

## RESEARCH ARTICLE

# Mapping the ecological resilience of Atlantic postglacial heathlands

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**Handling Editor:** Lan Qie**Abstract**

1. Anthropogenic heathlands are semi-natural ecosystems with a unique cultural and biodiversity value, considered worthy of preservation across most of the world. Their rate of loss, however, is alarming. Currently, we know little about the heathlands' actual span of resilience affordances and their association with abiotic and anthropogenic factors, including how much additional intervention they need to persist. Consequently, we are missing out on vital knowledge for conservation, management and the historical persistence of heathlands.
2. This paper develops a method to assess the ecological resilience affordances of Atlantic postglacial heaths in the absence of human management. We use 12 existing cases of heathland succession to establish a four-step resilience grade for each site, which we regress onto a series of explaining factors and use it in predicting heath resilience across postglacial Atlantic Northern Europe.
3. We find that temperature, humidity, elevation and sandiness have a positive correlation with high heathland resilience. Our predictive mapping shows an uneven distribution of ecological heath resilience across Atlantic Northern Europe within an area of 1,000 × 1,200 km of 5 × 5 km resolution.
4. Historic heathland distributions far exceed areas that afford high heath resilience, suggesting that heath distribution and persistence depend on both abiotic and anthropogenic factors.
5. *Policy implications:* The map predicting the ecological resilience of Atlantic postglacial heaths can be used by managers working towards heath preservation and restoration to prioritize conservation efforts and to plan management practices across Atlantic Northern Europe. Together with the predictive model, it provides an important initial screening tool to assess heathland resilience in the absence of management as well as the impact of atmospheric nitrogen. The results are equally relevant for scholars who are interested in humans' role in increasing and decreasing ecosystem resilience. Our predictive method can be applied in other regions across the world by adding regionally specific variables.

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## KEYWORDS

Atlantic Northern Europe, *Calluna vulgaris*, conservation, heathland, historical management practices, resilience affordances, succession, tree encroachment

## 1 | INTRODUCTION

Atlantic dry inland heaths are open landscapes dominated by evergreen sclerophyllous plants and peatland. They are home to a wide range of specialized and nonspecialized plant and animal species, many of which are red-listed. Moreover, they play a crucial role in carbon sequestration as well as recreation, heritage conservation and landscape and biodiversity conservation (de Vries et al. 2009; Fagundéz, 2013). Their rate of loss, however, is alarming.

Atlantic inland heaths are plagioclimactic: They are constantly undergoing succession along different paths, including grasslands, shrublands and arboreal communities (Figure 1; Böcher, 1941). Depending on its age, *Calluna* has a variable competitive ability against other species in the heath community (Gimingham, 1972; Mallik & Gimingham, 1983; Watt, 1947). In the degeneration phase, the heath will make way for grasses and shrubs and pioneer trees (*Betula* spp. and *Pinus sylvestris*), in due course disappearing underneath a climax forest canopy. Therefore, in order to conserve heathlands for the future, human intervention is necessary. Such intervention may be palaeoecological (e.g. temperature, sea spray, strong winds, soil acidity, elevation, rainfall, oceanic exposure) or it may derive from humans (e.g. managed fires, turf cutting) or from nonhumans (e.g. wildfires, grazing and browsing).

Heathland succession has been the subject of a wide range of studies. In terms of ecological factors, sandy, nutrient-poor and acid soils are often pointed out as a primary driver of heathland resilience, hindering or delaying the invasion of other species. Additionally, temperature, elevation, distance to ocean, air humidity and average slope as well as wind, distance to nearest arboreal seed source, wildlife grazing, hours of sun and precipitation are also important factors for the competitive advantage of *Calluna* (Riis-Nielsen et al., 2005, table 7.1) as is the health and age of the *Calluna* plant, prior management history, frequency and severity of wildfires, drought and beetle attacks (Table 1).

In terms of anthropogenic factors, there has been a series of attempts to evaluate the impact of various management practices in delaying or halting succession. Studies have investigated livestock management strategies such as rotational grazing (Milligan et al., 2018; Rosa Garcia et al., 2013), flock size and flock composition (Bokdam & Gleichman, 2000), as well as the effects of wildlife (e.g. red deer) grazing (Riesch et al., 2019). Other studies have investigated the effects of chopping, mowing, sod-cutting (Berendse, 1990; Diemont, 1994, 1996; Dorland et al., 2004) and nutrient addition (Helsper et al., 1983; Niemeyer et al., 2007). Others again have focused on the effects of different fire management strategies with regard to the frequency and ultimately the age of the *Calluna* stands (Nilsen et al., 2005; Velle et al., 2012), fire temperature (Mallik & Gimingham, 1983) and species richness (Hobbs & Gimingham, 1984). Other disturbances are

documented to be destructive to heath regeneration, including beetle attacks, drought, unmanaged wildfires and overgrazing.

Within recent years, the importance of heathland management has been widely acknowledged in conservation and ecology management debates (Bak et al., 2020; Degn, 2019; Diemont et al., 2013; Fagundéz, 2013). A series of international steps, such as NATURA2000, and regional nature protection initiatives have been taken towards developing and intensifying management schemes. But due to elevated atmospheric nitrogen deposition and fundamental ruptures in management practices, postglacial heathlands have proven difficult to maintain and their decline is now an acknowledged issue across Europe (Fagundéz, 2013; Terry et al., 2004). This makes a study of ecological heath resilience highly pertinent in order to prioritize efforts in areas with the best chances of surviving.

The actual span of ecological resilience affordances of the heathlands—and, crucially, of its dependence on human intervention—has not yet been systematically investigated, however. This has implications both for the methods and policies used to protect them and for our understanding of their historical survival and expansion. Although several recent studies have explored the possibilities for reintroducing (pre) historic management practices such as heathland farming and burning (Jansen & Diemont, 2005; Mier & Tente, 2018; Woestenburg, 2018), there is yet no consistent knowledge about how human management practices translate into heathlands with different turnover rates.

Within the ecological disciplines, conventional ecosystem resilience is often defined as the rate at which a given ecosystem returns after a disturbance (Mitchell et al., 2000; see also Hodgson et al., 2015). However, we suggest that heathlands are fundamentally different from climax ecosystems in fundamental ways, involving their plagioclimactic and semi-cultural nature. This requires us to define ecological heath resilience differently, as *the rate at which heathlands turn into an alternative stable state*, such as grassland or forest, *in the absence of human intervention*.

Heathland longevity depends on the long-term persistence of relationships within socio-ecological systems in which stability and disturbance are intrinsically linked; heathlands require a certain level of (non)human disturbance to recalibrate and regain their relative instability and quantities (Løvschal, 2021). Moreover, the persistence of a given ecosystem—what Mitchell et al. (2000) call 'stability' and what Holling calls 'resilience' (1973)—cannot be adequately measured without taking longer time frames into consideration than are normally applied in the ecological realm. Not only is heathland resilience crucially dependent on the historical, social and environmental context, including previous land-use patterns, but a long-term scale is also necessary to capture its longer term entrapment in cycles of disturbance and rejuvenation. In this way, instead of leaving humans out of the equation, we support a multispecies, multidirectional understanding of resilience (Costanza et al., 2007), given that human

**FIGURE 1** Dry inland heath at Vrads Sande, Central Jutland, Denmark, in different succession stages, surrounded by a pine plantation. The foreground shows dense heather canopy encroached by shrubs; the background shows heathland succeeded by grass. Credit: Mette Løvschal



**TABLE 1** Underlying data for the 12 sites (Figure 2), including the basis for the vegetational resilience factor calculation, observation span/years, any additional uncontrolled factors and key biographical references. All sites are characterised by the vegetation community *Calluna vulgaris*. N = natural

