Ecosystem dynamics in dry heathlands: spatial and temporal effects of environmental drivers on the vegetation

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Abstract

To understand and estimate the effects of environmental drivers on temperate dry heathland vegetation, pin-point cover data from 102 Danish sites sampled during a 16-year period was regressed onto selected environmental variables. The effects of nitrogen deposition, soil pH, soil C-N ratio, soil type, precipitation and grazing on the heathland vegetation was modelled in a spatio-temporal structural equation model using a Bayesian hierarchical model structure. The results suggest that the modelled environmental variables have important regulating effects on the large-scale spatial variation as well as plant community dynamics in dry heathlands. The cover of the dwarf shrub *Calluna vulgaris*, which is the characteristic species of dry heathlands, increased in relatively sandy soils with a relatively high C/N ratio. The cover of the grass *Avenella flexuosa* increased markedly at relatively high nitrogen deposition and low precipitation. The cover of other graminoids, of which *Molinia caerulea* is the most abundant, increases with a relatively low C/N ratio, low grazing pressure, and clayey soils. It was concluded that the modeled environmental variables are sufficient for predicting the *average* plant community dynamics of dry heathlands. Consequently, the model may be used to make forecasts for the effect of different management scenarios at a specific site and thus provide important input to setting up local adaptive management plans.

Keywords: Plant community dynamics of dry heathlands; spatial and temporal variation of plant cover; hierarchical Bayesian models; pin-point cover data; structural equation modelling; ecological predictions, adaptive management plans.

Introduction

To appropriately manage semi-natural dry heathland ecosystems under the influence of climate change and altered land use practices, it is important to understand and be able to predict the effects of environmental drivers on the vegetation. Improved quantitative understanding of the effects of the different environmental drivers will enable us to make quantitative predictions at the local site level to future ecosystem responses to changes in e.g. climate and grazing regimes, as well as, provide important input for local adaptive management plans (Damgaard 2022a; 2025b). Consequently, to better understand the causal relationships underlying the observed large-scale variation and temporal changes in dry heathlands as well as estimate the effect of the environmental drivers, a structural equation model of the dry heathland ecosystem was hypothesized and fitted to spatial and temporal ecological data from 102 Danish dry heaths in the period 2007 to 2022.

The dynamics of semi-natural heathland ecosystems, and especially *Calluna* dominated heaths, were first studied by Watt (1947), who gave a detailed account of possible ecological processes that lead to different spatial vegetation patterns. This line of work has since been extended by several authors (e.g. Gimingham 1978; Gimingham 1988; Gimingham et al. 1981; Løvschal and Damgaard 2022; Usher and Thompson 1993), who describe the spatial patterns of heathland vegetation at different scales and how they are regulated by management.

The conservation status and resilience of dry heathlands are hypothesized to be highest when a low nutrient status is maintained, succession to forest or grassland is actively prevented by maintaining traditional land-use practices, and ensuring spatial heterogeneity in disturbance patterns (Damgaard et al. 2024; Olmeda et al. 2020). An analysis of the Danish dry heathland vegetation from 2004 to 2021 revealed declines in all three dominant species, *Calluna vulgaris*, *Empetrum nigra*, and *Avenella flexuosa* (the decline in *C. vulgaris* was only marginally significant). These species are ecosystem engineers, and their decline threatens the structure and function of heathland ecosystems. In contrast, the increasing cover of purple moor-grass, a tussock-forming species, may drive substantial ecological shifts (Damgaard 2025c). Overall, the conservation status of Danish dry heaths is deteriorating and unfavorable in about 40% of the areas (Nygaard et al. 2020).

The *a priori* selection of the studied environmental drivers was based on current ecological knowledge, where specific environmental drivers, e.g. atmospheric nitrogen deposition, soil type, soil pH and disturbance, have been shown to have an effect on heathland vegetation (e.g. Aerts et al. 1990; Aerts and Heil 1993; Britton et al. 2003; Damgaard et al. 2024; Damgaard et al. 2020; De Graaf et al. 2009; Vogels et al. 2020). However, dry heathland vegetation is expected to be regulated by more environmental drivers than it was possible to include in this study because of missing data, e.g. species-specific herbivores and pests and previous natural management actions. Some of these more or less unknown factors can have a geographical regional structure that may be partly explored using latent geographic factors (Ovaskainen et al. 2016), and possible significant effects of such latent geographic factors can generate new testable causal hypotheses. Furthermore, it is expected that soil type and nitrogen deposition may have both direct and indirect effects by affecting soil pH (Damgaard et al. 2014), and such direct or indirect causal pathways are often best modelled using structural equation models (SEM) that are fitted to observed ecological data (Grace et al. 2010). Generally, the effects of changes in environmental variables, e.g. climate, soil physical properties and disturbance regimes, on plant communities are expected to occur with some time-lags (e.g. Svenning and Sandel 2013). Furthermore, the regulating environmental variables are expected to vary considerably among different sites, and it is critical to integrate this large-scale spatial variation into the analysis of the ecosystem dynamics.

The objective of this study is to investigate the effects of selected environmental and ecological drivers (nitrogen deposition, soil type, soil pH, soil C-N ratio, precipitation, and grazing) on the vegetation at dry heaths, which is summarized by the multivariate relative cover of six species or aggregated species groups

(*Calluna vulgaris*, *Empetrum nigra*, *Avenella flexuosa*, other graminoids, other herbs, and cryptogams). Previously, similar models have been fitted to wet heathlands (Damgaard 2019; 2025a), as well as, acid (Damgaard 2022c), and calcareous grassland (Damgaard 2023).

Materials and Methods

Dry heathlands

Dry heathlands are semi-natural ecosystems on sandy, nutrient-poor soils, which first became widespread in prehistoric times under the influence of extensive agricultural practices (Løvschal 2021; Olmeda et al. 2020). In Denmark, the dry heathlands are mainly situated in the western part of Denmark that were not covered by ice during the last (Weichselian) glacial period. The vegetation is mainly comprised of dwarf shrubs and graminoids, where especially *C. vulgaris, E. nigra*, and *A. flexuosa* are characteristic and often dominating species (Damgaard 2025c).

