Limited selection on leaf traits in Danish grasslands

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Abstract

Only limited trait selection was observed on leaf traits (SLA and LDMC) in a study of an extensive ten-year Danish grassland vegetation dataset. The negative result of this study may partly be due to the relatively conservative analysis, where the continuous plant trait variables are used for grouping plant species into functional types, which are then treated as dependent variables. This procedure is in contrast to most other analyses of trait selection, where it is the community weighted mean of the traits that are used as the dependent variable. However, it is not the traits, but rather individual plants that are sampled and, consequently, it is important to consider the sampling of species abundance in the statistical modelling of plant traits. This misapprehension has not received sufficient proper attention in the plant trait literature.

Keywords: Plant trait selection, leaf economics spectrum (SLA and LDMC), plant functional types, multi-species joint distribution, pin-point cover data, Dirichlet - multinomial distribution, hierarchical Bayesian models, STAN

Introduction

The observed covariation among plant traits and the environment has been the focus of plant ecology since its early days and has been demonstrated in numerus cases (e.g. Garnier *et al.*, 2016). Furthermore, trait selection, i. e. a change in the distribution of plant traits in a specific area, has been observed in manipulated experiments (e.g. Laliberté *et al.*, 2012, Pellissier *et al.*, 2014) and during successional processes (e.g. Garnier *et al.*, 2004, Garnier *et al.*, 2007, Douma *et al.*, 2012). Based on the above findings, it has been suggested to focus on the analysis of changes in mean plant traits rather than species abundance in order to understand community assembly rules and the causal mechanisms underlying species coexistence patterns (e.g. Stegen & Swenson, 2009, Shipley, 2010).

However, little work has been done to demonstrate trait selection in natural areas that are not subjected to large changes, such as successional processes. Conversely, in time-series analysis of plant species abundance in such natural areas it has frequently been demonstrated that species composition changes over time (e.g. Smart *et al.*, 2006, Timmermann *et al.*, 2015), but it has often been difficult to determine the causal mechanisms of the observed patterns of change in species abundance.

An often-studied suite of plant traits is the leaf economics spectrum, which is an important trade-off between plant resource acquisition and storage, where some plant species characterized by relatively thin leaves have a strategy of rapid carbon gain with rapid foliar turnover and fast growth. These thin-leaved species often have a competitive advantage in high-productive ecosystems with fertile soil. Whereas other plant species characterized by relatively thick leaves invest more resources into leaf construction and have a relatively slower foliar turnover and slow growth. These thick-leaved species often have a competitive advantage in low-productive ecosystems with infertile soil (e.g. Westoby *et al.*, 2002, Craine, 2009, Reich, 2014).

In the past sixty years, there has been a dramatic anthropogenic increase in atmospheric nitrogen deposition and significant effects on the plant vegetation has been demonstrated in some grassland habitats, although the deposition recently has levelled off and even shown a decreasing tendency (Stevens *et al.*, 2004, Damgaard *et al.*, 2011). According to leaf economics spectrum theory, the increase in plant available nitrogen is expected to lead to selection in favor of thin-leaved fast growing plant species, although it is generally unknown how fast plant populations respond to environmental changes (Svenning & Sandel, 2013).

Usually, trait selection is investigated using community weighted mean trait values (CWMs) as the dependent variable; where the CWMs are calculated from a fixed species-trait matrix and the measured

species abundances in a plot (e.g. Garnier *et al.*, 2016). However, as pointed out by Clark (2016), it is not the CWMs that are sampled, but rather species abundances, and the stochastic properties of CWMs do not arise from variation in traits, but depend on the used sampling protocol to estimate species abundance. The fact that it is not the traits, but the individual plants that are sampled is potentially critical for the statistical modelling of the covariance between traits and environment as well as trait selection (Clark, 2016), and this misapprehension has not received sufficient proper attention in the plant trait literature. One of the ways to solve the problem is to work with discrete plant functional types (PFTs) with known statistical sampling properties as the dependent variable rather than CWMs (Clark, 2016). However, depending on the studied problem, it may not always be possible to define suitable PFTs, and then you have to model the covariance between plant abundance and trait variation (Clark, 2016).