Site	Basis for vegetational resilience factor calculation	Additional uncontrolled factors	Key references
The Poole Basin, Dorset (GB)	Aerial photographs 1946/47, 1972/73, 1986. Controlled observation (quadrants) 1978–1987	Sheep grazing and controlled fires, fracturing	Webb (1990), Webb and Haskins (1980) and Mitchell et al. (1997)
Dwingeloo Heath, Drenthe (NL)	Controlled observations (quadrants)	Beetle attack, some grazing	Lippe et al. (1985), Berendse (1990) and Diemont (1996)
The Muir of Dinnet, Aberdeenshire (GB)	Controlled observations (quadrants)	N (wildlife grazing)	Mallik and Gimingham (1983), Hobbs and Gimingham (1984) and Gong (1976)
Howden Moor, Sheffield (GB)	Aerial photographs	N (wildlife grazing)	Harris et al. (2011) and Allen et al. (2016)
Knettishall Heath, East Anglia (GB)	Aerial photographs 1946, 1951, 1967, 1976	Some tree removal 1979	Marrs et al. (1986)
Kringsjå, Rogaland (NO)	Aerial photographs	N (wildlife grazing)	Gjedrem and Log (2020), pers com
Lüneburg Heath, Lower Saxony (DE)	Controlled observations (quadrants)	Sheep grazing and controlled fires	Kaiser and Stubbe (2004), Kaiser (2015) and Lütkepohl and Stubbe (1997)
Buelund, Djursland (DK)	Controlled observations (quadrants)	Shifting grazing pressure	Buttenschön and Buttenschön (2015)
Randbøl Hede, Central Jutland (DK)	Controlled observations (experimental and control plots)	Some burning, mowing, cutting. Farming	Böcher (1941) and Degn (1996), Nilsen et al. 2005
Nørholm Hede, Western Jutland (DK)	Controlled observations (quadrants)	N (wildlife grazing)	Ransijn et al. (2015), Schmidt et al. (2015) and Riis-Nielsen et al. (2005)
Tarva, Trøndelag (NO)	Controlled observations (quadrants) and uncontrolled observations	Sheep grazing	Nilsen et al. (2005) and Måren and Nilsen (2008)
Hard Hill Moor, North West England (GB)	Controlled observations (quadrants and plots)	N (wildlife grazing)	Marrs (1992; Marrs et al., 2018) and Milligan et al. (2016)

disturbances can have a positive, even crucial impact on ecosystem stability (Løvschal, 2022). However, to be able to assess humans' role in increasing/decreasing heathland resilience, both in the past and with respect to future management, we suggest to focus on factors indicative ecological resilience in the following analytical approach.

In this paper we ask: In the absence of any systematic human management, what are the resilience affordances of heathlands across Atlantic Northern Europe, based on a scale of ecological resilience? How much additional management is necessary for their long-term persistence? What are the most critical ecological factors

for keeping the heathlands in place? And how does this scale of ecological resilience correlate with the archaeological evidence for past heathland regimes?

First, based on a review of existing research literature, we identify factors that have been associated with heathland persistence. Second, based on published case studies of heathland succession, we present a classification of heathland resilience in the absence of human intervention. Third, we regress ordinal resilience classification data onto the identified factors to test their respective impacts on resilience and map the expected ecological resilience on a Northern European scale. On this basis, we estimate the most significant factors in heathland resilience and, implicitly, how much additional disturbance is necessary for their persistence. Classifying heathlands on a scale of resilience enables us to make a qualitative comparison of the heathland resilience affordances against the heathlands' historical distribution in prehistoric times. On this basis, we discuss how people in the past actively increased/decreased diverse heathland (in)stabilities across a long-term perspective.

We believe that the predictive model provides an important initial screening tool for assessing heathland resilience for nature conservationists and managers, but also for biologists, archaeologists and historical ecologists. Estimating the resilience affordances, even on this primary and geographically crude basis, creates a new basis for international management plans and land prioritization. This will enable managers and conservationists to identify and prioritize areas most suitable for heathland conservation as well as the necessary intensity of associated management forms. The model is capable of further expansion and can be tested against archaeological meta-analyses, for example, how different anthropogenic and abiotic factors change causal influence on heath resilience over time. Moreover, the integration of ecology and archaeology provides new and extended horizons—both temporal and human-integrated—in debates over semi-cultural landscape resilience.

## 2 | MATERIALS AND METHODS

### 2.1 | Analytical approach

Our main analytical approach is based on a six-step procedure involving:

1. Factor identification that can be quantified on a European scale (based on the existing literature on heathland succession)
2. Site selection based on vegetation succession studies, preferably 15+ years
3. Site classification into four ordinal classes of resilience
4. Statistical factor-based analysis of resilience using ordinal regression
5. Predictive modelling and mapping
6. Regional comparison with archaeological and palaeoecological evidence

The study did not require ethical approval.

### 2.2 | Factor identification

Based on existing studies of heathland vegetation, we identified six abiotic factors assumed to influence the resilience of *Calluna* heaths and capable of quantification on a European scale. Our six a priori chosen factors are temperature (Temp), elevation (Elev), sandiness (Sand), distance to ocean (Dist), air humidity (Humid) and average slope (Slope), since they were the main identified resilience factors where consistent data existed and could be obtained for this study. Nitrogen deposition would have been a highly relevant additional resilience driver (MET Norway). However, currently data are not available in terms of how much Ndep varied over the years at the different sites.

Temperature is the mean annual temperature 1950–2010 at the weather station closest to the site's GPS location (Wolfram, 2020). Elevation is calculated from the procedure GeoElevationData in *Mathematica* (Wolfram, 2020). The sandiness of the dominant surface for each site was obtained from a polygon-based map of European topsoils with a resolution of 10x10 km (European Commission, 2005). The classification of soil texture is on an ordinal scale with 1: coarse, 2: medium, 3: medium fine, 4: fine and 5: very fine. Distance to ocean is the shortest distance from the site point to the ocean and used as a proxy for cation input due to airborne sea salt and soil humidity. Air humidity is the mean annual humidity 1950–2010 at the weather station closest to the site's GPS location using WeatherData in *Mathematica* (Wolfram, 2020). Average slope was calculated at distances of 2.5 km around the GPS point using GeoElevationData in *Mathematica* (Wolfram, 2020).

We investigated the correlation between these variables in a pairwise scatterplot (Supporting Information).

### 2.3 | Site selection

We selected 12 case study sites for 20th and 21st century Northern European heathland on which detailed information is documented on vegetation succession (Figure 2, Supporting Information). The sites were non-randomly selected on the basis of a literature review of succession studies with an observation span of +15 years.

### 2.4 | Site classification

We assigned each site an ordinal resilience classification according to identified cut-off points related to its relative stability. The scale (the response variable) spans low/moderate–low/moderate–high/high resilience reflecting the rate at which after a major resetting—typically a fire and in the absence of additional human intervention—heather is outcompeted by other species. Sites which are wood- or grass-dominated (*Molinia*) with some *Calluna* within the first 10 years are classified as 'low'. Sites which are shrub-dominated with some *Calluna*



within the first 10 years are classified as moderate–low. Sites which are *Calluna*-dominated with little shrub or wood encroachment within the first 20 years are classified as moderate–high. Sites which are still *Calluna*-dominated after 30 years are classified as high. This rate is established qualitatively on the basis of existing succession studies describing the turnover rate for our 12 sites. This approach is consistent with Mitchell et al. (2000), who have also suggested using plant species abundances in time-series data to quantify the ecological resilience of heathlands. On this basis, we have scored each site on a four-step ordinal scale, from ‘high’ resilience where no immediate tree succession occurs when heather moves into the degenerate phase (after 20 or more years), to ‘low’ resilience where alternative shrub, grass or tree vegetation encroaches and takes over within up to 20 years.

