Date: 13 November 2023
Our ref: 451605
Your ref: TR010032

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Mr Rynd Smith
Lead Member of the Examining Authority
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Bristol BS1 6PN

By email only, no hard copy to follow

Dear Mr Smith

Application by National Highways for an Order Granting Development Consent for the Lower Thames Crossing
Natural England's response to Deadline 5 – supplementary reference material
Natural England User Code: 20034784

The Examining Authority is in receipt of Natural England's Deadline 5 response. It has come to our attention that not all of the references provided within that response were included in full as appendices, and we therefore provide those here so as to ensure the Examining Authority, Applicant and Interested Parties as appropriate have full access to the information referenced within our DL5 response. We request that the Examining Authority accepts this supplementary DL5 response at it's discretion. For ease, we have provided our comments in the following Appendices to this letter:

Annex A: European Court Ruling (C-127/02) *Waddennzee*, 7th September 2004
Annex B: Natural England's approach to advising competent authorities on the assessment of road traffic emissions under the Habitats Regulations (NEA001)
Annex C: Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance (NECR210)
Annex D: NBN Atlas occurrence download at https://nbnatlas.org accessed on 28th June 2023.
Annex E: Olff, H., Leeuw, de L., Bakker, J.P., Platerink R. J. & van Wijnen H. J. (1997). Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology, Vol. 85, No. 6 pp. 799-814.
Annex F: Nolte, S., Waner, A., Stock. M., & Jensen K. (2019) Elymus athericus encroachment in Wadden Sea salt marshes is driven by surface-elevation change. Applied Vegetation Science, Vol. 22. No. 3, pp. 454 – 464.
Annex G: Bockelmann, A.C. (2002). Ordinary and successful: The invasion of Elymus athericus in European salt marshes. Doctor of Philosophy, Groningen.
Annex H: New Forest Local Plan air quality monitoring
Annex I: Shrewsbury Northwest Relief Road
Annex J: British Bryological Society Records

Yours sincerely

James Seymour
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John Torlesse
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Annex A: European Court Ruling (C-127/02) *Waddenzee*, 7th September 2004

JUDGMENT OF THE COURT (Grand Chamber)

7 September 2004 [*]

In Case C-127/02,

REFERENCE for a preliminary ruling under Article 234 EC

from the Raad van State (Netherlands), made by decision of 27 March 2002, registered at the Court on 8 April 2002, in the proceedings brought by

Landelijke Vereniging tot Behoud van de Waddenzee,

Nederlandse Vereniging tot Bescherming van Vogels

against

Staatssecretaris van Landbouw, Natuurbeheer en Visserij,

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[*] Language of the case: Dutch.

intervener:

Cooperatieve Producentenorganisatie van de Nederlandse Kokkelvisserij UA,

THE COURT (Grand Chamber),

composed of: V. Skouris, President, P. Jann, C.W.A. Timmermans, C. Gulmann (Rapporteur), J.-P. Puissochet and J.N. Cunha Rodrigues, Presidents of Chambers, R. Schintgen, S. von Bahr and R. Silva de Lapuerta, Judges,

Advocate General: J. Kokott,
Registrar: M.-F. Contet, Principal Administrator,

having regard to the written procedure and further to the hearing on 18 November 2003,

after considering the observations submitted on behalf of:

Landelijke Vereniging tot Behoud van de Waddenzee, by C.A.M. Rombouts, advocaat,

Nederlandse Vereniging tot Bescherming van Vogels, by A.J. Durville, advocaat, Cooperatieve Producentenorganisatie van de Nederlandse Kokkelvisserij VA, by G. van der Wal, advocaat,

the Netherlands Government, by H.G. Sevenster and N.A.J. Bel, acting as Agents,

the Commission of the European Communities, by G. Valero Jordana, acting as Agent, and J. Stuyck, avocat,

after hearing the Opinion of the Advocate General at the sitting on 29 January 2004,

gives the following

Judgment

The reference for a preliminary ruling concerns the interpretation of Article 6 of Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (OJ 1992 L 206, p. 7, 'the Habitats Directive').

2 The reference was made in proceedings between the Landelijke Vereniging tot Behoud van de Waddenzee (National association for conservation of the Waddenzee, 'the Waddenvereniging') and the Nederlandse Vereniging tot Bescherming van Vogels (Netherlands association for the protection of birds, 'the Vogelbeschermingsvereniging') on the one hand and the Staatssecretaris van Landbouw, Natuurbeheer en Visserij (Secretary of State for agriculture, nature conservation and fisheries, 'the Secretary of State') on the other in respect of licences which the latter issued to the Cooperatieve Producentenorganisatie van de Nederlandse Kokkelvisserij UA (Cooperative producers' association of Netherlands cockle fisheries, 'the PO Kokkelvisserij') for the mechanical fishing of cockles in the special protection area (SPA) of the Waddenzee, classified within the meaning of Article 4 of Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds (OJ 1979 L 103, p. 1) ('the Birds Directive').

Legal framework

The Birds Directive

3 Article 4(1) and (2) of the Birds Directive requires Member States to classify as SPAs the territories satisfying the ornithological criteria established by those provisions.

1 Article 4(4) of the Birds Directive provides:

'In respect of the protection areas referred to in paragraphs 1 and 2 above, Member States shall take appropriate steps to avoid pollution or deterioration of habitats or any disturbances affecting the birds, in so far as these would be significant having regard to the objectives of this article. Outside these protection areas, Member States shall also strive to avoid pollution or deterioration of habitats.'

The Habitats Directive

s Article 6 of the Habitats Directive states :

'l. For special areas of conservation, Member States shall establish the necessary conservation measures involving, if need be, appropriate management plans specifically designed for the sites or integrated into other development plans, and appropriate statutory, administrative or contractual measures which correspond to the ecological requirements of the natural habitat types in Annex I and the species in Annex II present on the sites.

2. Member States shall take appropriate steps to avoid, in the special areas of conservation, the deterioration of natural habitats and the habitats of species as well as disturbance of the species for which the areas have been designated, in so far as such disturbance could be significant in relation to the objectives of this Directive.

3. Any plan or project not directly connected with or necessary to the management of the site but likely to have a significant effect thereon, either individually or in combination with other plans or projects, shall be subject to appropriate assessment

of its implications for the site in view of the site's conservation objectives. In the light of the conclusions of the assessment of the implications for the site and subject to the provisions of paragraph 4, the competent national authorities shall agree to the plan or project only after having ascertained that it will not adversely affect the integrity of the site concerned and, if appropriate, after having obtained the opinion of the general public.

4. If, in spite of a negative assessment of the implications for the site and in the absence of alternative solutions, a plan or project must nevertheless be carried out for imperative reasons of overriding public interest, including those of a social or economic nature, the Member State shall take all compensatory measures necessaiy to ensure that the overall coherence of Natura 2000 is protected. It shall inform the Commission of the compensatmy measures adopted.

Where the site concerned hosts a priority natural habitat type and/or a priority species, the only considerations which may be raised are those relating to human health or public safety, to beneficial consequences of primary importance for the environment or, further to an opinion from the Commission, to other imperative reasons of overriding public interest.'

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[6] Article 7 of the Habitats Directive states that 'obligations arising under Article 6(2), (3) and (4) of this Directive shall replace any obligations arising under the first sentence of Article 4(4) of [the Birds Directive] in respect of areas classified pursuant to Article 4(1) or similarly recognised under Article 4(2) thereof, as from the date of implementation of this Directive or the date of classification or recognition by a Member State under [the Birds Directive], where the latter date is later'.

National legislation

7 Under Article 12(1) of the Natuurbeschermingswet (Nature Conservation Law), it is prohibited to carry out, to have carried out or to allow actions which are harmful to the natural integrity or the scientific importance of a protected natural site or disfigure it, without authorisation by the Minister van Landbouw, Natuurbeheer en Visserij (Minister for Agriculture, nature conservation and fisheries, 'the Minister') or in breach of the conditions accompanying that authorisation. Under Article 12(2), activities harmful to the essential characteristics of a protected natural site, as set out in the designation decision, are always to be considered harmful to the natural integrity of such a site or its interest in natural science terms.

s It is clear from the order of 17 November 1993 designating the Waddenzee as a national natural site and from the explanatory memorandum for that order, which is an integral part of it, that the policy of authorisations and revocations under the Natuurbeschermingswet is linked to that followed under the Planologische Kernbeslissing Waddenzee (Key planning decision for the Waddenzee, hereinafter 'the PKB Waddenzee'). According to that explanatory memorandum, applying the procedures of the Natuurbeschermingswet creates an adequate framework for controlling activities which might harm the main objective of the PKB Waddenzee, namely, sustainable protection and development of that sea as a natural site and, in particular, of feeding, nesting and resting areas for birds frequenting that site. Human activities for economic purposes are allowed subject to an adequate assessment in the light of the main objective. Activities envisaged in the Waddenzee must therefore be examined in the light of the abovementioned objective and policy guidelines and assessed in terms thereof.

9 The section in the PKB Waddenzee devoted to coastal fisheries management is implemented in the Government decision of 21 January 1993, namely, the Structuurnota Zee- en kustvisserij 'Vissen naar evenwicht' (Structure Document on Marine and Inshore Fisheries 'Fishing for equilibrium'). This establishes the policy for shellfish fishing, inter alia in the Waddenzee, for the years 1993 to 2003 and includes a number of restrictions as regards cockle fishing. Certain areas in the national natural site are permanently closed to cockle fishing and in years in which food is scarce, 60% of the average food requirement of birds in the form of cockles and mussels is reserved for them. While 100% of their average food requirement is not thus reserved, that is because they can also turn to alternative food sources (Baltic clams, surf clams and shore crabs).

10 Under the PKB Waddenzee, it follows from the precautionary principle that where the most reliable information available leaves obvious doubt as to the absence of possible significant adverse effects on the ecosystem, the benefit of the doubt will favour conservation of the Waddenzee. The order for reference makes clear that most of the available scientific studies consulted do not unequivocally indicate the existence of significant adverse effects on the ecosystem of the Waddenzee linked to mechanical cockle fishing.

The main action and the questions referred

11 By decisions of 1 July 1999 and 7 July 2000 ('the decisions at issue in the main action'), the Secretary of State issued licences to PO Kokkelvisserij, subject to certain conditions, to engage in mechanical cockle fishing in the Waddenzee SPA during the periods from 16 August to 25 November 1999 and 14- August to 30 November 2000 respectively.

12 The Waddenvereniging and the Vogelbeschermingsvereniging challenged those decisions before the Secretary of State, who, by decisions of 23 December 1999 and 19 February 2001, held that the complaints made against the decisions at issue in the main action were not founded and rejected the applications against them.

13 Those nature protection associations brought an action against those rejections before the Raad van State (Council of State). They claimed in essence that cockle fishing, as authorised by the decisions at issue in the main action, causes permanent damage to the geomorphology, flora and fauna of the Waddenzee's seabed. They also submitted that such fishing reduces the food stocks of birds which feed on shellfish, causing a decline in their populations, in particular for oystercatchers and eider ducks. The Waddenvereniging and the Vogelbeschermingsvereniging also claimed that those decisions were contrary to the Habitats and Birds Directives.

14 As regards the correct transposition of Article 6(2) to 6(4) of the Habitats Directive into Netherlands law, the Raad van State states that Article 12 of the Natuurbeschermingswet, although not expressly intended to implement the obligations laid down in Article 6(2) of the Habitats Directive, may be interpreted in a manner consistent with that provision. Similarly, the Natuurbeschermingswet does not contain rules which implement Article 6(3) and (4),of that directive. Nor are there generally binding rules intended to implement the provisions of those two paragraphs which are otherwise applicable to the Waddenzee.

15 The national court also states that according to the Waddenvereniging and the Vogelbeschermingsvereniging, in view of the expansion of cockle fishing in the Waddenzee SPA, there is a 'plan or project' which should be subject to 'appropriate assessment' in accordance with Article 6(3) of the Habitats Directive whereas the Secretary of State contends that the activity in question, inasmuch as it has been

carried on for many years without any intensification, falls within Article 6(2) of that directive.

16 As regards the relationship between Article 6(2) and 6(3) of the Habitats Directive, the Waddenvereniging and the Vogelbeschermingsvereniging submit that although the activity for which licences were granted must be described as a 'plan' or 'project' within the meaning of Article 6(3), it must nevertheless be examined in the light of Article 6(2). It is therefore appropriate to consider whether Article 6(3) must be regarded as a specific application of the rules in Article 6(2), so that those two paragraphs must be applied cumulatively, or as a provision with a separate, independent purpose, so that Article 6(2) relates to existing use while Article 6(3) applies to new plans or projects.

17 The Raad van State asks under what conditions an 'appropriate assessment' of the effect of the plan or project on the site concerned must be carried out. In addition, it asks what the criteria are on the basis of which it must be determined whether 'appropriate steps' or an 'appropriate assessment' are concerned, also in the light of the requirement laid down in Article 6(3) of the Habitats Directive for the competent authorities to agree to a plan or project only after having ascertained that it will not adversely affect the integrity of the site concerned.

1s Finally, the national court considers it relevant to know whether Article 6(2) and (3) of the Habitats Directive has direct effect.

19 In those circumstances, the Raad van State decided to stay the proceedings and to refer the following questions to the Court of Justice for a preliminary ruling:

'1. (a) Are the words "plan or project" in Article 6(3) of Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora to be interpreted as also covering an activity which has already been carried on for many years but for which an authorisation is in principle granted each year for a limited period, with a fresh assessment being carried out on each occasion as to whether, and if so in which sections of the area, the activity may be carried on?

(b) If the answer to Question 1(a) is in the negative, must the relevant activity be regarded as a "plan or project" if the intensity of this activity has increased over the years or an increase in it is made possible by the authorisations?

2. (a) If it follows from the answer to Question 1 that there is a "plan or project" within the meaning of Article 6(3) of the Habitats Directive, is Article 6(3) of the Habitats Directive to be regarded as a special application of the rules in Article 6(2) or as a provision with a separate, independent purpose in the sense that, for example:

(i) Article 6(2) relates to existing use and Article 6(3) to new plans or projects, or

(ii) Article 6(2) relates to management measures and Article 6(3) to other decisions, or

(iii) Article 6(3) relates to plans or projects and Article 6(2) to other activities?

(b) If Article 6(3) of the Habitats Directive is to be regarded as a special application of the rules in Article 6(2), can the two subparagraphs be applicable cumulatively?

3. (a) ls Article 6(3) of the Habitats Directive to be interpreted as meaning that there is a "plan or project" once a particular activity is likely to have an effect on the site concerned (and an "appropriate assessment" must then be carried out to ascertain whether or not the effect is "significant") or does this provision mean that an "appropriate assessment" has to be carried out only where there is a (sufficient) likelihood that a "plan or project" will have a significant effect?

(b) On the basis of which criteria must it be determined whether or not a plan or project within the meaning of Article 6(3) of the Habitats Directive not directly connected with or necessary to the management of the site is likely to have a significant effect thereon, either individually or in combination with other plans or projects?

4. (a) When Article 6(3) of the Habitats Directive is applied, on the basis of which criteria must it be determined whether or not there are "appropriate steps" within the meaning of Article 6(2) or an "appropriate assessment", within the meaning of Article 6(3), in connection with the certainty required before agreeing to a plan or project?

   (b) Do the terms "appropriate steps" or "appropriate assessment" have independent meaning or, in assessing these terms, is account also to be taken of Article 174(2) EC and in particular the precautionary principle referred to therein?

   (c) If account must be taken of the precautionary principle referred to in Article 174(2) EC, does that mean that a particular activity, such as the cockle fishing in question, can be authorised where there is no obvious doubt as to the absence of a possible significant effect or is that permissible only where there is no doubt as to the absence of such an effect or where the absence can be ascertained?

5. Do Article 6(2) or Article 6(3) of the Habitats Directive have direct effect in the sense that individuals may rely on them in national courts and those courts must provide the protection afforded to individuals by the direct effect of Community law, as was held inter alia in Case C-312/93 *Peterbroeck* [1995] ECR 1-4599?'

20 By order of 28 April 2004, the application by PO Kokkelvisserij to be allowed to submit written observations in response to the Advocate General's Opinion or otherwise to be given an opportunity to respond to that Opinion was rejected.

The questions referred

First question

Question l(a)

21 By Question l(a), the national court in essence asks whether mechanical cockle fishing which has been carried on for many years but for which a licence is granted annually for a limited period, with each licence entailing a new assessment both of the possibility of carrying on that activity and of the site where it may take place, falls within the concept of 'plan' or 'project' within the meaning of Article 6(3) of the Habitats Directive.

22 The 10th recital in the preamble to the Habitats Directive states that 'an appropriate assessment must be made of any plan or programme likely to have a significant effect on the conservation objectives of a site which has been designated or is designated in future'. That recital finds expression in Article 6(3) of the Directive, which provides inter alia that a plan or project likely to have a significant effect on the site concerned cannot be authorised without a prior assessment of its effects.

23 The Habitats Directive does not define the terms 'plan' and 'project'.

24 By contrast, Council Directive 85/337/EEC of 27 June 1985 on the assessment of the effects of certain public and private projects on the environment (OJ 1985 L 175, p. 40), the sixth recital in the preamble to which states that development consent for projects which are likely to have significant effects on the environment should be granted only after prior assessment of the likely significant environmental effects of these projects has been carried out, defines 'project' as follows in Article 1(2):

the execution of construction works or of other installations or schemes,

other interventions in the natural surroundings and landscape including those involving the extraction of mineral resources.'

2s An activity such as mechanical cockle fishing is within the concept of 'project' as defined in the second indent of Article 1(2) of Directive 85/337.

26 Such a definition of 'project' is relevant to defining the concept of plan or project as provided for in the Habitats Directive, which, as is clear from the foregoing, seeks, as does Directive 85/337, to prevent activities which are likely to damage the environment from being authorised without prior assessment of their impact on the environment.

27 Therefore, an activity such as mechanical cockle fishing is covered by the concept of plan or project set out in Article 6(3) of the Habitats Directive.

2s The fact that the activity has been carried on periodically for several years on the site concerned and that a licence has to be obtained for it every year, each new issuance of which requires an assessment both of the possibility of carrying on that activity and of the site where it may be carried on, does not in itself constitute an obstacle to considering it, at the time of each application, as a distinct plan or project within the meaning of the Habitats Directive.

29 The answer to Question l(a) must therefore be that mechanical cockle fishing which has been carried on for many years but for which a licence is granted annually for a limited period, with each licence entailing a new assessment both of the possibility of carrying on that activity and of the site where it may be carried on, falls within the concept of 'plan' or 'project' within the meaning of Article 6(3) of the Habitats Directive.

Question 1(b)

30 In the light of the reply to Question l(a), there is no need to reply to Question l(b).

Second question

31 By its second question, the national court in essence asks what the relationship is between Article 6(2) and Article 6(3) of the Habitats Directive.

32 It should be recalled that Article 6(2) of the Habitats Directive, in conjunction with Article 7 thereof, requires Member States to take appropriate steps to avoid, in SPAs, the deterioration of habitats and significant disturbance of the species for which the areas have been designated.

33 Article 6(3) of the Habitats Directive provides that the competent national authorities are to authorise a plan or project not directly connected with or necessary to the management of the site but likely to have a significant effect thereon only after having ascertained, by means of an appropriate assessment of the implications of that plan or project for the site, that it will not adversely affect the integrity of the site.

34 That provision thus establishes a procedure intended to ensure, by means of a preliminary examination, that a plan or project which is not directly connected with or necessary to the management of the site concerned but likely to have a significant effect on it is authorised only to the extent that it will not adversely affect the integrity of that site.

3s The fact that a plan or project has been authorised according to the procedure laid down in Article 6(3) of the Habitats Directive renders superfluous, as regards the action to be taken on the protected site under the plan or project, a concomitant application of the rule of general protection laid down in Article 6(2).

36 Authorisation of a plan or project granted in accordance with Article 6(3) of the Habitats Directive necessarily assumes that it is considered not likely adversely to affect the integrity of the site concerned and, consequently, not likely to give rise to deterioration or significant disturbances within the meaning of Article 6(2).

37 Nevertheless, it cannot be precluded that such a plan or project subsequently proves likely to give rise to such deterioration or disturbance, even where the competent national authorities cannot be held responsible for any error. Under those conditions, application of Article 6(2) of the Habitats Directive makes it possible to satisfy the essential objective of the preservation and protection of the quality of the environment, including the conservation of natural habitats and of wild fauna and flora, as stated in the first recital in the preamble to that directive.

38 The answer to the second question must therefore be that Article 6(3) of the Habitats Directive establishes a procedure intended to ensure, by means of a preliminary examination, that a plan or project which is not directly connected with or necessary to the management of the site concerned but likely to have a significant effect on it is authorised only to the extent that it will not adversely affect the integrity of that site, while Article 6(2) of the Habitats Directive establishes an obligation of general protection consisting in avoiding deterioration and disturbances which could have significant effects in the light of the Directive's objectives, and cannot be applicable concomitantly with Article 6(3).

Third question

Question 3(a)

39 According to the first sentence of Article 6(3) of the Habitats Directive, any plan or project not directly connected with or necessary to the management of the site but likely to have a significant effect thereon, either individually or in combination with other plans or projects, is to be subject to appropriate assessment of its implications for the site in view of the site's conservation objectives.

40 The requirement for an appropriate assessment of the implications of a plan or project is thus conditional on its being likely to have a significant effect on the site.

41 Therefore, the triggering of the environmental protection mechanism provided for in Article 6(3) of the Habitats Directive does not presume - as is, moreover, clear from the guidelines for interpreting that article drawn up by the Commission, entitled 'Managing Natura 2000 Sites: The provisions of Article 6 of the "Habitats" Directive (92/43/EEC)' - that the plan or project considered definitely has significant effects on the site concerned but follows from the mere probability that such an effect attaches to that plan or project.

42 As regards Article 2(1) of Directive 85/337, the text of which, essentially similar to Article 6(3) of the Habitats Directive, provides that 'Member States shall adopt all measures necessary to ensure that, before consent is given, projects likely to have significant effects on the environment ... are made subject to an assessment with regard to their effects', the Court has held that these are projects which are likely to

have significant effects on the environment (see to that effect Case C-117/02 *Commission* v *Portugal* [2004] ECR 1-5517, paragraph 85).

43 It follows that the first sentence of Article 6(3) of the Habitats Directive subordinates the requirement for an appropriate assessment of the implications of a plan or project to the condition that there be a probability or a risk that the latter will have significant effects on the site concerned.

44 In the light, in particular, of the precautionary principle, which is one of the foundations of the high level of protection pursued by Community policy on the environment, in accordance with the first subparagraph of Article 174(2) EC, and by reference to which the Habitats Directive must be interpreted, such a risk exists if it cannot be excluded on the basis of objective information that the plan or project will have significant effects on the site concerned (see, by analogy, inter alia Case C-180/96 *United Kingdom* v *Commission* [1998] ECR 1-2265, paragraphs 50, 105 and 107). Such an interpretation of the condition to which the assessment of the implications of a plan or project for a specific site is subject, which implies that in case of doubt as to the absence of significant effects such an assessment must be carried out, makes it possible to ensure effectively that plans or projects which adversely affect the integrity of the site concerned are not authorised, and thereby contributes to achieving, in accordance with the third recital in the preamble to the Habitats Directive and Article 2(1) thereof, its main aim, namely, ensuring biodiversity through the conservation of natural habitats and of wild fauna and flora.

1s In the light of the foregoing, the answer to Question 3(a) must be that the first sentence of Article 6(3) of the Habitats Directive must be interpreted as meaning that any plan or project not directly connected with or necessary to the management of the site is to be subject to an appropriate assessment of its implications for the site in view of the site's conservation objectives if it cannot be excluded, on the basis of objective information, that it will have a significant effect on that site, either individually or in combination with other plans or projects.

Question 3(6)

46 As is clear from the first sentence of Article 6(3) of the Habitats Directive in conjunction with the 10th recital in its preamble, the significant nature of the effect on a site of a plan or project not directly connected with or necessary to the management of the site is linked to the site's conservation objectives.

47 So, where such a plan or project has an effect on that site but is not likely to undermine its conservation objectives, it cannot be considered likely to have a significant effect on the site concerned.

48 Conversely, where such a plan or project is likely to undermine the conservation objectives of the site concerned, it must necessarily be considered likely to have a significant effect on the site. As the Commission in essence maintains, in assessing the potential effects of a plan or project, their significance must be established in the light, inter alia, of the characteristics and specific environmental conditions of the site concerned by that plan or project.

49 The answer to Question 3(b) must therefore be that, pursuant to the first sentence of Article 6(3) of the Habitats Directive, where a plan or project not directly connected with or necessary to the management of a site is likely to undermine the site's conservation objectives, it must be considered likely to have a significant effect on that site. The assessment of that risk must be made in the light inter alia of the characteristics and specific environmental conditions of the site concerned _by such a plan or project.

Fourth question

50 By Questions 4(a) to 4(c), the national court in essence asks the Court to clarify the concepts of 'appropriate steps' within the meaning of Article 6(2) of the Habitats Directive and 'appropriate assessment' within the meaning of Article 6(3) thereof and the conditions under which an activity such as mechanical cockle fishing may be authorised.

51 In the light of the context of the main action, as well as the foregoing observations, and in particular the answers to the first two questions, there is no need, as stated in point 116 of the Advocate General's Opinion, to answer the fourth question as regards Article 6(2) of the Habitats Directive.

52 As regards the concept of 'appropriate assessment' within the meaning of Article 6(3) of the Habitats Directive, it must be pointed out that the provision does not define any particular method for carrying out such an assessment.

53 None the less, according to the wording of that provision, an appropriate assessment of the implications for the site concerned of the plan or project must precede its approval and take into account the cumulative effects which result from the combination of that plan or project with other plans or projects in view of the site's conservation objectives.

54 Such an assessment therefore implies that all the aspects of the plan or project which can, either individually or in combination with other plans or projects, affect those objectives must be identified in the light of the best scientific knowledge in the field. Those objectives may, as is clear from Articles 3 and 4 of the Habitats Directive, in particular Article 4(4), be established on the basis, inter alia, of the importance of the sites for the maintenance or restoration at a favourable conservation status of a natural habitat type in Annex I to that directive or a species in Annex II thereto and for the coherence of Natura 2000, and of the threats of degradation or destruction to which they are exposed.

55 As regards the conditions under which an activity such as mechanical cockle fishing may be authorised, given Article 6(3) of the Habitats Directive and the answer to the first question, it lies with the competent national authorities, in the light of the conclusions of the assessment of the implications of a plan or project for the site concerned, to approve the plan or project only after having made sure that it will not adversely affect the integrity of that site.

56 It is therefore apparent that the plan or project in question may be granted authorisation only on the condition that the competent national authorities are convinced that it will not adversely affect the integrity of the site concerned.

57 So, where doubt remains as to the absence of adverse effects on the integrity of the site linked to the plan or project being considered, the competent authority will have to refuse authorisation.

5s In this respect, it is clear that the authorisation criterion laid down in the second sentence of Article 6(3) of the Habitats Directive integrates the precautionary principle (see Case C-157/96 *National Farmers' Union and Others* (1998] ECR 1-2211, paragraph 63} and makes it possible effectively to prevent adverse effects on the integrity of protected sites as the result of the plans or projects being considered. A less stringent authorisation criterion than that in question could not as effectively ensure the fulfilment of the objective of site protection intended under that provision.

59 Therefore, pursuant to Article 6(3) of the Habitats Directive, the competent national authorities, taking account of the conclusions of the appropriate assessment of the implications of mechanical cockle fishing for the site concerned, in the light of the site's conservation objectives, are to authorise such activity only if they have made certain that it will not adversely affect the integrity of that site. That is the case where no reasonable scientific doubt remains as to the absence of such effects (see, by analogy, Case C-236/01 *Monsanto Agricoltura Italia and Others* (2003] ECR 1-8105, paragraphs 106 and 113).

60 Otherwise, mechanical cockle fishing could, where appropriate, be authorised under Article 6(4-) of the Habitats Directive, provided that the conditions set out therein are satisfied.

61 In view of the foregoing, the answer to the fourth question must be that, under Article 6(3) of the Habitats Directive, an appropriate assessment of the implications for the site concerned of the plan or project implies that, prior to its approval, all the

aspects of the plan or project which can, by themselves or in combination with other plans or projects, affect the site's conservation objectives must be identified in the light of the best scientific knowledge in the field. The competent national authorities, taking account of the appropriate assessment of the implications of mechanical cockle fishing for the site concerned in the light of the site's conservation objectives, are to authorise such an activity only if they have made certain that it will not adversely affect the integrity of that site. That is the case where no reasonable scientific doubt remains as to the absence of such effects.

Fifth question

62 In the light of the finding in paragraph 51 above, it is not necessary to consider the fifth question in so far as it relates to Article 6(2) of the Habitats Directive.

63 It is therefore appropriate to consider that question only in so far as it concerns Article 6(3) of the Habitats Directive.

64 By its fifth question, the national court asks in essence whether, when a national court is called on to ascertain the lawfulness of an authorisation for a plan or project within the meaning of Article 6(3) of the Habitats Directive, it may examine whether the limits of discretion of the competent national authorities laid down by that provision have been complied with even though it has not been transposed into the legal order of the Member State concerned despite the expiry of the time-limit laid down for that purpose.

65 It should be recalled that the obligation of a Member State to take all the measures necessary to achieve the result prescribed by a directive is a binding obligation imposed by the third paragraph of Article 249 EC and by the directive itself. That duty to take all appropriate measures, whether general or particular, is binding on all the authorities of Member States including, for matters within their jurisdiction, the, courts (see Case C-72/95 *Kraaijeveld and Others* [1996] ECR I-5403, paragraph 55).

66 As regards the right of an individual to rely on a directive and of the national court to take it into consideration, it would be incompatible with the binding effect attributed to a directive by Article 249 EC to exclude, in principle, the possibility that the obligation which it imposes may be relied on by those concerned. In particular, where the Community authorities have, by directive, imposed on Member States the obligation to pursue a particular course of conduct, the effectiveness of such an act would be weakened if individuals were prevented from relying on it before their national courts, and if the latter were prevented from taking it into consideration as an element of Community law in order to rule whether the national legislature, in exercising the choice open to it as to the form and methods for implementation, has kept within the limits of its discretion set by the directive (see *Kraaijeveld and Others*, paragraph 56). That also applies to ascertaining whether failing transposition into national law of the relevant provision of the directive concerned, the national authority which has adopted the contested measure has kept within the limits of its discretion set by that provision.

67 More particularly, as regards the limits of discretion set by Article 6(3) of the Habitats Directive, it follows from that provision that in a case such as that in the main action, the competent national authorities, taking account of the conclusions of the appropriate assessment of the implications of mechanical cockle fishing for the site concerned in the light of the site's conservation objectives, are to authorise

such an activity only if they have made certain that it will not adversely affect the integrity of that site, that being the case if there remains no reasonable scientific doubt as to the absence of such effects (see paragraph 59 above).

6s Such a condition would therefore not be observed were the national authorities to authorise that activity in the face of uncertainty as to the absence of adverse effects for the site concerned.

69 It follows that Article 6(3) of the Habitats Directive may be taken into account by the national court in determining whether a national authority which has granted an authorisation relating to a plan or project has kept within the limits of the discretion set by the provision in question.

70 Consequently, the answer to the fifth question must be that where a national court is called on to ascertain the lawfulness of an authorisation for a plan or project within the meaning of Article 6(3) of the Habitats Directive, it can determine whether the limits on the discretion of the competent national authorities set by that provision have been complied with, even though it has not been transposed into the legal order of the Member State concerned despite the expiry of the time-limit laid down for that purpose.

Costs

71 Since these proceedings are, for the parties to the main proceedings, a step in the action pending before the national court, the decision on costs is a matter for that court. Costs incurred in submitting observations to the Court, other than the costs of those parties, are not recoverable.

On those grounds, the Court (Grand Chamber) rules as follows:

I. Mechanical cockle fishing which has been carried on for many years but for which a licence is granted annually for a limited period, with each licence entailing a new assessment both of the possibility of carrying on that activity and of the site where it may be carried on, falls within the concept of 'plan' or 'project' within the meaning of Article 6(3) of Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora.

2. Article 6(3) of Directive 92/43 establishes a procedure intended to ensure, by means of a preliminary examination, that a plan or project which is not directly connected with or necessary to the management of the site concerned but likely to have a significant effect on it is authorised only to the extent that it will not adversely affect the integrity of that site, while Article 6(2) of that directive establishes an obligation of general protection consisting in avoiding deterioration and disturbances which could have significant effects in the light of the Directive's objectives, and cannot be applicable concomitantly with Article 6(3).

3. (a) The first sentence of Article 6(3) of Directive 92/43 must be interpreted as meaning that any plan or project not directly connected with or necessary to the management of the site is to be subject to an appropriate assessment of its implications for the site in view of the site's conservation objectives if it cannot be excluded, on the basis of objective information, that it will have a significant effect on that site, either individually or in combination with other plans or projects.

(b) Pursuant to the first sentence of Article 6(3) of Directive 92/4,3, where a plan or project not directly connected with or necessary to the management of a site is likely to undermine the site's conservation objectives, it must be considered likely to have a significant effect on that site. The assessment of that risk must be made in the light inter alia of the characteristics and specific environmental conditions of the site concerned by such a plan or project.

4. Under Article 6(3) of Directive 92/43, an appropriate assessment of the implications for the site concerned of the plan or project implies that, prior to its approval, all the aspects of the plan or project which can, by themselves or in combination with other plans or projects, affect the site's conservation objectives must be identified in the light of the best scientific knowledge in the field. The competent national authorities, taking account of the appropriate assessment of the implications of mechanical coclde fishing for the site concerned in the light of the site's conservation objectives, are to authorise such an activity only if they have made certain that it will not adversely affect the integrity of that site. That is the case where no reasonable scientific doubt remains as to the absence of such effects.

5. Where a national court is called on to ascertain the lawfulness of an authorisation for a plan or project within the meaning of Article 6(3) of Directive 92/43, it can determine whether the limits on the discretion of the competent national authorities set by that provision have been complied with, even though it has not been transposed into the legal order of the Member State concerned despite the expiry of the time-limit laid down for that purpose.

Signatures.

Annex B: Natural England’s approach to advising competent authorities on the assessment of road traffic emissions under the Habitats Regulations (NEA001)

FOR INTERNAL USE ONLY

Natural England's approach to advising competent authorities on the assessment of road traffic emissions under the Habitats Regulations

Version: June 2018

Green-winged orchids *Anacamptis morio* on a roadside verge (by kind permission of Mark Meijrink @ http://markmeijrink.wordpress.com)

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Natural England Internal Note on Ways of Working:

Natural England's approach to advising competent authorities on the assessment of road traffic emissions under the Habitats Regulations

1. Introduction

1.1 This internal operational Guidance Note describes how Natural England advises competent authorities and others on the assessment of plans and projects (as required by the Conservation of Habitats and Species Regulations 2017 ('the Habitats Regulations')) likely to generate road traffic emissions to air which are capable of affecting European Sites[1].

The terms used throughout this note are referred to with regard to the Habitats Regulations assessment (HRA) procedure. The meaning of these terms is separate and distinct from the meaning of similar terms associated with Environmental Impact Assessment (EIA) procedures[2]. HRA and EIA can be compared as follows:

Framework	**Relevance step**	**Detailed assessment step**
Habitats Regulations Assessment	Likely Significant Effect Test	Adverse Effect Test
Environmental Impact Assessment	Screening	Significance Test

Natural England's Role as Advisor under the Habitats Regulations

1.2 Natural England plays several roles in the implementation of the Habitats Regulations, acting as an advisory 'nature conservation body' under Regulation 5 and as a 'competent authority' as defined under Regulation 7. As a competent authority, Natural England must formally assess new plans or projects which are (a) subject to the section 28 SSSI notice and consent procedures under Regulation 24 and (b) any plans or projects we are planning to undertake ourselves or give our authorisation or permission to under regulation 63.

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[1] The term 'European Site' applies here to the following Protected Sites occurring in England; Special Areas of Conservation (SACs), candidate SACs, Special Protection Areas (SPAs), Sites of Community Importance (SCIs), potential SPAs, possible SACs, listed or proposed Ramsar sites and sites identified, or required, as compensatory measures for adverse effects on these European sites (see also page 28 of the National Planning Policy Framework 2012 and regulation 8 of the Habitats Regulations 2017.

[2] The EIA of certain projects under the EU Directive (2014/52/EU) on the assessment of the effects of certain public and private projects on the environment as transposed by the UK into various EIA Regulations covering town and country planning, infrastructure planning, forestry, agriculture and marine works (for an overview see https://www.gov.uk/guidance/environmental-impact-assessment)

1.3 This guidance is concerned with Natural England's other role as advisor to other competent authorities, acting as a '*nature conservation body*' according to regulation 5, also referred to in the Regulations as '*the appropriate nature conservation body*'. This definition also includes our sister agencies the Natural Resources Wales and Scottish Natural Heritage.

1.4 It is a statutory requirement under regulation 64(3) for competent authorities to consult Natural England for its views when they are carrying out an Appropriate Assessment (AA) and to '*have regard*' to any representations that we may make. Although there is no statutory requirement at the earlier step of determining 'likely significant effect', we are also likely to be consulted by other competent authorities for a 'screening opinion' or for further advice on the scope of an appropriate assessment, particularly where they do not have access to ecological expertise. This advice is increasingly delivered through Natural England's Discretionary Advice Service.

Who is this Guidance Note for?

1.5 This is internal guidance designed to assist Natural England staff when giving practical and proportionate advice to competent authorities and others about their assessment of the potential impacts from road traffic emissions on the qualifying features of European Sites. This Guidance Note has been prompted by the High Court judgment in Wealden v SSCLG [2017] ('the Wealden Judgment 2017').

1.6 It is worth noting the Dutch courts request for a preliminary ruling from the Court of Justice of the European Union ('CJEU') in C-294/17 on a series of questions relating to the implementation of the Dutch State's national nitrogen strategy[3] in light of the Habitats Directive. Any ruling subsequently provided by the CJEU is also likely to be of interest to the UK and may affect the contents of this guidance.

1.7 This Guidance Note has been drafted to reflect Natural England's current operational approach to advising competent authorities on air quality matters affecting European Sites. External stakeholders should be mindful that this note may be subject to review in light of operational feedback, new authoritative decisions and any subsequent reform of or changes to Natural England's general approach to giving its advice.

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[3] See http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:62017CN0294

Why has this guidance note been made public?

1.8 This internal guidance has been made public for general information purposes to explain Natural England's approach to assessing the effects of road traffic emissions on European Sites particularly in light of the Wealden Judgment 2017. This version of Natural England's internal guidance note has been modified to remove references to Natural England internal information sources so that it is clear to an external audience.

1.9 Natural England has provided this general guidance to its staff on the factors to consider when advising a competent authority on the HRA of plans and projects generating road traffic and air pollution effects. It cannot cater for all situations and where local factors or information indicate that it would be inappropriate to rely on this guidance, it advises staff to seek further internal advice and/or advise that the plan or project should progress to appropriate assessment.

1.10 Publication of this internal guidance does not replace the need for competent authorities to consult Natural England where appropriate. Competent authorities and other third parties seeking Natural England's advice in relation to specific plans or projects should continue to consult Natural England in the usual way.

1.11 In addition to this guidance note, competent authorities and other third parties may also wish to seek the expert advice of other relevant statutory bodies as appropriate, such as the Environment Agency, and refer to other technical guidance on air quality matters or the Habitats Regulations Assessment process.

This internal Guidance Note includes Natural England's own interpretation of the law as it applies to air quality matters affecting European Sites. It does not constitute legal or professional advice to competent authorities or to any other third party. No warranty is given nor liability accepted for the contents of this internal Guidance Note. Competent authorities and other parties should seek their own legal advice.

What's covered by this Internal Guidance Note

1.12 This guidance outlines Natural England's approach to advising competent authorities on air quality assessment and identifies data sources to:

- allow competent authorities to have regard to these matters when they undertake their statutory duties and reach their conclusions on Habitats Regulations Assessments

- identify when Natural England is likely to advise no further assessment is required

- identify when Natural England is likely to advise detailed assessment and bespoke advice may be required, and,

- assist Natural England staff when drafting advice on potential impacts from air pollution.

1.13 **This guidance is applicable when Natural England gives its advice on plans and projects involving the following;**

- Emissions from road traffic likely to be generated by new development projects including residential, mixed use and industrial/commercial developments

- Emissions from road traffic likely to result from allocations in strategic Local Plans

- Emissions from proposed road schemes

What's not covered by this Internal Guidance Note

1.14 This guidance focusses on ecological receptors and does not cover human health.

1.15 This guidance is limited to plans or projects with road traffic emissions. It does not apply where the subject plan or project relates to non-road point sources or Environmental Permitting of intensive livestock units.

1.16 This guidance does not specifically cover nationally significant sites such as Sites of Special Scientific Interest (SSSIs), which are covered by a different regulatory framework. However, the general principles for air quality assessment outlined here for European Sites are likely to be equally relevant for this and other designations.

1.17 This guidance does not cover the further stages of the HRA process (tests for alternative solutions, imperative reasons of overriding public interest and compensation measures (stages 3 and 4 in Figure 1) which will be based on more bespoke advice and should be led by the competent authority responsible for the HRA.

2. Overview - how might European sites be adversely affected by air pollution?

2.1 Air pollution that typically affects habitat will include dust and particulate matter (PM), nitrogen oxides (NOx), ammonia (NH_3) and sulphur dioxide (SO_2). Each proposal type will have emissions typically associated with its specific activity. For example, ammonia is typically associated with farming or waste management. Combustion sources such as industry or traffic are more likely to be associated with nitrogen oxides and particulate matter.

2.2 Generally speaking, the risks to qualifying features from air pollution (in simple terms) most frequently arise from:

- The direct effects which arise when a pollutant which is dispersed in the air is taken up by vegetation (through pores on the surface called stomata). Pollutants taken up by vegetation can cause adverse impacts to plant health and viability. The relevant assessment benchmark for pollutant concentrations ‘in the air’ is referred to as a **critical level** expressed in units of µg/m^3 (micrograms per cubic metre).

- There are indirect effects which arise when the pollutant settles onto the ground (referred to as ‘deposition’) causing nutrient enrichment of the soil (‘eutrophication’) or changes to the soil pH (‘acidification’). These effects can decrease the ability of a plant to compete with other plants and can hinder the inherent capacity for self-repair and self-renewal under natural conditions. In other words, nitrogen acts as a fertiliser for plants that can thrive on high nitrogen levels and can dominate plant communities. The speed with which a given pollutant settles (or deposits) after it is released into the atmosphere is different for each pollutant, and is influenced by how dense (or heavy) the particles are. Some pollutants travel a long distance before deposition occurs whilst others will settle much closer to their source. Wind speed and direction will also have an influence on deposition properties.

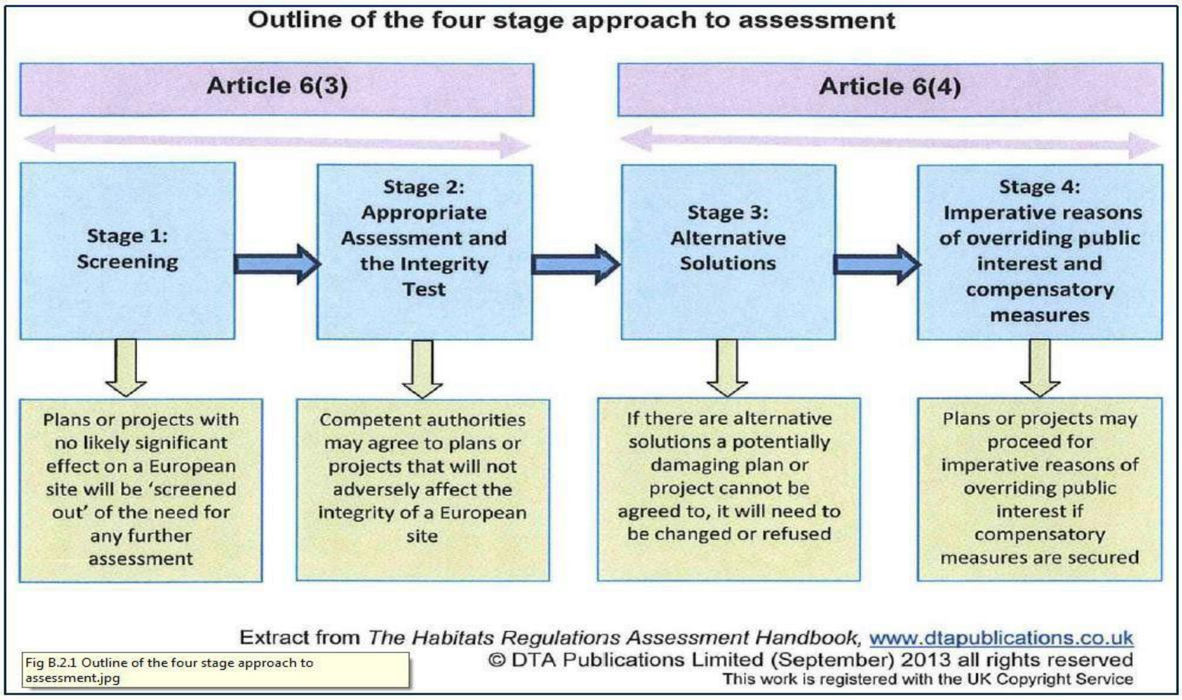
  The relevant assessment benchmark for pollutant levels which settle from the air onto a surface (or deposit) is referred to as a **critical load** expressed in units of kilograms of nitrogen per hectare per year (Kg N/ha/yr) for nitrogen deposition or kilo-equivalents per hectare per year (Keq/ha/yr) for acid deposition**.**

2.3 The UK’s Air Pollution Information System (APIS; http://www.apis.ac.uk/) provides an overview of deposition, air pollution effects on habitat and typical emissions arising from different proposal types in the APIS Starter’s Guide to Air Pollution Sources. Further description of critical loads (deposition benchmarks) and critical levels (air concentration benchmarks) can be found on APIS Guide to Critical Loads and Levels. These topics are covered in more detail in subsequent sections of the guidance. All assessment stages rely on sufficient information to make a determination.

2.4 Road traffic is a source of NOx emissions, meaning that increases in traffic can represent a risk with regard to the potential effects associated with the exceedance of critical levels for sensitive vegetation. Traffic emissions can also be a short range contributor to nitrogen deposition.

3. Overview – an approach to the HRA of plans or projects with road traffic emissions

3.1 There are four stages to assessment for European Sites (see Figure 1). This guidance relates primarily to Stage 1 of the process and the scoping of a stage 2 appropriate assessment (as illustrated in Figure 1 below).



Extract from *The Habitats Regulations Assessment Handbook*, www.dtapublications.co.uk
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Figure 1: Overview of the Habitats Regulations Assessment procedures

3.2 Under the Habitats Regulations, it is the competent authority[4] who must carry out an appropriate assessment of any plan or project which is either not directly connected with or necessary to the management of a European Site and which is likely to have a significant effect on a European site. A competent authority should therefore decide for itself as to the likelihood of a significant effect on a site (stage 1 of Figure 1 above), but it is often the case that it may seek advice on this from Natural England (see section 4 below).

3.3 Furthermore, there is a statutory requirement for a competent authority to formally consult Natural England for the purposes of an appropriate assessment (Stage 2 in Figure 1 above). This is the only statutory input required from Natural England during the HRA process under the Habitats Regulations.

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[4] The Habitats Regulations define a 'competent authority' as including any Minister of the Crown, government department, statutory undertaker, public body of any description or persons holding public office, or any person exercising those functions (regulation 7(1)).

Staff should be aware that, in accordance with Government's guidance on competent authority co-ordination when applying the Habitats Regulations, it is generally permissible for a competent authority to adopt, if it can, the assessment, reasoning and conclusions of another competent authority relating to the same plan or project, thus avoiding unnecessary duplication of effort. Staff are therefore encouraged to advise competent authorities to first check, at an early stage, the extent to which this might apply in relation to assessing road traffic emissions from an individual proposal. For example, the likely effects of a development proposal might have already been considered by a HRA of a Local Plan made by the same or another competent authority.

3.4 When specifically **advising** a competent authority at this screening stage of HRA as to whether the road traffic emissions associated with a plan or project are likely to have a significant effect on a European site, Natural England suggests a sequential approach can be taken to quickly filter out those proposals posing no credible risk.

3.5 Firstly it considers the evidence about emission types and distance that emissions are likely to travel to identify whether a plan or project might pose a risk to a European site (***step 1***).If a proposal gives rise to emissions that are likely to reach a designated site, the screening assessment should, secondly, consider the sensitivity of the qualifying feature(s) at the designated site (***step 2***). Next, if the necessary information is available, establish the feature's location and its likely exposure to emissions (***step 3***) to confirm the presence or absence of a credible risk.

3.6 Where there is the potential for interaction between a sensitive feature and emissions, ascertain either the predicted increase in flow of road traffic associated with the plan or project ('AADT flow') or the predicted process-contribution as a % of the pollution benchmark to act as a screening threshold alone (***step 4a***) and, where the threshold is not exceeded alone, in-combination (***step 4b & 4c***). These steps inform a decision as to whether a more detailed 'appropriate assessment' is required. The requirement to specifically consider the risks of 'in-combination' effects is explained further starting at paragraph 4.31. Together, these steps represent the "likely significant effect" or "screening" stage. If a proposal alone is above the likely significant effect thresholds, there is no need to also look for the risk of in-combination effects before proceeding to the appropriate assessment stage.

3.7 If the likelihood for significant effect cannot be ruled out, Natural England should advise the competent authority that an appropriate assessment is needed (***step 5***). Appropriate assessment is intended to be proportionate to the risk from a plan or project and does not always require detailed modelling or large amounts of reporting. The appropriate assessment should focus on assessing more precisely the ecological impacts of the emissions on the site in view of its qualifying features and conservation objectives. It should take into account any detailed modelling that is or becomes available, the best available evidence as to ecological impacts, background levels and likelihood for future reductions. Natural England will be consulted by the competent authority for the purposes of the assessment and asked for its advice (***step 6***).

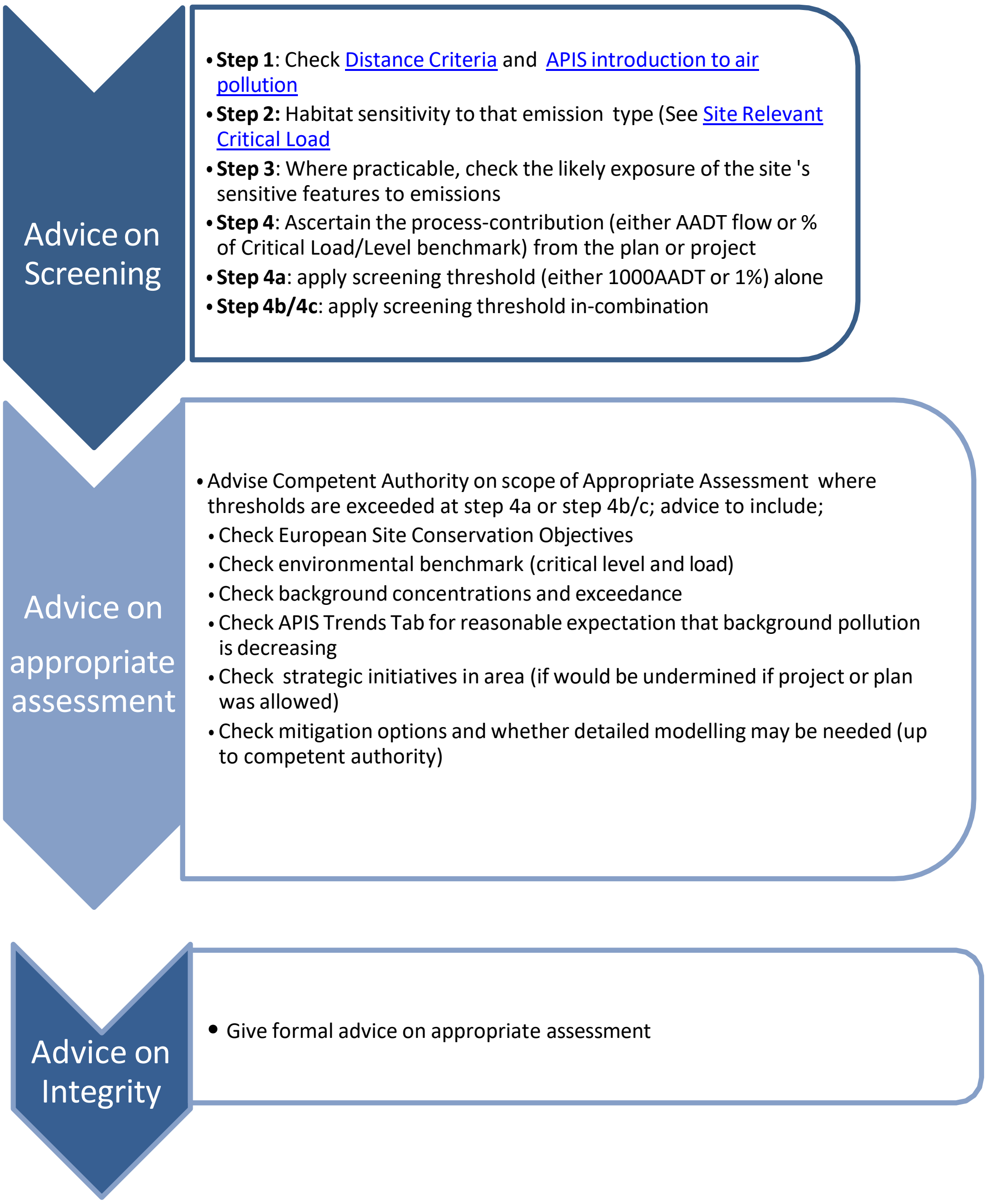
3.8 Natural England can direct competent authorities to further information they will find useful for undertaking an appropriate assessment and further guidance to inform the scope of an appropriate assessment is given in Section 5. It is at this stage that we would also detail why a likely significant effect could not be ruled out either because of the risk to a European site from the plan or project 'alone' or due to a risk of 'in-combination' effects.

3.9 A summary flowchart has been produced in *Appendix A* to this guidance, which is linked to the screening steps described in more detail below. It can help to guide staff in coming to a view as to the advice to be given on the assessment of plans or projects.

3.10 Staff should note that this document and the flowchart only provides general guidance on the factors to consider when advising a competent authority on the HRA of those plans and projects generating road traffic and air pollution effects. It cannot cater for all situations. Where there is information available that indicates it would be inappropriate to rely on this guidance (for example, there is uncertainty in the evidence base, there are development clusters that need to be accounted for or specific local evidence is available which undermine the application of this guidance), it will be necessary to consider whether further internal advice is needed and/or whether we should advise that the plan or project should progress to appropriate assessment. This adapted advice will need to be explained on a case by case basis.

Figure 2: Overview of stages and steps when advising a competent authority on the HRA of a road traffic project or plan

For road traffic emissions the distance criteria applied is 200m. Distance criteria applied to other emission sources is available on request and under review;



- **Step 1**: Check Distance Criteria and APIS introduction to air pollution
- **Step 2:** Habitat sensitivity to that emission type (See Site Relevant Critical Load
- **Step 3**: Where practicable, check the likely exposure of the site 's sensitive features to emissions
- **Step 4**: Ascertain the process-contribution (either AADT flow or % of Critical Load/Level benchmark) from the plan or project
- **Step 4a**: apply screening threshold (either 1000AADT or 1%) alone
- **Step 4b/4c**: apply screening threshold in-combination

- Advise Competent Authority on scope of Appropriate Assessment where thresholds are exceeded at step 4a or step 4b/c; advice to include;
  - Check European Site Conservation Objectives
  - Check environmental benchmark (critical level and load)
  - Check background concentrations and exceedance
  - Check APIS Trends Tab for reasonable expectation that background pollution is decreasing
  - Check strategic initiatives in area (if would be undermined if project or plan was allowed)
  - Check mitigation options and whether detailed modelling may be needed (up to competent authority)

- Give formal advice on appropriate assessment

4. Advice on Screening for Likely Significant Effects

4.1 The purpose of the screening stage of the HRA process is to initially identify the risk or the possibility of significant adverse effects on a European site which could undermine the achievement of a site's conservation objectives and which therefore require further detailed examination through an appropriate assessment (see also paragraph 4.3 below). If risks which might undermine a site's conservation objectives can clearly be ruled out (based on the consideration of objective information), a proposal will have no likely significant effect and no appropriate assessment will be needed.

4.2 The Habitats Regulations place the responsibility for the screening decision as to whether appropriate assessment is required on the competent authority (see, for example, the text of regulations 63 and 105). There is no statutory requirement for a competent authority to seek or to rely on Natural England's screening opinion – it can come to its own view on likely significant effect. However, a competent authority, and/or the promoters or proposers of a plan/project, may request Natural England's advice on screening at formal consultation or at pre-application stages (under our Discretionary Advice Service). This section is intended to cover such circumstances.

4.3 In undertaking an assessment of 'likely significant effects' under the Habitats Regulations, authoritative case law has established that:

- An effect is likely if it '*cannot be excluded on the basis of objective information'*[5]
- An effect is significant if it '*is likely to undermine the conservation objectives'*[6]
- In undertaking a screening assessment for likely significant effects '*it is not that significant effects are probable, a risk is sufficient'….* but there must be credible evidence that there is '*a real, rather than a hypothetical, risk'*'[7].

4.4 The Advocate General's opinion in *Sweetman* also offers some simple guidance that the screening step '*operates merely as a trigger'* which asks *'should we bother to check?'*'[8].

4.5 As such, when determining whether air pollution from a plan or project has a 'likely significant effect' upon a given qualifying feature under the Habitats Regulations, the extent to which there are risks of air pollution that might undermine the conservation objectives for the site is central.

4.6 It is recommended that Natural England staff follow the sequential steps 1 – 5 outlined below to apply this screening procedure when Natural England is asked

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[5] Case C127-02 *Waddenzee* (refer para 45)
[6] Case C127-02 *Waddenzee* (refer para 48)
[7] Boggis v Natural England and Waveney DC [2009] EWCA Civ 1061 (refer paras 36-37)
[8] Case C 258/11 *Sweetman* Advocate General Opinion (refer paras 49-50)

to advise competent authorities on the risks of air quality impacts within the framework of a HRA.

Step 1: Does the proposal give rise to emissions which are likely to reach a European site?

4.7 Any emissions from road traffic associated with a specific proposal and the proximity to European sites should be considered in the consultation documents. If they are not, further information should be requested from the competent authority consulting Natural England.

4.8 A key factor to consider at this initial screening step for air pollution assessment is the distance between an emission source and the receptor (in this case a European site). Emissions to air may have effects over both long and short ranges depending on the size, source and nature of the emission.

4.9 Distance-based criteria have been established for several sectors to identify consultations requiring consideration for potential effects from air pollution. These are listed on Natural England's Technical Information Exchange (TIE) air pollution pages (Distance Criteria) and currently under review[9].

4.10 With regard to potential risks from road traffic emissions, Natural England and Highways England are in agreement that protected sites falling within 200 metres of the edge of a road affected by a plan or project need to be considered further. This is based on evidence presented in ENRR580 (Bignal *et al.* 2004[10]) and is consistent with more current literature (Ricardo-AEA, 2016[11]). However, where (unusually) there is a credible risk that air quality impacts might extend beyond 200 metres from a road, Natural England may advise that additional sites should also be scoped into the HRA.

4.11 The distance between roads where increased traffic levels are predicted and specific designated sites can be checked using Magic.

4.12 If the consultation does not fall within the distance criterion for designated sites (i.e. 200m for road traffic proposals), no further steps of the assessment are necessary. Such proposals are likely to have no effect on sites at all and so do not need to be subject to assessment in-combination with other plans and projects. A screening conclusion of no likely significant effect on the site can be advised with regard to the risk of road traffic emissions affecting air quality.

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[9] Available upon request

[10] BIGNAL, K., ASHMORE, M. & POWER, S. 2004. *The ecological effects of diffuse air pollution from road transport*. English Nature Research Report No. 580, Peterborough.

[11] RICARDO-AEA, 2016. *The ecological effects of air pollution from road transport: an updated review*. Natural England Commissioned Report no.199.

Step 2: Are the qualifying features of sites within 200m of a road sensitive to air pollution?

4.13 The qualifying features of European Sites can be identified by reference to Natural England's formal advice on their Conservation Objectives, which include a definitive list of legally-qualifying features. These objectives are available here. Alternatively a list of qualifying features can also be found by searching for the European Site on Designated Sites View.

4.14 There are several ways to establish whether a qualifying feature is sensitive to the type of air emissions expected from a proposal. These range from broad, internationally agreed pollution benchmarks (critical loads and levels) to site specific information such as survey data.

4.15 APIS provides key information about feature sensitivity to specific pollutants:

- by broad category (habitat, ecosystem and species) and,
- by qualifying feature on each designated European site (Site Relevant Critical Loads Search Tool).

4.16 Where none of a site's qualifying features are considered to be sensitive to a pollutant, then no further assessment is required for that pollutant. For example a chalk river will not typically be sensitive to acid deposition because of its natural buffering capacity. In these circumstances a screening conclusion of no likely significant effect on the site can be reached with regard to air quality.

Where at least one of a site's features is known to be sensitive, further screening is advised at step 3 (where information is available) or at step 4. Where there is uncertainty over the sensitivity of the feature in close proximity to a road affected by the plan or project, then a precautionary approach should be taken with an assumption made that the feature may be sensitive.

Step 3: Could the sensitive qualifying features of the site be exposed to emissions?

4.17 Usually, only those European sites present within 200m of the edge of a road on which a plan or project will generate traffic will need to be considered when checking for the likelihood of significant effects from road traffic emissions (but see also paragraph 4.10).

4.18 Many sites are designated for several different qualifying features. Not all features are present within a given location within the site. In some cases, a road surface and its adjacent verges may be included within a designated site boundary. This does not necessarily mean that it, and its associated verges, will be of nature conservation interest and form part of a qualifying feature. The inclusion of the hard surface of a road and/or its adjacent verges might simply have been unavoidable when denoting a boundary and included simply for convenience. These areas will therefore constitute 'site-fabric'[12], being of no special nature conservation interest. Conversely, at some sites, roadside verges may have been deliberately included within a site boundary and be an integral part of a designated habitat. Therefore, a site's conservation objectives are unlikely to apply equally to all parts of a site and a competent authority may need to be made aware of this as necessary.

4.19 An early understanding of the spatial distribution of features within a site can help to decide whether or not appropriate assessment will be required. This is particularly relevant as contributions to air pollution from a road will typically decrease with distance away from that road (e.g. Ricardo-AEA, 2016[13]). Where the applicant has provided reliable and precise information that models the likely deposition of road-based pollutants in relation to the distribution of a site's features and any sensitive qualifying features are not present within the area to be affected by emissions (and Natural England's advice is that there is no conservation objective to restore the features to that area), it will be relatively straightforward to ascertain that the plan or project poses no credible air quality risk to it.

Where no information is provided that is able to sufficiently predict the deposition of pollutants in relation to the site's sensitive features, further screening is advised at step 4.

4.20 Information about the precise location of features within sites may be available from a variety of sources. Preferably, up to date ecological information will have been provided by the applicant to the competent authority as part of the submitted proposal being consulted upon. This may include further survey and spatial information about the location of Protected Sites, the distribution of sensitive features and their sensitivity to emissions from a road that, subject to our checks and validation, could be relied upon to inform this step.

Information is held in Natural England's Designated Sites System Viewer about the spatial location of individual features. Each feature is assigned to an underpinning monitoring 'unit' for condition reporting purposes. If a sensitive feature is not assigned to a unit (or intended to be restored to the unit) within the distance criterion then effects can be screened out. (Note that the current

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[12] 'Site-fabric' is a general term used by Natural England to describe land and/or permanent structures present within a designated site boundary which are not, and never have been, part of the special interest of a site, nor do they contribute towards supporting a special interest feature of a site in any way, but which have been unavoidably included within a boundary for convenience or practical reasons. Areas of site-fabric will be deliberately excluded from condition assessment and will not be expected to make a contribution to the achievement of conservation objectives.

[13] Ricardo-AEA, 2016. The ecological effects of air pollution from road transport: an updated review' (NECR199).

reportable condition of a feature, based on latest condition assessment information, should not be used to justify screening out effects on a feature.)

4.21 If none of the site's sensitive qualifying features known to be present within 200m are considered to be at risk due to their distance from the road, there is no credible risk of a significant effect which might undermine a site's conservation objectives. The screening thresholds adopted in step 4 below need not be applied and no further assessment is required. In these circumstances, a screening conclusion of no likely significant effect on the site can be advised with regard to air quality.

4.22 If, at this stage, there is uncertainty over the presence or absence of the feature in close proximity to a road affected by the plan or project, then a precautionary approach should be taken with an assumption made that the feature may be present and step 4 undertaken.

Step 4: Application of screening thresholds

4.23 If a proposal has not been screened out by steps 1-3, the next step is to consider the risk from the road traffic emissions associated with the plan or project. Depending on the information available, this could be expressed in terms of either the predicted average annual daily traffic flow ('AADT' as proxy for emissions) or the predicted emissions themselves (the actual process-contribution). Each of these parameters have guideline thresholds to check whether the predicted change is likely to be significant (e.g.1000 AADT for traffic numbers or 1% of critical load or level for emissions). This information should have been provided to the competent authority by the applicant.

4.24 The use of the AADT screening threshold is advocated by Highways England in their Design Manual for Roads and Bridges[14] (DMRB) to check whether more detailed assessment of the impact of emissions from road traffic is required. This non-statutory or guideline threshold is based on a predicted change of daily traffic flows of 1,000 AADT or more (or heavy duty vehicle flows on motorways (HDV) change by 200 AADT or more).

4.25 The AADT thresholds do not themselves imply any intrinsic environmental effects and are used solely as a trigger for further investigation. Widely accepted Environmental Benchmarks for imperceptible impacts are set at 1% of the critical load or level, which is considered to be roughly equivalent to the DMRB thresholds for changes in traffic flow of 1000AADT and for HDV 200AADT. This has been confirmed by modelling using the DMRB Screening Tool that used average traffic flow and speed figures from Department of Transport data to calculate whether the NOx outputs could result in a change of > 1% of

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[14] HIGHWAYS ENGLAND. Design Manual for Roads and Bridges Volume 11 Section 3, Part 1 - Air Quality

critical/load level on different road types. A change of >1000 AADT on a road was found to equate to a change in traffic flow which might increase emissions by 1% of the Critical Load or Level and might consequentially result in an environmental effect nearby (e.g. within 10 metres of roadside).

As a result, the AADT thresholds and 1% of critical load/level are considered by Natural England's air quality specialists (and by industry, regulators and other statutory nature conservation bodies) to be suitably precautionary, as any emissions below this level are widely considered to be imperceptible and, in the case of AADT, undetectable through the DMRB model. There can therefore be a high degree of confidence in its application to screen for risks of an effect.

If there is already detailed, locally-based modelling available about the plan or project that shows the 1% of the environmental benchmark is *not* exceeded, even if 1000 AADT is, then this level of precision is sufficient to override the use of the very generic 1000 AADT guideline threshold above.

Remember that 1000 AADT has been adopted here to simply help trigger when to look further where traffic projection data is the sole means of assessment - it does not immediately mean there *will* be an effect.

Considering the effect of avoidance and mitigation measures already incorporated into the plan/project

4.26 In a recent authoritative decision in C-323/17 *People Over Wind*, the CJEU concluded that it is not appropriate, at the screening stage of a HRA, to take account of measures intended to avoid or reduce the harmful effects of the plan or project on a European Site. This overrules previously established UK case law in *Hart*[15] which concluded that incorporated measures could be taken into account at this screening stage when judging the risk of a significant effect. These matters can now only be taken into account as part of the appropriate assessment stage of a HRA.

4.27 Where Natural England's advice is requested at the screening stage, it should ensure that the competent authority and/or the promoters or proposers of a plan or project have clearly identified the nature of the plan or project under review and whether there are avoidance and/or mitigation measures that are to be excluded from the screening assessment. Where Natural England considers there is doubt in these matters, the precautionary principle should be applied and these matters should *not* be taken into account when Natural England is advising

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[15] Hart District Council v Secretary of State for Communities and Local Government, Luckmore Ltd and Barratt Homes Limited and Taylor Wimpey Developments Limited and Natural England [2008] EWHC 1204(Admin))

on applying the thresholds below to judge likely significant effect. Natural England should explain the reasoning for its advice, however the competent authority, as the decision maker, is entitled to disagree with this advice and reach its own reasoned and cogent decision.

Step 4a: apply the threshold alone

4.28 First consider the effects of the plan or project 'alone' against the screening threshold. Where a proposal is considered to have a likely significant effect because it breaches the screening threshold alone it should go through to an appropriate assessment 'alone' (at least initially). There is no need to consider the potential for in-combination effects (at steps 4b/c below) at this screening step as an appropriate assessment is needed in any event.

4.29 If the predicted change in traffic flow is less than 1000AADT (or the level of emissions is <1% of the critical load/level), the associated emissions are not likely to have a significant effect alone but the risk of in-combination effects should be considered further (go to step 4b/c).

4.30 At this stage, this is irrespective of the current background levels and whether critical load or level values are currently being exceeded or not. This is because 1% of the environmental benchmark or 1000AADT is considered to be so small that anything less than this will be, in any event, not likely to be perceptible and significant. We would advise that current background levels are considered later should appropriate assessment be needed.

