Both competition and frequency-dependence determine community dynamics in a dune heath ecosystem

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Abstract

To investigate community dynamics in a dune heath ecosystem, plant growth was measured in a five-block manipulated experiment with four nitrogen levels using the pin-point method. It was demonstrated that both Lotka-Volterra type interspecific competition and frequency-dependency play significant roles in determining plant growth. For modelling simplicity, plant taxa were divided into heather, wavy hair-grass, and all other vascular species. Significant interspecific competition was observed among all species, except wavy hair-grass on the growth of all other vascular species, and nitrogen addition was found to increase the competitive effect of heather on the growth of all other vascular species. Both heather and wavy hair-grass showed positive feedback dynamics on growth when they were relatively dominant at the plot scale and the effect increased with added nitrogen. Such positive feedback dynamics may lead to the formation of patches, which are a characteristic feature of heath ecosystems. Oppositely, there was a beneficial effect of being relatively rare on the growth of all other vascular species in plots with added nitrogen. The study highlights the importance of the combined effects of interspecific competition and frequency-dependency in regulating plant communities and, consequently, undermines both theoretical and empirical conclusions of modern coexistence theory.

keywords: plant-plant interactions, plant-soil feedback (PSF), frequency-dependence, unmeasured variables, measurement uncertainty, hierarchical modelling, structural equation modelling

Introduction

The governing hypothesis for understanding plant community dynamics is interspecific competition mediated by competition for resources, e.g. light, water and soil nutrients that are necessary for plant growth (Goldberg et al. 1990). This competition hypothesis is investigated empirically by modelling the observed net negative plant-plant interactions ("competition in the broad sense" sensu Weiner 1993) by Lotka-Volterra-type competition models (e.g Adler et al. 2018; Damgaard 1998; 2005; Law and Dieckmann 2000), although the use of net effects in the modelling of species interaction has been criticized and it has been argued that a more detailed description of species interaction with time may lead to qualitatively different conclusions on community dynamics (Gómez et al. 2023; Levine et al. 2024; Mougi 2024). Moreover, the specific mechanisms that influence plant growth and their importance may vary with the season and size of the competing plants (Gurevitch et al. 2006).

Theoretically, species coexistence has mainly been examined in Lotka-Volterra type models by investigating the conditions for invasion when the species is rare (Adler et al. 2018; Barabás et al. 2018; Chesson 1994; 2000), and this body of theory is sometimes referred to as "modern coexistence theory". However, other mechanisms of plant-plant interactions, soil-plant interactions and the behavior of herbivores and pathogens may also play important roles for species-specific plant growth and the assembly of plant communities, and the relative importance of the different mechanisms in regulating plant community dynamics in different ecosystems is still an open research question (e.g. De Long et al. 2023).

Lately, there has been increasing awareness that frequency-dependent species interactions may play an important role in the dynamics in plant communities (Chisholm and Fung 2020; Connell et al. 1984; Suding et al. 2024). Such frequency-dependency may be caused by species-specific soil-plant interactions by hindering local establishment and growth of conspecific dominant plant species (Heinen et al. 2020; Mazzoleni et al. 2015a; Mazzoleni et al. 2015b; van der Putten et al. 2013) or, oppositely, dominant plant species may be favored by positive feedback mechanisms, e.g. by resource monopolizing strategies (van der Putten et al. 2013).

One of the important abiotic factors that regulate plant community dynamics is the level of plant available nitrogen (Craine 2009), and nitrogen deposition, which is caused by the combustion of fossil fuels and animal husbandry, is known to play an essential role in heathland ecosystems (Alonso et al. 2001; Bähring et al. 2017; Damgaard 2019a; 2019b; Jones and Power 2012; Southon et al. 2013). If nitrogen input is sufficiently high, especially after the vegetation is opened by burning or beetle infestation, grass species may outcompete ericoid dwarf shrubs, e.g. heather (*Calluna vulgaris*), and the dwarf shrub vegetation may be replaced by acid grassland vegetation and, in the absence of management, the encroachment of trees (Alonso et al. 2001; Heil and Bobbink 1993; van Voorn et al. 2016). More specifically, wavy hair-grass (*Avenella flexuosa*) is expected to outcompete heather with increasing nitrogen availability, and this effect is partly due to a nitrogen monopolizing strategy of heather in nitrogen-limited environments, where slowly decaying heather litter is decomposed by ericoid mycorrhiza and absorbed by the roots of the heather plants (Diemont and Heil 1984; Johansson 2001; Smith and Read 2008; Talbot et

al. 2008). The positive feedback between heather and ericoid mycorrhiza may, again, lead to positive frequency-dependency in nitrogen limited environments, where the competitive growth of heather is accelerated when heather is dominant (Aerts et al. 1990). Species that alter the ecosystem in such a manner that the resource availability of other species is modified have been categorized as ecosystem engineers (Briones 2024).