Calluna vulgaris (L.) Hull (heather) is a 10 to 50 cm tall dwarf shrub that is dominant on dry heaths, though not tolerant to heavy grazing, and prefers at least moderately well-drained soils (Gimingham 1960). The developmental phases of heather include pioneer, building, mature and degenerate (Usher and Thompson 1993; Watt 1947), and without management actions such as burning, grazing or cutting, *C. vulgaris* plants degenerate when their age exceeds approximately 30 years, thereby leaving room for heathland succession.

Empetrum nigrum L. (black crowberry) is a low-growing, allelopathic, evergreen dwarf shrub typically forming dense mats on acidic, sandy, and nutrient-poor soils. It is well adapted to wind and salt aerosols. It is often found in late-successional or climax communities, though it can also act as a pioneer species in disturbed habitats. The dominant reproductive strategy is through adventitious rooting and sprouting from the basal parts (Tybirk et al. 2000).

Avenella flexuosa (L.) Drejer (wavy hair-grass) is a slender, tufted perennial grass typically 20 to 60 cm tall, which is found on acidic, sandy, and nutrient-poor soils. It is widely distributed across European heathlands and often increases in abundance following reduced grazing or elevated nitrogen deposition. It is tolerant of low nutrient availability but can become dominant under disturbance regimes that suppress dwarf shrubs (Aerts and Heil 1993).

The estimated cover and change in cover of the most common species in Danish dry heathland plots are shown in Table S1 (Damgaard 2025c).

Sampling design

Hierarchical time-series data from 102 dry heathland sites (Fig. 1) that had been monitored at least three times in the period from 2007 to 2022 were used in the analysis. Fifty-nine of the 102 sites are NATURA 2000 habitat sites and are protected under the Habitat Directive (EU 1992). All sites included several plots classified as dry heathland (EU habitat type: 4030) according to the habitat classification system used for the European Habitat Directive EU (EU 2013; Olmeda et al. 2020). The area of the sites ranged from 0.14 ha to 1030 ha, with a median area of 11.7 ha. A total of 883 unique plots were used in the analysis. The sampling was performed in the summer, and all plots at a site were sampled on the same day. Otherwise, sampling intensity was irregular among sites and years, but all sites were monitored within a six-year period. Typically, ten plots were sampled from each site each time. Including resampling over the years, a total of 3525 plots were used in the analyses. The plots were resampled with GPS-certainty (< 10 meters).

The data are a subset of the data collected in the Danish habitat surveillance program NOVANA (Nielsen et al. 2012; Nygaard et al. 2024).

Variables and measurements

Plant cover data

The plant cover, which is the relative projected area covered by a species, was measured for all higher plants by the pin-point method using a square frame (50 cm X 50 cm) of 16 grid points that were equally spaced by 10 cm (Nielsen et al. 2012). At each grid point, a thin pin was inserted into the vegetation and the plant species that were touched by the pin were recorded and used as an estimate of cover (Damgaard and Irvine 2019; Levy and Madden 1933; Lindquist 1931). Since the pin-point cover data after 2007 were recorded for each pin separately, the species cover data are readily aggregated into cover data for classes of species at a higher taxonomic or functional level. At each grid point, the pin may hit different plant species from the same species class and, in those cases, the hits are only counted as a single hit of the species class at the grid point.

In this study, the species were classified into six groups: *C. vulgaris, E. nigra*, and *A. flexuosa*, any other graminoids, any other herbs or cryptogams. The assumed distribution of pin-point cover data for single species and the joint distribution for multiple species are outlined in the electronic supplement (Appendix A).

Nitrogen deposition

Nitrogen deposition at each plot was calculated for each year using a spatial atmospheric deposition model in the period from 2005 to 2014 (Ellermann et al. 2012). The mean site nitrogen deposition ranged from 5.94 kg N ha^{-1} year to 21.89 kg N ha^{-1} $year^{-1}$, with a mean deposition of 13.80 kg N ha^{-1} $year^{-1}$. Anthropogenic nitrogen deposition has reached a maximum in Denmark and is currently decreasing (Ellermann et al. 2018).

Soil pH

Soil pH was measured in randomly selected plots from the uppermost 5 cm of the soil (four samples were amassed into a single sample). The soils were passed through a 2mm sieve to remove gravel and coarse plant material, and pH_{KCl} was measured on a 1 M KCl-soil paste (1:1). The soil sampling intensity was irregular among sites and years, but typically between one and four plots were sampled from each site at each time point. When a plot was resampled, the pH at the plot was calculated as the mean of the samples. In total, 704 independent soil pH values were used in the analysis. The measured soil pH ranged from 2.7 to 6.3, with a mean soil pH of 3.37.

C-N ratio in the soil

Soil C-N ratio was measured in randomly selected plots from the uppermost 5 cm of the soil (four samples were amassed into a single sample). Total C in each sample was determined by dry combustion and N by the Kjeldahl method. The soil sampling intensity was irregular among sites and years, but typically between one and four plots were sampled from each site at each time point. When a plot was resampled, the C-N ratio at the plot was calculated as the mean of the samples. Measurements outside of the domain [10, 60] were assessed to be unrealistic, and measurements outside the domain were set to either 10 or 60. The measured C-N ratio at the site level ranged from 12.2 to 60, with a mean site C-N ratio of 24.8. Moreover, the average soil C–N ratio on dry heathlands has been observed to decrease in the period from 2004 to 2014 (Strandberg et al. 2018).

Since soil C-N ratio is expected to be influenced by the vegetation, e.g. by the amount of slowly decomposing dwarf shrub litter, soil C-N ratio may be thought of more as an environmental covariable than an environmental driver.

Soil type

The texture of the topsoil for each site was obtained from a raster based map of Danish soils (Greve et al. 2007). The categorical classification of the soil (JB-nr.) was made on an ordinal scale with decreasing particle size, 1: coarse sandy soil, 2: fine sand soil, 3: coarse loamy soil, 4: fine loamy soil. There were some records with other soil types, but because of possible classification errors they were treated as missing values. The mean soil type was 1.70.