In this study, I will group grassland plant species according to leaf traits into PFTs and investigate whether the proportion among the abundance of the PFTs has changed over a ten-year period. The plant species will here be grouped with respect to two specific leaf traits, specific leaf area (SLA) and leaf dry matter content (LDMC), which are known to be important for determining the leaf economics spectrum and, consequently, the life history strategy of the plant species (e.g. Reich, 2014, Garnier *et al.*, 2016).

Materials and Methods

Sampling design and plant cover data

Hierarchical time-series plant cover data in the period from 2007 to 2016 from 236 Danish grassland sites were used in the analysis. All sites included several grassland plots with a total of 2946 plots that all were resampled three or more times with GPS-uncertainty (< 10 meters) over the sampling years. All plots at a site were either sampled or not sampled in a given year. Including resampling over the years, a total of 8859 vegetation plots were used in the analyses.

All plots were classified as belonging to one of four grassland habitat types: calcareous grasslands (or xeric sand calcareous grasslands, EU habitat type: 6120, 99 plots), dry grasslands (or semi-natural dry grasslands and scrubland facies on calcareous substrates, EU habitat type: 6210, 1155 plots), acid grasslands (or species-rich Nardus grasslands, EU habitat type: 6230, 1129 plots), and wet grasslands (or Molinia meadows on calcareous, peaty or clayey-siltladen soils, EU habitat type: 6410, 563 plots). The classification of the habitat type was performed according to the habitat classification system used for the European Habitat Directive (Nygaard *et al.*, 2009, EU, 2013).

The plant cover, i.e. the relative projected area covered by a species, of all higher plants was measured by the pin-point method (Lindquist, 1931, Levy & Madden, 1933, Damgaard, 2009) using a square frame (50

cm X 50 cm) of 16 grid points that were equally spaced by 10 cm (Nielsen *et al.*, 2012). One of the advantages of the pin-point method is that it is possible to aggregate taxa at the pin level. For example, if we want to aggregate the cover of two species, then we use the number of pins that hit either one or both of the species as an estimate of the aggregated cover of the two species.

The data are a subset of the ecological monitoring data collected in the Danish habitat surveillance program NOVANA (Nielsen *et al.*, 2012, Nygaard *et al.*, 2016).

Leaf traits and species groups

The values of the leaf traits SLA and LDMC were found in the LEDA trait database (Kleyer *et al.*, 2008), which is a homogenous trait database established from plant measurements in North Germany, which is geographically close to Denmark.

In order to group the higher plant species into PFTs, the trait values of the 542 grassland species where both leaf traits were available in the database were selected and analyzed in a principal component analysis (Fig. 1). The first principal component was used to group the species into four PFTs with similar mean abundance: 1: thin leaves ($PC_1 < 0$), 2: intermediary leaves ($0 \leq PC_1 < 1$), 3: thick leaves ($PC_1 \geq 1$), 4: the rest, i.e. species where no or only one of the two leaf traits were available in the trait database.

The classification of each species is shown in the Electronic Supplement, and the mean site cover of the four different species groups is shown in Fig. 2.

Statistical model

The pin-point cover data are modelled using a reparametrized Dirichlet-multinomial distribution (Damgaard, 2015, Damgaard, 2018), where the mean plant cover of a species group *i* is assumed to be a linear model of year (*y*), habitat type (*j*) and site (*k*).

$$\mu_{i,j,k,y} = invlogit\left(\alpha_i + \alpha site_{i,k} + \alpha habitat_{i,j} + \left(\beta_i + \beta site_{i,k} + \beta habitat_{i,j}\right) y\right) \quad (1),$$

where site and habitat are modelled as random effects. Each random effect, consisting of n groups $\{1, \ldots, m, \ldots, n\}$, is modelled as $z_m = \sigma\, \epsilon_m$, with a single standard deviation ($\sigma > 0$) and n group regressors, ϵ_m, that are assumed to have a strong prior distribution, $\epsilon_m \sim N(0,1)$. For example, $\beta habitat_{i,j} = \beta habitat_{\sigma,i}\, \beta habitat_{\epsilon,i,j}$, where the parameter $\beta habitat_{\sigma,i}$ is positive, and the n_j parameters $\beta habitat_{\epsilon,i,j}$ are assumed to be standard normally distributed. Other location parameters had a weak normally distributed prior distribution. Standard deviation parameters and the degree of spatial aggregation had a uniform prior distribution in the ranges 0.05 to 10, and 0.01 to 0.9, respectively.