In a previous study, Damgaard and Weiner (2021) suggested modelling the effect of neighbors on plant growth by the combined effect of Lotka-Volterra-type competition and frequency-dependency. This model was fitted to empirical growth data using a hierarchical Bayesian framework, where the possible role of *unmeasured variables* that influence individual plant performance and *measurement errors* are accounted for (Fig. 1). Generally, if an unmeasured variable either has an overall positive (e.g. more nutrients or beneficial mycorrhiza) or negative effect (e.g. more pathogens) on plant performance at both the early and later stages of plant development, then the estimated competitive effect from neighboring plants will be biased (Rinella et al. 2020). Furthermore, it has been demonstrated that sampling and measurement errors may lead to important model and prediction bias, a phenomenon known as "regression dilution" (Carroll et al. 2006; Damgaard 2020; Damgaard and Weiner 2021; Detto et al. 2019).

In this study, we test the hypothesis that *both* Lotka-Volterra-type competition and frequency-dependency play important roles in determining plant community dynamics in a dune heath ecosystem. More specifically, we will model the growth of heather and wavy hair-grass in a dune heath ecosystem along a manipulated nitrogen gradient. Growth

models, where both the effect of competition and frequency-dependency are parameterized, will be fitted to pin-point data sampled in both early and late summer during a three-year period. The competitive growth of heather, wavy hair-grass and all other higher plants grouped together are then modeled as a function of the cover in early summer (Damgaard and Weiner 2021).

Material and Methods

Competitive growth data

At a dune heath site, Vust hede (Fig. 1), with relatively low background nitrogen deposition (9 kg N ha^{-1} $year^{-1}$) five experimental blocks were established in 2018 (Kaae et al. 2024). In each block, there were four treatment plots with added nitrogen (0, 5, 10, 25 kg N ha^{-1} $year^{-1}$). At the sites there were natural populations of roe deer, red deer and fallow deer in an estimated combined density of 9.95 ha^{-1} day^{-1} (Appendix A). In the summer of 2020, approximately 70-80% of the heather plants were infested by the heather beetle *Lochmeae suturalis,* leading to discoloring of leaves and a possible reduction in growth.

To study the species interactions on plant growth, a 0.5 m x 0.5 m quadrat was permanently outlined within each plot. In the quadrat, plant abundance was measured non-destructively by the “pin-point” (also called “point intercept”) method (Kent and Coker 1992) using a pin-point frame with the same dimension as the quadrat and with 25 pin-positions regularly placed at distances of 10 cm. At each position, a pin with a diameter of 0.5 mm was passed vertically through the vegetation, and the number of contacts to each species was recorded.

The sampling was performed in early (June) and late summer (August to October).

The pin-point method provides estimates of two important plant ecological variables, plant cover and vertical density, which are well suited for studying species interactions in natural and semi-natural herbaceous perennial plant communities, where it is difficult to distinguish individual genets (Damgaard 2011; Damgaard et al. 2009). The cover of a specific plant species is defined as the proportion of pins in the grid that touch the species, thus, plant cover measures the cover of the plant species when it is projected onto the two-dimensional ground surface. The vertical density is defined as the number of times a pin touches a specific species, and this measure is correlated with plant biomass (Jonasson 1983; 1988; Kaae et al. 2024).

In the subsequent analysis, the observed plant taxa were grouped into heather, wavy hair-grass and an aggregated group of all other vascular plant species.

The pinpoint data may be found in an electronic supplement (Appendix B).50

Model

The effect of species interactions on plant growth was analyzed in a hierarchical model (Fig. 2c) by modelling how the vertical density of heather, wavy hair-grass and the other species at the end of the growing season depended on the cover at the beginning of the growing season. The underlying assumption is that the measure of vertical density at the end of the growing season as a function of the cover at the beginning of the growing season may be used as a measure of population growth (Damgaard 2011; Damgaard et al. 2009).

The used growth model is a modified version of the model used in Damgaard and Weiner (2021),

$$f_i(\boldsymbol{x}) = (a_i + an_i\, n)\, x_i^{b_i} Exp\left(\sum_{j=1, j\neq i}^{S} -(c_{ij} + cn_{ij} n)\, x_j^{d_j}\right) Exp\left(-(e_i + en_i\, n) \frac{x_i}{\sum_{j=1}^{S} x_j}\right) \quad (1),$$

where $f_i(\boldsymbol{x})$ is the expected vertical density of species *i* at the end of the growing season, and x_i is the cover of species *i* at the beginning of the growing season. The parameters a_i, an_i and b_i model the expected vertical density as a function of cover and nitrogen (*n*) in the absence of inter-specific interactions, c_{ij} , cn_{ij} and d_j model the inter-specific interactions of species *j* on the vertical density of species *i*. If $\left(c_{ij} + cn_{ij}\, n\right) > 0$, then there is evidence of competitive inter-specific interactions, otherwise there is evidence of facilitative inter-specific interactions. The parameters e_i and en_i model the frequency-dependent effect of species *i*. If $(e_i + en_i\, n) = 0$, then there is no evidence of frequency-dependence, and the population growth model (1) simplifies to a Lotka-Volterra competition model. If $(e_i + en_i\, n) > 0$, then rare species have an advantage over dominant species and, conversely, if $(e_i + en_i\, n) < 0$, then dominant species have an advantage over rare species. The parameters b_i and d_j model possible non-linearity in the effect of cover on vertical density with a domain in the interval (0.5, 2).