Precipitation

Site-specific precipitation was measured by the average annual precipitation in the period 2001 to 2010, with a spatial resolution of 10 km (DMI 2014). The annual precipitation ranged from 604 mm to 987 mm, with a mean precipitation of 824 mm.

Grazing

Land-use was summarized by possible signs of grazing, e.g. the presence of livestock or short vegetation within fences was recorded by the observer at each plot for each sampling year since 2007 as a binary variable (sign of grazing = 1, no sign of grazing = 0), i.e. if grazing was 0.5, then this probability may arise by a number of ways, e.g. if half the plots at the site showed signs of being grazed each year or all plots were grazed every second year. The mean grazing variable ranged from 0 to 1 among sites, but most sites had no grazing and the mean grazing intensity at the site level was 0.30. Unfortunately, the grazing variable does not include information on which animals were used for grazing, stocking densities or grazing duration, and is therefore a quite imprecise variable that must be interpreted together with general knowledge on the typically used grazing regime of dry heathlands.

Geographic regions

The 102 dry heathland sites were grouped into six arbitrary geographic regions without using prior information (Fig. 1). These regions were used to investigate possible latent geographic factors.

Spatio-temporal modelling

To further understand the observed changes in species composition at dry heathlands (Damgaard 2025c), and the deteriorating conservation status of Danish dry heaths (Nygaard et al. 2020), the observed changes in pin-point cover data were fitted to site variation in selected abiotic and land-use environmental variables in a spatio-temporal structural equation model (SEM) (Fig. 2).

It was decided to fit the SEM within a Bayesian hierarchical model structure using latent variables to model the effect of measurement and sampling uncertainties (Fig. 2). This use of a hierarchical model structure is important, since it has been demonstrated that ignoring measurement and sampling uncertainties may lead to model and prediction bias (Damgaard 2020; Damgaard and Weiner 2021). Furthermore, it is an advantage when making ecological predictions to separate measurement and sampling uncertainties from process uncertainty. The hierarchical SEM approach and the motivation for using it are explained further in (Damgaard 2025d). The mathematical and statistical details of the spatio-temporal modelling are explained in the electronic supplement (Appendix B)

The procedures for estimating the most important single species cover and change in species cover for all sampled dry heathland plots since the beginning of the monitoring program in 2004 are explained in the electronic supplement (Appendix C), and the used code and additional tests of fitting properties etc. may be found in Appendix D.

Results

The selected environmental variables covaried at the 102 dryland heath sites (Fig. S1), which again is expected to lead to covariance among parameter estimates and affect the fitting properties of the model negatively. Nevertheless, plots of the mean latent vs. expected logit-transformed cover variables demonstrated a relatively good fit of the large-scale spatial variation in cover (Fig. 3A; between 50% and 57% of the variation is explained, Table S3), and the model fitted the temporal process of the change in cover very well (Fig. 3B; > 97% of the variation is explained, Table S3). Furthermore, the Dunn–Smyth residuals of the marginal observed cover data of the six species classes were approximately normally distributed (Fig. S2).

To prevent possible prediction bias, the different sources of uncertainty, i.e. measurement and sampling uncertainty when measuring plant cover, nitrogen deposition, soil pH, soil C-N ratio and soil type, as well as the structural uncertainties due to the modelled soil pH, large-scale (among sites) spatial variation and the temporal processes, were modelled explicitly. The most important source of measurement uncertainty was the plant cover measurement due to the significant small-scale spatial aggregation of plant species, which was modelled by the parameter δ in the Dirichlet - multinomial mixture distribution. The median estimated value of δ was 0.19 with a relatively narrow credible interval (Table S2). Generally, the estimates of structural uncertainties were relatively low, although the large-scale spatial variation was relatively high (Table S2, Fig. 3A).

Many of the regression parameters that measure the large-scale spatial and temporal effect of the abiotic variables on the vegetation were significantly different from zero (Table S2), suggesting that the modelled environmental and land-use factors have a regulating effect on both the large-scale spatial variation in cover of the six species classes as well as plant community dynamics in dry heathlands. Soil type had significant effects on the large-scale spatial variation of all six species classes, whereas the other explanatory variables had significant effects on at least two species (Fig. 4A, Table S2) and, generally, there was significant geographic variation among the six assigned Danish regions, where the large-scale cover of *C. vulgaris* showed a qualitatively different geographic distribution than the other species (Fig. 4A, Table S2), but without showing a clear pattern (results not shown).

The selected environmental drivers, all had significant effects on the temporal variation of all six species classes, except for soil type, where four species were significantly affected (Fig. 4B, Table S2). Notably, relatively high nitrogen deposition was associated with an observed increase in the cover of *A. flexuosa*, and a decrease in the cover of other herbs. Relatively high C/N ratio in the soil was associated with an observed increase in observed cover of *C. vulgaris, E. nigra*, and *A. flexuosa*, and a decrease in the cover of other graminoids and cryptogams. Grazing was associated with a decrease in cover of other graminoids and other herbs. Finally, relatively high precipitation was associated with a decrease in the cover of *A. flexuosa* and an increase in cover of other graminoids (Fig. 4B).

In this study of dry heathlands, relatively high nitrogen deposition was associated with low soil pH (γ_N, Table S2), and soil pH was found to be significantly lower on more clayey soils compared to sandy soils (γ_S, Table S2).

Discussion

Environmental drivers and plant community dynamics

Many of the regression parameters that measure the effect of the environmental drivers on the change in plant species cover were significantly different from zero. These results suggest that the selected modelled environmental variables have regulating effects on the observed large-scale spatial variation as well as plant community dynamics in dry heathlands.

