Evidence for Acidification-Driven Ecosystem Collapse of Danish *Erica tetralix* Wet Heathland

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Abstract We report observations of disappearance of *Erica tetralix* in wet heathland, which is unlikely to be caused by competition, as *E. tetralix* is dying before its place is taken up by other species. To investigate the causes, we used both old and new data. Results showed that presence of *Molinia caerulea* and *Calluna vulgaris* were substantial in the former *E. tetralix* dominated areas. Measurements of the C/N ratio in the morlayer were between 21 and 26 under the *E. tetralix* stands. As the expected C/N ratio in a healthy nutrient poor ecosystem like the *E. tetralix* wet heathland is around 30, this indicates that the ratio is probably decreasing and, correspondingly, the probability of nitrogen leaching from the ecosystem is increasing. The morlayer pH was extremely low—between 3.03 and 3.78. This represents a pH decline since the 1960s, where pH values generally were above 4. This supports the hypothesis that the decrease in morlayer pH is the major factor explaining the disappearance of *E. tetralix* and that measures to increase pH should be considered as part of the recommendations for relevant future management.

Keywords Critical load · Nitrogen deposition · Management · Cross-leaved heath · Base cations

INTRODUCTION

Northern temperate European inland wet heathlands, characterized by *E. tetralix*, are nutrient poor dwarf shrub dominated ecosystems on podzolic soils with nutrient-poor

sand and a well-developed organic morlayer. Nowadays, they are associated with depressions in inland dry heathlands and are, typically, very easily distinguishable by their dominance of the pink cross leaved heath *E. tetralix*, a species appearing in a more or less narrow zone around nutrient poor bogs. The range of the zone depends on the inclination of the area around the bog, but according to older sources it can also be dominant in larger flat areas (Børgesen and Jensen 1904; Galløe and Jensen 1906; Jensen and Jensen 1979). The disappearance of these larger areas of wet heathland is likely to be the result of draining and use of ground water for irrigation.

In addition to draining and groundwater abstraction, other threats to this ecosystem include atmospheric nitrogen and sulphur deposition as major causes of ecosystem eutrophication and acidification (Aerts and Berendse 1988; Lovett et al. 2009; Bobbink et al. 2010; Maskell et al. 2010).

The vulnerability of dry heathlands dominated by *Calluna vulgaris* to nitrogen deposition, such as either nitrate or ammonium in the rain or dry deposition by nitrogen dioxide, nitric acid and ammonia, has been studied for a long period (e.g., Bobbink et al. 1992; Pitcairn et al. 1995). In Dutch wet heathlands, *E. tetralix* and accompanying rare species have been shown to be outcompeted by *Molinia caerulea*, especially at high levels of nitrogen deposition (Bobbink et al. 1992). The Dutch studies constitute the basis for the present critical load for nitrogen for wet heathlands at $10\text{--}20\text{ kg N ha}^{-1}\text{ year}^{-1}$ (Bobbink and Hettelingh 2011). The lower limit is set for protection of species.

In Denmark, the N deposition averaged $22\text{ kg N ha}^{-1}\text{ year}^{-1}$ at its peak in the 1980s and 1990s, and at present it averages $14\text{ kg N ha}^{-1}\text{ year}^{-1}$. This is a much lower deposition than in the Netherlands, which probably explains

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why *E. tetralix* dominated wet heathland in Denmark has been believed to be more stable than the *Calluna* dominated dry heathland, even though it is almost without management in the form of grazing or burning. As opposed to *E. tetralix*, *C. vulgaris* needs to be grazed, burnt or cut regularly to rejuvenate. Without this management, the *Calluna* stands grow too old and become unable to dominate the vegetation layer (Gimingham 1972). However, recently it has become evident in the inland wet heathlands of Denmark that *E. tetralix* is dying without a known cause. Observations show large areas of ground covered by grey areas of dead or dying *E. tetralix* (Fig. 1).

The possible causes of this collapse of the former *E. tetralix* dominated wet inland heathland ecosystem include nitrogen deposition, soil acidification, climatic stress, hydrological changes and plant disease. There was no clear indication of any plant disease being the explanation, and in the wet heathland areas situated in connection with depressions, the hydrology appears favourable for the wet heathland ecosystem. However, no obvious single factor could be identified as the dominant cause of the decline based on what was immediately observable.

Due to this lack of an obvious explanation of the causes of the decline, three approaches were selected to investigate the possible causes of the observed decline in wet heathland with *E. tetralix*.

