# The effect of nitrogen on the growth of *Calluna vulgaris* and *Avenella flexuosa* in a dune heath ecosystem: competition and frequency-dependence

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## Abstract

Nitrogen was manipulated in a dune heath ecosystem and using time-series pin-point data 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 undermine both theoretical and empirical conclusions of modern coexistence theory.

*keywords*: Plant competition, plant-plant interaction, interspecific interaction model, frequency-dependence, unmeasured variables, measurement uncertainty

## Introduction

Plants are sedentary and neighboring plants affect each other's growth. The most important effect of growing together is competition for resources, e.g. light, water and soil nutrients that are necessary for plant growth (Goldberg et al. 1990). However, other mechanisms of plant-plant interactions, soil-plant interactions, and the behavior of herbivores and pathogens also play important roles for species-specific plant growth and the assembly of plant communities (Damgaard and Weiner 2021). Furthermore, 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).

It is often not feasible to collect ecological and plant physiological data with sufficient detail to determine the importance of the different mechanisms, let alone model the underlying mechanisms that regulate plant growth. Consequently, the preferred way to empirically model the effects of neighboring plants on plant growth in a plant community is to model 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), where the negative effect of neighbors increases linearly with local density (Barabás et al. 2018; Chesson 1994; 2000). However, recently 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, there is an 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).

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 heathland vegetation may be replaced by acid grassland vegetation and in the absence of management the encroachment of tree (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 decomposing 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 are modified have been categorized as ecosystem engineers (Briones 2024).

In a previous study, Damgaard and Weiner (2021) suggested to model 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 address the possible roles of Lotka-Volterra-type competition and frequency-dependency on the growth of heather and wavy hair-grass in a dune heath ecosystem along a manipulated nitrogen gradient. More specifically, growth models will be fitted to pin-point data sampled at the same heathland plots 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).

**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 for competitive inter-specific interactions, otherwise there is evidence for 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 binomial 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 $\lambda$ and with a species-specific scale parameter $\upsilon_i$ 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 $\rho_i$ 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 $\sigma_i$ 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 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

188 additional constraints that $0 < a_i < 500, -5 < c_{ij} < 5, -5 < e_i < 5, 0.5 < \nu_i < 8$, and
189 $-0.5 < \rho_i < 0.8$, except for $\sigma_i$, which was assumed to be inverse gamma distributed with
190 parameters (0.1, 0.1).
191
192 Plots of the deviance and trace plots of parameters were inspected to check the fitting and
193 mixing properties of the used sampling procedure. Residual plots of the vertical density for
194 each species were inspected to check the fitting properties of the different models. The
195 statistical inferences were assessed using the calculated credible intervals, i.e. the 95%
196 percentiles of the marginal posterior distribution of the parameters, and the probabilities
197 that the marginal posterior distribution of the parameters were either above or below zero.
198
199 All calculations were done using Mathematica (Wolfram 2019). The software code and all
200 results are given as an electronic supplement (Appendix B).
201

202 **Results**

203 The MCMC iterations of the population growth model converged with acceptable mixing
204 properties although there was sizeable covariation among parameters (Appendix C). Based
205 on the residual plots (Fig. S1), the fit of the model was judged to be acceptable. A summary
206 of the marginal posterior probability distributions of all parameters are shown in Table 1.
207
208 The vertical density in the absence of interspecific species interaction was modelled by the
209 parameters $a_i$, $an_i$ and $b_i$. It was generally expected that the vertical density would be an
210 increasing function of added nitrogen, but this was only demonstrated in the case of all

211 other vascular species (Table 1, $an_3$).

212

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

223

224 There were significant frequency-dependent effects. For heather and wavy hair-grass there
225 were significant positive effects of being relatively dominant at the plot scale (Table 1,
226 $e_1, e_2$), and this effect increased significantly with added nitrogen (Table 1, $en_1, en_2$). On the
227 other hand, all other vascular species were significantly positively affected when relatively
228 rare in the plots (Table 1, $e_3, en_3$).