The cover of the dwarf shrub *C. vulgaris*, which is the characteristic species of dry heathlands, increased in relatively sandy soils with a relatively high C/N ratio. Notably, the cover of the grass *A. flexuosa* increased markedly at relatively high nitrogen deposition and low precipitation. These results corroborate earlier findings, that the ratio between the relative abundances of *C. vulgaris* and *A. flexuosa* at dry heathlands is associated with a precipitation and soil fertility gradient in Denmark (Damgaard 2015). The cover of other graminoids, of which *Molinia caerulea* is the most abundant (Table S1), increases with a relatively low C/N ratio, low grazing pressure, and clayey soils. Overall, these results corroborate the working hypothesis that the conservation status and resilience of dry heathlands hinge on nutrient-poor sandy soils (Damgaard et al. 2024). However, note that the current level of nitrogen deposition at dry heathland is within the current empirical critical load of dry heathlands between 5 and 15 kg N ha^{-1} $year^{-1}$ (Bobbink et al. 2022), and is expected to further decrease in the future. The annual precipitation in the future climate in Denmark is predicted to increase, but with decreasing summer precipitation and longer summer drought periods (DMI 2017). Generally, it is uncertain how this combination of more extreme weather will influence the future dry heathland vegetation (Olmeda et al. 2020).

There were significant effects of grazing on the observed changes in species composition at dry heathlands. However, except for the negative effects on other graminoids and other herbs, the observed effects on cover changes were relatively benign. Unfortunately, the Danish ecological surveillance program does not collect information on stocking rates or seasonality of grazing management, but only on whether grazing has taken place or not. This lack of resolution prevents a detailed analysis of the effect of the currently applied grazing on Danish dry heathland vegetation. It has been hypothesized that both grazing abandonment, which eventually may lead to a succession into a more woody vegetation, and overgrazing, where grass species are generally favored, may disfavor dwarf shrub species in dry heathlands (Newton et al. 2009; Olmeda et al. 2020). However, there is still considerable uncertainty as to the effect of grazing on dry heathland vegetation, and it will be beneficial if future grazing management actions monitor the effects and regulate stocking rates and seasonality using adaptive management procedures.

There were acidifying effects of nitrogen deposition and soil pH was found to be significantly higher on sandy soils compared to less sandy soils. The soil acidification effects of nitrogen deposition are due either to nitrate leaching or removal of base cations from the system by nature management (Williams and Anderson 1999), and the detrimental effects of this acidification, e.g. reduced biodiversity of higher plants, have clearly been demonstrated at heathlands in the Netherlands (Bobbink et al. 2022; Vogels et al. 2020), which generally have received higher nitrogen deposition than Danish heathlands.

In conclusion, this study has identified accumulated nitrogen in the soil due to nitrogen deposition and the associated soil acidification as some of the main threats to the conservation status of dry heathlands. This conclusion is in concordance with the background information in the EU habitat action plan for dry heathlands (Olmeda et al. 2020), who further points to the detrimental effects of too little grazing or over-grazing, and more generally, the abandoning of traditional agricultural practices and the following encroachments of trees from the border of the heathland areas.

Spatial variation

The short-scale spatial aggregation of the three species and the three aggregate classes of other plant species were modelled by the parameter δ in the Dirichlet - multinomial mixture distribution (Appendix A). The estimated amount of short-scale spatial aggregation significantly increased the measurement uncertainty of the expected cover data compared to the case of randomly distributed plant species. If this over-dispersion of the pin-point cover data relative to the random expectation is not taken into account in the statistical model, then the signal to noise ratio will be severely upward biased and, most likely, will lead to erroneous conclusions (Damgaard 2013).

All species classes had significant regional geographic variation among the six assigned regions (Fig. 1). This result indicates that some of the large-scale spatial residual variation that could not be explained by the modelled environmental drivers may be explained by hitherto unexplored factors that differ among the six regions. In future studies, it will be important to understand the historical causes for the observed large-scale spatial variation in species abundance, e.g. by collecting and analyzing detailed accounts of site-specific nature management actions and hydrological data.

Uncertainties and application of the model

Generally, a SEM does not allow us to prove the hypothesized causal relationships, but it is possible to test whether specific casual relationships are supported by data. To demonstrate causality, it is necessary to manipulate the system, e.g. in the form of a manipulated experiment, and observe whether the response predicted by the SEM actually takes place (Granger 1969; Pearl 2009). Moreover, there is an unknown time lag between the effect of environmental variables and the change in vegetation cover (e.g. Svenning and Sandel 2013), so it is uncertain which time period of a changing environmental variables to use in the model. However, since there typically is a high degree of spatial autocorrelation through time, i.e. sites that have a relatively high value of an environmental variable at one time period also have a relatively high at a following time period, the model is still able to estimate the relative effects of the environmental variables among the sites across years.

The statistical modelling uncertainty was partitioned into measurement uncertainty and uncertainties due to the modelled spatial – and temporal processes. The most important source of measurement uncertainty was the plant cover measurement due to the significant small-scale spatial aggregation of plant species (see above), but the measurement uncertainty of nitrogen deposition, soil pH, soil C – N ratio, and soil type was also estimated and, thus, accounted for in the model. Generally, the structural uncertainty of the temporal processes was relatively small, whereas the large-scale spatial processes entail a higher degree of structural uncertainty.

One of the advantages of partitioning the different types of uncertainties in the SEM is the use of the fitted SEM for predictive purposes (Damgaard 2022b; Damgaard 2025b), and since the fit of the temporal model was excellent, it is here suggested that the modeled environmental variables are sufficient for predicting the *average* plant community dynamics of dry heathlands. This optimistic conclusion is somewhat surprising in the light of several missing potentially important regulating variables, e.g. previous natural management actions. Due to the lack of an established causal understanding, caution and humbleness are required if the fitted model is used for generating local ecological predictions as input to a process of generating adaptive management plans for specific dry heathlands, since the modelled environmental variables in this study may be correlated to unknown causal factors of plant community dynamics, contingent event with large effects, or causal factors where we do not have access to relevant environmental data. On the other hand, the modelling results provide important information to site managers on the relative importance of the different environmental factors and management scenarios (Fig. 5). For example, since nitrogen deposition is invisible it is difficult to assess its effects without a statistical model and generally the effects of nitrogen deposition tend to be downplayed by site managers.