In order to ensure that the sum of the mean cover parameters does not exceed one, when the parameters in the linear model (1) were initialized to zero in the beginning of the MCMC sampling procedure, $invlogit(x) = \frac{0.322}{0.33+\mathrm{Exp}[-x]} + 0.01$, was used instead of transforming the linear model with the standard inverse logit function (Damgaard, 2018).

The model was fitted in STAN (Carpenter *et al.*, 2017) using four chains of 100,000 iterations after a warmup of 300,000 iterations. The STAN model is included as an electronic supplement.

Statistical inferences were based on the marginal posterior distributions of parameters and compound parameters, i.e. their 2.5%, 50%, and 97.5% percentiles, and the proportion of distribution that is larger than zero, P(>0).

Results

The fitted model had relatively many parameters, but, never the less, the MCMC iterations demonstrated good mixing properties and the marginal posterior distribution of the parameters had regular shapes (results not shown). Therefore, it was concluded that the model fitted the data adequately. The estimates of selected parameters and compound parameters are summarized in Tables 1, 2 and 3.

There were no significant changes in the cover of any of the PFTs in any of the four grassland habitat types during the ten-year period (Table 2). The strongest statistical signal was a negative trend for thin-leaved plant species in dry grasslands (Table 2).

The estimated standard deviations of the yearly change among habitats were higher than the standard deviations among sites (Table 1), which indicates that the variation in the yearly change is higher among habitats than sites and, consequently, that there is a tendency towards the yearly change in the plant cover of PFTs differing among grassland habitat types.

The standard deviations of the posterior distributions of the slope parameters that measure the yearly change in the cover of the PFTs were approximately 0.06 on the logit scale (Table 1). This width of the posterior distribution indicates that the statistical power of the analysis is only moderate, and, in connection with the observed non-significant changes in cover, it is concluded that trait selection for the studied leaf traits in Danish grasslands is limited.

The spatial aggregation of the FPTs were relatively benign and did not differ significantly among the grassland habitat types (Table 3).

Discussion

Only limited trait selection was observed on leaf traits (SLA and LDMC) in this study of an extensive ten-year Danish grassland vegetation dataset, and the hypothesis that the increase in plant available nitrogen the past sixty years should have selected for thin-leaved fast growing plant species cannot be corroborated. The result of the present study is also in contrast to the results reported by Timmermann et al. (2015), who in a shorter time-series observed that the winning plant species, i.e. the species that had an increasing cover, had a relatively small SLA. Generally, more times-series studies of trait selection in natural areas that are not subjected to large changes, such as successional processes, are needed in order to validate the predictions made in space-for-time studies of plant traits (Damgaard, 2019).

The negative result of this study may partly be due to the relatively conservative analysis, where the continuous variables SLA and LDMC are used for grouping plant species into PFTs and the aggregated cover of the PTFs are then treated as the dependent variable instead of treating the CWMs of SLA and LDMC as the dependent variable. However, as mentioned in the introduction, it is not the traits, but the individual plants that are sampled, and it is important to consider the sampling of species abundance in the statistical modelling of plant traits (Clark, 2016).

An alternative method of analyzing plant trait selection is to correlate trait values with estimated demographic parameters or change in abundance for individual species (Timmermann *et al.*, 2015, Garnier *et al.*, 2018, Herben *et al.*, 2019). However, it may be a problem that typically only point estimates of the plant ecological success are used without considering the covariance between plant abundance and trait variation (Clark, 2016). Furthermore, since many plant traits are correlated (e.g. Reich, 2014) it is problematic to infer from observed correlations to causal mechanisms. Especially, since the studied plant traits often are the traits that are most readily available in trait databases.