The measurement errors of cover and vertical density have previously been assumed to be binomially distributed and generalized-Poisson distributed, respectively (Damgaard et al. 2014). However, since we want to model the covariance between the early and later growth

stages to account for the possible effect of unmeasured variables (Rinella et al. 2020), both distributions are approximated by standard normal distributions, where (i) the observed pin-point cover measure, y, in a pin-point frame with n pin-positions and an expected cover q is transformed to $z_1(y;q) = \frac{y-n\,q}{\sqrt{n\,q(1-q)}}$, and (ii) the observed pin-point vertical density measure, vd, with an expected value λ and with a species-specific scale parameter υ_i is transformed to $z_2(vd;\lambda,\nu_i) = \frac{vd-\lambda}{\sqrt{\lambda}\,\nu_i}$. The measurement error of the standardized cover and vertical density measures is consequently modelled as

$$(z_1(y;q), z_2(vd;\lambda,\nu_i)) \sim N_2\left((0,0), \begin{pmatrix} 1 & \rho_i \\ \rho_i & 1 \end{pmatrix}\right) \quad (2),$$

where ρ_i is a species-specific correlation coefficient in the domain (-1, 1) (Damgaard and Weiner 2021). If $\rho_i = 0$, then the measurement errors of the standardized cover and vertical density measures are assumed to be uncorrelated, i.e. the covariance between the early and later growth stages is assumed to be accounted for by the competition model and not by additional unmeasured variables.

The structural uncertainty of the competitive growth model was assumed to be normally distributed and modelled as $vd_i \sim N(f_i(\boldsymbol{x}), \sigma_i)$, where σ_i is the species-specific process error.

Estimation

We have chosen to treat the three years of competitive growth data from each of the plots as independent events because i) the within-plots among-year covariation is expected to be minimal, since we model the plant growth of each year, and ii) considering plot as a random effect is not compatible with modelling covariance between early and late plant growth.

The joint Bayesian posterior probability distribution of the parameters in the model was calculated using Markov Chain Monte Carlo (Metropolis-Hastings) simulations of 900,000 iterations with a burn-in period of 800,000 iterations and normal candidate distributions (Carlin and Louis 1996). The prior probability distributions of all parameters and latent variables were assumed to be uniformly distributed in their specified domains under the additional constraints that $0 < a_i < 500, -5 < c_{ij} < 5, -5 < e_i < 5, 0.5 < \nu_i < 8$, and $-0.5 < \rho_i < 0.8$, except for σ_i, which was assumed to be inverse gamma distributed with parameters (0.1, 0.1).

Plots of the deviance and trace plots of parameters were inspected to check the fitting and mixing properties of the used sampling procedure. Residual plots of the vertical density for each species were inspected to check the fitting properties of the different models. The statistical inferences were assessed using the calculated credible intervals, i.e. the 95% percentiles of the marginal posterior distribution of the parameters, and the probabilities that the marginal posterior distribution of the parameters were either above or below zero.

All calculations were done using Mathematica (Wolfram 2019). The software code and all results are given as an electronic supplement (Appendix B).

Results

The MCMC iterations of the population growth model converged with acceptable mixing properties, although there was sizeable covariation among parameters (Appendix C). Based

on the residual plots (Fig. S1), the fit of the model was judged to be acceptable. A summary of the marginal posterior probability distributions of all parameters is shown in Table 1.

The vertical density in the absence of interspecific species interaction was modelled by the parameters a_i, an_i and b_i. It was generally expected that the vertical density would be an increasing function of added nitrogen, but this was only demonstrated in the case of all other vascular species (Table 1, an_3).

The competitive effect of wavy hair-grass and all other vascular species on within-season growth of heather was relatively large without added nitrogen (Table 1, c_{12}, c_{13}), but there was no significant effect of the nitrogen treatment (Table 1, cn_{12}, cn_{13}). Likewise, the competitive effect of all other vascular species on wavy hair-grass was relatively large without added nitrogen (Table 1, c_{23}), and there was no significant effect of the nitrogen treatment (Table 1, cn_{23}). We did not demonstrate significant competitive effects of wavy hair-grass on the growth of all other vascular species (Table 1, c_{32}, cn_{32}). Interestingly, the competitive effect of heather on all other vascular species was already significantly positive without added nitrogen (Table 1, c_{31}) and increased significantly with the level of added nitrogen (Table 1, cn_{31}).

There were significant frequency-dependent effects. For heather and wavy hair-grass, there were significant positive effects of being relatively dominant at the plot scale (Table 1, e_1, e_2), and this effect increased significantly with added nitrogen (Table 1, en_1, en_2). On the other hand, all other vascular species were significantly positively affected when relatively

rare in the plots (Table 1, e_3, en_3).