Figures

Fig. 1. Map of the selected 102 Danish dry heathland sites. The different colors represent a classification of the different sites into six geographical regions.

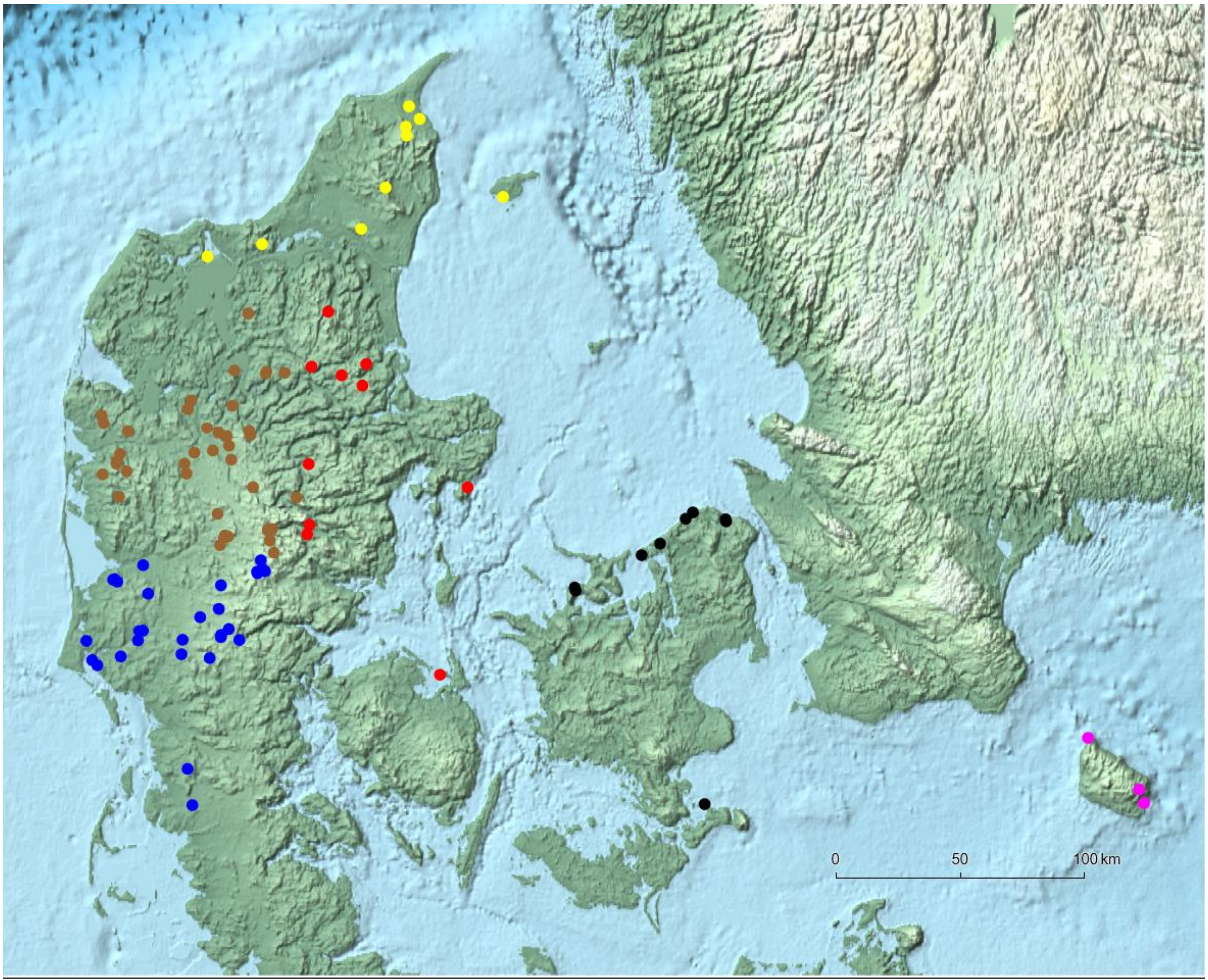


Fig. 2. Outline of hierarchical SEM. The spatial variation in vegetation cover in 2007 is modelled by nitrogen deposition (Ndep), soil pH (pH), soil C-N ratio (C/N), soil type and precipitation (Precipit.). The yearly change in vegetation cover from 2007 to 2022 (only a single yearly change is shown in the figure) is modelled by all the former variables as well as grazing. The black boxes are latent variables and the green ovals are data. The black arrows denote large-scale spatial processes, and the red arrows denote temporal processes (Appendix B).

