Selection towards lighter seeds in Danish grasslands over an eight-year period

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Abstract

Time-series analysis of cover data from 236 Danish grassland sites demonstrated community selection on seed mass. Across four grassland habitat types and during an eight-year period there was a benign but significant community selection towards lighter seeds. The relatively benign observed change in seed mass may partly be due to a 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 method was chosen in order to account for the sampling process of the vegetation data and is in contrast to most other analyses of trait selection, where the community weighted mean of the traits is used as the dependent variable. Generally, little is known on the underlying causes of possible plant trait community selection in semi-natural grasslands that are not subjected to successional processes.

Keywords: Plant trait selection, seed mass, plant functional types, multi-species joint cover distribution, multi-species pin-point cover data, Dirichlet - multinomial distribution, hierarchical Bayesian models, STAN

Introduction

In most plant communities, there is large interspecific variation in seed mass, and this variation has been suggested to play a role in a possible trade-off between fecundity and stress tolerance early in plant development (Muller-Landau 2010; Westoby et al. 2002). That is, if a certain amount of resources are allocated to seed production, then the plant species may either produce few heavy seeds or many light seeds and, generally, there is a negative correlation between seed mass and seed number (Coomes and Grubb 2003). Furthermore, there is substantial evidence that seedlings from heavy seeds are more likely to tolerate stressful conditions early in plant development (Coomes and Grubb 2003; Larios et al. 2014; Westoby et al. 2002). For example, Maron et al. (2021) found that the fitness of large seeds increased with competition intensity and that the fitness of small seeds increased with the level of seed predation in a study of 17 forb species in environments with variable competition intensity and rodent seed predation.

Generally, seed dispersal of wind-dispersed seeds is negatively correlated with seed mass (Skarpaas et al. 2011). However, the effect of seed mass on the dispersal distances of animal-dispersed seeds is more variable (Coomes and Grubb 2003), and a positive correlation between seed mass and dispersal distance has been documented when seeds are collected by animals with a hoarding strategy (Jansen et al. 2002).

Consequently, the trade-off between seed number (increased fecundity) and seed mass is intricate and depends on the environment, and it is expected that this trade-off may be undergoing selection at the community level (*sensu* Vellend 2010) as a response to changes in the abiotic and biotic environments. However, little work has been done to demonstrate such selection forces in natural habitats that are not subjected to large successional changes.

The ultimate goal of a community ecological investigation is to understand the underlying causes of an observed pattern, which would enable us to make credible ecological predictions. However, a specific ecological pattern may be caused by several different processes and involve several important contingencies (Vellend 2010), and the relationship between process and pattern may be influenced by time lags of unknown duration (Svenning and Sandel 2013). Consequently, it will not always be possible to link an observed ecological pattern to its underlying causes, and this is especially true if the investigation is performed at a relatively large spatial scale, where it is a more demanding task to monitor all the possible causal factors (Vellend 2010).

Recently, there has been increasing awareness that in order to avoid model bias in ecological models, it is important to model the sampling variance correctly. This has been demonstrated in model-based ordination (Damgaard et al. 2020; Hui et al. 2015) and, more specifically, in the statistical analysis of plant

trait changes (Clark 2016; Damgaard 2021). 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. 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; Damgaard 2021).

In this study, I will group grassland plant species into PFTs according to their seed mass and investigate whether the proportion among the PFTs has changed across four grassland habitats during the period from 2007 to 2014. This work is a companion study to Damgaard (2021), where the selection forces on the leaf economy spectrum in the same grassland habitats were investigated.