In this study, plant abundance is measured by plant cover using the pin-point method, which readily allows the aggregation of single cover into the cover of PFTs at the pin level. As demonstrated elsewhere, it is important to take the spatial aggregation of plant species into account when modelling plant cover (Damgaard, 2012, Damgaard, 2013, Damgaard & Irvine, 2019), and these results have been generalized into a multi-species setting, where it is recommended to analyze multispecies or PFTs pin-point cover data in a reparametrized Dirichlet-multinomial distribution (Damgaard, 2015, Damgaard, 2018). A further advantage of modelling trait selection by the change in the abundance of PFTs rather than the change in the continuous CWMs is that the class of missing values, i.e. the plant species with no or incomplete information on the trait values, is clearly defined (in this study as the rest group). Additionally, more complicated selection models than directional selection may be readily tested, e.g. stabilizing selection (the

intermediary PFT is positively selected) and disruptive selection (the intermediary PFT is negatively selected).

The studied vegetation plots were not real permanent plots, but were only resampled with GPS-uncertainty. However, if we had access to permanent plot time-series cover data, it would have been interesting to explore more sophisticated selection models, e.g. if the observed trait selection could be partitioned into direct selection and selection that is mediated by interspecific interactions (Damgaard, 2016, Pedersen *et al.*, 2019).

Figures

Fig. 1. A: Leaf trait values of SLA and LDMC of the 542 grassland species where both leaf traits were available in the database. PFTs: .thin leaves (blue), intermediary leaves (yellow) and thick leaves (green). B: histogram of the first principal component (PC_1), which was used to group the plants into PFTs with similar overall mean abundance

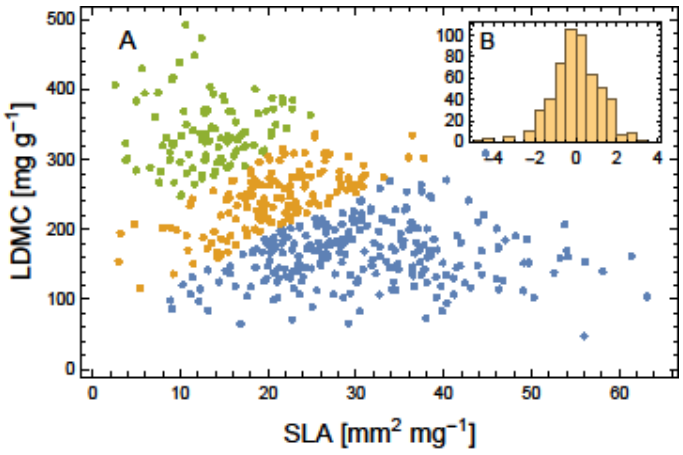
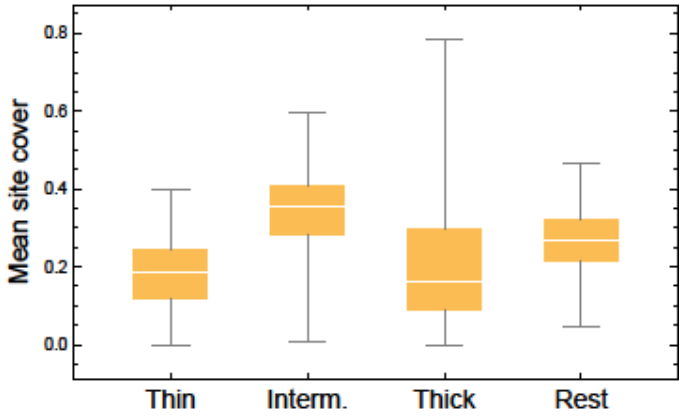


Fig. 2. The mean site cover of the four different species groups (PFTs).



Tables

Table 1. Summary of the posterior distribution of the general parameters in model (1) for the different plant functional types (PFTs).