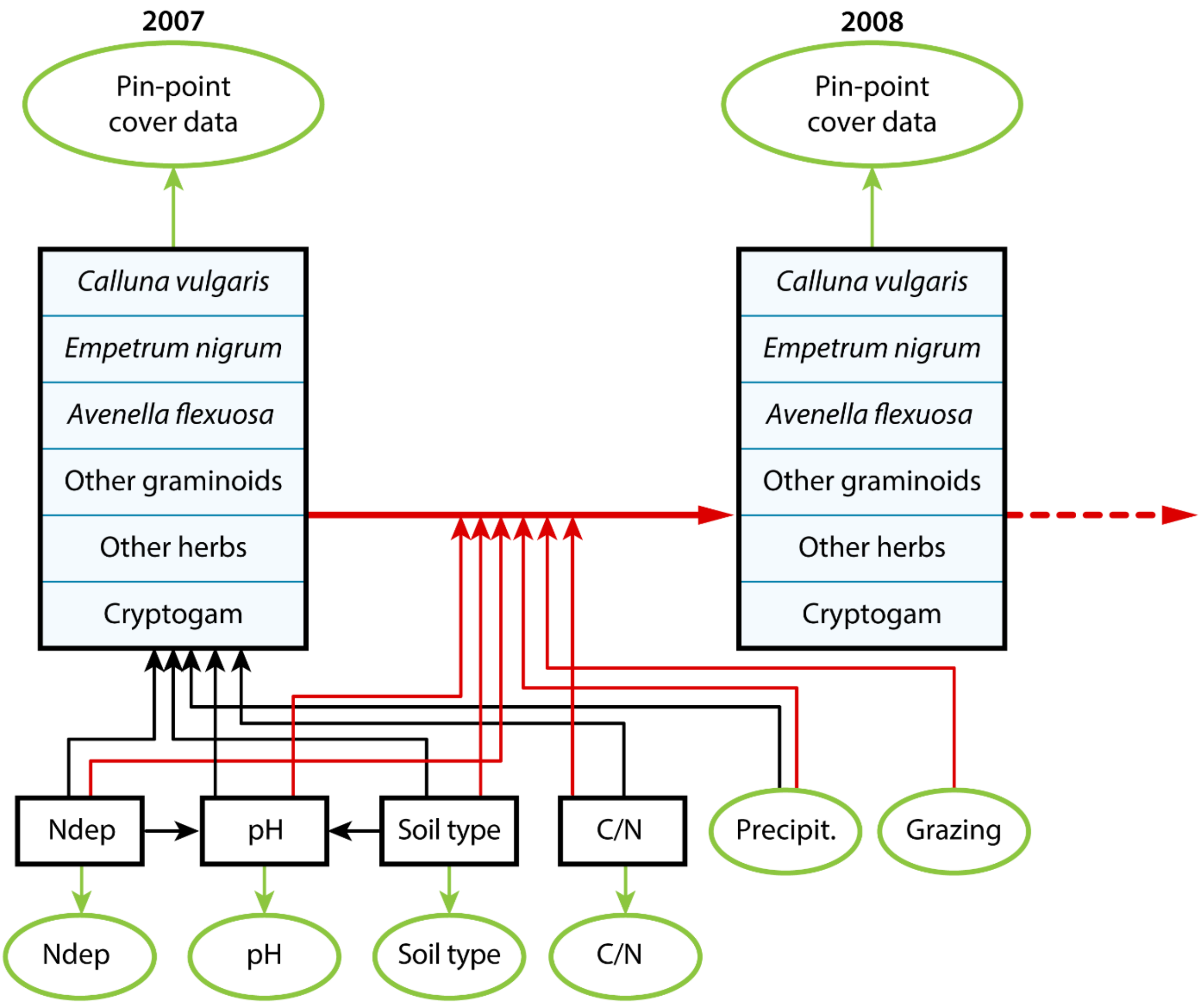
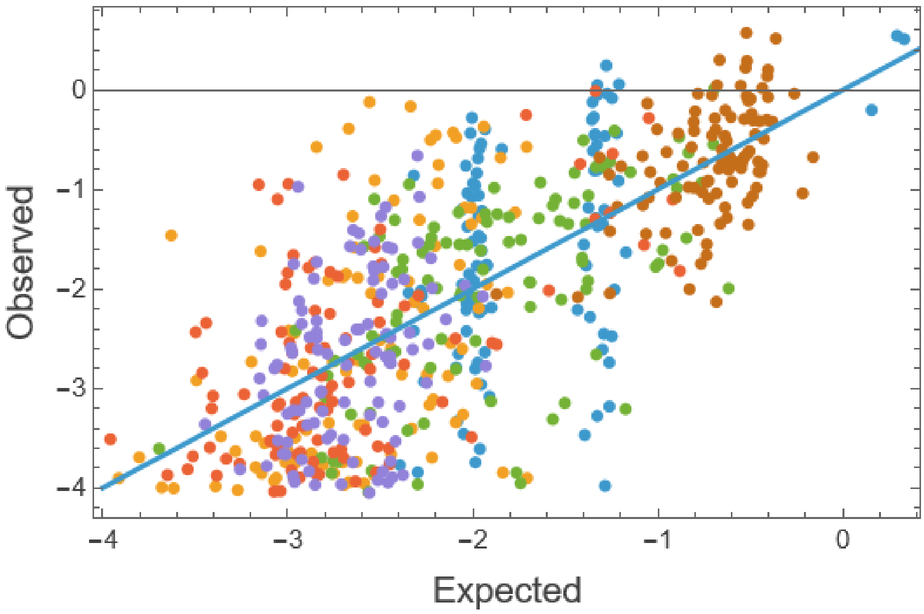


Fig 3. Plots of observed vs. expected logit-transformed cover of the large-scale spatial process (A) and the temporal (B). The proportions of the variance explained for each species may be found in Table S3. Blue: *Calluna vulgaris*, yellow: *Empetrum nigra*, green: *Avenella flexuosa*, red: other graminoids, purple: other herbs, blue: cryptogams.