Materials and Methods

Sampling design and plant cover data

Hierarchical time-series plant cover data in the eight-year period from 2007 to 2014 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 (xeric sand calcareous grasslands, EU habitat type: 6120, 99 plots), dry grasslands (semi-natural dry grasslands and scrubland facies on calcareous substrates, EU habitat type: 6210, 1155 plots), acid grasslands (species-rich Nardus grasslands, EU habitat type: 6230, 1129 plots) and wet grasslands (Molinia meadows on calcareous, peaty or clayey-silt laden soils, EU habitat type: 6410, 563 plots). The classification of the habitat types was performed according to the habitat classification system used for the European Habitat Directive (EU 2013; Nygaard et al. 2009). Since the habitat classification was performed for each plot, some sites may contain plots that were classified to different grassland habitat types. Only plots that over the years were consistently classified as belonging to the same grassland habitat type were used in the analyses.

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

square frame (50 cm X 50 cm) of 16 grid points that were equally spaced by 10 cm (Nielsen et al. 2012). Since the plots were resampled with GPS-uncertainty (< 10 meters), the probability that the location of resampled plots overlapped may be ignored.

In the present study, plant species were aggregated into PFTs according to their seed mass, and 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 a measure of the aggregated cover of the two species.

At the same time, when the vegetation was monitored it was recorded at each plot whether there were any signs of grazing by animal husbandry, which was used as a possible explaining variable.

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).

Seed mass

The seed mass values were found in the LEDA trait database (Kleyer et al. 2008), a homogenous trait database established from plant measurements in North-West Europe, which is geographically close to the studied sites. There will always be missing values when applying existing trait data sets to national survey data, and while more comprehensive plant trait databases exist, the priority in this study was to use a homogenous and geographically representative trait database in order to avoid data bias.

In order to group the higher plant species into PFTs, the trait values of all the 757 species, where seed mass data were available in the database, were used to group the species into PFTs with similar mean cover: 1: light seeds ($\log(seed\ mass\ in\ mg) < -1$), 2: intermediary seeds ($-1 \leq \log(seed\ mass\ in\ mg) < 0$), 3: heavy seeds ($\log(seed\ mass\ in\ mg) > 0$), 4: the rest, i.e. species without seed mass data (Fig. 1). The mean site cover of the four different species groups across habitat types and years is shown in Fig. 2.

The classification of each species that was observed in the four grassland types is shown in the Electronic Supplement

Statistical model

In this study, we consider multi-species (multi-PFTs) pin-point cover data, and it has previously been demonstrated that a reparametrized Dirichlet-multinomial distribution is a suitable candidate distribution to model multi-species pin-point cover data (Damgaard 2015; 2019b; Damgaard et al. 2017). The advantage of using the reparametrized Dirichlet-multinomial distribution is that the observed negative among-species covariation in mean cover are included in the model, and that the degree of within-species spatial

aggregation is taken into account and explicitly modelled by a parameter δ (Damgaard 2018). More specifically, 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 $\{1, \dots, m, \dots, n\}$, is modelled as $z_m = \sigma\, \epsilon_m$, with a standard deviation ($\sigma > 0$) and n group regressors, ϵ_m, that are assumed to have a strong prior probability 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 probability distribution. Standard deviation parameters were chosen to be uninformative in the positive domain using an exponential prior probability distribution ($\lambda = 0.5$), and the degree of spatial aggregation had an uninformative uniform prior probability distribution between 0.01 and 0.9.

In the applied general grassland model, there are two hierarchical levels (habitat type and site) with a total of 1469 parameters, and it was not computationally feasible to include plot as a third hierarchical level. This modelling choice was further motivated by the fact that it was unlikely that the location of resampled plots overlapped, and sampling could therefore be assumed to be performed at the site level. Furthermore, an autoregressive component at the plot level did not alter results qualitatively when modeling the change in cover of single heathland habitats, even though the vegetation at these habitats is rather spatially aggregated (Damgaard 2012; Damgaard 2019b).

In order to ensure that the sum of the mean cover parameters did not exceed one when the parameters in the linear model (1) were initialized to zero at 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 MathematicaStan (cmdstan-2.18.0) (Carpenter et al. 2017) using three chains of 100,000 iterations after a warmup of 100,000 iterations. The STAN model and the Mathematica notebook, including trace plots, are included as electronic supplements.

