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

Christian Damgaard, ORCID 0000-0003-3932-4312

Department of Ecoscience, Aarhus University, C.F. Møllers Allé 4, 8000 Aarhus C, Denmark

Corresponding author: Christian Damgaard, cfd@ecos.au.dk, +45-30183153

Abstract

Pin-point cover data from 81 Danish dune heathland sites collected over 16 years were analyzed to quantify the effects of key environmental drivers on vegetation dynamics. A spatio-temporal structural equation model within a Bayesian hierarchical framework was used to assess the influence of nitrogen deposition, soil pH, soil C–N ratio, soil type, precipitation, and grazing. The species composition at Danish dune heathlands is changing, and most regression parameters for environmental drivers were significantly different from zero, indicating strong regulatory effects on both large-scale spatial variation and temporal dynamics. Precipitation and soil pH emerged as the most influential factors, underscoring the role of hydrological and edaphic conditions in shaping the vegetation at dune heathlands. The model predicts plant community dynamics and can be applied to forecast the effect of different management scenarios, providing a basis for adaptive site-specific management planning.

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

Introduction

To effectively manage semi-natural dune heathland ecosystems under changing climate conditions and evolving land-use practices, it is essential to understand and predict how environmental drivers influence vegetation. Developing a robust quantitative understanding of these drivers will allow us to make site-specific predictions of future ecosystem responses to changes such as climate shifts and grazing regimes. This knowledge will also provide critical input for adaptive management plans at the local level (Damgaard 2022a; 2025c). To clarify the causal relationships driving the observed large-scale variation and temporal dynamics in dune heathlands, and to quantify the influence of environmental drivers, we developed and fitted a structural equation model of the dune heathland ecosystem using spatial and temporal ecological data from 81 Danish dune heaths collected between 2007 and 2022.

The conservation status and resilience of dune heathlands are increasingly compromised by interacting pressures, including nitrogen deposition, successional encroachment of e.g. *Pinus mugo*, and altered land-use practices. Indicators such as mor-layer C/N ratios approaching 25, reduced lichen to moss ratios, and dominance of invasive species signal declining ecological integrity and heightened vulnerability to eutrophication. Maintaining resilience requires management that restores disturbance-driven mosaics, limits nutrient enrichment, and curbs woody and invasive species (Nielsen 2005). Overall, the conservation status of Danish dune heaths is assessed as moderately unfavorable (Fredshavn et al. 2025)

The dynamics of semi-natural heathland ecosystems, particularly those dominated by *Calluna vulgaris*, were first investigated by Watt (1947), who provided a comprehensive analysis of the ecological processes underlying spatial vegetation patterns. Subsequent research has expanded upon this foundation (e.g. Gimingham 1978; Gimingham 1988; Gimingham et al. 1981; Løvschal and Damgaard 2022; Usher and Thompson 1993), offering detailed descriptions of heathland vegetation structure across multiple spatial scales and elucidating the role of management interventions in regulating these patterns.

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, dune heathland vegetation is likely influenced by additional environmental drivers that could not be incorporated into this study due to data limitations, such as species-specific herbivory, pest dynamics, and historical natural management interventions. 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 dune 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; 2025b), dry heathlands (Damgaard 2025a), as well as, acid (Damgaard 2022c), and calcareous grassland (Damgaard 2023).

Materials and Methods

Dune heathlands

Dune heathlands represent a dynamic coastal ecosystem characterized by nutrient-poor, acidic sandy soils and a mosaic of successional stages ranging from grey dunes to decalcified fixed dunes and wet dune slacks. The vegetation is typically composed of dwarf shrubs such as *Calluna vulgaris* and *Empetrum nigrum*, interspersed with graminoids (*Deschampsia flexuosa*, *Carex arenaria*) and cryptogams, particularly lichens of the genus *Cladonia* (Nielsen 2005).

Calluna vulgaris (L.) Hull (heather) is a 10 to 50 cm tall dwarf shrub that is dominant on dune 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).

Sampling design

Hierarchical time-series data from 81 dune 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-four of the 81 sites are NATURA 2000 habitat sites and are protected under the Habitat Directive (EU 1992). All sites included several plots classified as dune heathland (EU habitat type: 2140) according to the habitat classification system used for the European Habitat Directive EU (EU 2013). The area of the sites ranged from 0.36 ha to 2697 ha, with a median area of 15.5 ha. A total of 612 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 1530 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 5.83 kg N ha^{-1} year to 18.69 kg N ha^{-1} $year^{-1}$, with a mean deposition of 10.89 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, 595 independent soil pH values were used in the analysis. The measured soil pH ranged from 2.9 to 6.7, with a mean soil pH of 3.77.