A: large-scale spatial process



B: temporal process

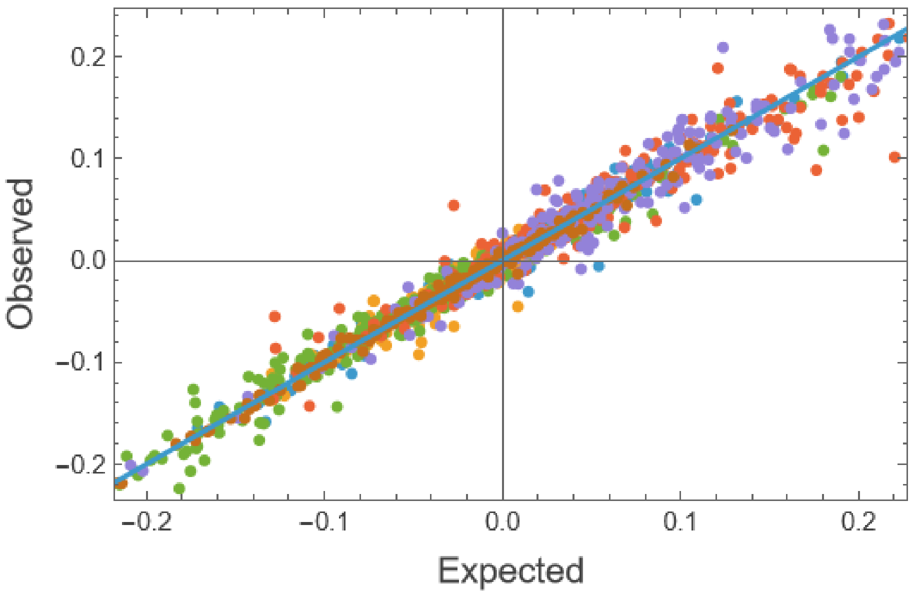
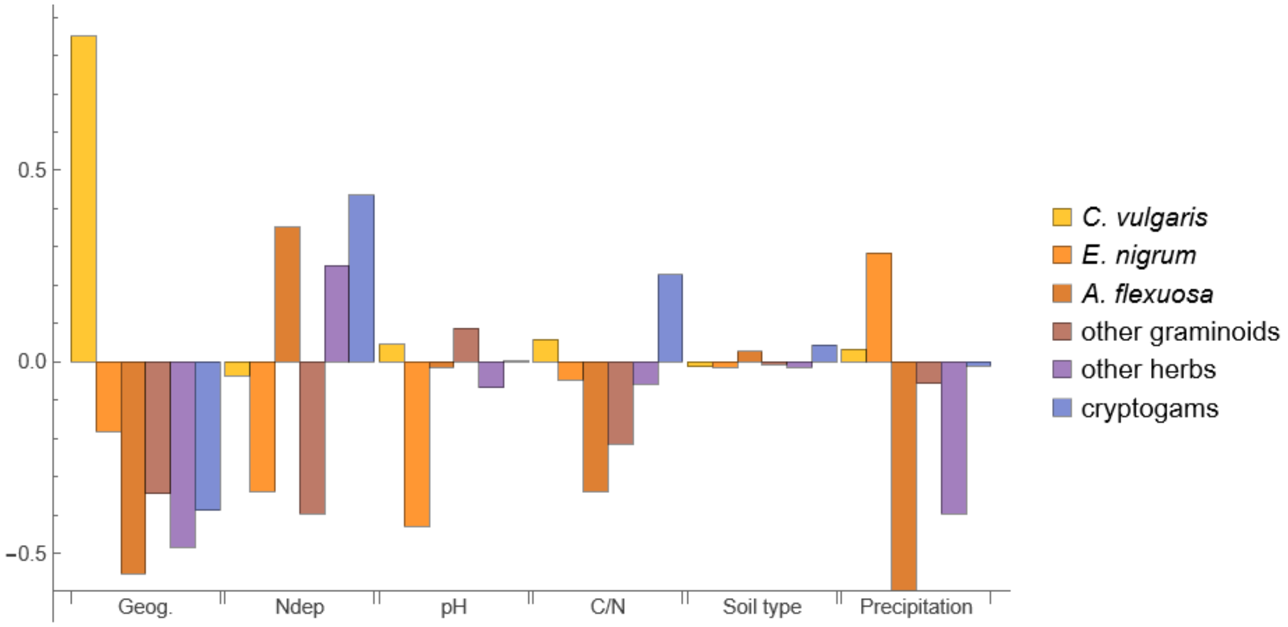


Fig 4. Standardized regression coefficients of the SEM for the large-scale spatial process (A) and the temporal (B).