## 2.5 | Statistical analysis

The ordinal resilience classifications were coded with integer values from one (low) to four (high) and analysed using linear ordinal regression models with the R procedure *polr* (Venables & Ripley, 2002) and the identified factors as fixed effects. Probably due to the relatively few independent data points, only a restricted number of potential models could be fitted. Different models were compared using the Akaike information criterion (AIC; Akaike, 1974), and the coefficient of determination with the method proposed by Nagelkerke (1991). The coefficient of determination is a measure of the proportion of the variance that is explained relative to a null model, and is analogous to  $R^2$  in a linear model with normally distributed residuals.

## 2.6 | Predictive modelling and mapping

Using the selected model and the R package ‘effects’, we predicted resilience across a c. 1,200 [N-S distance] by 1,000 km [E-W distance] spatial extent in Atlantic Northern Europe. Such a prediction was made using the multivariate interpolation algorithm Inverse Distance Weighting (IDW) in ArcGIS 10.8.2. The IDW was applied to a 5 × 5 km grid of Northern Europe at sites situated on sandy soil (sandiness = 1 or 2; European Commission, 2005). This spatial resolution seems to be a good compromise between calculation time, the spatial resolution of the soil map, and expected spatial variation of the response variable. However, we have not tested the sensitivity of the results against this decision.

## 2.7 | Comparison with archaeological and palaeoecological evidence

In order to assess how societies have responded and contributed to the different observed levels of heathland resilience in a historical perspective, we compared the hypothesised relative stability of heathlands with the historical distribution of moors and heathlands in Northern Europe, based on the Corine Land Cover (2018).

In order to qualify and explain our observations, and some of the processes leading to the historical heathland distribution, we drew upon a large multiproxy dataset comprising palaeoecological evidence, settlement and funerary sites as well as relict field systems from Northern Europe, collected as part of the ANTHEA project (<https://projects.au.dk/anthropogenic-heathlands/>). Because of space limits, this material is only involved in a qualitative fashion to assess the coarse historical contours in the human–heathland relationship.

## 3 | RESULTS

We found that the 12 heathland sites showed different levels of ecological resilience in the absence of systematic human intervention (Table 2). In cases of medium resilience areas such as the Muir of Dinnet, post-fire succession in both species-rich and species-poor heaths suggested that the moor was proceeding towards birch and pine forest after 10–15 years. Other sites with high resilience, such as those situated in the Tarva Archipelago, showed no tree encroachment (some *Empetrum*), although here *Calluna* was in the mature or degenerative phases and found in conjunction with mosses and lichen.

The only non-trivial model that could be fitted to the data was a model where the ordinal resilience classification depended on humidity, elevation, slope and sandiness (Table 3). This model supported the data better than a constant null model (the difference in AIC was –2.34) and 63% of the variation was explained according to the coefficient of determination. The effect of sandiness was included in the selected model even though the effect of sandiness was not significant (Table 3) since we have strong prior information that sandiness is important for resilience and we only had two sites with a sandiness classification of two.

The expected marginal probabilities of the resilience classes as functions of the independent variables are shown in Figure 3. Increasing temperature, humidity and elevation were found to have a positive effect on heathland resilience, whereas increasing slope had a negative effect. Heathlands were found to be more resilient on sandy soils (i.e. coarse soil texture) compared to soils of medium or fine texture, although this effect was not significant (Table 3, Figure 3).

The increased steepness of the curve for ‘soil’ and ‘slope’, referring to the expected change in resilience (Figure 3), indicates that soil and slope are more important than the other abiotic factors. In terms of sandiness, acidic, sandy and nutrient-poor are historically known to promote the expansion of heathlands. In terms of slope, a sloping terrain is more difficult to cultivate and has hence probably also historically been less utilized for ploughing and soil improvement.

Based on the selected model (Table 3), expected resilience was predicted on a Northern European scale (Figure 4) within an area of c. 1,200 × 1,000 km.

On coarse sandy soil, the selected model predicts that 12% of the area had a resilience below moderate–low, 18% are in the range between moderate–low and moderate–high and 70% of the selected European area is predicted to have high resilience affordances.



**FIGURE 2** The study's 12 case study sites, situated in Britain, the Netherlands, Denmark, Germany and Norway. The underlying map is based on a European elevation map (greyscale), and the dominant surface textural class (sandiness = 1 or 2) (green) is derived from ESDAC (European Commission, 2005). Based on ArcGIS 10.8.2. Credit: Mette Løvschal

Because of the uneven distribution case study sites that also do not cover the entire sampling area, a more conservative estimate based on a 50-km radius around them has been calculated.

Comparing our predictive map (Figure 4) with the historical distribution of heathlands (Figure 5), there is a high degree of accord. Larger areas that require explanation in, for example, Scotland and Western Ireland are outside our area of investigation (sandiness = 3–5).

## 4 | DISCUSSION

Our resilience prediction confirms several expectations as to how anthropogenic heathland is geographically and historically

distributed. A series of present-day heathland areas exist in what is predicted as high resilience heathland affordance, including those situated in Western Jutland, the uplands of Cornwall, the moorlands of Ireland and the heathlands of Northeast Netherlands. The sandy Saalian landscapes, however, are not as visible as expected. The discrepancy between areas predicted with high resilience affordances and today's deeply unstable heathlands suggests that, amongst others atmospheric nitrogen, plays a key role in ecological heathland resilience.

Areas with low/medium-low resilience have historically been used as managed forests and croplands, such as the Danish islands, Mid-Eastern England and Scania (Fyfe et al., 2013; Nielsen & Odgaard, 2010). Here, we see transformation phases, sometimes lasting several millennia, where grass pastures supersede forest,

**TABLE 2** Our 12 sites classified against an ordinal scale of relative stability, spanning high to low resilience. The descriptions derive from the reviewed studies underlying in [Table 1](#)

Site	Observation span/year	Observations	Resilience classification/ high to low
The Poole Basin	9 (20–50)	15% increase in shrubs and trees in 9 years. Annual succession rate is 1%	Moderate-low
Dwingeloo Heath	55	60% increase in grasses in 10 years.	Low
The Muir of Dinnet	19	Woodland ( <i>Betula</i> and <i>Pinus</i> ) dominance after 10–15 years, 'rapid colonization', reaches degeneration in 25–40 years	Low
Howden Moor	30	Fast reestablishment. Little tree encroachment at the fringes ( <i>Betula</i> and <i>Pinus s</i> ). Area dominated by +90% <i>Calluna</i>	High
Knettishall Heath	32	172% increase in woodland cover	Moderate–low
Kringsjå	57	Area completely overgrown with sitka forest	Moderate–low
Lüneburg Heath	17	<i>Calluna</i> domination (exc. Plot 85–5, where <i>Molinia caerulea</i> dominates). Tree encroachment after <10 years	Moderate–high
Buelund	35	70% woodland and shrub cover after 20 years	Low
Randbøl Hede	58	87% grass cover and some crowberry. Grass-dominated after 30 years	Moderate–high
Nørholm Hede	>100	Tree encroachment, the number of trees doubled in 10 years	High
Tarva	>50	No tree encroachment, some <i>Empetrum</i> . All <i>Calluna</i> plants are in the mature or degenerative phase	High
Hard Hill Moor	>60	No tree encroachment	High

which due to an increasing exhaustion and leaching, transgress more slowly into heath (Nielsen et al., 2012; Odgaard, 1994). In others, *Calluna* taxa are only present in smaller amounts or heathlands