For heather and wavy hair-grass, there was no significant effect of unmeasured environmental variables (Table 1, ρ_1, ρ_2) , i.e. the covariance between the early and later growth stages is assumed to be accounted for by the competition model (eq. 1) and not by additional unmeasured variables. However, for all other vascular species there was an indication that unmeasured environmental variables had a significant positive effect on the observed covariance between the early and later growth stages that was not accounted for by the species interaction model (Table 1, ρ_3).

Discussion

As previously demonstrated (Damgaard and Weiner 2021), there is compelling evidence that the standard use of the Lotka-Volterra model in studies of species interactions in plant communities is inadequate, and it is unfortunate that most empirical species interaction studies are modelled without considering frequency-dependency. Moreover, it has been argued that i) a more detailed description of species interaction with time may lead to qualitatively different conclusions on community dynamics (Gómez et al. 2023; Levine et al. 2024; Mougi 2024), ii) higher order interactions among species are important (Singh and Baruah 2020), and (iii) intraspecific genetic variation may play a role in the outcome of species interactions (Ehlers et al. 2016). Finally, it has been demonstrated that if the effects of measurement errors are ignored, model predictions may be biased (Carroll et al. 2006; Damgaard 2020; Damgaard and Weiner 2021; Detto et al. 2019). It is therefore also generally advisable to consider the possible effect of measurement errors when modelling

258 plant species interactions.

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260 In the studied dune heath ecosystem, we have demonstrated that both Lotka-Volterra type
261 interspecific competition and frequency-dependency play significant roles in determining
262 plant growth. There was significant interspecific competition among all species classes,
263 except wavy hair-grass, on the growth of all other vascular species (competition was still
264 more likely than facilitation in this case). *A priori*, we expected that nitrogen addition would
265 alter the species interactions, but this was only demonstrated in the case of heather on the
266 growth of all other vascular species, where nitrogen addition was found to increase the
267 competitive effect of heather. It has been suggested that heather may keep a competitive
268 advantage with increased deposition of nitrogen because of the vertical structure of the
269 leaves, the mature dense vegetation and the fact that leaves remain on the plant during
270 winter (Aerts et al. 1990; Aerts and Heil 1993). It is possible that nitrogen addition must take
271 place over more years before the level of plant available nitrogen has reached a new and
272 higher steady-state level, and it will be interesting to follow the effect of nitrogen on plant
273 species interactions in the coming years.

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275 Both heather and wavy hair-grass showed positive feedback dynamics on growth when they
276 were relatively dominant at the plot scale, whereas the growth of all other vascular species
277 was favored when they were relatively rare. The positive feedback dynamics of heather and
278 wavy hair-grass could be explained by the resource monopolizing strategy of heather
279 mediated by ericoid mycorrhiza (notice that typically when wavy hair-grass is relatively
280 dominant, then heather is relatively rare) (Diemont and Heil 1984; Johansson 2001; Smith

and Read 2008; Talbot et al. 2008), although it is surprising that the estimated positive feedback was found to increase with added nitrogen for both species. Oppositely, there was a beneficial effect of being relatively rare on the growth of all other vascular species in plots with added nitrogen. This advantage of being rare could be due to the absence of negative interactions with soil pathogens (e.g. van der Putten et al. 2013), and this hypothesis is corroborated by the finding that there was a positive covariation between early and late season (Rinella et al. 2020).

It is interesting that we in the same case study demonstrate positive effects of both being relatively rare and being relatively dominant for different species groups. Such frequency-dependent effects will clearly undermine both theoretical and empirical conclusions of modern coexistence theory (Adler et al. 2018; Barabás et al. 2018; Chesson 1994; 2000), where coexistence is examined in Lotka-Volterra type models by investigating the conditions for invasion when the species is rare.

Implicitly, it may be assumed that biomass at the end of the growing season in a species-specific way translates to cover at the start of the next growing season, so that the observed plant growth patterns may be used to predict community dynamics (Damgaard 2011; Damgaard et al. 2009). The demonstrated positive effects of being relatively dominant of both heather and wavy hair-grass at the plot scale are corroborated by previous studies, where it was concluded that the more locally dominant of the two species will outcompete the other (Damgaard et al. 2009), and observed divergent long-term successional patterns on dry heath plots, where plots either became dominated by grass or dwarf shrubs (Ransijn

et al. 2015). The cyclical successional processes leading to the typically found patchy distribution of grass or dwarf shrubs on heathlands were already described by Watt (1947), where a key feature is the life cycle of heather plants that senescence when they are 30–40 years old (Gimingham 1988; Watt 1955).

Crowberry (*Empetrum nigrum*) are often dominant on dune heaths, although animal trampling and different management actions, such as mowing, will adversely affect the species (Tybirk et al. 2000). A high local frequency of crowberry might affect the reported interactions, since it may increase in vigor at relatively high nitrogen deposition and may outcompete heather (Tybirk et al. 2000), although a time-series study from the same site indicates that heather will outcompete crowberry with increasing nitrogen levels, especially when heather or wavy hair-grass is relatively dominant (Kaae et al. 2024).