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 mean site C-N ratio was 22.9. Moreover, the average soil C–N ratio on 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 1.49.

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 587 mm to 903 mm, with a mean precipitation of 798 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 0.11. 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 dune heathlands.

Geographic regions

The 81 dune heathland sites were grouped into four 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 dune heathlands(Damgaard 2025d), and the causes for the moderately unfavorable conservation status of Danish dune heaths (Fredshavn et al. 2025; 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 2025e). 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 dune 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 estimated cover and change in cover of the most common species in Danish dune heathland plots are shown in Table 1. The most abundant species were *E. nigrum* and *C. vulgaris*, followed by *A. flexuosa* and *Carex arenaria*. Significant declines were observed for *E. nigrum*, *Erica tetralix*, *Salix repens*, and *Carex nigra*, with the latter showing the strongest negative trend on the logit scale. In contrast, *Cladonia sp.* exhibited significant positive trends, while *C. vulgaris* and graminoids remained relatively stable.

The selected environmental variables covaried at the 81 dune heathland 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 46% and 56% of the variation is explained, Table S2), and the model fitted the temporal process of the change in cover very well (Fig. 3B; > 97% of the variation is explained, Table S2). 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 0.188 with a relatively narrow credible interval (Table S1). Generally, the estimates of structural uncertainties were relatively low, although the large-scale spatial variation was relatively high (Table S1, Fig. 3A).

Most 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 S1), 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 dune heathlands. All explanatory variables had significant effects on the large-scale spatial variation of five or all six species classes (Fig. 4A, Table S1) and, there was significant geographic variation among the four assigned Danish regions, where the large-scale cover of other herbs and cryptogams showed a qualitatively different geographic distribution than the other species (Fig. 4A, Table S1), 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 nitrogen deposition on other graminoids (Fig. 4B, Table S1). Notably, relatively high nitrogen deposition was associated with an observed decrease in the cover of *C. vulgaris* and *A. flexuosa*, and an increase in the cover of *E. nigrum*. Relatively high soil pH was associated with an observed increase in *A. flexuosa* and a decrease in cryptogams. Relatively high C/N ratio in the soil was associated with an observed increase in the cover of *C. vulgaris, E. nigrum*, and *A. flexuosa*, and a decrease in the cover of

cryptogams. Grazing was associated with an increase in the cover of *C. vulgaris*. Sandy soil was associated with an observed increase in the cover of *C. vulgaris* and cryptogams. Finally, relatively high precipitation was associated with an increase in the cover of *E. nigrum* and a decrease in the cover of cryptogams (Fig. 4B).

In this study of dune heathlands, relatively high nitrogen deposition was associated with low soil pH (γ_N, Table S1), and soil pH was found to be significantly lower on more clayey soils compared to sandy soils (γ_S, Table S1).

Discussion

Plant community dynamics and environmental drivers

The species composition of Danish dune heathlands has changed since 2004. Several dwarf shrubs and wetland-associated species, such as *Carex nigra* and *Salix repens*, showed a decline in cover, while *Cladonia* species increased in cover. *C. vulgaris* and graminoids remained relatively stable throughout the monitoring period.

Most 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 dune heathlands.

Overall, precipitation and soil pH emerged as the most important drivers of dune heathland vegetation composition, highlighting the importance of hydrological and edaphic conditions in shaping species distributions. Precipitation showed the strongest overall effect, positively associated with *E. nigrum* while

reducing cryptogams. Soil pH was another key driver, promoting *A. flexuosa* but negatively affecting other herbaceous species, indicating a shift toward acid-tolerant graminoids under lower pH conditions.

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 dune heathland vegetation (Olmeda et al. 2020). The study demonstrated significant 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.

The C/N ratio exhibited moderate positive effects on *C. vulgaris*, *E. nigrum*, and graminoids, whereas cryptogams responded slightly negatively. Grazing intensity produced mixed responses: graminoids and other herbs showed slight positive associations, while cryptogams and *C. vulgaris* declined. Soil type effects were generally small, where clayey soils tended to favor graminoids and herbs. Nitrogen deposition had only minor positive coefficients across most groups, suggesting limited direct influence compared to other environmental gradients.

Spatial variation

The fine-scale spatial aggregation of the three focal species, along with the three aggregated classes of other plant species, was modeled using the parameter δ within the Dirichlet-multinomial mixture distribution framework (see Appendix A). The estimated degree of spatial aggregation at this scale significantly increased the uncertainty in the expected cover measurements compared to a scenario where

plant species are randomly distributed. If this overdispersion in the pin-point cover data is not accounted for in the statistical model, the signal-to-noise ratio will be substantially inflated, which is likely to result in misleading conclusions (Damgaard 2013).