Step 4b: apply the threshold in-combination with emissions from other road traffic plans and projects

4.31 Where a proposal is *below* the screening threshold *alone* at step 4a above (i.e. <1000 AADT or <1% depending on information available), step 4b must be considered to apply the same screening threshold 'in-combination'. This step is explicitly included here to reflect the requirements of the Habitats Regulations and in response to the recent clarification provided in the Wealden Judgment 2017.

4.32 This is also because projects and plans that increase road traffic flow have a high likelihood of acting together, or in-combination, with other plans or projects that would also increase traffic on the same roads. Vehicles generated by different plans or projects can end up on the exact same road(s) (forming a line source of emissions) within or close to the same site. In these cases, it is difficult to justify use of a threshold alone for determining likelihood for significant effect by applying it solely to the project being assessed. The threshold should be applied in-combination.

4.33 An in-combination effect is one which does not represent a likely significant effect 'alone' but, when added to similar effects from other live plans and projects, becomes significant.

4.34 The Wealden Judgment 2017 found that the use of the 1000 AADT guidelines (the proxy for 1% (on road) of the critical level/load (for the receiving habitat)) as the sole means of catering for in-combination effects lacked coherence, particularly where other figures are known which, when added together, would cause that threshold to be exceeded. From that, the Court concluded that where the likely effect of an individual plan or project does not itself exceed the threshold of 1000 AADT (or 1%), its effect must still be considered alongside the similar effects of other 'live' plans and projects (see paragraph 4.44 below) to check whether their added or combined effect on a site could be significant. The threshold itself was not questioned.

4.35 Natural England recognises that at both the screening and appropriate assessment stages of a HRA, the likely effects of a plan or project need to be thought about individually and in combination with other relevant plans or projects. This is a legal requirement of the Habitats Regulations and it helps to ensure that European sites are not inadvertently damaged by the additive effects of multiple plans or projects.

4.36 It may be very obvious that there are no other plans or projects which are 'live' at the time of the assessment (see 4.44 below) whose effects could act together with the subject proposal. A competent authority should clearly record this in their assessment in such cases. Natural England's advice is that where evidence concerning other live plans and projects is available, such as increases in road traffic from other plans or projects that will affect the same roads being assessed, the 1000 AADT threshold should also be applied to their combined value to screen for in-combination effects.

4.37 Natural England staff may be asked by a competent authority to advise on the scope of an in-combination screening step and how far they should look for other road traffic plans and projects which may be relevant to their risk assessment. In Natural England's view, staff in a competent authority can apply their professional judgment when considering this. An exhaustive search for relevant plans and projects by a competent authority is normally required to comply with the Habitats Regulations. However, a pragmatic approach to identifying the most pertinent ones may need to be taken where there is a large number of proposals. It might be reasonable to *initially* limit a search to those plans and projects which are of most direct relevance to the subject plan or project under HRA. This may be those which are simply the closest to the site or within a certain distance from it, or the most influential in nature).

4.38 Once screening thresholds have been exceeded to indicate that there is a risk of a significant combined effect from the subject proposal and other plans or projects and an appropriate assessment is warranted, the search for other live plans/projects may stop. This may mean that more minor plans or projects can be excluded from the in-combination assessment being undertaken.

4.39 This search should not be limited to other plans or projects being proposed within the jurisdiction of that competent authority; other relevant proposals affecting the same European Site(s) may occur within adjoining local planning authority areas for example.

4.40 Where the in-combination effect of the subject plan or project with more than one plan or project is greater than the 1000 AADT (when using traffic flow data) or 1% (when using emissions data) threshold, appropriate assessment is advised.

Step 4c: apply the threshold in-combination with emissions from other non-road plans and projects

4.41 When considering the potential for in-combination effects, a competent authority should also recognise that different proposal types ('sectors') and different pollutants (e.g. ammonia (NH_3), nitrogen oxides (NO_x and NO_2)) can combine together to have the same or similar effect on a given area of habitat. By way of example, nitrogen deposition on a site can result from both the emissions of ammonia from a farm source and also from emissions of nitrogen oxides from a traffic source, with both having an eutrophication effect.

4.42 Where the in-combination effect of the subject plan or project with other road traffic plans or projects has not exceeded the relevant 1000 AADT (or 1%) threshold, we should advise the competent authority to look further for any other insignificant effects of live 'non-road' plans/projects to check that the 1% threshold is not exceeded in this way.

4.43 Where the in-combination effect of the subject plan or project with one or more plan or project is greater than the 1% threshold, appropriate assessment is advised.

4.44 It is generally well-established that the scope of an in-combination assessment is restricted to plans and projects which are 'live' at the same time as the assessment being undertaken. These can potentially include:

- The incomplete or non-implemented parts of plans or projects that have already commenced;
- Plans or projects given consent or given effect but not yet started.
- Plans or projects currently subject to an application for consent or proposed to be given effect;

- Projects that are the subject of an outstanding appeal;
- Ongoing plans or projects that are the subject of regular review and renewal
- Any draft plans being prepared by any public body
- Any proposed plans or projects that are reasonably foreseeable and/or published for consultation prior to application

As stated above, when considering this scope, competent authorities can be mindful of the assessment, reasoning and conclusions included in any previous HRAs for these plans or projects.

What 'plans and projects' are already included in the nationally modelled background?

APIS provides information about background pollution concentrations for each European site through the Site Relevant Critical Load Tool (on the Concentrations/Deposition tab). Projects and plans operational **on or before** dates included in background pollution data on APIS are typically considered as an integral part of the background. These should **not** be included as projects or plans for in-combination assessment as this would effectively be double-counting the emission sources.

4.45 It is the role of the competent authority, not Natural England, to acquire sufficient knowledge and information on other plans and projects that are included within an in-combination assessment to enable it to make a fair and reasonable assessment of the likelihood of a significant combined effect. This may mean the plan or project proposer may be asked by the competent authority to provide or compile this.

4.46 Sources of information that project proposers or competent authorities can use to identify plans or projects that might act in-combination include:

- Planning Portals to locate applications awaiting permissions
- Environmental Permits Register of Applications and Register of Issued Permits
- Local plans (including brownfield registers with permission in principle) and any allocations not yet permitted.

4.47 In general terms, it is important for a competent authority to remember that the subject plan or project remains the focus of any in-combination assessment. Therefore, it is Natural England's view that care should be taken to avoid unnecessarily combining the *insignificant* effects of the subject plan or project with the effects of other plans or projects which can be considered *significant* in their own right. The latter should always be dealt with by its own individual HRA alone. In other words, it is only the appreciable effects of those other plans and projects that are not themselves significant alone which are added into an in-combination assessment with the subject proposal (i.e. ‘don’t combine individual biscuits (=insignificant) with full packs (=significant)’).

4.48 As stated above, an exhaustive search for relevant non-road plans and projects is normally required to comply with the Habitats Regulations. Where there is likely to be a large number of other live plans or projects which could all potentially fall within the scope of an in-combination assessment, it is Natural England’s view that staff in a competent authority can apply their professional judgment when considering this. It might be that a pragmatic approach to identifying the most pertinent ones may be required from the competent authority. It might be reasonable to initially limit a search to those plans and projects which are of most direct relevance to the subject plan or project under HRA (i.e. the likelihood of that plan or project’s effects impacting upon the same site in-combination with the proposed plan or project). This may be those which are simply the closest to the site or within a certain distance from it, or the most influential in nature.

4.49 As above, should screening thresholds be exceeded to indicate that there is a risk of a significant effect, this may mean that more minor plans or projects become immaterial to the in-combination assessment and can be discounted.

Similarly, this search should not be limited to other plans or projects being proposed within the jurisdiction or administrative boundaries of that competent authority; other relevant proposals affecting the same European Site(s) may occur within adjoining local authority areas for example.

Step 5: Advise on the need for Appropriate Assessment where thresholds are exceeded, either alone or in-combination

4.50 This can be summarised below:

Traffic Proxy or Process Contribution from a plan or project alone	**Advice on screening for likely significant effect**	**Is Appropriate Assessment required by the competent authority?**
More than 1000 AADT (or >1% of critical level/load)	There is a risk of a significant effect on air quality alone	Yes
Less than 1000 AADT (or <1% of critical level or load)	There is a risk of an appreciable effect on air quality but is unlikely to be significant alone and screen for in-combination effect	Either No – advise that appropriate assessment is not required if: • no other plans/projects can be identified that would act in-combination, or • **together** they add up to **less than** 1000 AADT (or 1% of critical level/load) Or Yes – advise that appropriate assessment is required if: • other plans/projects can be identified that would act in-combination, and • **together** they add up to **more than** 1000 AADT (or 1% of critical level/load)

5. Advising competent authorities on the scope and content of an Appropriate Assessment

About this section

5.1 This section aims to provide Area Team staff with further assistance when giving their advice to a competent authority on the scope and content of an appropriate assessment examining the likely effects of road traffic emissions.

5.2 This is not intended to provide a definitive or exhaustive checklist of factors to consider. A competent authority is entitled to make use of additional information and to seek the additional advice of others.

5.3 At this stage of HRA, it is a statutory requirement for competent authorities to formally consult Natural England '*for the purposes of*' an Appropriate Assessment (AA) and to '*have regard*' to any representations that Natural England may make. This consultation may include advice about further information that may be required from the applicant and advice as to whether the scope of the appropriate assessment fully addresses the likely risks to the site(s).

5.4 Typically, Natural England's expert advice is given significant weight; however a competent authority, as the decision maker, is also entitled to disagree with Natural England's advice and reach its own reasoned and cogent conclusion at Appropriate Assessment.

5.5 This section highlights a number of factors, in no particular order, that we could usefully advise a competent authority as being relevant for consideration in an assessment. It does **not** recommend sequential steps or provide definitive guidance about how or to what degree these factors should inform an assessment, which will depend on the facts and circumstances of each case.

Introduction

5.6 Having previously identified a risk or a possibility of a significant effect from a plan or project (either alone or in-combination), the purpose of the appropriate assessment stage is to more precisely assess the likely effects identified and to inform a conclusion as to whether an adverse effect on site integrity can be ruled out.

5.7 The 'integrity' of a site should be taken to mean the coherence of its ecological structure and function, across its whole area that enables it to sustain the habitat, complex of habitats and/or the levels of populations of the species for which it was, or will be, designated or classified. A site can also be described as having a high degree of integrity where '*the inherent potential for meeting site conservation objectives is realised, the capacity for self-repair and self-renewal* *under dynamic conditions is maintained and a minimum of external management is required*' (European Commission, 2000[16]).

5.8 Whilst the assessment should be an objective one which is contiguous with but more detailed than the previous screening stage, it should always be 'appropriate' in terms of its scope, content, length and complexity to the plan or project under assessment. This was recently reiterated by the Supreme Court decision in the case of *Champion*[17] which clarified:

> *'Appropriate' is not a technical term. It indicates no more than that the assessment should be appropriate to the task in hand: that task being to satisfy the authority that the project will not adversely affect the integrity of the site concerned'*.

5.9 It should not be assumed that appropriate assessment will necessarily involve detailed and complex monitoring or modelling work. Whilst complex work *might* be necessary in fully understanding what will happen to a site if the plan or project goes ahead, and asking whether that would be consistent with maintaining or restoring a site's integrity, it is equally possible that a fairly concise and straightforward assessment might be entirely 'appropriate'.

5.10 This section provides some information on additional factors which may be relevant to the scope of an appropriate assessment that seeks to assess the impacts from air pollution in a more detailed manner to ascertain whether there will be an adverse effect on site integrity. The impacts resulting from a change in the atmospheric concentration or deposition of pollutants as a result of the plan or project might include:

- Changes in the species composition of a designated or supporting habitat, especially in nutrient poor ecosystems, with an (unnatural) shift towards species associated with higher nitrogen availability (e.g. leading to the dominance of tall grasses);
- Reduction in the species richness of designated habitat
- Damage or loss of sensitive lichens and bryophytes (which may be strongly typical of a designated habitat) which receive their nutrients largely from the atmosphere
- Increases in nitrate leaching and changes in soil nutrient status which may affect the structure and function of a designated or supporting habitat

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[16] EUROPEAN COMMISSION, 2000. Managing Natura 2000 Sites (section 4.6.3).

[17] Champion v North Norfolk DC [2015] UKSC 52 (refer para 41)

5.11 Further technical guidance about the ecological impacts from road transport can also be found in the Natural England research report ‘The ecological effects of air pollution from road transport: an updated review’ (NECR199[18]).

5.12 The competent authority is therefore likely to require both ecological and air quality advice in order to undertake their appropriate assessment.

The use of thresholds at the appropriate assessment stage

5.13 At the previous screening stage, Natural England has advised that a threshold equivalent to 1% of the critical load/level can be applied as a guideline to initially check which road traffic plans and projects might require appropriate assessment. At appropriate assessment stage, Natural England recommends that this same 1% threshold is *not* used as a means of determining whether there is an adverse effect on site integrity from a road traffic project. Other factors are relevant which may mean that a plan or project that exceeds the 1% screening threshold can still demonstrate no adverse effect on site integrity through an appropriate assessment.

Issues recommended for further consideration by an appropriate assessment:

Consider whether the sensitive qualifying features of the site would be exposed to emissions

5.14 Where no information was available at the screening stage to consider the emissions from road traffic and the distance to sensitive qualifying features of sites within 200m of the road, this should be investigated further as part of the appropriate assessment.

5.15 This may require the applicant to provide further information about the actual predicted emissions at the behest of the competent authority to inform this assessment.

5.16 This is particularly relevant to this stage as contributions to air pollution from a road will typically decrease with distance away from that road (e.g. Ricardo-AEA, 2016[19]). Therefore, if, upon closer examination, the qualifying feature which is considered to be sensitive is shown not to be present within the area predicted to be affected by emissions (and Natural England’s advice is that there is no

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[18] RICARDO-AEA, 2016. *The ecological effects of air pollution from road transport: an updated review*. Natural England Commissioned Report no.199.

[19] Ricardo-AEA, 2016. The ecological effects of air pollution from road transport: an updated review’ (NECR199).

conservation objective to restore the feature to that area), it will be relatively straightforward to ascertain that the plan or project poses no credible risk to it and there is unlikely to be an adverse effect on the site's integrity.

5.17 Similarly, it may be possible at this stage to demonstrate that, despite their proximity, the sensitive features will actually only be exposed to emissions that are <1% of the Critical Load/Levels (both alone and in-combination) due to their distance from the affected road(s).

Consider the European Site's Conservation Objectives

5.18 The Habitats Regulations state that appropriate assessments of plans and projects must be undertaken '*in view of that site's conservation objectives*'. **The 'key question' for the appropriate assessment is, in view of these objectives, can it be ascertained that, should the plan or project go ahead, there will be no adverse effect from it on the site's integrity so that the site's conservation objectives will not be undermined.**

5.19 In England, Natural England provides formal advice on European Site Conservation Objectives, their purpose being in part to enable their effective use in HRAs and to expedite decision-making by competent authorities[20]. This advice is made publically available for all European terrestrial sites and European marine sites. This advice complements, but is broader than and different to, the narrower range of attributes and targets as set out in our SSSI 'Favourable Condition Tables' which are used for our own monitoring purposes to report on 'condition' status.

5.20 For Special Areas of Conservation, with reference to '*the key question'* above, the conservation objectives are to '*ensure that the integrity of the site is maintained or restored as appropriate, and ensure that the site contributes to achieving the Favourable Conservation Status of its Qualifying Features, by maintaining or restoring…'.*

The conservation objectives for any given site then go on to list a series of core attributes which form part of a site's integrity to be 'maintained' *or* ' restored'. When considering the risks associated with air pollution to a SAC, the attribute most likely to be undermined is '*the structure and function (including typical species) of qualifying natural habitats'*. These structural and functional changes might *in turn*, lead to changes to other attributes but most impacts from air pollution follow as a consequence of the structural and functional changes which are therefore of primary importance.

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[20] Defra, 2012. Report of the Habitats and Wild Birds Directives Implementation Review. Pages 26-27.

5.21 Special Protection Areas (SPA) are different; the qualifying features are the bird populations for which the site has been classified. The conservation objectives are to 'e*nsure that the integrity of the site is maintained or restored as appropriate, and ensure that the site contributes to achieving the aims of the Wild Birds Directive, by maintaining or restoring…'.*

As with SACs, the conservation objectives then go on to list a series of core attributes which form part of that site's integrity to be 'maintained' or 'restored'. When considering the risks associated with air pollution to a SPA, the attribute most likely to be 'undermined' is '*the structure and function of the habitats of the qualifying species'* (N.B. there is not reference to typical species in the case of SPA supporting habitat).

Where a Natural England Area Team has provided further **Supplementary Advice about a European Site's Conservation Objectives**, air quality will, where appropriate, be highlighted as a specific attribute of a site's structure and function with regard to any air quality sensitive features.

The conservation objective for the air quality attribute will typically be to ensure that, over the long-term, air pollutants are either maintained below or restored to below the site-relevant Critical Loads and Levels given on APIS. The inclusion of this objective in this advice on conservation objectives reflects the condition threat that exceedance poses. The objective will be tailored to distinguish where air quality should be maintained or restored dependent on whether these air quality benchmarks are currently being exceeded or not. Over time, this advice should be updated accordingly by Area Teams in light of best available information.

These objectives do not affect our existing condition assessments of these sites as air quality benchmarks do not currently inform condition reporting directly; the effects of exceedance might, over time, show up when measuring specific attributes of a habitat's structure e.g. the dominance of nitrogen-tolerant species or a decline in the extent of bare ground.

The trajectory of deposition and concentration trends illustrated on APIS is perhaps a better measure of whether the air quality objectives for a site are likely to be met or not.

NOTE OF CAUTION

When considering the sensitivity of SPA qualifying features, the extent to which changes to the structure and function of the *supporting* habitats might represent a risk to the integrity of an SPA will vary significantly, depending on the ecological role that the structure and function of a supporting habitat plays in maintaining the population for which the site has been classified. The site relevant critical load pages on APIS provide information on the sensitivity of each SPA feature.

5.22 When considering the ‘key question’ above in view of the conservation objectives, it follows that a decision as to whether a proposal ‘undermines’ the conservation objectives (or not) should also be informed by whether the conservation objectives are to ‘maintain’ or to ‘restore’.

Where background levels show the site is not currently exceeding relevant air quality benchmarks and the conservation objectives are to maintain the concentrations and deposition of air pollutants either at current levels or below the relevant benchmarks

5.23 Where there is currently no exceedance of relevant benchmarks (such as Critical Loads and Levels – see also para 5.31) the site’s conservation objectives are to ‘maintain the concentrations and deposition of air pollutants at current levels or below the relevant benchmarks’ to protect the site’s integrity in respect of air pollution. As such, a new plan or project could undermine the conservation objectives of such a site where it leads to a deterioration in air quality that is significant in the context of the site, even where that site is below a critical load or level. The evidence presented by Caporn *et al.* (2016)[21] in NECR 210 shows that small contributions of nitrogen deposition from the air have the potential to lead to *more* significant changes in vegetation composition where a site is below but near to the Critical Load, compared to a site which significantly exceeds a critical load. The appropriate assessment will need to examine such risks, and likely effects, in more detail.

5.24 Even where an additional contribution is small (e.g. <1% of critical load/level but >1% of the critical load/level in-combination), a competent authority should undertake a more considered assessment with regard to sites that are currently meeting their conservation objectives (which is considered to be appropriate to the specific circumstances).

Where the background levels show the site is already exceeding relevant air quality benchmarks and the conservation objectives are to ‘restore the concentrations and deposition of air pollutants to within benchmarks’.

5.25 Where the conservation objectives are to ‘restore the concentrations and deposition of air pollutants to within benchmarks’ (i.e. where the relevant benchmarks such as Critical Loads/Levels are *already* exceeded) they will be *undermined* by any proposals for which there is credible evidence that further emissions will compromise the ability of other national or local measures and initiatives to reduce background levels.

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[21] CAPORN, S., FIELD, C., PAYNE, R., DISE, N., BRITTON, A., EMMETT, B., JONES, L., PHOENIX, G., S POWER, S., SHEPPARD, L. & STEVENS, C. 2016. *Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance*. Natural England Commissioned Reports, Number 210.

5.26 An exceedance alone is insufficient to determine the acceptability (or otherwise) of a project**.** Exceedance will represent a threat to the condition and integrity of the site. Hypothetically, it could be argued that any increase above a currently exceeded state compromises the extent to which improvements from other initiatives will deliver the restoration aims of the conservation objectives as any additional pollution could slow the rate at which progress is made towards meeting the relevant air quality benchmarks.

5.27 In terms of whether an 'adverse' effect can be ruled out, the Advocate General's Opinion in *Sweetman*[22] indicated that, in her view, a plan or project involving *'some strictly temporary loss of amenity which is capable of being fully undone'* would not be an adverse effect on integrity. By comparison, the *'lasting and irreparable loss'* of part of the SAC feature in *Sweetman*[23] was ruled to be an adverse effect on integrity.

5.28 In practice, where a site is already exceeding a relevant benchmark, the extent to which additional increments from plans and projects would undermine a conservation objective to 'restore' will involve further consideration of whether there is credible evidence that the emissions represent a real risk that the ability of other national or local measures and initiatives to otherwise reduce background levels will be compromised in a meaningful manner. This is a judgement to be taken by the competent authority which should be informed by, amongst others, the extent to which any declining national trends in air pollution or strategic work to tackle emissions affecting the site more locally might otherwise lead to improvements, the rate at which such improvement are anticipated to be delivered, any credible evidence on the extent of the impacts of a plan or project and whether those impacts can properly be considered temporary and reversible.

Consider background pollution

5.29 European sites are unlikely to be pristine in terms of air quality effects, and our advice will therefore be mindful of the current condition of the site's features and the site's long-term conservation objectives. Factors already affecting the site which are not related to the plan/project being assessed count as the current prevailing or background conditions. These factors may be having an adverse effect independent of the proposal being assessed (and should be addressed separately) but nevertheless may be currently undermining the site's resilience to new and additional pressures.

5.30 The background condition of the site will provide some further context to judging the risk of an adverse effect on integrity. This section explores where to obtain

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[22] Advocate General Opinion in Case C-258/11 *Sweetman* (refer paras 58-61)
[23] Case C258-11 *Sweetman* (refer para 56)

background concentrations of air pollution to take into account as prevailing conditions.

(a) Review the Environmental Benchmarks ('critical loads and levels') and feature sensitivity to nitrogen

5.31 Habitats have varying sensitivity to air pollution effects. APIS provides environmental benchmarks for habitat either through the Site Relevant Critical Load Tool or the Habitat/pollutant impacts Tab on the home screen. These benchmarks are called critical loads or levels.

5.32 Critical levels and loads are set to take account of very long term contributions of pollution (20 – 30 year timeframe). Critical loads in particular are expressed as a range because they cover the situation across Europe for each nitrogen sensitive habitat. This range has to account for the variation in topography and precipitation/climate across Europe. In the UK, APIS outlines the part of the critical load range that is most appropriate based on available evidence (UK Indicative Critical Load Values).

5.33 Check whether the habitat being assessed has an environmental benchmark to assist with the assessment. If there is no benchmark on APIS that could mean there is lack of data. Absence of a benchmark is not assurance that a specific feature is insensitive to air pollution.

5.34 In addition, check and consider a feature's sensitivity to nitrogen more precisely. Some features and sites are much more sensitive to nitrogen than others; NECR 200 identifies three categories of sensitivity for traffic emissions; high (5-10 CL range), medium (10-20 CL range) and low (20-30 CL range).

5.35 Whilst the main impact mechanism of concern is through acid and nutrient nitrogen deposition (covered below), many assessments consider direct toxicity to vegetation from NOx. In this case the first relevant question to ask is the extent to which the relevant critical level might be exceeded as a result of the plan/project (either alone or in-combination with other plans and projects).

5.36 Ricardo-AEA (2016) in NECR200[24] found that background concentrations of NO_x in rural areas away from roads are typically in the range 15 – 20µg/m^3 i.e. some way off exceeding the critical level of 30µg/m^3.

Note that APIS provides background NOx values which are averaged over a 5km grid square. This means that higher levels along the roadside (but within a European site boundary) can be missed.

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[24] RICARDO-AEA, 2016. *Potential risk of impacts of nitrogen oxides from road traffic on designated nature conservation sites*. Natural England Commissioned Report no. 200.

5.37 NECR200 measured designated site exposure to NOx from road traffic taking account of other background sources of NOx for 2011 and predicted 2020 data. High (>30µg/m^3), medium (> 25µg/m^3) or low (<25µg/m^3) categories of exposure to NOx from road traffic are identified based on a combination of road traffic NOx and background levels. Whilst this is a national snapshot in time (based on modelled data available at the time of the study in 2014), it could provide useful contextual data to supplement site specific data from APIS. Further information is provided here at NECR200.

5.38 When considering the impacts of a plan or project in relation to critical levels, it is important to understand the distance from the road that the critical level is exceeded and whether this represents a credible risk to qualifying features. We may wish to advise for example on how site boundaries have been defined and how the conservation objectives should be interpreted and applied to roads and road verges within a site boundary (see also step 3 in the screening stage above).

(b) Check for exceedance of Environmental Benchmarks

5.39 Exceedance of the benchmarks is determined by comparing the CBED (the 'Concentration Based Estimated Deposition' model) results (at 5km or 1km grid resolution) with critical levels or loads. Through this very direct approach for determining exceedance, more than 80% of the area of sensitive European Sites is currently in this exceedance state. This approach does not account for variability within the 5km grid square.

5.40 National maps to demonstrate where habitat sensitive to air pollution is predicted to be above its environmental benchmarks are available on Defra's UK AIR website[25].

5.41 Whilst most sensitive European Sites will be in this exceedance state, it does *not* automatically mean that further plans or projects affecting them would have an adverse effect on site integrity. Rather, it provides another piece of information to consider when determining whether a proposal might have a benign impact on site integrity and be acceptable or whether a conclusion of no adverse effect on site integrity cannot be reached by the assessment.

(c) Consider trends and whether there is evidence to indicate that background levels are decreasing

5.42 Acquiring information on whether local background pollution levels are declining or not can provide useful context to an appropriate assessment.

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[25] 2013-2016 exceedances are in Defra AQ0826

5.43 This is available on the APIS Site Relevant Critical Load Tool and background concentrations are displayed under the “Trends” tab. This trend data currently covers the deposition and concentration trends over at least the last 8 years of national modelling. It is updated annually, though background trends are a 3-year average to account for weather variation (e.g. year 2005 is the average of years 2004, 2005 & 2006). The trend data is provided for maximum and minimum air concentrations (NOx, SOx, ammonia) as well as deposition (nutrient nitrogen and acid). A precautionary approach is to use the maximum value.

5.44 For deposition there are 3 sets of maximum and minimum values related to 3 rates of deposition:

- Moorland (or knee-high vegetation)
- Forest (or anything taller than knee high)
- Grid Average (average deposition for 5km grid square across habitat types)

5.45 Which value you use will depend on what type of habitat you are looking at. Figure 3 shows an example of nitrogen deposition trends at Breckland SAC. Nationally predicted declines in nitrogen deposition on heathland at Breckland SAC from 27 kg N/ha/year in 2005 to 24 kg N/ha/year in 2014 could mean that some increases in nitrogen from a plan or project (alone and in combination) may not impede this downward trend. Taking into account all relevant factors and information, it may be possible to consider some increases as temporary and reversible, which would be unlikely to undermine site objectives. In other words, we can still expect - even with the plan/project – the overall environmental loading will return to below critical level and loads within an appropriate timeframe.

5.46 While this may be a useful factor to consider in some cases, it should not be applied blindly. A range of matters will remain relevant, including whether any local survey evidence indicates that it is unsafe to rely on national modelling or where there are development clusters which would mean that any headroom that may be available should be more closely monitored or cannot be confidently relied on.

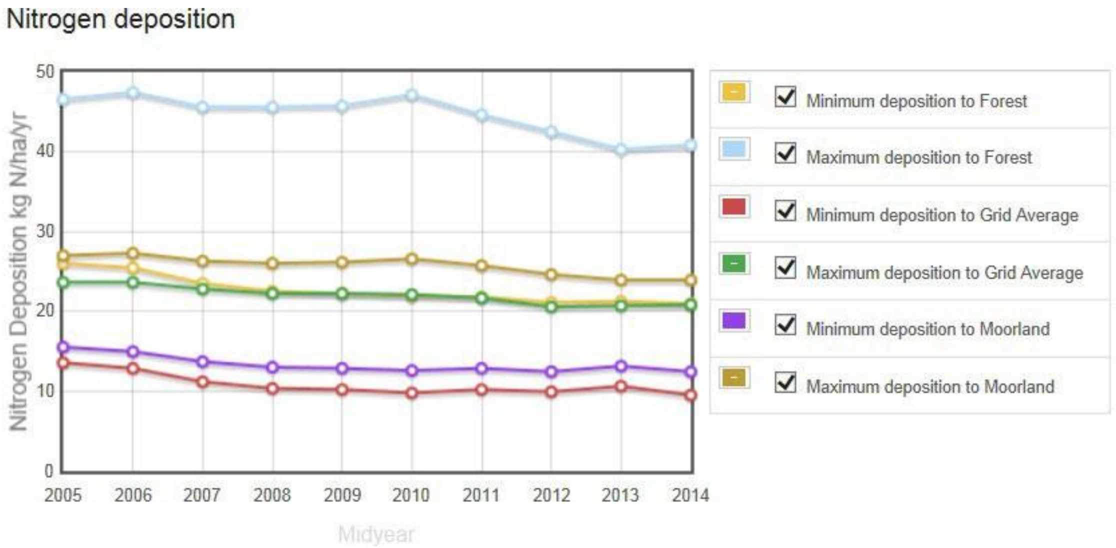

Figure 3: **APIS Trends Tab for Breckland SAC Nitrogen Deposition**

Consider the designated site in its national context

5.47 NECR200 provides contextual information to help inform relative risk within a wider national context. It provides an analysis of SAC and SSSI exposure to NOx from road traffic (taking into account other background sources of NOx), for 2011 and 2020 (based on 2014 modelling data).

5.48 It provides a relative categorisation of SSSI and SAC site exposure to road traffic NO_x in a national context and a relative risk categorisation of SACs based on exposure and site sensitivity. Whilst the data is a snapshot in time based on 2011 data and modelled 2020 data, it does provide a national context for local decision makers when assessing local plans and local development in relation to road traffic impacts on designated sites.

Consider the best available evidence on small incremental impacts from nitrogen deposition

5.49 When assessing likely adverse effects on site integrity, the Natural England Commissioned Report 210: *Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance* (referred to above) may be of relevance.

5.50 This research shows that habitats that have already been subject to high background nitrogen deposition can develop an effective tolerance to the effects of further deposition. However, this evidence is not appropriate for use to justify further exceedance on designated sites alone, without also considering all available factors and information and where this would undermine the conservation objectives to reverse this and restore pollutant levels to within an acceptable level.

5.51 The objective of this report was to examine recent vegetation survey data to understand the relationships that exist between species (composition and richness) and nitrogen deposition, and to determine the effect of incremental increases in nitrogen. Vegetation data were analysed from 226 sites, collected over 8 surveys of 5 UK priority habitats for conservation (sand dune, bog, lowland heath, upland heath, acid grassland). Further evidence was gained from published survey data and the network of UK nitrogen addition experiments.

5.52 This report provides detail about how much additional nitrogen might lead to a loss of one species on the following habitats (although in the case of bogs and sand dunes there was either insufficient information to develop a dose-response curve or the measure of effect (loss of one species) was too coarse to make a determination):

- Upland heath
- Lowland heath
- Bog (non-curvilinear response)
- Acid grassland
- Sand dunes

For certain habitats this information can inform a more precise assessment of the likely effect. The implications of any such predicted effects on overall species-richness should then be further evaluated in light of the site's Conservation Objectives to inform the conclusion of the appropriate assessment.

Consider the spatial scale and duration of the predicted impact and the ecological functionality of the affected area

5.53 The likely duration of any emission-impact(s) and the potential for recovery/reversibility of that impact are important factors to consider further when determining whether it is possible to demonstrate no adverse effect on integrity. For example, a conclusion of no adverse effect on integrity may be able to be reached in the case of a short-lived effect from which the site/feature can quickly recover (e.g. a peak caused by construction traffic).

5.54 The anticipated duration of any potential air quality impact, the ability for the affected feature to absorb or recover from that impact and the likely timescale of any anticipated recovery may be an important consideration in the assessment. The longer or more uncertain the feature's likely recovery time from an impact, the more difficult it may be to demonstrate no adverse effect on integrity.

5.55 A Natural England research report (NECR205) on how small scale effects[26] on European Sites have been considered in decision-making is of relevance here. Where the spatial extent of the affected area is small then the risk to the integrity of the site needs to be approached in a reasonable and proportionate manner. The Research Report concluded that:

> *'In the case of small scale effects on a qualifying Annex 1 habitat type for which a SAC had been designated, the decisions reviewed suggest that it is the relative importance of the area affected in terms of the rarity, location, distribution, vulnerability to change and ecological structure which is most influential. The contribution the affected area made to the overall integrity of the site (and hence that site's contribution to the conservation status of that habitat type at a member state level) exerted a stronger influence over decision makers than the spatial extent of the effect.*
>
> *In the case of small scale effects on a supporting habitat for a species (whether a designated SAC species or a classified SPA species), the decisions reviewed suggest it is the ecological functioning of that supporting habitat which is most influential: that is, what ecological function the affected area was performing, or could perform, and it's importance to the population of the species for which the site had been designated / classified.'*

Consider site survey information

5.56 Information available from site surveys will be relevant to an appropriate assessment. In particular any information which might indicate evidence of existing impacts from air pollution from similar sources which might introduce reasonable scientific doubt as to the absence of such adverse effects should the plan or project in question be permitted.

5.57 Such information which is available at the stage of the HRA could also enable a more detailed review of the likely exposure of sensitive features to emissions.

Consider national, regional and local initiatives or measures which can be relied upon to reduce background levels at the site

5.58 Where an existing national, regional or local initiative can be relied upon to lead to the reduction in background levels of pollution at a site, the competent authority should assess the implications of a plan or project against an improving background trend.

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[26] CHAPMAN, C. & TYLDESLEY, D. 2016. *Small-scale effects: How the scale of effects has been considered in respect of plans and projects affecting European sites - a review of authoritative decisions*. Natural England Commissioned Reports, Number 205.

5.59 In order to rely on the fact that national, regional or local initiatives will positively affect the environmental context within which a decision is taken on a plan or project (at appropriate assessment), a high degree of certainty is required in order to satisfy the precautionary nature of the legislation. Competent authorities should consider in their assessment the full details of the national, regional or local initiatives that they intend to rely on in an HRA and ensure that they are confident that such schemes will be implemented and achieve the results predicted within the relevant timescales.

5.60 An appropriate assessment would need to consider whether the additional contribution against a reliably predicted declining background level would adversely affect the integrity of the site in question. This question would be informed by a judgement by the competent authority over any delay that the new plan or project might introduce to the timeframe within which the benchmark might have otherwise been achieved (had the plan or project not been consented) and whether it considers any delay would be acceptable or not (having regard to Natural England's advice).

5.61 Examples of strategic work could include:

- Measures to implement Shared Nitrogen Action Plans (SNAPs) that are measured and demonstrated as a certainty, not simply an aspirational plan of potential measures. See Improvement Programme for England's Natura 2000 Sites Atmospheric Nitrogen Theme Plan IPENSTP013.
- National projections given in reports on NE Evidence Catalogue (NECR200 roads report)
- National Policy resulting in emission reductions (e.g. Clean Air Zones, Ultra-low emission zone actions) – these would need to have measureable outcomes for emissions that are certain; again they cannot be aspirational only.
- Evidence of uptake of emission-reduction measures in local agri-environment schemes (whilst recognising the timeframe of any commitments)

Note the request of the Dutch courts for a preliminary ruling from the CJEU in C-294/17 on the Dutch national nitrogen programme (see earlier paragraph 1.6).

Consider measures to avoid or reduce the harmful effects of the plan or project on site integrity

5.62 In a recent decision in C-323/17 *People Over Wind*, the CJEU concluded that any measures intended to avoid or reduce the harmful effects of the plan or project on a European Site should be taken into account at the appropriate assessment stage, rather than the preceding screening stage.

5.63 A submitted proposal subject to appropriate assessment by a competent authority may already contain such measures that have already been voluntarily proposed by the applicant. Further ‘additional’ mitigation measures can also be imposed by that competent authority on the proposal by way of formal conditions or restrictions subject to which a permission or authorisation may be given. These may be different to or go further than any mitigation measures already proposed by the applicant.

5.64 However, it is relevant to consider these matters at the appropriate assessment stage and Natural England may wish to advise a competent authority on such measures.

5.65 Avoidance and mitigation measures must be capable of preventing adverse effects on site integrity over the full lifetime of the plan or project. To be viable, such measures should be considered to be effective, reliable, timely, guaranteed and of sufficient duration.

5.66 As a result, the inclusion of these measures should be supported by evidence and confidence that they will be effective and that they can be adequately secured and legally enforced to ensure they are strictly implemented by the plan/project proposer.

5.67 Examples of plan/project specific measures to mitigate air quality effects might include;

- Traffic management measures which reduce emissions at source e.g. road speed reduction measures aimed at reducing impacts on sensitive sites/features
- Planting of wooded shelterbelts or other types of green barriers such as trees, green walls and hedges to intercept and limit the dispersal of traffic emissions to sensitive sites/features.

Consider any likely in-combination effects with other live plans and projects from other sectors

5.68 Where a plan or project has been screened in for appropriate assessment based on the likelihood of it having a significant effect alone, it should initially be subject to appropriate assessment on this basis.

5.69 If, after considering and applying any further mitigation measures to the plan or project, the competent authority considers that the risk of residual effects remain which are appreciable (i.e. not inconsequential) but no longer adverse in their own right, then a further in-combination assessment of these residual effects would be required at this stage to check for a combined adverse effect (see principles included in step 4b/c).

5.70 Other plans or projects that could add to the road traffic effects of the subject plan or project and have a cumulative effect on a particular site could originate from other sectors (e.g. applications for intensive livestock permits or industrial installations).

6. Giving Natural England's advice to the competent authority for the purposes of the appropriate assessment

6.1 The competent authority must have regard to any representations that Natural England makes about its assessment and can give its views considerable weight in coming to its decision[27]. However, Natural England's advice on an appropriate assessment is not binding and it does not have to be given such weight if cogent reasons can be given by a competent authority for departing from it[28].

6.2 Competent authorities may consult Natural England on their final appropriate assessment and the conclusions that have been reached Natural England's response will represent its formal opinion, as the appropriate nature conservation body, on the effects of the proposals on the integrity of the European Site(s) in accordance with the Habitats Regulations.

6.3 Natural England should advise on the competent authority's conclusion reached by its appropriate assessment. Where we do not agree with the conclusions of the assessment, we should explain why not with clear and credible reasoning. We may wish to advise on further modifications/conditions/restrictions that could, in our view, enable the competent authority to conclude no adverse effect on the integrity of the site, for instance.

6.4 Where an adverse effect on a European site's integrity cannot be ruled out by a competent authority, despite the application of additional mitigation, it does not necessarily follow that the plan or project will not be permitted. In accordance with the Habitats Regulations, the competent authority (in conjunction with the project proposers and the relevant Government department) could then consider whether the proposal can satisfy stages 3 and 4 of the Habitats Regulations Assessment (consideration of alternative solutions and imperative reasons of overriding public interest) subject to securing the necessary compensatory measures. In these circumstances, the competent authority should initially be referred to current Government guidance on applying these stages of HRA.

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[27] See (Ashdown Forest Economic Development LLP v SSCLG, Wealden District Council [2014] EWHC 406 (Admin) at paragraph 110)

[28] See R (Akester) v. DEFRA [2010] EWHC 232 (Admin) at paragraph 112; Wealden DC v. SSCLG [2016] EWHC 247 (Admin) at paragraphs 91 and 95; DLA Delivery v. Lewes District Council [2015] EWHC 2311 at paragraph 32; Mynydd y Gwynt at paragraph 20.

6.5 Natural England staff should act in accordance with Part 7 of Natural England's Non-Financial Schedule of Delegations when giving its advice to competent authorities on the appropriate assessment of certain plans and projects.

For further information about the content of this guidance note, please contact Natural England Planning Consultations Team at consultations@naturalengland.org.uk.

Appendix A: Summary Flowchart – advising on steps for HRA of plans/projects with road traffic emissions

Stage	**Flowchart step**		**Supplemental evidence/ basis for judgment**
Initial screening for credible risk of an effect	**1**	Check Distance criteria - could significant emissions reach a protected site? *Yes* = move to Step 2 *No* = no further HRA required	Industry standards based on likely distance for modelled emissions (scoping model); often related back to significance threshold Distance Criteria – 200m for roads and available upon request; note this is currently under review APIS Introduction to Air Pollution
	2	Check the sensitivity of qualifying habitats or supporting habitat of qualifying species. Are habitats in proximity sensitive to the emission type? *Yes* = move to Step 3 *No* = no further HRA required	APIS Site relevant Critical Loads and Levels (based on literature and professional judgement) http://www.apis.ac.uk/srcl
Detailed screening for determining whether screening thresholds are appropriate	**3**	Check habitat likelihood to be exposed to emissions Are the sensitive habitats where emissions are predicted to be? *Yes or Unsure* = move to Step 4a *No* = no further HRA required	Use application documents to understand predicted emissions (magnitude and location if available). If not available, assume emissions reach entire site in proximity. Investigate location of habitats determined as sensitive in Step 2. Use MAGIC priority habitat layers (internal staff: if necessary contact Site responsible Officer for advice to understand if sensitive habitats are present).
Applying screening thresholds	**4a**	Apply Screening Threshold Alone *If below threshold alone* = move to step 4b. *If above* = move straight to step 5.	Ascertain the Process Contribution (PC) or proxy increase in traffic from the plan or project (emissions and predicted deposition or AADT flow). This can be determined through application document, screening model results, detailed model results and information from APIS. Apply Screening threshold (1% of critical level or load or 1000AADT) alone.

Stage	Flowchart step		Supplemental evidence/ basis for judgment
	4b	Apply Screening Threshold In-combination with other traffic/roads *If below threshold in-combination* = move to step 4c. *If above* = move straight to step 5.	Use information from competent authority to determine if there are plans or projects in the pipeline (not in background pollution) that should be considered in-combination for emission from roads/ increase in traffic. For instance, add traffic increases/ emissions & deposition from other Local Plans together and apply 1000 AADT/ 1% to that sum.
	4c	Apply screening threshold in-combination across sectors *If below threshold in-combination*= no likely significant effect can be advised and no further assessment is required. *If above* = move to step 5.	Use information from other competent authorities (Planning Portal or Environmental Permitting register) to determine if there are nearby permissions that would have an in-combination effect with the roads being assessed. When all relevant proposals together (in-combination) fall below the 1% or 1000 AADT level of change, there is reasonable rationale to consider the proposal unlikely to have a significant effect.
Advise Appropriate Assessment is required and contribute scoping advice	**5**	Provide supporting evidence to Competent Authority (scoped as appropriate) Proceed to Step 6 when requested by competent authority and sufficient information is available to provide advice	• Check distance of sensitive habitats from emissions • Check European Site Conservation Objectives • Check environmental benchmark (critical level and load) • Check background concentrations and exceedance • Check APIS Trends Tab for reasonable expectation that background pollution is decreasing • Assess likely scale and duration of impacts on habitats from emissions • Check strategic initiatives in area (if would be undermined if project or plan was allowed) • Check mitigation options and whether detailed modelling may be needed (up to competent authority) • Consider any residual effects (after mitigation where practicable) and check for in-combination effects with other plans/projects
Advice on the appropriate assessment	**6**	Competent Authority has provided an Appropriate Assessment conclusion When requested by competent authority and information is available to provide advice	Give formal advice on appropriate assessment – provide reasoning for our advice

Annex C: Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance (NECR210)

Natural England Commissioned Report NECR210

Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance

First published 23 March 2016

www.gov.uk/natural-england

Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

The work was commissioned as part of a review of the thresholds used in air quality impact assessments that was required through the Inter-agency Air Quality Technical Advisory Group. The report aimed to analyse existing scientific data to demonstrate and quantify the effect of incremental additions of atmospheric nitrogen deposition (above the critical load) on different semi-natural habitat types.

The report will be used to inform specialist advice on air quality effects on habitat that is used in planning advice, agri-environment schemes and to protect and enhance designated sites. The Environment Agency have planned (subject to approval) to use this science report to review the thresholds they use for controlling ammonia emissions from intensive farming.

This report should be cited as:

CAPORN, S., FIELD, C., PAYNE, R., DISE, N., BRITTON, A., EMMETT, B., JONES, L., PHOENIX, G., S POWER, S., SHEPPARD, L. & STEVENS, C. 2016. *Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance*. Natural England Commissioned Reports, Number 210.

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Keywords - habitat, nitrogen deposition, heath, bog, dune, grassland, ammonia, air quality, air emissions

Further information
This report can be downloaded from the Natural England website: **www.gov.uk/government/organisations/natural-england**. For information on Natural England publications contact the Natural England Enquiry Service on 0845 600 3078 or e-mail **enquiries@naturalengland.org.uk**.

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Assessing the effects of small increments of atmospheric nitrogen deposition (above the critical load) on semi-natural habitats of conservation importance

Simon Caporn, Chris Field, Richard Payne, Nancy Dise, Andrea Britton, Bridget Emmett, Laurence Jones, Gareth Phoenix, Sally Power, Lucy Sheppard, Carly Stevens

Summary

1. Around two thirds of all Sites of Special Scientific Interest in the UK exceed their critical loads as a result of current atmospheric nitrogen (N) deposition. In regions where the critical load is already exceeded there is a need to understand how further increases in N deposition may affect ecological communities.
2. The objective of this report was to examine recent vegetation survey data to understand the relationships that exist between species (composition and richness) and nitrogen deposition, and to determine the effect of incremental increases in N. Vegetation data were analysed from 226 sites, collected over 8 surveys of 5 UK priority habitats for conservation (sand dune, bog, lowland heath, upland heath, acid grassland). Further evidence was gained from published survey data and the network of UK nitrogen addition experiments.
3. The relationships examined in this report use modelled annual N deposition as the pollutant variables; however, the relationships studied between N deposition and species richness and presence have developed over many years of pollution. The current rate of N deposition is used as a proxy for long-term cumulative N deposition. In some/many cases, sites will have experienced high N deposition for many years and, because of this legacy, it is unlikely that an increase or decrease in nitrogen deposition will immediately cause changes in species richness or composition.
4. Across the habitats and datasets, increasing N deposition (total, reduced or oxidised) was correlated with quantifiable declines in species richness and changes in species composition. Species richness was also correlated to climate, with increasing species richness being a function of increasing precipitation and decreasing temperature. Evidence from the literature review (N addition experiments where climatic drivers are controlled for and other field surveys) supports the findings from the data that N is driving considerable change within the habitats studied.
5. When all the habitats are considered separately, the response of species richness to long-term N deposition is curved, with sharper losses in diversity from well below the habitat-specific critical load range. At levels of N deposition at and above the upper end of each habitat-specific critical load, additional increments of long-term N are associated with further declines in species richness.
6. Not all species responded negatively, nitrogen loving plants such as the graminoids (grasses and sedges) *increased* their cover in response to increasing N deposition in bog, heath and sand dune habitats. This may result in the loss of key habitat species due to increased competition from faster-growing species, and further threaten site integrity. In addition, some species groups responded in some habitats but not in others, for example bryophyte species richness.
7. Gaps in the data mean that there remain many habitat types in the UK for which the responses to N deposition are not fully understood. Ecosystems which share similarities in species and soil type are likely to show similar responses to those found within this report. In these cases it is recommended that the findings in this report, subject to local conditions, be used to predict responses to an incremental increase in N deposition sustained over the long term. Further work should be undertaken to fill the data gaps in these habitats and those that are dissimilar to the ones studied.
8. The atmospheric concentration of NO_x and NH_3 can also influence responses. Over the long-term, changes in pollutant concentration are reflected by changes in deposition, therefore changes in annual mean concentrations could be converted to N deposition and responses predicted using the relationships developed in this report. However, it is important to recognise that the differing effects between concentration and deposition are unclear and high pollutant concentrations, even in the short-term, may be very damaging, especially for lower plants. Dose-response relationships to changes in N concentration are not fully understood and should be further researched experimentally.

9. The findings of this work, in conjunction with other recent studies, have important implications for the way that pollution regulators and the conservation agencies assess new or existing pollution sources and the assessment thresholds applied.

Acknowledgements

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1. Introduction

The nitrogen problem

Emissions to the atmosphere of ammonia (NH_3) and nitrogen oxides (NO_x) dramatically increased in the 20th century due to increased combustion of fossil fuels and intensification of agriculture. Ammonia is volatilised from intensive agricultural systems such as dairy farming and intensive animal husbandry, while nitrogen oxides come mainly from burning of fossil fuel by traffic and industry (Asman *et al*., 1988; Galloway, 1995; Bobbink and Hettelingh, 2011). These combined activities result in a more than doubling of the deposition of reactive nitrogen compounds to the earth's surface (Galloway *et al*., 2004). The problems that result from increased aerial deposition of reactive nitrogen compounds have been recognised only in recent decades but are now believed to be widespread in ecological communities on regional and global scales (Emmett, 2007; Phoenix *et al*., 2006; Bobbink *et al*., 2010). There is particular concern over the impacts on natural and semi—natural ecological communities, where the normal low rates of nitrogen supply often provide important limits to ecological processes. For this reason the most obvious potential influence of pollutant nitrogen deposition is as a fertilizer, i.e. eutrophication, threatening the natural composition of those ecological communities that are well adapted to nutrient-poor soils. Another ecological impact of nitrogen deposition results from soil and water acidification which affects some species directly but also causes impacts through release of toxic metals such as aluminium (Stevens *et al*., 2010). A wider range of biogeochemical changes are also likely to occur in impacted sites such as nitrogen leaching and nutrient imbalances in soils and vegetation (see RoTAP, 2012).

The evidence base

The scientific evidence demonstrating that nitrogen pollution can affect ecosystems in the UK and elsewhere has grown substantially in the past decade and has recently been re-evaluated in RoTAP (2012). Much of the early knowledge about nitrogen impacts on ecological communities came from laboratory and field experiments which have demonstrated the potential for change in structure and function of ecosystems and communities. An alternative approach using field-based monitoring and targeted vegetation surveys provides complementary and compelling evidence that the changes seen in nitrogen addition experiments have actually occurred in the field as a result of atmospheric deposition. Various vegetation monitoring schemes such as the UK Countryside Survey (Maskell *et al*., 2010) and specific habitat surveys across deposition gradients (e.g. Stevens *et al*., 2006), supported by experiments (see Emmett *et al*., 2007), indicate that long range nitrogen pollution is or has been responsible for community changes and significant losses of plant diversity across large areas of the UK.

Critical loads

The growing knowledge base from the combined experimental studies and field surveys enable us to generate, for several plant communities, nitrogen dose – ecological response relationships and these can be used to evaluate and position critical load guidelines. The Critical Loads approach is a tool used to judge the risk of harm to the environment from several forms of air pollutants. Critical Loads are defined as: *"a quantitative estimate of exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge"*. The empirical Nutrient nitrogen critical loads were revised in June 2010 (Bobbink and Hettelingh, 2011) and are shown for all EUNIS habitats in Appendix 6 and summarised in Table 1 where they relate to specific habitats studied here. Large areas of the country now exceed the critical loads for nutrient N and are predicted to continue to do so in 2020 despite reductions in emissions of reactive N gases (Hall *et al*., 2006). For an overview of Critical Loads see the UK Air Pollution Information System (http://www.apis.ac.uk/overview/issues/overview_Cloadslevels.htm).

Table 1: Summary of current critical loads relevant to the habitats studied in this report

Ecosystem type	EUNIS code	2011 critical load (kg ha^{-1} yr^{-1})	Indication of exceedance
Upland and lowland heath	F4.2	10-20	Transition from heather to grass dominance, decline in lichens, changes in plant biochemistry, increased sensitivity to abiotic stress
Sand dune grassland	B1.4	8-15	Increase in tall graminoids, decrease in prostrate plants, increased N leaching, soil acidification, loss of typical lichen species
Bog (raised and blanket)	D1	5-10	Increase in vascular plants, altered growth and species composition of bryophytes, increased N in peat and peat water
Acid grassland	E1.7	10-15	Increase in graminoids, decline of typical species, decrease in total species richness

Environmental protection

An application for an Environment Permit (under the Environmental Permitting Regulations 2010) from an industrial installation wishing to commence or expand activities triggers an assessment under the Conservation of Habitats and Species Regulations 2010 (known as the ‘Habitats and Species Regulations’), in relation to European protected sites, and the Wildlife & Countryside Act 1981, as amended by the Countryside & Rights of Way (CRoW) Act 2000 in relation to SSSIs. In accordance with the legislation, permits should only[1] be given where it is possible to conclude that the installation will have no adverse effect on the integrity of a European site (SAC, SPA or, by Government Policy, Ramsar site) and is not likely to damage a SSSI. This assessment is considered in context with the thresholds within the Environment Agency (EA) H1 guidance, together with the understanding that around two thirds of all protected sites are already predicted to exceed their nitrogen critical loads as a result of existing levels of air pollution (RoTAP, 2012).

This raises a key question for the Government nature conservation advisors and environmental regulator: if there is already an identified risk of harmful effects from existing air pollution (i.e. predicted critical load or critical level exceedance), what, if any, additional air pollution arising from a new installation is acceptable. Furthermore, what, if any, benefits are likely to be evident due to a reduction of pollutant exposure while the critical load or level remains exceeded?

In order to address these questions of the consequences of changes in nitrogen deposition above and below the critical load, this report will consider in detail the form and the quantitative nature of the relationships between atmospheric nitrogen deposition and ecological response in a number of different important UK ecological communities using

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[1] With the exception where Overriding Public Interest is determined by the Secretary of State or Welsh Assembly Government, under the Habitats Regulations.

recent evidence from surveys and experiments. The aim is to quantify the effect of incremental changes in long-term nitrogen deposition both above and below the critical load on important measures of plant community diversity and species composition.
The approach is to use recently available scientific data, including the UKREATE (Terrestrial Umbrella) survey dataset, and apply new statistical analysis such as canonical correspondence analysis, stepwise and LOESS (Locally weighted scatter plot smoothing) regression, and constrained cluster analysis to define and visualise the response variables within a range of habitats. Other published studies and experimental information are also assessed. The nature of the relationships between these response variables and nitrogen deposition are then examined. The results of our analysis are discussed in context with incremental increases in N deposition above and below the critical loads.

Report structure

First the report introduces the data sets and statistical methods used. The report is then structured by Tasks:

Tasks 1 and 2: To collate the relevant scientific information and categorise by habitat type
These tasks collated the available scientific information and categorised these data by habitat. Vegetation data sets from a number of surveys were used for the project, together with responses found at a number of nitrogen-addition experimental sites: details of these are provided here. In addition, key literature reporting survey responses from each habitat is also summarised in this section. In some habitats data were not available; these are identified and discussed separately in Task 6.

Task 3: To identify the relevant response variables for each habitat type
This studied each habitat for which vegetation survey data were available and how species richness or species composition varied across each dataset. The responses of these variables are analysed alongside ecological driver data such as nitrogen and sulphur pollution, temperature and precipitation and response variables strongly associated with nitrogen pollution are identified.

Task 4: To determine the relationship between nitrogen deposition and the key response variables
The nature of the relationship between the response variables identified in Task 3 and nitrogen pollution is considered further in Task 4.

Task 5: To assess the effects of different increments of nitrogen deposition above the critical load
Here the relationships identified in task 4 between N deposition and the response variables within each habitat were further considered and the effect of an incremental increase in long-term N pollution upon each was derived. This is reported as percent change in species richness or cover of selected indicator species for a 1 kg ha^{-1} yr^{-1} rise in long-term N pollution, and the amount of long-term N that would lead to a reduction in species richness of 1 species at different background levels of N pollution. Results for other increments of nitrogen are provided in Appendix 5. Comparable responses from dose-response experiments and the literature are also presented for Tasks 4 and 5.

Task 6:
This task reviews the information presented in the preceding tasks and assesses whether the relationships between the response variables and N can be applied to habitats where survey datasets were not available for analysis. Similarities between habitats in soil type and vegetation are used to complete this task. This task also considers whether the

relationships can be used when considering pollutants concentration i.e. critical levels rather than loads. A final discussion draws together the information presented within the report.

2. Methods

2.1 Vegetation survey data

This project analysed vegetation survey data collected during 8 surveys of 5 key UK semi-natural habitats between 2002 and 2009 encompassing the 2009 Terrestrial Umbrella (TU) multi-habitat survey, the 2006 TU Moorland Regional Survey (MRS), a 2002 Sand dune survey (Jones *et al*., 2004), and the BEGIN UK Acid Grassland dataset (Stevens *et al*., 2010). Mean vegetation data were collected over 5 separate quadrats per site (in most cases these quadrats were 2 x 2 m^2) and vegetation cover of all the species present within the quadrat was estimated. In the case of the Moorland Regional Survey, 0.5 x 0.5 m^2 quadrats were used. Full details of each survey are included under Tasks 1 and 2 and in Tables 2 and 3.

For the quadrat-survey technique to be directly comparable, quadrat size should be identical. It is important to note that this measure of species richness is a probability of finding a species at each site; it does not necessarily mean that fewer species are present at each location, although this may be the case. However, it does imply that the evenness of species is reduced and there is a tendency for the vegetation community to be dominated by fewer species and individual species to be present at lower frequencies. Figure 1 overleaf illustrates this concept.

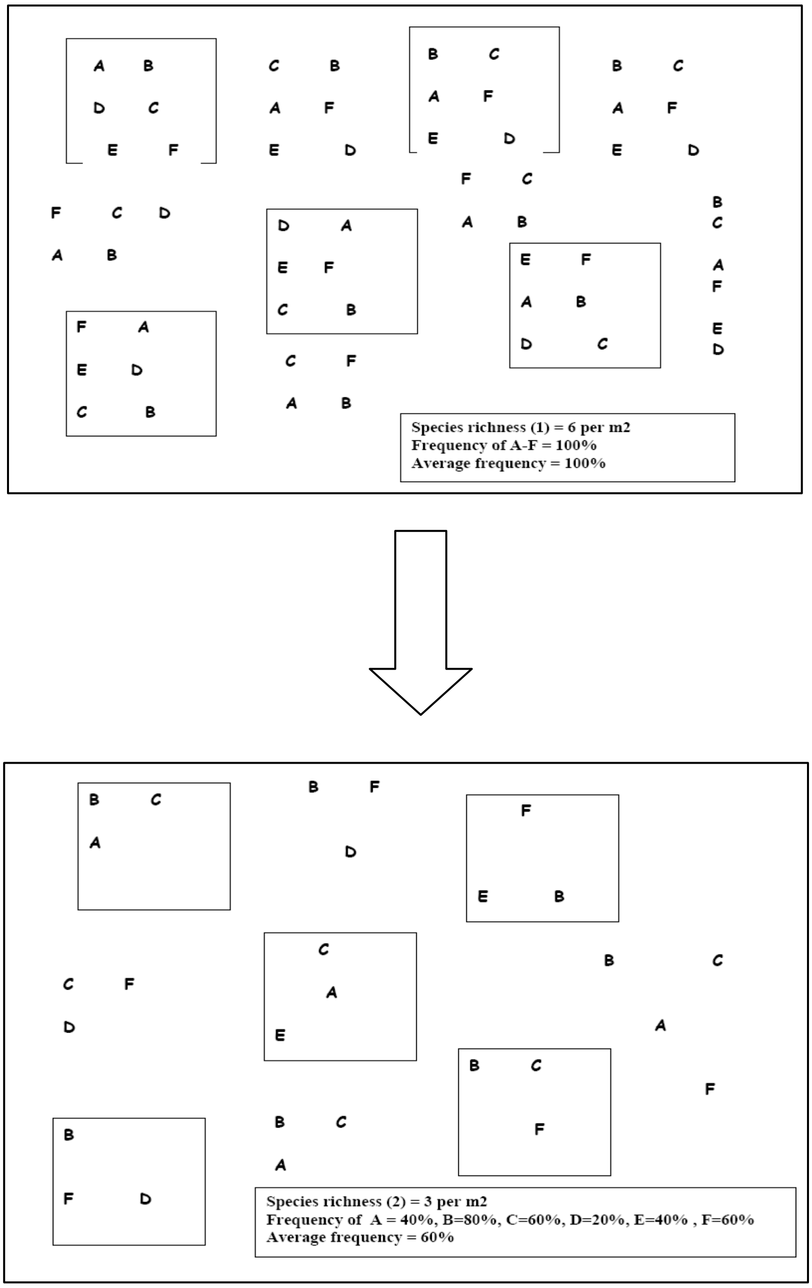


Figure 1: Species richness reduction vs. species loss. In both Figure 1a) and 1b), six species are present in the field. Both fields are surveyed using five 1 m^2 quadrats. In Figure 1 a, each quadrat surveyed contains 6 species and measured species richness is therefore 6. In Figure 1 b, each quadrat only contains 3 species, giving a species richness of 3. The same species are present in both fields, but at a lower frequency in the second: this generates a lower measure of species richness. Figure by N. Dise.

2.2 Environmental and pollutant driver variables

Species richness and composition may be affected by a number of physical and chemical variables. These drivers include variables such as temperature, precipitation, pH etc. Driver data shown in Table 2 were assembled from national datasets for use in the multivariate analyses. The climate data used were based upon UK 5 km^2 gridded data sets provided by the Met Office. Variables representing total annual precipitation and temperature were used, the latter represented by growing degree data (sum of degree days above 5^oC) in the TU and BEGIN survey data and by extreme temperature range in the MRS data. Both precipitation and growing degree data were averaged over the period 1997-2006.

The pollutant deposition data used were the 5 km^2 Concentration Based Estimated Deposition (CBED) values for 2004-2006, provided by the Centre for Ecology and Hydrology (CEH). Variables for total nitrogen deposition (further divided into wet and dry and reduced and oxidised forms), total sulphur deposition (split further into wet and dry) and non-marine calcium + magnesium deposition were included in the data analysis.

Co-correlation of deposition data between pollutant types and the response variable is acknowledged due to the intrinsic link between some pollutants, for example, nitrogen and sulphur are both by-products of fossil fuel combustion and therefore fluctuations in deposition of each follow broadly the same spatial pattern. Therefore in some cases a judgement was made of the ecological significance of a particular type of pollutant deposition. Such judgements were based where possible on the observed effects: for instance if nitrogen and sulphur were closely correlated but the effects were typical of eutrophication rather than acidification it was possible to exclude sulphur as a possible cause. It is also recognised that different forms of a pollutant have different effects on an ecosystem (e.g. oxidised and reduced nitrogen) and that more than one form of a pollutant can be correlated to ecological change. Separating closely correlated environmental variables is difficult in exploratory analyses such as the gradient studies presented here. We consider that it is better to include all possible environmental variables rather than to make *a priori* judgements about which variables are important. In cases where many variables are highly correlated the selection of one highly-correlated variable over another must be interpreted with caution. Although in many of our analyses we present results for the variable with strongest correlation statistics, in general these are best viewed as representing a broader gradient. So, for instance, although we might find strongest correlation statistics with dry deposition of oxidised nitrogen typically this variable is very strongly correlated with other forms of nitrogen deposition and the result is best seen as simply representing ‘nitrogen pollution’.

A further environmental variable included within the bog habitat was a hydrological index based upon field observations on a scale 1-5, with 1 relatively dry (similar to an upland heath) and 5 very wet: a quaking or floating bog. The environmental variables used in the statistical analysis and their acronyms when included on ordination plots are summarised in Table 2. Variables such as radiation index, latitude and longitude were not included as these are correlated with both climate and pollution; variability in these is accounted for by precipitation and growing degree days.

It is recognised that in these semi-natural habitats site management is an important determinant of vegetation structure. The term ‘management’ encompasses a range of human interventions (burning, grazing, drainage) that are difficult to quantify and for which national-scale data is rarely available. We attempt to account for these variables using field-observed indices. For the bog data, the hydrological index largely reflects the history of drainage and peat cutting. For the Moorland Regional Survey we included a ‘habitat’ term which captured the development phase of the *Calluna vulgaris* growth cycle i.e. ‘pioneer’, 'building', 'mature', 'degenerate' (Gimingham, 1972). For the TU heathland and sand dune data no management variables were included. In these studies (indeed in all of the studies) site and quadrat selection was carefully considered to maximise consistency between sites.

Table 2: Summary of driver variables used in the statistical analysis

Driver variables	Acronym	Comment
Growing degree days	growdeg	sum of degree days above 5°C
Precipitation	precip	
Extreme temperature range		Moorland regional survey only
Habitat		Moorland regional survey only
Grazing		Acid grasslands only
Altitude	altimetr	not sand dunes
Hydrology	bog_hydr	Bog habitat only
pH	pH	
Loss on ignition	LOI	
Total acid deposition	aciddepo	
Sulphur deposition	sulpdepo	
Nitrogen deposition	Nitrdepo	
Oxidised nitrogen deposition	oxiNdepo	
Reduced nitrogen deposition	redNdepo	
Calcium + magnesium deposition	Cmgdepo	
Wet sulphur deposition	wet_sulp	
Dry sulphur deposition	dry_sulp	
Wet oxidised nitrogen deposition	wet_oxiN	
Dry oxidised nitrogen deposition	dry_oxiN	
Wet reduced nitrogen deposition	wet_redN	
Dry reduced nitrogen deposition	dry_redN	

2.2.1 Cumulative N versus recent N deposition

The relationships examined in this report use modelled recent annual N deposition as the pollutant variable(s), however, the relationships studied between N deposition and species richness and presence have developed over many years (Dise *et al*., 2011). The recent rate of N deposition is primarily a proxy for longer-term cumulative N deposition. Thus we would not expect that a change in N deposition, either increasing or decreasing, would immediately change species richness or composition, but instead these would be gradually influenced by longer-term changes in N deposition. However, different plant groups respond in different ways: bryophytes and lichens are likely to respond quicker than vascular plants and the responses of both may be affected by management interaction which could alter inter-species composition.

Since cumulative deposition data from the survey locations was not available for use in this study, the current N deposition was instead used as a proxy for cumulative deposition. If cumulative data are estimated from current deposition patterns (as in Dupre *et al*., 2010) we would expect to see very similar results. However, if cumulative deposition data based on emission changes over time were available, this may show different results. An example of this could be in an area where agricultural N emissions have increased markedly in recent years: long term cumulative N deposition based upon current N deposition would over-estimate the total N deposited to the site. Conversely, the use of current N deposition estimates for an area to which N deposition has reduced dramatically over recent years at a rate different to broad-scale trends would under-estimate the cumulative N deposited. Fowler *et al*. (2004) calculated cumulative N deposition for 1900-2000 based upon historic emissions data. A comparison of the cumulative N deposition map for 1900-2000 with modelled nitrogen deposition maps for the year 2000 revealed that broad-scale patterns of N deposition across the country were very similar in these datasets; however, one area of notable difference is apparent. Relatively recent modelled N deposition in East Anglia is much greater than that indicated long-term cumulative N, presumably owing to growing agricultural emissions.

Given the potential impacts of high N deposition both over the long term and currently, a sensible approach would be to consider both N deposition scenarios when judging the vulnerability of a site to raised N and assessing the impact of N deposition at a site. However, given the similarities between the broad-scale spatial patterns of cumulative and contemporary N deposition for much of the UK, the use of current modelled deposition as a proxy for long-term N to predicting responses to increases in N deposition seems reasonable.

2.3 Experimental data

A number of long-term nitrogen addition experiments exist in the UK, many within the DEFRA ‘UK Research on The Eutrophication and Acidification of Terrestrial Ecosystems’ (UKREATE) project, and data from these were included where relevant to the findings of this project. These sites are summarised in Task 3 and Tables 5 and 6.

2.4 Data analysis

Several analytical techniques have been used to determine the effect of air pollution and environmental variables on key response variables in the survey data. Responses studied included species richness, species composition, changes in species richness of different functional groups and the response of certain individual species. The techniques used include ordination analysis, stepwise and conventional regression, LOESS (Locally weighted scatterplot smoothing) regression and cluster analysis.

2.4.1 Ordination analysis

Ordination analysis is a suite of techniques for the analysis of multivariate data in which the aim is to arrange samples along axes on the basis of their species compositions. At their simplest ordination techniques function as a dimension-reduction technique allowing the representation of difference or similarity in species composition of samples in a simple two-dimensional plot. Axes can be determined simply by the species composition of those samples (unconstrained ordinations, also termed indirect gradient analysis) or can be constrained to be composed of linear combinations of measurable environmental variables (constrained ordinations, also termed direct gradient analysis). In our analyses of gradient studies ordination techniques allowed us to understand and visualise the relationships between overall community composition and the environmental gradients which drive changes in that composition (pollution, climate etc). Furthermore, ordination plots allow us to identify individual species which are particularly responsive to individual environmental variables and which may function as indicator species. These analyses are therefore separate from, but complimentary to, analyses of univariate variables which integrate some aspect of community composition such as species richness or functional group ratios. Environmental controls on overall species composition are separate from, but often overlap with those on species richness.

A Detrended Correspondence Analysis (DCA) was first performed to analyse the length of environmental gradients underlying each dataset. Then either Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA) were used as appropriate, assuming linear and unimodal species responses along the environmental gradients respectively (Leps and Smilauer, 2003). We present two key outputs from RDA or CCA, the numerical results namely the % variance explained (analogous to the R^2 of a regression) and P-value (determined by Monte Carlo permutation test) and the ordination plot. Large-scale vegetation datasets will typically contain considerable noise due to non-measured variables and random variability so the proportion of variance explained by environmental variables is often low. However the relationships identified can still be highly significant with small P-values.