The observed widespread infestation of the heather beetle in 2020 had adverse effects on heather cover and growth. Such infestation may play an important role in transforming a dwarf shrub-dominated heath to a grass-dominated heath. However, our results suggest that one single outbreak of a heather beetle does not have long-term effects on the growth and competitive ability of heather at this dune heath site (Kaae et al. 2024). Heather is apparently able to recover relatively fast after the infestation event, however, recurrent events could result in a transformation to a grass-dominated heath.

If the local spatial effects of plant-plant interactions are modelled implicitly, then two distinct short-dispersal specializations are predicted, where parents disperse their offspring

locally, either to exploit empty patches quickly or to fill patches to exclude competitors (Bolker and Pacala 1999). However, generally, the theoretical and empirical investigations of plant patch dynamics are understudied, and dynamics at the patch scale, e.g. involving plant soil interactions, may be more important in some ecosystems than predicted and acknowledged under modern coexistence theory.

The traditional vegetation sampling in relatively small plots is not suited for studying patch dynamics that typically take place at a larger scale, and the widespread use of plot-based sampling methods may, in part, explain why plant patch dynamics have received limited attention. However, new drone-based sampling methods of plant abundance that operate at a larger spatial scale (e.g. Damgaard 2021) may provide much needed information for the study of plant patch dynamics.

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Tables

Table 1. Percentiles in the marginal posterior probability distribution of the parameters. The indices indicate the species, 1: heather, 2: wavy hair-grass and 3: all other vascular plant species.

Parameter	2.5%	50%	97.5%	P(X > 0)
a_1	60.354	66.953	72.629	-
a_2	12.062	16.665	23.747	-
a_3	37.188	62.952	68.653	-
an_1	-1.248	-0.588	0.351	0.208
an_2	-0.641	-0.405	0.697	0.100
an_3	0.228	0.961	1.910	**0.993**
b_1	1.541	1.820	1.987	-
b_2	0.939	1.459	1.941	-
b_3	1.635	1.916	1.996	-
c_{12}	2.086	3.127	4.295	**>0.999**
c_{13}	0.817	1.385	1.817	**>0.999**
c_{21}	-1.036	0.114	1.691	0.541
c_{23}	0.596	1.490	2.892	**>0.999**
c_{31}	0.222	0.651	1.568	**>0.999**
c_{32}	-0.719	0.117	0.872	0.636
cn_{12}	-0.118	0.008	0.228	0.548
cn_{13}	-0.006	0.022	0.079	0.877

cn_{21}	-0.256	-0.058	0.086	0.344
cn_{23}	-0.074	0.065	0.136	0.709
cn_{31}	0.118	0.236	0.346	**>0.999**
cn_{32}	-0.067	0.005	0.178	0.532
d_1	0.826	1.511	1.962	-
d_2	1.157	1.656	1.986	-
d_3	1.552	1.823	1.988	-
e_1	-0.260	-0.202	-0.133	**<0.001**
e_2	-0.663	-0.467	0.013	**0.027**
e_3	0.859	1.282	1.466	**>0.999**
en_1	-0.124	-0.104	-0.095	**<0.001**
en_2	-0.315	-0.250	-0.176	**<0.001**
en_3	-0.054	-0.005	0.006	0.244
σ_1	0.060	0.092	0.138	-
σ_2	0.036	0.080	0.145	-
σ_3	0.042	0.333	1.059	-
ν_1	7.437	7.889	7.996	-
ν_2	7.679	7.944	7.998	-
ν_3	7.796	7.960	7.999	-
ρ_1	-0.313	-0.048	0.283	0.372
ρ_2	-0.406	-0.062	0.341	0.390
ρ_3	0.671	0.773	0.799	**>0.999**

Figures

Fig. 1. Map showing the location of Vust hede. The rectangles are the blocks (1-5) with experimental manipulations (Kaae et al. 2024).