All species classes exhibited significant regional variation across the four designated geographic regions (Fig. 1). This finding suggests that part of the large-scale spatial residual variation, which is not explained by the modeled environmental drivers, may be attributed to yet unidentified factors that differ among these regions. Future research should aim to uncover the historical causes underlying this spatial variation in species abundance, for instance, by compiling and analyzing detailed records of site-specific nature management practices and hydrological conditions.

Uncertainties and application of the model

In general, structural equation modeling (SEM) does not provide definitive proof of hypothesized causal relationships. However, it does allow for testing whether specific causal pathways are supported by the data. Demonstrating true causality requires system manipulation to observe whether the responses predicted by the SEM actually occur (Granger 1969; Pearl 2009). Additionally, there is often an unknown time lag between changes in environmental variables and their effects on vegetation cover (e.g. Svenning and Sandel 2013), making it uncertain which temporal window of environmental change should be used in the model. Nevertheless, due to the typically high degree of temporal spatial autocorrelation, where sites with relatively high values of an environmental variable at one time tend to maintain those values over subsequent periods, the model can still reliably estimate the relative effects of environmental variables across sites and years.

The statistical modeling uncertainty was decomposed into measurement uncertainty and uncertainties associated with the modeled spatial and temporal processes. The primary source of measurement uncertainty stemmed from plant cover estimates, largely due to pronounced small-scale spatial aggregation

of plant species (see above). However, uncertainties in nitrogen deposition, soil pH, soil C–N ratio, and soil type were also quantified and incorporated into the model. Overall, the structural uncertainty linked to temporal processes was relatively minor, whereas the large-scale spatial processes introduced a greater degree of structural uncertainty.

One key advantage of partitioning different sources of uncertainty within the structural equation model (SEM) is its utility for predictive purposes (Damgaard 2022b; Damgaard 2025c). Given the excellent fit of the temporal model, it is suggested that the included environmental variables are sufficient for predicting the average dynamics of plant communities in dune heathlands. This optimistic conclusion is somewhat unexpected, considering the absence of several potentially influential regulatory factors such as historical nature management interventions. In the absence of a well-established causal framework, caution is warranted when applying the fitted model to generate site-specific ecological predictions for adaptive management planning. The environmental variables used in this study may be correlated with unknown causal drivers, rare but impactful contingent events, or relevant factors for which data are unavailable. Nevertheless, the modeling results offer valuable insights for site managers regarding the relative importance of various environmental drivers and management scenarios (Fig. 5). For instance, because the direct and indirect effects of nitrogen deposition are not readily observable, their impact is difficult to assess without a statistical model and is often underestimated by site managers.

Tables

Table 1: Maximum likelihood estimates of mean site cover for the most common species in Danish dune heathland sites. The cover is summarized by the maximum likelihood estimates of mean site cover (μ) and the beta distribution shape parameter (v) (Appendix C). The estimated trends in cover in the period 2004 - 2021 were calculated using a Bayesian framework using three linear models (Appendix C). The 2.5%, 50%, and 97.5% percentiles of the marginal posterior probability distribution of average yearly change (on a logit scale) in the model that was best supported by the data are reported (significant changes are shown in bold).

	Cover		Trends in cover			
Species	μ	v	2.50%	50%	97.50%	Model
Empetrum nigrum	0.297	1.17	**-0.064**	**-0.043**	**-0.023**	3
Calluna vulgaris	0.278	1.22	-0.043	-0.012	0.015	3
Avenella flexuosa	0.168	1.29	-0.009	0.011	0.03	3
Carex arenaria	0.148	2.59	-0.03	-0.013	0.003	3
Vaccinium uliginosum	0.063	1.17	-0.035	-0.009	0.018	3
Cladonia sp.	0.056	2.01	**0.003**	**0.037**	**0.065**	2
Molinia caerulea	0.054	0.58	-0.06	-0.025	0.011	3
Ammophila arenaria	0.047	1.62	-0.009	0.009	0.028	1
Erica tetralix	0.045	1.93	**-0.072**	**-0.045**	**-0.018**	3
Myrica gale	0.03	0.71	-0.12	-0.032	0.038	3
Salix repens	0.026	2.29	**-0.139**	**-0.081**	**-0.033**	3
Carex nigra	0.022	2.31	**-0.252**	**-0.155**	**-0.081**	3

Figures

Fig. 1. Map of the selected 81 Danish dune heathland sites. The different colors represent a classification of the different sites into four geographical regions.