Parameter	PFTs	Mean	SD	2.5%	50%	97.5%	P(>0)
α	Thin-leaved	-0.526	0.465	-1.415	-0.541	0.436	0.086
α	Intermediary	0.291	0.366	-0.466	0.286	1.083	0.852
α	Thick-leaved	-0.681	0.787	-2.246	-0.704	1.356	0.123
$\alpha site_{\sigma}$	Thin-leaved	0.674	0.043	0.594	0.673	0.765	-
$\alpha site_{\sigma}$	Intermediary	0.521	0.034	0.459	0.519	0.594	-
$\alpha site_{\sigma}$	Thick-leaved	1.120	0.066	0.996	1.118	1.259	-
$\alpha habitat_{\sigma}$	Thin-leaved	0.754	0.634	0.230	0.563	2.482	-
$\alpha habitat_{\sigma}$	Intermediary	0.629	0.490	0.203	0.477	2.006	-
$\alpha habitat_{\sigma}$	Thick-leaved	1.380	1.271	0.427	1.006	4.792	-
β	Thin-leaved	-0.050	0.068	-0.177	-0.050	0.067	0.130
β	Intermediary	0.002	0.056	-0.097	-0.001	0.118	0.488
β	Thick-leaved	-0.012	0.067	-0.132	-0.009	0.094	0.416
$\beta site_{\sigma}$	Thin-leaved	0.052	0.002	0.050*	0.052	0.059	-
$\beta site_{\sigma}$	Intermediary	0.052	0.002	0.050*	0.051	0.056	-
$\beta site_{\sigma}$	Thick-leaved	0.058	0.006	0.050*	0.056	0.072	-
$\beta habitat_{\sigma}$	Thin-leaved	0.101	0.092	0.051*	0.073	0.339	-
$\beta habitat_{\sigma}$	Intermediary	0.095	0.077	0.051*	0.072	0.279	-
$\beta habitat_{\sigma}$	Thick-leaved	0.099	0.086	0.051*	0.073	0.299	-

*The prior distribution of the parameter was in the range of 0.05 to 10.

Table 2. Summary of the posterior distribution of the change in cover $\left(\beta_i + \beta habitat_{\sigma,i}\ \beta habitat_{\epsilon,i,j}\right)$ for the different plant functional types (PFTs) in the different grassland habitat types

Habitat type	PFTs	Mean	SD	2.5%	50%	97.5%	P(>0)
calcareous grasslands	Thin-leaved	-0.046	0.065	-0.168	-0.046	0.081	0.175
calcareous grasslands	Intermediary	-0.012	0.079	-0.160	-0.011	0.132	0.422
calcareous grasslands	Thick-leaved	-0.012	0.081	-0.170	-0.012	0.146	0.409
dry grasslands	Thin-leaved	-0.060	0.058	-0.178	-0.059	0.051	0.090
dry grasslands	Intermediary	-0.002	0.075	-0.141	-0.002	0.135	0.486
dry grasslands	Thick-leaved	-0.022	0.078	-0.174	-0.021	0.128	0.324
acid grasslands	Thin-leaved	-0.055	0.058	-0.172	-0.055	0.057	0.103
acid grasslands	Intermediary	0.018	0.074	-0.122	0.017	0.157	0.654
acid grasslands	Thick-leaved	-0.012	0.078	-0.160	-0.012	0.139	0.395
wet grasslands	Thin-leaved	-0.033	0.060	-0.148	-0.034	0.085	0.202
wet grasslands	Intermediary	-0.009	0.075	-0.152	-0.007	0.126	0.441
wet grasslands	Thick-leaved	0.010	0.079	-0.140	0.007	0.167	0.566

Table 3. Summary of the posterior distribution of the degree of spatial aggregation in the different grassland habitat types.

Habitat type	Mean	SD	2.5%	50%	97.5%
calcareous grasslands	0.122	0.007	0.110	0.122	0.136
dry grasslands	0.103	0.002	0.099	0.103	0.107
acid grasslands	0.109	0.002	0.105	0.109	0.113
wet grasslands	0.124	0.003	0.117	0.123	0.130

Electronic Supplements

A: Species list (Excel csv file)

B: STAN model (text file)

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