1. Repeated analysis of a vegetation gradient from dry heathland to heathland bog first investigated in 1995, and repeated in 2010.
2. Refined statistical analyses of inland wet heathlands with *E. tetralix* from the Danish National Monitoring and Assessment Programme (Svendsen et al. 2005).
3. Transect analyses, including vegetation parameters and selected abiotic factors on the military shooting range Borris Hede in western Jutland DK, with the objective of quantifying current status and diagnosing possible causes for the decline of *E. tetralix*.

MATERIALS AND METHODS

Repeated Vegetation Analysis (Lønborg Hede)

In Lønborg Hede, Lange (1995) analysed the vegetation along a gradient from dry heathland over *E. tetralix* dominated wet heathland to nutrient poor heathland bog. This inland wet heathland site was revisited in 2010, and vegetation analysis along the 1995 gradient was repeated by use of Raunkjær circles applying the same method as in 1995 (Lange 1995), i.e., a method modified after Raunkjær (1909). The number of samples in 1995 and 2010 was 20 randomly placed Raunkjær circles in each of the three

zones recognized in 1995, i.e., (1) dry heathland dominated by *C. vulgaris* and *Empetrum nigrum*, (2) wet heathland dominated by *E. tetralix*, and (3) Bog dominated by *M. caerulea* and *C. vulgaris*. The plots were marked in 1995, and the markers identifying the three zones were re-found in 2010 to allow for an accurate re-analysis of the vegetation gradient.

Data from the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment (Svendsen et al. 2005; Nielsen et al. 2011)

The monitoring of inland wet heathland plant species cover has been carried out since 2004, and at present results including 2009 are available. Data include more than 500 wet heathland vegetation plots—that were subjected to refined statistical analyses including:

1. Analysis of cover of *E. tetralix* from 2004 to 2009
2. Analysis of the relation between model-calculated nitrogen deposition of dry and wet deposition of NH_3 , NH_4^+ and NO_3^- ($\text{kg ha}^{-1} \text{ year}^{-1}$) in 2008 at a resolution of $5.6 \text{ km} \times 5.6 \text{ km}$ (Ellermann et al. 2010) and cover of *E. tetralix* in wet heathlands.
3. The relation between the modelled base cation deposition and the cover of *E. tetralix* in wet heathlands.
4. The relation between morlayer (0–5 cm) $\text{pH}_{(\text{H}_2\text{O})}$ and cover of *E. tetralix*.

The trend in the pin-point cover data of *E. tetralix* over time at the level of the site was fitted to a linear model of time using a state-space model (see Electronic supplement), and the pin-point cover data of *E. tetralix* at the plot level were regressed to independent variables using the zero-inflated general-binomial distribution (see Electronic supplement; Damgaard 2008; Damgaard 2009).

In the monitoring programme, the cover of plant species is measured by the pinpoint method using the method described in the next section.

Gradient Analyses (Borris Hede)

Vegetation Analysis

The vegetation was analysed by transect analysis in two sites on the heathland “Borris Hede”, a military shooting range and EU-habitat area in central Jutland. The transects covered a gradient of increasing soil humidity starting in the dry *Calluna* dominated heathland through an area of intermediate humidity with *E. tetralix* and other wet heathland vegetation to a humid area with nutrient poor bog vegetation. The following vegetation parameters were measured along the gradient; species cover and species

Fig. 1 Photos of the wet heathland “Vejrup Søhede” in **a** 1999 and **b** 2010 clearly demonstrate that the ecosystem engineer *Erica tetralix* has disappeared during this time span. It is also evident that this is not a result of competition, as no other species has established in the vacant niche

compactness by the point intercept method (Kent and Coker 1992; Damgaard 2009). The cover of each species was calculated as the fraction of the pins touching the

specific species, whereas the vertical density was calculated as the total number of intercepts between the pin and every species present in the quadrat. Each quadrat

measured 0.25 m² and had 16 points of vertical pin insertions. The pin was 50 cm long and had a diameter of 1.6 mm. Apart from the fact that vertical density is not measured in the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment, the methods for registration were identical to those used in the programme (Svendsen et al. 2005). All individual sites in the transects were marked with white pins and the geographical coordinates were stored by GPS to allow for future visits.

Relative height in cm of individual plots along each transect was measured and these measurements are presented relative to the area where *E. tetralix* had its highest cover and vertical density (relative height 0). This was done to analyse the two gradients together.

Chemical analyses in the gradient were the same as in the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment (Svendsen et al. 2005)

Measurement of pH in the morlayer was done at 0–5 cm. Measurement of C and N in the morlayer was done at 0–5 cm.