Initially, all environmental variables were entered into each analysis and a forward selection procedure using Monte Carlo permutation tests carried out to establish a minimal suite of variables that independently explained significant variance in the data. The variable that explained greatest variance in the data (greatest marginal effect) was first selected in the analysis, and then included as a co-variable in subsequent analysis. The variance explained by all other variables was then tested to identify the next variable that then explained the greatest *additional* variance. This variable could then be tested for significance, and if $P<0.05$ included in the analysis. The selection process continued until no further variables explained significant additional variance. This approach enabled the statistical effect of climate and pollutant variables to be separated, however, it can mean that variables that are correlated with each other (such as different types of air pollution) may be excluded as only the variable with the strongest association is included, and when this variable is included as a covariable, the other variables that are correlated with it may be removed from the analysis as they explain no additional variation.

Subsequently variance partitioning was carried out to test the % variance and significance of each forward selected variable with other selected variables as co-variables. CANOCO software for Windows version 4.53 (ter Braak and Smilauer, 2004) was used for both CCA and RDA analysis.

An example ordination plot from an RDA analysis is provided below (Figure 2). In all ordination plots the values of the axes and the position of species relative to those axes is of less interest in general terms than the position of species relative to other species and environmental variables. The red arrows represent environmental variables and their direction of influence relative to the species shown in the diagram. The strength of each driver variable on species composition is represented by the relative length of arrow, in this example ‘redNdepo’ (reduced nitrogen deposition) has the longest red arrow and as such exerts the most influence on species composition. The correlation between environmental variables can be judged by their similarity of direction, arrows pointing in the same direction represent correlated variables. In the plot below it will be noted that the three red arrows point in different directions, there is little correlation between variables. Similarly, individual species are shown on the plot and positioned relative to the driver variables and the influence of the driver variables shown by relative length of grey arrow presented on the plot. The direction of an arrow relative to the axes does not imply a positive or negative direction of influence. In the example below, most species are ordinated away from redNdepo implying that the cover of these species is negatively affected by deposition of reduced N. These species are also correlated with each other, the vectors for *Cladonia portentosa* (cladport) and *Cladonia gracilis* (cladgrac) are adjacent to each other, most likely the species are found in the same sites. *Cladonia fimbriata* (cladfima) is the only species that appears positively associated to ‘redNdepo’, however, it also appears associated with ‘growdegr’ (growing degree days) suggesting that its relative cover is influenced both by reduced N deposition and temperature.

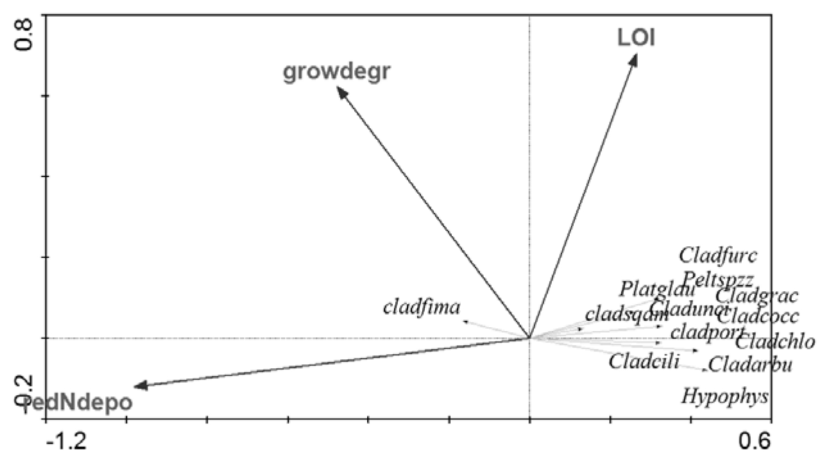


Figure 2: Example ordination plot

2.4.2 Stepwise and conventional regression

Regression techniques were used to model change in species richness with regard to an individual variable (simple regression) or a combination of variables (stepwise regression) that explain the most variation in the independent variable, in this case species richness. Stepwise regression is a form of multiple regression using a combination of forward and backward selection of variables. Variables are included if they explain significant variation in addition to those already in the model, and excluded if their removal does not increase the residual sum of squares. In both forms of regression a test for normality was performed and corrections made as necessary.

2.4.3 LOESS regression

LOESS (locally weighted scatterplot smoothing) regression is a form of non-parametric regression which acts as a ‘smoothing’ tool to aid visualisation of the response of taxa (individual species or functional groups) to a variable such as nitrogen pollution.

Linear regression techniques (including simple, multiple and stepwise) assume that the underlying relationship between dependent and independent variables is linear. LOESS regression enables a curve to be fitted to the data without making any assumptions about the form of the underlying relationship. In doing so it allows more flexibility than classical regression by fitting a smoothing function that varies with the data. However, simple mathematical equations describing the relationships cannot be generated with LOESS as with linear techniques.

PAST software version 2.06 (Hammer *et al*., 2001) was used for this analysis.

2.4.4 Cluster analysis, sample grouping and ecological thresholds

An important question that is rarely explicitly addressed is whether the response of plant communities to nitrogen deposition is linear, or if there are ecological thresholds. If threshold responses do exist, this may have important implications for regulation of pollution loading, suggesting that there are points above which, or below which, further nitrogen deposition may have a disproportionate impact on the ecosystem. As detailed elsewhere in this report, gradient studies are now available for a large number of semi-natural habitats within the United Kingdom. Results from these studies show a reduction in species richness along the nitrogen pollution gradient and characteristic changes in plant communities.

Here we apply constrained cluster analyses to these datasets. This analysis attempted to identify non-linearities in the community response using a variety of statistical techniques originally developed for time-series data from bio-stratigraphy but theoretically equally applicable to changes along any gradient. These techniques are similar to conventional cluster analysis techniques but with the constraint that clusters be composed of samples with similar levels of nitrogen deposition.

In the context of this report this analysis has two important functions. Firstly it enables us to validate the results of the ordination analyses (discussed below) which show nitrogen pollution to be an important environmental control on the species composition of many habitats. If significantly different groupings can be identified solely on the basis of their nitrogen-loading this provides convincing evidence that nitrogen is an important control on community composition. Secondly, the location of 'break-points' between sample groupings is of interest because these may relate to ecological threshold responses. It is important to note that our approach is subtly different from direct identification of a threshold. If a threshold is abrupt the groups of samples on either side of a break-point will be distinctly different and are likely to be easily separated by clustering, if however the threshold is more gradual there may be variability in the group to which marginal samples are assigned.

We trial three methods derived from two contrasting approaches. We first test an agglomerative approach: with groups built by successively combining samples, as for many conventional cluster analysis techniques. Our approach is based on Ward's method (Ward, 1963) where clusters are built so as to minimize the increase in total within-cluster sum of squares. Conventional cluster analysis produces groups that are difficult to interpret in terms of a single environmental variable. To avoid this problem we introduce a constraint that clusters must be composed of samples with adjacent levels of nitrogen deposition. Essentially, we force the cluster analysis to produce groups which represent differing levels of nitrogen deposition. This method – constrained incremental sum of squares (CONISS) – is widely used for temporally-structured data (Grimm, 1987). CONISS produces a dendrogram, but only the first few splits are likely to be ecologically meaningful. Table 1 presents the first two. A limitation of this technique is that Ward's method has an inherent tendency to produce clusters of similar size (e.g. Morse, 1980).

The other two methods take a contrasting approach: instead of building up groups by successively adding samples in an agglomerative approach, they consider the whole dataset and the reduction in overall variance which may be achieved by the insertion of zone boundaries. As such the methodology is more focused on the sequence as a whole, unlike the agglomerative methodology which is more focused on the individual samples. We treat our samples as a transect along the gradient of total nitrogen deposition (as for CONISS), and test the validity of inserting splits in all alternative positions. Two variants of this divisive methodology are examined, with variance assessed by information content (SPLITINF) or least squares (SPLITLSQ; Gordon and Birks 1972, Birks and Gordon 1985). The SPLITINF and SPLITLSQ techniques are binary approaches that first split the overall dataset in two and then successively split these zones into smaller sub-divisions. As for CONISS, the first two divisions are presented in Table 17. We apply all three of these techniques using ZONE vers.1.2 (Juggins, 1992) with a squared Euclidean distance matrix.

Results of constrained agglomerative techniques can be presented as a dendrogram showing the relationships of samples along the gradient. An example of such a dendrogram is shown in Figure 3 below. The relationships of individual samples are shown by the proximity of their branches. Although such dendrograms present a large amount of information, typically only the first 'branches' are significant and useful. In the results of this analysis we only present the locations of the first two sample divisions.

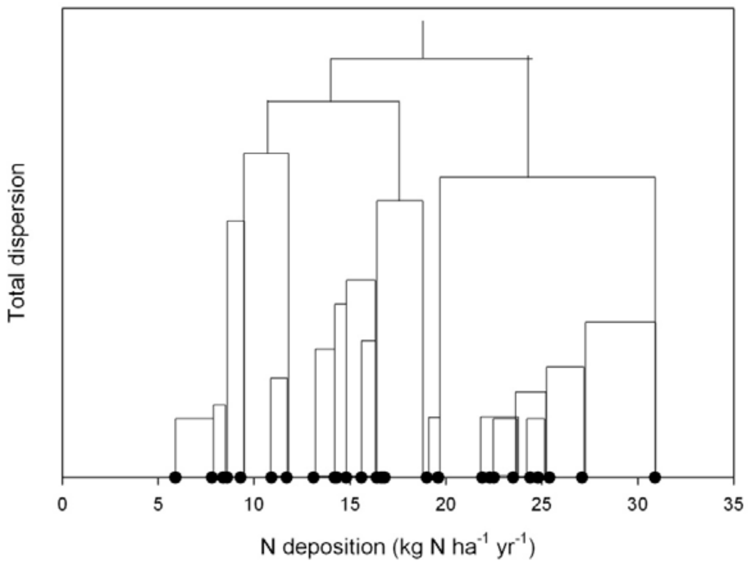


Figure 3: Example of a dendrogram showing the relationships of samples along a gradient

None of these three methods include a test of the validity of the clusters produced. To determine whether the community composition of the different clusters is significantly different, we apply a simple test of community similarity using ANOSIM. ANOSIM is a non-parametric test of similarity between pre-defined groups (Clarke, 1993). The test statistic (R_{ANOSIM}) has a value between -1 and +1 (although negative values are unusual); a value of 0 indicates the null hypothesis, that there is no difference between groups, while a value of 1 indicates that all samples within groups are more similar to one another than to any samples from different groups. Significance testing is achieved using permutation tests.

We applied ANOSIM with a Bray-Curtis distance measure and 10,000 permutations in PAST ver. 1.71 (Hammer *et al*., 2001). The ANOSIM results tell us whether the groups of samples are different, but give no assessment of whether those boundaries are in the optimum position (i.e. the probability of any random division producing a significant result in ANOSIM is relatively high). To give some assessment of the distinctness and validity of the cluster boundaries, we can compare the results of the three methods used. As these techniques rely on different underlying principles, if they identify similar cluster boundaries, this can give us confidence that the groupings are valid and useful. Additionally, where we have replication within an ecosystem type (acid grasslands and upland heaths) we can compare the results between the datasets.

Two general problems occur with all of these three approaches. Firstly there are issues with confounding environmental variables. In all of the datasets, many variables other than total nitrogen deposition affect plant communities, particularly climate. The response of the plant communities to these other variables is likely to complicate the identification of meaningful groups according to nitrogen deposition values. A second general problem is the size of the datasets and inconsistent sampling along the nitrogen gradient. With the exception of the larger Stevens *et al*. (2004, 68 sites) dataset the number of sites in each dataset is small (22-29 sites) and at the lower limit of the sample size for which many multivariate techniques are appropriate. Partly as a result of this limited sample size, the distribution of samples along the N deposition gradient is non-uniform, with gaps apparent in some datasets (for instance, no sites between 30.3 and 40.8 kg N ha^{-1} yr^{-1} in the TU-acid grasslands data, and no sites between 5.9 and 10.6 kg N ha^{-1} yr^{-1} in the TU-lowland heath data). Inconsistent sampling along the gradients both reduces the precision with which cluster boundaries can be located and increases the probability of false identification of a group boundary.

3. Tasks 1 and 2: Collation of scientific information and categorisation by habitat type

The bulk of the data used in this report is from a compilation of vegetation survey data from 8 field surveys encompassing vegetation quadrat data from a total of 226 UK sites surveyed between 2002 and 2009 (see Figure 4). The habitats are: dwarf shrub heathland (upland and lowland), acid grassland, bog and sand dune (fixed-dune grassland). Each represents a UK Biodiversity Action Plan (UK BAP) priority habitat for conservation (Natural England, 2011).

The surveys comprise of a 2002-2003 acid grassland survey, a 2002 sand dune survey, a 2006 upland heath survey, a 2007 acid grassland survey and 2009 surveys of sand dune, bog, upland and lowland heaths. Where data were comparable between surveys, results were combined. Details of the surveys are provided in Table 3.

Figure 4: The survey locations of the 226 sites from which data has been used in the analysis for this project

Within each survey, locations were carefully chosen to enable site comparisons to be made, ensuring vegetation structure between sites was consistent. Locations were identified along a UK nitrogen pollution gradient which was typically cleaner in the north and more polluted in the south. This UK pollution gradient also closely follows a climate gradient, with northern sites being cooler and wetter than their southern counterparts. For this reason an east-west gradient was also maximised within each habitat to provide survey locations that were ‘clean and warm’, ‘polluted and cooler’, ‘wetter and polluted’ and ‘drier and less-polluted’. Such an approach aided statistical partitioning of the effects of pollutant and climatic drivers of vegetation change.

Further data were obtained from a network of UK nitrogen addition experiments funded as part of the Terrestrial Umbrella (TU) UKREATE project (http://ukreate.defra.gov.uk/) which include habitats similar to the surveys. Data from these experiments that support or challenge findings from the gradient surveys are presented and details of these experiments are shown, in Tables 5 and 6.

Published data from similar habitats to the survey data have also been drawn upon and reviewed as part of this report: these are summarised in Task 4 and Table 4.

Table 3: Survey data sets by habitat type under new analysis as part of this report

Habitats	New analysis here or Reviewed	NVC	Survey date	Location	Method of data collection/ number of sites	Author /affiliation	Reference
Acid grassland	New	U4	2002/3	GB	Quadrat survey/68 sites	C. Stevens, Open University/CEH	Stevens *et al*. (2004)
	New		2007		Quadrat survey/22 sites	BEGIN grassland survey	Stevens *et al*. (2010)
Bogs	New	M19, M18	2009	GB	Quadrat survey/ 29 sites	TU consortium led by MMU	UKREATE, 2010 (TU report for 2007-2010)
Lowland heath	New	H2-H13	2009	GB	Quadrat survey/27 sites	TU consortium led by MMU	UKREATE, 2010 (TU report for 2007-2010)
Upland heath	New	H12	2009	GB	Quadrat survey/25 sites	TU consortium led by MMU	UKREATE, 2010 (TU report for 2007-2010)
Sand dunes	New	SD12, SD8 transitional	2009	GB	Quadrat survey/24 sites	TU consortium led by MMU	UKREATE, 2010 (TU report for 2007-2010)
Sand dunes	New	SD8, SD11, SD12 transitional	2002	GB	Quadrat survey/11 sites	L. Jones, CEH Bangor	Jones *et al*. (2004)
Upland heath	New	H12	2006	GB	Quadrat survey/20 sites	J. Carroll & S. Caporn, MMU	TU report, Caporn *et al*., (2007) JNCC report, Stevens *et al*., (2009)

Table 4: Published data by habitat type reviewed in this report

Habitats	**New analysis here or Reviewed**	**Survey date**	**Location**	**Method of data collection**	**Author /affiliation**	**Reference**
Acid grassland	Reviewed	2002-3	GB	Field survey	Stevens *et al*.	Stevens *et al*. (2004, 2006)
Acid grassland	Reviewed	2007	Europe inc. GB	Field survey	BEGIN consortium	Stevens *et al*. (2010)
Calcareous grassland	Reviewed		GB	Field survey	L. Van den Berg	Van den Berg *et al*. (2010)
Acid grassland **Calcareous grassland** **Mesotrophic grassland** **Heathland**	Reviewed	1998	GB	Field survey	CEH Countryside Survey	Maskell *et al*. (2010); JNCC report Stevens *et al*. (2009)
Acid grassland **Calcareous grassland** **Heathland** **Bogs**	Reviewed	Range	-	Collation of archived field survey	Stevens & CEH	Stevens *et al*. (2011)
Upland dry heath	Reviewed	2005	England, Wales	Field survey	J. Edmondson, MMU	Edmondson, *et al*. (2010)

Table 5: Name, location, vegetation type, soil type, and background atmospheric N deposition rates for the 9 TU sites

	Site name	Location in UK	Vegetation type: NVC classification	Soil type	Approx N dep. at site (kg N ha^{-1} yr^{-1})
Heath	Ruabon	North East Wales	Upland heath: H12 *Calluna –Vaccinium*	Peaty podzol	20 20
	Budworth	North west England	Lowland heath: H9 *Calluna –Deschampsia*	Humo ferric podzol	20
	Thursley	Southeast England	Lowland heath: H8 *Calluna*	Podsol, over lower greensand	10-15
	Culardoch	Northeast Scotland	Low Alpine Heath: H13 *Calluna-Cladonia*	Sub-alpine podsol	11
Bog	Whim	Southern Scotland	Ombrotrophic bog: M19, *Calluna-Eriophorum*	*Sphagnum* peat	8-10
Grassland	Pwllperian	Central Wales	Upland acid grassland U4	Shallow ferric stagnopodzol	25
	Wardlow	Central England	Acid grassland: U4e *Festuca-Agrostis-Galium*	Paleo-argillic	20-25
		Central England	Calcareous grassland: CG2d *Festuca –Avenula*	Rendzina	20-25
Sand dune	Newborough	Northwest Wales	Fixed sand dune grassland: SD8 *Festuca – Galium*	Rendzina	11

Table 6: Experimental site name and simulated N deposition treatments for the 9 TU sites. [1]= first experiment (treatments ceased in 1996 to follow recovery); [2]= ongoing experiment; [4] = plots where treatments are no longer ongoing. [5]=includes plots split in half with recovery since August 2005; [6]=includes plots split in half with recovery since spring 2003; [9]= a number of experiments have some plots where treatments have ceased in order to assess recovery.

	Site name	**N treatment rates (kg N ha^{-1} yr^{-1})**	**N form (as solution unless stated)**	**Year started**	**Duration of N treatment years to date or until ceased[9]**	**Key references to experiment**
Heath	Ruabon	0,40,80,120 0,10,20,40, 120	NH_4NO_3 solution	1989 1998	22 13[6]	Pilkington *et al*. (2005); Edmondson *et al*. (2010)
	Budworth	0,20,60,120	NH_4NO_3 solution	1996	115	Wilson (2003), Field (2010) Lageard *et al*. (2005)
	Thursley	0, 7.7, 15.4[1] 0, 30[2]	$(NH_4)_2SO_4$	1989-1996[1] 1998[2]	7[1] 12[2]	Power *et al*, 1998; Barker *et al*, 2004; Power *et al*, 2006 Barker, 2001, Green, 2005
	Culardoch	0, 10, 20, 50	NH_4NO_3	2000	11	Britton and Fisher, 2007
Bog	Whim	8,24,56 for wet dep. NH_3 transect 70-4	NH_4Cl $NaNO_3$ $NH_{3(g)}$	2002 2002	8 8	Sheppard *et al*. (2004). Sheppard *et al*. (2008)
Grassland	Pwllperian	10, 20	$NaNO_3$ NH_4SO_4	1996	12	Emmett *et al*. (2007)
	Wardlow	35, 70, 140 35, 140	NH_4NO_3	1990 1995	12[4] 15[5]	Morecroft *et al*. (1994) Horswill *et al*.(2008)
	Wardlow	35, 70, 140 35, 140	NH_4NO_3	1990[4] 1995[5]	12[4] 15[5]	Morecroft *et al*. (1994) Horswill *et al*.(2008)
Sand Dune	Newborough	7.5, 15	NH_4NO_3	2003	7	Plassmann *et al*. (2009)

4. Task 3: Identify the relevant response variables for each habitat

4.1 Introduction

This section of the report uses stepwise regression and ordination analysis to identify the key potential response variables in the survey datasets for each of the habitats studied. Stepwise regression considers overall changes in species richness and, where the data exist, by functional group. Ordination analysis considers changes in the composition of the vegetation community. Both analyses measure these changes relative to climatic and pollutant driver data.

Key potential response variables are also identified from published literature and from the Terrestrial Umbrella experiments.

4.2 Vegetation species richness responses to nitrogen pollution

Across all the datasets studied, increasing nitrogen deposition (total, reduced or oxidised) was correlated with reductions in species richness. This pattern was similar across all habitats. In many cases, climate was also correlated with species richness, with increasing species richness being a function of increasing precipitation and decreasing temperature (expressed as growing degree days or extreme temperature range). An exception to the latter was sand dunes, with pH ≥ 6.5 where increasing temperature was correlated with an increase in overall species richness. The output from the stepwise regressions are summarised in Table 7 and the relationship between nitrogen deposition and species richness presented in more detail in Task 4.

Consistency in survey methods and data collection in habitats visited as part of the TU 2009 survey enabled a direct comparison across all habitats (upland and lowland heath, sand dune, bog and acid grasslands – the latter representing a subset of 23 of the sites visited by Stevens *et al*. (2004)). For this cross habitat comparison, species richness was converted and expressed as a percentage of the maximum number of species recorded in that habitat. From this stepwise regression, nitrogen deposition explained most of the reduction in species richness (expressed as either total nitrogen deposition or dry-oxidised nitrogen deposition), followed by mean annual temperature.

Many plant groups were negatively associated with N pollution: within bogs the relationship was strongest in forbs including *Drosera rotundifolia* and *Narthcium ossifragum* and lichens; in upland heaths mosses and lichens reduced in diversity, although the change in the former was more significantly correlated with sulphur deposition; and in acid grasslands forbs showed a reduction in both richness and diversity (as previously reported in Stevens *et al*., 2006). For lowland heaths, wet-oxidised N deposition was significantly correlated with reductions in overall species richness however, climate explained more of the variation in species richness across the plant groups. This probably reflects the shift in lowland heath soil types as their geographical location changed from acid, base-poor, sandy soils of the Cornish heaths to the moister, more organic soils of the northern lowland heaths. Interestingly, across the ericaceous habitats which are often defined by a competitive balance between shrub, graminoid and moss species groups, graminoid species richness also fell as a function of rising N deposition. However, graminoid cover increased, suggesting a shift toward dominance by fewer species.

In sand dunes, moss species richness showed a strong reduction with increasing N deposition. Forb species richness was more weakly correlated with N pollution. However, when sand dune type was split by pH these responses were only seen in more calcareous sand dunes with pH ≥ 6.5, although limited data were available from sites with pH less than 6.5. In general, sand dune species richness was more strongly correlated to pH and the extent of decalcification. Some responses were, however, seen with soil N indicators in sand dunes (not shown in this report) such as N% and mineralisation at sites with pH lower than 6.5; this could indicate a longer-term response to N deposition.

The different forms of N pollution were also related to responses in species richness. However, it is difficult using modelled data to attribute change to a specific form of N pollution, and specific locations may be more vulnerable to either reduced or oxidised N dependent upon their proximity to a point source. In some cases, for example upland heath moss species richness and bog species richness, sulphur deposition was more strongly correlated with the species richness. It is difficult to be certain if these relationships are ecologically significant as sulphur levels are low across the range of the dataset, or indicative of a legacy effect from earlier years of high sulphur deposition. In general, significant correlations between pollutants exist and in both of these specific cases a form of N was also strongly correlated with the response variable and at levels more likely to elicit an ecological response.

Table 7: Summary of changes in overall species richness and the response of different functional groups (richness and cover where appropriate) using stepwise regression

Habitat /Survey	Response variable	Best fit model parameters from stepwise regression and influence of an increase in the parameter on the response variable (↑↓)	Variance explained by model and statistical significance
All habitats from TU 2009 survey	Overall species richness (% of maximum species recorded in each habitat)	Dry-oxidised nitrogen deposition (↓) Growing degree days (↓)	R^2=0.37, P<0.001
Upland heathland (TU 2009)	Overall species richness (total number of species recorded)	Reduced nitrogen deposition (↓)	R^2=0.39, P=0.002
	Moss species richness	Sulphur deposition (↓) (Wet-oxidised Nitrogen deposition also significant : ↓)	R^2=0.25, P=0.011 (R^2=0.21, P=0.021)
	Lichen species richness	Reduced nitrogen deposition (↓)	R^2=0.26, P<0.01
	Graminoid species richness	Dry-reduced nitrogen deposition (↓) Altitude (↓)	R^2=0.46, P<0.001
	Graminoid cover (%)	Dry-reduced nitrogen deposition (↑)	R^2=0.24, P=0.014
Upland heathland (MRS)	Overall species richness (total number of species recorded)	Dry-reduced nitrogen deposition (↓) Altitude (↑) Temperature extreme range (↑)	R^2=0.87, P=0.001
Lowland heathland (TU 2009)	Overall species richness (total number of species recorded)	Growing degree days (↓) Altitude (↓) Wet-oxidised nitrogen deposition (↓)	R^2=0.64, P<0.001
	Moss species richness	Growing degree days (↓) pH (↑)	R^2=0.42, P=0.005
	Lichen species richness	no combination of variables explain significant variation in the data	-
	Graminoid species richness	Growing degree days (↓)	R^2=0.46, P<0.001
	Graminoid cover (%)	Dry-reduced nitrogen deposition (↑)	R^2=0.35, P=0.001

Habitat /Survey	Response variable	Best fit model parameters from stepwise regression and influence of an increase in the parameter on the response variable (↑↓)	Variance explained by model and statistical significance
Bog (TU 2009)	Overall species richness (total number of species recorded)	Dry-sulphur deposition (↓) (Dry-oxidised Nitrogen deposition also significant : ↓)	R^2=0.56, P=0.01 (R^2=0.50, P=0.01)
	Moss species richness	no combination of variables explain significant variation in the data	-
	Lichen species richness	Dry-oxidised nitrogen deposition (↓)	R^2=0.37, P<0.01
	Forb species richness	Total acid deposition (↓) (Nitrogen deposition also significant : ↓)	R^2=0.39, P=0.002 (R^2=0.38, P=0.002)
	Graminoid cover (%)	Wet-reduced nitrogen deposition (↑) Growing degree days (↑)	R^2=0.68, P<0.001
Sand dunes TU 2009 (all sites)	Overall species richness (total number of species recorded)	pH (↑) Wet-oxidised nitrogen deposition (↓)	R^2=0.57, P<0.005
	Moss species richness	oxidised nitrogen deposition (↓) LOI (↑)	R^2=0.67, P<0.001
	Forb species richness	pH (↑) Wet-oxidised nitrogen deposition (↓) Wet-sulphur deposition (↓)	R^2=0.53, P<0.001
Sand dunes pH <6.5 (TU 2009)	Overall species richness (total number of species recorded)	no significant relationship with N	-
	Moss species richness	wet-sulphur deposition (↓)	
Sand dunes pH ≥6.5 (TU 2009)	Overall species richness (total number of species recorded)	Oxidised nitrogen deposition (↓) Ca + Mg deposition (↑) Growing degree days (↑)	R^2=0.76, P<0.001
	Moss species richness	Oxidised nitrogen deposition (↓)	R^2=0.62, P<0.001
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)	Overall species richness (total number of species recorded)	pH (↑) Nitrogen deposition (↓)	R^2=0.55, P<0.001
	Moss species richness	Total acid deposition (↓)*	R^2=0.31, P=0.001
Acid grasslands (BEGIN UK)	Overall species richness (total number of species recorded)	Nitrogen deposition (↓) Precipitation (↑)	R^2=0.38, P=0.001
	Forb species richness	Nitrogen deposition (↓)	R^2=0.48, P<0.001

*Total acid deposition incorporates both nitrogen and sulphur deposition as a total acid equivalent

Bryophyte species richness reduced in lowland heaths, sand dunes and the upland heath MRS survey – the latter included liverworts whereas the TU upland heath survey did not. Lichen species richness reduced in bogs and upland heaths and forb species richness reduced across acid grasslands, bogs and sand dunes. Graminoid species richness reduced in both heathland types whilst graminoid cover increased in all ecosystems except acid grasslands. However, within sand dunes, whilst this increase was significant, graminoid cover was more strongly associated with soil pH which could reflect either an interaction with precipitation and decalcification or acidification caused by pollutant deposition.

4.3 Vegetation community composition responses to nitrogen pollution

Table 8 presents the results from the ordination analysis. Vegetation community composition was also related to nitrogen (N), with a form N of nitrogen the first variable through the forward selection process in all habitats except sand dunes. In sand dunes, change was more strongly associated with climate (either growing degree days or precipitation) and the effect of rainfall on leaching of base cations, decalcification and acidification. Climate explained significant additional variation in the all the habitats after N pollution. In bogs, hydrology (typically influenced by management and drainage rather than rainfall) also was significantly related to change in species composition. Similarly, in upland heaths the amount of soil organic matter (LOI – loss on ignition) was related to community composition as was pH in lowland heaths: both these responses are indicative of changes in the soil from organic and peaty to calcareous and, at a broad-scale, driven by rainfall and climate.

The percentage of variance explained by these models is often low. Many factors drive variation within different habitats other than the ones chosen for this analysis and there is considerable heterogeneity between sites and also within a site. The fact that the relatively small number of environmental drivers explains as much variance as they do is testament to their strength as drivers of change in species composition.

Table 8: Summary of the analysis of species community composition using ordination (RDA) in CANOCO. ns = not significant

Habitat /Survey	Statistically significant drivers of change in species composition	Variance explained by model and statistical significance	Variance partitioning by driver*	Specific species showing a strong response to Nitrogen with good distribution across dataset (direction ↑↓)
Upland heathland (TU 2009)	Reduced nitrogen deposition Growing degree days Loss on ignition	36.3%	15.8% P=0.001 7.9% P=0.006 7.4% P=0.01	*Cladonia fimbriata* (↑) *Cladonia portentosa* (↓) *Deschampsia flexuosa* (↑) *Brachythecium rutabulum* (↑) *Hylocomium splendens* (↓)
Upland heathland (MRS 2006)	Dry-oxidised nitrogen deposition Reduced nitrogen deposition Consecutive dry days Habitat	87.8%	37.7% P=0.001 22.1% P=0.001 15.1% P=0.02 12.9% P=0.033	*Campylopus introflexus* (↑) *Hylocomium splendens* (↓)
Lowland heathland (TU 2009)	Dry-oxidised nitrogen deposition Growing degree days Soil pH	32%	8.2% P=0.005 13.3% P=0.001 6.5% P=0.019	*Cladonia fimbriata* (↑) *Cladonia portentosa* (↓) *Brachythecium rutabulum* (↑) *Campylopus introflexus* (↑) *Hylocomium splendens* (↓)

Habitat /Survey	Statistically significant drivers of change in species composition	Variance explained by model and statistical significance	Variance partitioning by driver*	Specific species showing a strong response to Nitrogen with good distribution across dataset (direction ↑↓)
Bog (TU 2009)	Dry-reduced nitrogen deposition	22.6%	7.0% P=0.004	*Eriophorum vaginatum* (↑) *Sphagnum fimbriatum* (↑) *Cladonia portentosa* (↓)
	Hydrological index		8.3% P=0.001	
	Dry-oxidised nitrogen deposition		5.9% P=0.011	
Sand dunes TU 2009 (all sites)	Growing degree days	36.6%	5.6% P=0.03	*Hylocomium splendens* (↓) *Ammophila arenaria* (↓)
	Precipitation		10.6% P=0.001	
	Dry-reduced nitrogen deposition		5.1% P=0.035	
	pH		14.6% P=0.001	
Sand dunes pH <6.5 (TU 2009)	Growing degree days	38.6%	*18.8%* *P=0.035*	*Hylocomium splendens* (↓)
	Dry-oxidised nitrogen deposition		*22.0%* *P=0.008*	
Sand dunes pH ≥6.5 (TU 2009)	Precipitation	29.3%	*17.1%* *P=0.001*	*Hylocomium splendens* (↓)
	Dry-reduced nitrogen deposition		*9.5%* *P=0.025*	
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)	Precipitation	28.1%	*4.9%* *P=0.06*	*Hylocomium splendens* (↓) *Carex arenaria* (↑ but ns). The relationship is significant when the 2002 data is analysed independently.
	Ca+Mg deposition		*3.2%* *ns*	
	Dry-sulphur deposition		*3%* *ns*	
	Dry-oxidised nitrogen deposition		*3%* *ns*	
	pH		*8.2%* *P=0.006*	
Acid grasslands (BEGIN UK)	Nitrogen deposition	15.5%	*3.1%* *P=0.002*	*Deschampsia flexuosa* (↑) *Hypnum cupressiforme (agg.)* (↑) *Nardus stricta* (↑) *Carex panicea* (↑) *Euphrasia officianlis* (↓) *Hylocomium splendens* (↓) *Lotus corniculatus* (↓)
	Growing degree days		*3.8%* *P=0.001*	
	Precipitation		*2.8%* *P=0.001*	
	Ca+Mg deposition		*2.1%* *P=0.02*	

*the sum of the variance explained by individual drivers will not always equal the total variance explained due to the use of covariables in the variance partitioning process

The species richness relationships detailed in the previous section were also largely reflected in community composition, for example, see Figure 5 which illustrates the response of sensitive lichen species in the upland heath habitat to N deposition: in this case reduced N deposition was the most strongly correlated variable (N.B. all species were included in the ordination but only lichen species are shown on the plot, for other ordination plots refer to appendix 1). The ordination process also suggested individual species that appeared strongly associated, either positively or negatively, with N and specific species for each habitat are suggested in Table 8. For example, in Figure 5, *Cladonia fimbriata* (cladfima) is the only species positively associated with N deposition while other lichen species are associated with low N conditions.

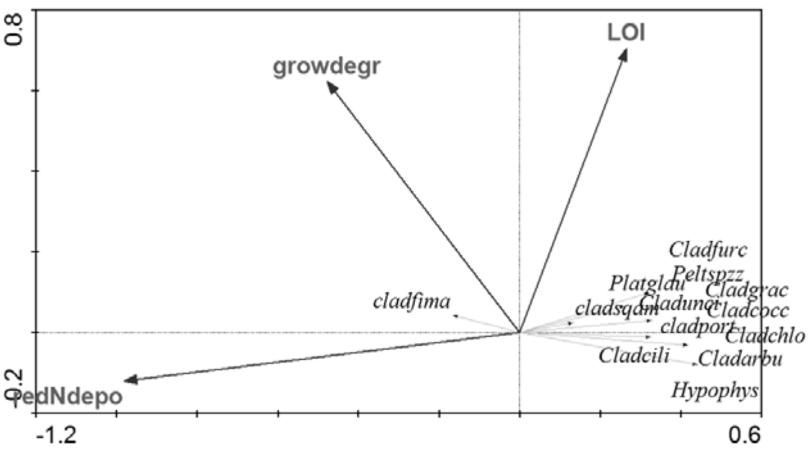


Figure 5: Ordination plot produced from RDA of upland heath data (TU 2009), lichen species only shown

In the example ordination plot above, many lichen species are ordinated away from N. This reflects reductions in lichen species richness as a function of N deposition, however, few lichen species are represented consistently across the dataset to enable a relationship with N to be examined with any statistical confidence. *Cladonia fimbriata* and *Cladonia portentosa* are two widely-represented lichen species, and these relationships alongside the other species shown in Table 8 are examined in greater detail in Task 4.

Typically, the strongest species related to N within the survey were mosses and lichens, showing both positive and negative relationships to N. Across the heathland, acid grassland, and sand dune datasets, the moss *Hylocomium splendens* showed a consistent negative response to N. The MRS survey of upland heaths also recorded presence of liverworts and these too were strongly sensitive to pollution. Within upland heath and bog habitats the graminoid species *Deschampsia flexuosa* and *Eriophorum vaginatum* showed positive responses to N deposition. In the 2009 sand dune survey, the grass *Ammophila arenaria* (marram grass) decreased in cover with increasing N deposition, however, this is at odds with findings from the 2002 survey where an increase in *A. arenaria* cover was found (Jones *et al*., 2004). *Carex arenaria* showed an increase with N, although this was non-signficant. This difference in response may be related to the differing types of sand dune surveyed between the surveys, since the 2009 survey focused on older de-calcified habitats where *Ammophila* persists only at low cover with low vigour, and is termed 'relict *Ammophila'*. Within the acid grassland habitat, forb species were strongly negatively correlated to N deposition, most notably *Lotus corniculatus* and *Euphrasia officianlis*.

Moss, lichen and forb species are an important component of the biodiversity within all the habitats studied, and key to maintaining high species richness and favourable habitat condition. Within the nature conservation agencies Common Standards Monitoring is a tool used to assess the condition of the habitat or feature. In heathlands, bryophytes and lichens play an important role in the overall habitat and are indicators of favourable condition in Common Standards Monitoring (CSM) (JNCC, 2006). The balance between graminoid and shrub cover is important in maintaining the intrinsic diversity in ericaceous habitats. In some cases, high graminoid cover may be detrimental to site integrity, for example, *Deschampsia flexuosa* cover above 25% in lowland heaths (JNCC, 2004). In two of the lowland heaths surveyed graminoid cover exceeded 30% and in several upland heaths graminoid cover was above 25 % suggesting that N deposition posed a long-term threat to site integrity.

4.4 Key response variables in the reviewed literature

Numerous vegetation categories have been described in the literature, such as individual species, botanical groups (grasses, bryophytes etc), functional groups (e.g. Ellenberg score) and plant characteristics (e.g. canopy height). The main ones relevant to N pollution response are listed in Table 9, while their relationships with nitrogen deposition are discussed under Task 4.

Table 9: Response variables frequently reported in the literature on vegetation and N deposition

Habitats	Reported response variable	Reference
Upland dry heath	Bryophytes richness	Edmondson *et al*. (2010)
Upland dry heath	Bryophytes richness, total spp. richness, individual species	Stevens *et al*. (2009) - pooled data of Edmondson *et al*. (2010) and Payne *et al*. 2014)
Acid grassland	Forbs, grass, bryophyte richness and cover, grass/forb ratio Individual species	Stevens *et al*. (2004, 2006, 2009)
Acid grassland (includes European sites)	Forbs, grass, bryophyte richness	Stevens *et al*. (2010)
Calcareous grassland	Species richness & diversity Functional groups species richness, Ellenberg N & R, individual species including (rare & scarce) species	Van den Berg *et al*. (2010)
Acid grassland **Calcareous grassland** **Mesotrophic grassland** **Heathland**	Vascular, bryophyte species richness	Maskell *et al*. (2010)
Acid grassland	Acid preference index Ellenberg N & R Competitive, stress tolerant, ruderal strategy	Stevens *et al*. (2010)
Acid grassland **Calcareous grassland** **Heathland** **Bogs**	Ellenberg N & R, canopy height, specific leaf area, species richness, individual species occurrence	Stevens *et al*. (2011)

4.5 Key response variables in the experimental site data

In the Terrestrial Umbrella (TU) experiments, vegetation and soils have been subjected to detailed study over many years, and several variables, both ecological and biogeochemical, were found to respond to additions of nitrogen. In relation to this report, the key response variables of interest considered were: changes in presence and abundance of individual species, botanical groups (vascular plants, bryophytes and lichens); changes in visible plant injury due to stress (winter damage, heather beetle); and changes in plant and soil chemistry (with potential consequences for nutrient imbalance, soil leaching and pH).

4.6 Conclusion and summary of response variables taken forwards to task 4

The results from the survey datasets strongly support the findings from the literature review. Increasing nitrogen deposition is strongly associated with both detrimental changes in species composition and reductions in species richness. In some cases a specific form of N was more strongly associated with a response however, to enable comparison with critical loads, total N deposition is used in further analysis. This will not affect the overall relationship as modelled total nitrogen deposition was strongly correlated with both modelled reduced and oxidised N deposition over the data used (R^2=0.89 and 0.72 respectively, both $P<0.01$). The nitrogen addition experiments provide data to support the hypothesis that nitrogen pollution, in the absence of change in other environmental variables, has a direct adverse effect on community composition in many different types of vegetation. Important changes in habitats were seen especially regarding the abundance of sensitive species and some of these are described under Task 4.

Table 10 below summarises the response variables that are strongly associated with N deposition for each habitat, these are further analysed in Task 4. The consistency shown between the new research discussed here and the published data is remarkable and reflects the strength of N as a driver of change within the UK's semi-natural ecosystems. The responses to N that are found are in addition to those explained by a climatic gradient and, in many instances, N deposition is statistically the strongest driver of change.

Table 10: Summary of the strongest response variables found during the statistical analysis that will be carried forward to Task 4. '#' indicates found within vegetation datasets analysed as part of this report, '$' indicates found within the literature reviewed as part of this report.

Response variable	Acid grassland	Bog	Upland heath	Lowland heath	Sand dune
Species composition	#$	#$	#$	#$	#
Total species richness	#	#$	#$	#$	#
Bryophyte species richness	$		#$	#	#
Lichen species richness		#	#		
Forb species richness	#$	#			#
Graminoid species richness			#	#	
Graminoid cover	$	#	#	#	#

In some cases, for example lowland heath mosses or lichens, N deposition did not emerge from the stepwise regression as a potentially significant driver of change in species richness. However, in these cases N deposition was associated with changes in species composition in the ordination analysis, with individual moss, lichen, forb and graminoid species strongly associated with changes in a form of N deposition.

Changes in certain individual species were related to changes in N deposition and these are summarised in Table 11 overleaf. Many more species appeared to show some relationship to N but, low frequency in the dataset meant that this was not significant. However, their response does contribute to changes in overall species richness and the species richness of functional groups.

Table 11: Summary of individual species that showed a strong response to N in the ordination analysis. The nature of these relationships with N deposition is examined further under task 4.

Habitat	Species with strong response (direction of response)
Upland heath (TU & MRS)	*Cladonia fimbriata* (↑) *Cladonia portentosa* (↓) *Deschampsia flexuosa* (↑) *Brachythecium rutabulum* (↑) *Hylocomium splendens* (↓) *Campylopus introflexus* (↑)
Lowland heath	*Cladonia fimbriata* (↑) *Cladonia portentosa* (↓) *Brachythecium rutabulum* (↑) *Campylopus introflexus* (↑) *Hylocomium splendens* (↓)
Acid grassland	*Deschampsia flexuosa* (↑) *Hypnum cupressiforme (agg.)*(↑) *Nardus stricta* (↑) *Carex panicea* (↑) *Euphrasia officianlis* (↓) *Hylocomium splendens* (↓) *Lotus corniculatus* (↓)
Bog	*Eriophorum vaginatum* (↑) *Sphagnum fimbriatum* (↑) *Cladonia portentosa* (↓)
Sand dune	*Hylocomium splendens* (↓) *Ammophila arenaria* (↓)

5. Task 4: Determine the relationship between N deposition and the key response variables

5.1 Introduction

The relationships between N deposition and the key response variables determined in Task 3 are examined in more detail here. This task presents results over 6 main sections: 1) those from the gradient surveys analysed in this report; 2) supporting evidence of change from the dose response experiments; 3) evidence from the literature; 4) a review of the relationships between N and the response variables found in the JNCC collation report (Stevens *et al*., 2011); 5) the use of cluster analysis to determine if any relationship exists between species composition and nitrogen deposition in the survey datasets and the possible presence of threshold responses and 6) Concluding comments.

The relationships examined in this chapter use modelled annual N deposition as the pollutant variables, however, the relationships studied between N deposition and species richness and presence have developed over many years. The current rate of N deposition is primarily a proxy for long-term cumulative N deposition. Thus we would not expect that a change in N deposition, either increasing or decreasing, would immediately change species richness or composition, however, long-term changes in N deposition are likely to affect species richness and composition. Furthermore, different species groups will respond in different ways: bryophytes and lichens with no root structure are likely to respond quicker than vascular plants and the responses of both may be affected by management interaction which could alter inter-species composition. Refer to the methods section for further information.

5.2 Relationships determined in the gradient surveys

The nature and strength of the relationships between N deposition and total species richness, functional group richness and plant cover, where significant, are summarised in Table 12 and the relationships between N and individual species cover or presence are presented in Table 13. Regression curves for each of these relationships are provided in Appendix 2 for total and functional group species richness and Appendix 3 for the individual species responses, however, the broad relationship between N and the percentage of the maximum number of species within habitats with comparable survey techniques (TU 2009 upland heath, lowland heath, bog, sand dune and subset of BEGIN/Stevens *et al*. (2004) grasslands) is shown in Figure 6.

Across the 135 survey sites represented in this plot, a highly significant pattern of species richness reduction as a function of increasing atmospheric nitrogen deposition is apparent with a wedge shaped response. The pattern indicates that at low N deposition the species number can be both high and low, but at high N deposition the species number is always low. The large scatter in the data is related to the variation between- as well as within- habitats. Within this overall dataset, a negative-linear relationship best describes the response, however, within each habitat and functional group a negative, curvi-linear relationship is more common, indicating a more rapid loss of species associated with increasing N deposition at

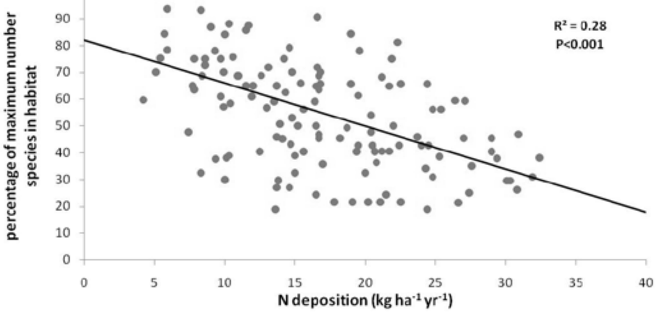


Figure 6: Change in % of maximum species richness as N deposition increases at 135 sites studied in the TU 2009 multi-habitat survey

lower levels of N pollution. Species richness curves from the TU sand dune (all pH) and TU upland heath surveys and are shown in Figure 7 below, and a complete set of response curves provided in Appendix 2. A curvi-linear response suggests that less-polluted sites are more sensitive to increases in N deposition and that at sites already receiving high levels of pollution, much species diversity has already been lost. In all habitats, the magnitude of the response is large, with 50-75% fewer species in the least diverse sites within each habitat, compared with the most diverse.

Loss of species richness related to increases in N deposition is consistent across all the habitats and functional groups, with the exception of sand dunes with a pH less of than 6.5, where limited data and strong climatic effects occurred. Whilst graminoid species richness also declined, graminoid cover increased, and this relationship was also curvilinear, indicating more rapidly increasing cover of fewer graminoid species as N deposition increased. In this respect, the potential for adverse change in each habitat increased at locations with a higher background N deposition.

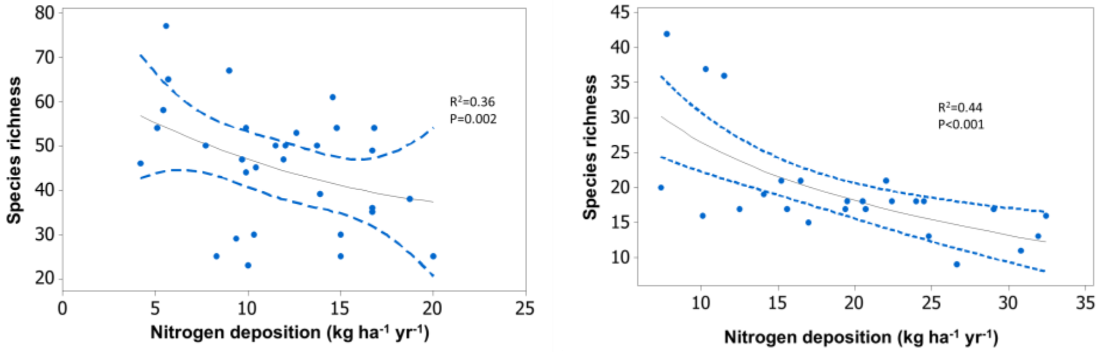


Figure 7: Measured species richness within a) TU 2009 survey sand dunes (all pH) and b) TU survey upland heaths as nitrogen deposition increases

To further examine the range over which the response variables from Task 3 show the most rapid change, each variable was analysed using LOESS regression. Summary data from these analyses are presented in Tables 12 and 13 and example regression curves for TU Sand dune (all pH) and TU Upland heath surveys are shown in Figure 8.

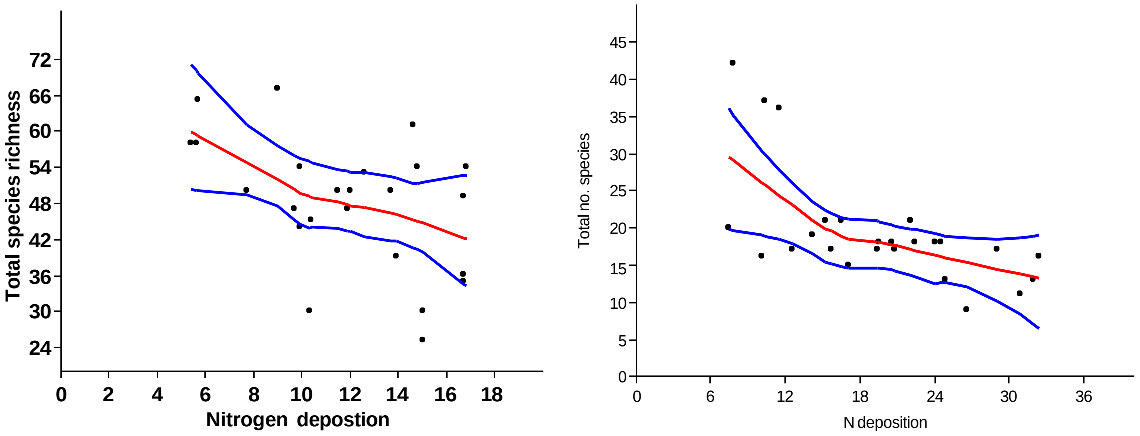


Figure 8: LOESS regression curves showing change in species richness as nitrogen deposition increases for a) TU 2009 survey sand dunes (all pH) and b) TU survey upland heaths. Best fit to data line in red, 95% confidence limits shown in blue and fitted by bootstrapping.

Although data in most habitats is limited to around 25 sites, clear response points were usually found, and these mostly supported the curvilinear relationships from the linear regressions. In many cases the inflection was at an N deposition level typically between 17 and 22 kg N ha^{-1} yr^{-1} for many negative and positive responses to N. The general exception to this was *Cladonia fimbriata* cover which showed a ‘humpback’ uni-modal response in upland (16-25 kg N ha^{-1} yr^{-1}) and lowland heaths (17-28 kg N ha^{-1} yr^{-1}).

Table 12: Summary of relationship type and direction between modelled nitrogen deposition (kg ha^{-1} yr^{-1}) and species richness/cover for each habitat. Relationship equations shown: y=species richness; x=nitrogen deposition (kg ha^{-1} yr^{-1}). LOESS regression range highlights the range over which the species response is the most responsive, a dash indicates no tipping point was apparent.

Habitat/ Survey	Response variable	Direction of response to N	Relationship type	Statistical significance	Relationship equation	LOESS regression range of max. loss or gain
All habitats (from TU 2009)						
	Total species richness	negative	linear	$R^2=0.28$ $P<0.001$	$y=1.56*x + 82.9$	n/a
Upland heathland (TU 2009)						
	Total species richness	negative	mild curvilinear	$R^2=0.44$ $P<0.001$	$y=54.37 - 12.11*\ln(x)$	7-17 kg N
	Moss species richness	negative	curvilinear	ns	-	-
	Lichen species richness	negative	linear	$R^2=0.23$ $P=0.015$	$y=11.34 – 3.18*\ln(x)$	7-16 kg N
	Graminoid species richness	negative	mild curvilinear	$R^2=0.27$ $P<0.01$	$y=9.62- 2.28*\ln(x)$	7-22 kg N
	Graminoid cover	positive	mild curvilinear	$R^2=0.31$ $P=0.017$	$y=0.042x^2 - 0.88x + 9.19$	>22 kg N
Upland heathland (MRS)						
	Total species richness	negative	mild curvilinear	$R^2=0.61$ $P<0.001$	$y = 0.011*x^2 - 0.709*x + 19.8$	20 kg N
Lowland heathland (TU 2009)						
	Total species richness	negative	mild curvilinear	$R^2=0.32$ $P=0.002$	$y=-11.25*\ln(x) + 47.27$	< 17 kg N
	Moss species richness	negative	mild curvilinear	$R^2=0.15$ $P<0.05$	$y = -3.29*\ln(x) + 14.685$	-
	Graminoid species richness	negative	mild curvilinear	$R^2=0.26$ $P<0.01$	$y=0.16+38.99/x$	-
	Graminoid cover	positive	mild curvilinear	$R^2=0.25$ $P<0.05$	$y=8.45-1.15*x+0.05x^2$	> 23 kg N
Bog (TU 2009)						
	Total species richness	negative	linear	$R^2=0.23$ $P=0.009$	$y=27.9 - 0.30*x$	> 19 kg N
	Lichen species richness	negative	linear	$R^2=0.19$ $P=0.018$	$y= 4.79 - 0.13*x$	-
	Forb species richness	negative	mild curvilinear	$R^2=0.46$ $P<0.001$	$y = 8.07 - 2.33*\ln(x)$	-
	Graminoid cover	linear	linear	$R^2=0.27$ $P=0.004$	$y=1.35*x + 17.4$	-
Sand dunes TU 2009 (all sites)						
	Total species richness	negative	mild curvilinear	$R^2=0.36$ $P=0.002$	$y=30.4 + 194.6/x$	< 10 kg N
	Moss species richness	negative	strong curvilinear	$R^2=0.81$ $P<0.001$	$y= -1.3 + 84.4/x$	< 12 kg N
	Graminoid cover	positive	mild curvilinear	$R^2=0.17$ $P<0.05$	$y=75.3 - 214.8/x$	< 10 kg N
	Forb species richness	negative	mild curvilinear	$R^2=0.17$ $P<0.05$	$y=12.8 + 84.1/x$	-
Sand dunes TU 2009 (pH <6.5)						
	Total species richness	too few data points	-	-	-	-

Habitat/ Survey	Response variable	Direction of response to N	Relationship type	Statistical significance	Relationship equation	LOESS regression range of max. loss or gain
Sand dunes TU 2009 (pH ≥6.5)						
	Total species richness	negative	mild curvilinear	R^2=0.42 P=0.009	y=94.1-16.8*ln(x)	-
	Moss species richness	negative	mild curvilinear	R^2=0.85 P<0.001	y= -1. + 86.1/x	
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)						
	Total species richness	negative	mild curvilinear	R^2=0.27 P<0.001	y=104.3-22.6*ln(x)	-
	Moss species richness	negative	mild curvilinear	R^2=0.26 P=0.002	y=22.9-6.98*ln(x)	
Acid grasslands (BEGIN)						
	Total species richness	negative	mild curvilinear	R^2=0.29 P<0.001	y = 0.0052x^2 - 0.68*x + 34.6	-
	Forb species richness	negative	linear	R^2=0.48 P<0.001	Y= 11.8 - 0.35*x	-

Some of the individual species also revealed an apparent threshold level above or below which the response was strong. Most notable were the rapid reduction in the probability of presence (number of quadrats in which a species was found) of *Hylocomium splendens* in both upland heath surveys and the sand dunes at N deposition above 20 kg N ha^{-1} y^{-1} and the rapid increase in *Brachythecium rutabulum* at a similar point. *H. splendens* is thought to be sensitive to N however, its absence should not lead to the assumption that a site is negatively affected by N as the moss generally only occurs at less-polluted sites that are also moist. Similarly, *B. rutabulum* exhibits a preference for moister sites. It is therefore important that other factors be considered when making judgement of a site's N-status by the presence or absence of a single species.

Table 13: Summary of key relationships between nitrogen deposition and the individual species in each habitat identified in Task 3. Type, direction, statistical significance and equation of curve shown.

Habitat/ Survey	Response variable	Direction of response to N	Relationship type	Statistical significance	Relationship equation
Upland heathland (TU 2009)					
	Hylocomium splendens cover (%)	negative	mild curvilinear	R^2=0.16 P<0.05	y = 0.038x^2 - 2.37*x + 36.44
	Hylocomium splendens probability of presence	negative	threshold	ns	-
	Cladonia portentosa cover	negative	curvilinear	ns	-
	Deschampsia flexuosa cover	positive	mild curvilinear	R^2=0.30 P=0.018	y = 0.04x^2 - 0.75*x + 6.52
	Cladonia fimbriata cover	positive	curvilinear	ns	-
	Brachythecium rutabulum cover	positive	curvilinear	ns	-
	Brachythecium rutabulum probability of presence	positive	threshold	ns	-
Upland heathland (MRS)					
	Hylocomium splendens presence (%)	negative	threshold	R^2=0.65 P<0.001	y= -1.33 +39.74/x
	Campylopus introflexus presence (%)	positive	threshold	R^2=0.39 P=0.01	y = 0.003x^2 – 0.05*x + 0.23

Habitat/ Survey	Response variable	Direction of response to N	Relationship type	Statistical significance	Relationship equation
Lowland heathland (TU 2009)					
	Hylocomium splendens cover (%)	negative	curvilinear	R^2=0.44, P<0.001	y=6.21+ 119.51/x
	Hylocomium splendens probability of presence	negative	curvilinear	R^2=0.35, P<0.001	y=6.69-2.14 *ln(x)
	Cladonia portentosa cover	negative	mild curvilinear	R^2=0.35, P<0.001	y=11.08 -3.60 * ln(x)
	Cladonia portentosa presence	negative	strong curvilinear	R^2=0.37, P<0.001	y=8.72 -2.69 *ln(x)
	Cladonia fimbriata cover	positive	linear	ns	
	Cladonia fimbriata presence	positive	linear	R^2=0.14, **P=0.06**	-
	Campylopus introflexus cover	positive	curvilinear	ns	-
	Brachythecium rutabulum cover	positive	curvilinear	ns	-
	Brachythecium rutabulum presence	positive	strong curvilinear	R^2=0.25, P<0.05	$y=0.06 -0.014*x + 0.005*x^2$
Bogs (TU 2009)					
	Cladonia portentosa cover	negative	linear	R^2=0.13, **P=0.055**	-
	Cladonia uncialis cover	negative	mild curvilinear	R^2=0.25, P=0.006	y=0.89 – 0.29*ln(x)
	Cladonia uncialis presence	negative	mild curvilinear	R^2=0.53, P<0.001	y= -1.17 +24.52/x
	Eriophorum vaginatum cover	positive	linear	R^2=0.41, P<0.001	y=1.48*x + 5.27
	Sphagnum fimbriatum cover	positive	mild curvilinear	R^2=0.20, P=0.015	y= -0.58 + 0.24*ln(x)
	Sphagnum fimbriatum presence	positive	mild curvilinear	R^2=0.21, P=0.013	y= -2.0 + 0.83*ln(x)
Sand dunes (TU 2009 all sites)					
	Hylocomium splendens cover	negative	mild curvilinear	R^2=0.21, P<0.01	y= -5.84 +106.88/x
Acid Grasslands (BEGIN)					
	Hylocomium splendens cover	negative	mild curvilinear	R^2=0.16, P=0.001	y= -1.01 +42.06/x
	Hypnum cupressiforme cover	positive	linear	R^2=0.16, P<0.001	y = 0.19*x - 2.07
	Nardus stricta cover	positive	linear	R^2=0.11, P=0.003	y = 0.30*x - 2.38
	Carex panacea cover	positive	linear	R^2=0.08, P=0.014	y = 0.072*x – 0.88
	Euphrasia officianlis cover	negative	mild curvilinear	R^2=0.11, P=0.005	y= 1.83 - 0.54*ln(x)
	Lotus corniculatus cover	negative	mild curvilinear	R^2=0.09, P=0.009	y= 3.58 – 1.03*ln(x)

5.3 Evidence from Dose–response relationships in the TU experiments

The UKREATE Terrestrial Umbrella (TU) project is funded by the Department for Environment Food and Rural Affairs (Defra) and the Natural Environment Research Council (NERC). The nine UKREATE sites (see Tables 5 and 6) are long term experiments in locations representing a broad range of priority UK habitats. Although established at different times over the past 22 years and involving different levels of nitrogen additions, the common features of their research design and monitoring enable consistent comparisons to be made among the sites. A recent overview is presented in RoTAP (2012), while the published sources of results from individual sites are given in Table 6 as well as in the report section on the UKREATE web site (http://ukreate.defra.gov.uk/publications/reports/index.htm).

5.3.1 Complementary nature of the Field surveys and the UKREATE experiments

The national-scale field surveys and the UKREATE experiments provide different, but complementary information. The changes observed in the spatial field surveys take place in the 'real-world' under normal timescales but may also be driven by climate, management, air pollution, soil chemistry and a host of other factors. Where air pollution, and in particular nitrogen deposition, is separated out as a main driver of change, the timescales of the influence of pollutants are very lengthy, possibly at least over the two centuries since the Industrial Revolution and periods of agricultural expansion but certainly over recent decades (Fowler *et al*., 2004).

The UKREATE experiments are short by comparison and in most cases involve nitrogen additions that are beyond the normal range of current deposition starting from ambient loadings which are already around the critical load. However, the controlled experiments provide evidence for ecosystem responses that result directly from nitrogen addition since other factors (soils, climate management etc) are a constant. They can also reveal the potential for changes that may occur at higher levels of nitrogen deposition but are not yet detectable in the natural landscape. Furthermore, some of the UKREATE experiments include the cessation of treatments along with maintained monitoring in order to investigate the consequences of reduction of nitrogen inputs.

Within this report the results of the UKREATE experiments are used to provide evidence regarding the nature of changes in plant community composition and individual species in response to added nitrogen.

5.3.2 Responses of vegetation to nitrogen addition and recovery

Selected examples of responses of vegetation to nitrogen additions in the UKREATE experiments are presented below. A general outcome from the experiments to date is that bryophytes and lichens are strongly and negatively affected by the nitrogen additions, but that changes in the vascular flora are modest and have appeared more slowly (RoTAP, 2012; Phoenix *et al*, 2012). One important exception is that both vascular species as well as lower plants in the Whim bog experiment have been greatly affected by gaseous ammonia treatments (Figure 9). The data from Whim bog show that responses in the most sensitive plants, in this case the bryophytes, are evident even at the lowest level of N addition i.e. 8 kg N ha^{-1} y^{-1} above a background of the same. At the higher end of the nitrogen addition range there is evidence of increasing damage to bryophytes at additions beyond the critical load range (for bogs 5-10 kg N $ha^{-1}y^{-1}$). In the gaseous NH_3 experiment, increased nitrogen also led to substantial community change with large increases in *Eriophorum* and loss of *Calluna* (Figure 9, top).

The sensitivity of bryophytes and lichens to wet deposited nitrogen treatments was also demonstrated at the original Ruabon upland heath (heather moorland) experiment (Carroll *et al*., 1999). In the newer Ruabon experiment, which used a wider range of treatments, a gradual pattern of change in lichen cover (mainly *Cladonia portentosa*) was observed (Figure 10) which after 5 years showed sensitivity to just 10 kg N $ha^{-1}y^{-1}$ above the ambient input of around 20 kg N $ha^{-1}y^{-1}$. This being the upper end of the critical load range for heathland (Pilkington *et al*., 2007). At Ruabon the same experiment also found that certain liverworts were particularly sensitive to increasing nitrogen additions (Figure 11), and again their abundance continued to decline as loadings were raised above the heathland critical load (Edmondson, 2007).

The sensitivity of lichens to nitrogen pollution, a clear outcome of the JNCC collation report (Stevens *et al*, 2011) was further confirmed in the experiment at Culardoch in the Cairngorms where lichens are an important part of the *Calluna-Cladonia* montane heath (Figure 12). Lichen cover was also very sensitive to nitrogen additions of just 7.7 kg N ha^{-1} y^{-1} (above a background deposition of around 8 kg N ha^{-1} y^{-1}) at Thursley Common (Figure 13) and here the effect still persisted at least 8 years after the nitrogen treatments had ceased (Power *et al*., 2006).

The above examples from the UKREATE experiments are consistent with the overall results from the field surveys since they show that small, realistic nitrogen additions can have adverse effects on the abundance of sensitive vegetation, even where the site is already close to the critical load. Increasing nitrogen inputs beyond the critical load can also change the character of the community by increasing the cover of dominant graminoid species.

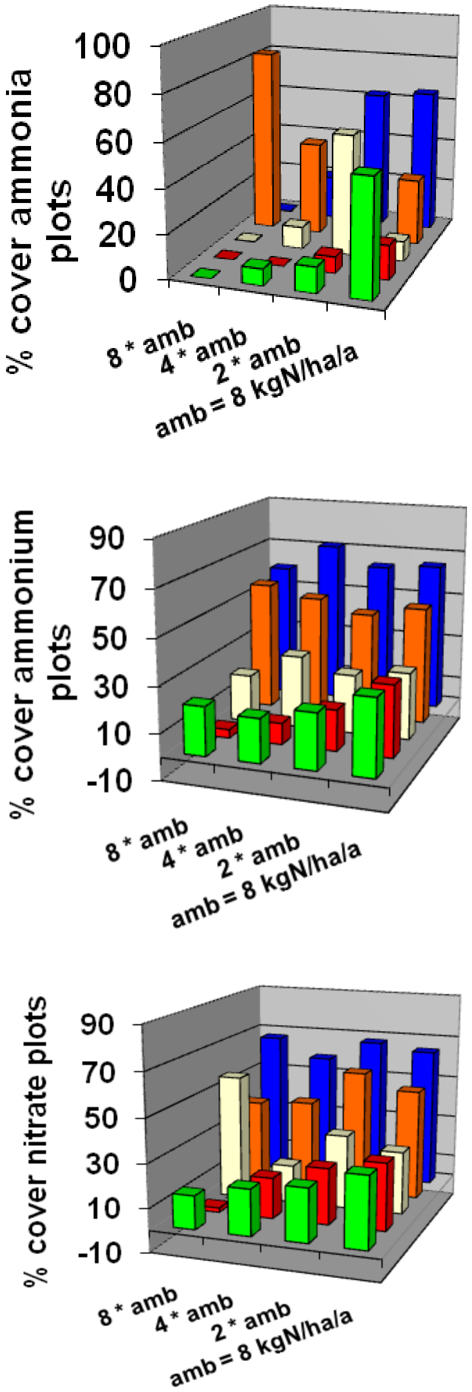


Figure 9: Response to different forms of nitrogen addition on Whim bog in 2009 after seven years treatment: ammonia gas (top), wet ammonium (middle), wet nitrate (lower) in different plants from front to back – *Sphagnum capillifolium, Pleurozium schreberi, Hypnum jutlandicum, Eriophorum vaginatum, Calluna vulgaris* (Sheppard, unpub). Ambient (amb) nitrogen deposition (approx. 8 kg N ha^{-1} yr^{-1}) at the right hand side of each graph, increasing N deposition towards the left.

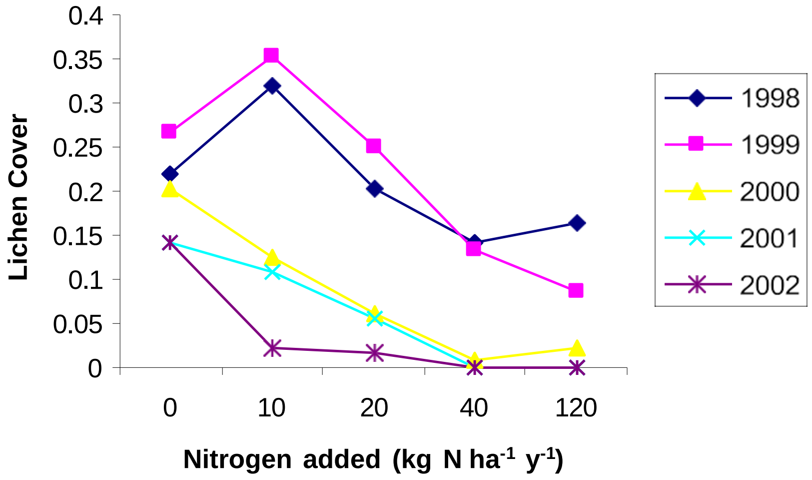


Figure 10: Nitrogen dose-response of lichen cover (mean touches/pin) at the Ruabon upland heath experiment new plots in the first 5 years of treatment. Ambient deposition circa 20 kg N ha^{-1} yr^{-1}. (Pilkington *et al*., 2007).