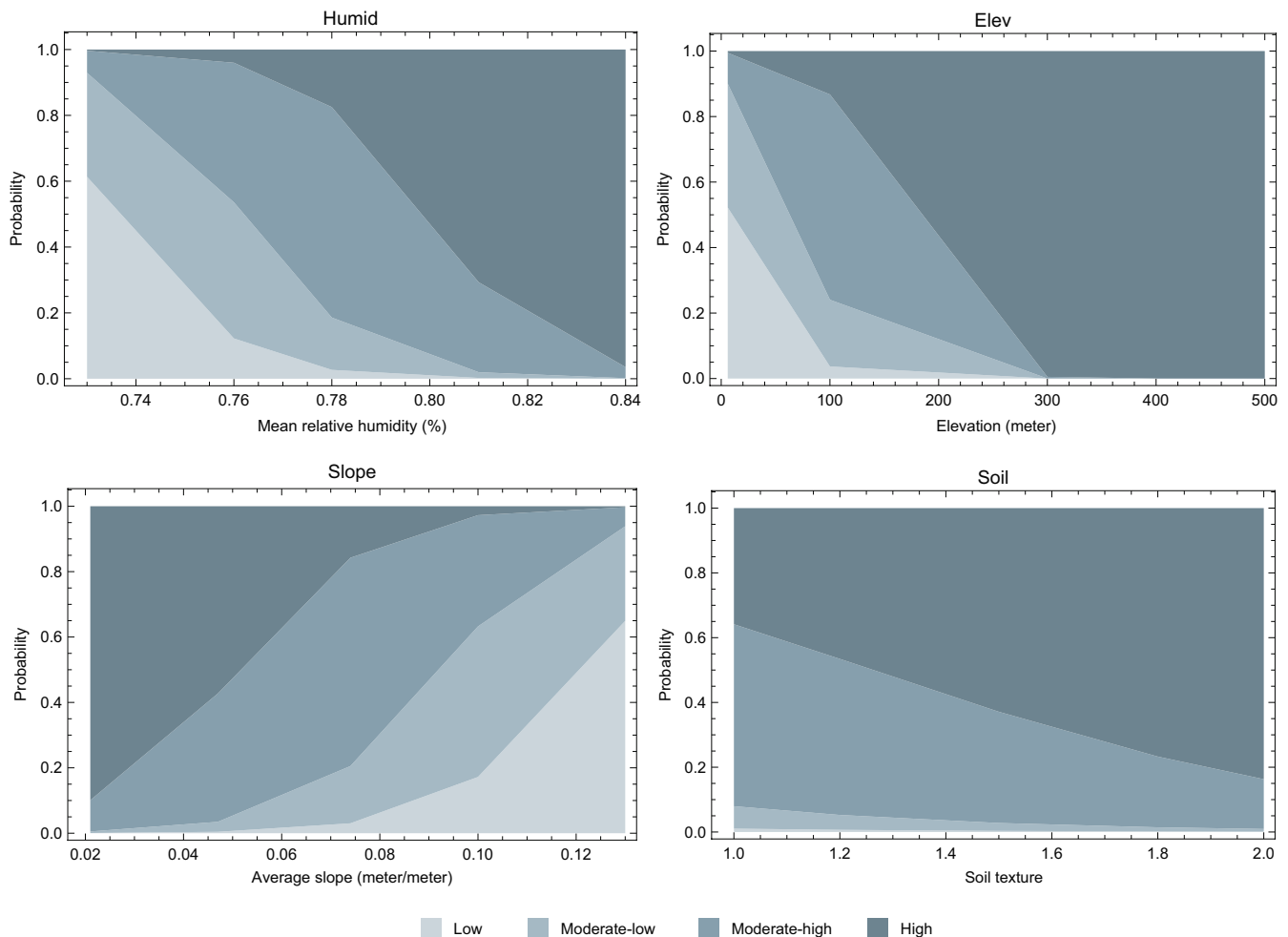
**TABLE 3** Coefficient table of the selected model

Variable	Coefficient	Standard error	p value
Humidity	81.08	18.81	<0.0001
Elevation	0.036	0.0073	<0.0001
Slope	–72.92	24,74	0.003
Sandiness	2.22	1.99	0.265

remain a short-term ecosystem, quickly shifting to another stable state (e.g. Behre & Kučan, 1986; Simmons & Innes, 1996).

If we combine our resilience prediction with the historical distribution of heathland and evidence of its associated land use practices across a time-scale of 5000 years, a series of interesting observations emerge. One is that the historical distribution of heathlands far exceeds the distribution of areas with medium–high resilience affordances. These include heathlands situated on Djursland and Northern Zealand (DK), the Llŷn Peninsula (GB) and Lower Saxony (DE). This discrepancy requires explanation. It suggests that significant human intervention such as burning, grazing and/or turf cutting must have been involved in the past in order to expand and maintain these areas as heaths. And that by applying such methods and practices, heathlands that are—ecologically—low–medium resilient can turn medium–high resilient in the systematic intervention with human cultural and land-use systems. Alternatively, and equally likely, heathland resilience has changed significantly since historical times. The modern-day input of nitrogen by atmospheric deposition differs in our study not only by region but also radically from the situation in the past. The answer must probably be sought in a combination of the two, and would be intriguing to pursue in a further future development of this study.

In a deep time perspective, different resilience affordances also shaped the botanical evolution and land use strategies of the sandy landscapes of Northern Europe. Geological formations played a crucial role for the post-glacial heathland succession that was initiated with the human opening of the landscape through the systematic and extensive combination of deforestation, burning and livestock grazing. In some areas of high resilience, such as Western Jutland, we see that heathlands directly replace forest (Odgaard, 1994). Rising levels of microscopic charcoal dust, correlating with increasing levels of *Calluna* pollen in these areas, indicate that agro-pastoral communities deliberately maintained heathlands and invested labour in burning and grazing them (Odgaard, 1994). In these areas, the heath pastures became part of mosaic agro-pastoral systems, including summer and winter pastures in combination with wetlands, meadows, forests, some croplands and potentially gardens (Andreasen, 2009). The archaeological evidence of such maintenance practices also suggests that even in areas of high-resilience affordances, the heathlands would have required a substantial management. Unfortunately, since there does not yet exist any consistent data on microscopic charcoal at a European scale, a systematic comparison between management intensity and heath resilience is not yet possible.



**FIGURE 3** Stacked expected marginal probabilities of the resilience classes, when analysed with Model 2 as a function of the independent variables.