Measurements of N in annual shoots were taken in *Calluna* and *Erica*.

Samples of the morlayer, defined as the upper 5 cm of the soil, were taken by a steel cylinder with a diameter of 48 mm. The samples were dried at 80°C, homogenised, crushed, and weighed into sample boats. Total carbon and nitrogen content were analysed on an elemental analyser (Europe Scientific RoboPrep-C/N). Shoots of *C. vulgaris* and *E. tetralix* were analysed for total nitrogen using the same method. Determinations of pH were measured in samples of the morlayer by a field pH meter with addition 10 ml distilled water to create good contact.

RESULTS

Development from 1995 to 2010 (Lønborg Hede)

The re-analysis of the vegetation from Lønborg Hede demonstrated that the broad zone dominated by *E. tetralix* in 1995 has disappeared, and in 2010 no clear zone dominated by living *E. tetralix* could be identified (Table 1).

The table demonstrates the extent of the disappearance of *E. tetralix* from the gradient. The area formerly dominated by *E. tetralix* has been substituted by a narrower zone of a mixture of *Calluna* and *Erica*, and the wet area dominated by *Calluna* has increased in size. Visual inspection of the site in 2011 showed dead *Erica* clones seen as patches of grey withered vegetation in the *Calluna* dominated vegetation.

National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment—Results for Inland Wet Heathland

Analysis of the data from the National Monitoring Programme showed that the cover of *E. tetralix* in the inland wet heathlands as an average has decreased by approximately 36%, from an average cover of 28% in 2004 to an average cover of 18% in 2009 (Fig. 2).

The analysis of data from the National Monitoring Programme demonstrated a significant negative relation between the cover of *E. tetralix* and nitrogen deposition (likelihood ratio test, $P < 0.001$; Fig. 3b), indicating a threshold at a deposition between 8.3 and 13.2 kg N ha⁻¹ year⁻¹ (95% credibility interval of threshold parameter x_0 (see Electronic supplement)). A significant positive relation between the base cation deposition and the cover of *E. tetralix* was also demonstrated (likelihood ratio test, $P < 0.001$; Fig. 3a). The reason that some individual points indicate a poor relation is likely due to geographical differences in soil properties, either favouring or disfavouring the presence of *E. tetralix*.

The use of distance to the coast as a proxy for the base cation deposition showed a significant positive relation with the cover of *E. tetralix* in the inland wet heathlands (likelihood ratio test, $P < 0.001$; Fig. 4).

Gradient Analyses (Borris Hede)

The cover of the four dominant species (*E. tetralix*, *C. vulgaris*, *M. caerulea* and *Trichophorum caespitosum*) in the transect was fitted to four different models (see Electronic supplement), and for each species the model that best fitted the observed distribution of species is presented in Fig. 5. The four models applied were sigmoid, unimodal optimum, constant and exponential increase or decrease. Except for *E. tetralix*, which showed its best fit with the unimodal model, the other three species were best fitted by sigmoid models.

It is seen that *C. vulgaris* dominates the dry zone, *E. tetralix* dominates the intermediate zone and *M. caerulea* and *T. caespitosum* the wet zone.

The C/N ratio shows a decrease along the gradient from dry heathland to nutrient poor bog, with values above 30 in the driest part and below 20 in the wettest part (Fig. 6). The C:N ratio ranges between 21 and 26, where *Erica* dominates.

The pH along the gradient was generally low and on average only slightly above pH 3, where the cover of *E. tetralix* was highest (Fig. 6).

In summary, observations and results showed that the distribution of *E. tetralix*, both at individually investigated sites and in general, has been decreasing and that the condition of individual plants appeared poor relative to

Table 1 Vegetation zones in Lønborg Hede in 1995 when *Erica* still thrived in the wet heathland and 2010 when *Erica tetralix* population has declined

Vegetation zone	Year		Graphic representation
	1995	2010	
Dry Calluna heathland	12	14	
Erica heathland/Dry Calluna	1	0	
Erica heathland	11	0	
Erica/wet Calluna	9	3.5	
Wet Calluna heathland	19	33.5	
Myrica/Molinia bog	8	9	

After Lange (1995) and Strandberg et al. (2011)