A: large-scale spatial process



B: temporal process

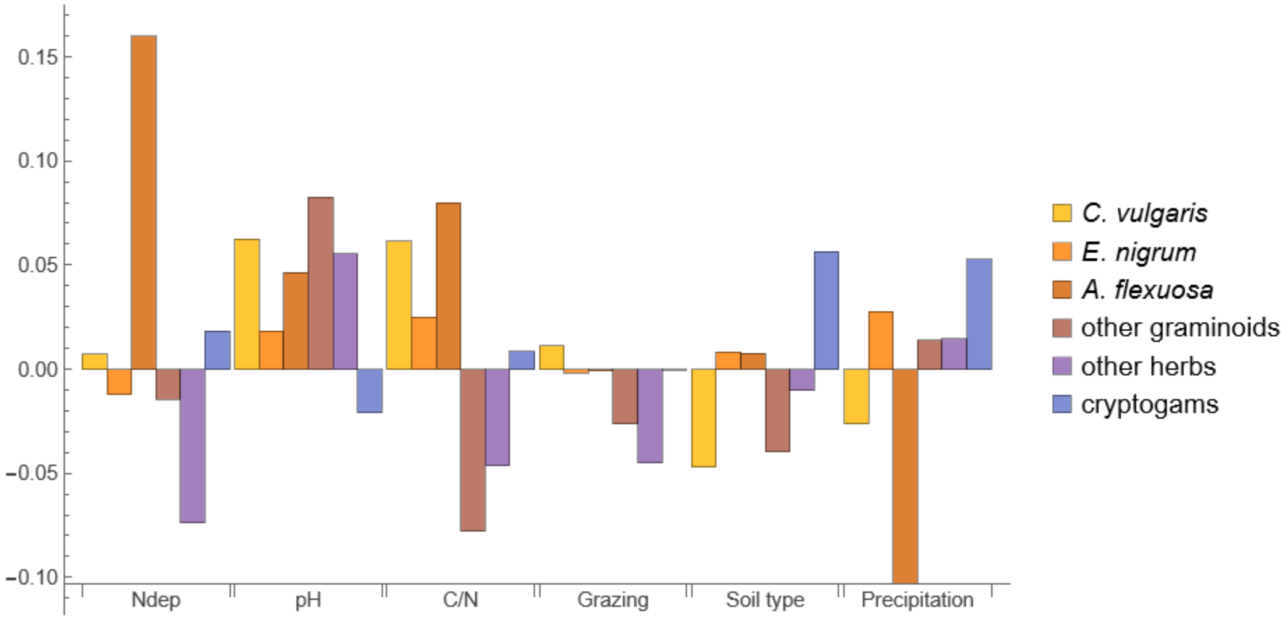
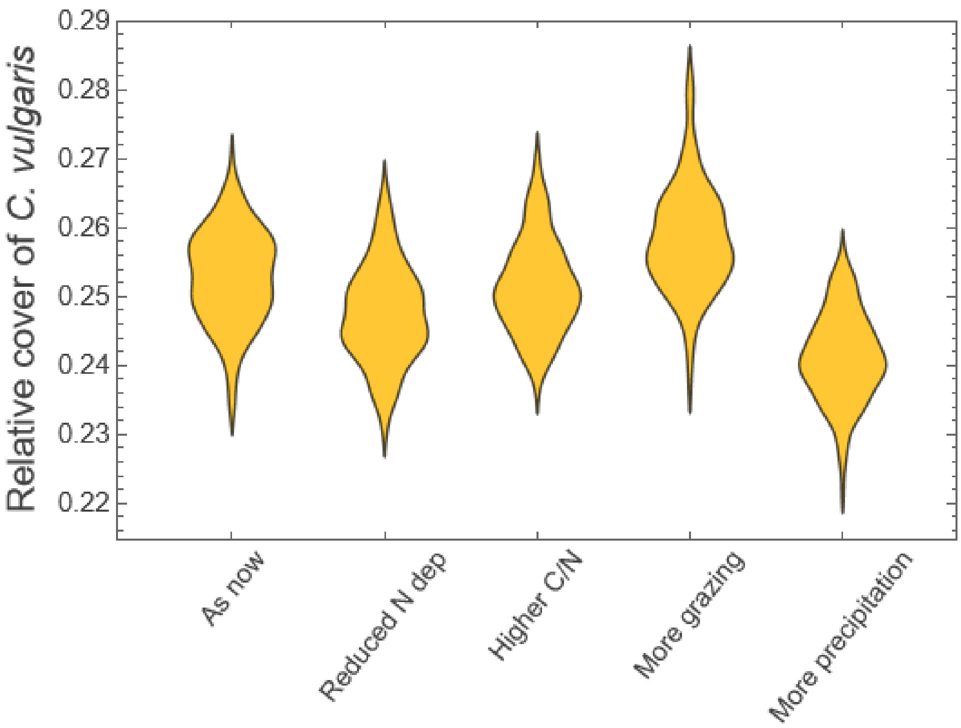
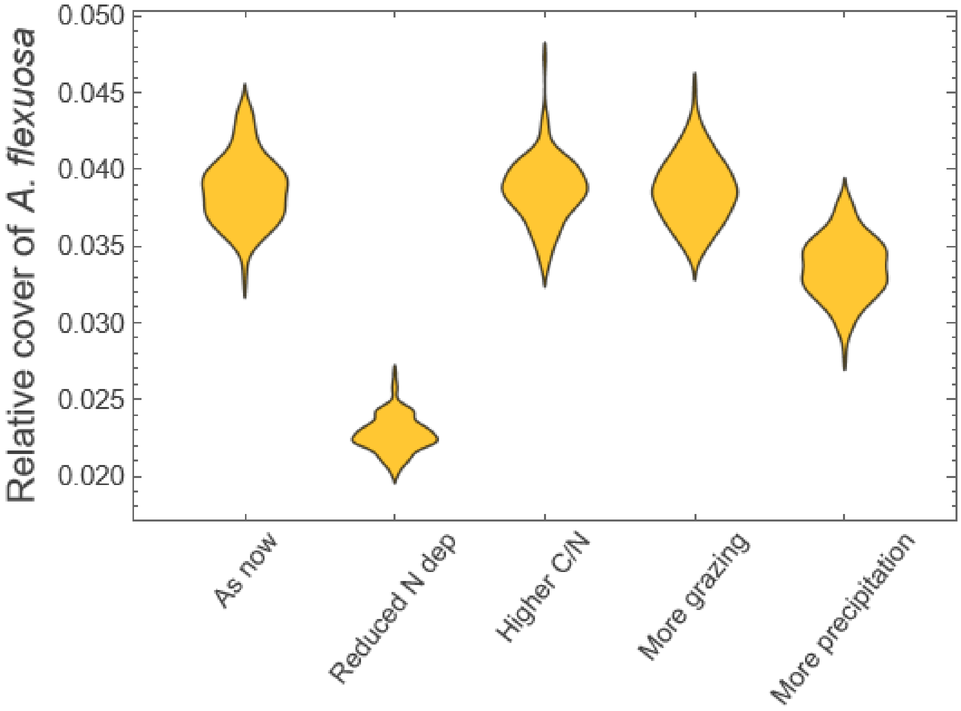


Fig. 5. Predicted distribution of the cover of *C. vulgaris* and *A. flexuosa* for a specific dry heathland site (Højsande in West Jutland) after five years under four different scenarios (Damgaard 2022a; 2025b). The initial cover of *C. vulgaris* and *A. flexuosa* was 0.31 and 0.06, respectively. The scenarios were 1: As now, 2: more grazing, from 0 to 0.5, 3: reduced N deposition, from 15.5 kg N ha^{-1} year^{-1} to 8 kg N ha^{-1} year^{-1} (note that it will require intensive mangement actions to reduce plant available N in the soil to the level expected at equlibrium under the reduced N deposition scenario), 3: Higher C/N ratio in soil, from 26 to 40, 4: more grazing 0 to 0.5 (average of a binary variable where 0 is no grazing) 5: more precipitation, from 987 mm year^{-1} to 1100 mm year^{-1}. The other environmental variables were pH in soil: 3.27, soil texture (jb nr.): 1 (coarse sandy soil).




Relative cover of A. flexuosa
0.050
0.045
0.040
0.035
0.030
0.025
0.020
As now
Reduced N dep
Higher C/N
More grazing
More precipitation

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Electronic supplements

The following electronic supplements may be downloaded from https://osf.io/4ezan/

Table S1 – Cover and change in cover of single species at Danish dry heathlands

Table S2 - Marginal distribution of parameters

Table S3 – Proportion of variance explained

Fig. S1 – Pairwise scatter plot of variables

Fig. S2 - Dunn–Smyth residuals

Appendix A - Distribution of pin-point plant cover data

Appendix B - Spatio-temporal modelling

Appendix C - Estimating species cover and change in species cover

Appendix D – Mathematica notebook (a free reader may be downloaded from https://www.wolfram.com/player/)