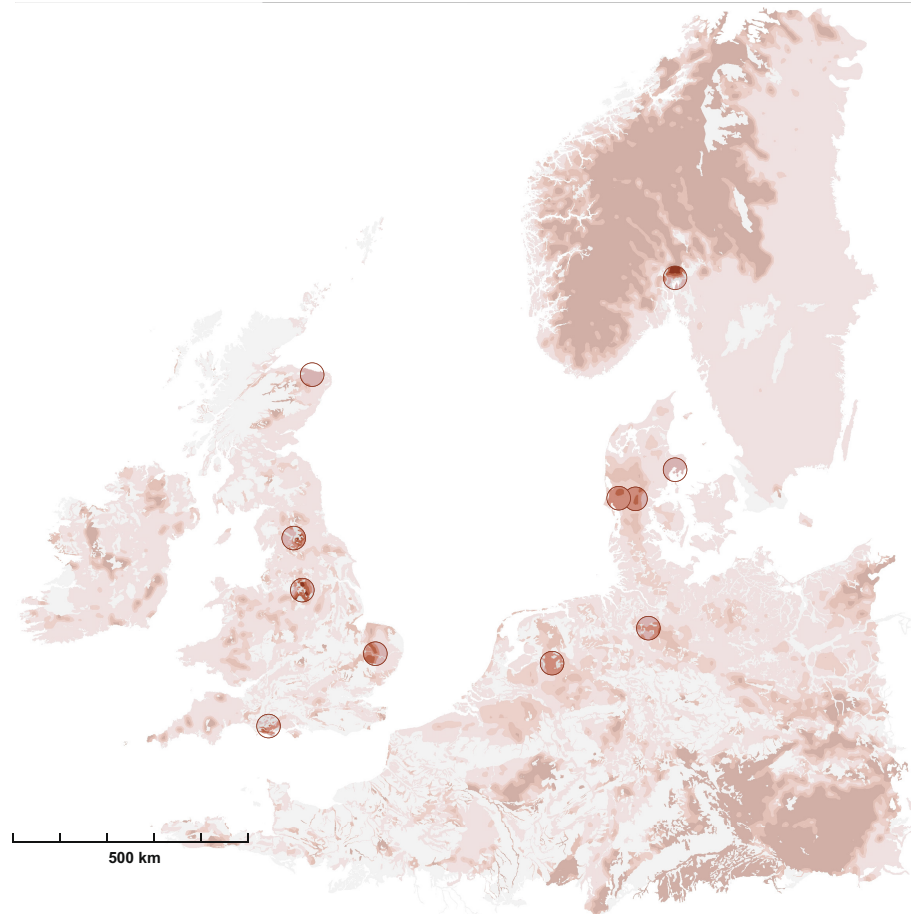
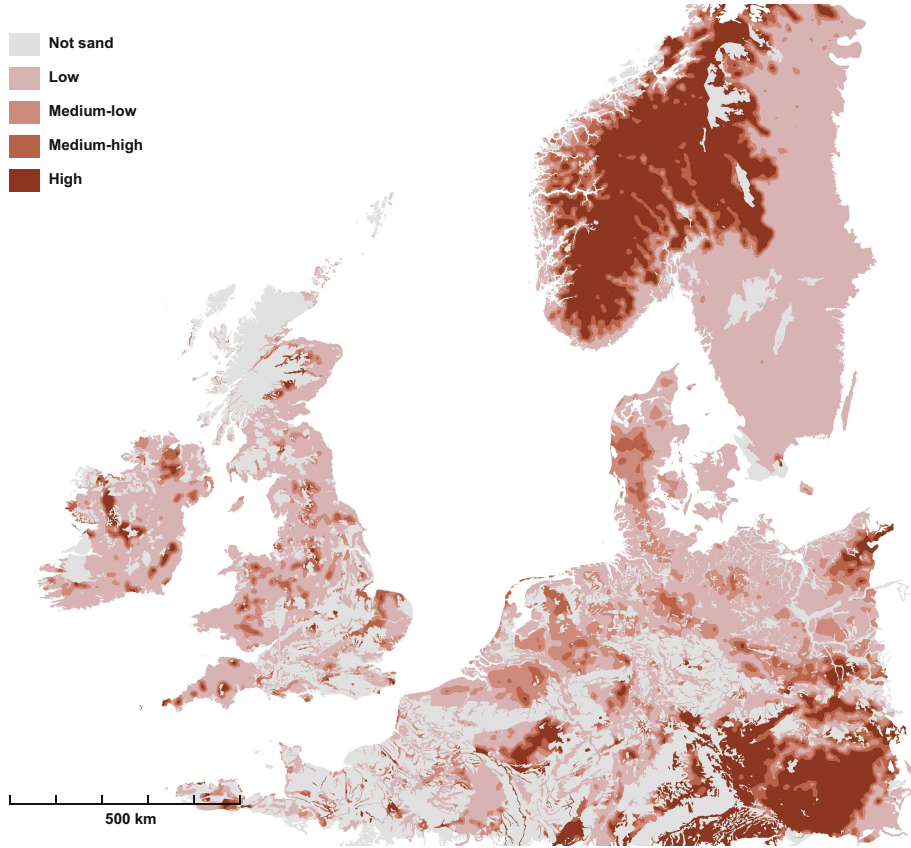
Since the Neolithic and into historical times, we can follow how different human uses of the heathlands involved extraction and management practices of different rejuvenation cycles that contributed in different levels to heath resilience and succession patterns. From the Late Neolithic–Early Bronze Age onwards, heath turfs were used in Western Jutland for fuel and heating, as reflected in the archaeological record of charcoal from heather found in hearths placed inside houses. Heathlands also served as sods for funerary barrows, which became a striking feature of the heathlands (Hübner, 2005: 467 ff.; Holst et al., 2013) as well as for building houses. Over time, they were systematically used in plaggen- and træk-based concentrational farming in Denmark, Germany and the Netherlands, where sods were systematically removed from the heathlands to concentrate and intensify crop production in smaller infields (Christiansen, 1996, 2002).

It remains an open question, how differences in ecological resilience, vice versa, affected social organization and governance in the past. For example, is it so that the more ecologically resilient a heathland, the less need for human governance, the less developed rules pertaining to grazing and burning? Or were heathlands kept as commons, with well-developed grazing and access rules and with clearly distributed requirements of rights and obligations? This is something that future research could shed light on to provide further inspiration for the governance of heathland conservation.

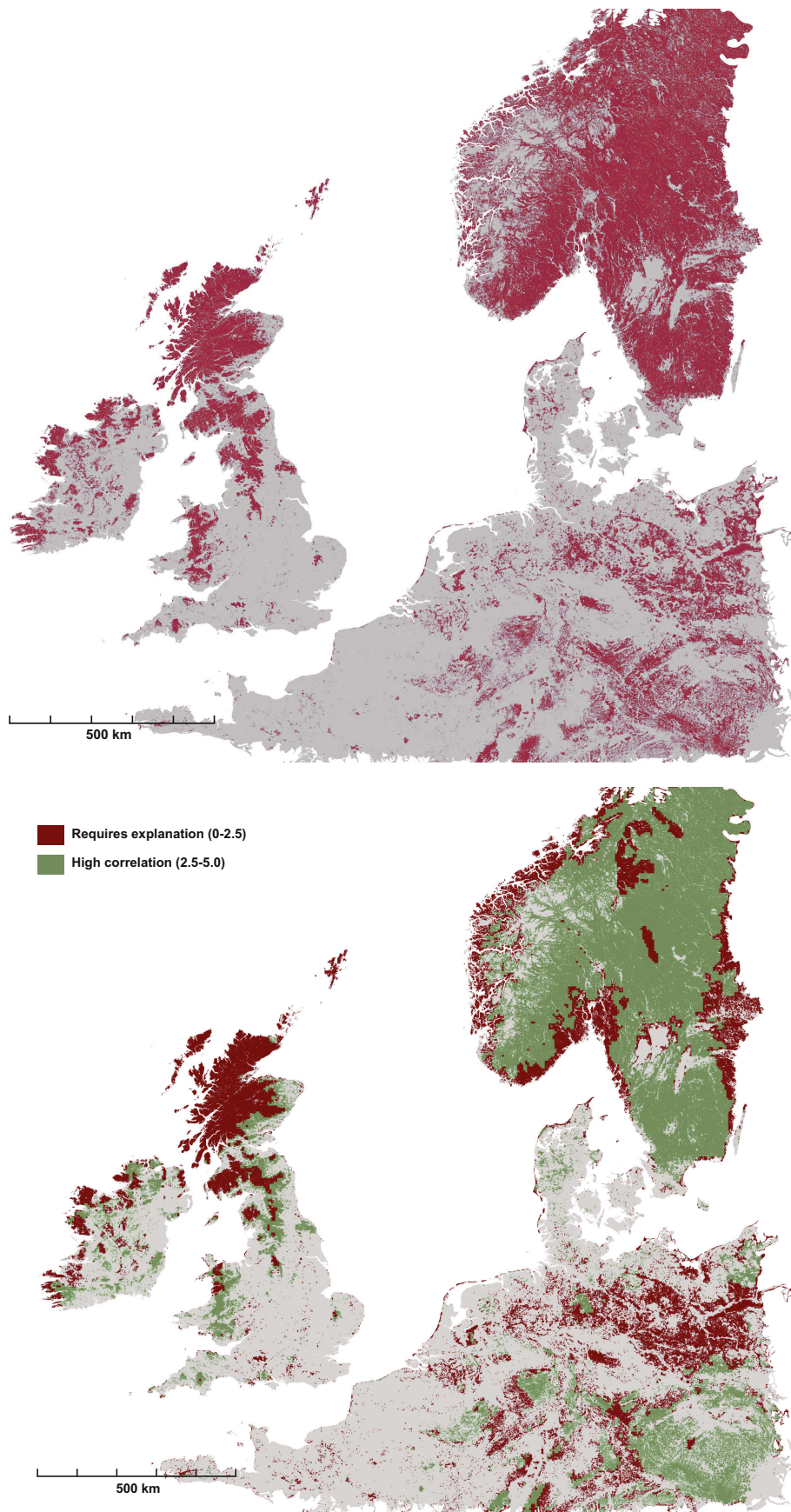
#### 4.1 | Method evaluation

Our results are characterized by several biases and shortcomings that require caution and careful interpretation. Our predictive model

**FIGURE 4** Upper: Prediction mapping of heathland resilience in Northern Europe. Colours range from light red (low resilience) to dark red (high resilience). Light grey is topsoil not classified as sand. In the absence of sampling points for Ireland, Sweden, France, Northeast Germany, and further towards the southeast, we consider the mapping to be invalid for these areas. Additionally, predictive accuracy of the model is limited where elevation is above 300m. Based on ArcGIS 10.8.2. Lower: Indication of a 50-kilometre radius around the 12 case study sites, reflecting the areas where we assume the prediction to have the highest validity. Credit: Ane Kjeldgaard and the authors.