Fig. 2 Significant reduction in the cover of *Erica tetralix* from 2004–2009 in inland wet heathlands in Denmark (from Bruus et al. 2010)

expectations from observations gathered in the 1980s and 1990s. The fact that especially *M. caerulea* and *C. vulgaris* were present in the former *E. tetralix* dominated areas indicated that ecosystem change was taking place (Table and Fig. 5). The analysis of data from the National Monitoring Programme demonstrated a significant relation between decline of *E. tetralix* and nitrogen deposition, indicating a threshold at a deposition between 8.3 and 13.2 kg N ha⁻¹ year⁻¹ (Fig. 3b). However, the observation of the relation between distance to coast and nitrogen deposition (Fig. 4) and the observation that there is a positive relation between the relative base cation deposition and the cover of *E. tetralix* (Fig. 3a) indicate that other factors apart from nitrogen influence the system. The measurement of the C:N ratio in the morlayer under the *E. tetralix* stands, and even lower in the nutrient poor bog, and pH was generally low, between 3.03 and 3.78, in all ecosystems represented in the transect (Fig. 6).

Fig. 3 Relation between base cation (a) and nitrogen (b) deposition on cover of *Erica tetralix* in Danish inland wet heathland

DISCUSSION

A summary of yet unpublished Danish observations from wet heathland has demonstrated that the decline of *E. tetralix* in Danish inland wet heathland has started and that it has been accelerating since the mid-1990s, where large

Fig. 4 Relation between nitrogen deposition and distance to the coast, showing that the N deposition generally increases with distance to the west coast of Jutland, which is mainly caused by the dominating wind direction from the North Sea and the occurrence of large nature areas at the west coast

Fig. 5 Modelled cover of *Erica tetralix* (blue line), *Calluna vulgaris* (red), *Molinia caerulea* (green) and *Trichophorum caespitosum* (yellow) along the transects studied in Borris Hede. The relative height is measured with x axis zero as the point where *Erica tetralix* had maximum cover. (Color figure online)

Fig. 6 The C:N ratio (empty circles) and the pH (filled circles) in the morlayer (0–5 cm) in the transect investigated in the Borris shooting range. The relative height is measured with x axis zero as the point where *Erica tetralix* had maximum cover

coherent areas with nearly 100% cover of *E. tetralix* still existed (Strandberg et al. 2011). Lovett et al. (2009) state that species mortality is often observed only at experimentally elevated exposure levels or in combination with other stresses such as drought, freezing, or pathogens. This study suggests that the collapse of the *E. tetralix*-dominated ecosystem in the wet inland heathland probably is the result of soil acidification from >50 years accumulated effects of nitrogen and sulphur deposition, with nitrogen accumulation most likely playing a minor role. The effect may be the result of a combination with other stress factors such as drought and frequent shifts in soil hydrology and influence on ericoid mycorrhizas. Investigations by Horswill et al. (2008) confirm acidifying effects of nitrogen deposition, i.e., effects such as base cation depletion and aluminium mobilisation were observed in grassland ecosystems. The effects in grasslands include decline in species richness, attributed both to acidification and eutrophication (Stevens et al. 2010; Vergeer et al. 2003).

Further, a review of management literature made it clear that no proven methods for successful management of wet heathland have been published so far (Strandberg et al. 2011). In the 1960s, the morlayer pH of Danish heathland generally was above 4 (Hansen 1976), whereas today it is generally between 2.9 and 4.3 (95% quartile; mean 3.34) (unpublished data from the National Monitoring Programme). This makes the low pH a prominent candidate for explaining the observed changes. Another likely explanation is morlayer nitrogen accumulation, which is known to influence ericoid species tolerance to stress factors such as drought, soil acidification, plant pathogens, and resource competition (Finlay 2008). An effect that often occurs through effect on ericoid mycorrhizal associates such as the ericoid mycorrhizal fungus *Rhizoscyphus ericae* (Strandberg and Johansson 1999). The question is whether the die back of *E. tetralix* is a single event or just the first in a coming series of sudden changes of nutrient poor ecosystems. The situation for *E. tetralix* in the coastal heathlands is still stable, none of the coastal heaths visited have shown any sign of *E. tetralix* being influenced, despite the fact that pH measurements there also show low values and that the C:N ratio is only slightly above those measured in the inland wet heathlands (Strandberg et al. 2011).

Nitrogen deposition in Denmark reached its highest levels in the 1980s and early 1990s with an average deposition of 22 kg N ha⁻¹ year⁻¹. Since then, the average N deposition has been reduced to 14 kg N ha⁻¹ year⁻¹. The present critical load (CL) for wet heathland suggests 10–20 kg N ha⁻¹ year⁻¹ (Bobbink and Hettelingh 2011). The results from the National Monitoring Programme (fig. 3b) suggest that at least the higher value (i.e., 20 kg N ha⁻¹ year⁻¹) represents an exceedance of the CL for inland wet heathlands. The rather short span of years

with depositions averaging $22 \text{ kg N ha}^{-1} \text{ year}^{-1}$ further suggests that the actual CL should be lower than 20, probably around the present average deposition, which is close to the calculated threshold value (Fig. 3b). Other observations and results from our investigations indicate that factors other than nitrogen deposition are important for the understanding of the collapse of the Danish inland wet heathland ecosystem.