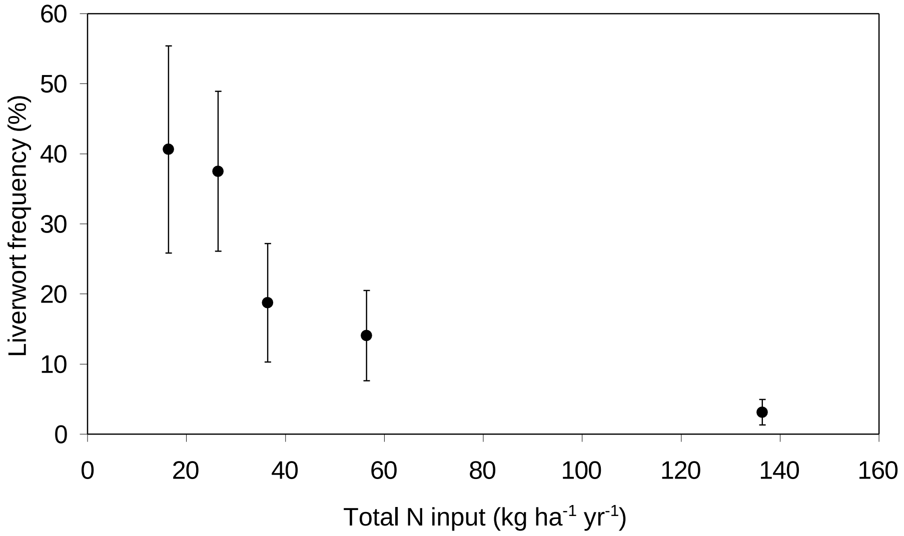


Figure 11: Relationship between total N input (N treatment + ambient deposition) and total liverwort frequency at the Ruabon upland heath experiment new plots. Ambient deposition circa 20 kg N ha^{-1} yr^{-1} (Edmondson, 2007).

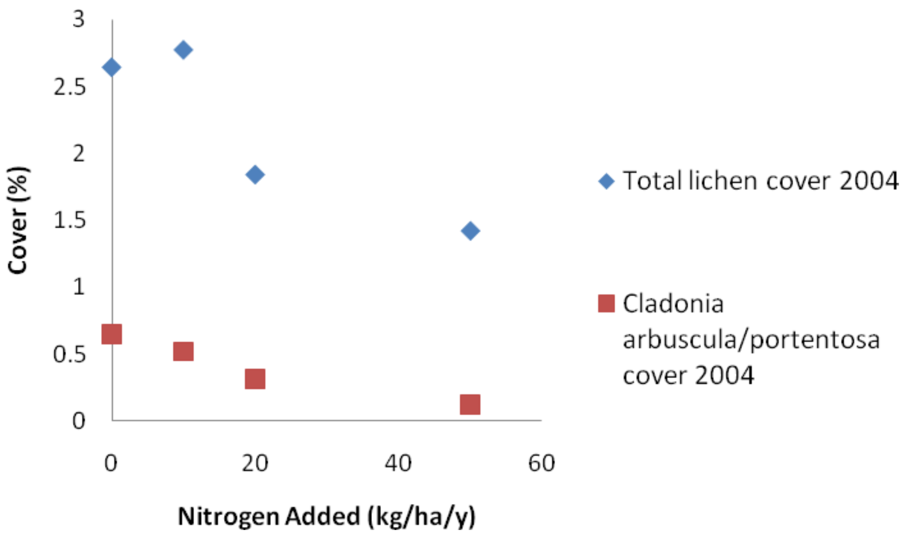


Figure 12: Response of lichens to nitrogen addition in montane heath at Culardoch in the Cairngorms (Britton & Fisher, 2007). Background N deposition circa 10 kg N ha^{-1} yr^{-1}.

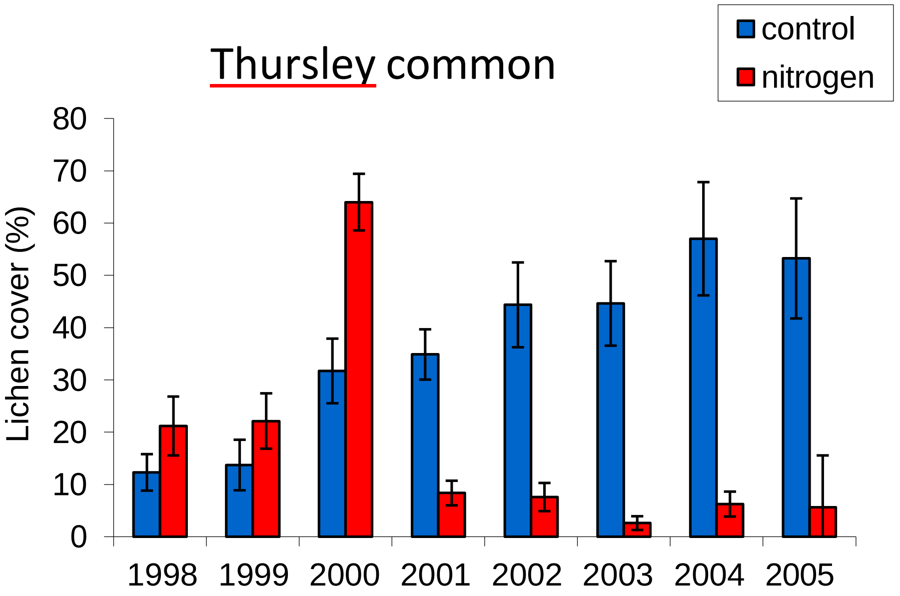


Figure 13: Effect of nitrogen additions (30 kg N ha^{-1} y^{-1}) on lichen cover at Thursley common, lowland heathland in Surrey (Sally Power, pers. comm.). The large decrease between 2000 and 2001 is thought to be related to a closing higher plant canopy following management interaction in 1998.

5.4 Reviewed literature – relationship between N deposition and the key response variables in the Countryside Survey and targeted habitat spatial surveys

The form of the relationship between nitrogen pollution and plant community composition is reviewed here for two types of survey: firstly the Countryside Survey of Great Britain, using a stratified randomised approach, which in this case used data collected in 1998 (Maskell *et al*., 2010). Secondly, several smaller scale surveys that have deliberately targeted particular habitats and enabled separation of air pollution signals from other important influences such as precipitation, temperature and management (Table 14).

The main focus of the Countryside Survey and targeted habitats spatial surveys was change in plant species richness, with further interest in individual sensitive species and functional groups. A range of important UK habitats was addressed, but some significant habitat gaps, notably woodland, remain. Data were gathered using small quadrats (2 x 2 m or 0.5 m^2 for bryophytes only) and analysed by multivariate statistical methods that examined a range of potential drivers including climate, air pollution and in some cases management (in other studies management level was kept a constant).

5.4.1 Habitat differences

The results of these surveys (Table 14) show a large degree of agreement, but also some important differences, between habitats. In upland heath, acid grassland and mesotrophic grassland, the different studies show strong agreement i.e. species richness was negatively correlated with nitrogen deposition. However, the two independent studies examining calcareous grassland found no correlation between nitrogen deposition and species richness. The contrast between base-rich calcareous habitats and the others suggests at least one of the likely mechanisms of change in less buffered soils is a long-term shift in soil pH (Stevens *et al*., 2010 Functional ecology paper) that could result from increased nitrogen deposition. While the calcareous grassland spatial survey in 1990-93 reported by Van den Berg *et al*. (2010) found no significant correlation with nitrogen deposition, the smaller repeat survey of 2006-2009 found an reduction in plant species diversity over the two decades that was greater in high-N deposition regions of the UK, particularly in the 25-35 kg N ha^{-1} y^{-1} areas. These changes comprised a decline in the frequency of characteristic calcareous grassland species and a lower number of rare and scarce species.

5.4.2 Taxonomic groups respond differently

In surveys where a significant drop in overall species richness in response to nitrogen deposition was recorded, different plant groups did not always respond in the same way. In acid grasslands, Stevens *et al*. (2006) found a strong decline in richness of forbs, a much weaker (but significant) reduction in grass species richness and no change in bryophyte species richness although the moss *Hylocomium splendens* was consistently reduced. In the Countryside Survey, both bryophyte and total species richness significantly declined in acid grasslands but not in heathlands and mesotrophic grasslands, where total species richness reduced but, bryophytes showed no change (Maskell *et al*., 2010). Bryophytes declined significantly with increasing nitrogen in the upland heath surveys.

5.4.3 The shape of the relationships between species richness and nitrogen deposition, and the critical load.

The decline in total species richness with increasing nitrogen demonstrated in all surveys apart from calcareous grasslands are described by either linear or curvilinear mathematical relationships. Over the nitrogen range investigated in the UK there is no evidence of a limit at the low end of the range below which negative change does not occur. The linear responses to increasing nitrogen found in a number of the studies (or plant groups within the studies) indicate that the rate of change in richness is constant across the nitrogen deposition range while the curvilinear fit that better describes other relationships indicate that reduction in species richness is greater at low than at high N deposition.

The slope of species richness vs nitrogen deposition is remarkably similar for the studies 1-5 (Table 11) (all except calcareous grassland, study 6) falling in a range of between minus 2.5 – 4.3 fewer species per quadrat per 10 kg $ha^{-1}y^{-1}$. Where curvilinear gradients were described (study 4) the rate of change was greater (minus 4.3) below 10 kg $ha^{-1}y^{-1}$ and minus 2.9 above 20 kg $ha^{-1}y^{-1}$. These figures compare broadly with the survey data analysed in this report: see task 5, Table 19.

Note however, that fewer species in a quadrat, or a reduction in species richness, means neither species 'loss' from a site, nor local species extinction – it means that the frequency of at least one species has been reduced. Also note that it is very likely that any inferred reduction in species richness due to N is the product of many years of N deposition, so that the current rate of N deposition is primarily a proxy for this long-term cumulative N.

5.4.4 Species richness declines in relation to the critical load

For acid grasslands and heathlands (Table 14, studies 1-4 and part of 5) the critical load range is 10-15 kg N $ha^{-1}y^{-1}$ and 10-20 kg N $ha^{-1}y^{-1}$ respectively. These fall towards the lower end (left) of the nitrogen deposition range surveyed. This has the following important implications:

(a) as would be expected, *above* the critical load range there is a substantial reduction in species richness (for both linear and curvilinear responses);
(b) what was more unexpected is that where curvilinear responses in species richness are described, the greatest decline in richness is *below* the critical load.

Table 14: Details of other surveys that have targeted specific habitat types along pollution and climatic gradients

Habitats	Significant Trend in response to increasing N deposition	Critical Load N kg ha^{-1}y^{-1}	Nitrogen Range kg ha^{-1}y^{-1}	Slope	Type of Relationship of response variable with N deposition	Comment	Reference
Upland dry heath	Bryophytes richness declines	10-20	19.5-30.5	3.1 bryophyte species / 10 kg N	Linear best fit		Edmondson *et al*., 2010
Upland dry heath	Bryophytes richness declines	10-20	8-31	2.4 bryophyte species/ 10 kg N	Linear best fit		Combined data of Edmondson & Carroll & Caporn (Stevens *et al*., 2009)
Acid grassland	Forbs & grass richness declines, Bryophytes no change Plant acid preference index score increases	10-15	6-36	4 species (all) / 10 kg N	Linear best fit to NHy and total N deposition; Exponential curvilinear best fit with NOx deposition Linear best fit of plant acid preference with total N deposition	Greater decline at low N deposition	Stevens *et al*., 2004, 2006, 2010
Acid grassland	Forbs Grasses Bryophytes All groups richness decline	10-15	2-44	4.3 species (all) / 10 kg N below 20 kg /ha/y 2.9 species (all) / 10 kg above 20 kg N/ha/y	Exponential curvilinear best fit with total N	Greater decline at low N deposition BEGIN project Analysis included GB and European sites	Stevens *et al.*, 2010

Habitats	Significant Trend in response to increasing N deposition	Critical Load N kg ha^{-1}y^{-1}	Nitrogen Range kg ha^{-1}y^{-1}	Slope	Type of Relationship of response variable with N deposition	Comment	Reference
Acid grassland	(Vascular + bryophyte) richness decline Bryophyte (alone) Decline	10-15	c. 5-40	2.5 (vasc+bryo species) / 10 kg N	Linear best fit	Countryside Survey 1998	Maskell *et al*., 2010
Calcareous grassland	No response in richness	15-25	c. 5-40	No change	No change	Countryside Survey 1998	
Mesotrophic grassland	(Vascular + bryophyte) richness decline	15-25	c. 5-40	Not given	Linear fit	Countryside Survey 1998	
Heathland	(Vascular + bryophyte) richness decline	10-20	c. 5-40	3.2 (vasc+bryo) species / 10 kg N	Linear fit	Countryside Survey 1998	
Calcareous grassland	No response in richness (1990-1993 survey)	15-25	7-41	No change	Above 25 kg N/ha/y there was a lower number of rare and scarce species	1990-3 survey part repeated in 2006-9; Increasing decline in species diversity and evenness over +20 years	Van den Berg *et al*., 2010

5.5 Review of relationships between N deposition and the key response variables from the JNCC Collation report

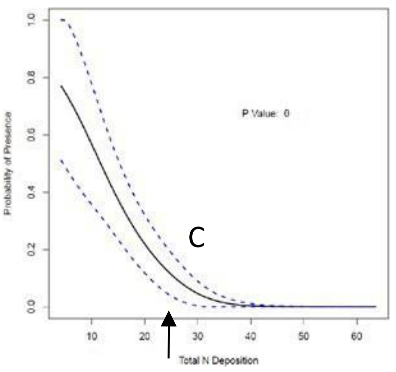
Two recent studies for JNCC have collated and analysed several different vegetation surveillance data sets (within UK or GB) in order to investigate relationships between community composition and nitrogen deposition (Stevens *et al*., 2011) and the impact of this on critical loads and policy (Emmett *et al*., 2011). A summary of relationships in selected data sets from the JNCC report is given here (Tables 16-17). This report will focus on the analysis of the vegetation datasets held within Stevens *et al*. (2011) although for a broader overview of policy implications the reader is directed to Emmett *et al*. (2012).

This JNCC collation study examines in detail the responses to nitrogen in a selection of habitats: heathlands, acid grasslands, calcareous grasslands and bogs. Large scale geographical distributions of plant species in relation to nitrogen deposition were examined using eight different surveillance data sets. Stevens *et al*. (2011) analysed spatial and in addition temporal changes over recent decades where data was available.

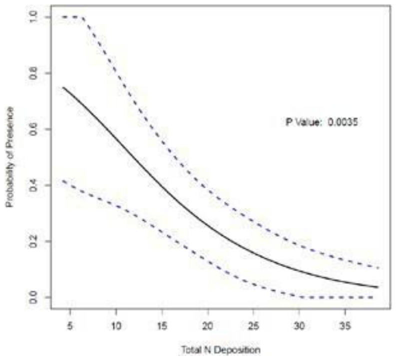
Discussion in this report is limited to examining the nature or shape of the spatial dose response relationships described in the collation report and covers the main databases providing detailed information on individual species over a wide geographical range: Vascular plant database (VPD), Botanical Society of the British Isles (BSBI), British Lichen society (BLS). Comment here is made regarding the British Bryological Society (BBS) data set.

A range of dose-response relationships was mathematically described and plotted in the JNCC Collation report (Stevens *et al*., 2011). Species presence - N relationships were not analysed by Stevens *et al*. (2011) where there were insufficient samples across the nitrogen deposition range. In the current report four types of relationships are proposed, the first three are negative responses of species to nitrogen, while the fourth is a positive response. In the cases of negative responses, an approximate deposition to result in 50% probability of presence is given based on visual assessment of the relationships; this is termed ND_{50}. Examples of these responses taken from Stevens *et al* (2011) are shown below overleaf. The four response types are categorised in the following way and illustrated in Figure 14. The mathematical relationships are represented by the solid line. Dotted lines illustrate the confidence intervals, where narrow our understanding of the response is strong, where the distance between these lines widens this reflects a less understanding of responses usually at extremes of the N deposition range:

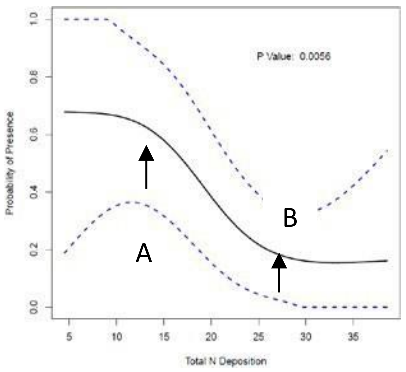
Type 1:	Strong negative curvilinear fall with a turning point (‘heel’) at point C
Type 2:	Mild negative curvilinear fall, the shape approaching linear within the normal deposition range (up to 30-35 kg N)
Type 3:	Reverse sigmoid fall, indicating a shoulder at point A and a heel at point B
Type 4:	Increase within normal deposition range



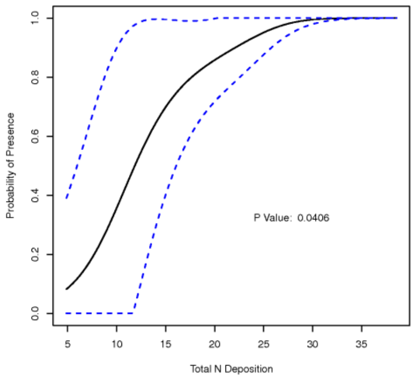
Type 1: strong curvilinear fall
Spatial change in the probability of presence of *Cladonia subulata* in heathland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS.



Type 2: mild curvilinear fall
Spatial change in the probability of presence of *Peltigera didactyla* in acid grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS.



Type 3: reverse sigmoid fall
Spatial change in the probability of presence of *Cladonia foliacea* in calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from BLS.



Type 4: Increase
Spatial change in the probability of presence of *Alchemilla xanthochlora* in upland calcareous grassland with increasing total current inorganic N deposition (kg N ha^{-1} yr^{-1}). Data from Vascular Plant Database.

Figure 14: Examples of relationships between individual species probability of presence and nitrogen deposition from JNCC report 447 (Stevens *et al*., 2011) with proposed inflexion points A,B,C which are discussed here in the text

5.5.1 Other types of responses within the VPD, BSBI, BLS and BBS databases

In addition to the cases listed in the Tables 15-17 and shown in the graphs (see Stevens *et al*. 2011), there were also other cases of: no significant relationship; hump-backed responses, U-shaped responses; ‘small magnitude changes.’ These are not reported in the Tables 15-17 in the current report because they are difficult to interpret and suggest the strong influence of other factors. The tables below show cases where there were clear-cut, significant relationships with nitrogen deposition, both positive and negative.

Where there were sufficient data available for analysis, numerous observations of ‘no significant response’ were reported. Where significant changes were found the majority of these were negative i.e. decline in presence with increasing nitrogen deposition. There were also a significant number of species showing increasing presence, particularly amongst bryophytes, but the majority of responses within any plant group were negative.

The strongest responses were in the lichen data set (BLS) and these were consistently negative changes. All three decline curve types were seen, but the majority were Type 1 or 2, indicating that there was no minimum threshold and the decline in presence started from a very low dose (around 5 kg N ha^{-1} y^{-1}). The fewer cases found of the reverse sigmoid curve type (Type 3) suggested that a decline commenced above a nitrogen deposition of approximately 15 kg N ha^{-1} y^{-1}. The approximate value for the ND_{50} was, for the lichens, within or around the low end of the critical load range for the habitats, with an average of 14 kg N ha^{-1} y^{-1} for those lichens shown in Table 14.

There were fewer cases of clear relationships with nitrogen in the BSBI higher plant data sets (Table 16), but these were all negative with either Type 1 or Type 3 curves over the normal range of deposition. Sigmoid type curves (Type 3) for three species showed that decline commenced above a nitrogen deposition of approximately 5, 8, 18 kg N ha^{-1} y^{-1} respectively. The mean ND_{50} for these vascular plants was approximately 16 kg N ha^{-1} y^{-1}.

The Vascular Plant Database (VPD) analysis showed a larger number of significant positive and negative relationships between vascular species presence and Nitrogen deposition (Table 17). The most common decline was described by a strong curvilinear response (Type 1) with a 50% drop by around 8-15 kg N ha^{-1} y^{-1}. A few species declined in a sigmoid manner (Type 3) with a shoulder at around 10-15 kg N ha^{-1} y^{-1}.

Bryophyte response curves in the JNCC collation report were not analysed to the same level of detail in the current study. The individual species data for bryophytes are difficult to interpret with some species increasing and other decreasing and the authors could not find any clear and general trends in the data (Stevens *et al*. 2011).

5.5.2 Response patterns above the critical load

Examination of the individual responses from the BLS, BSBI and VPD datasets suggests that at the higher levels of deposition there usually is a turning point or ‘heel’ to a slower rate of decline (position C in a type 1 curve, and position B in a type 3 curve - see Figure 14). In the significant negative responses this turning point was observed around an average approximate nitrogen deposition of 25 kg N ha^{-1} y^{-1} in lichens (BLS datasets) and 23 kg N ha^{-1} y^{-1} in vascular plants (VPD and BSBI datasets).

5.6 Summary from the review of published dose response relationships between species richness or individual species presence and nitrogen deposition

Evidence from the BLS, BSBI and VPD national datasets (summarised over Tables 15 to 17) which are based on national botanical surveillance data sets or targeted habitat surveys show a remarkable degree of consistency demonstrating evidence for nitrogen enrichment across several UK habitats. All habitats examined here show evidence of either broad scale reductions in species richness, decline in individual species or plant groups or increases in some nitrophilous species such as graminoids. However, it is also clear that species and habitats do not all respond in the same way to nitrogen deposition. For example, individual bryophytes show a range of different responses to nitrogen, some declining and others increasing that probably reflect the importance of other aspects of habitat/micro-habitat over nitrogen deposition in many species of this group. Calcareous habitats are less affected by nitrogen deposition than less well pH buffered systems suggesting a role for acidification in changes in plant communities.

Negative relationships with nitrogen in species richness or individual species presence tend to show a similar response form – namely either linear indicating an equal rate of decline across the nitrogen deposition range or curvilinear suggesting a greater rate of change at low nitrogen than at high deposition rates. The JNCC Collation study revealed a number of plant species that started to decline with increasing nitrogen inputs only after a level of deposition was reached, but in the majority of affected species no level was apparent implying that within the normal UK deposition range the vulnerable species start to decline with any increasing level of nitrogen and that this is typically at or below the critical load range for the habitats.

At the higher end of the nitrogen deposition scale, all the data sets investigated demonstrated clear evidence that species declines continue to occur above the habitat critical loads, so that small increments of nitrogen pollution within the range of 20-35 kg N ha^{-1} y^{-1} still have the potential to cause adverse and continuing change. Even in the less sensitive calcareous habitat, the temporal change study in calcareous grasslands found the greatest decline in individual species was in the areas receiving 25-35 kg N ha^{-1} y^{-1}. The importance of changes in nitrogen deposition at the higher end of the UK range should not be underestimated.

Table 15: Relationship between probability of presence and nitrogen deposition for lichen species from the BLS database spatial analysis for which significant responses were found. The turning point and ND50 (these are defined in section 5.5) values refer to nitrogen deposition (kg N ha^{-1} y^{-1}) and were estimated by eye from published figures of Stevens *et al*. (2011) and Emmett *et al*. (2012). Examples of response types and turning points are shown in Figure 14.

British lichen society database Habitat / Species (Critical load)	**Direction of change**	**Response Type**	**Turning Points (kg N ha^{-1} y^{-1})**	**ND_{50}**
Acid grassland (10-15 kg N ha^{-1} y^{-1})				
Cetraria aculeata	Negative	1	C=22	15
Peltigera didactyla	Negative	2		12
Calcareous grassland (15-25 kg N ha^{-1} y^{-1})				
Cladonia foliacea	Negative	3	A=15, B=30	17
Bog (5-10 kg N ha^{-1} y^{-1})				
Cladonia portentosa	Negative	3 (between 5-30 kg N)	A=15, B=30	22
Heathland (10-20 kg N ha^{-1} y^{-1})				
Cetraria aculeata	Negative	1	C=20	10
Cetraria muricata	Negative	1	C=20	10
Cladonia cervicornis cervicornis	Negative	1	C=15	8
Cladonia cervicornis verticillata	Negative	2 (between 5-35 kg N)		10
Cladonia portentosa	Negative	2 (between 5-30 kg N)		15
Cladonia subulata	Negative	1	C=27	12
Cladonia uncialis biuncialis	Negative	1	C=18	9
Peltigera hymenina	Negative	3	A=15, B=40	25
				Mean = 14

Table 16: Relationship between probability of presence and nitrogen deposition for vascular plant species from the BSBI database local change spatial analysis for which significant responses were found. The turning point and ND_{50} values refer to nitrogen deposition (kg N ha^{-1} y^{-1}) and were estimated by eye from published figures of Stevens *et al*. (2011) and Emmett *et al*. (2012). Examples of response types and turning points are shown in Figure 14.

BSBI database Habitat/Species (Critical load)	**Direction of change**	**Curve Type**	**Turning Points (kg N ha^{-1} y^{-1})**	**LD50**
Calcareous grassland				
Lowland (15-25 kg N ha^{-1} y^{-1})				
Bromopsis erecta	Negative	1 (over 5-25 kg N range)	C= 12	8
Campanula glomerata	Negative	3	A=18, B=30	27
Carex spicata	Negative	1	C=18	14
Ononis repens	Negative	3	A=8, B=18	15
Upland Heathland (10-20 kg N ha^{-1} y^{-1})				
Vaccinium vitis-idaea	Negative	3	A=5 , B=27	18
				Mean = 16

Table 17: Relationship between probability of presence and nitrogen deposition for vascular plant species for which significant responses were found in the vascular plant database spatial analysis. The turning point and ND_{50} values refer to nitrogen deposition (kg N ha^{-1} y^{-1}) and were estimated by eye from published figures of Stevens *et al*. (2011) and Emmett *et al*. (2012). Examples of response types and turning points are shown in Figure 14.

Vascular plant database Habitat/Species (critical load)	**Direction of change**	**Curve Type**	**Turning Points**	**LD_{50}**
Acid grassland: Lowland (10-15 kg N ha^{-1} y^{-1})				
Cerastium arvense	Negative	1	C=15	8
Cerastium semidecandrum	Negative	1	C=22	12
Trifolium arvense	Negative	1	C=19	12
Vicia lathyroides	Negative	1	C=19	10
Viola canina	Negative	1	C=24	15
Calcareous grassland (15-25 kg N ha^{-1} y^{-1})				
Lowland				
Allium vineale	Negative	1	C=25	9
Anacamptis pyramidalis	Negative	1	C=30	8
Carlina vulgaris	Negative	2 (between 5-30)		16
Cynoglossum officinale	Negative	3	A=10, B=35	25
Echium vulgare	Negative	3	A=10, B= 30	Outside range
Geranium columbinum	Negative	1	C=25	12
Lathyrus nissolia	Positive	4 (between 15-30)		
Ononis repens	Negative	3	A=10, B= 22	20
Spiranthes spiralis	Negative	1	C=15	8
Stachys officinalis	Positive	4 (between 5-30)		
Upland				
Alchemilla xanthochlora	Positive	4 (between 5-30)		
Melica nutans	Negative	3	A=15, B=27	17
Heathland (10-20 kg N ha^{-1} y^{-1})				
Lowland				
Platanthera bifolia	Positive	4 (between 5-35)		
Viola canina	Negative	3	A=12, B=25	18
Upland				
Arctostaphylos uva-ursi	Negative	1	C=15	9
				Mean = 13

5.7 Cluster analysis, sample grouping and ecological thresholds results

The analysis in this section of Task 4 sought to establish coherent ecological groupings along the N deposition gradient to support the suggestion that N is an important control on community composition and locate putative loads of N deposition where community composition is found to change significantly. Full details of the methodology used are provided in the methods section of this report.

The results are summarised in Table 18, split by survey dataset. In the acid grassland data (BEGIN) there are significant differences between the first two groups identified by both CONISS and SPLITLSQ. The break-points identified by these methods are different but rather similar, falling around 14.1 and 14.4 kg N ha^{-1} yr^{-1}. In the TU sand dune dataset significantly different groups are identified with only one method and the groups identified are only marginally significant. In the TU bog dataset two methods identify first divisions in adjacent positions around 11-12 kg N ha^{-1} yr^{-1}. In the TU upland heath data CONISS and SPLITINF identify adjacent break-points around 17 kg N ha^{-1} yr^{-1}, SPLITLSQ identifies a slightly lower first break at around 14.6 kg N ha^{-1} yr^{-1} and then a second significant break around 25-26 kg N ha^{-1} yr^{-1}. In the TU lowland heath data identical breaks are identified by all methods with only a first break significant at around 14.6 kg N ha^{-1} yr^{-1}.

Table 18: Results of CONISS, SPLITLSQ and SPLITINF for seven nitrogen gradient studies. Results show only the first two break-points listing the samples (e.g. N14.4, N14.5 etc) between which a division falls and the total nitrogen deposition (N) values for those samples in kg N ha^{-1} yr^{-1}. Analyses were based on squared Euclidean distance using proportion data (mean percent cover in most datasets, proportion of total species occurrences in five quadrats in the moorland regional survey). Differences between groups were tested on the same datasets using ANOSIM with Bray-Curtis dissimilarity, significance testing with permutation tests (10,000 permutations). *=P<0.05, **=P<0.01, ***=P<0.001, grey shading shows non-significant results. Second break-points are only counted as significant if all groups are significantly different (maximum P value between groups shown).

Dataset	CONISS		SPLITLSQ		SPLITINF	
	1st division	2nd division	1st division	2nd division	1st division	2nd division
BEGIN- acid grassland	(N14.4/14.5)**	(N22.8/23.8)	(N14.0/14.2)*	(N14.4/14.5)	(N24.8/25.0)	(11.0/13.4)
Moorland regional survey	N26.1/28.1)***	N20.4/20.6)**	(12.9/20.4)***	N26.1/28.1)***	(12.9/20.4)***	(N26.1/28.1)***
TU-sand dune	(N13.9/14.6)	(N15/16.7)	(N13.9/14.6)	(N15/16.7)	(N5.7/7.7)*	(N10.4/11.5)
TU-bogs	N10.9/11.7)***	(N19.6/21.9)	(N19.6/21.9)	(N14.2/14.3)	(N11.7/13.1)**	(16.6/16.6)
TU- Upland heath	(N16.5/17)**	(N24.5/28)	(N14.1/15.2)***	(N24.8/26.6)**	(N17/19.4)***	(N24.8/26.6)
TU-lowland heath	(N14.6/14.7)**	(N13/13.6)	(N14.6/14.7)**	(N13/13.6)	(N14.6/14.7)**	(N13/13.6)

Comparing the results between different surveys of the same or similar habitat types the case for consistent break-points is not overly strong. In the upland heath data from the TU and MRS there is overlap in some of the break-points however given the inconsistent sampling along the gradient it is difficult to place great confidence in the significance of this observation. The 16.5/17, 14.1/15.2 and N17/19.4 break-points in the TU data all lie within the wide gap between the MR15 and MR20 samples (12.9-20.4 kg N ha^{-1} yr^{-1}) in the MRS data. As discussed above, comparison of the MRS results with other results is particularly difficult due to the differing methodologies. Comparing the TU upland and lowland heath data there is similarity in the position of a first break-point in the lowland heath dataset and the first break-point with SPLITLSQ in the upland heath data while the upland heath first splits with SPLITINF and CONISS are slightly higher.

The results show that although break-points are identified in all cases, not all of the identified groups are significantly different. In only two cases are groups identified by a second split in the data significantly different from each other. The most significant results are identified with the moorland regional survey with all methods producing significantly different groups; however these results should be treated with caution particularly in comparison to the other datasets. In contrast to other datasets instead of recording percent cover this survey recorded presence/absence in each of five quadrats; the data we analyse here is a proportion of total species count and therefore although incorporating some measure of abundance is more weighted towards presence/absence.

In general there is some similarity between the results of different methods, but in many cases also substantial differences. Perhaps surprisingly the results of the two divisive methods are not substantially more similar to each other than to the results of the agglomerative method.

In most datasets our analyses succeed in identifying groups of samples with significantly different plant communities according to levels of nitrogen deposition. In itself this is an interesting result, supporting the suggestion from the ordinations that nitrogen deposition modifies plant community structure. The identification of such groups may be a useful way to approach the output of gradient studies. For instance the identification of indicator species for these groups may allow new sites to be categorised according to their levels of nitrogen-loading, which may be a useful approach to bioindication.

In some datasets different statistical techniques suggest the same break-point locations whereas in others there are differences. Where there are similar results by different methods this provides evidence for the validity of these values. However, where results differ between methods it does not necessarily mean the results are invalid. As different methods work on different principles and responded to different elements in the data it is quite possible for different methods to identify different, but equally valid break-points.

This analysis has studied the relationship between species composition and nitrogen deposition. The analysis of the lowland and upland heath and acid grassland datasets suggest that significant changes in composition may occur at 15 – 17 kg N ha^{-1} yr^{-1}. This value is in broad agreement with the conventional and LOESS regressions which looked for ‘heels’ in the species richness curves. Analysis of the bog vegetation data suggested a breakpoint where change occurs in species composition of 10-13 kg N ha^{-1} yr^{-1} which is lower than the 19-20 kg N ha^{-1} yr^{-1} suggested in the regression analysis of species richness data. Analysis of the sand dune data also suggested that changes in species composition may occur at much lower levels of N deposition than changes in overall species richness, 5-8 kg N ha^{-1} yr^{-1} compared to 10 kg N ha^{-1} yr^{-1}.

These findings broadly support the species richness regressions and the levels of N deposition where the rate of change in species richness altered, however, they do highlight the possibility that a change in species composition may occur before it is measured by a change in overall species richness. The implication of this is that ecosystems may be showing sensitivity to N deposition at much lower levels of N deposition than previously thought and certainly at the lower end of the critical load ranges.

5.8 Summary

The responses to nitrogen (N) across the habitats studied in the survey datasets are remarkably consistent with strong reductions in measured species richness associated with increases in N deposition. The fact that N deposition is so consistently related to changes in species richness (and composition) demonstrates the deleterious effects of N pollution on biodiversity. In many cases, bryophytes and lichens were shown to be most sensitive to N deposition although in grasslands, the intrinsic biodiversity of the habitat was affected by N through reductions in forb species richness. Within the heathland, bog and sand dune survey datasets graminoid cover increased exponentially with rising N deposition.

The results from the survey datasets are consistent with the findings from the dose-response experiments and the literature review. At a number of heathland experiments bryophyte and lichen diversity or cover reduced as N addition increased, notably so at the Culardoch montane heath where background N deposition was at the low end of the critical load range for heathlands (10 kg N ha^{-1} yr^{-1}). Reductions specifically in *Cladonia portentosa* cover at Ruabon and Culardoch supported the reductions seen in the heathland and bog surveys. Vascular plants were not strongly affected by N in the experiments although this perhaps reflects the dose/time compromise made. An exception to this was increase in *Eriophorum vaginatum* cover at Whim Bog along the gaseous ammonia release transect which reflected increases in cover this sedge as N deposition increased in the survey dataset. It should also be noted that the timescales of even the longest N-addition experiments are short by comparison to real-world N driven changes which have occurred over many decades. Furthermore, experiments tend to be limited by plot size which limits the possible response of vascular plants which may be reflected in change over a wider area. For these reasons, many of the experiments fail to show significant loss of vascular species although in some cases declines in cover are observed. Indeed, as has been observed, cover of certain graminoid species increased with N deposition although graminoid species richness tended to fall.

The similarity in responses seen at the experimental sites provides important supporting evidence that N deposition is driving the changes seen in the survey datasets and that change is not solely driven by a climatic gradient. Larger national survey datasets including the Countryside Survey and plant databases from the British Lichen Society (BLS) and the Botanical Society of the British Isles (BSBI) also provide evidence for widespread changes in response to N deposition. However, it is also accepted that climate plays an important role in influencing species richness and diversity with a tendency towards greater species richness in wetter and colder sites.

Much of the data presented and reviewed in this report suggested a curvilinear response to N with steeper responses at lower background levels of N (< 10 kg ha^{-1} yr^{-1}), decreasing at higher background N (>20 kg) with a turning point or heel in the response curves generally occurring between 15 – 22 kg N ha^{-1} yr^{-1}. These N deposition loads were broadly supported by the cluster analysis that studied change using species composition as the variable, however, in sand dunes and bogs species composition appeared sensitive at much lower levels of N highlighting that ecosystem change occurs across the N deposition range. This is reflected by some of the changes in seen in individual species that are poorly distributed across the datasets but typically found at the less polluted sites. The change in the frequency of presence or cover of some species may therefore be good indicators of N deposition even where a change in overall species richness is not observed.

Table 19 below summarises some of the key findings from the analysis of the vegetation datasets and supporting reviews of literature and experimental site work. The relationships found in the species richness, cover and individual species data will be carried forward to Task 5 where the effect of incremental increases in N deposition on the variables will be examined further. Other relationship exist with the review literature and the experiments as discussed in this chapter, however, where these were not found to be significant in the data analysed as part of this project they have not been carried forward.

Table 19: Summary of the key findings from the analysis of the vegetation datasets and supporting reviews of literature and experimental site work. [1]Details of the UKREATE experiments in this report is presented in Tasks 2, 3 and 4 summarised in Phoenix *et al* (2012). [2]For details of studies included in the literature review see Tasks 2 and 3.

Habitat	Response curve shape from data analysis	Supported by UKREATE experiments[1]	Literature[2]	Spp. richness LOESS max. sensitivity	Spp. composition Cluster analysis change range	Individual species
All habitats						
Species richness (SR)	linear	#	#	n/a	n/a	*Hylocomium splendens*
Upland heath					14-20 kg N	*Hylocomium splendens* *Deschampsia flexuosa*
Total SR	mild curvilinear		#	7-20 kg N		
Lichen SR	curvi-linear	#	#	7-16 kg N		
Graminoid SR	mild curvilinear			7-22 kg N		
Graminoid cover	mild curvilinear			>22 kg N		
Lowland heath					14-15 kg N	*Hylocomium splendens* *Cladonia portentosa* *Brachythecium rutabulum*
Total SR	mild curvilinear	#	#	< 17 kg N		
Moss SR	mild curvilinear	#	#	none		
Graminoid SR	mild curvilinear			none		
Graminoid cover	mild curvilinear			> 23 kg N		
Bog					10-13 kg N	*Cladonia uncialis* *Eriophorum vaginatum* *Sphagnum fimbriatum*
Total SR	linear			> 19 kg N		
Lichen SR	linear			none		
Forb SR	mild curvilinear			none		
Graminoid cover	linear	#		none		
Sand dune					5-8 kg N	*Hylocomium splendens*
Total SR	mild curvilinear					
Moss SR	strong curvilinear					
Forb SR	mild curvilinear					
Graminoid cover	mild curvilinear		#			

Habitat	Response curve shape from data analysis	Supported by UKREATE experiments[1]	Literature[2]	Spp. richness LOESS max. sensitivity	Spp. composition Cluster analysis change range	Individual species
Acid grassland					14-15 kg N	*Hylocomium splendens* *Hypnum cupressiforme* *Europhrasia officianalis* *Lotus corniculatus* *Carex panacea* *Nardus stricta*
Total SR	mild curvilinear		#			
Forb SR	linear		#			

6. Task 5: Determine the relative effect of incremental N

6.1 Introduction

The implications of the relationships between the response variables and nitrogen (N) deposition that were detailed within Task 4 are explored further within this task and the effect of incremental increases in long-term N deposition upon these response variables is considered.

6.2 Habitat specific difference in species richness along the survey gradients associated with different levels of N deposition

As described previously, the relationships between species richness and N deposition described by the spatial surveys have developed over many years, and the current rate of N deposition is primarily a proxy for this long-term cumulative N. Thus we would not expect that a change in N deposition, either increasing or decreasing, would immediately change species richness or composition. However, the spatial relationships described above can be examined to estimate how the species richness of different habitats has responded to different levels of long-term N deposition, as represented by differences in current N deposition. Recall from previously that a reduction in species richness does not necessarily mean that any species are 'lost' (see Figure 1), but that the frequency of some species is reduced.

This section 1) compares the difference in species richness for a 1 kg N ha^{-1} y^{-1} increment of long-term N deposition along the gradient studies, expressed as a reduction of percentage of the maximum number of species recorded in each habitat (Table 20**,** other increments are shown in appendix 5), 2) expresses the response relationship as the difference in long-term N deposition associated with a species richness reduction of one species along the gradient (Table 21). For reference, the current (2011) critical load for each habitat is included in the results tables and full details of critical loads for all habitats are provided in appendix 6 with a summary in the introduction to this report).

When the linearly related TU survey data are combined, 1.6% of the maximum number of species within each habitat is reduced with every incremental increases of 1 kg ha^{-1} yr^{-1} of long-term N deposition. When all the habitats are considered separately, the typically curvilinear response of species richness to N deposition produces sharp losses in diversity from well below the habitat-specific critical load ranges. However, even at levels of N deposition at and above the upper end of each habitat-specific critical load, the effect of a 1 kg increase of N is considerable and at the mid-point of the critical load range the losses and subsequent threat to habitat integrity from loss of sensitive species and increases in graminoid cover are considerable. For example, within the upland and lowland heath habitats in the TU 2009 survey, species richness is reduced by nearly 1.0 (around 2 % of the maximum species richness) for each 1 kg $ha^{-1}yr^{-1}$ increase in long-term N above the mid-point of the critical load range (15 kg N $ha^{-1}yr^{-1}$) and by 1.0 for each 2 kg increase (above 1 % of maximum) increase in N deposition well above the critical load: 25 kg N $ha^{-1}yr^{-1}$. The magnitude of change is less in the MRS Upland heath survey probably due to a different recording technique and the use of smaller survey quadrats due to the focus towards the lower plant species. These results from the heathland surveys reveal remarkably high losses in diversity in what are naturally low-diversity systems, typified by specialist low-nutrient plants and these losses highlight the vulnerability of this habitat to eutrophication by N enrichment.

The results from the other habitats follow a similar pattern of reductions in species richness as long-term N deposition increases. Sand dune ecosystems in particular appear to be strongly sensitive to N deposition with a very rapid loss of species diversity as N increases from below the lower end of the critical load range. Even when sand dune type is split between decalcified and calcareous, species richness reduces by 1.2 % species for every 1 kg increase in long-term N deposition above the upper end of the habitat specific critical load (15 kg N $ha^{-1}yr^{-1}$), equivalent to 1 a fall of 1 species for every 1.1 kg N $ha^{-1}yr^{-1}$. Moss diversity is particularly negatively related to N. Within the bog habitat, losses are less severe with species richness reducing by around 1 % for approximately every 3 kg increase in long-term N deposition across the range studied. This is likely due to the hydrology regime limiting species responses to N. The much larger acid grassland dataset (BEGIN) also showed reductions in richness to N and, due to a flatter response curve, these remain high with a 1 species drop in richness for approximately every 2 kg N increase above the upper end of the critical load range. Interestingly, when non-UK European grasslands are included (not included in this report) a curvilinear response is also apparent (Stevens *et al*., 2010).

Table 20: Summary of relationships between nitrogen deposition and species richness/cover by habitat expressed as a percentage of the maximum in a habitat. Change in species richness associated with a 1 kg ha^{-1} y^{-1} difference in long-term N deposition along the survey sites is shown. Modelled relationship only applied over N deposition range in which survey sites fell, where no sites were surveyed at a given N deposition level '-' is shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load (kg N ha^{-1} yr^{-1})	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 1 kg increase in long-term N deposition at different background N deposition levels					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
All habitats (TU 2009)								
Total species richness	77 spp.	10-20	-1.6 % of maximum number of species/kg N increase					
Upland heath (TU 2009)								
Total species richness	42 spp.	10-20	-5.7 %	-2.9 %	-2.0 %	-1.4 %	-1.2 %	-1.0 %
Lichen species richness	11 spp.	10-20	-5.4 %	-2.7 %	-1.8 %	-1.8 %	-1.0 %	-1.0 %
Graminoid species richness	7 spp.	10-20	-7.0 %	-2.9 %	-2.9 %	-1.4 %	-1.4 %	-1.0 %
Graminoid cover	n/a	10-20	-0.5 %	no change	+0.4 %	+0.8 %	+1.2 %	+1.6 %
Upland heath (MRS)*								
Total species richness	16 spp.	10-20	-3.4 %	-3.1 %	-2.5 %	-1.9 %	-1.3 %	-0.3 %
Lowland heath (TU 2009)								
Total species richness	37 spp.	10-20	-6.2 %	-3.5 %	-2.2 %	-1.6 %	-1.4 %	-1.0 %
Moss species richness	12 spp.	10-20	-5.8 %	-2.5 %	-1.7 %	-1.7 %	-1.7 %	-0.9 %
Graminoid species richness	9 spp.	10-20	-17.8%	-4.4 %	-2.2 %	-1.1 %	-1.1 %	-0.5 %
Graminoid cover	n/a	10-20	-0.6 %	no change	+0.5 %	+1.05 %	+1.6 %	+2.2 %
Bog (TU 2009)								
Total species richness	32 spp.	5-10	-0.9 % of maximum number of species/kg N increase					
Lichen species richness	6 spp.	5-10	-1.7 %					
Forb species richness	6 spp.	5-10	-7.7 %	-3.9 %	-2.6 %	-1.9 %	-1.6 %	-1.3%
Graminoid cover	-	5-10	+1.5 % cover/kg N increase					
Sand dunes (TU 2009, all sites)								
Total species richness	77 spp.	8-15	-10.1%	-2.6 %	-1.2 %	-0.6 %	-	-
Moss species richness	16 spp.	8-15	-21.3%	-5.0 %	-2.5 %	-1.3 %	-	-
Graminoid cover	n/a	8-15	+8.6 %	+ 2.2 %	+ 1.0 %	+ 0.5 %	-	-
Forb species richness	33 spp.	8-15	-10.3%	-2.4 %	-1.2 %	-0.6 %	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total species richness	77 spp.	8-15	-4.4 %	-2.2 %	-1.4 %	-1.0 %	-	-
Moss species richness	16 spp.	8-15	-21.3%	-5.6 %	-2.5 %	-1.3 %	-	-
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)								
Total species richness	77 spp.	8-15	-4.4 %	-2.2 %	-1.4 %	-1.0 %	-	-
Moss species richness	16 spp.	8-15	-8.9 %	-4.4 %	-3.1 %	-2.5 %	-	-

Survey/ Habitat/	Max. species richness	Habitat/species critical load (kg N ha^{-1} yr^{-1})	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 1 kg increase in long-term N deposition at different background N deposition levels					
Acid grasslands (BEGIN)								
Total species richness	42 spp.	10-15	-1.5 %	-1.4 %	-1.2 %	-1.1 %	-1.0%	-0.9%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

The incremental effect of long-term N on species richness reduces as deposition levels increase above the upper end of the critical load for each habitat due to the curvilinear nature of the relationship between N and species richness. However, the positive, curvilinear relationship between graminoid cover in the heathlands means that graminoid cover increases dramatically above the critical load. This outcome is of key importance to site integrity, particularly within heathlands which have been shown to be vulnerable to conversion to grassland, most notably in the highly N-polluted areas of the Netherlands. Within the bog habitat, graminoid cover (principally the sedge, *Eriophorum vaginatum*) was found to increase by 1.5% per additional kg N across the deposition range studied suggesting that the balance between shrubs, graminoid and moss (mainly *Sphagnum* spp.) is at risk of moving towards dominance by sedge species. A similar result was obtained from the sand dune survey data although the relationship with N was weaker and more strongly associated with pH. Nevertheless, other studies have found sand dune integrity vulnerable to increases in graminoid cover (Remke *et al*., 2009).

It is also important to highlight the differing results between surveys, particularly the TU 2009 Upland Heath Survey and the Moorland Regional Survey (MRS). The reason behind this is the different quadrat sizes used to measure species richness: the TU survey used 2 x 2 m quadrats whilst the MRS used 0.5 x 0.5 m quadrats. Both produce valid measures of species richness although the MRS was more focussed on lower plants. For this reason the TU 2009 survey provides the strongest data as the bigger quadrats capture more of a site’s biodiversity and therefore are more representative of the changes that occur across the dataset.

Table 21: Summary of relationships between long-term nitrogen deposition and species richness by habitat expressed as the amount of incremental N deposition (in kg N ha^{-1} yr^{-1}) associated with a reduction in species richness of one species along the survey gradient sites. Modelled relationship only applied over N deposition range in which survey sites occurred; where no sites were surveyed at a given N deposition level '-' is shown.

Survey/ Habitat/	**Max. species richness**	**Habitat/ species critical load kg N ha^{-1} yr^{-1}**	**Increase in N deposition (in kg N ha^{-1} yr^{-1}) required to reduce measured species richness by 1 at different background long-term N deposition levels**					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
Upland heath (TU 2009)								
Total species richness	42 spp.	10-20	0.4 kg	0.8 kg	1.3 kg	1.7 kg	2.0 kg	2.4 kg
Upland heath (MRS)*								
Total species richness	16 spp.	10-20	1.7 kg	2.0 kg	2.5 kg	3.3 kg	5.0 kg	20.0 kg
Lowland heath (TU 2009)								
Total species richness	37 spp.	10-20	0.4 kg	0.8 kg	1.3 kg	1.7 kg	2.0 kg	2.4 kg
Bog (TU 2009)								
Total species richness	32 spp.	5-10	3.3 kg					
Sand dunes (TU 2009, all sites)								
Total species richness	77 spp.	8-15	0.1 kg	0.5 kg	1.1 kg	2.0 kg	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total species richness	77 spp.	8-15	0.3 kg	0.6 kg	0.9 kg	1.3 kg	-	-
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)								
Total species richness	77 spp.	8-15	0.3 kg	0.6 kg	0.9 kg	1.3 kg	-	-
Acid grasslands (BEGIN)								
Total species richness	42 spp.	10-15	1.7 kg	1.7 kg	2.0 kg	2.0 kg	2.5 kg	2.5 kg

*in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

Table 22: Summary of relationships between long-term nitrogen deposition and species cover (C) or probability of presence (P) by habitat expressed as a percentage of the maximum in a habitat. Difference in species richness associated with a 1 kg ha^{-1} y^{-1} difference in long-term N deposition along the survey sites is shown. Modelled relationship only applied over N deposition range in which survey sites fell, where no sites were surveyed at a given N deposition level '-' is shown. When the relationship between N and species richness was not significant 'ns' is shown.

Habitat (Survey) /Species	**Max cover/ presence (no. of quadrats)**	**Change in species cover expressed as a % of maximum species cover recorded in habitat with a 1 kg increase in long-term N deposition at different background N deposition levels**					
		5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
Upland heath (TU 2009)							
Hylocomium splendens cover (C)	73	-2.0 %	-1.6 %	-1.2 %	-0.8 %	-0.4 %	-0.1
Deschampsia flexuosa (C)	37	-0.3 %	0.1 %	0.5 %	0.9 %	1.3 %	1.7
Upland heath (MRS)*							
Hylocomium splendens presence (P)	5	-1.3 %	-0.4 %	-0.2 %	-0.1 %	-0.1 %	-0.04
Campylopus introflexus (P)	2	0.0 %	0.02 %	0.04 %	0.07 %	0.10 %	0.13
Lowland heath (TU 2009)							
Hylocomium splendens (C)	31	-4.0 %	-1.1 %	-0.5 %	-0.3 %	-0.2 %	-0.1
Hylocomium splendens (P)	5	-0.4 %	-0.2 %	-0.1 %	-0.1 %	-0.1 %	-0.1
Cladonia portentosa (C)	11	-0.7 %	-0.3 %	-0.2 %	-0.2 %	-0.1 %	-0.1
Cladonia portentosa (P)	5	-0.5 %	-0.3 %	-0.2 %	-0.1 %	-0.1 %	-0.1
Brachythecium rutabulum (P)	5	0.0 %	0.1 %	0.1 %	0.2 %	0.2 %	0.3
Bog (TU 2009)							
Cladonia uncialis (C)	1	-0.1 %	0.0 %	0.0 %	-0.01 %	-0.01 %	-0.01
Cladonia uncialis (P)	4	-0.8 %	-0.2 %	-0.1 %	-0.06 %	-0.04 %	-0.03
Eriophorum vaginatum(C)	65	1.5 %					
Sphagnum fimbriatum (C)	1	0.0 %	0.0 %	0.0 %	0.01 %	0.01 %	0.01
Sphagnum fimbriatum (P)	3	0.2 %	0.1 %	0.1 %	0.04 %	0.03 %	0.03
Sand dunes (TU 2009 all sites)							
Hylocomium splendens (C)	30	-3.6 %	-1.0 %	-0.4 %	-0.3 %	-	-
Acid Grasslands (BEGIN)							
Hylocomium splendens (C)	11	-1.4 %	-0.4 %	-0.2 %	-0.1 %	-0.1 %	0.0
Hypnum cupressiforme (C)	19	0.2 %					
Nardus stricta cover (C)	42	0.3 %					
Carex panacea cover (C)	13	0.1 %					
Euphrasia officianlis cover (C)	1	-0.1 %	-0.1 %	0.0 %	0.0 %	0.0 %	0.0
Lotus corniculatus cover (C)	11	-0.2 %	-0.1 %	-0.1 %	-0.1 %	0.0 %	0.0

6.3 Applicability of this work to pollutant (NO_x and NH_3) concentrations and critical levels

The work in this chapter has focused upon the relationship between nitrogen deposition, critical loads and species richness, however, it is recognised that the concentration of a pollutant and its critical level may also influence species responses. Critical levels were identified in order to protect particular species or groups of plants, for example the critical level for NH_3 is 3 μgm^{-3} for vascular plants but 1 μgm^{-3} for lower plants such as lichens. By contrast critical loads are habitat specific.

Nitrogen deposition data is based on measured concentration data (for wet deposition, ion concentrations in precipitation and the amount of rainfall, and for dry deposition, gas concentrations in air, measured at a specified height, usually 1.5 m from the ground surface, which represent an average over a defined period). Thus deposition reflects pollutant concentration and over the longer-term, vegetation responses to changes in deposition would be comparable to changes in pollutant concentrations of a similar magnitude. It would therefore be reasonable to use the data in this chapter to approximate the response of vegetation to a percentage increase in concentration and to compare responses between changes in long-term deposition and long-term mean concentrations. This could be done by converting an increment in concentration to an increment in N deposition. However, this would only be relevant over the longer-term, and it is important to understand that the differing effects between concentration and deposition over time are unclear. High pollutant concentrations in particular may be very damaging, especially for lower plants (Pearce and van der Waal, 2008).

At present, air concentrations of dry deposited gases are regulated through critical levels. Gaseous NH_3 and NO_x concentrations can be measured relatively easily using passive samplers, normally exposed for one month, so that routine monthly measurements can be made to estimate an annual mean. However, the conversion of a gas concentration to an N load is not straightforward, as deposition velocity varies by species group, and meteorological conditions also affect deposition. In addition, the precise positioning of a new or expanding installation would also influence the frequency of high concentrations.

Much experimental evidence concerning the responses of a number of ecosystem types to changes in nitrogen deposition, mainly in form of wet NH_4NO_3, is available and we are confident that nitrogen deposition is in many cases the strongest driver of the changes in species richness and composition found in the survey data. However, the interactive effects of pollutant concentration and deposition are unclear and within the current report it was not the intention to attribute responses to specific forms of pollutant or changes in modelled concentration owing to co-correlation between these variables and the difficulty in separating out these across the survey sites.

Field experiments investigating the response of ecosystems to changing concentrations in wet deposition are rare and no contemporary experiments have studied the response of semi-natural ecosystems to changes in dry deposition of NO_x at realistic concentrations, however, one notable UK experiment has studied the response of bog vegetation to gaseous NH_3. The CEH Edinburgh Whim Bog experiment adds wet nitrogen deposition in oxidised and reduced N forms and dry-gaseous N deposition in the reduced form as NH_3 to a raised bog consisting mainly of ericoids, *Sphagnum* and cotton grass vegetation (Leith *et al*., 2004; Sheppard *et al*., 2004). Per unit N deposited, gaseous NH_3 has a much greater effect on soils and vegetation in comparison to similar deposition of the wet forms of N (Sheppard *et al*., 2011). The stronger responses to gaseous NH_3 are thought to be linked to effects on the foliage which may in part reflect the intermittent high concentrations, although deposition is not linearly linked to concentration (Jones, 2006) and applying the critical level

of ammonia (1 µg m^{-3}) to the bog provides greater protection than the critical load (5-10 kg N ha^{-1} y^{-1}).
In conclusion, caution should be applied when using the approach developed in this report to legislate for small incremental increases in pollutant concentration as the incremental responses developed within this report are not directly comparable between deposition and concentration and the level of uncertainty from a direct conversion of load to level would be quite large. Projected increases in deposition are more appropriate in understanding the likely long-term change and mean levels of concentration could be converted to deposition to give an indication of the changes that would occur over many decades. However, particular care should be taken where installations are likely to produce high levels of a pollutant over short-timescales as these may be very damaging to vegetation within close proximity to the source.

With the exception of the Whim Bog facility, dose response relationships to changes in N concentration are not fully understood and should be further researched experimentally. Further work on the datasets used in this report could also be carried out to study responses to changes in NH_3 concentration and deposition based on forthcoming 1 km gridded modelled pollutant datasets and the effect on bog vegetation based upon current experimental evidence. Given the commonalities between soil type and vegetation, this could also be used to experimentally support responses seen in some heathland systems and it may be possible to produce similar incremental relationships to those found with N deposition.

6.4 Summary

Even relatively small increases in long-term N deposition of 1 - 2 kg N $ha^{-1}yr^{-1}$ were found to have an impact on species richness across all habitats with the sand dune habitat appearing the most sensitive at low levels of N and the bog habitat the least. As N deposition increased upwards through the critical load range the rate of fall in species richness lessened but still existed and within the gradient of UK N deposition responses were still marked. These changes in rate of response reflected the curvi-linear relationships that were developed in Task 4.

Contrasting the falls in species richness, graminoid cover increased markedly with long-term N deposition and highlighted a potential threat to site integrity in the sand dunes, bogs and heaths. In the latter, cover increased exponentially and at some sites was above a level likely to cause concern and tip the balance between shrubs, lower plants and grasses.

The impacts illustrated in this chapter are calculated from the modelled relationships found in chapter 4. Only the relationships that were statistically significant were used to consider the impact of incremental N and in the most part these relationships were strong, however, with the exception of the acid grassland habitat, only 25-30 sites were visited within each habitat and this has produced some scatter within the data which is to be expected given the heterogeneous nature of site vegetation. The fact that the relationships found *were* so strong demonstrates the strength of the nitrogen signal in the data and if more sites were visited it is likely that the strength of the relationship would increase further.

The measures of species richness used in calculating the incremental effect of long-term N were obtained from a specific survey methodology that was consistently applied across all sites. The relationships produced are not rigid and they are not intended to be a precise prediction of the impact of incremental N although the direction of the impact of N (usually negative), the relative magnitude of the response and the shape of the response (often curvi-linear) would not be expected to change across an alternative selection of sites. In addition, many factors that impact biodiversity vary across the sites surveys including climate and other pollutants such as sulphur and these may also be correlated with changes in species richness. It is important to remember that these, and the relationships used in this report are based upon correlations and which does not imply causation, however, the findings of this work are also supported by significant literature on the subject and work from experimental sites which control for N addition.

The data used in this chapter illustrates what the effect of long-term N deposition has been, and could be used in the assessment of the relative effects of incremental increases in N over the long-term from new sources at different background levels of N deposition. The impact of N on individual species should be more cautiously used as many factors may influence the response of a species at a particular site and the data on individual species within the surveys was limited.

7. Task 6: Applicability of results to other habitats with limited dose-response information

7.1 Introduction

This report has studied the responses of vegetation to long-term N deposition within data from five semi-natural UK habitats: acid grasslands, upland heath, lowland heath, bog and sand dunes, however, evidence suggests that other important UK habitats are also negatively affected by N. Task 6 will consider whether the results and relationships presented within this report can be reasonably applied to other habitats given similarities in soil type and vegetation. Focus will be given to Calcareous grasslands, vegetated shingle, fens and deciduous woodlands.

7.2 Comparisons of responses between habitats

Reductions in total species diversity were found in all the habitats studied in this report. Figure 15 below compares the response curves within each based upon the percentage of the maximum number of species at a given N deposition. Both heaths showed similar response gradients, and this reflects the changes in species richness illustrated in Task 5.

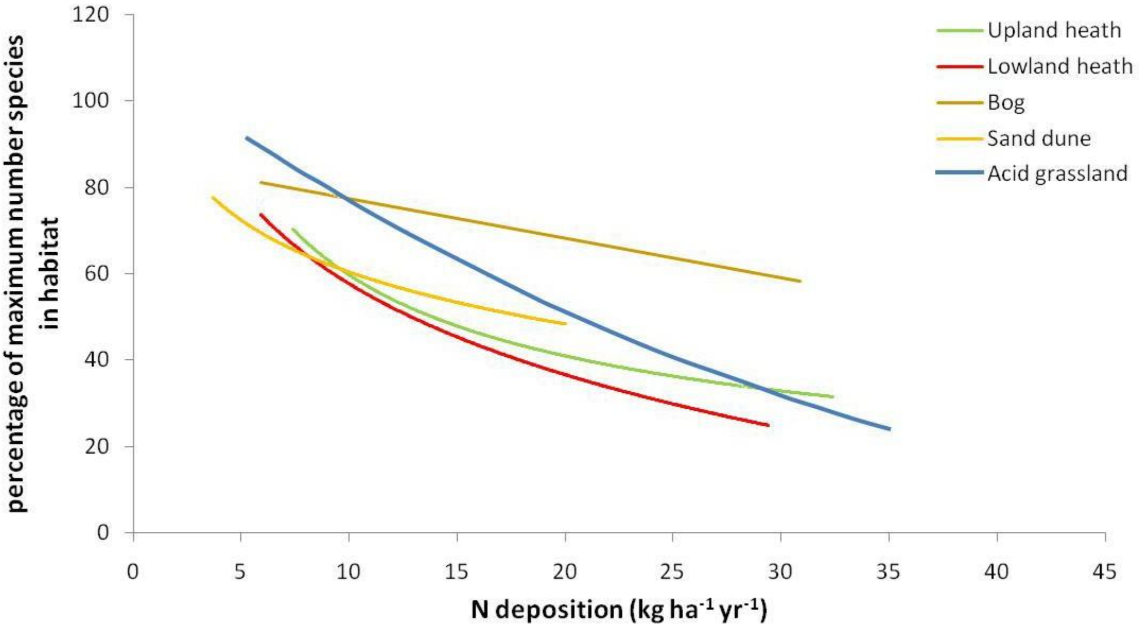


Figure 15: Modelled response curves showing the rate of change in species richness across the habitats studied as part of the TU 2009 multi-habitat survey.

Acid grasslands show a similar magnitude of response as the heaths, albeit less curvilinear, perhaps reflecting similarities in acidic, humus soil types. Changes in species richness in the bog habitat are shallower, indicative of the strong effects of hydrology limiting the response to N and a slightly less diverse habitat than the others. Sand dune response occurs more rapidly initially, then shallow over a much smaller range than the other habitats.

Whilst there is variability between the responses of the different habitats, the general magnitude of response is similar and when all the above data is considered together, as in Tasks 4 and 5, species richness reduces by 1.6% per 1 kg increase in long-term N. This broad approach could be used in similar habitats to those studied in this report, however, would be unsuitable for habitats which do not show change in species richness. An example of the latter would be calcareous grasslands where survey work has found that species richness does not appear affected by N deposition but species composition does change and the frequency of rare or scare plants reduces.

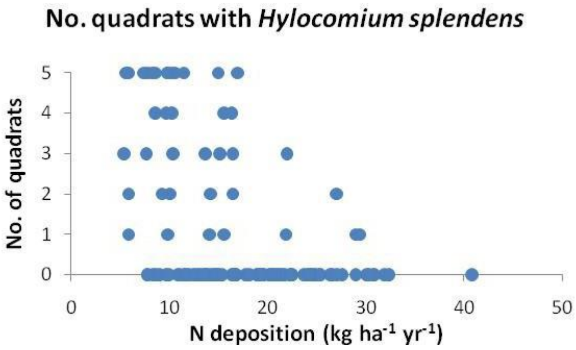


Figure 16. The presence of *Hylocomium splendens* across the habitats studied as part of the TU 2009 multi-habitat survey.

Task 3 showed that changes in overall diversity were often driven by changes in specific functional groups. Within upland heaths the reductions were apparent in total species richness, moss and lichens; in lowland heaths total species richness only; sand dunes moss species richness was strongly affected; in bogs forbs and lichens reduced and in acid grasslands forbs showed the strongest response. The lower plants, where present in significant numbers, are often the most sensitive to N. Of these, the moss *Hylocomium splendens* showed a remarkably consistent negative response to N across all the habitats except bogs, see Figure 16**,** with an abrupt reduction in probability of presence (number of quadrats the species was found in) above 17 kg N ha^{-1} yr^{-1}. The lichen *Cladonia portentosa* was also consistently negatively associated with N deposition in both upland and lowland heath sites and the bog survey.

7.3 Deciduous broadleaf woodland

Elevated nitrogen deposition has driven strong biogeochemical responses in woodlands with many authors documenting reductions in soil CN, acidification and increased nitrate leaching (Dise and Wright, 1995; Emmett *et al*., 1998; Dise *et al*., 2009). However, the impact of N deposition on vegetation composition is poorly understood partly due to the strong influence that tree canopy structure places on ground flora through inception of light, rainfall and pollution and the effect of woodland management and nitrogen deposition upon this structure.

Nevertheless, work has demonstrated that understory plants such as bryophytes, lichens and forbs can be negatively affected by N. Studies of mixed woodlands around four Scottish intensive livestock units showed marked changes in species composition within 300 m downwind of the units (Pitcairn *et al*., 1998; Pitcairn *et al*., 2009), the grasses *Deschampsia flexuosa* and *Holcus lanatus* increased in abundance close to the units as did the shrub *Rubus idaeus* and the forb *Urtica dioica*. Mosses in general were found to decrease in abundance downwind of the farm as did the forbs *Oxalis acetosella*, *Galium odoratum*, *Potentilla erecta* and *Dactylorhiza fuchsii*. A much broader scale survey of 103 woodlands in 1971 and revisited in 2001 found that overall species richness was unaffected by N but changes in composition were found with some species responding positively to N (*Poa nemoralis/trivialis, Galium aparine, Allium ursinum, Athyrium filix-femina, Carex pendula, Urtica dioica*) and others negatively (*Deschampsia flexuosa, Agrostis capillaris, Ajuga reptans, Holcus lanatus, Pteridium aquilinum, Vaccinium myrtillus*). The lack of an overall response in species richness was attributed to three main reasons: 1) much woodland ground flora tends towards the upper and middle of the Ellenberg spectrum; 2) impacts on woodlands may be from localised ammonia sources and unapparent over a national N gradient and 3) the interaction of canopy shading damping responses of the lower plants to N (Kirby *et al*., 2005).

Experimental work in Sweden well summarised by Cunha *et al*. (2002) found that N addition altered the composition of species towards *Deschampsia flexuosa* and ruderal species. In addition bryophyte abundance changed with increases in some *Brachythecium* species and reductions in others including *Hylocomium splendens*. These effects are similar to those found in the datasets studied in this report. Other studies have shown detrimental effects of N deposition on growth of bryophyte species *Isothecium myosuroides, Dicranum scoparium, Frullania tamarisci* in transplant experiments between Atlantic Oak woods (Mitchell *et al*., 2004) and shifts in species composition of epiphytic lichens between nitrophytes and acidophytes (Sutton *et al*., 2009).

A recent study has attempted identify the contribution of N deposition to vegetative change in addition to changes in woodland structure and age. Verheyen *et al*. (2012) studied data from over 1200 vegetation plots and found a shift towards shade tolerant and nutrient demanding species, however, N deposition did not explain these responses. Verheyen *et al* (2012) concluded that the effects of N deposition could be obscured by changes in the tree canopy and highlighted a potential N 'time bomb' which could explode when the canopy opens up again.

Some of the species responses highlighted by the above studies showed a significant response in the survey datasets in this report including the grass *Deschampsia flexuosa* which increased in cover in upland heaths supporting the findings by Pitcairn *et al*. (1998) but contradictory to Kirby *et al*., (2005), and the mosses *H. splendens* and *Brachythecium* species which showed respective decreased and increased in presence. This lack of an overall relationship between species richness and N deposition makes it difficult to assume a dose-response relationship to broad-scale N deposition in woodlands over a national gradient, however, it seems likely that the edges of the woodlands are likely to be more strongly affected by a nearby pollutant source such as an intensive livestock farm (Kirby *et al*., 2005).

7.4 Vegetated shingle

Vegetated shingle is an important habitat for conservation in the UK (Natural England, 2011) yet there is limited knowledge of its responses to N deposition and no experimental data from this community is available for analysis. Vegetated shingle community species composition shifts from pioneer species close to the sea shore able to tolerate high salinity and sea spray to more stable gravel communities consisting of grassland with important moss and lichen assemblages (UK BAP, 2008). In the survey datasets studied in this report the closest analogue are the acidic dune grasslands (sites with pH <6.5) which share their dry, acidic nature with the gravel communities of vegetated shingle.

Results from analysis of the acidic dune grasslands in this report suggests that nitrogen deposition (in the form dry-oxidised N) alongside climate plays an important role in determining species composition but no overall relationship between species richness and N deposition was found. This lack of a relationship between N and species richness is likely due to the limited number of acidic-dune sites that were surveyed (only 9). However, a recent study of 19 coastal dunes around the Baltic Sea on acid soils found that high N deposition increased growth of the sedge *Carex arenaria* and reduced the species richness of lichen, grass and forb species (Remke *et al*., 2009). These responses were strongest in the sites with the lowest pH suggesting the influence of acidification on species richness and the ability for *C. arenaria* to dominate under these conditions. The acidic-dune grassland survey data within this report showed that cover of *C. arenaria* appears to increase with N deposition although the number of data points is limited and the relationship non-significant. Moss species richness was most strongly correlated with Sulphur (S) deposition (in dunes with pH <6.5) and a correlation with N deposition was almost significant; in general a greater number of moss species were present at lower levels of N deposition. As discussed elsewhere in this report it is difficult to ascertain if this relationship with S is ecologically significant, however, both N and S deposition are likely to increase acidity and may be responsible for the decline in moss species richness and concurrent increases in *C. arenaria*.