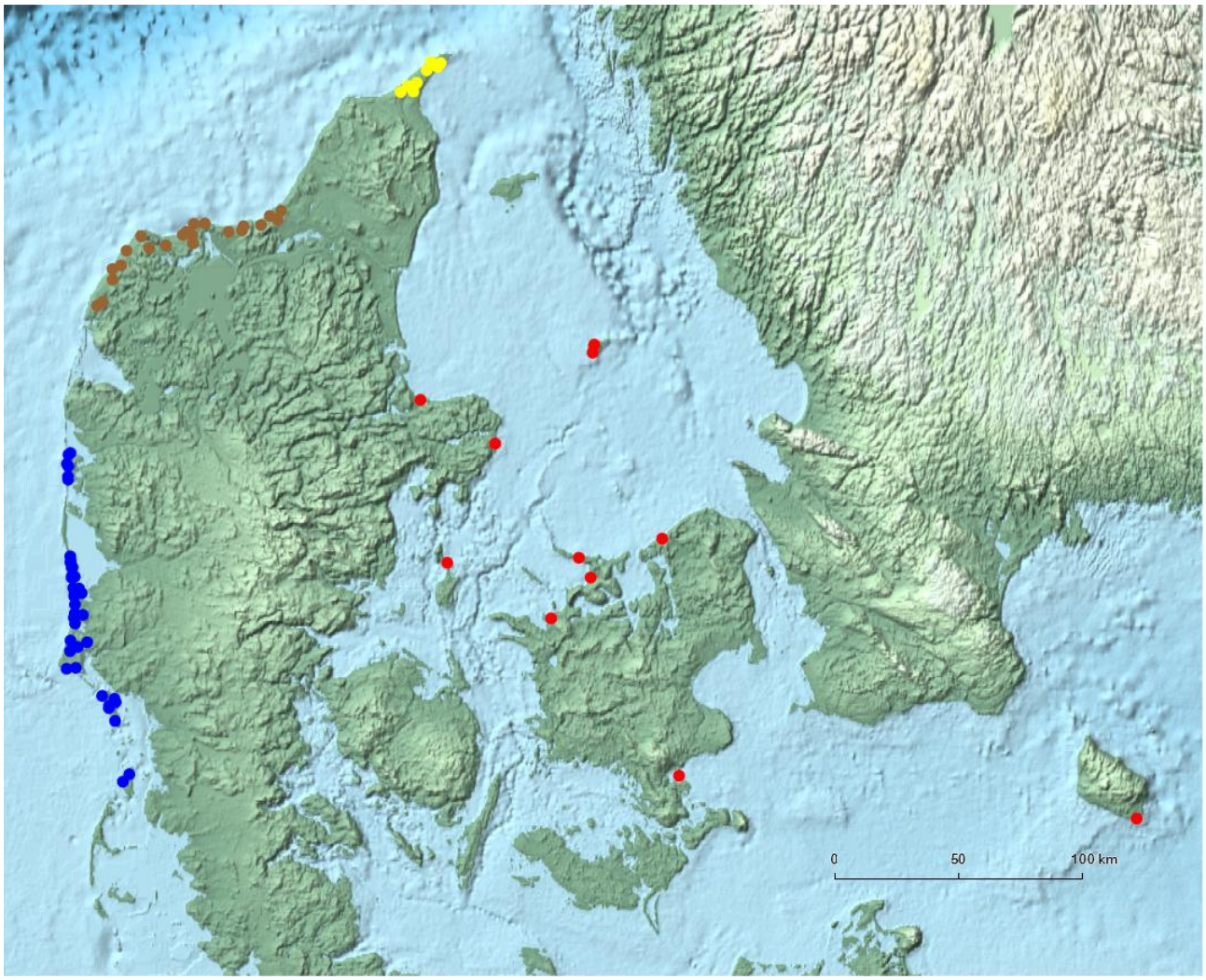


Fig. 2. Outline of hierarchical SEM. The spatial variation in vegetation cover in 2007 is modelled by nitrogen deposition (Ndep), soil pH (pH), soil C-N ratio (C/N), soil type and precipitation (Precipit.). The yearly change in vegetation cover from 2007 to 2022 (only a single yearly change is shown 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).