- First and most important, the observation of dead *E. tetralix* without the presence of competing species (Fig. 1) clearly indicates that competition with other species is not the obvious cause of the decline.
- Secondly, the low pH observed in the morlayer of the ecosystem indicates that acidification may be the most important factor explaining the decline of *E. tetralix* (Fig. 6, and the analyses of data from the National Monitoring Programme reported here).
- Thirdly, the observation that the cover of *E. tetralix* in wet heathlands is increasingly affected with distance to the coast, which could be explained by the decrease in deposition of base cations (Na^+ , Mg^{2+} , Ca^{2+} , K^+) with distance to coast (Fig. 3a). The explanation is that the deposition of base cations could counteract the depletion of base cations, which is a known effect of acidification (Horswill et al. 2008). Another effect of acidification is the occurrence of free aluminium ions in the soil water which is toxic to plants, this effect may be neutralised by reaction with chloride ions deposited from the sea.

The second and third explanations support the hypothesis that acidification is the primary cause of the collapse of *E. tetralix* stands observed in the wet inland heathlands.

Finally, the observation of healthy *E. tetralix* dominated ecosystems in the dune heaths close to the coast (Strandberg et al. 2011) raised the question—what factors are different between coastal areas and inland heathland areas? A likely explanation is effects of deposition from the sea, because the results showed that pH was equally low in both ecosystems (Strandberg et al. 2011). The use of distance to coast as a proxy for base cation deposition from the sea has been established earlier by Lövblad et al. (2004).

Almost all literature on management of heathland ecosystems has concentrated on *C. vulgaris* heathland, e.g., little has been published on methods to manage inland wet heathlands. Calvo et al. (2002) observed that when *C. vulgaris* was cut in a humid mountainous *Calluna* dominated heathland, it was replaced by *E. tetralix*, whereas after burning and ploughing *E. tetralix* only reappeared after the sixth and eighth years, respectively. Dorland et al. (2003) observed reduced germination of wet heathland species in an experiment with addition of ammonium and explained the observation of reduced

germination after sod removal by the removal of nitrifying microorganisms having the highest abundance in the upper soil layer. This tells us that the management of the wet heathlands is not easy, especially after *E. tetralix* has disappeared. Bååth and Arnebranth (1993) investigated the effects of lime and wood ash addition on the soil pH and found that wood ash addition is able to increase pH as much as 2.5 points by addition of $5 \text{ t wood ash ha}^{-1}$. This indicates that a more effective burning of the morlayer of the wet heathland than is currently allowed with Danish legislation would be able to increase pH. However, most likely such extensive burning would only have temporary effect on morlayer pH as the ash will tend to disappear due to effects of leaching and wind, and stimulation of new growth will further increase the potential for soil acidification (Hovmand and Petersen 1984; Pilkington et al. 2007).

CONCLUSIONS

The overall conclusion is that a decrease in morlayer pH from an average above 4 to between 2.9 and 4.3 (95% quartile; mean 3.34) since the 1960s is the most likely explanation of the collapse of *E. tetralix* in the inland wet heathlands. There are two major hypotheses that explain the observations:

1. The low pH leads to toxic concentrations of aluminium ions in the soil that cause *E. tetralix* to die.
2. The low pH has depleted the soil from base cations to a degree that causes *E. tetralix* to die.

Both hypotheses are supported by the fact that there is a negative relation between distance to the coast and the status of *E. tetralix* in the wet inland heathlands, i.e., the longer the distance to the coast, the lower the amount of living *E. tetralix* in the heathlands.

Other factors that may be involved in the explanations are:

- Nitrogen deposition and associated accumulation of nitrogen in the morlayer with a very low C:N ratio as the result.
- Management practice including burning, grazing, and cutting depleting the ecosystem from a range of nutrients, in this way increasing nutrient imbalances that makes *E. tetralix* sensitive to fluctuation of climate.

We suggest that investigations are initiated to elucidate the interactions between soil chemistry and plant health in wet and dry heathlands under different management regimes. Such investigations are to include deposition of N, S, base cations, plant–plant interactions, plant–mycorrhiza,

and soil microbiology interaction, and should relate these measures to soil chemistry.

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