229

230 For heather and wavy hair-grass there were no significant effect of unmeasured
231 environmental variables (Table 1, $\rho_1, \rho_2$) , i.e. the covariance between the early and later
232 growth stages is assumed to be accounted for by the competition model (eq. 1) and not by
233 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, $\rho_3$).

## Discussion

As previously demonstrated (Damgaard and Weiner 2021), there is compelling evidence that the standard use of the Lotka-Volterra model in empirical 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), or (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) so it is therefore generally advisable to consider the possible effect of measurement errors when modelling plant species interactions.

In the studied dune heath ecosystem, we have demonstrated that both Lotka-Volterra type interspecific competition and frequency dependency play significant roles in determining plant growth. There was significant interspecific competition among all species classes, except wavy hair-grass on the growth of all other vascular species (competition was still

more likely than facilitation in this case). *A priori*, we expected that nitrogen addition would alter the species interactions, but this was only demonstrated in the case of heather on the growth of all other vascular species, where nitrogen addition was found to increase the competitive effect of heather. It has been suggested that heather may keep a competitive advantage with increased deposition of nitrogen because of the vertical structure of the leaves, the mature dense vegetation and the fact that leaves remain on the plant during winter (Aerts et al. 1990; Aerts and Heil 1993). Possibly nitrogen addition must take place over more years before the level of plant available nitrogen has reached a new and higher steady-state level, and it will be interesting to follow the effect of nitrogen on plant species interactions in the coming years.

Both heather and wavy hair-grass showed positive feedback dynamics on growth when they were relatively dominant at the plot scale, whereas the growth of all other vascular species was favored when they were relative rare. The positive feedback dynamics of heather and wavy hair-grass could be explained by the resource monopolizing strategy of heather mediated by ericoid mycorrhiza (notice that when wavy hair-grass is relatively 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 translate 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 is 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 bidirectional long-term successional patterns on dry heathland 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 N deposition and may outcompete heather (Tybirk et al. 2000), although a time-series study from the same site indicate 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 heathland 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 investigation of plant patch dynamics is 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.

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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 |
| $\sigma_1$ | 0.060 | 0.092 | 0.138 | - |
| $\sigma_2$ | 0.036 | 0.080 | 0.145 | - |
| $\sigma_3$ | 0.042 | 0.333 | 1.059 | - |
| $\nu_1$ | 7.437 | 7.889 | 7.996 | - |
| $\nu_2$ | 7.679 | 7.944 | 7.998 | - |
| $\nu_3$ | 7.796 | 7.960 | 7.999 | - |
| $\rho_1$ | -0.313 | -0.048 | 0.283 | 0.372 |
| $\rho_2$ | -0.406 | -0.062 | 0.341 | 0.390 |
| $\rho_3$ | 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).