**FIGURE 5** Upper: The historical distribution of heathlands in Northern Europe derived from Corine land cover 2018. Lower: The historical distribution of heathlands in Northern Europe compared against our prediction (Figure 4). Based on QGIS 3.24.2-Tisler. Credit: Mark Haughton and Mette Løvschal.

is first and foremost an initial screening tool, one that is subject to future modification. Although generated on a small number of sites ( $N = 12$ ), we consider it adequate to fulfil this role and to be further improved as future studies will add geographical detail and refinement. We expect the predictions to be most accurate for coarse sandy soils and near the sampling points, in [Figure 4](#) suggested to be within a 50-km radius.

The degree of explained variance was 63%. However, the accuracy of the performed modelling is constrained by the relatively few sites where we were able to quantify resilience. In this respect, there is a real risk that the model is somewhat over-fitted. Surprisingly, the effect of proximity to the coast does not clearly show in [Figure 4](#). Although it is uncertain how many additional Northern European sites exist where resilience might be credibly estimated, it should be possible to add additional sites, even if associated with a more uncertain resilience estimation, so long as this is combined with a modelling of the measurement uncertainty (Damgaard, 2022). Moreover, the fact that 70% of the area with coarse sandy soils are classified as highly resilient suggests that our criteria for 'high resilience' were potentially too low and could be adjusted towards, for example, shorter succession spans.

Ten of our sites were situated on 'coarse' sandy soil, but only two on 'medium'. This biased distribution in the soil texture variable may in itself be seen as an indication of the importance of soil texture for modern land use of former heathland sites, and indirectly of the resilience of heathland ecosystems, since possible former heathland sites with less sandy soil have now been converted to agriculture or forest. Generally, it is difficult to obtain good soil data without performing local soil sampling, and the data quality of the polygon-based map of European topsoils (European Commission, 2005), which we used, is, in our opinion, too coarse. The characterization of the soil texture is uncertain due to interpolation from a limited number of soil samples and a classification of the raw soil texture data into an ordinal scale. Finer resolution soil data exist, including pH value and previous land-use patterns, but currently still only for regional and national levels (e.g. Geus, VSK).

In addition to our chosen a priori factors, there exist a series of additional contributing factors to the relative (in)stability of heathlands (see 'Introduction'). As mentioned, unfortunately, we have not been able to locate this information consistently in order to include them in this study; we do, however, consider them equally important. The results could also be significantly improved by more and longer succession studies of unmanaged heaths, with a specific focus on controlling and specifying the range of disturbance factors, and with a focus on currently 'empty' areas, such as Scania, Southwestern Norway, Wales and Ireland.

## 4.2 | Policy recommendations

We see significant future potential in combining archaeology and palaeoecology in the conceptualisation and study of resilience, in order to estimate how heath resilience has changed over time,

its integration in human economic and cultural systems as well as how humans, in a deep time perspective, have dealt with and managed various speeds in vegetation succession. This provides valuable information in terms of planning what kind of and how much additional human intervention is needed in order to prevent heathlands from turning into shrublands, grasslands or forest. Moreover, [Figure 4](#) provides a tool for prioritizing which heathlands are most suitable for conservation and restoration projects.

We recommend that heathland conservation efforts are focused on areas, predicted as high or medium-high resilience and that heath management efforts are differentiated in relation to heath resilience. In low resilience heaths, human intervention in the form of frequent managed burning and grazing, combined with tree removal, is necessary to remove sufficient amounts of nutrients for the heath to retain stability. In high resilience heaths, grazing by sheep alone will sometimes be enough to keep the heath in a habitat-characteristic state, but must often be supplemented with burning.

## 5 | CONCLUSIONS

Few scholars have explicitly addressed when, how and why heathlands emerged and persisted as a cultural landscape for so long. Most consider heathland persistence as primarily the unintended consequence of soil exhaustion and poor soil conditions, rather than a purposive and integrated part of agro-pastoral regimes (Ombashi & Løvschal, 2022). This has marginalised heathlands somewhat in relation to other kinds of landscapes such as croplands and grass pastures. In this paper, we have attempted to systematically address the resilience of Atlantic unmanaged inland heaths and their ability to move along a varying spectrum of trajectory and pace towards alternative stable states. Rather than being characterised by *one* particular state, *one* dominant plant species or *one* management form, heathland is a highly context dependent, dynamic and constantly drifting multispecies assemblage. 70% of the selected European area with coarse sand was predicted to have a high heath resilience. Differences in this 'heath drift', we show, have provided very different bases for past heathland regimes, as well as modern-day conservation programmes. We have used these insights to soften the boundaries between ecological definitions of resilience and definitions building on a stronger integration of human co-dependency. Our study provides a basis for further exploring the nature, magnitude, intensity and frequency of additional anthropogenic and abiotic disturbances that are necessary for the heathlands to remain in, or return to, a habitat-characteristic state—in the present as well as in the past. A deep time approach to this prediction is useful for both understanding the historical processes of how humans have increased and decreased heath resilience affordances as well as for advising management in the conservation of these semi-natural habitats.

## AUTHOR CONTRIBUTIONS

Mette Løvschal conceived the initial ideas and analytical set-up and study and Mette Løvschal and Christian F. Damgaard designed the methodology; Mette Løvschal collected the vegetation succession and archaeological data and Mette Løvschal and Christian F. Damgaard collected the abiotic proxy data; Mette Løvschal and Christian F. Damgaard analysed the data; Mette Løvschal led the writing of the manuscript with contributions by Christian F. Damgaard. Both authors gave final approval for publication.

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## CONFLICT OF INTEREST

We have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

The data underlying our results in Figure 4 have been made available in the Supporting Information file via the Dryad Digital Depository <https://doi.org/10.5061/dryad.7m0cfxpxr> (Løvschal & Damgaard, 2022).