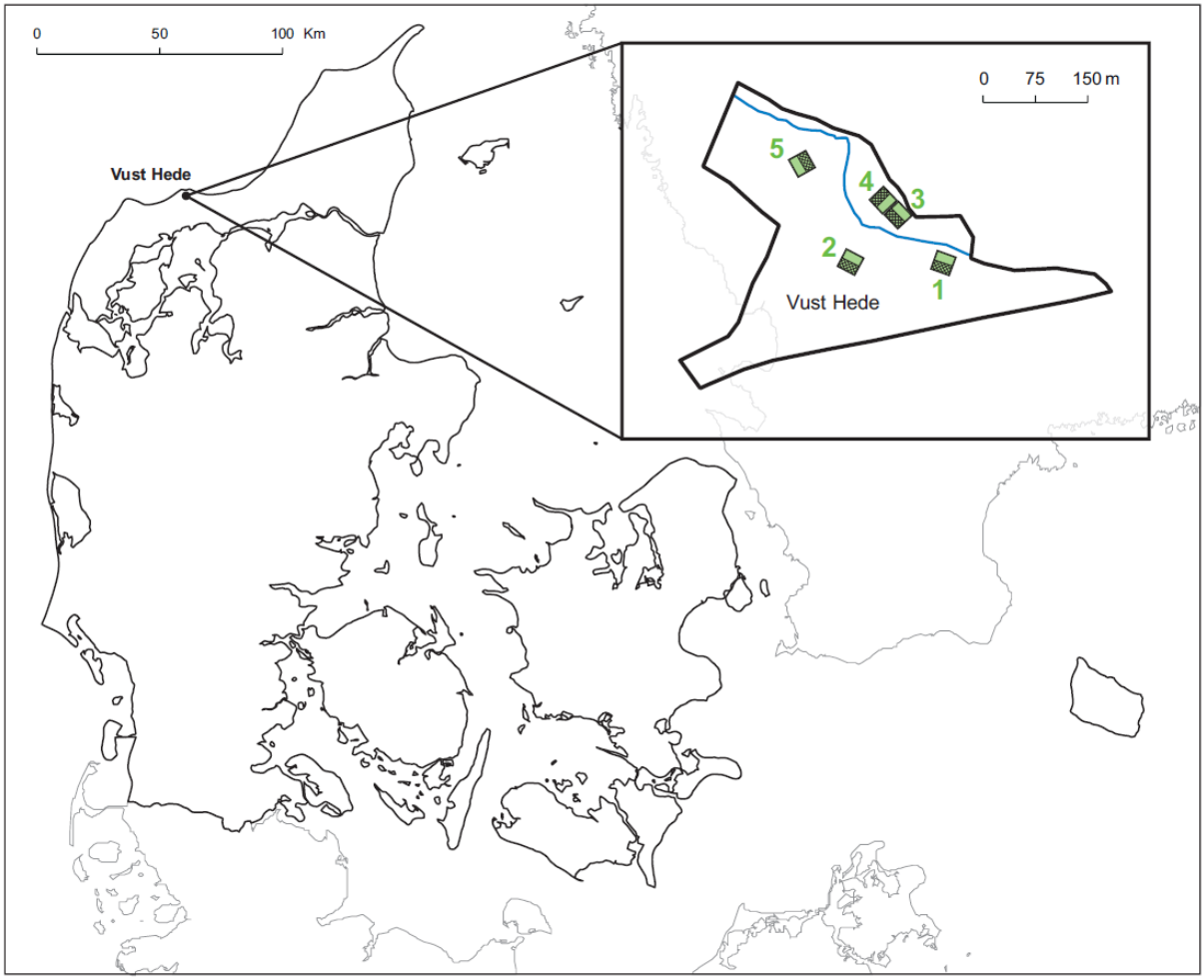
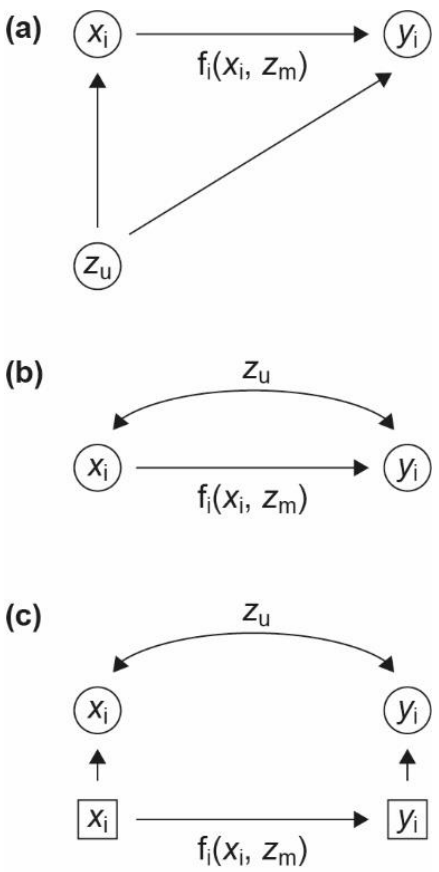


Fig. 2. (a) The effect of an unmeasured variable (z_u) on individual plant performance at both an early (x_i) and later growth stage (y_i) of plant species i. The competitive growth process is modelled by the function, f_i, which depends on x_i and possibly on some measured environmental variables (z_m). (b) The effect of the unmeasured variable affecting both earlier and later growth stages is modelled as the part of the covariance between the early and later growth stages that is not explained by the independent factors in the competition model. (c) Hierarchical model in which true but unknown factors affecting plant performance are modelled by latent variables (squares) and measurement errors are separated from process errors. Data are denoted by circles.



Electronic Supplements

The electronic supplements are located at https://osf.io/n6s9w/

Appendix A: Deer densities at Vust heath

Appendix B: Pin-point data (Excel file)

Appendix C: Software code (Mathematica notebook, get free viewer at https://www.wolfram.com/player/)

Fig. S1: Residual plots of vertical density

References

Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, Meiners JM, Tredennick AT, Veblen KE. 2018. Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. Ecol Lett. 21(9):1319-1329.