Whilst caution should therefore be applied in attempting to extrapolate relationships between species richness and N deposition from the sand dune survey data presented it this report, it would seem reasonable to assume that the widespread reductions in species richness observed across all habitats, particularly in lower plant species, would also occur in vegetated shingle, especially above the recommended critical load range of 8-15 kg ha^{-1} yr^{-1}.

7.5 Fens

Fen nutrient budgets are characterized by inputs and outputs of nutrients via groundwater and surface water, and are tightly linked with local hydrology. The extent to which these systems receive and lose nutrients with in- and out-flowing water determines for a large part their sensitivity to excess N (ECE, 2010). Open wetland ecosystems such as floodplain fens would be expected to show little sensitivity to deposition of atmospheric N, whereas the impact on fens with a closed N cycle is likely to be much more significant. Fens with lowered water tables, as a result of drainage or over-abstraction, may also exhibit increased nutrient availability through decomposition of surface layers following drying, so knowledge of hydrological status of sites is important in assessing impact and risk.

Fens are found across a wide range of base cation and nutrient levels, from acid to strongly alkaline, and from oligotrophic to eutrophic. In all of these fen types, elevated N deposition has been found to increase cover of vascular plants including graminoids and dwarf shrubs and reduce cover of bryophytes (ECE, 2010). The vegetation of acidic, oligotrophic fens closely resembles the bog habitat studied in this report however; the critical load for this habitat has been estimated to be higher at 10-15 kg N ha^{-1} yr^{-1} compared with 5-10 kg N ha^{-1} yr^{-1} for bogs, due to the assumed higher buffering capacity of these minerotrophic fens. It has been recommended that the upper end of this range is used for soligenous, acidic valley mires, while the lower end of this range is used for quaking bogs and transition mires (ECE, 2010), which are in many cases functionally ombrotrophic systems.

Experimental work on a mesotrophic fen in Ireland (Verhoeven *et al*., 2011) has demonstrated significant responses to N additions of 35 and 70 kg ha^{-1} yr-^{1} on top of a low background N of 4-8 kg N ha^{-1} yr-^{1} and particularly to reduced-nitrogen. In these plots, vascular plant biomass increased strongly (from 170 g m^{-2} to 340 gm^{-2}) and bryophyte cover reduced considerably (from 350 g m^{-2} to 60 g m^{-2}) as did bryophyte species richness (from an average of 7 to 4). The authors attributed these changes in bryophytes to a combination of increased vascular plant cover and the direct toxic effect of ammonia. Other studies have also found N related increases in vascular plant biomass and shifts in vegetation composition in both mesotrophic and oligotrophic base-rich Dutch fens (Verhoeven and Schmitz, 1991; Verhoeven *et al*., 1996; Paulissen *et al*., 2004). Only limited evidence is available for the impacts of N on base-rich fens and the recommended critical load spans a wide range (15-30 kg N ha^{-1} yr-^{1}). The lower end of this range is recommended for oligotrophic types, such as montane fens,

These responses found in fens closely mirror those found in the bogs habitat survey and by the Whim Bog experiment discussed earlier in this report. It would seem reasonable therefore, given strong similarities in vegetation composition, soil type and hydrological regime to apply the relationships found in the bog survey data also to oligotrophic and mesotrophic fens, particularly in reference to changes in bryophyte, lichen and sedge cover and species richness around intensive livestock units with the caveat that the slightly higher pH may offer marginally greater protection from acidification, however, not from eutrophication.

8. Discussion and overall conclusion

The objective of this report was to determine the effects of incremental increases in long-term nitrogen deposition on species composition and richness for a range of different habitat types. This was carried out by examining recent vegetation survey data in order to understand the relationships that exist between species composition and richness and nitrogen (N) deposition.

Tasks 1 and 2 studied the available datasets and sought other supporting data that existed from N addition experiments and in recent published literature. The survey data chosen consisted of data from 226 sites, across 8 surveys and 5 UK priority habitats encompassing the Terrestrial Umbrella (TU) 2009 multi-habitat survey, the BEGIN UK Acid Grassland dataset, the 2006 TU Moorland Regional Survey (MRS) and a 2002 Sand dune survey.

Task 3 then used statistical techniques to understand the ecological responses within the survey data for each habitat, be it changes in overall species composition, species richness, functional groups or individual species abundance, and related these to key environmental variables including climate and pollutant deposition data. Table 23 below summarises the responses variables that were significantly related to nitrogen deposition resulting from this task.

Table 23: Summary of the response variables found during the statistical analysis of vegetation datasets in Task 3 that were significantly related to atmospheric nitrogen deposition. MRS = Moorland Regional Survey.

Response variable	Acid grassland	Bog	Upland heath	Lowland heath	Sand dune
Species composition	#	#	#	#	#
Total species richness	#	#	#	#	#
Bryophyte species richness			# (MRS only)	#	#
Lichen species richness		#	#		
Forb species richness	#	#			#
Graminoid species richness			#	#	
Graminoid cover		#	#	#	#

Task 4 examined the nature of the relationship between total species richness, the relevant functional groups and key individual species and N deposition. In many cases a strong, curvi-linear relationship existed between N and the response variables. This means that sites located in areas of low background N deposition responded to additional nitrogen with a greater fall in species richness than sites located in more polluted parts of the country. However, contrasting this, graminoid[2] cover *increased* with increasing N deposition in bog, heath and sand dune habitats. Depending on the specific graminoid species affected, and the balance between graminoids and other functional groups, this could have a negative effect on the condition of the site and prevent the site achieving its conservation objectives. This task also examined the data for levels or ranges of pollution over which an ecosystem appeared to be more sensitive and whilst these results are difficult to interpret it was

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[2] Graminoid functional group includes species from the grass, sedge and rush families.

apparent that much ecological change occurred between approximately 14 to 23 kg N ha^{-1} yr^{-1}.

Task 5 used the relationships developed within Task 4 and quantified them in terms of change per *x* kg long-term N. This information could be used to understand the likely effect of additional increments in long-term nitrogen deposition (e.g. from a new pollution source) and assist with decisions making under the planning and/or environmental permitting regimes. It was apparent that even though a curvi-linear response dominates the relationship between the response variable and N deposition, significant falls in species richness were modelled for increases in long-term N deposition levels above the upper end of the critical load. Similarly, the positive relationship between graminoid cover and N in the sand dune, heath and bog habitats was reflected by marked increases in cover of grasses and sedges at the higher levels of long-term N. These simultaneous events may be interactive, with graminoids (and shrubs to some degree) enjoying a competitive advantage as N increases and shading out forbs and lower plants, or be a direct toxic effect of N on the lower and less nutrient-tolerant plants.

Consequently, the data suggests that habitat quality is affected across the UK N deposition range. The decline in species richness commences at the low end of the N deposition range and by upper end of the critical load range a substantial loss has already occurred. This reduces the inherent biodiversity of habitats through the loss of more sensitive and rare species. At higher loads of long-term N deposition beyond the critical load range, the integrity of sites may be threatened by graminoid domination and structural change to the habitat. Furthermore, all of the data sets examined as well as the reviewed published studies, show that at high rates of long-term N deposition, above for example 25 kg N ha^{-1} yr^{-1} (i.e. beyond the upper range of all critical loads of the communities addressed in this report) there is significant decline in species richness. Table 24 below summarises the relationships found in the vegetation datasets in Task 4 and indicates where these findings are supported by N addition experiments and the literature reviewed in this report. It should be highlighted that many of these responses are also supported by the broader scientific literature.

Table 24: Summary of the key findings from the analysis of the vegetation datasets and supporting reviews of literature and experimental site work. [1]Details of the UKREATE experiments in this report is presented in Tasks 2, 3 and 4, summarised in Phoenix *et al* (2012) and additionally in the literature cited in the table below. [2]For details of studies included in the literature review see Tasks 2 and 3 and the references in the table below.

Habitat	**Response curve shape from data analysis in this report**	**Direction of change**	**Supported by** UKREATE experiments[1]	Literature[2]
All habitats				
Total species richness (SR)	linear	↓	#	#
Upland heath				
Total SR	mild curvilinear	↓	*lichens and bryophytes only*	Edmondson *et al*, 2010; Stevens *et al*, 2009; Maskell *et al*, 2010; Payne *et al*, 2014
Lichen SR	mild curvilinear	↓	Carroll *et al*, 1999; Pilkington *et al*, 2007	Southon *et al*, 2013; Field *et al*, 2014
Graminoid SR	mild curvilinear	↓	*no*	Southon *et al*, 2013; Field *et al*, 2014
Graminoid cover	mild curvilinear	↑	*no*	Southon *et al*, 2013; Field *et al*, 2014

Habitat	Response curve shape from data analysis in this report	Direction of change	Supported by UKREATE experiments[1]	Literature[2]
Lowland heath				
Total SR	mild curvilinear	↓	*no*	Southon *et al*, 2013; Field *et al*, 2014
Moss SR	mild curvilinear	↓	*no* *(but lichen cover reduced)*	
Graminoid SR	mild curvilinear	↓	*no*	Southon *et al*, 2013; Field *et al*, 2014
Graminoid cover	mild curvilinear	↑	Barker *et al*, 2004	Southon *et al*, 2013; Field *et al*, 2014
Bog				
Total SR	linear			
Lichen SR	mild curvilinear	↓	*cover only* (Sheppard *et al*, 2011)	Field *et al*, 2014
Forb SR	mild curvilinear	↓		
Graminoid cover	linear	↑	(Sheppard *et al*, 2011)	Field *et al*, 2014
Sand dune				
Total SR	mild curvilinear	↓	*no*	Jones *et al*, 2004; Field *et al*, 2014
Moss SR	strong curvilinear	↓	*biomass only* (Plassman *et al*, 2009)	Remke *et al*, 2009; Field *et al*, 2014
Forb SR	mild curvilinear	↓	*no*	Remke *et al*, 2009; Field *et al*, 2014
Graminoid cover	mild curvilinear	↑	*no*	Jones *et al*, 2004; Remke *et al*, 2009
Acid grassland				
Total SR	curvi-linear	↓	*no*	Stevens *et al*, 2004; Maskell *et al*, 2010; Stevens *et al*, 2010
Forb SR	linear	↓	*no*	Stevens *et al*, 2006

Some individual species appeared to show a response at a specific point in the N deposition range, for example presence of *Hylocomium splendens* declined sharply above 17 kg N ha^{-1} yr^{-1}, whilst overall species richness changed more gradually. It is possible that many more species have a range of N pollution over which they can thrive up to a particular deposition load, however, the relatively small datasets used in this analysis has meant that some of the rarer species within each habitat are present at only a small number of locations. In these cases it was not possible to develop a mathematical relationship with N but each individual species contributed to an overall change in species composition and gradual fall in species richness. The relatively small datasets mean that caution should be applied when drawing conclusions on site integrity based on the presence or absence of individual species and that this information be used in conjunction with changes in species richness and composition.

Equally, some species groups responded in certain habitats (see Table 21) but not others. The reasons for these differences are not immediately obvious as many factors interact to govern how a habitat or species responds. In some cases the effect of a pollutant may be direct, for example a particular plant may be intolerant of N, and in others it could be a competitive interaction as discussed above. In addition to eutrophication and its fertilisation effect, N deposition can also acidify the soil. This could cause a response in rooted plants (and less in bryophytes and lichens), particularly in the poorly-buffered acidic habitats and less so in well-buffered calcareous habitats.

Due to a lack of root structure the lower plants are more directly responsive to current N and are likely to respond quickly to increases in pollution, whilst changes in the dominant species present within the vascular plant community are likely to occur more slowly in response to changes in soil N. Management interaction such as grazing can also alter the competitive interaction between lower plants and faster growing higher plants through competition for light. The relationships determined in this report were based upon modelled recent annual nitrogen deposition, and no attempt was made to consider long-term cumulative N deposition which occurs over many years. Whilst current day N deposition can be used as a good proxy for long-term deposition and gives a strong indication of changes with regard to N deposition, it would be advised to further consider pollution over the longer-term. However, the overall findings of this report would not be expected to change dramatically if cumulative N deposition is used instead of present day N deposition.

These alternative mechanisms for change mean that species richness is a better indicator of N deposition in some habitats and changes in species composition more suitable in others. An example of the latter is the Calcareous Grassland habitat where existing survey work (Van den Berg *et al*., 2010) has suggested that species richness is not affected by increasing N but found changes in species composition and the less presence of rare or scarce species as N increases. New data studying the Calcareous Grassland habitat has been obtained as part of recent survey work by the BEGIN project and this should be reviewed to develop understanding further.

Whilst the general trend in reducing species richness as N increases holds true across the habitats that were studied in this report, not all of the habitats behaved in the same way. The bog habitat is probably affected more strongly by site hydrology whilst in sand dunes, precipitation and decalcification were the more dominant drivers. For bogs, this means that the species richness response to N is buffered by the hydrological status and the response curve is shallower per unit N than the habitats that are more freely drained. The approach used to predict the response to incremental N can still be used, however, sites with lower rainfall may be more sensitive to N and the relationships expressed in this report for the bog habitat should be regarded as conservative. For sand dunes, site location and rainfall drive acidity with the more acidic sites being less biodiverse. This situation is complicated by the fact that N (and sulphur) deposition can also acidify a habitat. The relationships found in Task 5 can still be used to understand the likely impact, however, limited data is available for sites with a pH less than 6.5 and a conservative approach would be to use the relationships obtained for the largest datasets. These are the TU 2009 all site dataset and the combined TU 2009 and 2002 surveys.

Task 6 used the relationships developed from the survey data and considered if they may be reasonably applied to habitats where significant data is not currently available. Many UK ecosystems share similarities in species and soil type and it seems likely that where this is the case similar responses to those found within this report would occur. However, local site conditions, management interactions affecting canopy structure, and natural variation within a habitat should be carefully considered when applying these relationships to a new habitat. Gaps in data do exist and mean that there remain large habitat types in the UK where the impact of N deposition is not fully understood, for example, woodlands, fens, vegetated shingle and mesotrophic grasslands and further work. Experimentally work and gradient studies should be performed to understand the changes that occur with increases in N. The incremental effect of changes in pollutant concentration is also not fully understood as the differing effects between concentration and deposition over time are unclear. High pollutant concentrations in particular may be very damaging, especially for lower plants and these should be further researched experimentally. Further work on the datasets used in this report could also be carried out to study the evidence of response to changes in NH_3 concentration and deposition based upon current experimental work.

The overall goal in the management of pollution deposition levels should be one of reduction but it should be stressed that lowering current N deposition may not reverse the declining trend in species richness. Indeed it is likely that lowering current N deposition may only slow the decline in species richness. Considerable N remains stored within the soil and management such as cutting or burning may only remove small amounts of the N pool. However, as the rate of decline may be slowed by a reduction in N, management may help tip the competitive balance in favour of lower plants that are not directly affected by the pollutant.

The effects of N deposition extend beyond its impact on biodiversity and species composition. Many experiments have demonstrated an impact on soil biodiversity, ecosystem services and the onset of leaching. Depending upon the ecosystem studied and the timescale of deposition, these responses can have broader implications upon water quality and aquatic systems. The focus of this report has been the study of botanical datasets, further work should be carried out to quantify the effects on incremental N on soils and biogeochemistry. The relationship between N concentration and ecosystem response is poorly understood and further work should be carried out experimentally to develop our knowledge.

The main weaknesses of the analyses performed in this report fall in two main areas. Firstly, due to the time-consuming survey methods used to obtain the data, and with the possible exception of the acid grassland habitat, the size of the datasets is inevitably limited. However, the fact that N deposition still comes through the analysis reflects its strength as a driver of change. Secondly, across the large north-south pollution gradient that exists in the UK a similar climatic gradient also occurs, with cooler, wetter sites in the north and warmer, drier sites in the south. The design of the surveys and choice of site locations attempted to cross these climatic boundaries as much as possible within a given habitat type by also choosing cooler, dryer sites and warmer, wetter sites. However, in a gradient survey it is difficult to completely separate the simultaneous and interactive effects of climate and pollutant.

Overall, in all of the analysis of species composition and species richness, N comes through as a strong driver of change and in many cases is the strongest driver. The fact that this does happen adds considerable assurance to the belief that N is driving considerable change within our semi-natural habitats. This is supported with many years of experimental manipulation of N with climatic change controlled for within the main habitats studied. This provides confidence in using the data presented in Task 5 of this report to understand the relative effects of incremental increases in N over the long-term from new or existing sources at different background levels of N deposition.

References

Asman, W. A. H., B. Drukker and A. J. Janssen (1988). "Modelled historil concentrations and depositions of ammonia and ammonium in Europe." Atmospheric Environment 22: 725-735.

Barker, C.G., 2001. The impact of management on heathland response to increased nitrogen deposition. PhD Thesis, Imperial College, London.

Barker, C. G., S. A. Power, J. N. B. Bell and C. D. L. Orme (2004). "Effects of habitat management on heathland response to atmospheric nitrogen deposition." Biological Conservation 120(1): 41-52.

Birks, H. J. B., and Gordon, A. D. 1985. Numerical methods in Quaternary pollen analysis. Academic Press, New York.

Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J. W. Erisman, M. Fenn, F. Gilliam, A. Nordin, L. Pardo and W. De Vries (2010). "Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis." Ecological Applications 20(1): 30-59.

Bobbink, R. and Hettelinghl, J-P. Eds. (2011) Review and revision of empirical critical loads and dose response relationships. Proceedings of an expert workshop, Noordwijkerhout, 23-25th June 2010.

Britton, A.J. and Fisher, J.M. (2007) Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate Calluna vulgaris heathland. Journal of Applied Ecology, 44, 125-135.

Caporn, S.J.M., Edmondson, J., Carroll, J.A., Pilkington, M., and Ray, N. (2007). Long term impacts of enhanced and reduced nitrogen deposition on semi-natural vegetation. UKREATE (2007) Terrestrial Umbrella: Effects of Eutrophication and Acidification on Terrestrial Ecosystems. CEH Contract Report. Defra Contract No. CPEA 18.

Carroll, J. A., S. J. M. Caporn, L. Cawley, D. J. Read and J. A. Lee (1999). "The effect of increased deposition of atmospheric nitrogen on Calluna vulgaris in upland Britain." New Phytologist 141: 423-431.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18, 117-143.

Cunha, A., Power, S. A., Ashmore, M. R., Green, P. R. S., Haworth, B. J. and Bobbink, R. (2002) Whole ecosystem nitrogen manipulation: an updated review. JNCC: 126.

Dise, N. B. and R. F. Wright (1995). "Nitrogen leaching from European forests in relation to nitrogen deposition." Forest Ecology and Management 71(1-2): 153-161.

Dise, N. B., J. J. Rothwell, V. Gauci, C. van der Salm and W. de Vries (2009). "Predicting dissolved inorganic nitrogen leaching in European forests using two independent databases." Science of the Total Environment 407(5): 1798-1808.

Dise, N. B., Ashmore, M., Belyazid, S. Aleeker, A., Bobbink, R., de Vries, W., Erisman, J.W., Spranger, T., Stevens, C.J. and van den Berg, L. (2011) Nitrogen as a threat to European terrestrial biodiversity. In: Th e European Nitrogen Assessment, eds M. A. Sutton, C. M. Howard, J. W. Erisman *et al*. Cambridge University Press.

Dupre, C., C. J. Stevens, T. Ranke, A. Bleeker, C. Peppler-Lisbach, D. J. G. Gowing, N. B. Dise, E. Dorland, R. Bobbink and M. Diekmann (2010). "Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition." Global Change Biology 16(1): 344-357.

ECE/EB.AIR/WG.1/2010/14, 2010. Empirical critical loads and dose-response relationships. Prepared by the Coordination Centre for Effects of the International Cooperative Programme on Modelling and Mapping Critical Levels and Loads and Air Pollution Effects, Risks and Trends, Report to the Working Group on Effects; http://www.unece.org/env/lrtap/WorkingGroups/wge/29meeting_Rev.htm

Edmondson, J.L. (2007) Nitrogen pollution and the ecology of heather moorland. PhD. thesis. Manchester Metropolitan University.

Edmondson, J. L., Carroll, J. A., Price, E. A. C. and Caporn, S. J. M. (2010) "Bio-indicators of nitrogen pollution in heather moorland." Science of the Total Environment, 408(24), 6202-6209.

Emmett, B. A., D. Boxman, M. Bredemeier, P. Gundersen, O. J. Kjønaas, F. Moldan, P. Schleppi, A. Tietema and R. F. Wright (1998). "Predicting the Effects of Atmospheric Nitrogen Deposition in Conifer Stands: Evidence from the NITREX Ecosystem-Scale Experiments." Ecosystems 1(4): 352-360.

Emmett, B. A. (2007) Nitrogen saturation of terrestrial ecosystems: Some recent findings and their implications for our conceptual framework. Water Air and Soil Pollution, Focus 7, 99-109.

Emmett, B.A., Griffiths, B., Williams, D., and Williams, B. (2007) Task 6: Interactions between grazing and nitrogen deposition at Pwllpeiran: Effects of eutrophication and acidification on terrestrial ecosystems. Final Report (July 2007) NERC-Defra Terrestrial Umbrella (Contract No CPEA18).

Emmett, B.A, Rowe, E.C, Stevens, C.J, Gowing, D.J, Henrys, P.A, Maskell, L.C. and Smart, S.M. (2011) Interpretation of evidence of nitrogen impacts on vegetation in relation to UK biodiversity objectives. JNCC Report, No. 449.

Field, C.D. (2010). The effect of nitrogen deposition on carbon sequestration in semi-natural ericaceous dominated ecosystems. PhD Thesis, Manchester Metropolitan University, Manchester, UK.

Field, C., Dise, N., Payne, R., Britton, A., Emmett, B., Helliwell, R., Hughes, S., Jones, L., Lees, S., Leake, J., Leith, I., Phoenix, G., Power, S., Sheppard, L., Southon, G., Stevens, C. and Caporn, S. M. (2014). "The Role of Nitrogen Deposition in Widespread Plant Community Change Across Semi-natural Habitats." Ecosystems: 1-14.

Fowler, D., O'Donoghue, M., Muller, J.B.A., Smith, R.J., Dragosits, U., Skiba, U., Sutton, M.A. and Brimblecombe, P. (2004) A chronology of nitrogen deposition in the UK between 1900 and 2000. Water, Air and Soil Pollution Focus, 4, 9-23.

Galloway, J. N. (1995). "Acid deposition: Perspectives in time and space." Water, Air, & Soil Pollution 85(1): 15-24.

Galloway, J.N., F.J. Dentener, D.G. Capone, E.W. Boyer, R.W. Howarth, S.P. Seitzinger, G.P. Asner, C.C. , Cleveland, P.A. Green, E.A. Holland, D.M. Karl, A.F. Michaels, J.H. Porter, A.R. Townsend, and C.J. Vorosmarty. (2004) Nitrogen cycles: Past, present and future. Biogeochemistry, 70, 153-226.

Gimingham, C. H. (1972) Ecology of Heathlands. London, Chapman and Hall Limited, 242.

Gordon, A.D. and Birks, H.J.B. (1972) Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. New Phytologist, 71, 961.

Green ER (2005) The effect of N deposition on lowland heath ecosystems. PhD thesis, Imperial College London, London, UK.

Grimm, E.C. (1987) CONISS: A Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers and Geosciences, 13, 13-35.

Hall, J., Dore, A., Heywood, E., Broughton, R., Stedman, J., Smith, R., and O'Hanlon, S. (2006) Assessment of the Environmental impacts Associated with the UK Air Quality Strategy: London, DEFRA.

Hall, J., Emmett, B., Garbutt, A., Jones, L., Rowe, E., Sheppard, L., Vanguelova, E., Pitman, R., Britton, A., Hester, A., Ashmore, M., Power, S. and Caporn, S. (2011) UK Status Report March 2011: Update to empirical critical loads of nitrogen. Report to Defra under contract AQ801 Critical Loads and Dynamic Modelling. http://cldm.defra.gov.uk/Status_Reports.htm

Hammer, O., Harper, D.A.T. and Ryan, P.D. (2001) Paleontological Statistics software package for education and data analysis. Paleontologica Electronica, 4(1), 9 pp.

Horswill, P., O'Sullivan, O., Phoenix, G. K., Lee, J. A. and Leake, J. R. (2008) Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. Environmental Pollution, 155(2), 336-349.

JNCC (2004). Common Standards Monitoring Guidance for Lowland Heathland. JNCC. ISSN: 1743-8160. http://jncc.defra.gov.uk/pdf/CSM_lowland_heathland.pdf

JNCC (2006). Common Standards Monitoring Guidance for Upland Habitats. JNCC. ISSN: 1743-8160. http://jncc.defra.gov.uk/pdf/CSM_Upland_Oct_06.pdf

Jones, M.L.M., Wallace, H.L., Norris, D., Brittain, S.A., Haria, S., Jones, R.E., Rhind, P.M., Reynolds, B.R., and Emmett, B.A. (2004) Changes in vegetation and soil characteristics in coastal sand dunes along a gradient of atmospheric nitrogen deposition. Plant Biology, 6(5), 598-605.

Jones, M.R. (2006). Ammonia deposition to semi-natural vegetation. PhD Thesis. University of Dundee.

Juggins, S. (1992). The ZONE program, version 1.2, Unpublished program, University of Newcastle.

Kirby, K.J., Smart, S.M., Black, H.I.J., Bunce, R.G.H.,Corney,P.M.and Smithers,R.J. (2005). *Long term ecological change in British woodland* (1971-2001). Peterborough: English Nature (Research Report 653).

Leith, I., L. Sheppard, D. Fowler, J. N. Cape, M. Jones, A. Crossley, K. Hargreaves, Y. S. Tang, M. Theobald and M. Sutton (2004). "Quantifying Dry NH3 Deposition to an Ombrotrophic Bog from an Automated NH3 Field Release System." Water, Air, & Soil Pollution: Focus 4(6): 207-218.

Leps, J. and Smilauer, P. (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, 260pp.

Maskell, L. C., S. M. Smart, J. M. Bullock, K. E. N. Thompson and C. J. Stevens (2010). "Nitrogen deposition causes widespread loss of species richness in British habitats." Global Change Biology 16(2): 671-679.

Mitchell, R.J., Sutton, M.A., Truscott, A.M., Leith, I.D., Cape, J.N., Pitcairn, C.E.R. and van Dijk, N. (2004) Growth and tissue nitrogen of epiphytic Atlantic bryophytes: effects of increased and decreased atmospheric N deposition. Functional Ecology, 18, 322-329.

Morecroft, M.D.; Skellers, E.K.; Lee, J.A. 1994 An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands Journal of Ecology 82 475-483.

Morse, J.N. (1980) Reducing the size of the non-dominated set: Pruning by clustering, Computers and Operations Research, 7, 55-66.

Natural England (2011) UK list of priority habitats and species. http://www.naturalengland.org.uk/ourwork/conservation/biodiversity/protectandmanage/prioritylist.aspx

Paulissen, M. P. C. P., van der Ven, P. J. M., Dees, A. J. and Bobbink, R. (2004) Differential Effects of Nitrate and Ammonium on Three Fen Bryophyte Species in Relation to Pollutant Nitrogen Input. New Phytologist, 164(3), 451-458.

Payne, R., Caporn, S.J.M., Field, C., Carroll, J., Edmondson, J., Britton, A. and Dise, N. (2014). "Heather Moorland Vegetation and Air Pollution: A Comparison and Synthesis of Three National Gradient Studies." Water, Air, & Soil Pollution 225(7): 1-13.

Pearce, I. S. K. and R. Van der Wal (2008). "Interpreting nitrogen pollution thresholds for sensitive habitats: The importance of concentration versus dose." Environmental Pollution 152(1): 253-256.

Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C.I, Stock, W.D., Dentener, F.J., Giller, K.E., Austin, A.T., Lefroy, R.D.B., Gimeno, B.S., Ashmore, M.R. and Ineson, P. (2006) Atmospheric Nitrogen Deposition in World Biodiversity Hotspots: the need for a greater global perspective in assessing N deposition impacts. Global Change Biology, 12, 470-476.

Phoenix, G. K., Emmett, B. A., Britton, A. J., Caporn, S. J. M., Dise, N. B., Helliwell, R., Jones, L., Leake, J. R., Leith, I. D., Sheppard, L. J., Sowerby, A., Pilkington, M. G., Rowe, E. C., Ashmorek, M. R. and Power, S. A. (2012). "Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments." Global Change Biology 18(4): 1197-1215.

Pilkington, M. G., Caporn, S. J. M., Carroll, J. A., Cresswell, N., Lee, J. A., Emmett, B. A. and Johnson, D. (2005). "Effects of increased deposition of atmospheric nitrogen on an upland Calluna moor: N and P transformations." Environmental Pollution 135(3): 469.

Pilkington, M. G., Caporn, S. J. M., Carroll, J. A., Cresswell, N., Lee, J. A., Emmett, B. A. and Bagchi, r. (2007). "Phosphorus supply influences heathland responses to atmospheric nitrogen deposition." Environmental Pollution 148(1): 191-200.

Pitcairn, C. E. R., I. D. Leith, L. J. Sheppard, M. A. Sutton, D. Fowler, R. C. Munro, S. Tang and D. Wilson (1998). "The relationship between nitrogen deposition, species composition and foliar nitrogen concentrations in woodland flora in the vicinity of livestock farms." Environmental Pollution 102(1, Supplement 1): 41-48.

Pitcairn, Carole E.R.; Leith, Ian D.; van Dijk, Netty; Sheppard, Lucy J.; Sutton, Mark A.; Fowler, David. 2009 The application of transects to assess the effects of ammonia on woodland groundflora. In: Sutton, Mark A.; Reis, Stefan; Baker, Samantha M.H., (eds.) Atmospheric Ammonia: Detecting emission changes and environmental impacts. Results of an Expert Workshop under the Convention on Long-range Transboundary Air Pollution. Springer, 59-69.

Plassmann, K., Edwards-Jones, G., and Jones, M.L.M. (2009) The effects of low levels of nitrogen deposition and grazing on dune grassland. Science of the Total Environment, *407(4), 1391-1404.*

Power, S. A., M. R. Ashmore and D. A. Cousins (1998). "Impacts and fate of experimentally enhanced nitrogen deposition on a British lowland heath." Environmental Pollution 102(1, Supplement 1): 27-34.

Power, S.A., Green, E.R., Barker, C.G. & J.N.B. and Ashmore, M.R. (2006) Ecosystem recovery: heathland response to a reduction in nitrogen deposition. Global Change Biology, 12, 1241-1252.

Remke, E., Brouwer, E., Kooijman, A., Blindow, I. and Roelofs, J. G. M. (2009) Low atmospheric nitrogen enrichment loads leads to grass encroachment in coastal dunes, but only on acid soils. Ecosystems, 12, 1173-1188.

RoTAP (2012). Review of Transboundary Air Pollution: Acidification, Eutrophication, Ground Level Ozone and Heavy Metals in the UK. Contract Report to the Department for Environment, Food and Rural Affairs. Centre for Ecology & Hydrology.

Sheppard, L. J., Crossley, A., Leith, I. D., Hargreaves, K. J., Carfrae, J. A., Dijk, N. v., Cape, J. N., Sleep, D., Fowler, D. and Raven, J. A. (2004) An automated wet deposition system to compare the effects of rediced and oxidised N on ombrotrophic bog species: practical considerations. Water, Air, and Soil Pollution, 4, 197-205.

Sheppard, L. J., Leith, I. D., Crossley, A., Van Dijk, N., Fowler, D., Sutton, M. A. and Woods, C. (2008) Stress responses of Calluna vulgaris to reduced and oxidised N applied under `real world conditions'. Environmental Pollution, 154(3), 404-413.

Sheppard, L.J., Leith, I.D., Kivimaki, S.K., Gaiawyn, J. (2011) The form of reactive nitrogen deposition is important for the provision of ecosystem services. In: Nitrogen Deposition, Critical Loads and Biodiversity (Eds. Sutton M.A. *et al*.) (Proceedings of the INI/CLRTAP/CBD Expert Workshop, 16-18 November 2009).

Southon, G. E., Field, C., Caporn, S. J. M., Britton, A. J. and Power, S. A. (2013). "Nitrogen Deposition Reduces Plant Diversity and Alters Ecosystem Functioning: Field-Scale Evidence from a Nationwide Survey of UK Heathlands." PLoS ONE 8(4): e59031.

Stevens, C. J., Dise, N. B., Mountford, J. O. and Gowing, D. J. (2004) Impact of nitrogen deposition on the species richness of grasslands. Science, 303, 1876-1879.

Stevens, C. J., N. Dise, D. J. Gowing and J. O. Mountford (2006). "Loss of forb diversity in relation to nitrogen deposition in the UK: regional trends and potential controls." Global Change Biology 12: 1823-1833.

Stevens, C. J., Caporn. S.J.M., Maskell, L. C., Smart, S. M. Dise, N. and Gowing, D. J. (2009). Detecting and attributing air pollution impacts during SSSI condition assessment. , JNCC report 426.

Stevens, C. J., Thompson, K., Grime, J. P., Long, C. J. and Gowing, D. J. (2010a) Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. Functional Ecology, 24, 478-484.

Stevens, C.J., Dupre, C., Dorland, E., Gaudnik, C., Gowing, D., Bleeker, A., Diekmann, M., Alard, D., Bobbink, R., Fowler, D., Corcket, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller, S. and Dise, N.B. (2010b). Nitrogen deposition threatens species richness of grasslands across Europe. Environmental Pollution, 158, 2940-2945.

Stevens, C.J., Smart, S.M., Henrys, P., Maskell, L.C., Walker, K.J., Preston, C.D., Crowe, A., Rowe, E., Gowing, D.J. and Emmett, B.A. (2011). Collation of evidence of nitrogen impacts on vegetation in relation to UK biodiversity objectives. JNCC report 447.

Sutton, M.A., Wolseley, P.A., Leith, I.D., van Dijk, N., Tang, Y.S., James, P.W., Theobald, M.R., and Whitfield, C. (2009) Estimation of the Ammonia critical levels for epiphytic lichens based on observations at farm, landscape and national scales. In Sutton, M.A., Reis, S. and Baker, S.M.H. (Eds.) (2009). Atmospheric Ammonia. Springer Press. 464pp.

ter Braak, C.J.F. and Smilauer, P. (2004) Canoco Software for Windows 4.53. Biometris Plant Research International, Wageningen, The Netherlands.

UKBAP (2008). Coastal vegetated shingle. UK Biodiversity Action Plan; Priority Habitat Descriptions.

UKREATE (2010) Terrestrial Umbrella: Effects of Eutrophication and Acidification on Terrestrial Ecosystems. CEH Contract Report NEC03425. Defra Contract No. AQ0802.

Van Den Berg, L. J. L., Vergeer, P., Rich, T. C. G., Smart, S. M., Guest, D. A. N. and Ashmore, M. R. (2010) Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. Global Change Biology.

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M. and Verstraeten, G. (2012). "Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests." Journal of Ecology 100(2): 352-365.

Verhoeven, J. T. A. and Schmitz, M. B. (1991) Control of plant growth by nitrogen and phosphorus in mesotrophic fens. Biogeochemistry, 12(2), 135-148.

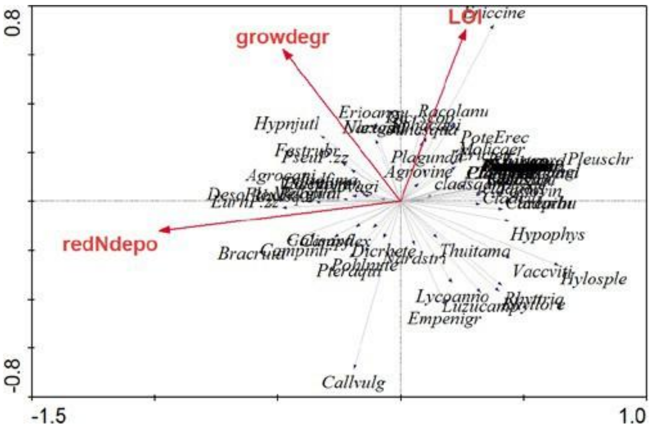
Verhoeven, J., Beltman, B. and De Caluwe, H. (1996) Changes in plant biomass in fens in the vechtplassen area, as related to nutrient enrichment. Aquatic Ecology, 30(2), 227-237.

Verhoeven, J. T. A., B. Beltman, E. Dorland, S. A. Robat and R. Bobbink (2011). "Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes." Applied Vegetation Science 14(2): 149-157.

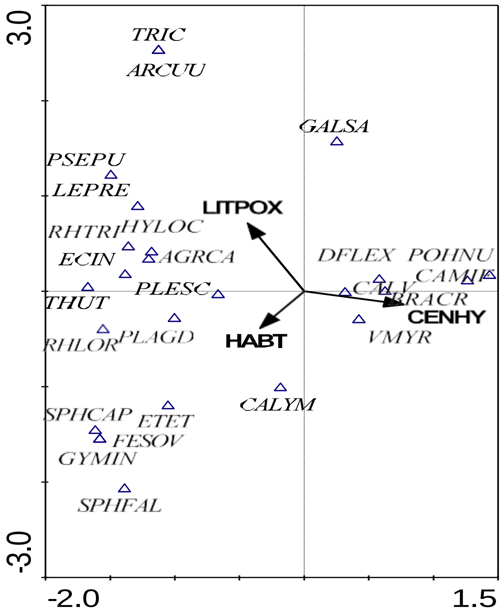
Ward, J.H. (1963) Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association, 58, 236-244.

Appendix 1: Key ordination plots

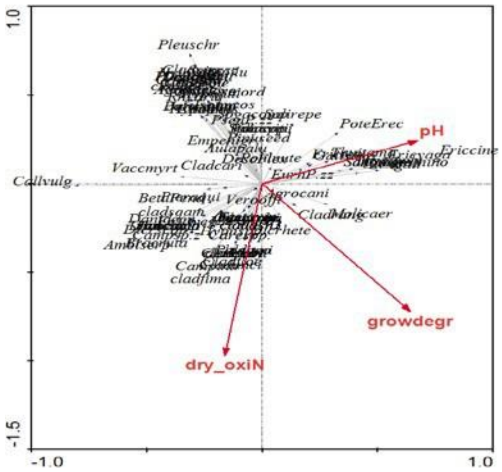
Upland heaths (TU 2009): RDA ordination plot



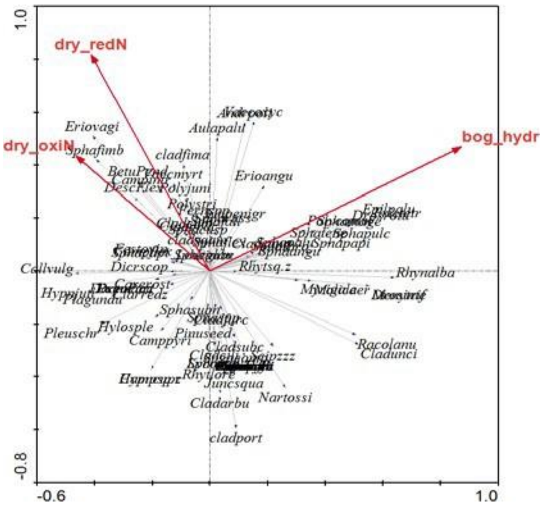
Upland heaths (MRS): CCA ordination plot



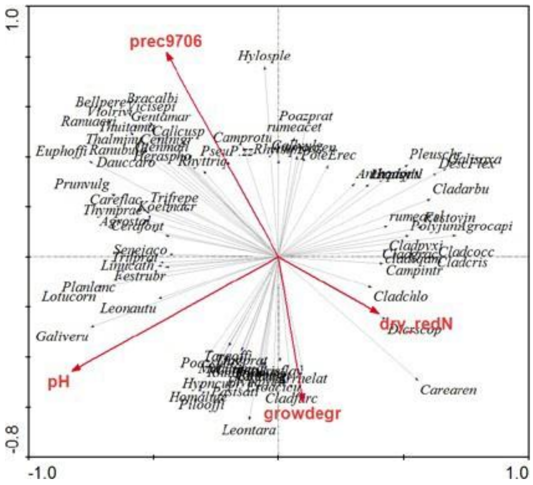
Lowland heaths (TU 2009): RDA ordination plot



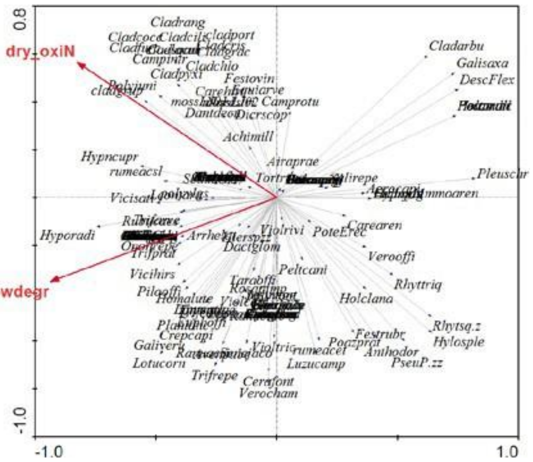
Bog (TU 2009): RDA ordination plot



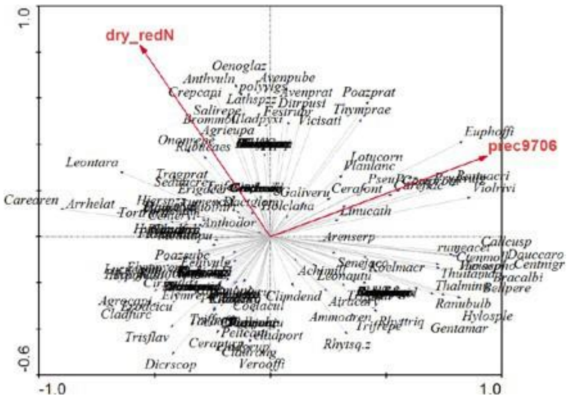
Sand dune (TU 2009 all pH): RDA ordination plot showing response of species with 15% minimum fit to axes



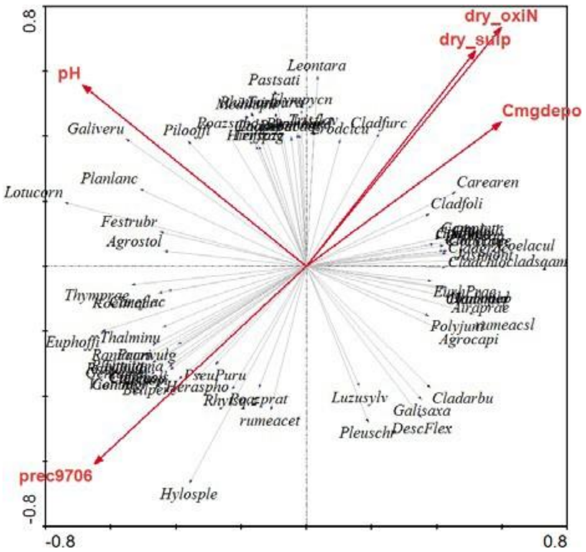
Sand dune (TU 2009 pH< 6.5): RDA ordination plot



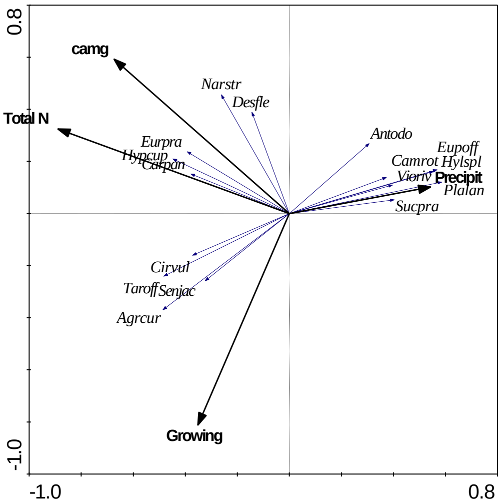
Sand dune (TU 2009 pH≥ 6.5): RDA ordination plot



Sand dune (TU 2009 all pH plus 2002 fixed-dune grasslands): RDA ordination plot showing response of species with 15% minimum fit to axes



Acid grasslands (BEGIN): RDA ordination plot

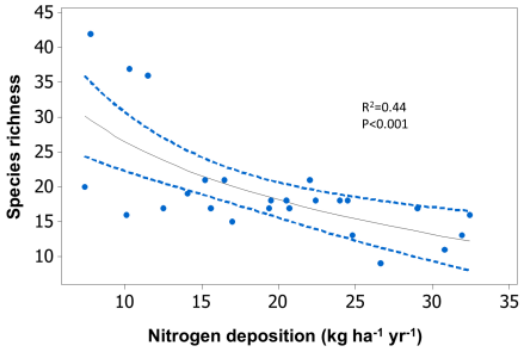


Appendix 2: Species richness nitrogen response curves.

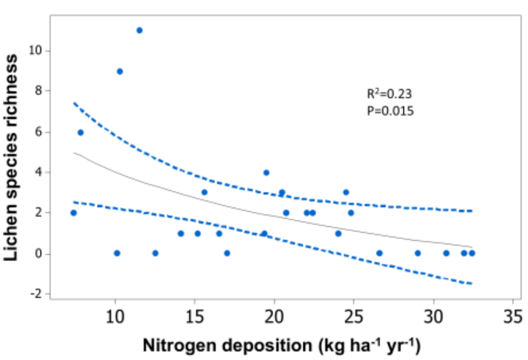
Only those with a significant relationship to nitrogen deposition are shown.

Upland heath: TU Survey 2009

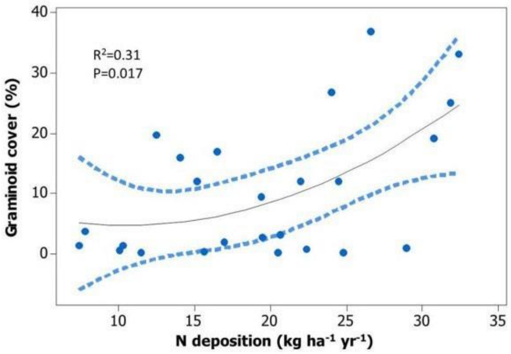
Upland heath: total species richness



Upland heath: lichen species richness

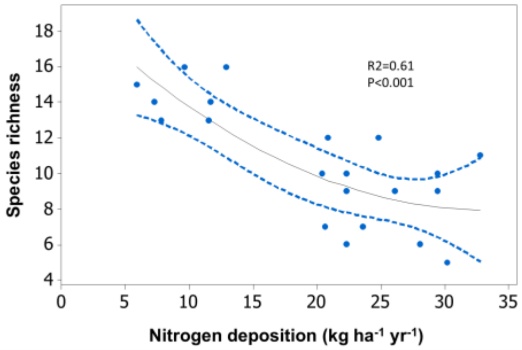


Upland heath: graminoid cover

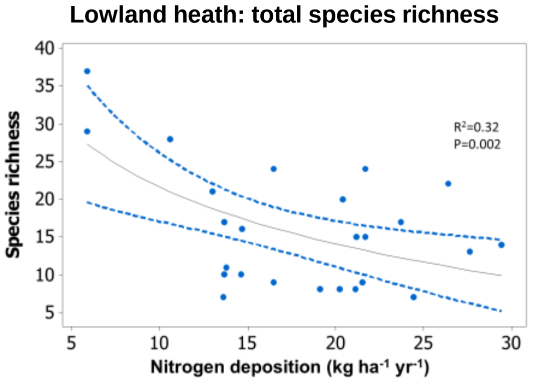


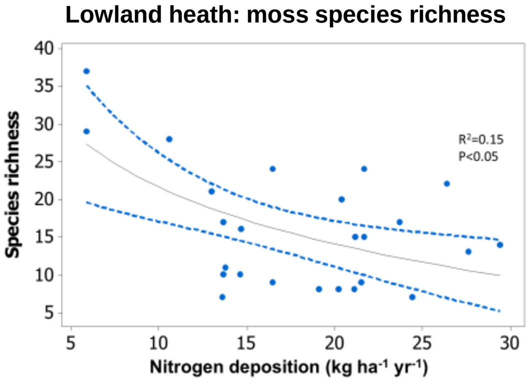
Upland heath: MRS

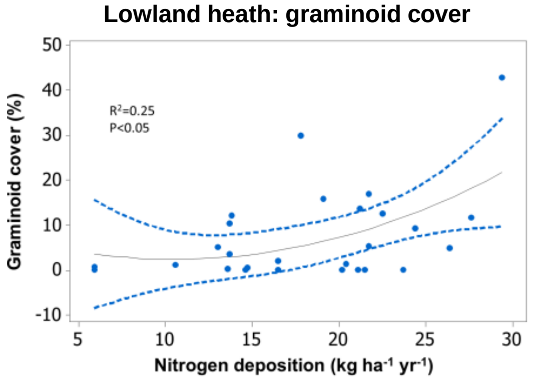
Upland heath: total species richness



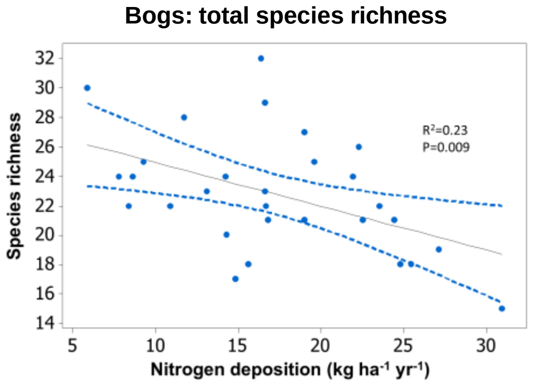
Lowland heath: TU Survey 2009

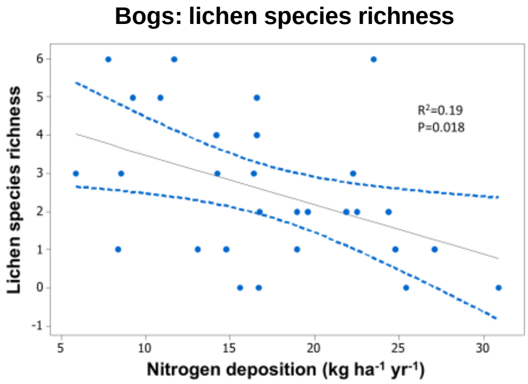


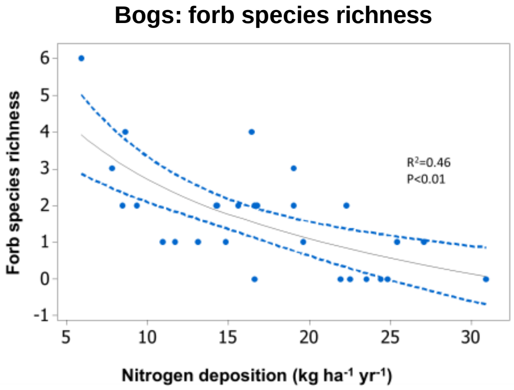


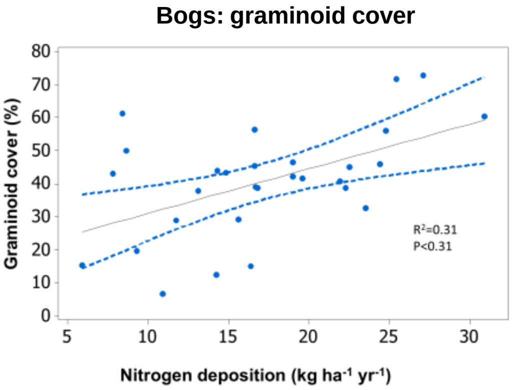


Bog: TU Survey 2009

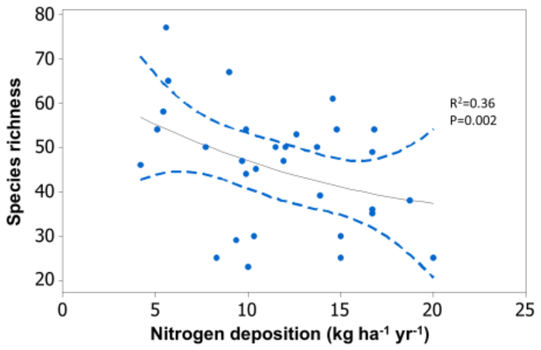


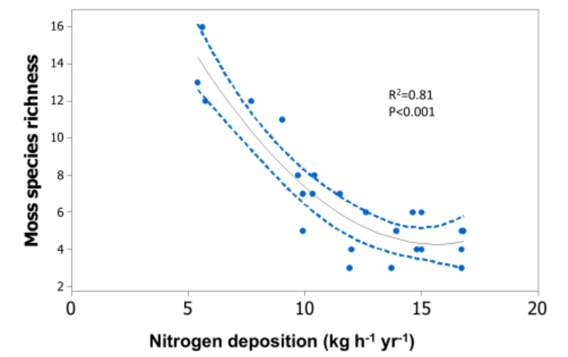




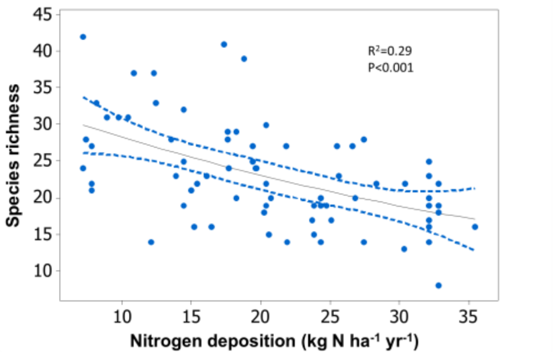


Sand dunes (TU 2009 all pH)


Sand dunes: total species richness

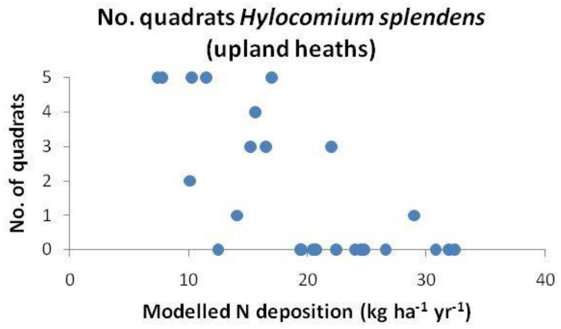

Sand dunes: moss species richness

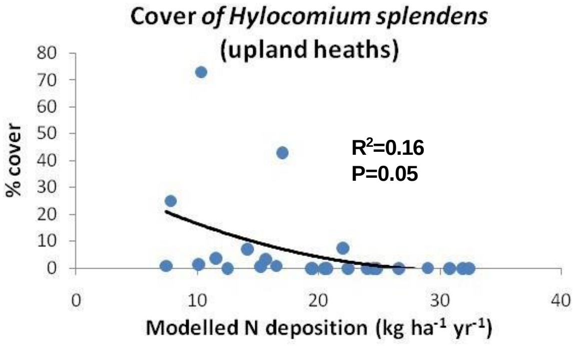
Acid grasslands (BEGIN)

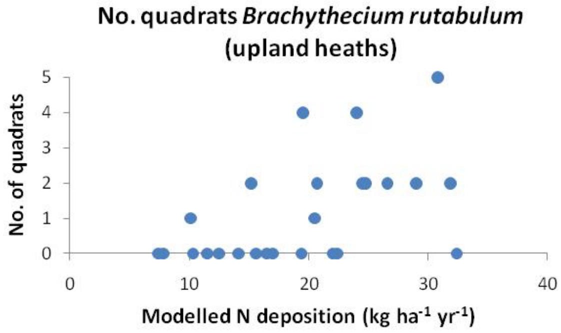

Acid grassland: total species richness

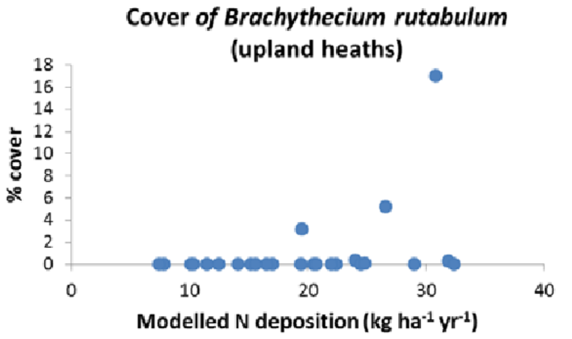
Appendix 3: Individual species N response curves

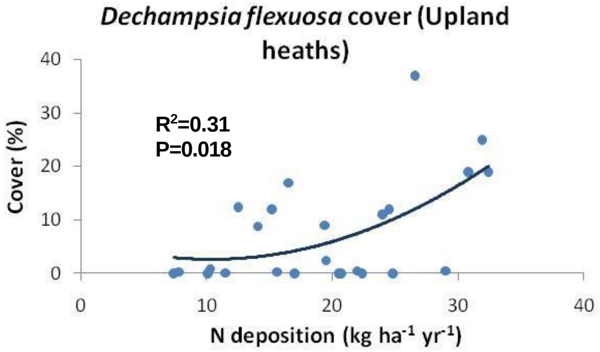
Upland heaths: TU 2009



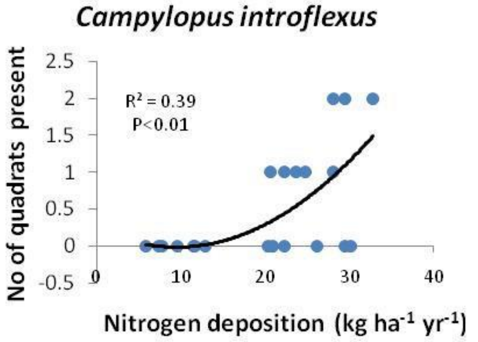


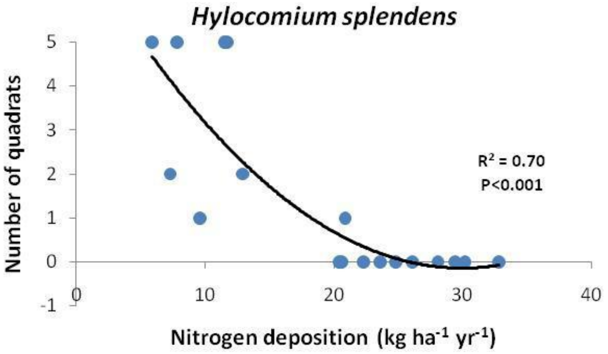




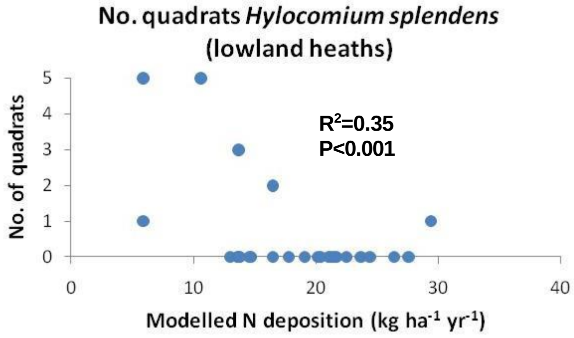


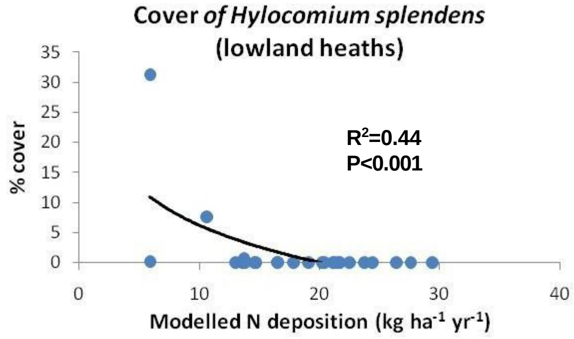
Upland heaths (MRS)

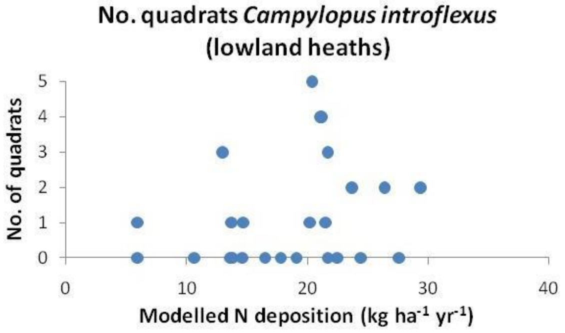


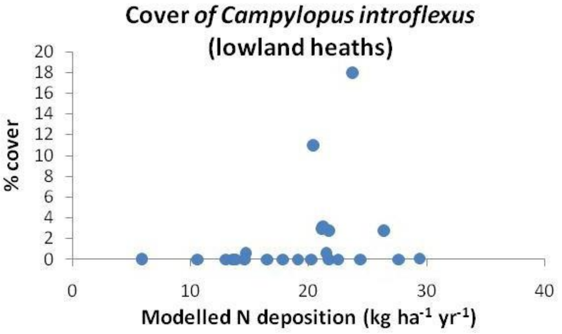


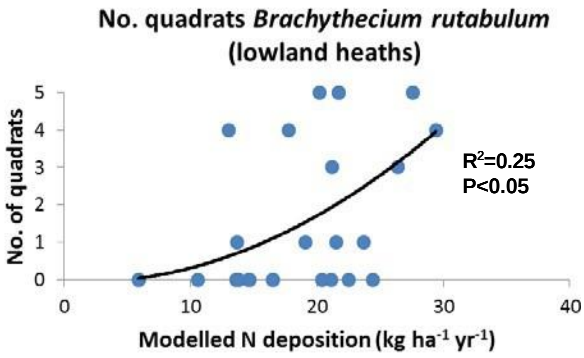
Lowland heaths: TU 2009

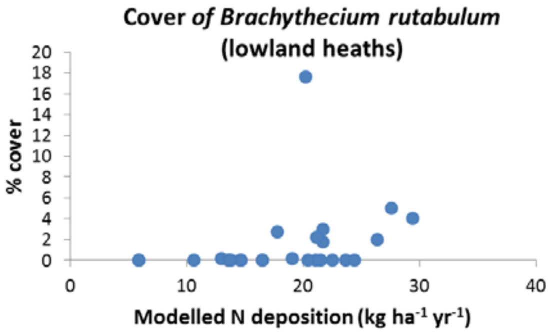


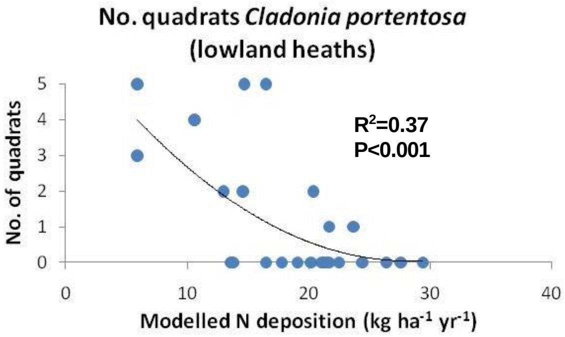


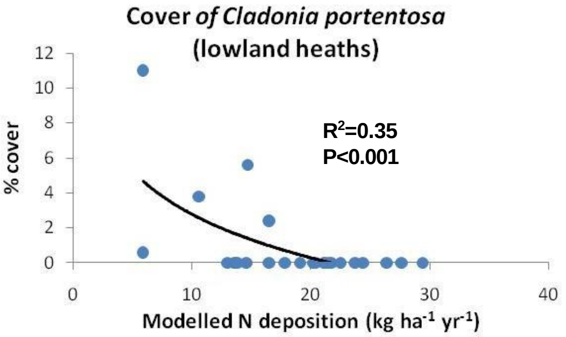


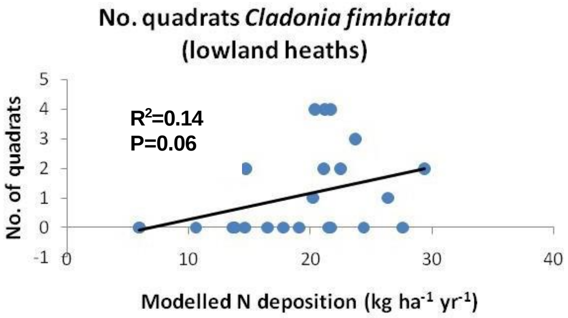


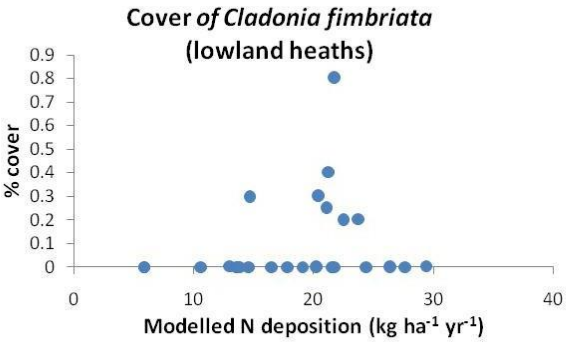




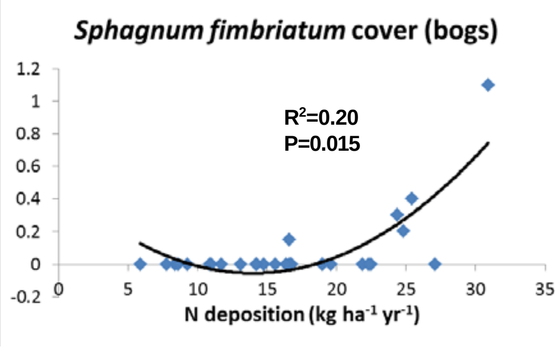


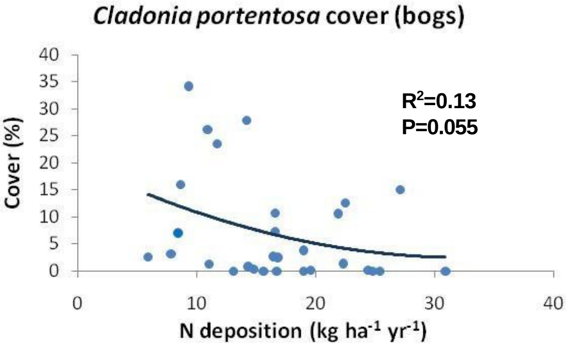




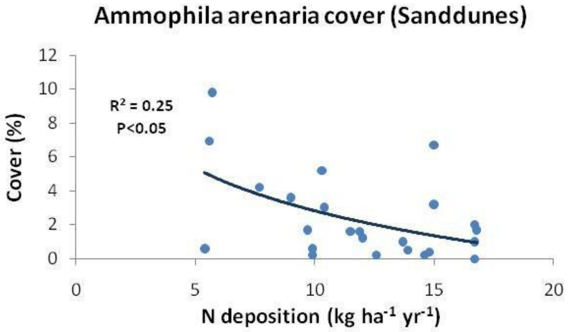


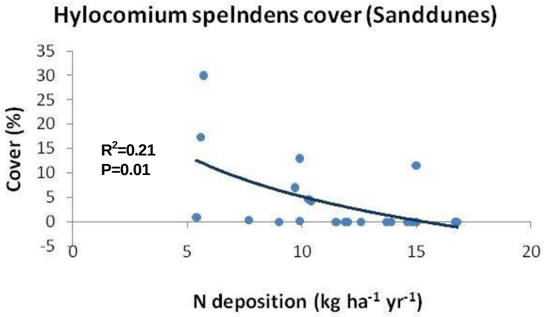
Bogs: TU survey 2009

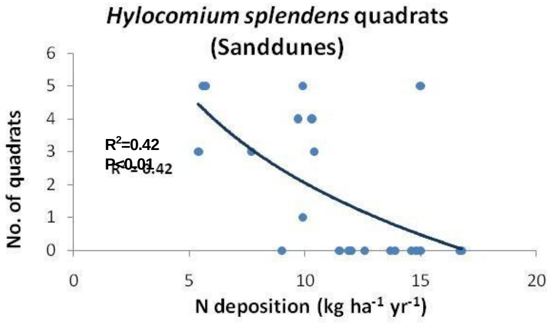




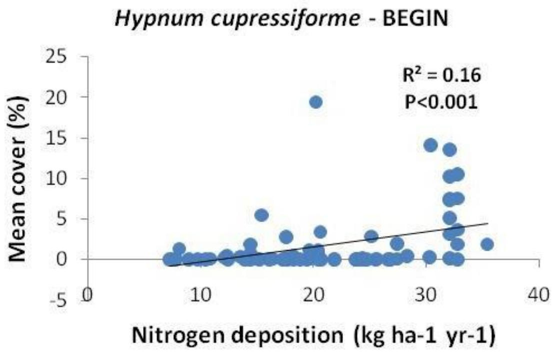
Sand dunes (TU 2009 all sites)

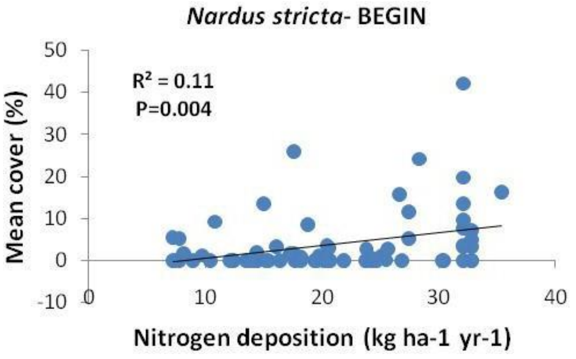


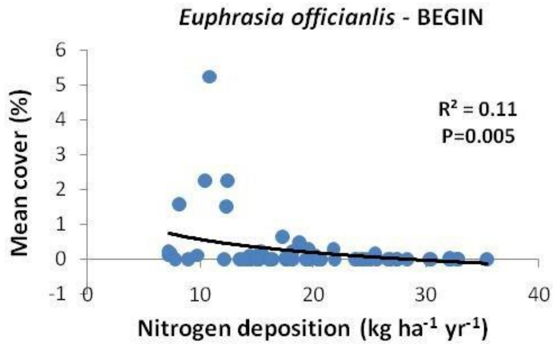


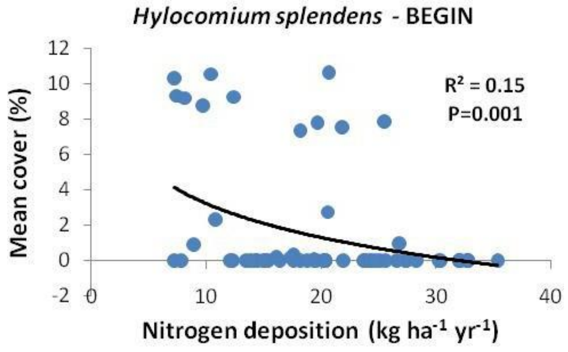


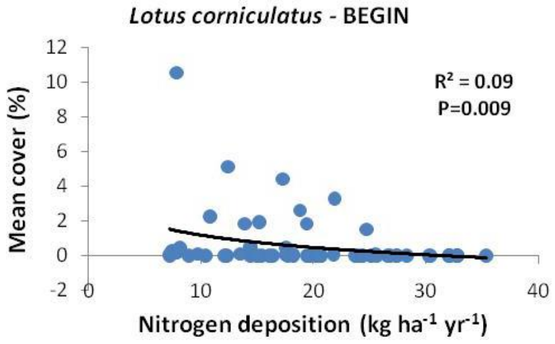
Acid grasslands (BEGIN)

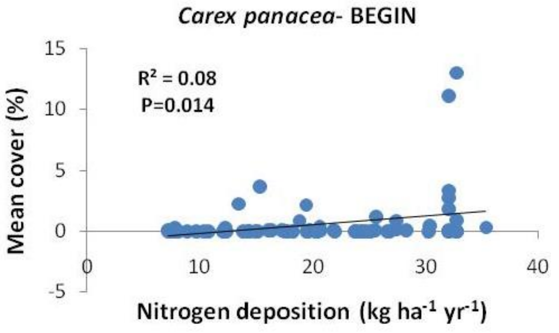

Hypnum cupressiforme - BEGIN


Nardus stricta- BEGIN


Euphrasia officianlis - BEGIN


Hylocomium splendens - BEGIN

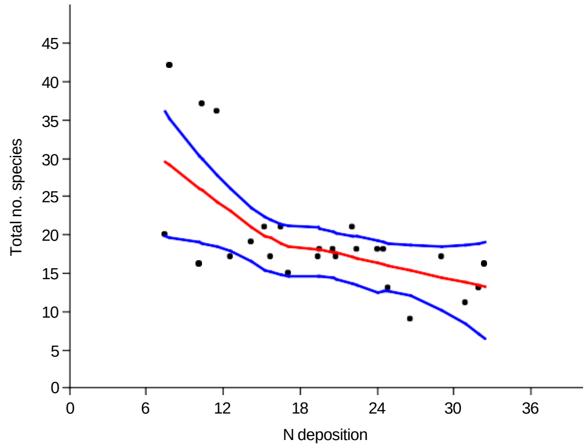

Lotus corniculatus - BEGIN

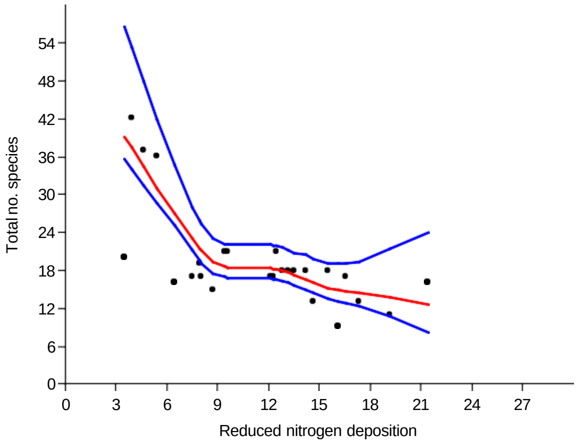

Carex panacea- BEGIN

Appendix 4: LOESS regression curves

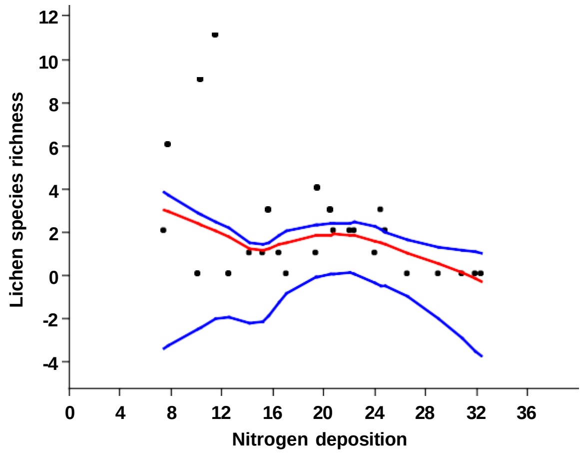
Best fit to data line in red, 95% confidence limits shown in blue and fitted by bootstrapping.