Statistical inferences were based on the marginal posterior probability 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, nevertheless, the MCMC iterations demonstrated good mixing properties and the marginal posterior probability distribution of the parameters had regular shapes (see Appendix S4). Therefore, it was concluded that the model fitted the data adequately. The marginal posterior probability distributions of selected parameters and compound parameters are summarized in Tables 1, 2 and 3.

Across the four grassland habitat types, there was community selection towards lighter seeds. The cover of heavy seeds decreased significantly during the eight-year period (Table 1: heavy seeds, $P(\beta > 0) = 0.048$) and the cover of intermediary showed a tendency towards a decrease (Table 1: intermediary seeds, $P(\beta > 0) = 0.099$). The probability of both these observed decreases in cover should occur by chance is 0.005. However, the selection towards lighter seeds was not significant when considering each of the four grassland habitats separately (Table 2), possibly due to reduced statistical power. The distribution of the mean site cover at the four grassland habitat types over the years is shown in Fig. 3.

In order to examine possible patterns of the among-site variation the mean of the random effects for the different aggregated species groups, $E(\beta site_{i,k})$ were compared to information on whether signs of grazing were observed in each plot during the years, which was assumed to be a proxy for management intensity. However, no significant patterns were observed (Appendix S4).

The estimated standard deviations of the yearly change among sites were approximately of the same size as the standard deviations among habitats (Table 1), which indicates that there is a sizeable variation in the yearly change among sites of the same grassland habitat type.

The standard deviations of the posterior probability distributions of the slope parameters that measure the yearly change in the cover of the PFTs were approximately 0.02 on the logit scale (Table 1). This width of the posterior probability distribution indicates that the statistical power of the analysis is moderate and, in connection with the mostly non-significant changes in cover, it is concluded that trait selection for seed mass in Danish grasslands over the eight-year period generally is benign.

The spatial aggregation of the FPTs was significantly higher in calcareous grasslands and wet grasslands than in the two other grassland habitat types (Table 3).

Discussion

Across the four grassland habitat types, there was benign selection at the community level towards lighter seeds during an eight-year period. I am not aware of other studies that have investigated selection on seed

mass at the community level using time-series data from a large number of grassland sites. Unfortunately, a general theory on community level selection on seed mass in a changing environment and motivated hypotheses on what to expect under different circumstances are underdeveloped (although see e.g. Larios and Venable 2018). To further generate such hypotheses, possible patterns between the among-site variation and observed signs of grazing were examined, but did not reveal any significant patterns.

In the past seventy years, there has been a dramatic change in the land-use of grassland habitats, where the use and management of semi-natural grasslands have changed towards intensified agricultural production and fertilization in some areas and abandonment of traditional practices (e.g. cessation of extensive livestock grazing) in others (Poschlod et al. 2005). Concurrently, there has been an increase in atmospheric nitrogen deposition, although nitrogen deposition recently has levelled off and has even shown a decreasing tendency in Denmark (Ellermann et al. 2019). The effects of these land-use changes vary, but, generally, there has been a change in the vegetation towards taller and more competitive plant species (Timmermann et al. 2015), and these land-use changes may also have had an effect on the seed mass. Moreover, possibly as a selection response to these environmental changes, a significant decrease in the proportion of thin-leaved plant species has been observed in Danish grasslands (Damgaard 2021).

Most existing theories and empirical studies on the seed number – seed mass trade-off focus on intra-specific selection and trade-off mechanisms. There has, however, been an extensive exploration of the role of different plant traits, including the role of seed mass, to characterize different plant life history strategies and how the different strategies are more or less suited to different environments (e.g. Garnier et al. 2016; Westoby et al. 2002). However, more time-series studies are needed in order to understand the relevant ecological processes rather than relying on the commonly performed space-for-time approach (Damgaard 2019a).

In order to model the sampling variance correctly and avoid possible model bias (Clark 2016), the continuous variable, seed mass, is used for grouping plant species into PFTs, and the aggregated cover of the PTFs is then treated as the dependent variable. This method is relatively conservative compared to treating the CWMs of seed mass as the dependent variable. However, in order to ensure that the reported results are representative and may be generalized to other areas, it is of utmost importance that the sampling variance is modelled correctly.