Aerts R, Berendse F, Caluwe Hd, Schmitz M. 1990. Competition in heathland along an experimental gradient of nutrient availability. Oikos. 57:310-318.

Aerts R, Heil GW. 1993. Heathlands. Patterns and processes in a changing environment.: Kluwer Academic Publishers.

Alonso I, Hartley SE, Thurlow M. 2001. Competition between heather and grasses on scottish moorlands: Interacting effects of nutrient enrichment and grazing regime. Journal of Vegetation Science. 12(2):249-260.

Barabás G, D'Andrea R, Stump SM. 2018. Chesson's coexistence theory. Ecological Monographs. 88(3):277-303.

Bolker BM, Pacala SW. 1999. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. American Naturalist. 153:575-602.

Briones MJI. 2024. Special feature on ecosystem engineers: Cross-scale and cross-system perspectives. Functional Ecology. 38(1):4-7.

Bähring A, Fichtner A, Ibe K, Schütze G, Temperton VM, von Oheimb G, Härdtle W. 2017. Ecosystem functions as indicators for heathland responses to nitrogen fertilisation. Ecological Indicators. 72:185-193.

Carlin BP, Louis TA. 1996. Bayes and empirical bayes methods for data analysis. London: Chapman & Hall.

Carroll RJ, Ruppert D, Stefanski LA, Crainiceanu C. 2006. Measurement error in nonlinear models: A modern perspective. Boca Raton: CRC.

Chesson P. 1994. Multispecies competition in variable environments. Theoretical Population Biology. 45(3):227-276.

Chesson P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics. 31:343-366.

Chisholm RA, Fung T. 2020. Janzen-connell effects are a weak impediment to competitive exclusion. Am Nat. 196(5):649-661.

Connell JH, Tracey JG, Webb LJ. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. Ecological Monographs. 54(2):141-164.

Craine JM. 2009. Resource strategies of wild plants. Princeton University Press.

Damgaard C. 1998. Plant competition experiments: Testing hypotheses and estimating the probability of coexistence. Ecology. 79:1760-1767.

Damgaard C. 2005. Evolutionary ecology of plant-plant interactions - an empirical modelling approach. Aarhus, Denmark: Aarhus University Press.

Damgaard C. 2011. Measuring competition in plant communities where it is difficult to distinguish individual plants. Computational Ecology and Software. 1:125-137.

Damgaard C. 2019a. Is the degree of spatial aggregation of calluna vulgaris regulated by nitrogen deposition or precipitation? Acta Oecologica. 97:1-5.

Damgaard C. 2019b. Spatio-temporal structural equation modeling in a hierarchical bayesian framework: What controls wet heathland vegetation? Ecosystems. 22:152-164.

Damgaard C. 2020. Measurement uncertainty in ecological and environmental models. Trends Ecol Evol. 35:871-873.

Damgaard C. 2021. Integrating hierarchical statistical models and machine-learning algorithms for ground-truthing drone images of the vegetation: Taxonomy, abundance and population ecological models. Remote Sensing. 13(6).

Damgaard C, Riis-Nielsen T, Schmidt IK. 2009. Estimating plant competition coefficients and predicting community dynamics from non-destructive pin-point data: A case study with *calluna vulgaris* and *deschampsia flexuosa*. Plant Ecol. 201:687–697.

Damgaard C, Strandberg B, Mathiassen SK, Kudsk P. 2014. The effect of glyphosate on the growth and competitive effect of perennial grass species in semi-natural grasslands. Journal of environmental science and health Part B, Pesticides, food contaminants, and agricultural wastes. 49(12):897-908.

Damgaard C, Weiner J. 2021. The need for alternative plant species interaction models. Journal of Plant Ecology.

De Long JR, Heinen R, Heinze J, Morriën E, Png GK, Sapsford SJ, Teste FP, Fry EL. 2023. Plant-soil feedback: Incorporating untested influential drivers and reconciling terminology. Plant and Soil. 485(1):7-43.

Detto M, Visser MD, Wright SJ, Pacala SW. 2019. Bias in the detection of negative density dependence in plant communities. Ecol Lett. 22(11):1923-1939.

Diemont WH, Heil GW. 1984. Some long-term observations on cyclical and serial processes in dutch heathlands. Biol Conserv. 30(3):283-290.

Ehlers BK, Damgaard CF, Laroche F. 2016. Intraspecific genetic variation and species coexistence in plant communities. Biology letters. 12(1):20150853.

Gimingham CH. 1988. A reappraisal of cyclical processes in calluna heath. Vegetatio. 77(1/3):61-64.

Goldberg DE, Grace J, Tilman D. 1990. Components of resource competition in plant communities. In: Grace J, Tilman D, editors. Perspective on plant competition. San Diego: Academic press. p. 27-49.

Gómez JM, Iriondo JM, Torres P. 2023. Modeling the continua in the outcomes of biotic interactions. Ecology. 104(4):e3995.