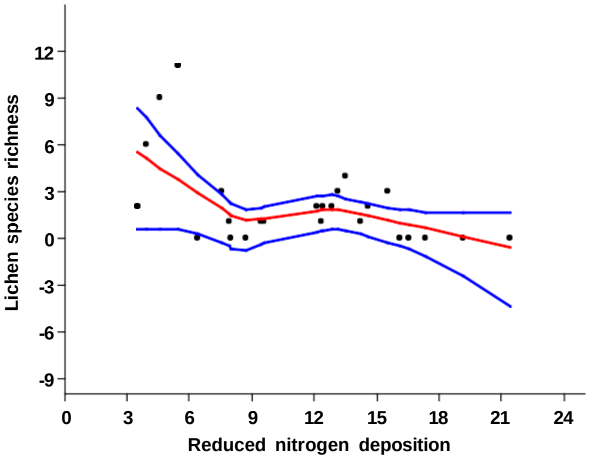
Upland heaths (TU): total species richness



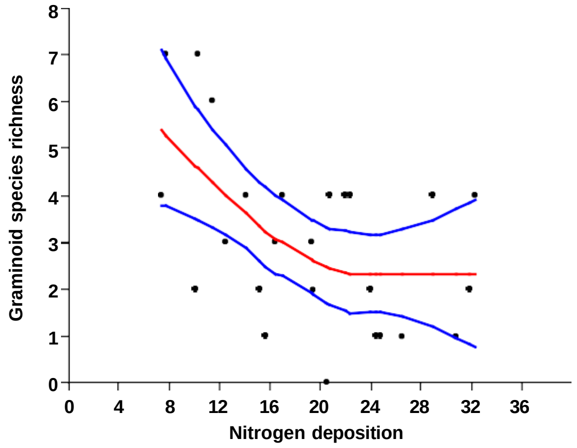


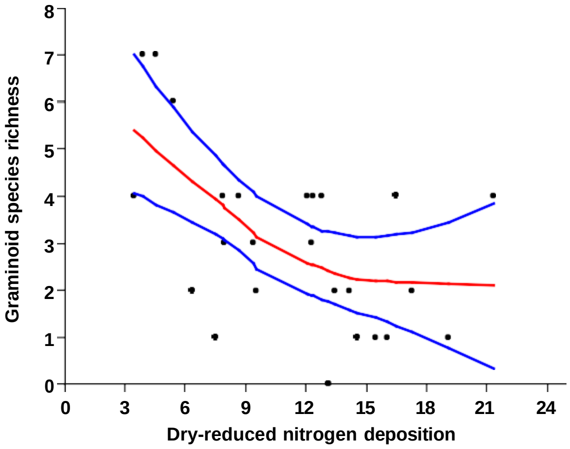
Upland heaths (TU): lichen species richness



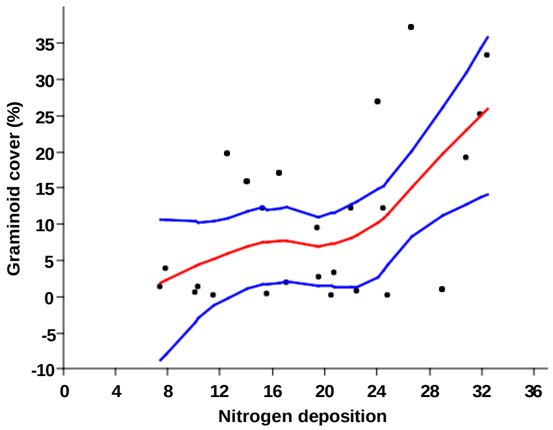


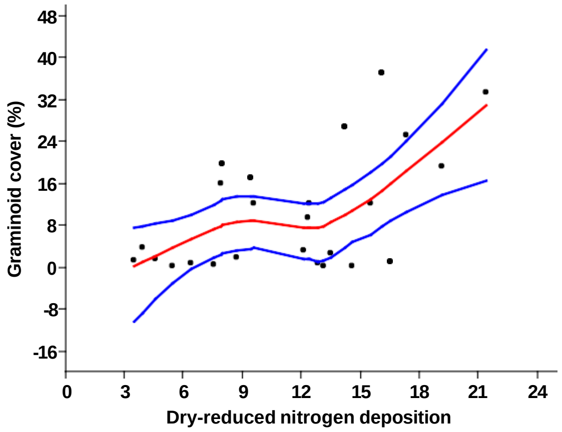
Upland heaths (TU): graminoid species richness



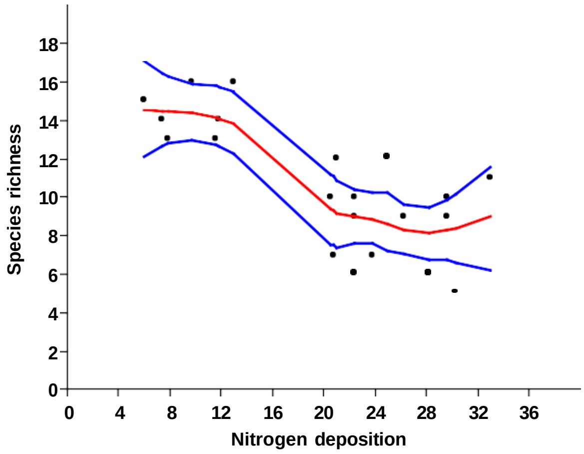


Upland heaths (TU): graminoid cover

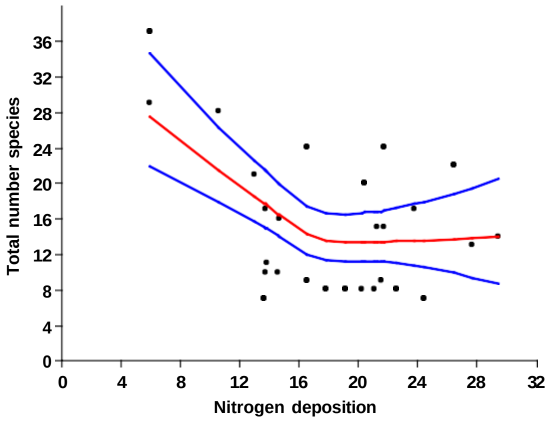


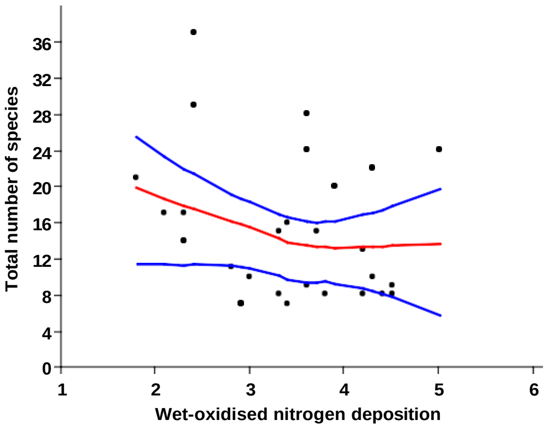


Upland heaths (MRS): total species richness

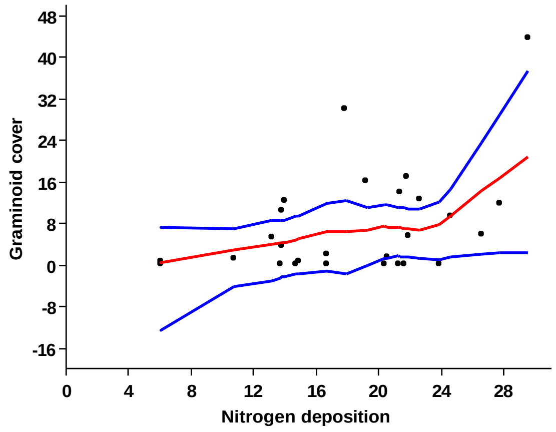


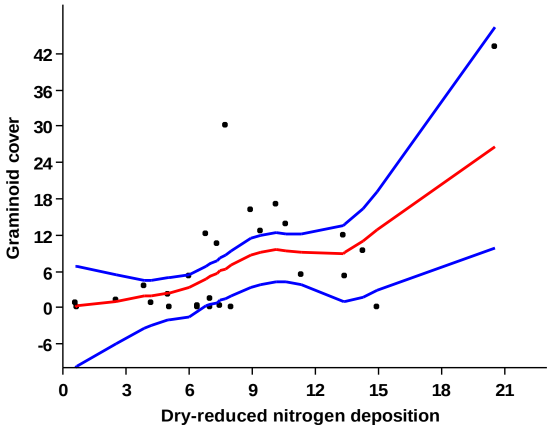
Lowland heaths: total number species



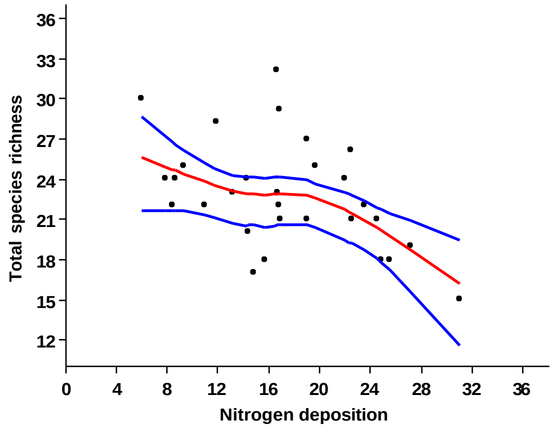


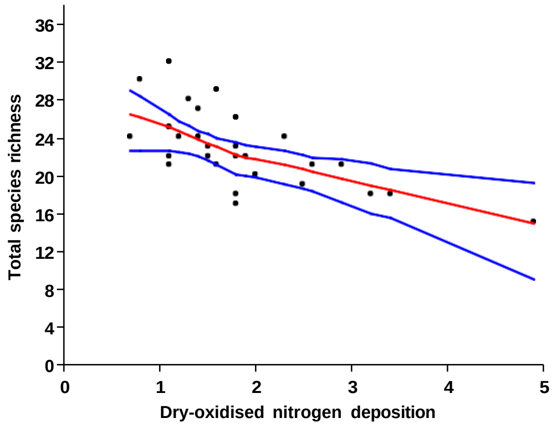
Lowland heaths: Graminoid cover



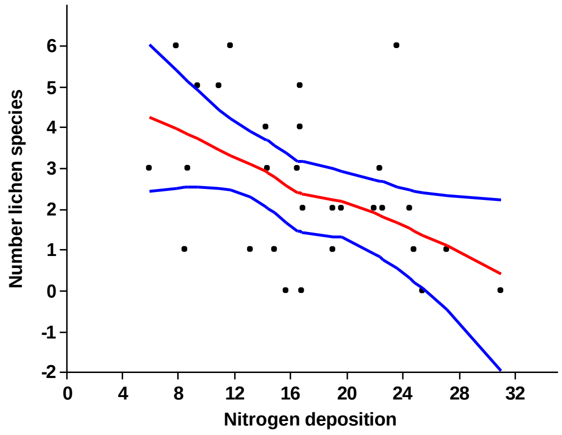


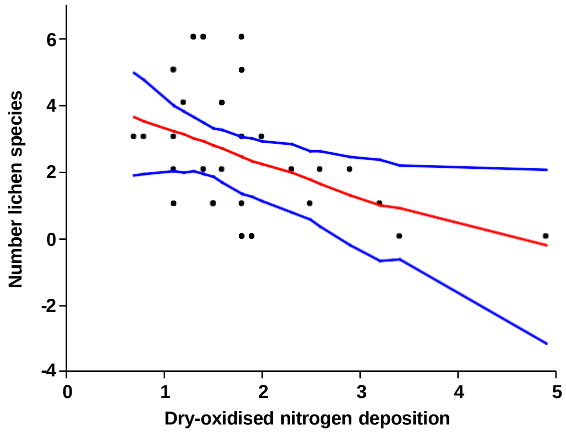
Bogs: total species richness



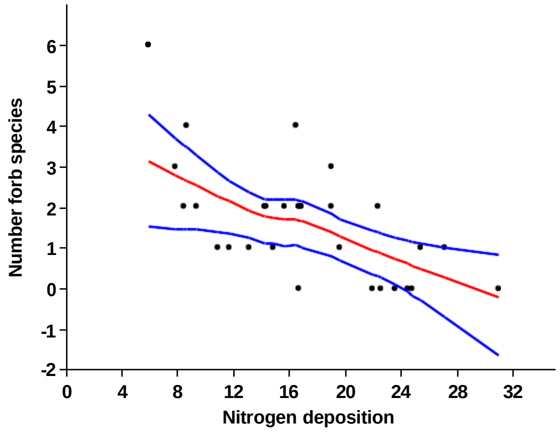


Bogs: lichen species richness

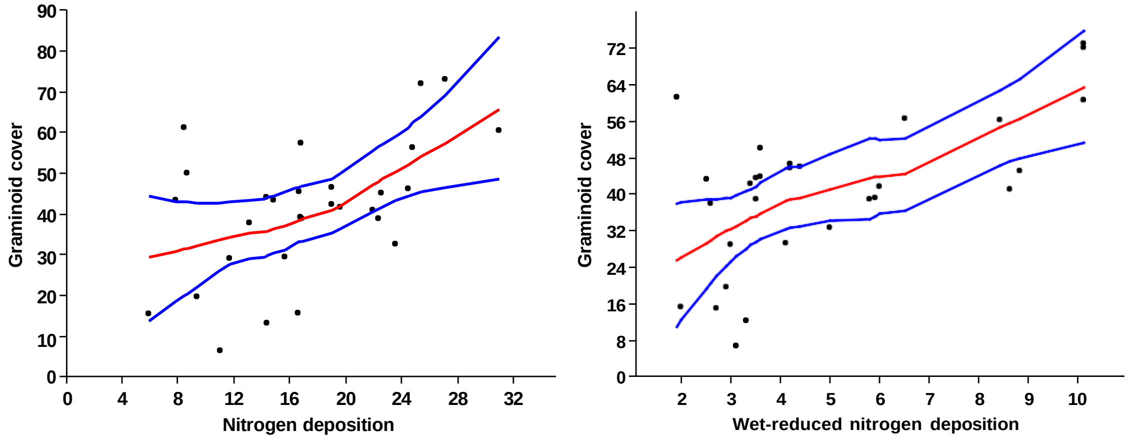




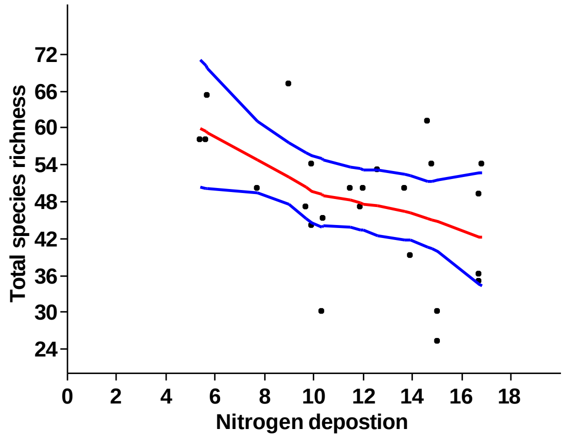
Bogs: Forb species richness



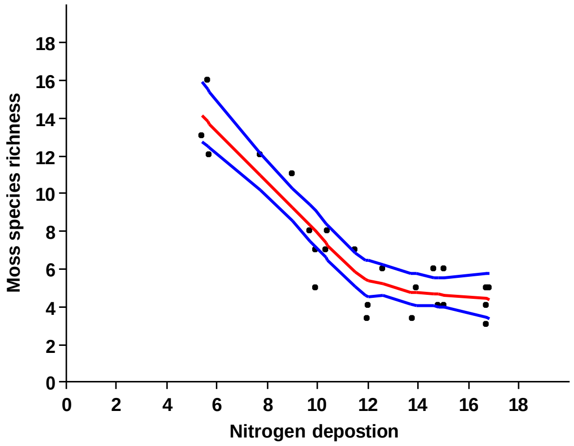
Bogs: Graminoid cover



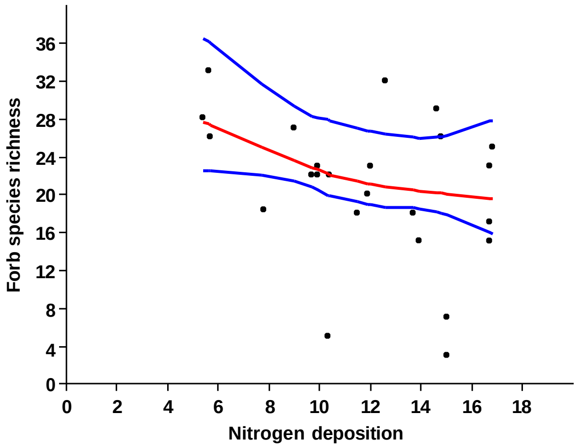
Sand dunes (all TU 2009): Total species richness



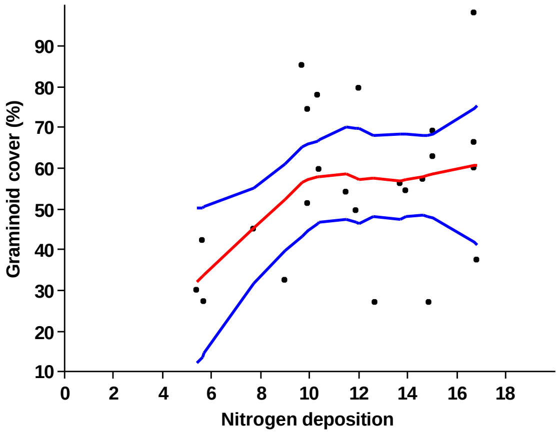
Sand dunes (all TU 2009): Moss species richness



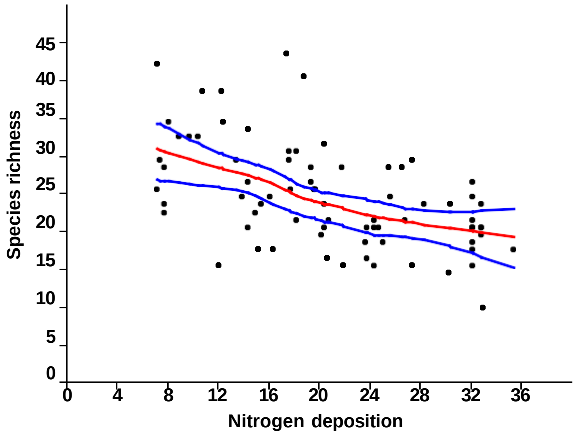
Forb species richness



Sand dunes (all TU 2009): Graminoid cover



Acid Grasslands (BEGIN): Total species richness



Appendix 5: Effect of incremental increases in N deposition upon species richness

Summary of relationships between nitrogen deposition and species richness by habitat expressed as a percentage of the maximum in a habitat. Change in cover expresses as an absolute percentage. Incremental effect of a 0.3 kg increase in N deposition shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 0.3 kg increase in N deposition at different background N deposition levels					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
All habitats (TU 2009)								
Total Species Richness (SR)	77 spp.	10-20 kg N ha^{-1} yr^{-1}	-0.5 % of maximum number of species					
Upland heath (TU 2009)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.7%	-0.9%	-0.6%	-0.4%	-0.3%	-0.3%
Lichen SR	11 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.7%	-0.9%	-0.6%	-0.4%	-0.3%	-0.3%
Graminoid SR	7 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.9%	-1.0%	-0.6%	-0.5%	-0.4%	-0.3%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.13%	-0.01%	+0.11%	+0.24%	+0.37%	+0.5%
Upland heath (MRS)*								
Total SR	16 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.1%	-0.9%	-0.7%	-0.5%	-0.3%	-0.1%
Lowland heath (TU 2009)								
Total SR	37 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.8%	-0.9%	-0.6%	-0.5%	-0.4%	-0.3%
Moss SR	12 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.6%	-0.8%	-0.5%	-0.4%	-0.3%	-0.3%
Graminoid SR	9 spp.	10-20 kg N ha^{-1} yr^{-1}	-4.9%	-1.3%	-0.6%	-0.3%	-0.2%	-0.1%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	n/a	-0.04%	+0.11%	+0.26%	+0.41%	+0.56%
Bog (TU 2009)								
Total SR	32 spp.	5-10 kg N ha^{-1} yr^{-1}	-0.3%					
Lichen SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-0.6%					
Forb SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-2.3%	-1.1%	-0.8%	-0.6%	-0.5%	-0.4%
Graminoid cover	-	5-10 kg N ha^{-1} yr^{-1}	+0.41%					
Sand dunes (TU 2009, all sites)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-2.9%	-0.7%	-0.3%	-0.2%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-6.0%	-1.5%	-0.7%	-0.4%	-	-
Graminoid cover	n/a	8-15 kg N ha^{-1} yr^{-1}	+2.43%	+0.63%	+0.28%	-0.16%	-	-
Forb SR	33 spp.	8-15 kg N ha^{-1} yr^{-1}	-2.9%	-0.7%	-0.3%	-0.2%	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-1.7%	-0.9%	-0.6%	-0.4%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-2.5%	-1.3%	-0.9%	-0.6%	-	-
Acid grasslands (BEGIN)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-0.4%	-0.4%	-0.4%	-0.3%	-0.3%	-0.3%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

Summary of relationships between nitrogen deposition and species richness by habitat expressed as a percentage of the maximum in a habitat. Change in cover expresses as an absolute percentage. Incremental effect of a 0.5 kg increase in N deposition shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 0.5 kg increase in N deposition at different background N deposition levels					
			5 kg N	10 kg N	15 kg N	20 kg N	25 kg N	30 kg N
All habitats (TU 2009)								
Total SR	77 spp.	10-20 kg N ha^{-1} yr^{-1}	-0.8 % of maximum number of species					
Upland heath (TU 2009)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-2.7%	-1.4%	-0.9%	-0.7%	-0.6%	-0.5%
Lichen SR	11 spp.	10-20 kg N ha^{-1} yr^{-1}	-2.8%	-1.4%	-0.9%	-0.7%	-0.6%	-0.5%
Graminoid SR	7 spp.	10-20 kg N ha^{-1} yr^{-1}	-3.1%	-1.6%	-1.1%	-0.8%	-0.6%	-0.5%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.22%	-0.01%	+0.20%	+0.41%	+0.62%	+0.83%
Upland heath (MRS)*								
Total SR	16 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.9%	-1.5%	-1.2%	-0.8%	-0.5%	-0.1%
Lowland heath (TU 2009)								
Total SR	37 spp.	10-20 kg N ha^{-1} yr^{-1}	-2.9%	-1.5%	-1.0%	-0.8%	-0.6%	-0.2%
Moss SR	12 spp.	10-20 kg N ha^{-1} yr^{-1}	-2.6%	-1.3%	-0.9%	-0.7%	-0.5%	-0.2%
Graminoid SR	9 spp.	10-20 kg N ha^{-1} yr^{-1}	-7.9%	-2.1%	-0.9%	-0.5%	-0.3%	-0.2%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.31	-0.06%	+0.19%	+0.44%	+0.69%	+0.94%
Bog (TU 2009)								
Total SR	32 spp.	5-10 kg N ha^{-1} yr^{-1}	-0.5%					
Lichen SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-1.1%					
Forb SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-3.7%	-1.9%	-1.3%	-1.0%	-0.8%	-0.6%
Graminoid cover	-	5-10 kg N ha^{-1} yr^{-1}	+0.68%					
Sand dunes (TU 2009, all sites)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-4.6%	-1.2%	-0.5%	-0.3%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-9.6%	-2.5%	-1.1%	-0.6%	-	-
Graminoid cover	n/a	8-15 kg N ha^{-1} yr^{-1}	+3.91%	+1.02%	+0.46%	+0.26%	-	-
Forb SR	33 spp.	8-15 kg N ha^{-1} yr^{-1}	-4.6%	-1.2%	-0.5%	-0.3%	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-2.8%	-1.4%	-1.0%	-0.7%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-4.2%	-2.1%	-1.4%	-1.1%	-	-
Acid grasslands (BEGIN)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-0.7%	-0.7%	-0.6%	-0.6%	-0.5%	-0.4%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

Summary of relationships between nitrogen deposition and species richness/cover by habitat expressed as a percentage of the maximum in a habitat. Incremental effect of 1 kg increase in N deposition shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 1 kg increase in N deposition at different background N deposition levels					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
All habitats (TU 2009)								
Total species richness (SR)	77 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.6 % of maximum number of species/kg N increase					
Upland heath (TU 2009)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-5.7 %	-2.9 %	-2.0 %	-1.4 %	-1.2 %	-1.0 %
Lichen SR	11 spp.	10-20 kg N ha^{-1} yr^{-1}	-5.4 %	-2.7 %	-1.8 %	-1.8 %	-1.0 %	-1.0 %
Graminoid SR	7 spp.	10-20 kg N ha^{-1} yr^{-1}	-7.0 %	-2.9 %	-2.9 %	-1.4 %	-1.4 %	-1.0 %
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.5 %	no change	+0.4 %	+0.8 %	+1.2 %	+1.6 %
Upland heath (MRS)*								
Total SR	16 spp.	10-20 kg N ha^{-1} yr^{-1}	-3.4 %	-3.1 %	-2.5 %	-1.9 %	-1.3 %	-0.3 %
Lowland heath (TU 2009)								
Total SR	37 spp.	10-20 kg N ha^{-1} yr^{-1}	-6.2 %	-3.5 %	-2.2 %	-1.6 %	-1.4 %	-1.0 %
Moss SR	12 spp.	10-20 kg N ha^{-1} yr^{-1}	-5.8 %	-2.5 %	-1.7 %	-1.7 %	-1.7 %	-0.9 %
Graminoid SR	9 spp.	10-20 kg N ha^{-1} yr^{-1}	-17.8%	-4.4 %	-2.2 %	-1.1 %	-1.1 %	-0.5 %
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.6 %	no change	+0.5 %	+1.05 %	+1.6 %	+2.2 %
Bog (TU 2009)								
Total SR	32 spp.	5-10 kg N ha^{-1} yr^{-1}	-0.9 % of maximum number of species/kg N increase					
Lichen SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-1.7 %					
Forb SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-7.7 %	-3.9 %	-2.6 %	-1.9 %	-1.6 %	-1.3%
Graminoid cover	-	5-10 kg N ha^{-1} yr^{-1}	+1.5 % cover/kg N increase					
Sand dunes (TU 2009, all sites)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-10.1%	-2.6 %	-1.2 %	-0.6 %	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-21.3%	-5.0 %	-2.5 %	-1.3 %	-	-
Graminoid cover	n/a	8-15 kg N ha^{-1} yr^{-1}	+ 8.6 %	+ 2.2 %	+ 1.0 %	+ 0.5 %	-	-
Forb SR	33 spp.	8-15 kg N ha^{-1} yr^{-1}	-10.3%	-2.4 %	-1.2 %	-0.6 %	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-4.4 %	-2.2 %	-1.4 %	-1.0 %	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-21.3%	-5.6 %	-2.5 %	-1.3 %	-	-
Sand dunes TU 2009 + 2002 (Fixed dune grasslands)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-4.4 %	-2.2 %	-1.4 %	-1.0 %	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-8.9 %	-4.4 %	-3.1 %	-2.5 %	-	-
Acid grasslands (BEGIN)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-1.5 %	-1.4 %	-1.2 %	-1.1 %	-1.0%	-0.9%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

Summary of relationships between nitrogen deposition and species richness by habitat expressed as a percentage of the maximum in a habitat. Change in cover expresses as an absolute percentage. Incremental effect of a 2 kg increase in N deposition shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 2.0 kg increase in N deposition at different background N deposition levels					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
All habitats (TU 2009)								
Total Species Richness (SR)	77 spp.	10-20 kg N ha^{-1} yr^{-1}	-3.2 % of maximum number of species					
Upland heath (TU 2009)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-9.7%	-5.3%	-3.6%	-2.7%	-2.2%	-1.9%
Lichen SR	11 spp.	10-20 kg N ha^{-1} yr^{-1}	-9.7%	-5.3%	-3.6%	-2.8%	-2.2%	-1.9%
Graminoid SR	7 spp.	10-20 kg N ha^{-1} yr^{-1}	-11.0%	-5.9%	-4.1%	-3.1%	-2.5%	-2.1%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-0.8%	+0.1%	+0.9%	+1.8%	+2.6%	+3.5%
Upland heath (MRS)*								
Total SR	16 spp.	10-20 kg N ha^{-1} yr^{-1}	-7.2%	-5.8%	-4.5%	-3.1%	-1.7%	-0.3%
Lowland heath (TU 2009)								
Total SR	37 spp.	10-20 kg N ha^{-1} yr^{-1}	-10.2%	-5.5%	-3.8%	-2.9%	-2.3%	-2.0%
Moss SR	12 spp.	10-20 kg N ha^{-1} yr^{-1}	-9.2%	-5.0%	-3.4%	-2.6%	-2.1%	-1.8%
Graminoid SR	9 spp.	10-20 kg N ha^{-1} yr^{-1}	-24.8%	-7.2%	-3.4%	-2.0%	-1.3%	-0.9%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-1.1%	-0.1%	+0.9%	+1.9%	+2.9%	+3.9%
Bog (TU 2009)								
Total SR	32 spp.	5-10 kg N ha^{-1} yr^{-1}	-1.9%					
Lichen SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-4.3%					
Forb SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-13.1%	-7.1%	-4.9%	-3.7%	-3.0%	-2.5%
Graminoid cover	-	5-10 kg N ha^{-1} yr^{-1}	+2.7%					
Sand dunes (TU 2009, all sites)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-14.4%	-4.2%	-2.0%	-1.1%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-30.1%	-8.8%	-4.1%	-2.4%	-	-
Graminoid cover	n/a	8-15 kg N ha^{-1} yr^{-1}	+12.3%	+3.6%	+1.7%	+1.0%	-	-
Forb SR	33 spp.	8-15 kg N ha^{-1} yr^{-1}	-14.6%	-4.2%	-2.0%	-1.2%	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-9.9%	-5.4%	-3.7%	-2.8%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-14.7%	-8.0%	-5.5%	-4.2%	-	-
Acid grasslands (BEGIN)								
Total species richness	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-2.9%	-2.7%	-2.4%	-2.2%	-2.0%	-1.7%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

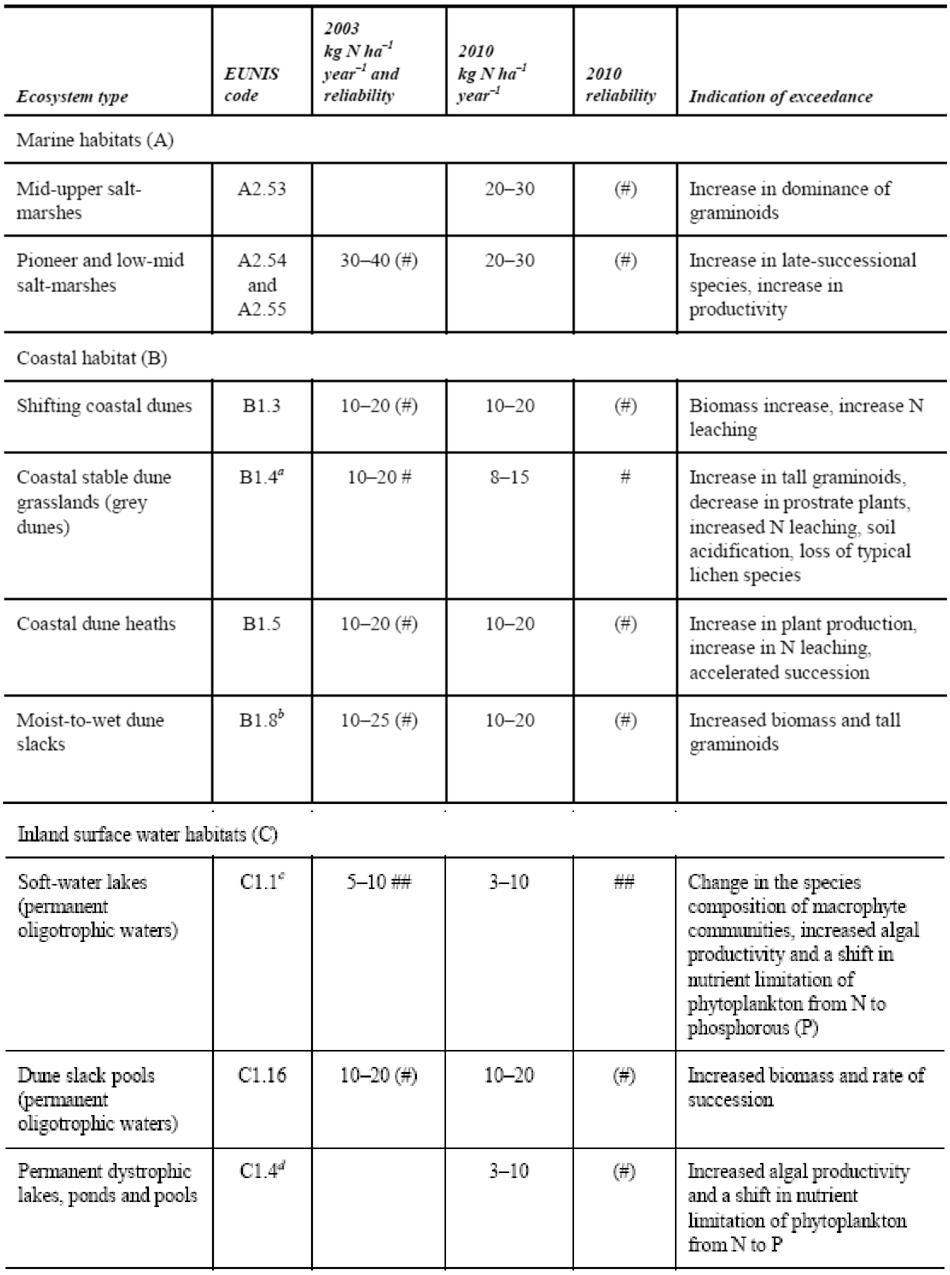
Summary of relationships between nitrogen deposition and species richness by habitat expressed as a percentage of the maximum in a habitat. Change in cover expresses as an absolute percentage. Incremental effect of a 5.0 kg increase in N deposition shown.

Survey/ Habitat/	Max. species richness	Habitat/species critical load	Change in species richness expressed as a % of maximum species richness recorded in habitat with a 5.0 kg increase in N deposition at different background N deposition levels					
			5 kg N	**10 kg N**	**15 kg N**	**20 kg N**	**25 kg N**	**30 kg N**
All habitats (TU 2009)								
Total species richness (SR)	77 spp.	10-20 kg N ha^{-1} yr^{-1}	-8 % of maximum number of species					
Upland heath (TU 2009)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-20.0%	-11.7%	-8.3%	-6.4%	-5.3%	-4.4%
Lichen SR	11 spp.	10-20 kg N ha^{-1} yr^{-1}	-20.0%	-11.7%	-8.3%	-6.5%	-5.3%	-4.5%
Graminoid SR	7 spp.	10-20 kg N ha^{-1} yr^{-1}	-22.6%	-13.2%	-9.4%	-7.3%	-5.9%	-5.0%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-1.3%	+0.9%	+3.0%	+5.1%	+7.2%	+9.3%
Upland heath (MRS)*								
Total SR	16 spp.	10-20 kg N ha^{-1} yr^{-1}	-17.0%	-13.6%	-10.1%	-6.7%	-3.3%	-
Lowland heath (TU 2009)								
Total SR	37 spp.	10-20 kg N ha^{-1} yr^{-1}	-21.1%	-12.3%	-8.7%	-6.8%	-5.5%	-4.7%
Moss SR	12 spp.	10-20 kg N ha^{-1} yr^{-1}	-19.0%	-11.1%	-7.9%	-6.1%	-5.0%	-4.2%
Graminoid SR	9 spp.	10-20 kg N ha^{-1} yr^{-1}	-43.3%	-14.4%	-7.2%	-4.3%	-2.9%	-2.1%
Graminoid cover	n/a	10-20 kg N ha^{-1} yr^{-1}	-2.0%	+0.5%	+3.0%	+5.5%	+8.0%	+10.5%
Bog (TU 2009)								
Total SR	32 spp.	5-10 kg N ha^{-1} yr^{-1}	-4.7%					
Lichen SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-10.8%					
Forb SR	6 spp.	5-10 kg N ha^{-1} yr^{-1}	-26.9%	-15.7%	-11.2%	-8.7%	-7.1%	-6.0%
Graminoid cover	-	5-10 kg N ha^{-1} yr^{-1}	+6.8%					
Sand dunes (TU 2009, all sites)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-25.3%	-8.4%	-4.2%	-2.5%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-52.8%	-17.6%	-8.8%	-5.3%	-	-
Graminoid cover	n/a	8-15 kg N ha^{-1} yr^{-1}	+21.5%	+7.2%	+3.6%	+2.2%	-	-
Forb SR	33 spp.	8-15 kg N ha^{-1} yr^{-1}	-25.5%	-8.5%	-4.2%	-2.5%	-	-
Sand dunes TU 2009 (pH ≥6.5)								
Total SR	77 spp.	8-15 kg N ha^{-1} yr^{-1}	-20.3%	-11.9%	-8.4%	-6.5%	-	-
Moss SR	16 spp.	8-15 kg N ha^{-1} yr^{-1}	-30.2%	-17.7%	-12.6%	-9.7%	-	-
Acid grasslands (BEGIN)								
Total SR	42 spp.	10-20 kg N ha^{-1} yr^{-1}	-7.2%	-6.5%	-5.9%	-5.3%	-4.7%	-4.1%

* in the upland heath MRS survey quadrat size was 0.5 x 0.5 m. This produced different results than the other surveys which used 2 x 2 m quadrats.

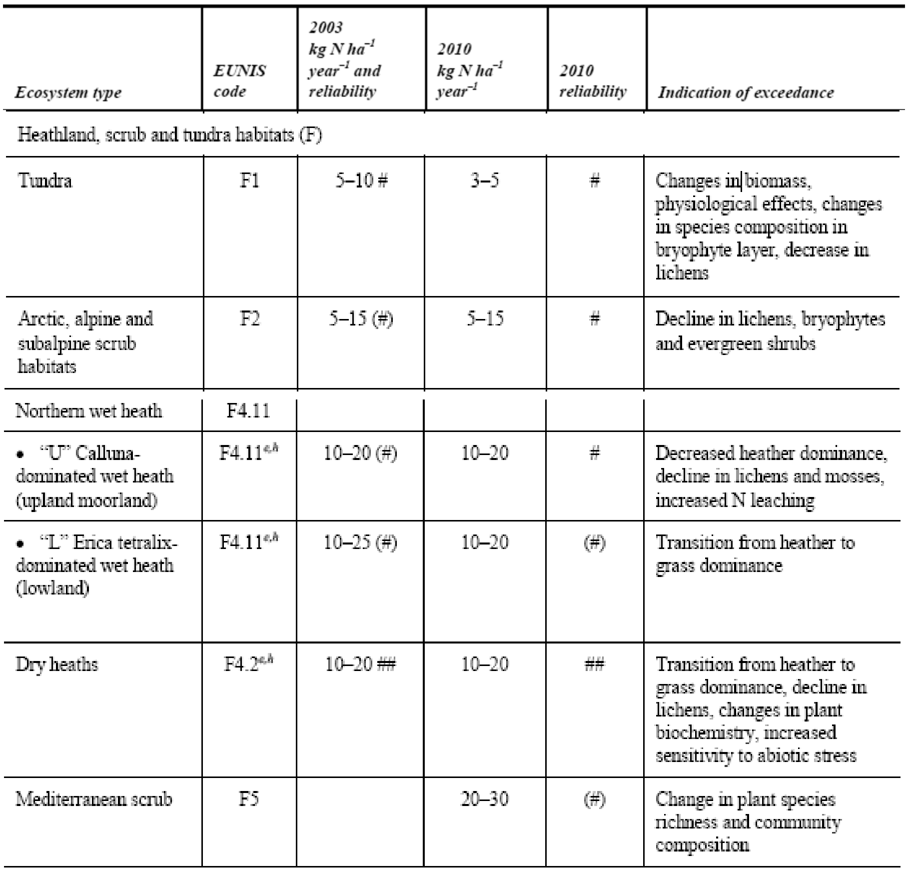
Appendix 6: Current critical loads for all habitats taken from ECE Empirical critical loads and dose-response relationships

Overview of empirical critical loads for nitrogen deposition (kg N ha^{-1} year^{-1}) to natural and seminatural ecosystems (column 1), arranged according to EUNIS class and level (column 2), as originally established in 2002 and reported in 2003 (column 3) and as revised in 2010 (column 4). The reliability is expressed in qualitative terms: ## reliable; # quite reliable; and (#) expert judgement (column 5). Column 6 provides a selection of effects that can occur when critical load are exceeded. Changes with respect to values of 2003 are indicated in bold.) For more information see Defra Report AQ801 Hall *et al*. (2011).



Ecosystem type	*EUNIS code*	*2003 kg N ha^{-1} year^{-1} and reliability*	*2010 kg N ha^{-1} year^{-1}*	*2010 reliability*	*Indication of exceedance*
Marine habitats (A)					
Mid-upper salt-marshes	A2.53		20–30	(#)	Increase in dominance of graminoids
Pioneer and low-mid salt-marshes	A2.54 and A2.55	30–40 (#)	20–30	(#)	Increase in late-successional species, increase in productivity
Coastal habitat (B)					
Shifting coastal dunes	B1.3	10–20 (#)	10–20	(#)	Biomass increase, increase N leaching
Coastal stable dune grasslands (grey dunes)	B1.4[a]	10–20 #	8–15	#	Increase in tall graminoids, decrease in prostrate plants, increased N leaching, soil acidification, loss of typical lichen species
Coastal dune heaths	B1.5	10–20 (#)	10–20	(#)	Increase in plant production, increase in N leaching, accelerated succession
Moist-to-wet dune slacks	B1.8[b]	10–25 (#)	10–20	(#)	Increased biomass and tall graminoids
Inland surface water habitats (C)					
Soft-water lakes (permanent oligotrophic waters)	C1.1[c]	5–10 ##	3–10	##	Change in the species composition of macrophyte communities, increased algal productivity and a shift in nutrient limitation of phytoplankton from N to phosphorous (P)
Dune slack pools (permanent oligotrophic waters)	C1.16	10–20 (#)	10–20	(#)	Increased biomass and rate of succession
Permanent dystrophic lakes, ponds and pools	C1.4[d]		3–10	(#)	Increased algal productivity and a shift in nutrient limitation of phytoplankton from N to P

Ecosystem type	*EUNIS code*	*2003 kg N ha^{-1} $year^{-1}$ and reliability*	*2010 kg N ha^{-1} $year^{-1}$*	*2010 reliability*	*Indication of exceedance*
Mire, bog and fen habitats (D)					
Raised and blanket bogs	D1[e]	5–10 ##	5–10	##	Increase in vascular plants, altered growth and species composition of bryophytes, increased N in peat and peat water
Valley mires, poor fens and transition mires	D2[f]	10–20 #	10–15	#	Increase in sedges and vascular plants, negative effects on bryophytes
Rich fens	D4.1[g]	15–35 (#)	15–30	(#)	Increase in tall graminoids, decrease in bryophytes
Montane rich fens	D4.2[g]	15–25 (#)	15–25	(#)	Increase in vascular plants, decrease in bryophytes
Grasslands and tall forb habitats (E)					
Subatlantic semi-dry calcareous grassland	E1.26	15–25 ##	15–25	##	Increase in tall grasses, decline in diversity, increased mineralization, N leaching; surface acidification
Mediterranean xeric grasslands	E1.3		15–25	(#)	Increased production, dominance by graminoids
Non-Mediterranean dry acid and neutral closed grassland	E1.7[h]	10–20 #	10–15	##	Increase in graminoids, decline of typical species, decrease in total species richness
Inland dune pioneer grasslands	E1.94[h]	10–20 (#)	8–15	(#)	Decrease in lichens, increase in biomass
Inland dune siliceous grasslands	E1.95[h]	10–20 (#)	8–15	(#)	Decrease in lichens, increase in biomass, increased succession
Low and medium altitude hay meadows	E2.2	20–30 (#)	20–30	(#)	Increase in tall grasses, decrease in diversity
Mountain hay meadows	E2.3	10–20 (#)	10–20	(#)	Increase in nitrophilous graminoids, changes in diversity
Moist and wet oligotrophic grasslands					
• Molinia caerulea meadows	E3.51	15–25 (#)	15–25	(#)	Increase in tall graminoids, decreased diversity, decrease of bryophytes
• Heath (Juncus) meadows and humid (Nardus stricta) swards	E3.52	10–20 #	10–20	#	Increase in tall graminoids, decreased diversity, decrease of bryophytes
Moss- and lichen-dominated mountain summits	E4.2	5–10 #	5–10	#	Effects upon bryophytes or lichens
Alpine and subalpine acid grasslands	E4.3		5–10	#	Changes in species composition; increase in plant production
Alpine and subalpine calcareous grasslands	E4.4		5–10	#	Changes in species composition; increase in plant production



Ecosystem type	*EUNIS code*	*2003 kg N ha^{-1} year^{-1} and reliability*	*2010 kg N ha^{-1} year^{-1}*	*2010 reliability*	*Indication of exceedance*
Heathland, scrub and tundra habitats (F)					
Tundra	F1	5–10 #	3–5	#	Changes in biomass, physiological effects, changes in species composition in bryophyte layer, decrease in lichens
Arctic, alpine and subalpine scrub habitats	F2	5–15 (#)	5–15	#	Decline in lichens, bryophytes and evergreen shrubs
Northern wet heath	F4.11				
• "U" Calluna-dominated wet heath (upland moorland)	F4.11^{e,h}	10–20 (#)	10–20	#	Decreased heather dominance, decline in lichens and mosses, increased N leaching
• "L" Erica tetralix-dominated wet heath (lowland)	F4.11^{e,h}	10–25 (#)	10–20	(#)	Transition from heather to grass dominance
Dry heaths	F4.2^{e,h}	10–20 ##	10–20	##	Transition from heather to grass dominance, decline in lichens, changes in plant biochemistry, increased sensitivity to abiotic stress
Mediterranean scrub	F5		20–30	(#)	Change in plant species richness and community composition

Ecosystem type	*EUNIS code*	*2003 kg N ha^{-1} year^{-1} and reliability*	*2010 kg N ha^{-1} year^{-1}*	*2010 reliability*	*Indication of exceedance*
Forest habitats (G)					
Fagus woodland	G1.6		10–20	(#)	Changes in ground vegetation and mycorrhiza, nutrient imbalance, changes soil fauna
Acidophilous Quercus-dominated woodland	G1.8		10–15	(#)	Decrease in mycorrhiza, loss of epiphytic lichens and bryophytes, changes in ground vegetation
Meso- and eutrophic Quercus woodland	G1.A		15–20	(#)	Changes in ground vegetation
Mediterranean evergreen (Quercus) woodland	G2.1		3–7	(#)	Changes in epiphytic lichens
Abies and Picea woodland	G3.1		10–15	(#)	Decreased biomass of fine roots, nutrient imbalance, decrease in mycorrhiza, changed soil fauna
Pinus sylvestris woodland south of the taiga	G3.4		5–15	#	Changes in ground vegetation and mycorrhiza, nutrient imbalances, increased N_2O and NO emissions
Pinus nigra woodland	G3.5		15	(#)	Ammonium accumulation
Mediterranean Pinus woodland	G3.7		3–15	(#)	Reduction in fine root biomass, shift in lichen community
Spruce taiga woodland	G3.A[i]	10–20 #	5–10	##	Changes in ground vegetation, decrease in mycorrhiza, increase in free algae
Pine taiga woodland	G3.B[i]	10–20 #	5–10	#	Changes in ground vegetation and in mycorrhiza, increase occurrence of free algae
Mixed taiga woodland with Betula	G4.2		5–8	(#)	Increased algal cover
Mixed Abies-Picea Fagus woodland	G4.[0]		10–20	(#)	
Overall					
Broadleaved deciduous woodland	G1[k)]	10–20 #	10–20	##	Changes in soil processes, nutrient imbalance, altered composition mycorrhiza and ground vegetation
Coniferous woodland	G3[k,l]	10–20 #	5–15	##	Changes in soil processes, nutrient imbalance, altered composition mycorrhiza and ground vegetation

[a] For acid dunes, use the 8–10 kg N ha-1 year-1 range, for calcareous dunes use the 10–15 kg ha-1 year-1 range.

[b] Use the lower end of the range with low base cation availability. Use the higher end of the range with high base cation availability.

[c] This critical load should only be applied to oligotrophic waters with low alkalinity with no significant agricultural or other human inputs. Use the lower end of the range for boreal and alpine lakes, use the higher end of the range for Atlantic softwaters.

[d] This critical load should only be applied top waters with low alkalinity with no significant agricultural or other direct human inputs. Use the lower end of the range for boreal and alpine dystrophic lakes.

[e] Use the high end of the range with high precipitation and the low end of the range with low precipitation. Use the low end of the range for systems with a low water table, and the high end of the range for systems with a high water table. Note, that water table can be modified by management.

[f] For D2.1 (quaking fens and transition mires) use lower end of the range (#).

[g] For high latitude systems use lower end of the range.

[h] Use the high end of the range when sod cutting has been practiced; use the lower end of the range with low intensity management.

[i] In 2003 presented as overall value for boreal forests.

[j] Included in studies which were classified into G1.6 and G3.1.

[k] In 2003 presented as overall value for temperate forests.

[l] For application at broad geographical scales.

Annex D: NBN Atlas occurrence download at https://nbnatlas.org accessed on 28th June 2023. Data provided by the following providers:

- Records provided by British Bryological Society, accessed through NBN Atlas website. (). For more information: [redacted]@ceh.ac.uk, or https://registry.nbnatlas.org/public/show/dp74
- Blockeel TL, Bosanquet SDS, Hill M , Preston C (eds) 2014. Atlas of British and Irish bryophytes. Newbury: Pisces Publications. (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email [redacted]@ceh.ac.uk, or https://registry.nbnatlas.org/public/show/dr859

Annex E: Olff, H., Leeuw, de L., Bakker, J.P., Platerink R. J. & van Wijnen H. J. (1997). Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology, Vol. 85, No. 6 pp. 799-814.

Vegetation succession and herbivory in a salt marsh

Olff, H; de Leeuw, J; Bakker, J P; Platerink, R J; van Wijnen, H J; de Munck, W

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Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient

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Summary

1 The relationships between soil development, vertical vegetation zonation, vegetation succession and herbivory by Brent geese, *Branta bernicla,* were studied in a coastal salt marsh. We were able to analyse up to 100 years of salt marsh development by comparing sites where vegetation succession had progressed for various periods of time. These data were related to a continuous daily record of high water levels measured since 1824.

2 Most elevational variation in edaphic conditions (and therefore vertical vegetation zonation) could be attributed to variation in height of the sandy subsoil, as rapid dune formation occurs on the beaches early in succession. In the intermediate part of this elevational gradient, the maximum annual increase of 1.2 mm of silt corresponded to an annual increase of 5.6 g N m-^{2} in the topsoil (0-50cm). The average sea level rise in this area over the last 170 years was 0.63 mm yeac^{1}. A sedimentation model suggests that this has had strong effects on sedimentation and the annual inundation frequency in the mid-part of the elevational gradient, thus affecting vegetation zonation on the salt marsh. For the major part of the investigated transects, sea level rise has probably speeded up succession due to an increased rate of sedimentation.

3 The occurrence and dominance of all plant species were recorded in 3927 plots, and and for the 11 most common species response surfaces were calculated for their dependence on elevation and transect age. Most plant species were clearly separated along these axes. Most halophytic species, which were preferred by the geese, occurred early in succession and low on the gradient, where we observed the highest densities of Brent geese grazing. Forage quality of *Festuca rubra* increased towards the lower salt marsh. Other preferred forage species *(Puccinellia maritima* and *Plantago maritima)* were gradually displaced during succession by the tall grass *Elymus athericus,* especially in the mid- and upper salt marsh. Few geese grazed in areas where *Elymus* was dominant.

4 Herbivores first increased in numbers but then declined along a gradient of primary productivity. We propose that declining forage quality (due to changing vegetation composition during succession) is a better explanation for this pattern than the classic explanation of predator control of herbivores at high levels of primary productivity. This quality threshold hypothesis, as an alternative explanation of the exploitation ecosystem hypothesis, is expected to hold especially where smaller (quality-sensitive) herbivores such as geese are present.

5 Grazing by cattle in a 200-year-old part of the salt marsh led to the disappearance

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of *Elymus athericus*, to establishment of early successional halophytes and a return of Brent geese. Grazing by a larger herbivore therefore facilitated conditions for smaller herbivores by preventing the dominance of plant species that were good light competitors, and thus improved forage quality. Populations of these small herbivores could then become regulated by predators, although none was present at our site.

Keywords: facilitation, herbivory, nitrogen accumulation, salt marsh, sea level rise, succession

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Introduction

Vegetation succession on initially bare substrates involves the accumulation of nutrients in the soil, leading to an increase in nutrient availability, an increase in plant biomass and changes in species composition of the vegetation (Crocker & Major 1955; Bormann & Sidle 1990; Olff *et al.* 1993). Herbivore densities are predicted to increase with increasing primary production (Oksanen *et al.* 1981; McNaughton *et al.* 1989), until a level of primary production is reached where either regulation of herbivores by predators becomes important (Hairston *et al.* 1960; Oksanen *et al.* 1981) or where the food quality of the plant biomass itself becomes a limiting factor to herbivores (van de Koppel *et al.* 1996). This latter effect may occur when tall, late successional plant species (with support structures) represent poor quality forage. A simultaneous analysis of changes in soil nutrients, plant species' abundances and herbivore densities during primary succession has not yet been performed for any terrestrial ecosystem, and may provide a test of these contrasting explanations.

The salt marsh in the eastern part of the island of Schiermonnikoog offers an opportunity for investigating the interactions between soil changes, vegetation and herbivory, since different stages of salt marsh development are spatially contiguous, as the island is gradually extending eastwards. The formation of primary dunes on the islands leads to differences in elevation that are associated with differences in inundation frequency and sedimentation rate and result in the vertical zonation of salt-marsh vegetation (Gray 1992; De Leeuw *et al.* 1993). Besides changing nutrient availability, shifts in tidal inundation rates may explain part of the observed successional dynamics. The potential importance of this was investigated by modelling the changes in the tidal inundation frequency during the last 100 years using data on sea level change and silt accretion.

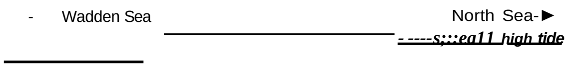
The area is important for spring staging of Brent geese, *Branta bernicla* (Prop & Deerenberg 1991). During April and May, the geese increase their body mass by about 33% while foraging in this area (Ebbinge 1992) and variation in their breeding success in the Arctic could be partially explained by their body weight at the end of spring staging (Ebbinge 1992). This means that selection of a suitable area for foraging, based on the presence of appropriate food plant species, is important for the geese. The large increase in body size is only possible through very selective foraging for only those plant species of high nutritional quality (Prop & Deerenberg 1991). Since the geese leave the area in late May (at the start of the growing season) they might not be able to exert much control over the vegetation composition of this salt marsh, in contrast to the situation on their breeding grounds (Kerbes *et al.* 1990; Hik *et al.* 1992; Srivastava & Jefferies 1996).

We examined the long-term dynamics of inundation frequency, silt accretion, plant species distribution and Brent goose densities at different elevations on the salt marsh, utilizing the salt-marsh chronosequence. We hypothesized that silt accretion and soil nitrogen accumulation during primary succession are linked with an increase in goose densities, up to a point where unpalatable plant species become dominant in the vegetation, which becomes unattractive for the geese. Bigger herbivores with a lower requirement for high-quality forage, however, may be able to utilize such late successional species and, may again attract geese by removing tall, productive, relatively unpalatable species (facilitation). This hypothesis was tested in a late successional stage on the salt marsh at Schiermonnikoog, where we analysed the effect of cattle grazing on vegetation composition and goose densities.

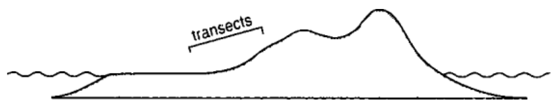
Outline of the system and hypotheses

Figure 1 gives a schematic view of the process of salt-marsh formation on Schiermonnikoog, one of the Dutch West Frisian islands 53°30'N, 6°10'E). In the first stage, embryonic dunes are formed on bare beach surfaces, mainly due to sand trapping by *Elymus farctus.* During the next phase of dune succession, establishment of *Ammophila arenaria* and continued sand trapping leads to formation oflarge dunes. After dunes are formed, the sand flat behind the dunes is no longer frequently inundated by tidal water from the North Sea: inundation occurs only from the Wadden sea at high spring tides, and the reduced

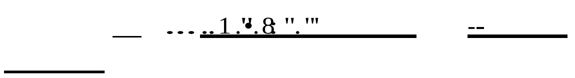
(a) Initial situation: bare sand plate



(b) Sand dune formation



(c) Salt marsh formation due to sedimentation



(d) Cliff formation during transgression

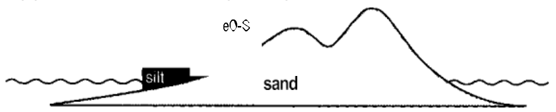


Fig. 1 Four stages of salt-marsh formation on coastal bar islands; the black layer represents the silt that is deposited on the sandy subsoil.

turbulence of the water results in silt sedimentation. Inundation rates decrease to zero towards the foot of a dune, leading to decreased sedimentation, whereas at the lowest elevational positions, high rates of water movement also prevent sedimentation. Sedimentation will therefore be highest at intermediate elevational positions on the young salt marsh (Fig. 1c). During episodes of strong sea level rise, the lower part of the salt marsh may be eroded (Dijkema *et al.* 1991) (Fig. 1d).

A hypothetical scheme for salt marsh development is given in Fig. 2. Increasing sedimentation is expected to lead to a higher nutrient (especially N) availability, resulting in more plant biomass to contribute to silt trapping. In the longer term, the surface level will increase with continued sedimentation, leading to a decreased inundation frequency. Sedimentation therefore results in a negative feedback that increasingly restricts further sedimentation (Fig. 2). The increased primary productivity provides more food for herbivores, which potentially could enhance their density. The forage quality at lower elevations and in the earlier stages of salt marsh succession is predicted to be very high, due to constraints on primary productivity imposed by salinity and waterlogging (i.e. high protein/biomass ratio) (White 1993). However, when herbivores are not able to graze down vegetation to a short sward, tall plants (good light competitors) may become dominant as succession progresses, leading to a decrease in forage quality and to a decrease in abundance of quality-sensitive herbivores.

Description of the chronosequence

Several different stages of salt-marsh development can be found adjacent to one another on the island of Schiermonnikoog, since changing sea currents cause the island to extend eastwards, so that the western part of the island is the oldest part and young stages of salt marsh development can be found in the eastern part of the island. This process was quantified by mapping the vegetated areas from aerial photographs, taken in 1927, 1952, 1969 and 1980 (Fig. 3). In addition, we used a topographical map (1:50000) surveyed in 1853 that gave a good indication of the extent of vegetated areas. Based on this information, we placed seven transects, representing sites of different stages of salt-marsh development (Fig. 3). Primary succession on these transects was estimated to have progressed by 1992 for 10 years (transect 1), 25 years (transect 2), 35 years (transect 3), 60 years (transect 4) and 100 years (transect 5). We also established two transects on the oldest part of the salt marsh (transects 6 and 7), where silt accretion has occurred for at least 200 years and grazing by heifers from local farms has taken place for most of that time (Bakker 1989). In 1972, grazers were excluded from transect 6 in order to study the effect of grazing on the vegetation composition (Bakker 1989). Each transect was positioned at the foot of a dune slope (Fig. 1). Along the length of these transects we determined elevation, rates of silt accretion and nitrogen accumulation, vegetation composition and faecal dropping rates of Brent geese (reflecting duration of grazing measured over the whole season). Transects 6 and 7 were not used in the reconstruction of salt-marsh succession, since we expected that cattle grazing had had a strong impact on the species composition of the vegetation.

During the early 1980s, the prime area for grazing by Brent geese was in the vicinity of transect 3. Since then, the prime area for grazing has moved gradually eastwards, and was located in the vicinity of transect 2 in the early 1990s (R. Drent, personal communication).

Methods

ELEVATION MEASUREMENTS AND SOIL SAMPLING

Each transect consisted of a grid of 11 columns and a variable number of rows of 1-m^2 plots (51-60, depending on the local topography) located adjacent to each other in a grid, with the longest dimension of the grid extending up the slope of the main elevational gradient. For every 1-m^2 plot we measured elevation (m) with respect to Dutch Ordnance Level **(NAP)** using a theodolite. In the middle of each plot we took a soil sample with an auger, resulting in a total of 561-660 soil samples for each transect. In each sample, a clear distinction could be made between the subsoil consisting of coarse sand, and a dark, organic, silty sediment layer situated on top of this. The thickness of the silt layer was measured for every sample. Elevational variation has two components, the time-inde-

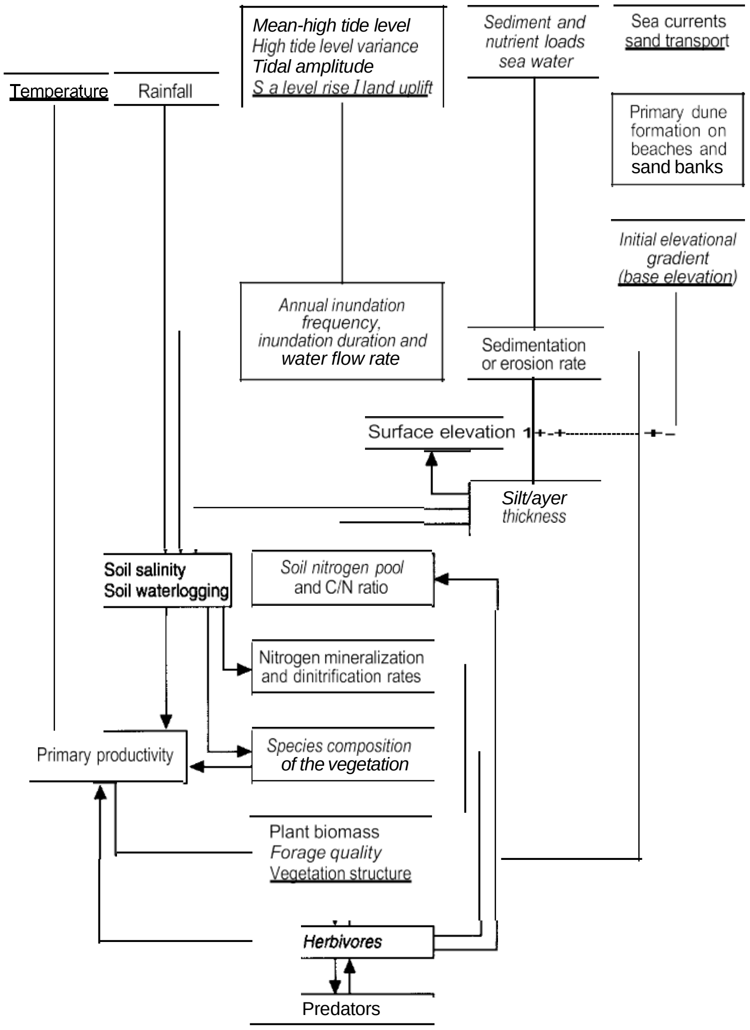


Fig. 2 Schematic view of the relationships between climate, sea level, geomorphology, soil development, vegetation succession, herbivores and predators in coastal salt marsh ecosystems. The features given in italics were investigated in the present study.

pendent elevation of the sandy subsoil (base elevation) and the time-dependent thickness of the silt layer. Surface elevation is thus correlated with age, but by using base elevation (surface elevation minus silt layer thickness), succession can be reconstructed for a given location, and the dependence of silt accumulation and plant species composition on this independent variable can be studied.

At three positions along each transect (low, middle and high elevations) we measured the amount of nitrogen in the topsoil (0-50 cm) by taking samples from the soil layers at 0-5 cm, 5-25 cm and 25-50 cm. Whenever the border between sand and silt fell within one of these layers, we treated that layer as two separate samples. Ten random samples were taken per transect and position and separated into layers, and equivalent samples were pooled prior to the chemical analysis. The bulk density of each layer was determined using volumetric rings (100 cc). The samples were dried for 48 h at 70 °C and finely ground. Total nitrogen concentrations were determined using a Carlo-Erba element analyser. The N accumulation per layer was then calculated by multiplying the N concentration by the bulk density and the thickness of each layer, and these values were added for all layers between 0 and 50cm to obtain the total N amount in the top soil. This N amount was then related to the thickness of the silt layer using linear regression analysis.