An alternative method of analyzing plant trait selection is to correlate trait values with estimated demographic parameters or change in abundance for individual species (Garnier et al. 2018; Herben et al. 2019; Timmermann et al. 2015). 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; 2013; Damgaard and 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; 2018). A further advantage of modelling trait selection by the change in the cover 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. whether 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. Histogram of seed mass of all the 757 species that was available in the database. The seed mass data were used to group the species into PFTs with similar mean cover; yellow: light seeds, blue: intermediary seeds, green: heavy seeds.

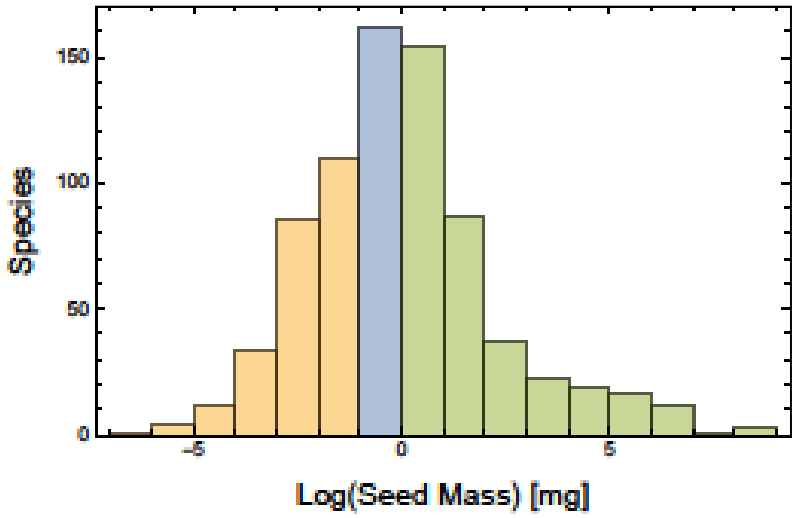


Fig. 2. Distribution of the mean site cover of the four different species groups (PFTs).