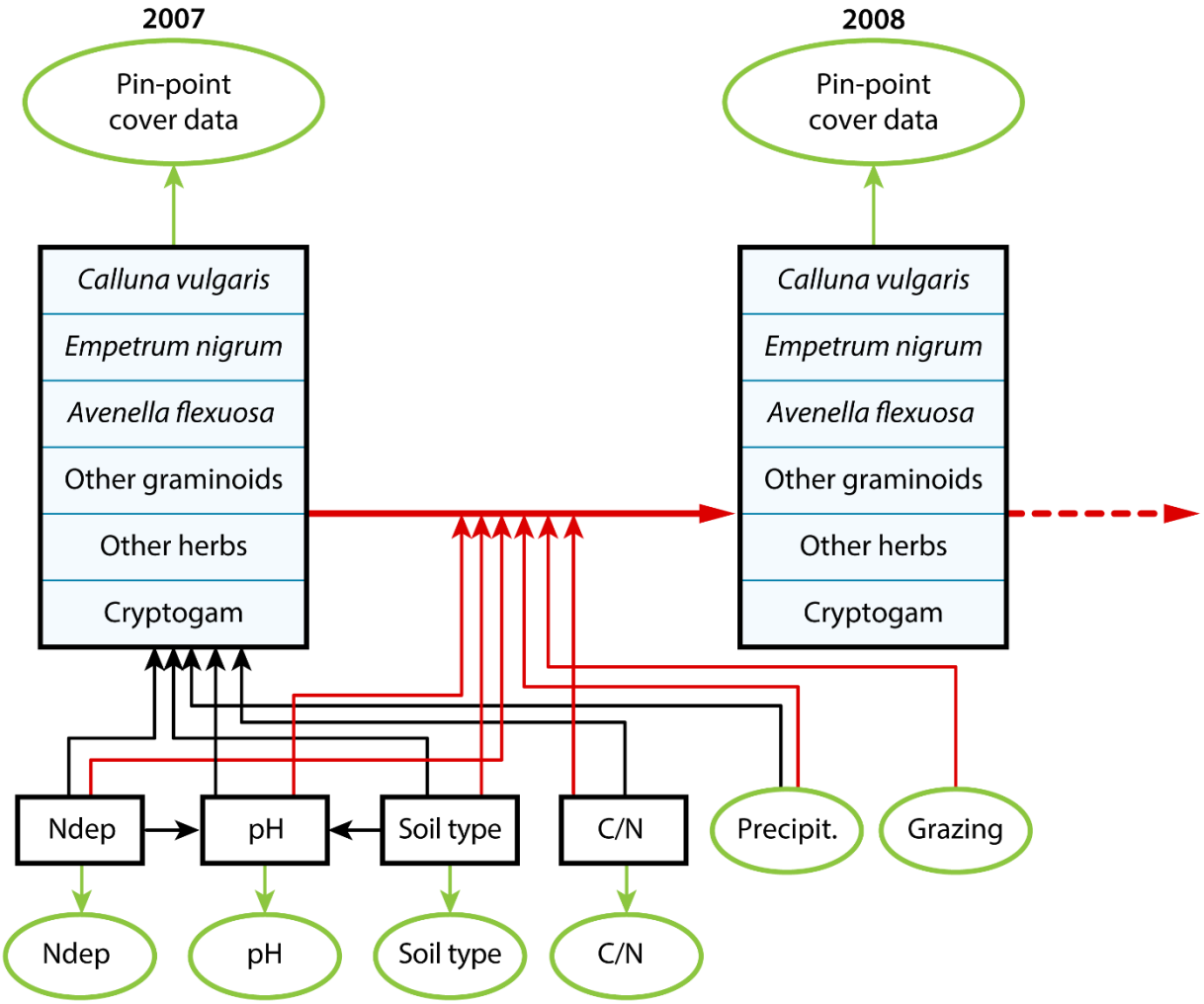
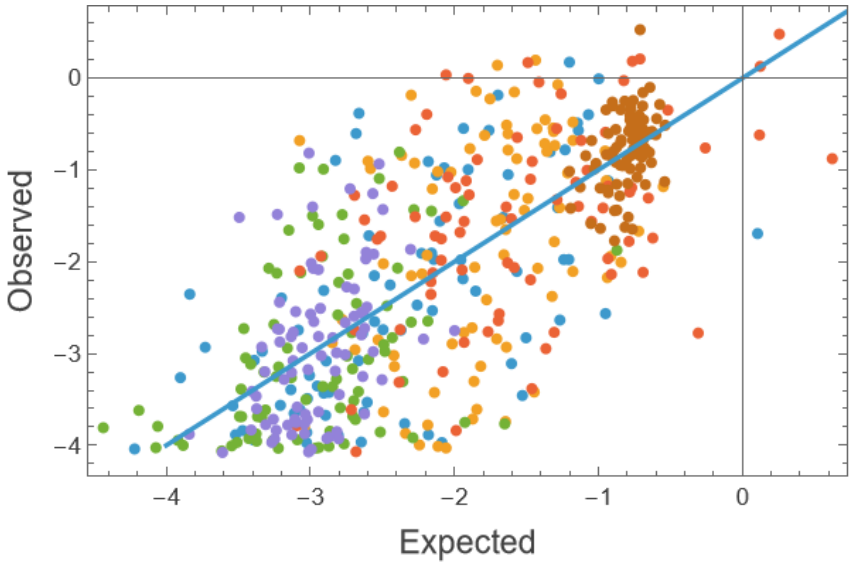
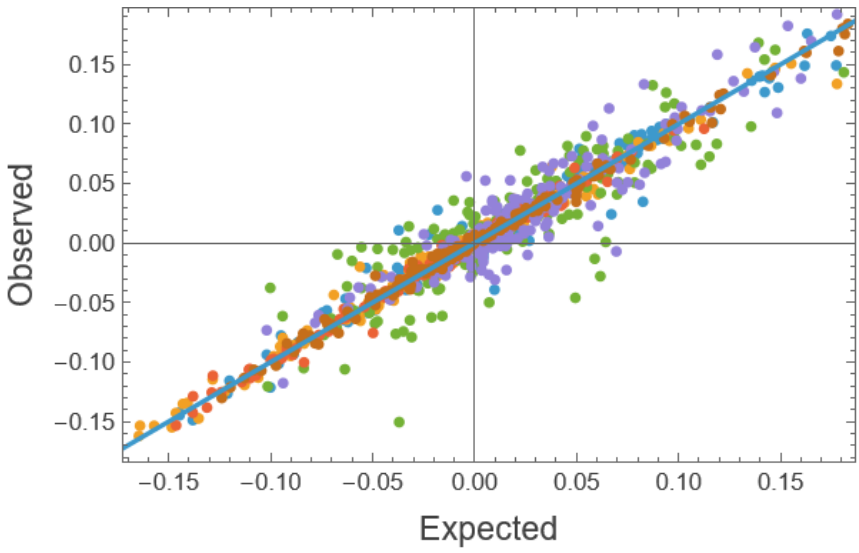