SEA LEVEL RISE, INUNDATION FREQUENCY AND SEDIMENTATION MODELLING

High-water levels of each tide have been recorded by Rijkswaterstaat at Schiermonnikoog since 1965. For investigations of longer-term changes we also used similar data recorded at the mainland stations of Zoutkamp (1824-36), Oostmahorn 1927-69 and Lauwersoog 1970-93. Due to the construction of local embankments along the mainland coast, we could not use the same station for the whole period, but at the time periods selected the sites were relatively unaffected by these local embankments and therefore could be used as an indication of high water levels at Schiermonnikoog (K. Doekes, Rijkswaterstaat, personal communication). All data were converted to give an

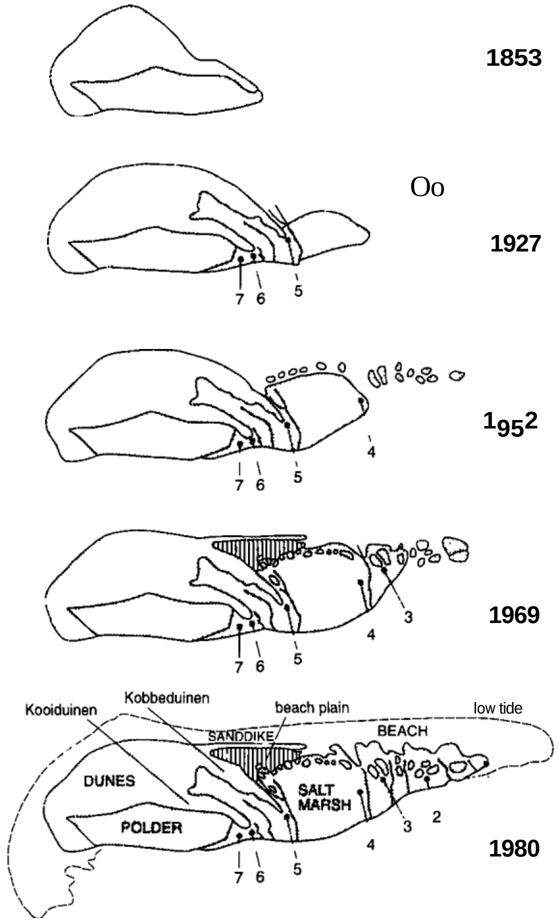


Fig. 3 Reconstruction of salt-marsh development on the Dutch island of Schiermonnikoog. Vegetated areas were mapped from aerial photographs 1927-80 and a topographic map (1853, 1:50000). Three major vegetation types were distinguished: salt-marsh vegetation (heavily shaded), dry-dune vegetation (lightly shaded) and dune-slack vegetation (hatched). The numbers refer to the position of the different aged transects where salt marsh succession in 1992 had progressed for about 10 years(!), 25 years (2), 35 years (3), 60 years (4), 100 years (5) and 200 years (6, 7).

annual mean tidal height. We obtained the average tidal transgression frequencies at Schiermonnikoog (number of times a location at a given elevation is inundated each year) for 5-cm height classes, over the period 1965-92. From these data we calculated the parameters of a regression equation that predicts the annual inundation frequency of a site based on its surface elevation and the annual mean height of tides.

We then utilized the data on silt accretion along the transects of different ages to calibrate a sedimentation model (outlined in Appendix 1), which enables the silt layer thickness at any time at any base elevation to be predicted. The model was developed to investigate whether the observed sedimentation patterns could be understood from a few simple geomorphological and hydrological principles. It was used to evaluate the consequences of the observed sea level rise on sedimentation in this salt marsh.

PLANT SPECIES DISTRIBUTION

During June and July of 1991, we determined in each plot which species were present, and which were the three most abundant species (highest percentage cover, determined subjectively); these were called the dominant species. With the use of these rapid methods we were able to assess all 3927 plots, which would not have been possible with more precise techniques.

For the 11 most frequently recorded species, the observed data on presence and dominance were first related to the base elevation (20-cm classes) and age, by calculating the probability of occurrence of each species for each combination of transect age and height class. For the same species, the statistical significance of the dependence on age and base elevation was tested for transects 1-5 (3180 plots) by calculating a second order response surface including a linear interaction term, after logit transformation of the dependent variable, where the probability P of being present or dominant is given by:

$$P = 1/1 + \exp(c_1 + c_2E + c_3A + c_4E^2 + c_5A^2 + c_6EA) \quad (1)$$

where $c_1, \dots, c_6$ are the parameters of the model, E denotes the base elevation, and A denotes the transect age. Each term was tested for entry in a forward stepwise logistic regression analysis. This model has the advantage that the dependent variable is bound between 0 and 1, and that it fits a bell-shaped response surface, which is an ecologically realistic response (Ter Braak & Looman 1986; Huisman *et al.* 1992). Although skewed response surfaces can theoretically occur, they could not be fitted with this approach; a satisfactory technique for fitting skewed models in more than one dimension is not yet available (Huisman *et al.* 1992). We omitted the vegetation data of transects 6 and 7 from this response analysis, since their history of cattle grazing affected species composition (Bakker 1985; Bakker *et al.* 1985; Bakker 1989). Response surfaces were only calculated for those species which occurred in more than 25% of the plots.

We also calculated for each species a so-called dominance index, which was the ratio of the numbers of plots in which a species was one of the three dominants, divided by the number of plots in which it occurred. A low value of this index indicates species that rarely attain dominance, even when present at high frequencies (subordinates), while a high value indicates species that dominate the vegetation as soon as they establish.

FORAGE QUALITY

Data on forage quality were not collected in this study, but we used unpublished data collected by H. H. T. Prins and R. Ydenberg in the vicinity of transect 3 (Fig. 1) in May 1979. Fifteen samples of *Festuca* *rubra* leaves were taken at different positions on the elevational gradient, which at that time had undergone about 20 years of salt-marsh development. Only the top parts of leaves were collected, as these were the portions grazed by geese. The plant samples were analysed colormetrically for total N after Kjeldahl digestion. Total N amounts were transformed to crude protein concentrations by multiplying values by 6.25.

BRENT GEESE HERBIVORY

Changes in densities of grazing Brent geese in this chronosequence were made based on counts of faecal densities along transects I, 2, 3 and 5, which represent 100 years of succession undisturbed by cattle grazing (Fig. 3). Faeces were also counted along transect 7, in order to investigate the effect of cattle grazing on goose herbivory. Along each transect, we placed two parallel, adjacent lines of 10 circular plots, each of 4 m2, and all plots within and between lines were separated by a distance of 6 m. The 20 plots were therefore equally distributed along each of the transects. Since transect 6 was surrounded by a stout fence to prevent cattle grazing, which also excluded geese, we could not investigate directly the effect of excluding cattle on densities of geese. On 6, 14, 21 and 28 May 1992 we counted numbers of fresh faecal droppings in every plot, and droppings were removed after each count. Fresh droppings were no more than 7 days old, and could be distinguished visually from older droppings that were sometimes deposited in plots by high tides or wind. The faecal dropping counts were used to calculate weekly dropping rates for each plot. This method gives a reliable estimate of the rate of utilization of vegetation by geese (Prop & Deerenberg 1991). These authors concluded, based on visual observations of grazing, removal rates of vegetation by geese and plant remains in faeces, that *Puccinellia maritima, Plantago maritima* and *Triglochin maritima* were the principal food sources of Brent geese. *Festuca rubra* acts as a replacement for *Puccinellia maritima,* when the production of the latter drops. In areas with the highest intensities of grazing by geese (i.e. in the vicinity of transect 2), all newly produced tissue of *Plantago* and *Puccinellia* was effectively removed during the grazing period in April and May (Prop & Deerenberg 1991).

Results

SILT ACCRETION AND NITROGEN ACCUMULATION

We investigated the thickness of the silt layer in relation to base elevation and sediment age (duration of sedimentation) along transects. Average values for 10-cm classes are shown for transects 1-5 in Fig. 4a, together with the number of observations (Fig. 4d).

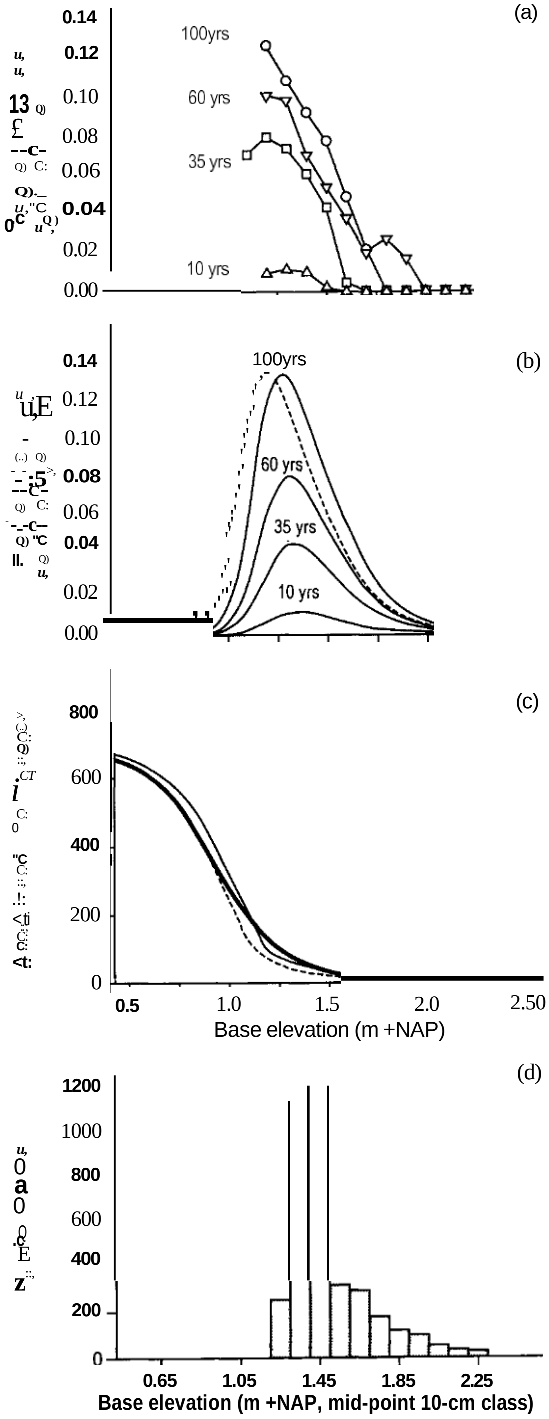


Fig. 4 (a) Dependence of the thickness of the silt layer on the elevation of the sandy subsoil (base elevation) along four transects where vegetation succession had proceeded for 10, 35, 60 and 100 years. Average values are given for 10-cm classes of base elevation. (b) The predicted sedimentation at different base elevations after 10, 35, 60 and 100 years, under the current sea level rise (solid lines) and the predicted sedimentation after 100 years but without sea level rise (dashed line), using the sedimentation model described in Appendix I. (c) The predicted annual inundation frequency of different base elevations after 0 years of sedimentation (thick solid line), 100 years of sedimentation with the current sea level rise (thin solid line, see Fig. 6) and after 100 years of sedimentation without sea level rise (dashed line). (d) The frequency distribution of base elevation for all investigated transects.

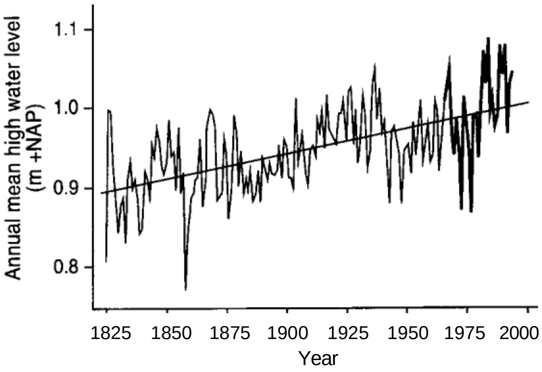


Fig. 6 Sea level rise since 1825 in the eastern part of the Dutch Wadden Sea, reconstructed from different stations (see text), with the linear regression line ($y = -0.2580 + 0.00063x$, $r^2 = 0.34$, $n = 169$, $P < 0.001$). For the recent decades, tidal data from both the mainland station Lauwersoog (thin line) and Schiermonnikoog are shown.

The data show that most plots within transects were situated between 1.30 and 1.50m above Dutch Ordnance Level **(NAP). A** thin silt layer was found along the entire gradient on young transects, while a thicker layer occurred at lower elevations on old transects. Within each transect, silt accretion was highest at about 1.3 m above **NAP** (Fig. 4a). The results indicate that silt accretion over the last century caused a maximum elevational difference of 12cm, which was rather small compared to differences in base elevation, which were found to exceed 100 cm along the transects (Fig. 4).

Total amounts of nitrogen (g m^{-2}) in the upper 50 cm of the soil significantly increased with the thickness of the silt layer (in cm), according to the regression equation $y = 186 + 43x$, $r = 0.90$, $P < 0.001$ (Fig. 5). The intercept of the regression equation represented an estimate of the initial total nitrogen (186 g m^{-2}) in 50cm of sand. The slope indicates that the size of the N pool in the topsoil increased by 43 g m^{-2} with every additional centimetre of silt. The maximum accretion of the silt layer was 12 cm over 100 years, equivalent to an increase in total soil nitrogen of 5.16 g m^{-2} year^{-1}.

SEA LEVEL RISE, INUNDATION FREQUENCY AND SILT ACCRETION

Annual mean high water levels have increased in the area at least since 1824, at an average rate of 0.63 mm yeac^{1} (Fig. 6; $y = -0.2580 + 0.00063x$, $r^2 = 0.34$, $n = 169$, $P < 0.001$). These tidal data and the observed sedimentation rates (Fig. 4a) were used to calibrate a dynamic simulation model for sedimentation (see Appendix 1). Although the model predictions were not independent from the observations, the simulations (Fig. 4b) were similar to the recorded patterns, and suggested that sedimentation in this salt marsh is a relatively simple geomorphological process, dependent on the relationship between elevation and inundation frequency (tidal height and amplitude) and on water sediment loads. It was not necessary to incorporate a feed-back effect of plant biomass on sedimentation rates in order to produce realistic simulations. The simulations were performed using the observed increase in tidal height (Fig. 6) as input data, and also for a scenario where the sea level had remained at the 1824 level of 0.891 m + **NAP** (y-intercept of the linear regression in Fig. 6). The simulations showed that the observed sea level rise has had a profound effect on the amount of sedimentation (Fig. 4b) and on the annual inundation frequency (Fig. 4c) for different parts of the elevation gradient. Peak rates of sedimentation have occurred at higher elevations on the marsh, which has resulted in less sedimentation at low elevations and more sedimentation at higher elevations than would have been found without sea level rise. The largest decrease was predicted at 1.10 m above **NAP** (- 5 cm, a reduction of about 50%), with the largest increase at 1.60m above **NAP** (+2cm, an increase of about 20%): at 1.20 m above **NAP** there would have been little change. Without a sea level rise, the inundation would have decreased during succession over the entire gradient from 1.0 to 1.8 m above **NAP,** but with the observed sea level rise, the inundation frequency decreased during succession at elevations greater than 1.1 m above **NAP,** and increased at lower elevations (Fig. 4c). The decrease in inundation frequency at higher elevations was less then that predicted in the 'no sea level change' scenario (Fig. 4c). Since most observed base elevations were between 1.35 and 1.55 m above **NAP** (Fig. 4d), the observed sea level rise has resulted in increases in both sedimentation and inundation in the majority of plots, compared with simulations assuming a constant sea level (the interpolated 1824 level, Fig. 4c)

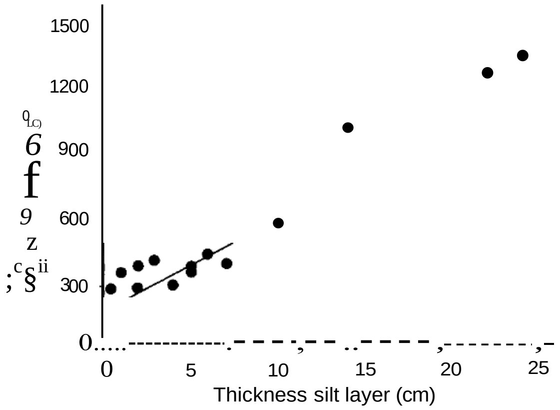


Fig. 5 Total nitrogen pool in the top 50 cm of the soil in relation to the thickness of the silt layer across different ages (duration of sedimentation) and different base elevations.

PLANT SPECIES ZONATION AND VEGETATION SUCCESSION

Only 25 vascular plant species (all halophytes) were recorded in the 3180 plots of transects 1-5, and 11 species that occurred in more than 25% of the plots were used in the regression analyses (basic data in Fig. 7). A significant logistic regression was fitted, for both presence and dominance of each of these species (Table 1). The effect of age was always significant, indicating that for every species these variables showed a trend with time. Values for presence and dominance for about half of the species reached a maximum during succession (significant quadratic effect of age; Table 1), while corresponding values for all other species either increased or decreased continuously. A similar pattern was found for the effect of elevation. The interaction effect of age x elevation was significant for almost every species (Table 1), which can be interpreted as either the distribution of species along the elevational gradient changed with succession, or the successional dynamics of individual species were different for each elevational position. The interaction term was not significant for the presence/absence data of *Elymus athericus.* The curves based on the calculated logistic regression equations (Figs 8 and 9 and Table 1) gave a good fit to the recorded observations (compare with Fig. 7). Results of the presence and dominance of plant species were qualitatively similar but the distributions in time and space of dominance were more constrained than those for presence (Figs 7, 8 and 9).

After 10 years of succession on the lowest sections of the transects (base elevation 1.2 m above **NAP),** the vegetation was dominated by *Spergularia maritima, Suaeda maritima, Limonium vulgare* and *Puccinellia maritima* (Figs 7 and 8). *Limonium* increased further and maintained dominance along the entire successional sequence on the low salt marsh, while the remainder of the above species decreased in dominance. *Spergularia* disappeared, but *Puccinellia* and *Suaeda* remained present at relatively high frequencies. *Festuca rubra, Glaux maritima* and *Artemisia maritima* all increased in presence and dominance during the successional sequence. *Juncus gerardi* increased after 40 years, and became one of the most dominant species in the later stages of succession. The only species which showed a clear maximum in presence and dominance in time was *Atriplex por-*

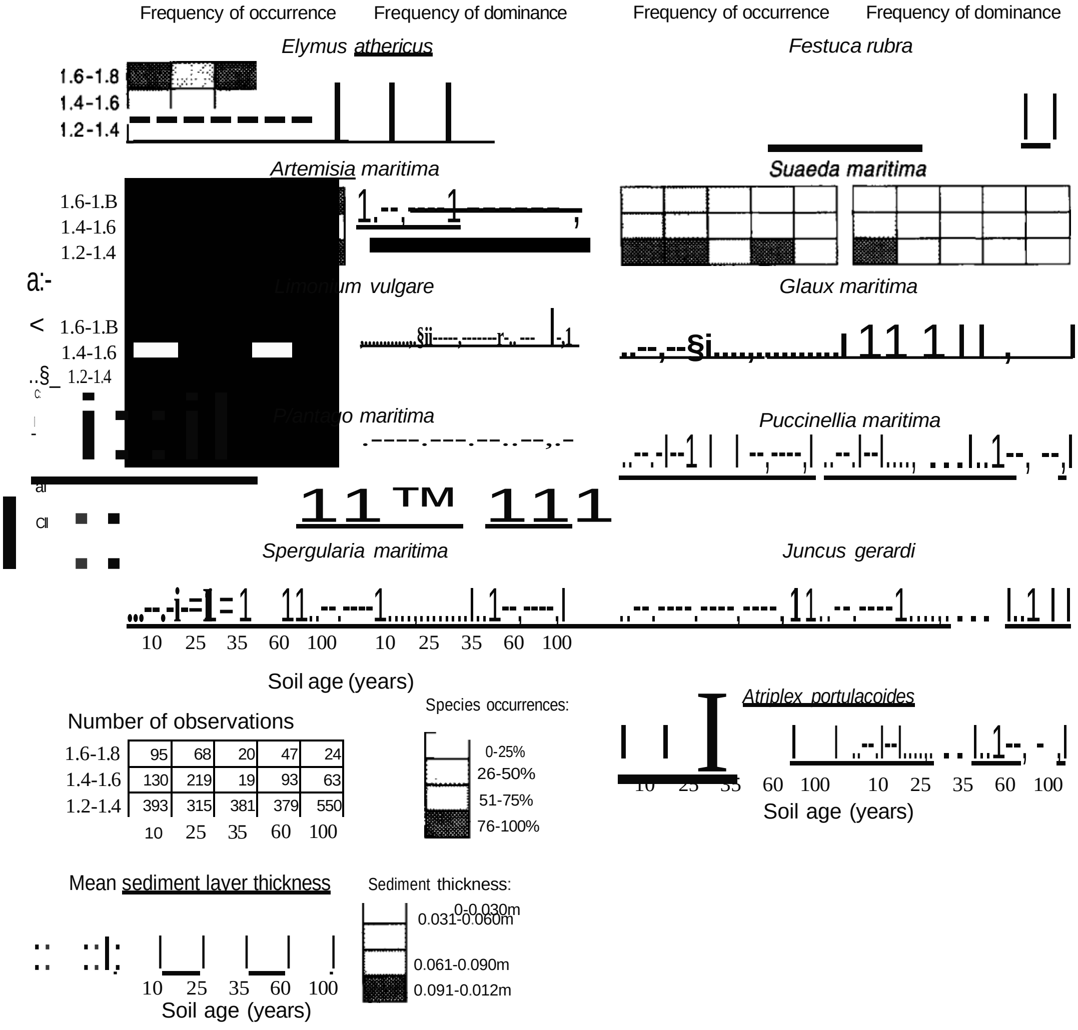


Fig. 7 Observed frequency of occurrence and frequency of dominance (based on cover) of 11 salt-marsh species, as related to transect age (duration of succession) and elevation of the sandy subsoil (base elevation). The average silt layer thickness and the number of observations are given for each combination of age and base elevation class. The darker shades of grey represent higher values of frequency of occurrence or dominance.

Table 1 Parameters of the step-wise logistic regression equation* for the dependence of species presence and dominance on base elevation (in m above **NAP)** and soil age (in years). The number of years succession had progressed was divided by 100 for the parameter calculation. Also the total abundance (% of plots present or dominant) is given for each species, as well as the dominance index

Speciest (with abbreviation)	Regression parameter						Abundance (%)	Dominance indext
	Age	Elevation	Age^2	Elevation^2	Age x elevation	Constant		
Presence								
Elymus athericus (Ea)	20.52	65.08	-14.96	-16.47	0.00	-64.56	30	0.80
Artemisia maritima (Am)	23.37	4.08	-8.30	0.00	-7.93	-7.83	68	0.63
Festuca rubra (Fr)	3.70	48.67	-11.83	-12.69	-13.19	-43.30	65	0.72
Plantago maritima (Pm)	9.51	22.57	1.52	5.96	5.95	-19.80	50	0.36
Puccinellia maritima (Pa)	44.42	92.76	0.00	-34.14	-36.19	-61.38	41	0.39
Juncus gerardi (Jg)	101.84	123.48	-14.64	-37.03	-59.18	-103.91	51	0.24
Spergularia maritima (Sm)	-7.26	11.59	0.00	-5.17	2.70	-5.16	35	0.29
Limonium vulgare (Lv)	15.63	-5.39	-5.85	0.00	-7.44	8.70	80	0.71
Suaeda maritima (Sa)	12.35	-5.01	0.00	0.00	-11.44	8.75	58	0.33
Glaux maritima (Gm)	45.97	40.81	0.00	-11.95	-34.20	-32.80	56	0.34
Atriplex portulacoides (Ap)	22.44	0.00	-11.85	0.00	-6.95	-2.33	48	0.19
Dominance								
Elymus athericus (Ea)	9.67	57.08	-12.41	-15.00	5.87	-56.32	24	
Artemisia maritima (Am)	22.70	13.45	-10.91	-3.40	-5.90	-15.68	43	
Festuca rubra (Fr)	15.65	44.60	-2.32	-12.01	-8.31	-39.70	47	
Plan/ago maritima (Pm)	13.28	34.95	-3.01	-9.72	-7.38	-31.62	18	
Puccinellia maritima (Pa)	38.51	134.71	0.00	-50.44	-34.05	-89.17	16	
Juncus gerardi (Jg)	158.50	213.28	-26.93	-64.37	-93.87	-179.96	12	
Spergularia maritima (Sa)	-109.18	39.22	0.00	-20.55	64.03	-12.65	10	
Limonium vu/gare (Lv)	43.75	0.00	0.00	0.00	-32.32	0.38	57	
Suaeda maritima (Sm)	36.73	120.50	0.00	-43.56	-31.67	-82.40	19	
Glaux maritima (Gm)	61.88	41.42	0.00	-12.01	-47.49	-34.78	19	
Atriplex portulacoides (Ap)	11.97	-6.47	-19.41	0.00	6.56	2.41	9	

*Parameters indicated by zero did not improve the regression model significantly when added.

tOther species present in less then 25% of the plots not included in the regression analysis (with frequency of occurrence): *Armeria maritim* 15, *Elymus fare/us* 6, *Spartina anglica* 7, *Atriplex prostrata* 2, *Cochlearia danica* 2, *Plantago coronopus* 3, *Agrostis stolonifera* 3, *Juncus maritimus* 4, *Ammophila arenaria* I, *Triglochin maritima* 22, *Aster tripolium* 23, *Carex extensa* 3, *Parapholis stricta* I, *Sonchus arvensis* I

tCalculated as(% of plots dominant)/(% of plots present).

tulacoides. The highest abundances of this species were recorded at sites that had undergone between 40 and 60 years of succession. *Elymus athericus* was never an abundant species on the lowest sections of the transects. *Plantago maritima* occurred in one-third of the plots, but was almost never a dominant species, and did not show a clear successional trend in abundance.

The successional sequence in the middle part of the transects (base elevation I. 5 m above **NAP)** was different from that described above. *Festuca* and *Limonium* were initially the most dominant species (Fig. 7), but whereas *Festuca* remained abundant, *Limonium* decreased as succession progressed. Both *Elymus* and *Artemisia* increased during succession at these middle elevations and *Elymus* finally became codominant with *Festuca,* while *Artemisia* decreased in the later stages of succession. *Suaeda, Glaux, Spergularia* and *Puccinellia* also decreased as succession progressed.

At the highest elevations of transects (base elevation 1.8 m above NAP), the successional dynamics in species composition was different again. Initially, *Festuca* was abundant, with some *Elymus* and *Plantago,* but *Elymus* rapidly increased and ultimately became the single dominant in many plots. *Artemisia* decreased after an initial increase.

A different perspective of the regression relationships for *Elymus, Festuca, Plantago* and *Puccinellia* is provided in Fig. 9. The same regression equations in Table I were used, but now the complete distributions along the elevational gradient have been graphed, for the different phases of succession. They show that *Elymus* initially occurred only in the higher part of the salt marsh, but the species has extended gradually to the lower parts of the salt marsh during succession. There was no significant age x elevation interaction, so the maximum values with respect to elevation did not change. Initially, *Festuca* was absent at the lowest levels, it increased in presence and dominance at this elevational position, but at the highest sections of the transects it decreased in dominance, although it remained present. In the upper part of the salt marsh, *Plantago* was present for up to 25 years after the start of succession, but by I00 years it had decreased. In the lower salt marsh, *Plantago* did not change in abundance. At the lower sections of the gradient where it was initially among the most abundant species, *Puccinellia* decreased in dominance during the course of succession, but remained present in many plots.

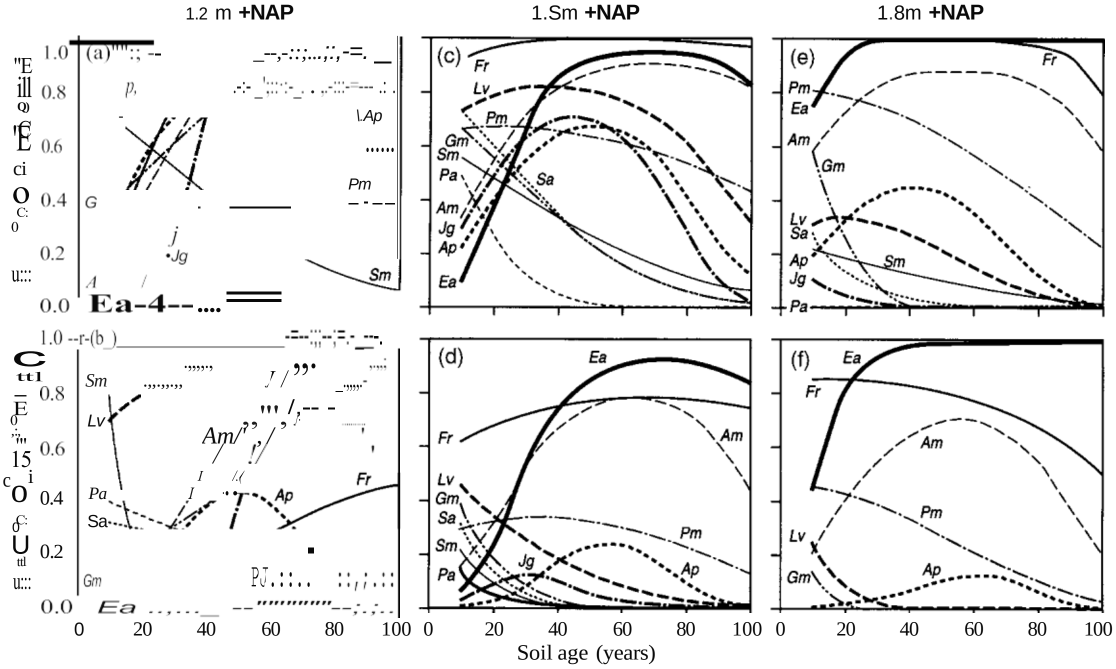


Fig. 8 Calculated trends fitted by logistic regression for 11 salt-marsh species, representing the probability of presence (a, c, e) and dominance (b, d, f) as related to the age of the transect (duration of vegetation succession) at three elevations of the sandy subsoil (base elevation, in m above Dutch Ordnance Level (NAP)). Regression parameters are given in **Table 1.** Although the equations were fitted with both age and elevation as independent variables, a cross-section of the response surfaces at each base elevation is presented here. See Table 1 for complete species names.

FORAGE QUALITY

Data on the composition of *Festuca* leaf tissue (Fig. 10) collected at a 20-year-old successional stage showed that amounts of crude protein in tissues increased from 18 to 24% from the upper to the lower elevations of the salt marsh ($y = -0.0051x + 21.631$, $r = -0.97$, $P < 0.001$).

ZONATION, SUCCESSION AND GEESE HERBIVORY

The highest densities of faecal droppings were recorded at the lower end of the elevational gradient, on the second transect (25 years of age) (Fig. 11). Along younger and older transects, dropping densities were lower. A one-way analysis of variance of the faecal dropping densities within the base elevation range 1.2-1.4 m above NAP yielded a significant difference between transects ($F_{3,44} = 31.95$, $P < 0.001$). A posteriori contrasts showed that the faecal dropping rate along the 25-year-old transect was significantly higher than those along the first and last transects (Fig. 11e; $P < 0.05$). The 35-year-old transect was significantly lower than the previous stage but higher than the last stage ($P < 0.05$), while it was not different from the 10-year-old stage (Fig. 11e). The faecal densities in the first and the last stage of succession (10 and 100 years, respectively) were low, and not significantly different from each other ($P > 0.05$). Clearly, geese preferred within the lower salt marsh the mid-successional stage (25-35 years.).

EFFECT OF CATTLE GRAZING IN A LATE-SUCCESSIONAL STAGE ON VEGETATION ZONATION AND GOOSE HERBIVORY

Transect 7 has undergone 200 years of succession, during which time there has been almost continuous cattle grazing. Transect 6 has also undergone 200 years of succession, but large herbivores have been excluded from this transect in the last 20 years. The differences in vegetational composition between transects 6 and 7 therefore have developed during the last 20 years. This has resulted in the dominance of *Elymus athericus* over the entire gradient in transect 6; in contrast, *Plantago maritima* and *Festuca rubra* have become restricted to the higher part of the transect, while *Puccinellia* has become rare along the whole transect (Fig. 12c; note that low plots (< 1.30 m above **NAP)** are lacking in these transects). Although the fence along transect 6 prohibited goose grazing, the results from the 100-year-old transect 4 suggest that dominance of *Elymus* (Figs 9b and 11e) would have prevented their grazing even if the geese had had access to the vegetation. In contrast, continued cattle grazing (transect 7) maintained the dominance of early successional salt-marsh species, even after 200 years (such as *Puccinellia;* compare Figs 9h and 12a). Cattle grazing led to strong suppression of *Elymus* (Fig. 12a,c) and allowed the Brent geese to forage on the early successional species that established (Fig. 12b). Faecal densities were higher towards the lower part of the gradient along transect 7 ($y = 36380e^{-8.26x}$, $n = 20$, $r = 0.86$, $P < 0.001$,

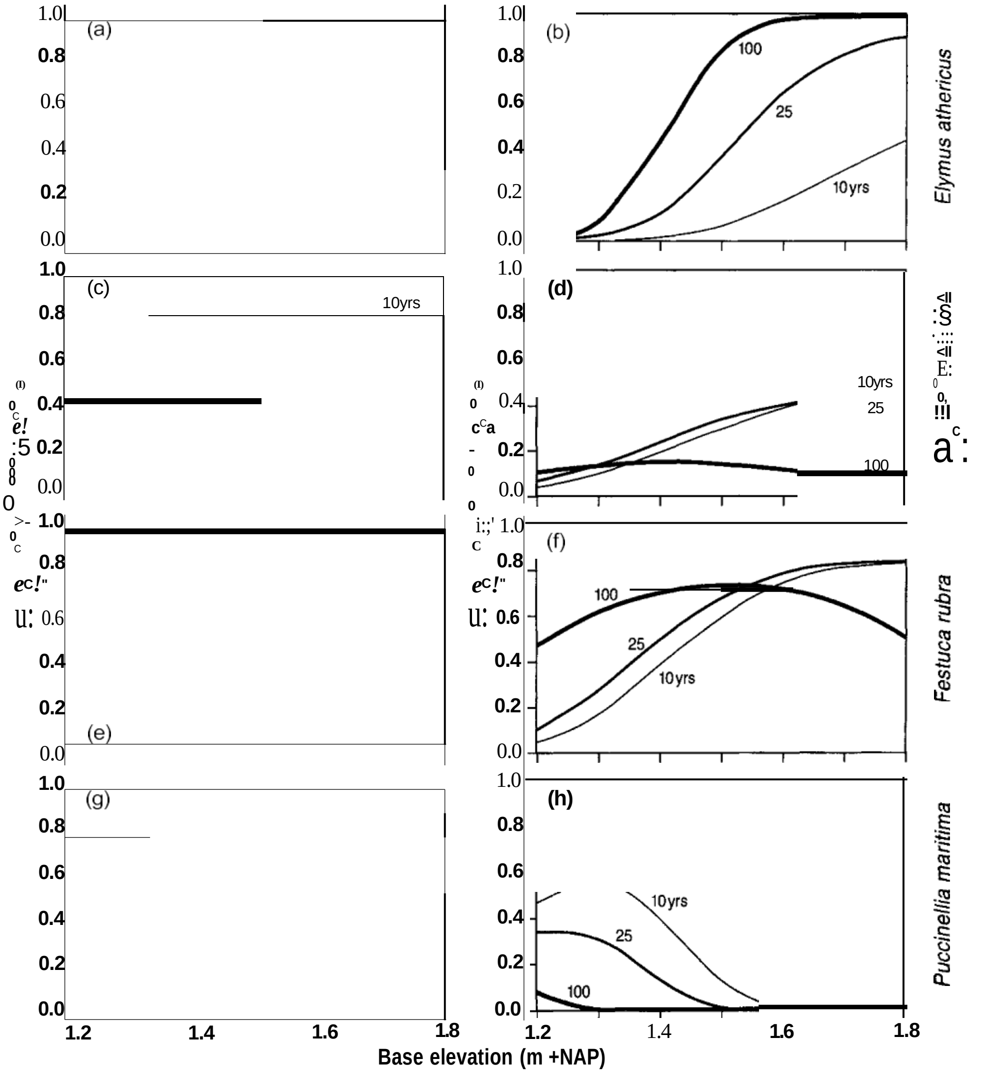


Fig. 9 Changes during succession in vertical distribution along an elevational gradient of four salt-marsh species important as a food source for Brent geese (see text). Base elevation denotes elevation of the sandy subsoil. The same response surfaces are used as in Fig. 8 (see **Table 1** for parameters), but now a cross-section along the elevational gradient is shown at 10, 25 and 100 years of vegetation succession. Plant species abundances are expressed either as the proportion of plots in which the species occurred (a, c, e, g), or as the proportion of plots in which the species was one of the three dominants (b, d, f, h).

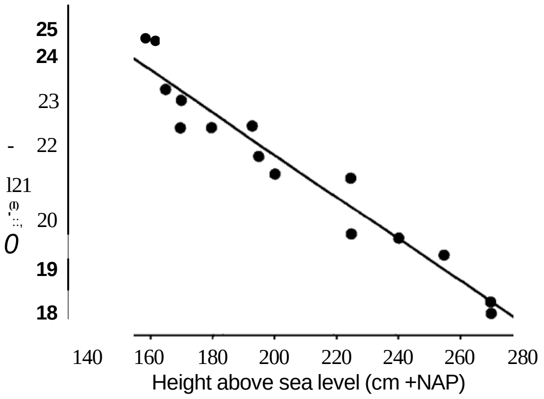


Fig. 10 Tissue crude protein concentrations (6.25 x total N¾) of *Festuca rubra* along a elevational gradient in a 20-year-old part of the salt marsh. Only young leaf tips were collected for the analyses, as they are grazed by Brent geese. Note that in contrast to the other figures, the actual surface elevation is given in this graph, not base elevation.

Fig. 12b), where the frequently dominant *Triglochin maritima* is especially favoured by geese (Fig. 12; personal observations; see also Mulder *et al.* 1996).

Discussion

Changes in salt-marsh ecosystems result from a complex interplay of changes in geomorphology, flooding regime, water sediment loads and salinity, soil characteristics, vegetation type and herbivory, and this may produce many feedbacks (Fig. 2). Geographic variation in the relative importance of these factors in their effect on sedimentation and surface elevation will lead to different geomorphological types of salt marshes (Dijkema 1987; Adam 1990; Gray 1992; de Leeuw *et al.* 1993). Primary productivity and species composition of the vegetation depend on the inundation frequency, which in turn depends on geomorphology. However, the vegetation also alters the

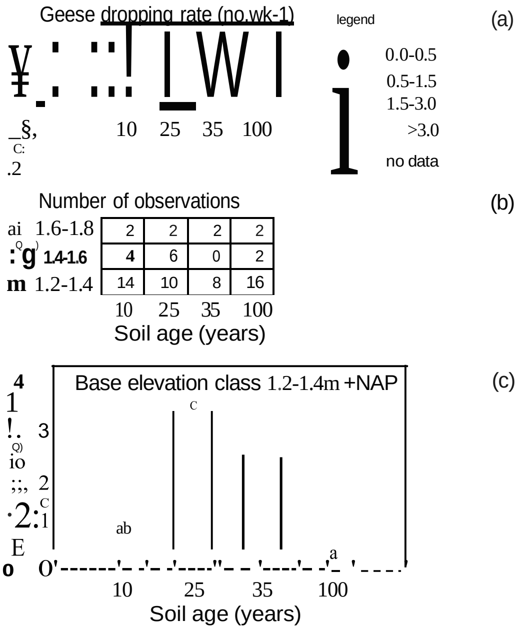


Fig.11 (a) Average faecal dropping rates (number m^{-2} weeks^{-1}) of geese at different elevations of the sandy subsoil (base elevation, in m above NAP) (Dutch Ordnance Level) (as 20-cm height classes) and successional stage. (b) The number of observations for each combination. (c) Mean faecal dropping rates at the lowest base elevation class. Means with the same letter were not significantly different (Student-Newman-Keuls test after one-way analysis of variance).

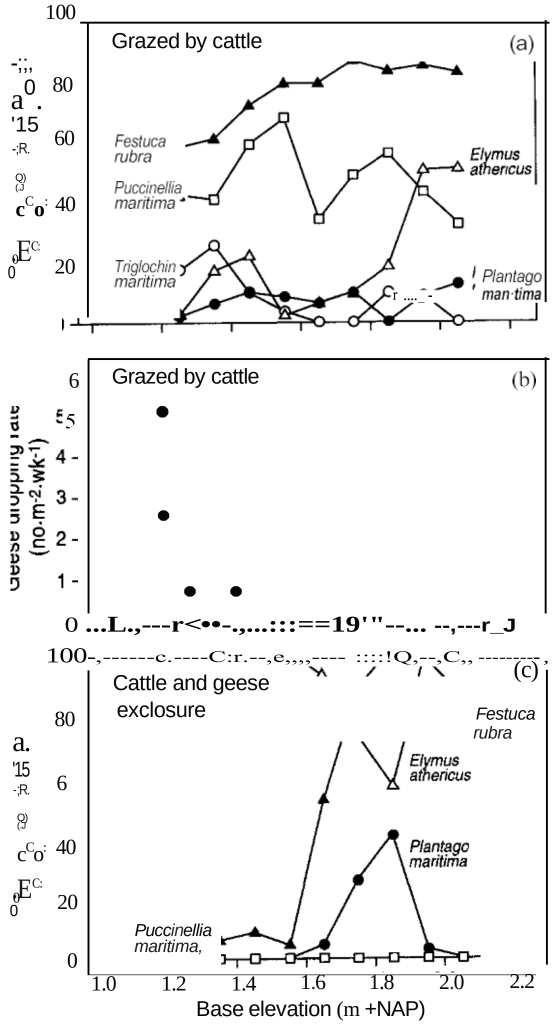


Fig.12 The distribution of (a) various plant species important for geese grazing along the elevational gradient of transect 7 (200 years of succession, grazed by cattle for the last 20 years) and (b) faecal deposition rates of Brent geese, *Branta bernicla*, along this transect ($y = 36380e^{-\bullet 26}$\ $n = 20$, $r = 0.86$, $P < 0.001$), and (c) the distribution of plant species along transect 6 (200 years of succession, ungrazed by cattle and geese for the last 20 years).

geomorphology by trapping sediment, thereby altering the inundation frequency and inducing soil changes. Herbivores respond to the vegetation because of their preference for certain plant species, directed by their physiological and morphological constraints in handling food. Herbivores, however, also affect the salt marsh vegetation, by removing plant biomass and altering the light environment, nutrient availability and soil salinity (Bakker *et al.* 1985; Srivastava & Jefferies 1996; Wilson & Jefferies 1996).

In our study site, most elevational variation could be linked to elevational differences in the sandy subsoil (Figs 1 and 2). These 'coastal bar' type salt marshes of the Wadden Sea are characterized by low sediment loads in the water, resulting in relatively slow sedimentation rates. In contrast, salt marshes along river deltas of the Dutch, British and German North Sea coasts are generally characterized by less initial elevational variation (little sand dune formation), and much higher rates of sedimentation (> 1 m per century; De Leeuw *et al.* 1993). In these salt marshes, most elevational variation is caused by different periods of sedimentation, so that lower salt marshes are also younger salt marshes. This is not true for the coastal bar-type salt marsh described in this study: each elevational position has its own characteristic successional sequence (Figs 7 and 8). A third geomorphological type of salt marsh is found along the Hudson Bay coast and along the Baltic coast. In these cases, most elevational variation originates from isostatic land uplift attended by slow sedimentation rates, and here again lower elevations are of a younger successional age (Jefferies *et al.* 1979).

The relatively strong sea level rise occurring in this part of the Wadden Sea over the last two centuries (Fig. 6) has probably had a strong impact on vegetation zonation and succession on the salt marsh. Interestingly, this appears to have led to a decreased rate of sedimentation on the lowest salt marsh, and increased sedimentation on the higher salt marsh, with little change in the intermediate zone (Fig. 46). However, the majority of plots were located at relatively high elevations, so increased sedimentation has probably occurred in most plots. Since increased silt accretion leads to increased nitrogen accumulation (Fig. 5), it is likely to be an important cause of plant species replacement and, hence, vegetation succession may have been speeded up by sea level rise.

The simulations showed that the assumption of a constant sedimentation rate during succession produced predicted patterns of silt accumulation that agreed well with the observations (Fig. 4). This implies that the increase in vegetation height and density during succession does not exert a profound effect on sedimentation rate.

A general dogma of salt marsh zonation is that the lower vertical limit of species is controlled largely by tolerance of tidal factors, while the upper limit is fixed by interspecific competition (Snow & Vince 1984; Gray 1992; Pennings & Callaway 1992). Rozema *et al.* (1985) tested the salt and flooding tolerance of 12 species from this same salt marsh in growth experiments, and concluded that their ranking in salt tolerance corresponded to the order of their vertical zonation on the salt marsh. A similar conclusion was reached by Snow & Vince (1984), who found that the ability of species to tolerate extreme edaphic factors (salinity, flooding) determined the seaward limit of distribution within a salt marsh. When potential distributions overlapped, especially at the higher end of the gradient, they found that competition was important in maintaining the zonation pattern. An interesting result of the present study is that the upper and lower elevational limits of species changed during succession (Fig. 9), possibly as a result of changing competitive abilities associated with nutrient accumulation. Perennial grasses, such as *Elymus athericus* and *Festuca rubra,* are able to extend towards the lower salt marsh (Fig. 9) with the progress of nutrient accumulation. *Elymus* moved about 40 cm down the elevational gradient, while silt accretion was only 12cm at its maximum, indicating that the increase in surface elevation was not the main explanation for the behaviour of this species in different transects. It is possible that the salt tolerance of some species is increased at higher nutrient availability, or that the soil salinity decreased with biomass accumulation towards later successional stages (see Srivastava & Jefferies 1996). Small halophytes, such as *Plantago maritima* and *Puccinellia maritima,* became much less abundant at higher elevations, but remained at lower elevations as silt accumulated. Competitive interactions possibly may become important at progressively lower elevations as succession continues. However, *Elymus* does not become dominant below 1.3 m above **NAP** during the first 100 years of succession (Fig. 9b), so that the most salt-tolerant species can survive in a refugium at the lower elevations. Rozema *et al.* (1985) found that *Elymus* was one of the least salt-tolerant species, while *Puccinellia, Glaux* and *Salicornia* were the most salt-tolerant species occurring in this marsh.

With increased nitrogen accumulation due to sedimentation, plant species with a low stature *(Puccinellia rnaritima, Salicornia* sp., *Spergularia maritima)* were replaced by taller species *(Elyrnus athericus, Arternisia maritima, Atriplex portulacoides),* which suggested that light competition becomes more important with increasing nutrient availability (Tilman 1985; Olff *et al.* 1993). However, interspecific differences in colonization ability may also be important in accounting for the changes. Annual salt marsh plants *(Suaeda, Salicornia,* with high seed production) were the first to be present and the first to disappear along transects. This may imply that a trade-off between colonization and competitive ability (Tilman 1994) was important in determining the successional pattern of species. Indirect evidence for this can be obtained from the dominance index data (Table 1). The perennials *Lirnoniurn, Elymus, Festuca* and *Artemisia,* which increased in later successional stages, had high dominance indices, which indicated that whenever they established they rapidly became dominant. Low values for the dominance index were recorded for short-lived plants (like *Salicornia)* which decreased in abundance after 10 years of succession. Although they sometimes occurred in high frequencies, they rarely became dominant. In this marsh, therefore, a low value of the dominance index is indicative of high colonizing ability, while a high value indicates **high competitive ability.**

High densities of Brent geese were observed on the lower part of the elevational gradient in mid-successional stages (25-35years) (Fig.11). We observed a good correspondence between the distribution of goose droppings and high abundances of three of their principal food species, *Festuca* (maximally 24% protein in May), *Puccinellia* (28% protein in **May)** and *Plantago* (28% protein **in May)** (Figs 7, 8 and **11**; protein concentrations from Prop & Deerenberg 1991). *Elyrnus,* which dominated the highest part of the gradient, had a much lower protein content (12% protein; Bakker 1989) and was avoided by the geese. The restriction of geese to lower elevations was probably not only determined by the distribution of food species, but also by an increasing quality of plants of the same species at lower elevations (Fig. 10). Other studies are in line with the conclusion that 'stressed' plants are more beneficial to herbivores because their nutritional quality is higher (Breman & De Wit 1983; Bink 1986; White 1993; Crawley 1997). Although *Puccinellia* dominated the lower part of the first transect (10 years of succession; Figs 7 and 8), we observed low dropping densities here, probably because the plants were too small and sparsely distributed. With the increasing dominance of *Festuca* and *Elymus* on the lower and mid-sections of the transects, *Puccinellia rnaritima* and *Plantago maritirna* decreased in dominance, and the abundance of goose droppings declined (Fig. l l).

Classic exploitation theory (Hairston *et al.* 1960; Oksanen *et al.* **1981**; Oksanen 1990; Crawley 1997) predicts that productive environments are capable of supporting natural predators that are sufficiently abundant to keep herbivores scarce, but below a threshold level of primary productivity the impact of natural predators becomes trivial because the secondary productivity of their prey becomes too low to sustain the predator populations. Below this threshold, herbivore densities decrease towards lower primary productivity because they become increasingly limited by their food. This so-called exploitation ecosystem hypothesis to explain why herbivore densities level off at intermediate productivity is, however, an unlikely explanation for the patterns observed in this study, since the geese have no natural enemies on this island. Instead we think that vegetation succession, attended by nutrient accumulation, is generally associated with increasing abundance of superior light competitors (tall species like *Elymus* and *Artemisia).* A high investment in structural tissues is an important trait enabling these species to attain dominance under productive conditions. However, these tissues are generally low in nutrients (especially nitrogen), and difficult to digest, which reduces the quality of tall plants as a food source for herbivores. Furthermore, tall rhizomateous grasses like *Elymus* withdraw nutrients efficiently from senescing leaves (enabling them to regrow fast in the next spring), so that large quantities of standing dead material (oflow forage quality) are left in autumn (Bobbink *et al.* 1989). In the subsequent spring, these dead leaves can comprise up to 50% of the above-ground biomass (van de Koppel *et al.* 1996), making it difficult for the geese to select fresh leaves. We call this explaination of why herbivore densities may peak at intermediate productivity the quality threshold hypothesis (van de Koppel *et al.* 1996; Huisman *et al.*, in press; Prins & Olff, in press). An important consequence of quality limitation for herbivores at high net primary productivity is that it may cause multiple stable states in plant-herbivore systems (van de Koppel *et al.* 1996). Although we did not measure population sizes, we hypothesize that productive environments may not be capable of supporting large populations of smaller herbivores because the food quality is too low, and herbivore densities will thus show a maximum at intermediate levels of net primary productivity. In a recent review, Cebrian & Duarte (1994) found that herbivore consumption across ecosystems was especially low in areas with very high plant production. More data on herbivore densities along productivity gradients are needed to show whether the observed patterns are explained best by the exploitation ecosystem hypothesis or the quality threshold hypothesis.

We found that cattle grazing of vegetation in a late successional stage that would otherwise be dominated by *Elymus athericus* caused the re-appearance of early successional species such as *Puccinellia maritima,* and also the re-appearance of Brent geese (Fig. 12). Cattle grazing caused plant species normally characteristic of the lower part of the elevational gradient to colonize these higher positions on the elevational gradient (Fig. 12; see also Bakker *et al.* 1985; Bakker 1989). Cattle can utilize forage of a much lower quality than geese, and sometimes they prefer *Elymus* (Bakker 1989). This prevents *Elymus* from becoming dominant, and leaves are grazed before they can become standing dead biomass. Large herbivores, such as cattle, therefore appear to prevent the mechanisms stated in the quality threshold hypothesis from becoming operative, and may perhaps even induce predator control of small herbivores. Since cattle grazing in these salt marshes causes the sward to be opened without impoverishing the soil (Bakker 1989), and increases salinity in the top soil (Bakker *et al.* 1985), these observations support the hypothesis that light competition, together with increasing nutrient availability (due to sedimentation) and decreasing soil salinity, has caused the disappearance of early successional halophytes. Whereas cattle were able to arrest succession and cause a retrogression (Bakker 1989), the geese were apparently not able to prevent *Elymus* from becoming dominant. Large effects of geese on vegetation composition do, however, occur in Arctic breeding grounds, where they forage during almost the entire period of vegetation growth (Bazely & Jefferies 1989; Ruess *et al.* 1989; **Hik** *et al.* 1992; Srivastava & Jefferies 1996). On the salt marsh at La Perouse Bay, Canada, vegetation succession in the presence of goose grazing proceeds from a *Puccinellia-Carex* assemblage to a *Calamagrostis-Festuca* assemblage, changes which have been attributed to isostatic uplift. The geese delay vegetation succession in this area but are also not able to stop it completely (Bazely & Jefferies 1985). In both this case and on our study site, the geese seem to depend on vegetation that is at a particular stage in a succession that is primarily driven by a combination of changes in geomorphology and soil conditions.

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References

Adam, **P.** (1990) *Salt Marsh Ecology.* Cambridge University Press, Cambridge.

Bakker, J.P. (1985) The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio,* **62,** 391-398.

Bakker, J.P. (1989) *Nature Management by Cutting and Grazing.* Kluwer Academic Publishers, Dordrecht.

Bakker, J.P., Russchen, P.T. & Dijkstra, M. (1985) Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh. *New Phytologist,* **101,** 291-308.

Bazely, **D.R.** & Jefferies, R.L. (1985) Changes in the composition and standing crop of salt marsh communities in response to the removal of a grazer. *Journal of Ecology,* **74,** 693-706.

Bazely, **D.R.** & Jefferies, **R.L.** (1989) Lesser snow geese and the nitrogen economy of a grazed salt marsh. *Journal of Ecology,* **77,** 24-34.

Bink, F.A. (1986) Acid stress in *Rumex hydrolapathum* (Polygonaceae) and its influence on the phytophage *Lycena dispar* (Lepidoptera; Lycenidae). *Oecologia,* **70,** 447-451.

Bobbink, R., Den Dubbelden, **K.** & Willems, J.H. (1989) Seasonal dynamics ofphytomass and nutrients in chalk grassland. *Oikos,* **55,** 216-224.

Bormann, B.T. & Sidle, R.C. (1990) Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay, Alaska. *Journal of Ecology,* **78,** 561-578.

Breman, H. & De Wit, C.T. (1983) Rangeland productivity and exploitation in the Sahel. *Science,* **221,** 1341-1347.

Cebrian, J. & Duarte, C.M. (1994) The dependence of herbivory on growth rate in natural plant communities. *Functional Ecolog,* **8,** 518-525.

Crawley, M.J. (1997) Plant-herbivore dynamics. *Plant Ecology* (ed. **M.J.** Crawley), pp. 401-474. Blackwell Science, Oxford.

Crocker, R.L. & Major, **J.** (1955) Soil development in relation to vegetation and surface age at Glacier Bay. *Journal of Ecology,* **43,** 427-448.

De Leeuw, J., De Munck, W., Olff, H. & Bakker, J.P. (1993) Does zonation reflect the succession of salt-marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in the Netherlands. *Acta Botanica Neerlandica,* **42,** 435-445.

Dijkema, K.S. (1987) Geography of salt marshes in Europe. *Zeitschriftfar Geomorphologie* **31,** 489-498.

Dijkema, K.S., Bossinade, J.H., Bouwsema, P. & de Glopper, **R.J.** (1991) Salt marshes in the Wadden Sea: rising high tide levels and accretion enhancement. *Expected Effects of Climate Change on Marine Coastal Ecosystems* (ed. J. **J.** Beukema), pp. 173-188. Elsevier, Amsterdam.

Ebbinge, B. (1992) *Population limitation in arctic-breeding geese.* Thesis, University of Groningen.

Gray, A.J. (1992) Salt marsh plant ecology: zonation and succession revisited. *Salt Marshes: Morphodynamics, Conservation and Engineering* (eds J.R.L. Allen & **K.** Pye), pp. 63-69. Cambridge University Press, Cambridge.

Hairston, **N.G.,** Smith, F.E. & Slobodkin, **L.B.** (1960) Community structure, population control, and competition. *American Naturalist,* **94,** 421-425.

Hik, D.S., Jefferies, R.L. & Sinclair, A.R.E. (1992) Foraging by geese, isostatic uplift and symmetry in the development of salt-marsh plant communities. *Journal of Ecology,* **80,** 395-406.

Huisman, J., Grover, J.P., van der Wal, **R.** & van Andel, J. (in press) Competition for light, plant species replacement, and herbivory along productivity gradients. *Herbivores Between Plants and Predators* (eds H. Olff, V.K. Brown & E.H. Drent). Blackwell Science, Oxford.

Huisman, J., Olff, H. & Fresco, L.F.M. (1992) A hierarchical set of models for species response analysis. *Journal of Vegetation Science,* 4, 37-46.

Jefferies, R.H., Jensen, A. & Abraham, K.F. (1979) Vegetation development and the effect of geese on vegetation at La Perouse Bay, Manitoba. *Canadian Journal of Botany,* **57,** 1439-1450.

Kerbes, **R.H.,** Kotanen, **P.M.** & Jefferies, **R.L.** (1990) Destruction of wetland habitats by lesser snow geese: a keystone species of the west coast of Hudson Bay. *Journal of Applied Ecology,* **27,** 242-258.

van de Koppel, J., Huisman, J., van de Wal, **R.** & Olff, H. (1996) Patterns ofherbivory along a gradient of primary productivity: an emperical and theoretical investigation. *Ecology,* **77,** 736-745.

McNaughton, S.J., Oesterheld, **M.,** Frank, **D.A.** & Williams, **K.J.** (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature,* **341,** 142-144.

Mulder, C.P.H., Ruess, R.W. & Sedinger, J.S. (1996) Effects of environmental manipulations on *Triglochin palustris:* implications for the role of goose herbivory in controlling its distribution. *Journal of Ecology,* **84,** 267-278–

Oksanen, **L.** (1990) Predation, herbivory and plant strategies along gradients of primary productivity. *Perspectives on Plant Competition* (eds **J.B.** Grace & D. Tilman), pp. 445-474. Academic Press, New York.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist,* **118,** 240-261.

Olff, H., Huisman, J. & Van Tooren, B.F. (1993) Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *Journal of Ecology,* **81,** 693-706.

Pennings, S.C. & Callaway, R.M. (1992) Salt marsh plant zonation - the relative importance of competition and physical factors. *Ecology,* **73,** 681-690.

Prins, H.H.T. & Olff, H. (in press) Species richness of African grazer assemblages: towards a functional explanation. *Dynamics of Tropical Communities* (eds D. Newbery, H.H.T. Prins & G. Brown). Blackwell Science, Oxford.

Prop, J. & Deerenberg, C. (1991) Spring staging in Brent Geese *Branta bernicla:* feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia,* **87,** 19-28.

Rozema, J., Bijwaard, P., Prast, G. & Broekman, R. (1985) Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio,* **62,** 499-521.

Ruess, R.W., Hik, D.S. & Jefferies, R.L. (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. *Oecologia,* 79, 23-29.

Snow, A.A. & Vince, S.W. (1984) Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology,* 72, 669-684.

Srivastava, D.S. & Jefferies, R.L. (1996) A positive feedback: herbivory, plant growth, salinity, and the desertification of an antarctic salt marsh. *Journal of Ecology,* **84,** 31-42.

Ter Braak, C.J.F. & Looman, C.W.N. (1986) Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio,* **65,** 3-11.

Tilman, **D.** (1985) The resource-ratio hypothesis of plant succession. *American Naturalist,* **125,** 827-852.

Tilman, **D.** (1994) Competition and biodiversity in spatially structured habitats. *Ecology,* **75,** 2-16.

White, T.C.R. (1993) *The Inadequate Environment. Nitrogen and the Abundance of Animals.* Springer-Verlag, Berlin.

Wilson, D.J. & Jefferies, R.L. (1996) Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. *Journal of Ecology,* **84,** 841-851.

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Appendix 1

A SIMPLE INUNDATION/SEDIMENTATION MODEL

In order to understand the process of sedimentation in this type of salt marsh and to analyse the consequences of the observed sea level changes for sedimentation, zonation and succession, we developed a sedimentation model for which the parameters can be fitted from simple measurements.

After the initial phase of sand-dune formation, a rather steep elevational gradient exists, which is important in understanding the spatial variation in sedimentation rate. The lower part of the gradient is inundated every day, and the sedimentation rate will be almost zero, mainly because the flow rate of the water is high. At the higher end of the gradient, inundation takes place only very rarely, so sedimentation is low or zero. In the intermediate part of the elevational gradient (initially the elevation of the sandy subsoil) sedimentation is expected to be at its maximum. The dependence of annual transgression frequency *(T)* on elevation (E) can be described by the empirical model:

$$T = \frac{m}{1 + e^{a(E-H)}} \qquad (I)$$

where *m* is the maximum number of tides per year, *a* is a parameter denoting the relative rate of decrease in *Twith E* and His the annual mean high water level (m above **NAP):** which might change with time due to sea level rise. Note that *H* in this cumulative model only represents the mean high tide provided the levels of the high tide follow a symmetric distribution; this assumption is valid in this case. If ***H*** shows a simple linear change with time (I) over a certain period then:

$$H = h_0 + rt \qquad (2)$$

where *ho* is the mean high water level at the start of the period, and *r* is the annual rate of change in mean high water level.

As outlined above, the annual sedimentation rate S depends on the transgression frequency, with a maximum at intermediate frequencies. A simple model for this is:

$$S = \frac{bT}{1 + e^{cT}} \qquad (3)$$

where the empirical parameters *b* and *c* determine the height and width of the curve. When band Tare both positive, the function described by eqnuation 3 goes through the origin, then rises with *T* towards a maximum, and then declines towards zero.

The elevation of a point in a certain year will be determined by the elevation in the previous year, plus the sedimentation in that year, so that:

$$E_{t+1} = E_t + S \qquad (4)$$

Combining equations I, 2, 3 and 4 results in the final sedimentation model:

$$E_{,+\ I} = E, + \frac{I;\ !}{I+\ e''}$$

with

$$T = \frac{m}{1 + e^{(a(E_t - h_0 - rt))}} \qquad (5)$$

Dynamic simulation of *E* using this equation with an annual time step allows for the calculation of the soil surface elevation starting from any initial elevation E_0 (base elevation) after any number of years.

The thickness of the silt layer *(D)* after *n* years can then be calculated as:

$$D_n = E_n - E_0 \qquad (6)$$

Parameter Estimation

The values of the parameters h_0 and *r* can be obtained from a linear regression of the observed annual mean high tide vs. time. In our case, these data were measured from 1824 to 1993, and the annual mean high tide indeed significantly increased ($R^2 = 0.34$, $n = 169$, $P < 0.001$).

The parameter value for *a* can subsequently be calculated by substituting equation 2 in equation I, and fitting the resulting equation by non-linear regression to observations on annual transgression frequencies of different elevations. In our case, transgression frequencies were measured for 5-cm elevational classes, and the model fitted very well ($r^2 = 0.99$, $n = 169$). The parameter values for hand *c* might be obtained from sedimentation experiments with simultaneous measurement of transgression frequencies. In our case, however, these parameters were not measured independently, but calibrated to the observed silt-layer thickness after 10, 25, 35, 60, 100 and 200 years, at different base elevations (every 10cm for each transect). In addition to the measured data, we added points at 0.2, 0.3, 0.4 and 0.5 m **NAP,** with zero sedimentation, since sedimentation was never observed at this low elevation in the field. Adding these points made it much easier to calibrate the model to the field data. The calibration was done by solving the model starting with an initial guess of *b* and *c*, evaluating the sum of the squared differences between observed and predicted values, and subsequently adjusting *b* and/or *c* until this residual sum of squares was minimal. The Solver procedure from Microsoft Excel 6.0 was used to find a best combination for *b* and *c*, using automatic scaling, quadratic extrapolation and forward differencing. The R^2 of the regression between observed and predicted values for the solution was 0.86 ($n = 116$).

Using these statistical procedures, we obtained the following parameter values for the Schiermonnikoog salt marsh:

a	5.648	relative decrease in annual transgression frequency with increasing elevation (m above **NAP),** indicating the temporal variance in high tide level;
b	7.97E-05	linear coefficient for the dependence of annual sedimentation rate (m) on annual transgression frequency, related to tidal amplitude and sediment load;
c	1.63E-02	exponential coefficient for the dependence of annual sedimentation rate (m) on annual transgression frequency, related to tidal amplitude and sediment load;
	0.891	initial annual mean high tide (m above **NAP)** in 1824 (intercept of the linear regression);
	6.3×10^{-4}	average annual change in mean high tide (m), indicating sea-level rise, over the period 1824-I993 (slope of the linear regression);
m	706	total number of tides per year (irrespective of elevation).

Annex F: Nolte, S., Waner, A., Stock. M., & Jensen K. (2019) Elymus athericus encroachment in Wadden Sea salt marshes is driven by surface-elevation change. Applied Vegetation Science, Vol. 22. No. 3, pp. 454 – 464.

Title: *Elymus athericus* encroachment in Wadden Sea salt marshes is driven by surface-elevation change

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Abstract:

Question: What are the main drivers of vegetation succession and the encroachment of *Elymus athericus* (Link) Kerguélen in ungrazed Wadden Sea salt marshes? Is (1) elevation, a proxy for tidal inundation and thus abiotic conditions, limiting the expanse of *Elymus*. Does sedimentation increase the spread of *Elymus* by (2) leading to surface-elevation change or does it (3) add nitrogen and thereby allows *Elymus* to grow in lower elevation?

Location: salt marsh at Sönke-Nissen-Koog, Wadden Sea National Park Schleswig-Holstein, Germany

Methods: The experiment was established in 2007 in the high marsh and consisted of four blocks of 12 m x 8 m. The blocks differed in surface-elevation change during the experiment. Each block was subdivided into 24 plots of 1 m x 1 m. The original elevation of all plots in relation to the German ordnance datum (NHN) was assessed at the start of the experiment. Plots within the blocks were randomly assigned to one of the three N-fertilisation treatments.Within each plot we planted five randomly chosen individuals of *Elymus*. After four years of treatment, the vegetation composition and cover was recorded in all plots and aboveground biomass was collected.

Results: Original elevation was found to be a main driver of succession favouring *Elymus* and other late successional plants. No effect of N-fertilisation, but a positive effect of surface-elevation change on *Elymus*-cover was detected.

Conclusions: We can therefore conclude that the positive effect of surface-elevation change on *Elymus* is based on the resulting higher elevation and more favourable abiotic conditions caused by sedimentation, but not the addition of nitrogen with the freshly deposited sediment. This case,

therefore, is an example for an ecosystem in which encroachment is driven by a natural factor, rather than anthropogenic eutrophication.

Keywords:

Biomass; *Halimione portulacoides;* N-deposition; N-fertilisation; *Puccinellia maritima*; sedimentation; succession

1. Introduction

The concept of succession, originally described by Clements (1916) as the unidirectional development of vegetation through a series of stages until a stable climax vegetation is reached, has been extensively studied in vegetation ecology (van Andel et al. 1993; McCook 1994). The first vegetation stage is often dominated by small pioneer plants which are then replaced by a diverse community of short herbaceous plants. These intermediate communities are then progressively replaced by later successional stages, which are often dominated by taller plants such as grasses (Berendse and Elberse 1990), shrubs or trees (Eldridge et al. 2011). This replacement of small plants by tall ones in late successional stages can be driven by belowground competition for nutrients (Chapin et al. 1994; Casper and Jackson 1997) or aboveground competition for light (Olff et al. 1997; Veer and Kooijman 1997). In the latter case, taller plants reduce the amount of light available for small plants, which are then outcompeted. This invasion of tall plants is sometimes also defined as encroachment (Eldridge et al. 2011) and can lead to a loss of plant species richness as only few competitive species prevail (Veer and Kooijman 1997).

The natural succession of the vegetation, however, can also be influenced by various other factors such as herbivory (van Andel et al. 1993). Herbivores reduce the standing biomass by grazing (Nolte et al. 2014) and can open gaps in the canopy for seedling establishment (Bullock et al. 1994; Bakker and Olff 2003). Thereby, herbivores decrease the light competition and enable small plants to persist while tall grazing-sensitive species are unable to establish or are reduced (Kuijper et al. 2005). Herbivores thus can halt or set-back vegetation succession (Kuijper and Bakker 2003). Therefore, grazing with herbivores is sometimes used in nature conservation e.g. in semi-natural grasslands to prevent encroachment of tall plants and maintain intermediate successional stages with a higher plant species richness (Bouchard et al. 2003; Rook et al. 2004; Metera et al. 2010). In contrast to this set-back of succession, the addition of nitrogen to an ecosystem, e.g. by atmospheric N-deposition, was found to speed up succession and encroachment (Berendse and Elberse 1990; WallisDeVries and Bobbink 2017). Especially in nutrient-poor habitats, a high N-availability can favour tall growing plants (Gaucherand et al. 2006) and thereby enhances light competition leading to low plant species richness (Veer and Kooijman 1997; Bird and Choi 2016; Soons et al. 2016).