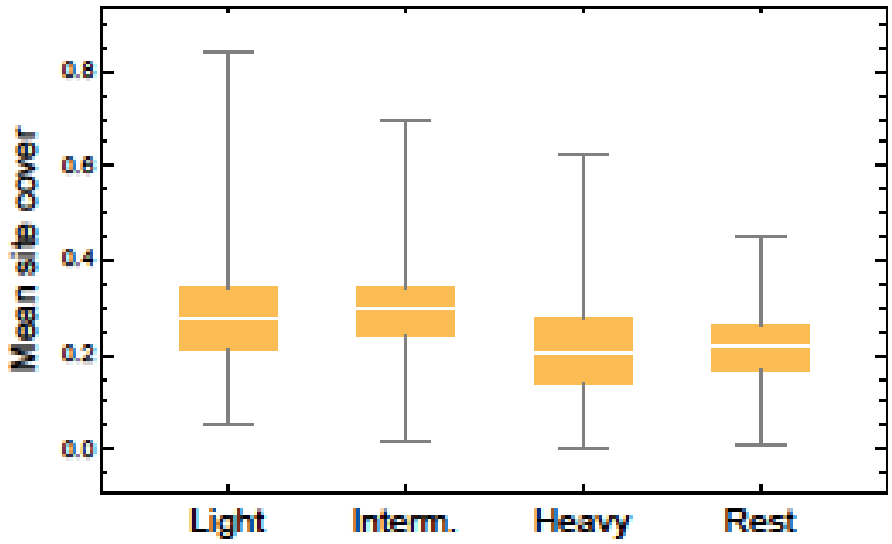
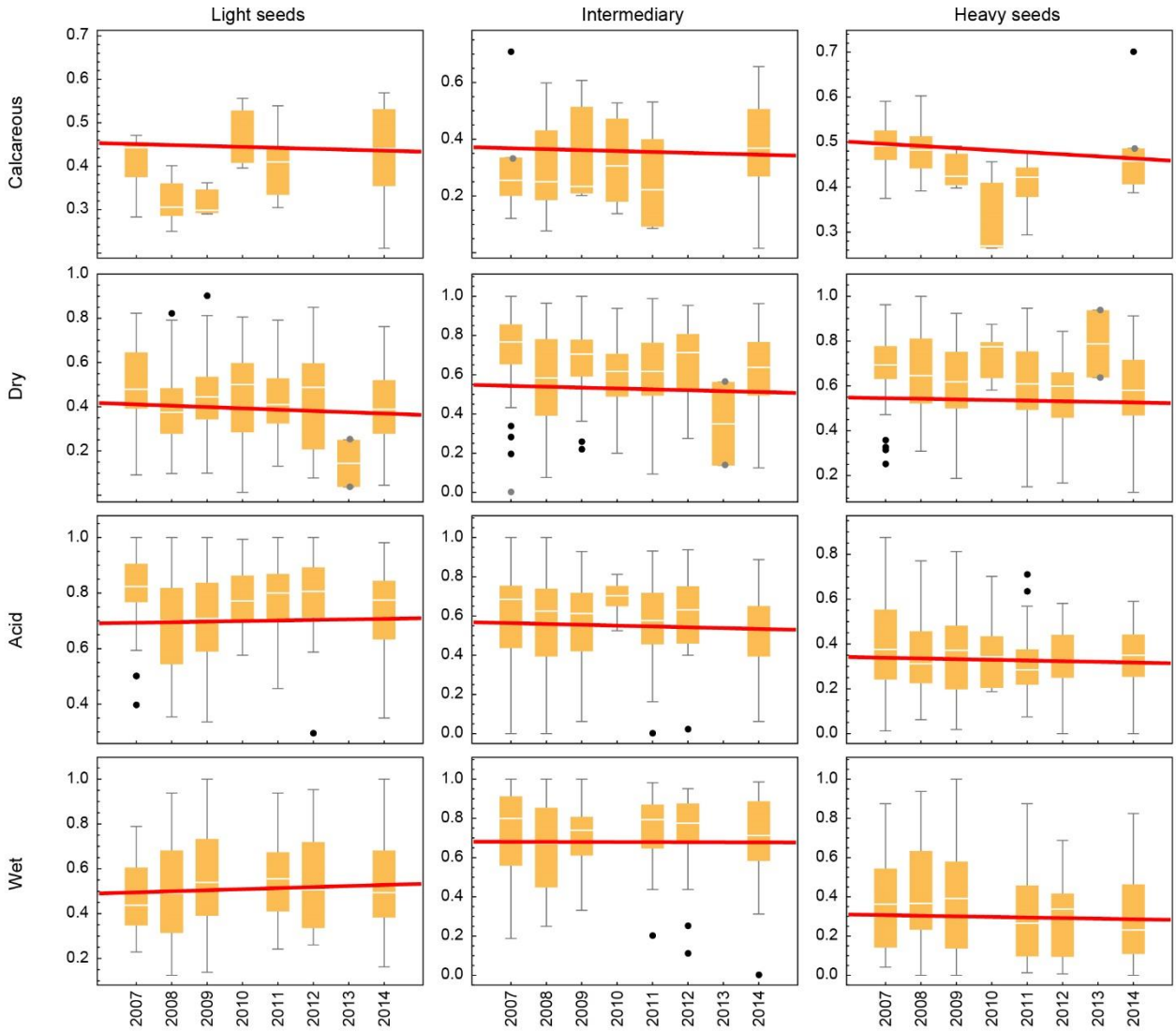


Fig. 3. Distribution of the mean site cover at the four grassland habitat types over the years. The estimated slopes are illustrated approximately with the red lines.