Fig 3. Plots of observed vs. expected logit-transformed cover of the large-scale spatial process (A) and the temporal (B). The proportions of the variance explained for each species may be found in Table S3. Blue: *Calluna vulgaris*, yellow: *Empetrum nigra*, green: *Avenella flexuosa*, red: other graminoids,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

A: large-scale spatial process



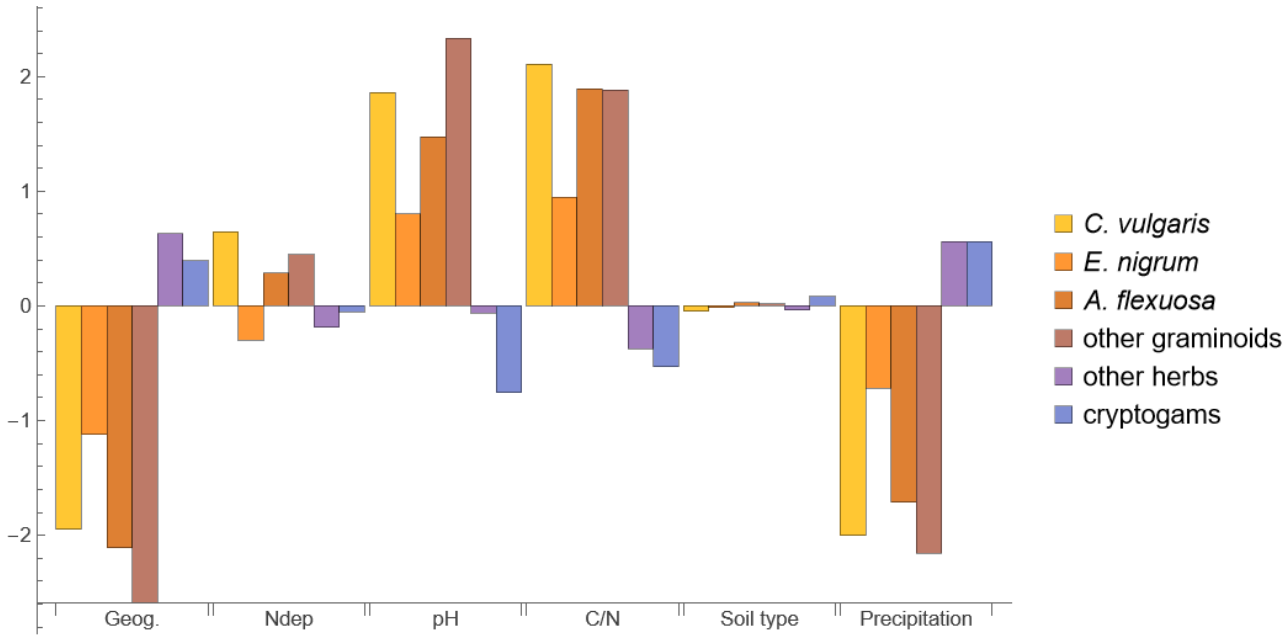
B: temporal process



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

340 temporal (B).