An example for such an encroachment of a tall grass species which can lead to a loss of plant diversity is the invasion of *Elymus athericus* (hereafter referred to as *Elymus*) in salt marshes of the Wadden Sea (Andresen et al. 1990; Leendertse et al. 1997; Kiehl et al. 2007; Esselink et al. 2009; Veeneklaas et al. 2013). In the Wadden Sea area, most salt marshes along the mainland coast are the result of man-made sedimentation fields, which were built to create new land (Dijkema 1987). These salt marshes are coastal, natural or semi-natural grasslands characterised by regular flooding with sea water (Adam 1990) resulting in salt stress for plants. The frequency of tidal inundation, mainly determined by the salt-marsh elevation, leads to a distinct zonation of vegetation along an elevation gradient (Suchrow and Jensen 2010). The lowest zones are flooded frequently and are thus dominated by halophytes such as *Salicornia europea* (Suchrow and Jensen 2010). The vegetation types of the lowest elevation additionally represent the early stages of salt-marsh succession (Olff et al. 1997). However, frequent tidal inundations in low elevations also deliver sediment to the marsh, thus leading to a positive surface-elevation change of the marsh platform (Nolte et al. 2013a) and consequently less frequent inundations. With higher elevation the vegetation composition shifts to intermediate and then late successional stages in the high marsh zone, the latter often being dominated by the tall grass species *Elymus*. Thus surface-elevation change was identified as a main driver of succession in salt marshes (Rupprecht et al. 2015b).

Salt marshes in the Wadden Sea region have been used for livestock grazing for centuries (Esselink et al. 2000). In the past decades, however, grazing has been stopped in many salt-marsh areas to allow a more natural habitat and vegetation development within the National parks (Bakker et al. 2003; Esselink et al. 2009; Stock and Maier 2016). This cessation of grazing led in many locations to the encroachment of the tall, late-successional grass *Elymus* (Andresen et al. 1990; Kiehl et al. 2007; Rupprecht et al. 2015b). *Elymus* is a high-marsh species which grows in dense mono-specific stands and therefore locally reduces the plant species richness (Leendertse et al. 1997; Kiehl et al. 2007; Wanner et al. 2014) and is sensitive to grazing with livestock. In the last decades it has also spread widely in areas that have never been grazed (Veeneklaas et al. 2013; Rupprecht et al. 2015b). Therefore, researchers and nature managers were wondering which factors, next to the cessation of grazing, are driving the encroachment of *Elymus* (Van Wijnen and Bakker 1999; Veeneklaas et al. 2013). The elevation as a proxy for flooding frequency and therefore also for abiotic conditions has been identified as a major constriction for the distribution of *Elymus* (Bockelmann and Neuhaus 1999). Yet, *Elymus* has been found to expand into lower marsh areas over the last decades (Olff et al. 1997; Veeneklaas et al. 2013).

It has been argued that the encroachment of *Elymus* in the Wadden Sea salt marshes is driven or sped up by eutrophication (Van Wijnen and Bakker 1999). Although salt marshes are relatively rich in nutrients, the high stress environment with salt and hypoxia forces plants to respond physiologically leading to a high nutrient cost (Adam 1990). The addition of nitrogen in a fertilization experiment therefore led to an increase of biomass in *Elymus* and sped up vegetation succession (Van Wijnen and Bakker 1999). Nitrogen is often added to ecosystems through anthropogenic atmospheric deposition, but in salt marshes it is also added naturally during inundations with sediment deposition. To disentangle the effects of these two deposition pathways, Veeneklaas et al. (2013) analysed time series of vegetation maps and chronosequence data of four naturally developed salt marshes varying in sediment deposition rates. They found that expansion rates of *Elymus* were highest on young salt marshes which have high sediment deposition rates. This was interpreted by Veeneklaas et al. (2013) as an indicator that *Elymus* expansion is mainly driven by spatially varying natural sediment deposition rates and not by the evenly spread atmospheric deposition. However, in this observational study it was not possible to disentangle whether the high sediment deposition rates affected the encroachment of *Elymus* by the added N, or whether the positive effect of sediment deposition on the surface-elevation change (Nolte et al. 2013a) and thus elevation caused the shift. Yet, elevation as a proxy for inundation frequency and abiotic conditions has previously been found to be an important predictor of the distribution of *Elymus* (Suchrow and Jensen 2010).

The aim of this study is therefore to unravel the effects of experimental nitrogen fertilization, elevation and surface-elevation change on the vegetation succession (i.e. the shift from early towards late successional plant-species composition), the cover of *Elymus* and plant biomass in an ungrazed salt marsh. We hypothesize that (1) elevation as a proxy for flooding frequency is a driving factor of succession, with a sufficiently high elevation allowing the establishment of *Elymus* and other late-successional plants with a higher biomass production. Additionally, we hypothesize that (2) *Elymus* is N-limited and therefore the experimental N-fertilisation will lower the elevation at which *Elymus* can establish. Furthermore, we expect experimental N-fertilisation to speed up the succession towards the late-successional plant communities, as it will increase the production of biomass. Finally, we hypothesize that (3) a high surface-elevation change will lead to an increase in elevation, so *Elymus* will be able to establish, even if the original elevation at the start of the experiment was below the establishment threshold. This high surface-elevation change furthermore increases the spread of other late-successional plant communities with a higher biomass.

We carried out a field experiment in which different levels of experimental N-fertlisation were applied in blocks with a comparable range of elevation at the start of the experiment, hereafter referred to as original elevation. Additionally, the plots were positioned along a gradient of surface-elevation change, which is caused by an increasing distance of plots to the sediments source (i.e. the edge of the marsh). If the experiment shows both fertilisation and a high surface-elevation change to lower the original elevation limit for *Elymus*, we can assume that the plant is indeed nitrogen limited. If, however, no effect of experimental N-fertilisation, but an effect of surface-elevation change is found, we can conclude that the positive effect of surface-elevation change at the end of the experiment is based on the resulting higher elevation, but not the addition of nitrogen with the freshly deposited sediments.

2. Material and Methods

2.1 Experimental design

The experiment was setup in the Sönke-Nissen Koog (SNK) salt marsh on the mainland coast of the Wadden Sea in the North of Germany (Fig. 1). The area is characterised by an artificial drainage system, but maintenance of ditches and livestock grazing stopped in 1991 after the salt marsh became part of the Wadden Sea National Park in 1986 (Stock et al. 2005). The area has been previously described in context of a grazing experiment in the Northern part of the marsh (Kiehl et al. 1996; Kiehl et al. 1997; Nolte et al. 2013b).

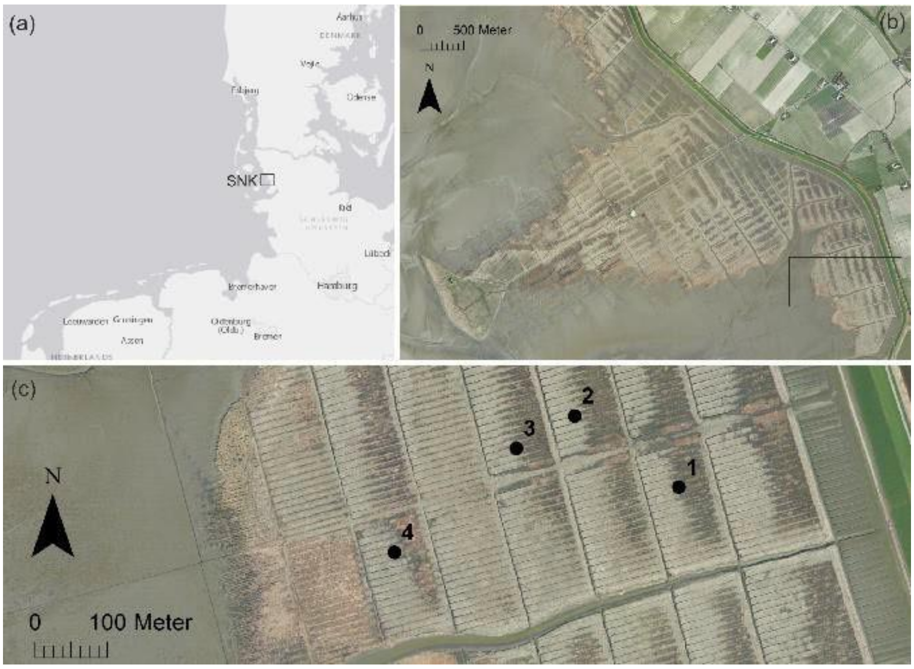

Figure 1: A) Map of the German Bight with the position of the Sönke-Nissen Koog (SNK) study site indicated. B) Aerial photograph of the Sönke-Nissen Koog & Hamburger Hallig salt marsh area with the position of the experimental site. C) The experimental site with the position of the 4 plots. World Imagery - Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

The *Elymus* experiment was established in 2007 in the high marsh and consisted of four blocks of 12 x 8 m. A rectangular shape was chosen for the blocks to exclude former ditches, which still prevail in the marsh as depressions and are evenly spaced with a distance of 10 m. Each block had a comparable mean elevation at the start of the experiment (i.e. original elevation). Within plots the prevalent micro-topography lead elevation ranges between the lowest and highest point of the respective plot of 7.0 cm to 12.5 cm. Additionally, the plots were positioned along a gradient of surface-elevation change, which is caused by an increasing distance of plots to the sediments source (i.e. the edge of the marsh; Schröder et al. 2002). Blocks were positioned close to sedimentation-erosion bars (van Wijnen and Bakker 2001; Nolte et al. 2013a) previously installed by the National Park administration along a transect from the intertidal flats to the seawall to monitor surface-elevation change (Stock 2011). Measurements of surface-elevation change continued during the experimental period. From these data, mean surface-elevation change [mm yr^{-1}] for the duration of the experiment was calculated and assigned to the blocks as surface-elevation change value. During the study period, these values for the blocks one to four are 2.7 mm yr^{-1}, 4.9 mm yr^{-1}, 7.3 mm yr^{-1}, and 8.1 mm yr^{-1}, respectively. Each block was subdivided into 24 plots of 1 m x 1 m separated by one metre wide buffer zones. Thus while the original elevation represents the conditions at the start of the experiment, the surface-elevation change assesses the mean increase of elevation as a result of sediment deposition and soil autocompaction over the course of the experiment. The position of the plots was marked in the field using plastic sticks. The original elevation of all plots in relation to the German ordnance datum (NHN) was assessed at the start of the experiment using an optical levelling device (Nolte et al. 2013a).

A total number of 850 individual *Elymus* plants were collected close to the experimental blocks in June 2007 from an area dominated by the plant. An automatic planting device with a diameter of 8 cm and depth of 16 cm was used for extraction and individuals were transplanted together with the field substrate into pots of the same size. Pots were transported to the greenhouse where plants were cut back and cultivated for 5 weeks. In case one pot contained more than one individual the surplus individuals were removed. Only intermediate sized individuals were further used for planting. Within each plot we planted five randomly chosen individuals of *Elymus* on 24.07.2007. The automated planting device was used to remove the soil in the field to create a hole, so that plants could be transplanted including their substrate. Previous to the experiment *Elymus* was not present in the blocks. Vegetation composition in blocks 1 to 3 was heterogeneous with a mix of *Aster tripolium, Halimione portulacoides* , *Puccinellia maritima* and *Spartina anglica*. Only block 4 was characterised by the dominance of *Halimione portulacoides* in most plots. Almost 50% of all planted individuals died in the autumn of 2007, probably due to extremely high precipitation. To continue the experiment dead individuals were therefore replaced in April 2008.

Plots within the blocks were randomly assigned to one of the three N-fertilisation treatments, namely 0 g N m^{-2} yr^{-1} (control), 20 g N m^{-2} yr^{-1} (N20) and 40 g N m^{-2} yr^{-1} (N40), resulting in eight replicates per treatment per block. These Nitrogen addition treatments were chosen to be relatively high, as fertilisation treatments representing atmospheric N-input of 4 g N m^{-2} yr^{-1} (Bockelmann and Neuhaus 1999) or 5 g N m^{-2} yr^{-1} (Van Wijnen and Bakker 1999) were found to have no effect. A powdered slow-release N-fertilizer (Floranid® 32-0-0) was used and was dissolved in water obtained from the closest salt-marsh creek. The same volume of creek water without fertilizer was added to control plots. Fertilizer was applied three times per year during the main growing season in Mai, June and July every year from the start of the experiment in 2007 to 2011.

After four years of treatment, the vegetation composition and cover was recorded in all plots on 30.09.2011 using the Londo decimal scale (Londo 1976). Nomenclature follows (Haeupler and Muer 2007). Additionally, total aboveground biomass was collected from a 20 cm x 20 cm subplot in each plot on 30.09.2011 as an indicator of general light competition. Biomass was stored in perforated permeable plastic bags (Sealed Air Cryovac) and air dried at 60°C for two days to constant weight. Additionally, five empty bags were weighed and the mean weight used to subtract the weight of the bag from the biomass samples.

2.2 Statistical analyses

To assess succession (i.e. the shift from early towards late-successional plant-species composition following Olff et al. (1997) and Petersen et al.(2014)) the effect of surface-elevation change, original elevation and N-fertilisation on plant-species composition in plots was analysed with redundancy analysis (RDA). Species cover recorded using the Londo decimal scale was recalculated as a percentage cover value, log(x+1)-transformed and centred. As environmental factors, we added original elevation, surface-elevation change and N-fertilisation in a stepwise forward procedure to the analysis. Both surface-elevation change and N-fertilisation were treated as factors, as they had only four and three levels, respectively. Significance was tested based on Monte-Carlo permutation tests, with 499 permutations.

In addition to the RDA we tested the effect of surface-elevation change, elevation and N-fertilisation on the cover of *Elymus* at the end of the experiment using a negative binomial generalized linear model (GLM). The full model included the cover of *Elymus* as a response variable and the explanatory variables original elevation, surface-elevation change and N-fertilisation, with the latter two being factorial variables. All interaction effects were included. Overdispersion was detected and therefore standard errors were corrected using a quasi-GLM model. Backward stepwise model selection was performed using the drop1 command based on χ^2-test (Zuur et al. 2009).

The effect of surface-elevation change, original elevation and N-fertilisation on the biomass was analysed using Analysis of Covariance (ANCOVA) as assumptions of normality and homogeneity of variance were met by the data. Original elevation, surface-elevation change and N-fertilisation, as well as all possible interaction terms, were included as explanatory variables. To compare the biomass between treatments, we used a Tukey posthoc-test. No spatial autocorrelation was detected in the models when variograms of the residuals were plotted (Zuur et al. 2009). All statistical analyses except for the RDA were performed using the statistical software ‘R’ version 3.2.4 (R Development Core Team 2017). The RDA was performed using the statistical software CANOCO 5 (Smilauer and Lepš 2014)

3. Results

3.1 Plant-species composition

In the RDA we found that 32.2 % and 8.4 % of the variation in the plant-species composition were explained by the first and second axis, respectively. The final model included surface-elevation change, original elevation and N-fertilisation and was significantly different from a random model (pseudo F = 13.5; p = 0.002). The single values of the surface-elevation change factor are organised along the first axis, with the surface-elevation change 4.9 mm yr^{-1} and 2.7 mm yr^{-1} positioned relatively close together (Fig. 2). The second axis corresponds with the single values of the N-fertilisation factor, with N 20 being close to the centre of the plot. Original elevation lies between axes. *Elymus* corresponds with the first axis. This indicates that *Elymus* cover is mainly explained by surface-elevation change, with the highest percentage covers at the surface-elevation change 8.1. Furthermore, cover of *Elymus* in plots is positively correlated with original elevation, while the N-fertilisation seems to have little influence on the cover of *Elymus*. The same pattern can be observed for *Halimione protulacoides*, another late-successional species. Here it needs to be noted, however, that *Halimione portulacoides* already had a higher percentage cover in the respective block with surface-elevation change 8.1 at the start of the experiment. Characteristic pioneer and low marsh species such as *Salicornia europea* L. s. I. and *Puccinellia maritima* lie close to the low surface-elevation change values and are negatively correlated with original elevation. The typical mid-marsh species such as *Aster tripolium*, *Spergularia maritima* and *Limonium vulgare* are clustered around the mid-elevations and intermediate surface-elevation change value. The high N-fertilisation seems to be positively associated only with *Suaeda maritima*, while most species cluster around the N 0 and N 20 treatment.

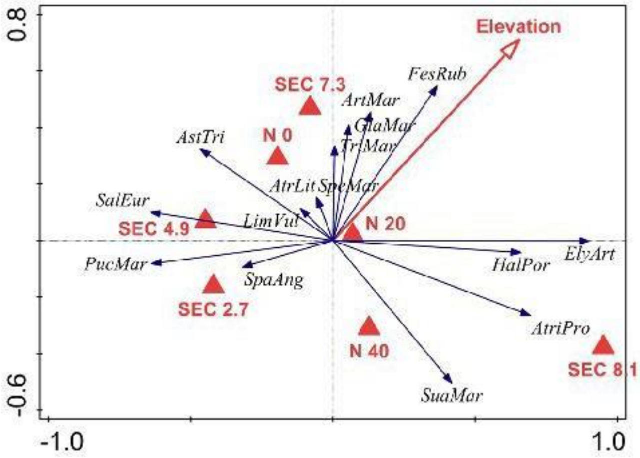

Figure 2: Biplot of the RDA analysis illustrating the effect of the environmental variables surface-elevation change (SEC) and N-fertilisation (▲), as well as original elevation range (elevation, open arrow) on species composition. Species abbreviations: ***ArtMar*** *Artemisia maritima*, ***AstTri*** *Aster tripolium*, ***AtriPro*** *Atriplex prostrata*, ***AtrLit*** *Atriplex littoralis*, ***ElyArt*** *Elymus athericus*, ***FesRub*** *Festuca rubra*, ***GlaMar*** *Glaux maritima*, ***HalPor*** *Halimione portulacoides*, ***LimVul***

Limonium vulgare, ***PlaMar*** *Plantago maritima,* ***PucMar*** *Puccinellia maritima,* ***SalEur*** *Salicornia europea,* ***SpaAng*** *Spartina anglica,* ***SpeMar*** *Spergularia maritima,* ***SuaMar*** *Suaeda maritima,* ***TriMar*** *Triglochin maritimum*

3.2 Cover of *Elymus*

The final model explaining the percentage cover of *Elymus* included a significant interaction of surface-elevation change and original elevation (Tab. 1), while N-fertilisation did not remain in the model. If surface-elevation change is low, *Elymus* is only present with a low percentage cover at the highest original elevation of the elevation range within the blocks (Fig. 3 A & B). With a higher surface-elevation change of 7.3 mm yr^{-1} *Elymus* is present more often, but cover percentage is higher only in the highest elevation within this block (Fig. 3 C). At a high surface-elevation change of 8.1 mm yr^{-1} *Elymus* is present at all original elevations within the plot (Fig. 3 D), and its percentage cover increases along the elevation range within the blocks with increasing original elevation.

TABLE 1 Summary statistics of GLM analyzing effects of N fertilization, original elevation and surface elevation change (SEC) and their interactions (*) on the percentage cover of *Elymus*

	estimate	t-value	P
N			ns
Elev	4.18 ± 1.22	3.42	**< 0.001**
SEC	107.6 ± 32.31	3.33	**< 0.01**
N*Elev			ns
N*SEC			ns
Elev*SEC	-0.51 ± 0.15	-3.31	**<0.01**
N*Elev*SEC			ns

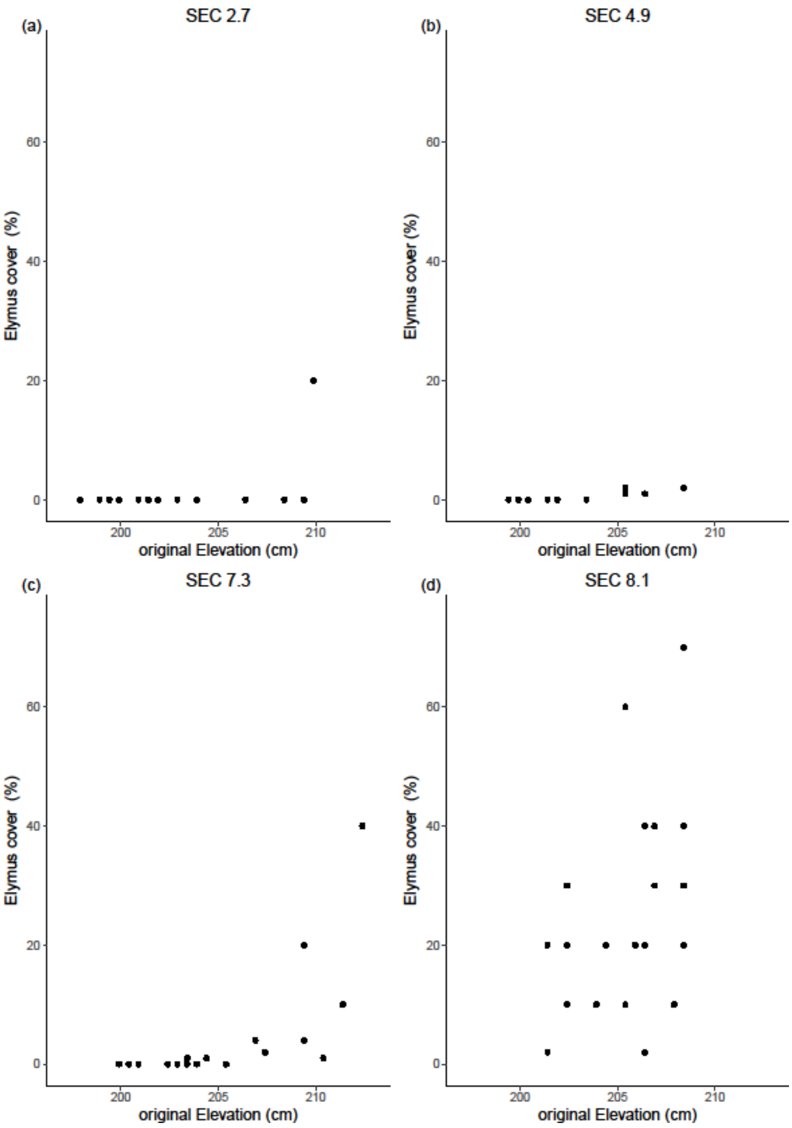

Figure 3: Point plots illustrating the effect of the range of original elevation within blocks on the percentage cover of *Elymus* at four different rates of surface-elevation change (SEC) in mm yr^{-1} (A-D).

3.3 Biomass

The ANCOVA results (Tab. 2) showed N-fertilisation and surface-elevation change to be the factors explaining the total biomass within plots. Furthermore, post-hoc tests showed biomass to be lowest at a surface-elevation change of 7.3 mm yr^{-1} and highest at surface-elevation change of 8.1 mm yr^{-1}, while both low surface-elevation change values showed an intermediate biomass (Fig. 4 A). N-fertilisation was found to have a positive effect on biomass compared to the control treatment, but the amount of fertiliser had no effect in our experiment (Fig. 4B). Elevation had no effect on biomass (Fig 4C).

TABLE 2 Summary statistics of ANCOVA analyzing effects of N fertilization, original elevation and surface elevation change (SEC) and their interactions (*) on the total biomass in plots

	DF	F-value	P
N	2	4.49	**< 0.05**
Elev			ns
SEC	3	30.65	**< 0.001**
N*Elev			ns
N*SEC			ns
Elev*SEC			ns
N*Elev*SEC			ns

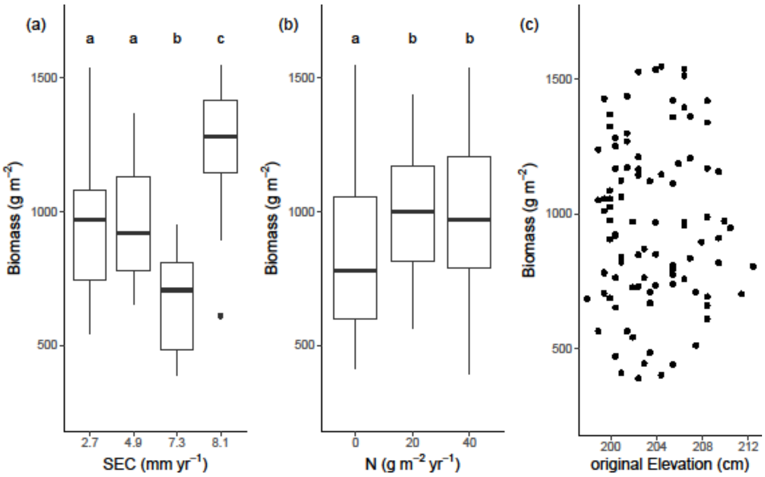

Figure 4: A) and B) boxplots illustrating the effect of surface-elevation change (SEC) and N-fertilization on biomass in plots. Boxplots represent: median (middle line), interquartile range (box), 1.5 times interquartile range (bar) and outliers (dots). Letters indicate significant differences between treatments based on PostHoc-tests. C) Point plot illustrating the effect of the range of original elevation on total biomass.

4. Discussion

In line with our first hypothesis, original elevation was found to be a main driver of succession favouring *Elymus* and other late successional plant species such as *Halimione portulacoides*, as well as increasing the cover of *Elymus*. Contrastingly, no effect of original elevation on biomass could be found. N-addition increased the biomass in comparison to the control treatment, but had no effect on succession as seen in the RDA, or the cover of *Elymus*. We therefore find no support for hypothesis 2 and conclude that *Elymus* is not N-limited. In support of hypothesis 3 we found that surface-elevation change is a main driver of succession as seen in the RDA. The significant interaction effect of original elevation and surface-elevation change on the cover of *Elymus* indicates that a high surface-elevation change quickly raises the original elevation to a level, at which *Elymus* can establish. Thus as no effect of N-fertilisation, but an effect of surface-elevation change was detected, we can conclude that the positive effect of surface-elevation change on *Elymus* is based on the resulting higher elevation caused by sedimentation, but not the addition of nitrogen with the freshly deposited sediments.

4.1 Elevation

Elevation is clearly one of the most important factors determining the succession and therefore also the presence and dominance of *Elymus* in Wadden Sea salt marshes (Olff et al. 1997; Suchrow and Jensen 2010; Davy et al. 2011; Rupprecht et al. 2015b). Generally, a high elevation is interpreted as a proxy for low flooding frequency and duration and therefore also for favourable abiotic conditions for high-marsh plants such as *Elymus* (Suchrow and Jensen 2010). In these less stressful parts of the marsh, the dominance of *Elymus* is often explained with its high biomass and the competitive exclusion of other species based on the limitation of light for shorter plants (Olff et al. 1997). Yet, we found no effects of original elevation on biomass which thus means that elevation might not favour tall plants and could indicate that light competition plays no role. However, the plots were chosen to be very similar in elevation and therefore only represent a small part of the entire elevation gradient in salt marshes. Additionally, biomass might not be the most suitable indicator to quantify light competition between species, because there is no clear linear relationship between biomass and the relative absorbed irradiance (Rupprecht et al. 2015a). Therefore, we cannot rule out light competition as a driving mechanism of succession in this case.

Furthermore, we are unable to rule out effects of belowground competition, as this study only included the assessment of aboveground biomass. An experiment using the grass species *Agrostis capillaris* for example, showed that the negative effect of this invasive species on the native vegetation was driven by belowground competition (Broadbent et al. 2017). Interestingly, the authors found this effect regardless of N-availability. Yet, in a mainland salt marsh in Germany with clay soil, N-availability was found to have no effect on the fine-root mass (Redelstein et al. 2018). However, the fine-root mass was significantly lower in the *Elymus*-dominated high marsh, compared to the low marsh (Redelstein et al. 2018). Both Redelstein et al. (2018) and Ford et al. (2016) found the fine-root mass to increase with plant species richness, probably because the species in the more diverse low-marsh community also represent diverse belowground space occupation strategies. Yet, the total fine-root mass of a group of species does not rule out potential belowground competition and therefore these interactions should be further investigated in salt marshes.

4.2 N-fertilisation vs. surface-elevation change

We found no effect of N-fertilisation on the cover of *Elymus* and on succession. Likewise, Bockelmann and Neuhaus (1999) found no effect of N-fertilisation on *Elymus* in their study in a mainland salt marsh, thus drawing the conclusion that *Elymus* is not N-limited. In contrast, a positive effect of N-fertilisation on the succession and the relative contribution of *Elymus* to the total biomass was found by Van Wijnen and Bakker (1999) in a back-barrier island salt marsh. Thus, these contrasting results might be explained by the differences between mainland salt marshes and island salt marshes, with the latter being characterised by a much shallower clay layer on top of the sandy subsoil (de Groot et al. 2011; Elschot et al. 2013). The thickness of the clay layer was found to be a good predictor of the N-pool (Olff et al. 1997). Therefore, *Elymus* might be N-limited in island salt marshes (Van Wijnen and Bakker 1999), but not in mainland salt marshes (Bockelmann and Neuhaus 1999) such as in this experiment. In an indirect approach, comparing time series of vegetation maps and chronosequence data of four island salt marshes differing in sediment deposition rates, it was also concluded that *Elymus* expansion is mainly driven by spatially varying natural sediment deposition rates including the resulting N-addition, and not by the evenly spread atmospheric N-deposition (Veeneklaas et al. 2013). We can now corroborate this conclusion by the results of our experiment that sedimentation leading to a high surface-elevation change enabled *Elymus* to grow at originally lower elevation, while N-fertilisation had no effect. Sediment deposition rate in our study area is 2.8 – 8.3 kg m^{-2} yr^{-1} (Nolte et al. 2013b). Furthermore, we know that the N-content of the freshly deposited sediment collected using sediment traps is around 0.28% of the total mass (Mueller et al. unpublished data). Therefore the input of N via sediment deposition in the study site ranges roughly between 7.8 and 23.0 g m-2 yr-1 and thus is representative of the lower N-fertilization treatment. For comparison, on a back-barrier island in the Netherlands sediment deposition rate was found to range from roughly 1.0 to 2.5 kg m^{-2} yr^{-1} (Elschot et al. 2013). No data on the N-content of freshly deposited sediment is available for this specific site, but assuming similar values to those of Mueller et al. (unpublished data), the input of N via sediment deposition would range between 2.8 and 7.0 g m^{-2} yr^{-1}. This illustrates that natural N-input in in these island marshes is probably much lower and can thus, together with the resulting shallower clay layer, explain that *Elymus* is limited by Nitrogen in these salt marshes. Furthermore, surface-elevation change can also vary between mainland marshes. This is in accordance with a landscape scale study of succession in the salt marshes of the Schleswig-Holstein Wadden Sea coast, which found early successional stages to be more persistent in the northern Wadden Sea (Rupprecht et al. 2015b). It is argued that this is due to large scale gradients of e.g. surface-elevation change (Rupprecht et al. 2015b), which was found to be lower in the North (Suchrow et al. 2012) and might therefore reduce *Elymus* encroachment.

4.3 Individual establishment vs. clonal growth

In this experiment planted individuals of *Elymus* were used to assess which factors drive the encroachment of the species. In natural succession, however, vegetative propagation was found to be an important pathway for *Elymus,* especially in young marshes (Veeneklaas et al. 2011). The spread of *Elymus* along the coast of Schleswig Holstein was also found to be positively affected by a shorter distance to the nearest established *Elymus* patch (Rupprecht et al. 2015b), which might also indicate the importance of vegetative spreading. Vegetative spreading can enable plants to grow into unfavourable habitats as daughter ramets can be supported by the adult plants via the rhizome

(Hutchings and Bradbury 1986). This physiological integration can increase the chance of survival for daughter ramets in stressful conditions (D'Hertefeldt and Jónsdóttir 1999; Zhou et al. 2014). Furthermore, clonal grasses such as e.g. *Leymus scalinus*, were found to adapt the length of their ramets under different conditions, switching to the so-called guerrilla growth form with spreading ramets in patches with low nutrient supply (Ye et al. 2006). Whether *Elymus* is also using physiological integration to invade the otherwise unfavourable low marsh, remains to be further investigated.

4.4 Succession in salt marshes

Our results highlight that elevation and the change of elevation through sedimentation (i.e. surface-elevation change) is a key driver of the succession from mid-successional low marsh communities to a late successional high marsh community dominated by *Elymus*. The elevation as a key variable determining the distribution of salt-marsh plant species in Wadden Sea salt marshes (Olff et al. 1997; Schröder et al. 2002; Suchrow and Jensen 2010) and the increase in elevation over time as a main factor leading to vegetation change has been widely described here (Leendertse et al. 1997; Olff et al. 1997; Veeneklaas et al. 2013; Rupprecht et al. 2015b). However, while the zonation represents the succession in mainland salt marshes (de Leeuw et al. 1993), this is not necessarily true for back-barrier island salt marshes (de Leeuw et al. 1993; Olff et al. 1997). Here the marsh elevation is a result of the underlying sand layer and the clay sediment that deposited on top of it (Olff et al. 1997; Bakker 2014). Additionally, the thickness of the clay layer in back-barrier island marshes is a good predictor of the N-pool (Olff et al. 1997). This might explain why studies with N-fertilization found much clearer effects in island salt marshes with a thin clay layer (van Wijnen and Bakker 2001), compared to mainland salt marshes with a thick clay layer (Bockelmann and Neuhaus 1999).

4.5 Conclusions

We can conclude that the main driver of the *Elymus*-encroachment in the ungrazed Wadden Sea mainland salt marshes is a high surface-elevation change, raising the original elevations and thereby probably generating more favourable abiotic conditions. In contrast to many other studies on grass encroachment, N-fertilisation had no effect on the encroachment of *Elymus* in this mainland salt marsh and we therefore conclude that eutrophication by atmospheric N-deposition probably plays only a minor role. This case, therefore, is an example for an ecosystem in which encroachment is driven by a natural factor, rather than anthropogenic eutrophication. Thus, when attempting to halt or slow down grass or shrub encroachment, we suggest nature managers to assess different potential causes of the development before decisions on actions such as grazing, cutting or burning are made. In case of the Wadden Sea salt marshes, it furthermore needs to be monitored whether *Elymus* is indeed the climax vegetation. On the oldest parts of the island salt marshes, *Elymus* has been partly replaced by stands of *Phragmites australis* and *Juncus gerardii*, probably due to waterlogging and low rates of sediment deposition and thus low sediment supply. Whether this development will also lead to a reduced encroachment or even reduction of *Elymus* in mainland salt marshes, remains to be seen.

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Data availability statement:

Data is available in PANGAEA. https://doi.org/10.1594/PANGAEA.899893

Literature

Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge

Andresen H, Bakker JP, Brongers M, et al (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89:137–148.

Bakker ES, Olff H (2003) Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. J Veg Sci 14:465–474.

Bakker JP (2014) Ecology of salt marshes - 40 years of research in the Wadden Sea. Wadden Academy

Bakker JP, Bos D, de Vries Y (2003) To graze or not to graze : that is the question. In: Wolff WJ, Essink K, Kellermann A, van Leeuwe MA (eds) Challenges to the Wadden Sea - Proceedings of the 10th international scientific Wadden Sea Symposium. pp 67–87

Berendse F, Elberse WT (1990) Competition and nutrient availability in heathland and grassland ecosystems. Perspect plant Compet 93–116. doi: http://dx.doi.org/10.1016/B978-0-12-294452-9.50010-2

Bird EJ, Choi YD (2016) Response of native plants to elevated soil nitrogen in the sand dunes of Lake Michigan, USA. Biol Conserv. doi: 10.1016/j.biocon.2016.12.001

Bockelmann AC, Neuhaus R (1999) Competitive exclusion of Elymus athericus from a high-stress habitat in a European salt marsh. J Ecol 87:503–513.

Bouchard V, Tessier M, Digaire F, et al (2003) Sheep grazing as management tool in Western European saltmarshes. C R Biol 326:148–157. doi: 10.1016/S1631-0691(03)00052-0

Broadbent A, Stevens CJ, Peltzer DA, et al (2017) Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. Oecologia. doi: 10.1007/s00442-017-4039-5

Bullock JM, Hill BC, Dale MP, Silvertown J (1994) An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. J Appl Ecol 31:493–507.

Casper BB, Jackson RB (1997) PLANT COMPETITION UNDERGROUND. Annu Rev Ecol Syst. doi: 10.1146/annurev.ecolsys.28.1.545

Chapin FSII, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol Monogr. doi: 10.2307/2937039

Clements FE (1916) Plant Succession.

D’Hertefeldt T, Jónsdóttir IS (1999) Extensive physiological integration in intact clonal systems of Carex arenaria. J Ecol 87:258–264. doi: 10.1046/j.1365-2745.1999.00345.x

Davy AJ, Brown MJH, Mossman HL, Grant A (2011) Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. J Ecol 99:1350–1357. doi: 10.1111/j.1365-2745.2011.01870.x

de Groot A V, Veeneklaas RM, Kuijper DPJ, Bakker JP (2011) Spatial patterns in accretion on barrier-island salt marshes. Geomorphology 134:280–296.

de Leeuw J, de Munck W, Olff H, Bakker JP (1993) Does Zonation Reflect the Succession of Salt-Marsh Vegetation - a Comparison of an Estuarine and a Coastal Bar Island Marsh in the Netherlands. Acta Bot Neerl 42:435–445.

Dijkema KS (1987) Geography of Salt Marshes in Europe. Zeitschrift Fur Geomorphol 31:489–499.

Eldridge DJ, Bowker MA, Maestre FT, et al (2011) Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. Ecol. Lett. 14:709–722.

Elschot K, Bouma TJ, Temmerman S, Bakker JP (2013) Effects of long-term grazing on sediment deposition and salt-marsh accretion rates. Estuar Coast Shelf Sci 133:109–115.

Esselink P, Petersen J, Arens S, et al (2009) Salt Marshes. Thematic Report No. 8. In: Marencic H, de

Vlas J (eds) Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group,

Esselink P, Zijlstra W, Dijkema KS, van Diggelen R (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. Biol Conserv 93:61–76.

Ford H, Garbutt A, Ladd C, et al (2016) Soil stabilization linked to plant diversity and environmental context in coastal wetlands. J Veg Sci. doi: 10.1111/jvs.12367

Gaucherand S, Liancourt P, Lavorel S (2006) Importance and intensity of competition along a fertility gradient and across species. J Veg Sci 17:455–464. doi: 10.1658/1100-9233(2006)17[455:IAIOCA]2.0.CO;2

Haeupler H, Muer T (2007) Bildatlas der Farn- und Blütenpflanzen Deutschlands. Verlag Eugen Ulmer

Hutchings MJ, Bradbury IK (1986) Ecological Perspectives On Clonal Perennial Herbs. Bioscience 36:178–182. doi: 10.2307/1310305

Kiehl K, Eischeid I, Gettner S, Walter J (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. J Veg Sci 7:99–106.

Kiehl K, Esselink P, Bakker JP (1997) Nutrient limitation and plant species composition in temperate salt marshes. Oecologia 111:325–330.

Kiehl K, Schröder H, Stock M (2007) Long-term vegetation dynamics after land-use change in Wadden Sea salt marshes. Coastline Reports 7:17–24.

Kuijper D, Dubbeld J, Bakker J (2005) Competition between two grass species with and without grazing over a productivity gradient. Plant Ecol 179:237–246.

Kuijper DPJ, Bakker JP (2003) Large-scale effects of a small herbivore on salt-marsh vegetation succession – A comparative study on three Wadden Sea islands. J Coast Conserv 9:179–188.

Leendertse PC, Roozen AJM, Rozema J (1997) Long-term changes (1953-1990) in the salt marsh vegetation at the Boschplaat on Terschelling in relation to sedimentation and flooding. Plant Ecol 132:49–58.

Londo G (1976) The Decimal Scale For Releves Of Permanent Quadrats. Vegetatio 33:61–64.

McCook LJ (1994) Understanding ecological community succession: Causal models and theories, a review. Vegetatio 110:115–147.

Metera E, Sakowski T, Sloniewski K, Romanowicz B (2010) Grazing as a tool to maintain biodiversity of grassland - a review. Anim Sci Pap Reports 28:315–334.

Nolte S, Esselink P, Smit C, Bakker JP (2014) Herbivore species and density affect vegetation-structure patchiness in salt marshes. Agric Ecosyst Environ 185:41–47. doi: 10.1016/j.agee.2013.12.010

Nolte S, Koppenaal EC, Esselink P, et al (2013a) Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies. J Coast Conserv 17:301–325. doi: 10.1007/s11852-013-0238-3

Nolte S, Müller F, Schuerch M, et al (2013b) Does livestock grazing affect sediment deposition and accretion rates in salt marshes? Estuar Coast Shelf Sci 135:296–305. doi: 10.1016/j.ecss.2013.10.026

Olff H, de Leeuw J, Bakker J, et al (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. J Ecol 85:799–814.

Petersen J, Kers B, Stock M (2014) TMAP-Typology of Coastal Vegetation in the Wadden Sea Area. Wilhelmshaven

R Development Core Team (2017) R Development Core Team.

Redelstein R, Dinter T, Hertel D, Leuschner C (2018) Effects of Inundation, Nutrient Availability and Plant Species Diversity on Fine Root Mass and Morphology Across a Saltmarsh Flooding Gradient. Front Plant Sci. doi: 10.3389/fpls.2018.00098

Rook AJ, Dumont B, Isselstein J, et al (2004) Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biol Conserv 119:137–150. doi: 10.1016/j.biocon.2003.11.010

Rupprecht F, Möller I, Evans B, et al (2015a) Biophysical properties of salt marsh canopies — Quantifying plant stem flexibility and above ground biomass. Coast Eng 100:48–57. doi: 10.1016/j.coastaleng.2015.03.009

Rupprecht F, Wanner A, Stock M, Jensen K (2015b) Succession in salt marshes - large-scale and long-term patterns after abandonment of grazing and drainage. Appl Veg Sci 18:86–98. doi: 10.1111/avsc.12126

Schröder HK, Kiehl K, Stock M (2002) Directional and non-directional vegetation changes in a temperate salt marsh in relation to biotic and abiotic factors. Appl Veg Sci 5:33–44.

Smilauer P, Lepš J (2014) Multivariate Analysis of Ecological Data using CANOCO 5.

Soons MB, Hefting MM, Dorland E, et al (2016) Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. Biol Conserv. doi: 10.1016/j.biocon.2016.12.006

Stock M (2011) Patterns in surface elevation change across a temperate salt marsh platform in relation to sea-level rise. Coastline Reports 17:33–48.

Stock M, Gettner S, Hagge H, et al (2005) Salzwiesen an der Westküste von Schleswig-Holstein 1988 - 2001. Boyens Medien GmbH & Co. KG, Heide (Schriftenreihe / Nationalpark Schleswig-Holsteinisches Wattenmeer, 15)

Stock M, Maier M (2016) Salzwiesenschutz im Nationalpark Wattenmeer – ein Überblick. Vogelkundliche Berichte Niedersachsen 44:131–156.

Suchrow S, Jensen K (2010) Plant Species Responses to an Elevational Gradient in German North Sea Salt Marshes. Wetlands 30:735–746. doi: 10.1007/s13157-010-0073-3

Suchrow S, Pohlmann N, Stock M, Jensen K (2012) Long-term surface elevation changes in German North Sea salt marshes. Estuar Coast Shelf Sci 98:71–83. doi: 10.1016/j.ecss.2011.11.031

van Andel J, Bakker JP, Grootjans AP (1993) Mechanisms of vegetation succession: a review of concepts and perspectives. Acta Bot. Neerl. 42:413–433.

van Wijnen HJ, Bakker JP (2001) Long-term Surface Elevation Change in Salt Marshes: a Prediction of Marsh Response to Future Sea-Level Rise. Estuar Coast Shelf Sci 52:381–390. doi: 10.1006/ecss.2000.0744

Van Wijnen HJ, Bakker JP (1999) Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. J Ecol 87:265–272. doi: 10.1046/j.1365-2745.1999.00349.x

Veeneklaas R, Bockelmann A, Reusch T, Bakker J (2011) Effect of grazing and mowing on the clonal structure of Elytrigia atherica: A long-term study of abandoned and managed sites. Preslia 83:455–470.

Veeneklaas RM, Dijkema KS, Hecker N, Bakker JP (2013) Spatio-temporal dynamics of the invasive plant species Elytrigia atherica on natural salt marshes. Appl Veg Sci 16:205–216.

Veer MAC, Kooijman AM (1997) Effects of grass-encroachment on vegetation and soil in Dutch dry dune grassland. Plant Soil 192:119–128. doi: 10.1023/A:1004280300820

WallisDeVries MF, Bobbink R (2017) Nitrogen deposition impacts on biodiversity in terrestrial ecosystems: Mechanisms and perspectives for restoration. Biol. Conserv.

Wanner A, Suchrow S, Kiehl K, et al (2014) Scale matters: Impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. Agric Ecosyst Environ 182:69–79. doi: 10.1016/j.agee.2013.08.014

Ye XH, Yu FH, Dong M (2006) A trade-off between guerrilla and phalanx growth forms in Leymus secalinus under different nutrient supplies. Ann Bot 98:187–191. doi: 10.1093/aob/mcl086

Zhou C, Zhang Z, Wang Z, Yang Y (2014) Difference in capacity of physiological integration between two ecotypes of Leymus chinensis underlies their different performance. Plant Soil 383:191–202. doi: 10.1007/s11104-014-2169-7

Zuur AF, Ieno EN, Walker NJ, et al (2009) Mixed effects models and extensions in Ecology with R. Springer Science+Business Media

Annex G: Bockelmann, A.C. (2002). Ordinary and successful: The invasion of Elymus athericus in European salt marshes. Doctor of Philosophy, Groningen.

Ordinary and succesful

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Summary

Human alterations of the earth's ecosystems have led to profound changes in the landscape structure, the CO_2 concentration of the atmosphere, the hydrology and the global nitrogen cycle. As a major consequence, nearly all plant and animal communities in the semi-natural landscape of Central Europe are subject to a decrease of species diversity. This applies also to more natural landscapes, such as salt marshes, where species numbers are declining. Three major processes currently alter the salt-marsh ecosystem: change of land use, anthropogenic nitrogen input, and sea-level rise.

In the past two decades, the most notable change of vegetation in several abandoned salt marshes of the Wadden Sea area was the spread of native clonal grass *Elymus athericus* (Poaceae). *E. athericus* is expanding at higher elevations of the salt-marsh gradient, now frequently dominating extensive areas. In addition, this species recently also invaded lower elevations. A consequence of this expansion is a decline of species diversity in the entire salt marsh.

There are two different, non exclusive models that could explain the loss of species diversity through changing environmental conditions: (A) The ecological Model: The new, supposedly more homogeneous and nutrient-rich conditions could favour species with a high phenotypic plasticity that are able to spread very fast by means of vegetative reproduction, and that are strong competitors. (B) The evolutionary model: Changes in the environment could alter the natural selection pressure leading to rapid genetic adaptation of populations. In this thesis I followed the two outlined explanation models, one purely ecological and one integrating evolutionary and ecological processes, that could explain the success of *Elymus athericus* in expanding and invading new habitats. Ecological experiments, demographic investigations of the life history and analyses of genetic population and clone structure with molecular markers provided insight into factors that promote or hamper the invasion of this species. Figure 1.3 provides an overview on the research strategy.

In Chapter 2 we approached model (A) by testing in a field experiment at the North Frisian coast of Germany whether *E. athericus* can extend its distribution under enhanced nitrogen availability and whether its invasion can be prevented by competition with *Atriplex portulacoides*, a clonal dwarf shrub. The reciprocal effects on both species were measured as vegetation cover and above-ground biomass. *Elymus athericus* extended its distribution into the lower salt marsh when *Atriplex portulacoides* was removed. The lower distributional boundary of *Elymus athericus* in this experiment is thus probably a result of the competition with *Atriplex portulacoides.* Neither species showed a response to nitrogen fertilization. Improvement of nitrogen availability in concentrations of the annual atmospheric input had hence no detectable effect on plant zonation and growth.

A prerequisite for many experiments in this thesis is a proper characterisation of the gradient of inundation in salt marshes. In order to explain biological zonation, elevation above the Ordnance Sea Level is frequently used as an indicator of the abiotic gradient in intertidal ecosystems. This is based on the implicit assumption that tidal elevation is directly correlated with inundation frequency and/or duration. Despite the importance of inundation for tidal ecosystems, measurements have rarely been taken directly by measuring inundation at the site of investigation. We measured Mean High Tide (MHT) and flooding frequency at three sites on the Dutch Barrier Island of Schiermonnikoog (Chapter 3). To assess the scale dependence, we compared local measurements with the estimated inundation frequencies based on the official tide gauge at a distance of several kilometres. Locally measured MHT water levels differed among sites and were consistently higher than estimated MHT water levels. With this data we subsequently estimated the inundation frequency of vegetation plots and correlated it with species distribution. In an Analyses of Variance inundation frequency accounted for three times the variance in explaining different vegetation zones than elevation. The discrepancy in annual inundation frequency of the vegetation between sites was 300% for a given tidal elevation. Estimated and measured inundation frequencies reliably correlated at a small scale (meters), but not at a larger scale (hundreds of meters to kilometres). If inundation frequency is used as an explanatory variable, it will therefore be advisable to consider the scale dependence of the measurements, in particular if different sites are to be compared.

In the evolutionary model (B) I hypothesised that changes in the environment would lead to changes in the selection pressure acting upon populations. In one of the first analyses of the genetic population structure in salt-marsh species, we investigated population differentiation through isolation by distance, and among strongly divergent habitats (thereafter named low and high marsh, Chapter 4). We intended to test the impact of different selection regimes within these habitats. High and low marsh habitats were sampled at six sites throughout the Wadden Sea area. Contrary to our expectations, an analyses with polymorphic cross-species microsatellite primers revealed significant genetic differentiation already on a very small scale (<100 m to 5 km) and isolation by distance on larger scales (60 to 443 km). After Analyses of

Molecular Variance we found that 14% of the genetic variance could be explained by the differentiation between habitats, as compared to only 8.9% among six sites on a landscape scale. This suggests that strong abiotic and biotic differences between these habitats (e.g. in inundation frequency or presence of herbivores) represent different selection regimes, which result in restricted gene flow over distances as small as 80 m.

We were particularly interested in plant response to selection measured in life history traits. The selection pressure in salt marshes could lead to genetic habitat adaptation or adaptive phenotypic plasticity on a small spatial scale. We examined two times three populations of *E. athericus* from the low and high marsh by a reciprocal transplant experiment at three sites on Schiermonnikoog (Chapter 5). For each genet different growth and reproductive parameters were measured for adult ramets in each habitat and site. Population means in growth traits and vegetative reproduction mainly reacted by a plastic response to transplantation at all sites. A positive correlation of growth and reproductive traits indicated that there was no trade-off between these parameters but there was directive selection for longer shoots. However, if we analyse the genet separately plasticity was only beneficial for genets from the high marsh. Genets from the low marsh showed reduced reproductive output if they increased in growth traits after transplantation. Populations from the low marsh were superior to those in the high marsh in sexual reproduction, which indicated a genetic differentiation between habitats. The results were consistent over sites. We found no typical home site advantage at the population level but we did at the genet level, indicating ongoing evolution towards new population reaction norms. Possibly this indicates that the relatively young populations have not reached equilibrium but are still evolving. The evolutionary process in these young populations is probably constrained by small-scale temporal and spatial variation and thus limited predictability of the environment.

Alternatively selection could act stronger on other life history stages, such as germination or seedling survival, which we investigated in Chapter 6. Field experiments in salt marshes of different age and 'invasion status' on Schiermonnikoog revealed that germination rates are low. Hence, germination is probably the most critical life history stage in *E. athericus.* Accordingly, only low numbers of indigenous seedlings could be found. Once a seedling had emerged, between 35% and 80% survived during the first season, and 26% to 35% persisted until next spring. In two transplant experiments, survival and growth of seedlings depended on parent origin, which suggests habi-

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tat adaptation. We manipulated herbivory and competition in a factorial design, in order to disentangle which interactions are most important for explaining habitat adaptation. Differences in survival and growth among seed parent origin were only present when herbivory and competition with neighbouring species were allowed, which made maternal effects as predominant source for the observed differences unlikely. Superior seedlings originated from habitats with either intense herbivory or competition. We conclude that inherited life history traits resulting from different selection pressures in the parent populations can effect establishment at new sites.

In Chapter 7 we investigated the impact of management regimes of *E. athericus* to test their impact on the genetic population structure and adaptation. Since 1972 different management regimes (mowing, grazing, untreated control) have been applied experimentally to a salt marsh on Schiermonnikoog. We analysed life history traits in the field and tested their genetic basis in a common environment experiment. In addition, we tested genetic differentiation between management regimes using five polymorphic microsatellite markers. The analyses revealed significant differentiation between management regimes. In the common environment most life history differences observed in the field persisted. Plants invested less in growth if biomass had been repeatedly removed by grazing or mowing in the past. Moreover, ramets from grazed and mown plots invested more in vegetative reproduction. We interpret this as genetic adaptation to an environment where flowering is rare and clonal reproduction is advantageous. This is one of the first examples where experimental treatments lead to a genetic differentiation both visible in molecular markers and apparent in life history traits of a plant species.

In summary, I conclude that the success of *E. athericus* probably relies for a large part on its high rates of seedling establishment, a low adult mortality and the fact that this species is a strong competitor for light against other saltmarsh species. The importance of these features depends on the selection pressure in the actual habitat and modulated by rapid genetic habitat adaptation and adaptive plasticity. Intensive herbivory can reduce the abundance, while dense vegetation sward can hinder germination of *E. athericus.* This thesis shows that a combination of approaches from community ecology, population genetics and evolutionary biology can help to understand the population dynamics of an invasive species. The methods and results presented for *Elymus athericus* may serve as model system for other native or alien invaders.

Annex H: New Forest Local Plan air quality monitoring (text reproduced from https://newforest.gov.uk/article/2950/9-Air-quality-and-the-natural-environment)

9. Air quality and the natural environment

9.1 Modelling of traffic emissions from cumulative traffic growth over the Local Plan period identified the potential for significant adverse effects on parts of the New Forest SPA and SAC and Ramsar from nitrogen deposition and ammonia, particularly near main road corridors through the New Forest in areas lacking screening woodlands.

9.2 The Habitat Regulations Assessment which accompanied the Local Plan Part 1 concluded that implementation of the Local Plan and New Forest National Park Local Plan alone will not have an adverse effect on the integrity of any European site. While there is no evidence of current negative effects from traffic related air pollution, uncertainty remains about whether in-combination traffic growth and related air pollution could adversely affect the integrity of New Forest SAC, SPA and Ramsar site during the Local Plan period up to 2036.

9.3 With this uncertainty in the data, the precautionary principle applies requiring a modest financial contribution from development for ongoing monitoring of the effects of traffic emissions on sensitive locations, to trigger management or mitigation measures and developer contributions to implement them if harmful effects are confirmed in the future.

9.4 The Council has instigated a monitoring regime to monitor the condition of sensitive vegetation within the New Forest SPA, SAC and RAMSAR sites, to assess whether or not nutrient nitrogen deposition, acid deposition and ammonia levels from traffic emissions are having an adverse effect on these designated European sites.

9.5 If air quality monitoring identifies that significant adverse effects are occurring or likely, legal agreements or other appropriate mechanisms will be put in place to ensure that homes subsequently permitted would be required to make reasonable and proportionate developer contributions for air quality management or mitigation.

9.6 The project is monitoring any adverse impacts on short habitats (wet and dry heaths) and tall habitats (woodland) at selected sites and the air quality levels at those same sites. This establishes a monitoring framework and evidence base for measuring any adverse impacts on the integrity of New Forest designated internationally protected sites.

Annex I: Shrewsbury North West Relief Road

Natural England understands that, further to our Deadline 5 response (Examination Ref. REP5-109), the Shrewsbury Northwest Relief Road (reference 21/00924/EIA) has been granted permission, on 31st October 2023 (see https://newsroom.shropshire.gov.uk/2023/10/shrewsbury-north-west-relief-road-gets-council-go-ahead/#:~:text=The%20next%20step%20in%20completing,(Tuesday%2031%20October%202023).). We are not aware that the full details of that permission are yet publicly available, however Natural England anticipates that an air quality mitigation and monitoring scheme, to include ammonia, will be secured as part of that permission, as set out in Natural England's response to the Local Planning Authority, reproduced overleaf (where air quality monitoring, vegetation monitoring, and compliance monitoring are distinguished as important aspects of that monitoring scheme). Natural England is seeking equivalent monitoring to the Shrewsbury North West Relief Road (in terms of those three discrete elements) for the Lower Thames Crossing NSIP.

Date: 25 August 2023
Our ref:
Your ref: 21/00924/EIA

NATURAL
ENGLAND

Mr M Davies
Shropshire Council By
email only to
planning.northern@shropshire.gov.uk

Customer Services
Hornbeam House
Crewe Business Park
Electra Way
Crewe
Cheshire
CW1 6GJ

T 0300 060 3900

Dear Mr Davies,

Planning consultation: North West Relief Road Scheme
Location: Street Record, Welshpool Road, Bicton Heath, Shrewsbury, Shropshire

SUMMARY OF NATURAL ENGLAND'S ADVICE

NO OBJECTION - SUBJECT TO APPROPRIATE MITIGATION BEING SECURED

We consider that without appropriate mitigation the application would:
- have an adverse effect on the integrity of the Midland Meres & Mosses Phase 2 Ramsar Site
- damage the interest features for which Hencott Pool Site of Special Scientific Interest has been notified

In order to mitigate these adverse effects and make the development acceptable, the following mitigation measures are required:
- mitigation and monitoring scheme
- a planning condition obliging the developer to deliver the mitigation and monitoring scheme
- section 106 agreements obliging the applicable landowners to comply with the mitigation and monitoring scheme

We also have the following recommendations:
- revision of the timeline for securing mitigation
- further clarity on monitoring

Natural England is a non-departmental public body. Our statutory purpose is to ensure that the natural environment is conserved, enhanced, and managed for the benefit of present and future generations, thereby contributing to sustainable development.

Thank you for your consultation of on the final version of the Habitats Regulations Assessment which was completed by Shropshire Council on 22 August 2023.

General comments

Natural England notes that your authority, as competent authority, has undertaken a Habitats Regulations Assessment of the proposal in accordance with regulation 63 of the Conservation of Species and Habitats Regulations 2017 (as amended). Natural England is a statutory consultee on the appropriate assessment stage of the Habitats Regulations Assessment process, and a competent authority should have regard to Natural England's advice.

Your appropriate assessment concludes that your authority is able to ascertain that the proposal will not result in adverse effects on the integrity of the Midland Meres & Mosses Phase 2 Ramsar Site if the proposed mitigation can be secured. Natural England concurs with this view.

Natural England notes your comments at paragraph 3.1.19 of the Habitats Regulations Assessment that (i) further air quality monitoring surveys have been undertaken during 2023 which demonstrate that the application of mitigation will be more beneficial than originally presented, and (ii) as such changes to mitigation are being considered. Your organisation may wish to seek legal advice on this as Habitats Regulations Assessments do need to be based on the "best available scientific information". Paragraph D.7.2. of "The Habitats Regulations Assessment Handbook" states "*To conclude no adverse effect on integrity, the competent authority must be confident that no reasonable scientific doubt remains as to the absence of such effects. … scientific evidence which has become outdated or superseded by improved approaches would introduce reasonable doubt as to whether the competent authority is using the best available information."* Natural England have responded to this version of the assessment in the interest of expediency but if the underlying data and/or approach to mitigation substantially changes we would recommend that you conduct an updated assessment and consult us on it.

Specific comments

Screening assessment (section 2 of the Habitats Regulations Assessment)

We concur with the conclusions of the screening assessment.

Impact of the proposed new road alone (paragraphs 3.1.1 - 3.1.34 of the Habitats Regulations Assessment)

We confirm that this section contains an accurate reflection of our previous advice and we concur with the conclusions of this stage of the assessment.

Impact of the proposed new road in-combination (paragraphs 3.1.33 - 3.1.44 of the Habitats Regulations Assessment)

We confirm that the assessment of the two projects that have been identified has been conducted appropriately. We concur with the conclusions of this stage of the assessment. It should be noted that a contribution of "<3% of the critical load" is not in itself a "a level where any changes (changes to species composition/competitiveness) would be negligible/ imperceptible" (i.e. in all cases). However, in this case, the reasoning at 3.1.32 applies and it was concluded that an adverse effect on integrity could be excluded (as a result of the project alone). We concur that the additional ammonia concentration/ N deposition identified within the in-combination assessment would not undermine this conclusion – but this is not because the contribution (of N deposition) remains under 3%.

Securing mitigation measures (paragraphs 3.1.53 - 3.1.64 of the Habitats Regulations Assessment)

The proposed mitigation technique is novel, complex and will take time to deliver. We have previously advised that a level of detail is necessary to provide sufficient certainty that the mitigation technique can be delivered in practice. Whilst we are now of the view that sufficient information has been provided we have the following recommendations:

a. Overall timescales (paragraph 3.1.60). We are concerned that the timescales for negotiating section 106 agreements are unrealistic (three months). Our experience of using section 106 agreements to achieve land use change is that negotiations can be protracted. There is also no mention in this timeline of the proposed use of Compulsory Purchase Orders if negotiations fail to reach agreement. Conversely the timescales between preparing the final mitigation plan and commencing it on the ground appear to be quite long (two years). The timeline should be rebalanced to reflect this advice.

b. Monitoring. Whilst we welcome the monitoring proposals the assessment currently mixes up the different types of monitoring that have been proposed (especially in paragraph 3.1.62). The three types of monitoring that will be undertaken are:

Air quality monitoring - to investigate the amount of air pollution emitted by the new road and the amount that is being reduced by the mitigation scheme

Vegetation monitoring - at Hencott Pool to investigate any changes to the botanical communities of the SSSI

Compliance monitoring - to ensure that agricultural activities are not being undertaken within the fields that are part of the mitigation scheme.

We recommend clearly distinguishing between these three types of monitoring in the mitigation and monitoring scheme.

Please do not hesitate to contact me if you wish to discuss the advice in this letter. Please note that if your authority is minded to grant planning permission contrary to the advice in this letter, you are required under Section 28I(6) of the Wildlife and Countryside Act 1981 to notify Natural England of the permission, the terms on which it is proposed to grant it and how, if at all, your authority has taken account of Natural England’s advice. You must also allow a further period of 21 days before the operation can commence. Should the proposal change please consult us again.

[redacted]

Dr Paul Horswill
West Midlands Area Team

Annex J: British Bryological Society Records

Data referenced from the British Bryological Society (via the NBN Atlas) has been supplied to the Examining Authority as a separate Excel spreadsheet.

NBN Atlas record ID	Occurrence ID	Licence	Rightsholder	Scientific name	Taxon author	Name qualifier	Common r	Species ID	Taxon Ran	Occurrenc	Start date	Start date	Start date	Start date	End date	End date d	End date n	End date y	Locality	OSGR	Latitude (V	Longitude	Coordinate	Verbatim (	Recorder	Determine	Individual	Abundanc	Abundanc	Organism :	Organism	Sex	Life stage	Occur	Identificat	Basis of record	Survey key	Dataset name	Dataset ID	Data provider	Data provi	Institution	Kingdom	Phylum	Class	Order	Family	Genus	OSGR 100k	OSGR 10k	OSGR 2km	OSGR 1km	Country	State/Prov	Vitality
ffa9708b-2059-41a5-b18f-9d582e0349c3	8278949	CC-BY	British Bryological Society	Isothecium myosuroides	Brid.	s.str.		NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Lembophyllaceae	Isotheciun	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
f9107575-66a6-4091-97ee-f726d7226ba6	8278961	CC-BY	British Bryological Society	Tortella inflexa	(Bruch) Broth.		Sassari Cri	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Dicranales	Pottiaceae	Tortella	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
ee82fa96-ea44-486a-9615-888409c4b357	8278943	CC-BY	British Bryological Society	Fissidens taxifolius	Hedw.		Common F	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Dicranales	Fissidentaceae	Fissidens	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
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bb44545c-6c64-4a51-bc10-926415d336c5	8278956	CC-BY	British Bryological Society	Plagiothecium succulentum	(Wilson) Lindb.		Juicy Silk-n	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Plagiotheciaceae	Plagiothec	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
b196380e-18c0-49ca-bc1e-f71f0e4d39c8	8278962	CC-BY	British Bryological Society	Ulota bruchii	Hornsch. ex Brid.		Bruch's Pir	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Orthotrichales	Orthotrichaceae	Ulota	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
a1e72806-ecb7-4f65-ad41-f1b1960ae4a4	8278942	CC-BY	British Bryological Society	Eurhynchium striatum	(Hedw.) Schimp.		Common S	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Eurhynchiu	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
9c89c4f0-f26d-462c-a044-64be09d9010e	8278955	CC-BY	British Bryological Society	Plagiothecium nemorale	(Mitt.) A.Jaeger		Woodsy Si	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Plagiotheciaceae	Plagiothec	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
924e2c4e-7157-40eb-8b14-a1ce0f1930da	8278946	CC-BY	British Bryological Society	Homalothecium sericeum	(Hedw.) Schimp.		Silky Wall	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Homalothe	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
8a22626b-70ea-4826-bcc6-c7fc60dbe4bf	8278934	CC-BY	British Bryological Society	Barbula unguiculata	Hedw.		Bird's-claw	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Dicranales	Pottiaceae	Barbula	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
8865c21e-09f4-437d-83ea-c88fea7021d4	8278941	CC-BY	British Bryological Society	Kindbergia praelonga	(Hedw.) Ochyra		Common F	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Kindbergia	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
7e38ae45-bfaf-4d55-aa8a-ab0d84329f5c	8278935	CC-BY	British Bryological Society	Brachythecium rutabulum	(Hedw.) Schimp.		Rough-stal	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Brachythe	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
7b67ec1b-8450-4bbd-8e63-9e7ce44ff84a	8278945	CC-BY	British Bryological Society	Grimmia pulvinata	(Hedw.) Sm.		Grey-cushi	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Grimmiales	Grimmiaceae	Grimmia	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
77a444e3-e097-4294-9bbe-56dfabdfc564	8278957	CC-BY	British Bryological Society	Rhizomnium punctatum	(Hedw.) T.J.Kop.		Dotted Thy	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Bryales	Mniaceae	Rhizomniu	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
6d9561b3-849d-47a2-b6dc-3d6b1d5f37b0	8278959	CC-BY	British Bryological Society	Rhynchostegium confertum	(Dicks.) Schimp.		Clustered	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Rhynchost	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
69b44346-3b56-46e3-ad40-7daadc63ea2b	8278960	CC-BY	British Bryological Society	Thamnobryum alopecurum	(Hedw.) Gangulee		Fox-tail Fe	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Neckeraceae	Thamnobr	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
676484e3-6491-41d5-9642-edfb372f09da	8278951	CC-BY	British Bryological Society	Lophocolea bidentata	(L.) Dumort.		Bifid Crest	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Marchantiophyta	Jungermanniopsida	Jungermanniales	Lophocoleaceae	Lophocole	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
633bb172-e7c8-451f-848b-c5913d1319fb	8278939	CC-BY	British Bryological Society	Dicranella heteromalla	(Hedw.) Schimp.		Silky Forkl	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Dicranales	Dicranellaceae	Dicranella	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
5e372e20-cfeb-4efb-8354-bbc3e6cf8ad5	8278958	CC-BY	British Bryological Society	Rhynchostegiella tenella	(Dicks.) Limpr.		Tender Fea	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Brachytheciaceae	Rhynchost	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
5d12d53a-6b57-4243-b554-b19488eff71a	8278944	CC-BY	British Bryological Society	Frullania dilatata	(L.) Dumort.		Dilated Sca	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Marchantiophyta	Jungermanniopsida	Porellales	Frullaniaceae	Frullania	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
5ca0d955-f1ca-444c-b4b5-c2d3b98c8ca0	8278937	CC-BY	British Bryological Society	Cephaloziella hampeana	(Nees) Schiffn.		Hampe's T	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Marchantiophyta	Jungermanniopsida	Jungermanniales	Cephaloziellaceae	Cephalozie	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
5415b8a6-a308-4f4b-b0fa-92b906f290a8	8278952	CC-BY	British Bryological Society	Lophocolea heterophylla	(Schrad.) Dumort.		Variable-le	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Marchantiophyta	Jungermanniopsida	Jungermanniales	Lophocoleaceae	Lophocole	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
534d45b5-1eef-46a9-a978-ba0f5b2869f2	8278947	CC-BY	British Bryological Society	Hypnum andoi	A.J.E. Sm.		Mamillate	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Hypnaceae	Hypnum	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
3da2440f-d158-40f2-b0ae-21c9d85cfc76	8278948	CC-BY	British Bryological Society	Hypnum cupressiforme	Hedw.		Cypress-le	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Hypnales	Hypnaceae	Hypnum	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
3b2a4860-a5a3-45ca-9037-0b2523cd3435	8278953	CC-BY	British Bryological Society	Metzgeria furcata	(L.) Dumort.		Forked Vei	NHMSYS0	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Marchantiophyta	Jungermanniopsida	Metzgeriales	Metzgeriaceae	Metzgeria	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
29260c13-bac8-4872-aac4-632ad4f4cdbd	8278933	CC-BY	British Bryological Society	Atrichum undulatum	(Hedw.) P.Beauv.	s.str.		NHMSYS0	species ag	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Polytrichopsida	Polytrichales	Polytrichaceae	Atrichum	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
24e24987-e765-4eb5-8a1a-1de1f965c54e	8278938	CC-BY	British Bryological Society	Ceratodon purpureus	(Hedw.) Brid.		Redshank	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Dicranales	Ditrichaceae	Ceratodon	TQ	TQ76	TQ76K	TQ7560	United Kin	England	
0ee587b1-8ad3-4bd6-a908-31b61053caf3	8278936	CC-BY	British Bryological Society	Bryum capillare	Hedw.		Capillary T	NBNSYS00	species	present	08/09/2007	8	9	2007					Westfield	TQ754604	51.31611	0.516232	70.7		Hendey, J.I.										Accepted	HumanObservation	797	Bryophyte data for Great Britain from the British Bryological Society held by BRC: Atlas 2014	dr859	British Bryological Society	dp74	BBS	Plantae	Bryophyta	Bryopsida	Bryales	Bryaceae	Bryum	TQ	TQ76	TQ76K	TQ7560	United Kin	England	