Tables

Table 1. Summary of the marginal posterior probability distributions 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	Light seeds	0.050	0.335	-0.669	0.060	0.747	0.601
α	Intermediary	0.077	0.467	-1.084	0.104	1.005	0.630
α	Heavy seeds	-0.285	0.421	-1.134	-0.305	0.750	0.186
$\alpha site_{\sigma}$	Light seeds	0.406	0.024	0.361	0.406	0.456	-
$\alpha site_{\sigma}$	Intermediary	0.474	0.027	0.423	0.473	0.529	-
$\alpha site_{\sigma}$	Heavy seeds	0.554	0.033	0.492	0.552	0.622	-
$\alpha habitat_{\sigma}$	Light seeds	0.578	0.384	0.208	0.457	1.693	-
$\alpha habitat_{\sigma}$	Intermediary	0.873	0.732	0.268	0.644	3.636	-
$\alpha habitat_{\sigma}$	Heavy seeds	0.759	0.625	0.242	0.581	2.684	-
β	Light seeds	0.000	0.025	-0.047	-0.001	0.047	0.476
β	Intermediary	-0.013	0.017	-0.041	-0.013	0.016	0.099
β	Heavy seeds	-0.015	0.013	-0.040	-0.014	0.006	**0.048**
$\beta site_{\sigma}$	Light seeds	0.024	0.006	0.011	0.024	0.034	-
$\beta site_{\sigma}$	Intermediary	0.028	0.005	0.018	0.028	0.037	-
$\beta site_{\sigma}$	Heavy seeds	0.025	0.008	0.008	0.026	0.039	-
$\beta habitat_{\sigma}$	Light seeds	0.035	0.038	0.007	0.024	0.132	-
$\beta habitat_{\sigma}$	Intermediary	0.019	0.028	0.001	0.011	0.083	-
$\beta habitat_{\sigma}$	Heavy seeds	0.014	0.022	0.000	0.008	0.065	-

Table 2. Summary of the marginal posterior probability distribution of the change in cover $(\beta_i + \beta habitat_{\sigma,i}\, \beta habitat_{\epsilon,i,j})$ 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	Light seeds	-0.009	0.045	-0.098	-0.006	0.069	0.398
calcareous grasslands	Intermediary	-0.014	0.035	-0.073	-0.014	0.044	0.204
calcareous grasslands	Heavy seeds	-0.019	0.027	-0.071	-0.016	0.021	0.100
dry grasslands	Light seeds	-0.025	0.049	-0.130	-0.020	0.045	0.209
dry grasslands	Intermediary	-0.018	0.032	-0.076	-0.016	0.030	0.138
dry grasslands	Heavy seeds	-0.011	0.025	-0.051	-0.012	0.036	0.171
acid grasslands	Light seeds	0.009	0.043	-0.062	0.007	0.095	0.626
acid grasslands	Intermediary	-0.017	0.031	-0.074	-0.015	0.032	0.147
acid grasslands	Heavy seeds	-0.014	0.025	-0.057	-0.013	0.029	0.135
wet grasslands	Light seeds	0.019	0.046	-0.051	0.014	0.119	0.736
wet grasslands	Intermediary	-0.002	0.036	-0.048	-0.007	0.071	0.339
wet grasslands	Heavy seeds	-0.014	0.026	-0.060	-0.014	0.029	0.133

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

Habitat type	Mean	SD	2.5%	50%	97.5%
calcareous grasslands	0.128	0.007	0.116	0.128	0.142
dry grasslands	0.074	0.002	0.071	0.074	0.077
acid grasslands	0.077	0.002	0.073	0.077	0.080
wet grasslands	0.132	0.003	0.126	0.132	0.139

Data Accessibility statement

The used cover data may be found in Appendix S1

Electronic Supplements

All Appendices may be downloaded from https://osf.io/n7mu3/

Appendix S1: Cover data

Appendix S2: Species list (Excel file)

Appendix S3: STAN model (text file)

Appendix S4: Mathematica notebook with trace plots and simulated posterior probability distributions etc.

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