Gurevitch J, Scheiner SM, Fox GA. 2006. The ecology of plants. Sunderland, USA Sinauer.

Heil GW, Bobbink R. 1993. "Calluna", a simulation model for evaluation of impacts of atmospheric nitrogen deposition on dry heathlands. Ecological Modelling. 68:161-182.

Heinen R, Hannula SE, De Long JR, Huberty M, Jongen R, Kielak A, Steinauer K, Zhu F, Bezemer TM. 2020. Plant community composition steers grassland vegetation via soil legacy effects. Ecol Lett. 23(6):973-982.

Johansson M. 2001. Fungal associations of danish calluna vulgaris roots with special reference to ericoid mycorrhiza. Plant and Soil. 231(2):225-232.

Jonasson S. 1983. The point intercept method for non-destructive estimation of biomass. Phytocoenologia. 11:385-388.

Jonasson S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos. 52:101-106.

Jones AG, Power SA. 2012. Field-scale evaluation of effects of nitrogen deposition on the functioning of heathland ecosystems. J Ecol. 100(2):331-342.

Kent M, Coker P. 1992. Vegetation description and analysis. London: Belhaven Press.

Kaae ME, Hu F, Bak JL, Strandberg MT, Damgaard CF. 2024. How do nitrogen deposition, mowing, and deer grazing drive vegetation changes on dune heaths? Ecologies.5(1):116-131. doi:10.3390/ecologies5010008.

Law R, Dieckmann U. 2000. A dynamical system for neighborhoods in plant communities.

Ecology. 81:2137-2148.
Levine JI, Pacala SW, Levine JM. 2024. Competition for time: Evidence for an overlooked, diversity-maintaining competitive mechanism. Ecol Lett. 27(3):e14422.
Mazzoleni S, Bonanomi G, Incerti G, Chiusano ML, Termolino P, Mingo A, Senatore M, Giannino F, Cartenì F, Rietkerk M et al. 2015a. Inhibitory and toxic effects of extracellular self-DNA in litter: A mechanism for negative plant–soil feedbacks? New Phytologist. 205(3):1195-1210.
Mazzoleni S, Cartenì F, Bonanomi G, Senatore M, Termolino P, Giannino F, Incerti G, Rietkerk M, Lanzotti V, Chiusano ML. 2015b. Inhibitory effects of extracellular self-DNA: A general biological process? New Phytologist. 206(1):127-132.
Mougi A. 2024. Dual species interaction and ecological community stability. Ecology. 105(3):e4251.
Ransijn J, Kepfer-Rojas S, Verheyen K, Riis-Nielsen T, Schmidt IK. 2015. Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. Journal of Vegetation Science. 26(2):254-266.
Rinella MJ, Strong DJ, Vermeire LT. 2020. Omitted variable bias in studies of plant interactions. Ecology. 101(6):e03020.
Singh P, Baruah G. 2020. Higher order interactions and species coexistence. Theoretical Ecology. 14:71–83.
Smith SE, Read DJ. 2008. Mycorrhizal symbiosis. New York Academic Press.
Southon GE, Field C, Caporn SJM, Britton AJ, Power SA. 2013. Nitrogen deposition reduces plant diversity and alters ecosystem functioning: Field-scale evidence from a nationwide survey of uk heathlands. PLOS ONE. 8(4):e59031.
Suding KN, Collins CG, Hallett LM, Larios L, Brigham LM, Dudney J, Farrer EC, Larson JE, Shackelford N, Spasojevic MJ. 2024. Biodiversity in changing environments: An external-driver internal-topology framework to guide intervention. Ecology. 105(8):e4322.
Talbot JM, Allison SD, Treseder KK. 2008. Decomposers in disguise: Mycorrhizal fungi as regulators of soil c dynamics in ecosystems under global change. Functional Ecology. 22(6):955-963.
Tybirk K, Nilsson M-C, Michelsen A, Kristensen HL, Shevtsova A, Tune Strandberg M, Johansson M, Nielsen KE, Riis-Nielsen T, Strandberg B et al. 2000. Nordic empetrum dominated ecosystems: Function and susceptibility to environmental changes. AMBIO: A Journal of the Human Environment. 29(2):90-97, 98.
van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA et al. 2013. Plant–soil feedbacks: The past, the present and future challenges. J Ecol. 101(2):265-276.
van Voorn GAK, Kooi BW, Bregt AK. 2016. Over-shading is critical for inducing a regime shift from heathland to grassland under nitrogen enrichment. Ecol Complex. 27:74-83.
Watt AS. 1947. Pattern and process in the plant community. J Ecol. 35:1-22.
Watt AS. 1955. Bracken versus heather, a study in plant sociology. J Ecol. 43(2):490-506.
Weiner J. 1993. Competition among plants. Treballs de La Societat Catalana de Biologia. 44:99–109.
Wolfram S. 2019. Mathematica. 12.0.0.0 ed. Champaign, USA: Wolfram Research, Inc.