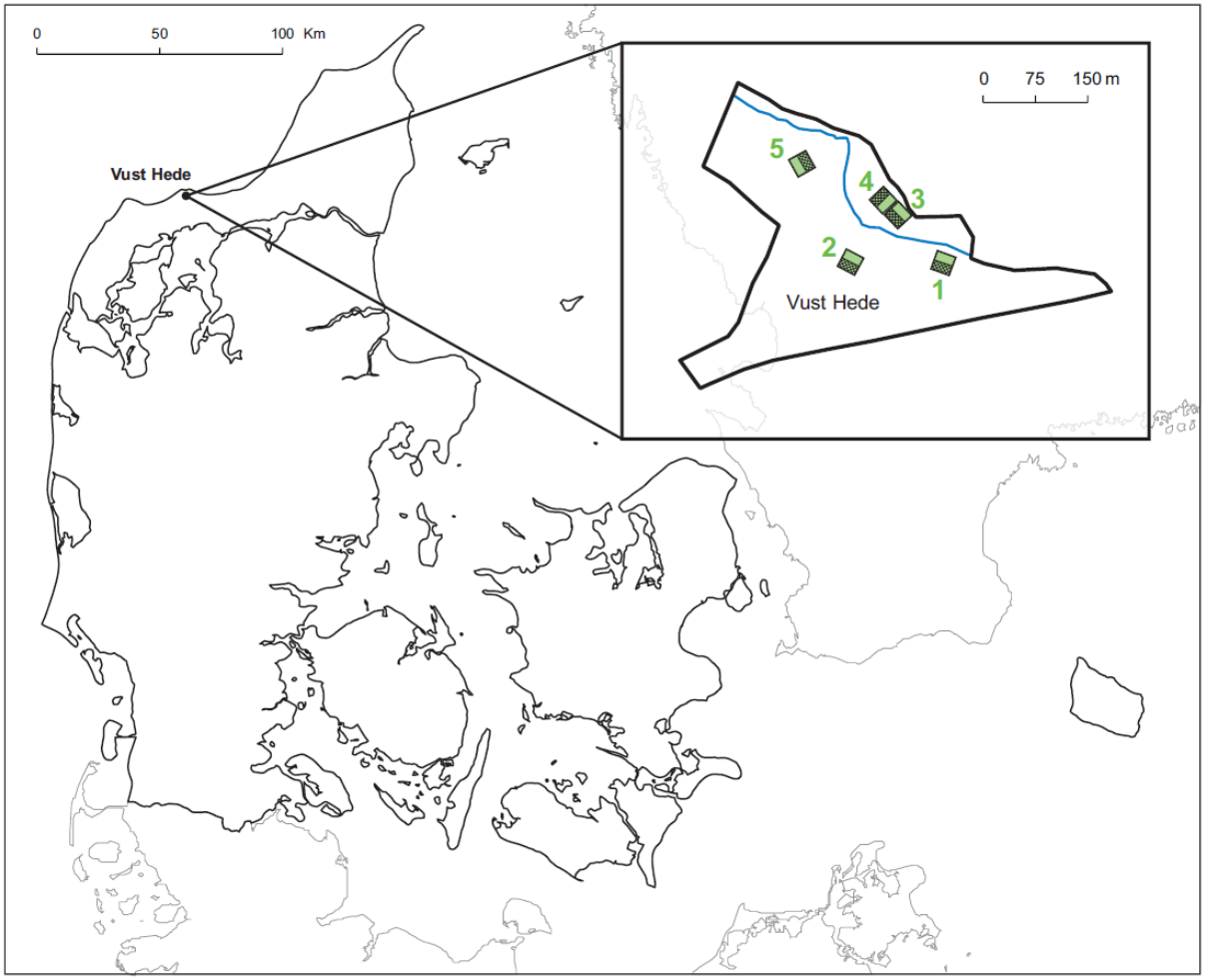
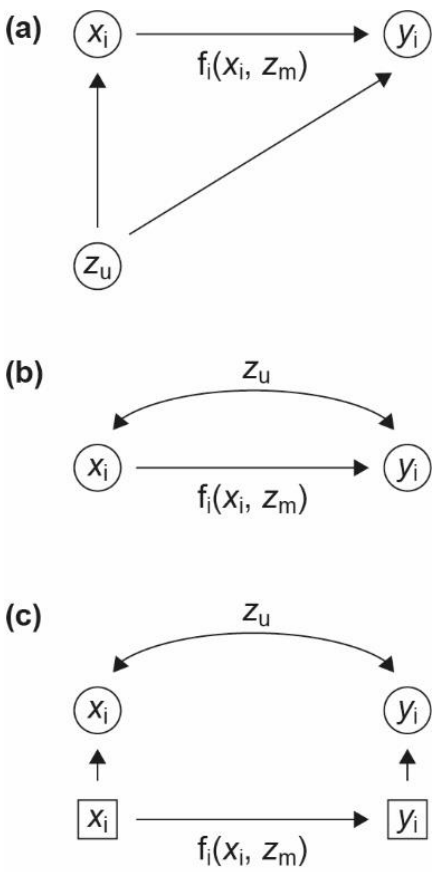


Fig. 2. (a) The effect of an unmeasured variable ($z_u$) on individual plant performance at both an early ($x_i$) and later growth stage ($y_i$) of plant species $i$. The competitive growth process is modelled by the function, $f_i$, which depends on $x_i$ and possibly on some measured environmental 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

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