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## REFERENCES

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Allen, K. A., Denelle, P., Ruiz, F. M. S., Santana, V. M., & Marrs, R. H. (2016). Prescribed moorland burning meets good practice guidelines: a monitoring case study using aerial photography in the Peak District, UK. *Ecological Indicators*, 62, 76–85. <https://doi.org/10.1016/j.ecolind.2015.11.030>
- Andreasen, M. H. (2009). Agerbruget i enkeltgravskultur. Senneolitikum og ældre bronzealder i Jylland belyst ud fra plantemakrofossiler. *Kuml*, 58, 9–55.
- Bak, J., Løvschal, M., & Damgaard, C. (2020). *Hvordan bevarer vi heden i Danmark? Tilstand, genopretning og mulig pleje*. Aarhus University.
- Behre, K. E., & Kučan, D. (1986). Die reflektion archäologisch bekannter siedlungen in pollendiagrammen verschiedener entfernungen—Beispiele aus der Siedlungskammer Flügeln, Nordwestdeutschland. In K. E. Behre (Ed.), *Anthropogenic indicators in pollen diagrams* (pp. 95–114). Balkema.
- Berendse, F. (1990). Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *Journal of Ecology*, 78(2), 413–427. <https://doi.org/10.2307/2261121>
- Böcher, T. W. (1941). *Vegetationen paa Randbøl Hede med særlig hensyntagen til det fredede areal*. Ejnar Munksgaard.
- Bokdam, J., & Gleichman, J. M. (2000). Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology*, 37(3), 415–431. <https://doi.org/10.1046/j.1365-2664.2000.00507.x>
- Buttenschön, R. M., & Buttenschön, J. (2015). Kvæggræsning som hedepleje. *Flora og Fauna*, 121(3), 95–104.
- Christiansen, S. (1996). Concentrational agriculture: types, functions and derivation. *Geografisk Tidsskrift-Danish Journal of Geography*, 96, 123–138.
- Christiansen, S. (2002). Flows of matter in a traditional heathland farm about 1840. An example from northern West Jutland, Denmark. *Geografisk Tidsskrift-Danish Journal of Geography*, 101(1), 43–66. <https://doi.org/10.1080/00167223.2001.10649450>
- Corine Land Cover. (2018). <https://land.copernicus.eu/>
- Costanza, R., Graumlich, L., Steffen, W., Crumley, C., Dearing, J., Hibbard, K., Leemans, R., Redman, C., & Schimel, D. (2007). Sustainability or Collapse: What can we learn from integrating the history of humans and the rest of Nature. *Ambio*, 36(7), 522–527. [https://doi.org/10.1579/0044-7447\(2007\)36\[522:SOCWCW\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[522:SOCWCW]2.0.CO;2)
- Damgaard, C. (2022). Adaptive management plans rooted in quantitative ecological predictions of ecosystem processes: Putting monitoring data to practical use. *Environmental Conservation*, 49(1), 27–32. <https://doi.org/10.1017/S0376892921000357>
- Degn, H. J. (1996). Ændringer af vegetationen 1954–1995. Randbøl Hede (p. 30). Arbejdsrapport fra DMU nr. 30.
- Degn, H. J. (2019). *Heden*. Aarhus Universitetsforlag.
- Diemont, H. (1996). *Survival of Dutch Heathlands*. Landbouwniversiteit.
- Diemont, W. (1994). Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science*, 5, 409–414. <https://doi.org/10.2307/3235864>
- Diemont, W. H., Heijman, W. J., Siepel, H., & Webb, N. R. (2013). *Economy and ecology of heathlands: heathland ecology and management*. BRILL.
- Dorland, E., van den Berg, L. J. L., van de Berg, A. J., Vermeer, M. L., Roelofs, J. G. M., & Bobbink, R. (2004). The effects of sod cutting and additional liming on potential net nitrification in heathland soils. *Plant and Soil*, 265, 267–277. <https://doi.org/10.1007/s11104-005-0363-3>
- European Commission. (2005). <https://esdac.jrc.ec.europa.eu>
- Fagundéz, J. (2013). Heathlands confronting global change: Drivers of biodiversity loss from past to future scenarios. *Annals of Botany*, 111(2), 151–172. <https://doi.org/10.1093/aob/mcs257>
- Fyfe, R. M., Twiddle, C., Sugita, S., Gaillard, M.-J., Barratt, P., Caseldine, C. J., Dodson, J., Edwards, K. J., Farrell, M., Froyd, C., Grant, M. J., Huckerby, E., Innes, J. B., Shaw, H., & Waller, M. (2013). The Holocene vegetation cover of Britain and Ireland: overcoming problems of scale and discerning patterns of openness. *Quaternary Science Reviews*, 73, 132–148. <https://doi.org/10.1016/j.quascirev.2013.05.014>
- Gimingham, C. H. (1972). *Ecology of Heathlands*. Chapman & Hall.
- Gjedrem, A. M., & Log, T. (2020). Study of heathland succession, prescribed burning, and future perspectives at Kringsjå, Norway. *Land*, 9, 485. <https://doi.org/10.3390/land9120485>
- Gong, W. K. 1976. *Birch regeneration in heathland vegetation* (PhD thesis). University of Aberdeen.
- Harris, M. P. K., Allen, K. A., McAllister, H. A., Eyre, G., Le Duc, M. G., & Marrs, R. H. (2011). Factors affecting moorland plant communities and component species in relation to prescribed burning. *Journal of Applied Ecology*, 48(6), 1411–1421. <https://doi.org/10.1111/j.1365-2664.2011.02052.x>
- Helsper, H. P. G., Glenn-Lewin, D., & Werger, M. J. A. (1983). Early regeneration of Calluna heathland under various fertilization treatments. *Oecologia*, 58, 208–214. <https://doi.org/10.1007/BF00399218>
- Hobbs & Gimingham. (1984). Studies on fire in Scottish Heathland Communities II. Post-fire vegetation development. *Journal of Ecology*, 72(2), 585–610. <https://doi.org/10.2307/2260069>



- Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, 30(9), 503–506. <https://doi.org/10.1016/j.tree.2015.06.010>
- Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4(1), 1–23.
- Holst, M. K., Rasmussen, M., Kristiansen, K., & Bech, J. H. (2013). Bronze age 'Herostrats': Ritual, political, and domestic economies in Early Bronze Age Denmark. *Proceedings of the Prehistoric Society*, 79, 265–296. <https://doi.org/10.1017/ppr.2013.14>
- Hübner, E. (2005). *Jungneolithische Gräber auf der Jütischen Halbinsel: Typologische und chronologische Studien zur Einzelgrabkultur*. Det Kongelige Nordiske Oldskriftselskab.
- Jansen, J., & Diemont, W. H. (2005). Prospects of the open Atlantic mountain landscape of Europe at its south western limit. In *Landscape ecology and management of Atlantic mountains*. IALE Publication Series.
- Kaiser, T., & Stubbe, A. (2004). *Mittelfristige vegetationsentwicklung auf pflgeflächen in sandheiden des naturschutzgebiets "Lüneburger Heide"* (p. 2). NNA-Berichte.
- Kaiser, T. (2015). *Das naturschutzgebiet lüneburger heide natur- und kulturerbe von europäischem rang* (p. 8). VNP-Schriften, Band.
- Lippe, E., De Smidt, J. T., & Glenn-Lewin, D. C. (1985). Markov models and succession: A test from a heathland in The Netherlands. *Journal of Ecology*, 73(3), 775–791. <https://doi.org/10.2307/2260146>
- Løvschal, M. (2021). Anthropogenic Heathlands: Disturbance ecologies and the social organisation of past super-resilient landscapes. *Antiquity*, 95, 1–6. <https://doi.org/10.15184/aqy.2021.46>
- Løvschal, M. (2022). Retranslating resilience theory in archaeology. *Annual Review of Anthropology*, 51(1). <https://doi.org/10.1146/annurev-anthro-041320-011705>
- Løvschal, M., & Damsgaard, C. (2022). Data from: Mapping the ecological resilience of Atlantic postglacial heaths. *Dryad Digital Depository*. <https://doi.org/10.5061/dryad.7m0cfxpxr>
- Lütkepohl, M., & Stubbe, A. (1997). Feuergeschichte in nordwestdeutschen Calluna-Heiden unter besonderer Berücksichtigung des Naturschutzgebietes Lüneburger Heide. *NNA-Berichte*, 10(5), 105–114.
- Mallik, A. U., & Gimingham, C. H. (1983). Regeneration of heathland plants following burning. *Vegetatio*, 53(1), 45–58. <https://doi.org/10.1007/BF00039771>
- Måren, I. E., & Nilsen, L. S. (2008). Kystlyngheier i Midt- og Nord-Norge. *Blyttia*, 66(1), 11–22.
- Marrs, R. H. (1992). An assessment of change in *Calluna* heathlands in Breckland, eastern England, between 1983 and 1991. *Biological Conservation*, 65(2), 133–139. [https://doi.org/10.1016/0006-3207\(93\)90442-4](https://doi.org/10.1016/0006-3207(93)90442-4)
- Marrs, R. H., Hicks, M. J., & Fuller, R. M. (1986). Losses of lowland heath through succession at four sites in Breckland, East Anglia, England. *Biological Conservation*, 36(1), 19–38. [https://doi.org/10.1016/0006-3207\(86\)90099-6](https://doi.org/10.1016/0006-3207(86)90099-6)
- Marrs, R. H., Sánchez, R., Connor, L., Blackbird, S., Rasal, J., & Rose, R. (2018). Effects of removing sheep grazing on soil chemistry, plant nutrition and forage digestibility: Lessons for rewilding the British uplands. *The Annals of Applied Biology*, 173, 294–301. <https://doi.org/10.1111/aab.12462>
- MET Norway. [https://emep.int/mscw/mscw\\_moddata.html](https://emep.int/mscw/mscw_moddata.html)
- Mier, M. F., & Tente, C. (2018). Transhumant herding systems in Iberia. In E. Costello, & E. Svensson (Eds.), *Historical archaeologies of transhumance across Europe* (pp. 219–232). Routledge.
- Milligan, G., Rose, R. J., & Marrs, R. H. (2016). Winners and losers in a long-term study of vegetation change at Moor house NNR: Effects of sheep-grazing and its removal on British upland vegetation. *Ecological Indicators*, 68, 89–101. <https://doi.org/10.1016/j.ecolind.2015.10.053>
- Milligan, G., Rose, R. J., O'Reilly, J., & Marrs, R. H. (2018). Effects of rotational prescribed burning and sheep grazing on moorland plant communities: Results from a 60-year intervention experiment. *Land Degradation & Development*, 29(5), 1397–1412. <https://doi.org/10.1002/ldr.2953>
- Mitchell, R. J., Auld, M. H. D., le Duc, M. G., & Robert, M. H. (2000). Ecosystem stability and resilience: A review of their relevance for the conservation management of lowland heaths. *Perspectives in Plant Ecology, Evolution and Systematics*, 3(2), 142–160. <https://doi.org/10.1078/1433-8319-00009>
- Mitchell, R. J., Marrs, R. H., Duc, M. G. L., & Auld, M. H. D. (1997). A study of succession on lowland heaths in Dorset, southern England: changes in vegetation and soil chemical properties. *Journal of Applied Ecology*, 34, 1426–1444. <https://doi.org/10.2307/2405259>
- Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78(3), 691–692.
- Nielsen, A. B., Giesecke, T., Theuerkauf, M., Feeser, I., Behre, K.-E., Beug, H.-J., Chen, S.-H., Christiansen, J., Dörfler, W., Endtmann, E., Jahns, S., de Klerk, P., Kühl, N., Latafowa, M., Odgaard, B. V., Rasmussen, P., Stockholm, J. R., Voigt, R., Wiethold, J., & Wolters, S. (2012). Quantitative reconstructions of changes in regional openness in north-central Europe reveal new insights into old questions. *Quaternary Science Reviews*, 47, 131–149. <https://doi.org/10.1016/j.quascirev.2012.05.011>
- Nielsen, A. B., & Odgaard, B. V. (2010). Quantitative landscape dynamics in Denmark through the last three millennia based on the Landscape Reconstruction Algorithm approach. *Vegetation History and Archaeobotany*, 19, 375–387. <https://doi.org/10.1007/s00334-010-0249-z>
- Niemeyer, M., Niemeyer, T., Fottner, S., Härdtle, W., & Mohamed, A. (2007). Impact of sod-cutting and choppers on nutrient budgets of dry heathlands. *Biological Conservation*, 134(3), 344–353. <https://doi.org/10.1016/j.biocon.2006.07.013>
- Nilsen, L. S., Johansen, L., & Velle, L. G. (2005). Early stages of *Calluna vulgaris* regeneration after burning of coastal heath in Central Norway. *Applied Vegetation Science*, 8(1), 57–64. <https://doi.org/10.1111/j.1654-109X.2005.tb00629.x>
- Odgaard, B. V. (1994). The Holocene vegetation history of northern West Jutland. *Opera Botanica*, 123, 1–171. <https://doi.org/10.1111/j.1756-1051.1994.tb00649.x>
- Ombashi, H., & Løvschal, M. (2022). Anthropogenic Heathlands in Prehistoric Atlantic Europe: Review and Future Prospects. *European Journal of Archaeology*. <https://doi.org/10.1017/eea.2022.42>
- Ransijn, J., Kepfer-Rojas, S., Verheyen, K., Riis-Nielsen, T., & Schmidt, I. K. (2015). Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. *Journal of Vegetation Science*, 26(2), 254–266. <https://doi.org/10.1111/jvs.12230>
- Riesch, F., Tonn, B., Meißner, M., Balkenhol, N., & Isselstein, J. (2019). Grazing by wild red deer: Management options for the conservation of semi-natural open habitats. *Journal of Applied Ecology*, 56, 1311–1321. <https://doi.org/10.1111/1365-2664.13396>
- Riis-Nielsen, T., Schmidt, I. K., & Binding, T. (2005). *Nørholm Hede: En langtidsundersøgelse af hedens vegetationsudvikling og tilgroning*. University of Copenhagen.
- Rosa Garcia, R., Fraser, M. D., Celaya, R., Ferreira, L. M. M., García, U., & Osoro, K. (2013). Grazing land management and biodiversity in the Atlantic European heathlands: A review. *Agroforestry Systems*, 87(1), 19–43. <https://doi.org/10.1007/s10457-012-9519-3>
- Schmidt, I. K., Riis-Nielsen, T., Kepfer-Rojas, S., & Ransijn, J. (2015). Naturlige processer på heden- Nørholm Hede. *Flora og Fauna*, 121(3–4), 83–94.
- Simmons, I. G., & Innes, J. B. (1996). The ecology of an episode of prehistoric cereal cultivation on the North York Moors, England. *Journal of Archaeological Science*, 23(4), 613–618. <https://doi.org/10.1006/jasc.1996.0057>
- Terry, A. C., Ashmore, M. R., Power, S. A., Allchin, E. A., & Heil, G. W. (2004). Modelling the impacts of atmospheric nitrogen deposition on *Calluna*-dominated ecosystems in the UK. *Journal of Applied Ecology*, 41, 897–909. <https://doi.org/10.1111/j.0021-8901.2004.00955.x>

- Velle, L., Nilsen, L. S., & Vandvik, V. (2012). The age of *Calluna* stands moderates post-fire regeneration rate and trends in northern *Calluna* heathlands. *Applied Vegetation Science*, 15, 119–128. <https://doi.org/10.1111/j.1654-109X.2011.01144.x>
- Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S*. Springer.
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, 35, 1–22. <https://doi.org/10.2307/2256497>
- Webb, N. R. (1990). Changes on the Heathlands of Dorset, England, between 1978 and 1987. *Biological Conservation*, 5, 73–286. [https://doi.org/10.1016/0006-3207\(90\)90113-4](https://doi.org/10.1016/0006-3207(90)90113-4)
- Webb, N. R., & Haskins, L. E. (1980). An ecological survey of heathland in the Poole Basin, Dorset, England, in 1978. *Biological Conservation*, 17, 281–296. [https://doi.org/10.1016/0006-3207\(80\)90028-2](https://doi.org/10.1016/0006-3207(80)90028-2)
- Woestenburg, M. (2018). Heathland farm as a new commons? *Landscape Research*, 43(8), 1045–1055. <https://doi.org/10.1080/01426397.2018.1503236>
- Wolfram, S. (2020). *Mathematica*. Wolfram Research, Inc.

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