341 A: large-scale spatial process



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343 B: temporal process

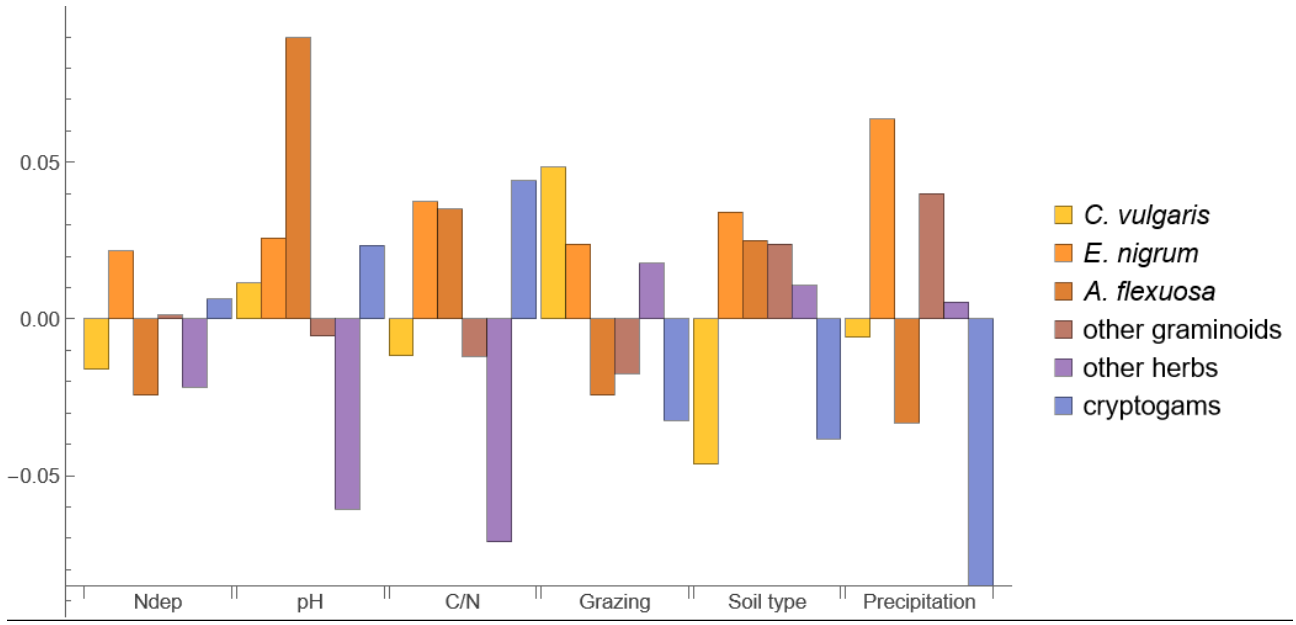

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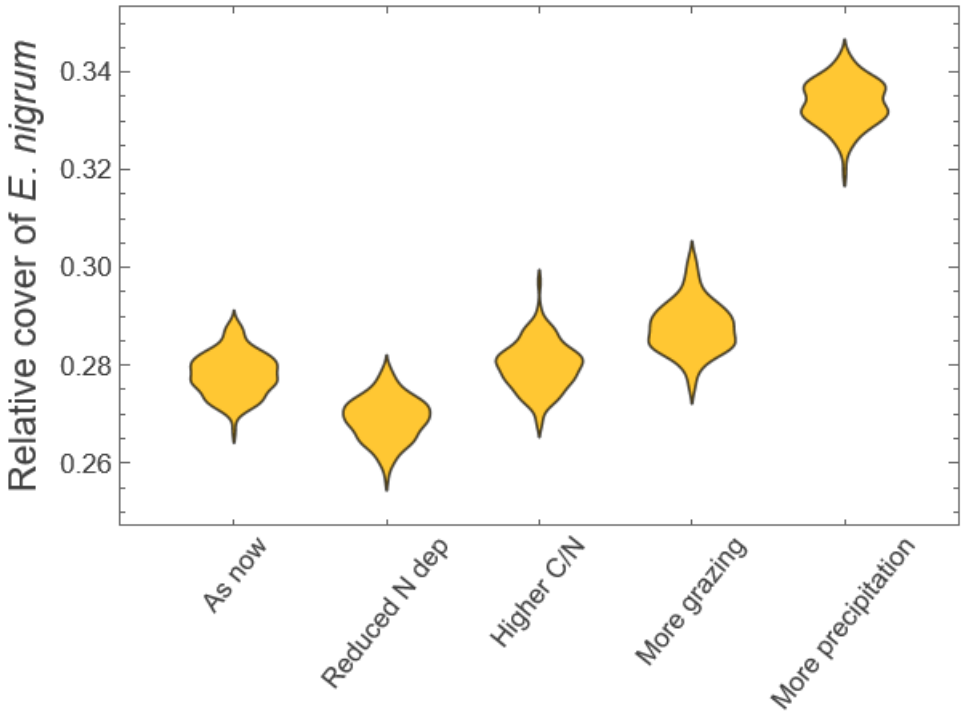
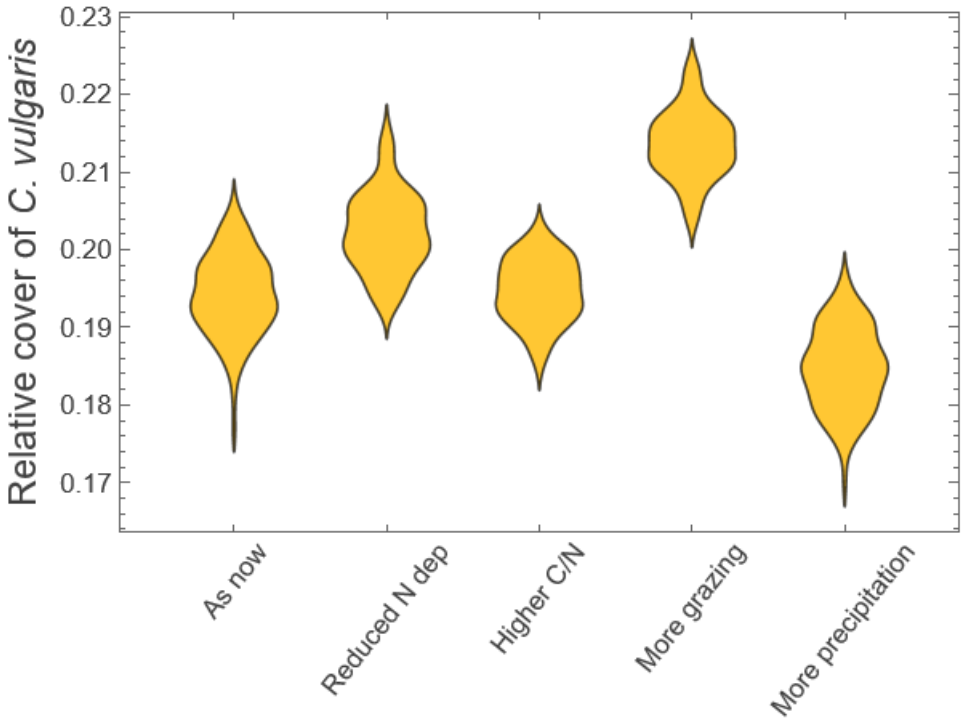
Fig. 5. Predicted distribution of the cover of *E. nigrum* and *C. vulgaris* for a specific dune heathland site (Husby klit in West Jutland) after five years under four different scenarios (Damgaard 2022a; 2025c). The initial cover of *E. nigrum* and *C. vulgaris* was 0.30 and 0.18, respectively. The scenarios were 1: As now, 2: reduced N deposition, from 12.2 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 19.7 to 40, 4: more grazing 0 to 0.5 (average of a binary variable where 0 is no grazing) 5: more precipitation, from 827 mm $year^{-1}$ to 1100 mm $year^{-1}$. The other environmental variables were pH in soil: 3.66, soil texture (jb nr.): 1 (coarse sandy soil).




Relative cover of C. vulgaris
0.23
0.22
0.21
0.20
0.19
0.18
0.17
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/ckhqy/overview

Table S1 - Marginal distribution of parameters

Table S2 – 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/)