Indication of a reduction in the cover of thin-leaved plants in Danish grasslands over an eight-year period

Christian Damgaard, Department of Bioscience, Aarhus University, Vejløvej 25, 8600 Silkeborg, Denmark
cfd@bios.au.dk, +45-30183153

Abstract

Across four grassland habitat types, the cover of thin-leaved plants was found to decrease significantly, but generally only limited trait selection was observed on leaf traits (SLA and LDMC) in a study of an extensive Danish grassland vegetation dataset from an eight-year period. The mostly 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 is 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

23 Introduction

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

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

37 An often-studied suite of plant traits is the leaf economics spectrum, which is an important trade-off
 38 between plant resource acquisition and storage, where some plant species characterized by relatively thin
 39 leaves have a strategy of rapid carbon gain with rapid foliar turnover and fast growth. These thin-leaved
 40 species often have a competitive advantage in high-productive ecosystems with fertile soil. Whereas other
 41 plant species characterized by relatively thick leaves invest more resources into leaf construction and have
 42 a relatively slower foliar turnover and slow growth. These thick-leaved species often have a competitive
 43 advantage in low-productive ecosystems with infertile soil (e.g. Westoby *et al.*, 2002, Craine, 2009, Reich,
 44 2014).

45 In the past sixty years, there has been a dramatic anthropogenic increase in atmospheric nitrogen
 46 deposition, and significant effects on the plant vegetation have been demonstrated in some grassland
 47 habitats (Stevens *et al.*, 2004, Damgaard *et al.*, 2011), although nitrogen deposition recently has levelled off
 48 and even shown a decreasing tendency in Denmark (Ellermann *et al.*, 2019). According to leaf economics
 49 spectrum theory, the increase in plant available nitrogen is expected to lead to selection in favor of thin-
 50 leaved fast growing plant species, although it is generally unknown how fast plant populations respond to
 51 environmental changes (Svenning & Sandel, 2013).

52 Usually, trait selection is investigated using community weighted mean trait values (CWMs) as the
 53 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. This 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 it is necessary 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 an eight-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 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 (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 none 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).

$$\mu_{i,j,k,y} = \text{invlogit}(\alpha_i + \alpha_{\text{site}_{i,k}} + \alpha_{\text{habitat}_{i,j}} + (\beta_i + \beta_{\text{site}_{i,k}} + \beta_{\text{habitat}_{i,j}}) y) \quad (1),$$

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 distribution, $\epsilon_m \sim N(0,1)$. For example, $\beta_{\text{habitat}_{i,j}} = \beta_{\text{habitat}_{\sigma,i}} \beta_{\text{habitat}_{\epsilon,i,j}}$, where the parameter $\beta_{\text{habitat}_{\sigma,i}}$ is positive, and the n_j parameters $\beta_{\text{habitat}_{\epsilon,i,j}}$ 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 0.01 to 10, and 0.01 to 0.9, respectively.

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 in the beginning of the MCMC sampling procedure,

$invlogit(x) = \frac{0.322}{0.33 + \text{Exp}[-x]} + 0.01$ 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 three 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, nevertheless, 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.

Across the four grassland habitat types, the cover of thin-leaved plants decreased significantly during the eight-year period (Table 1: β – thin-leaved, $P = 0.031$). However, within the four grassland habitat types there were no significant changes in the cover of any of the PFTs (Table 2); the strongest statistical signal was a negative trend for thin-leaved plant species in dry grasslands (Table 2: thin-leaved, $P = 0.090$).

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 distributions of the slope parameters that measure the yearly change in the cover of the PFTs were approximately 0.03 on the logit scale (Table 1). This width of the posterior 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 the studied leaf traits in Danish grasslands over the eight-year period generally is limited.

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

Discussion

Across the four grassland habitat types, the cover of thin-leaved plants was found to decrease significantly in this study of an extensive eight-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. This result may indicate that the observed decrease in nitrogen deposition over the last years is beginning to reverse earlier demonstrated effects of elevated nitrogen deposition on plant traits, but there are other possible explanations such as changed management, increase in soil moisture, and reduced grazing pressures on the studied grasslands (Cruz *et al.*, 2010, Zheng *et al.*, 2015). 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, were relatively thin-leaved (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 chosen method of analysis, where the continuous variables SLA and LDMC are used for grouping plant species into PFTs and the aggregated cover of the PFTs are then treated as the dependent variable instead of treating the CWMs of SLA and LDMC as the dependent variable, is relatively conservative. 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

174 reparametrized Dirichlet-multinomial distribution (Damgaard, 2015, Damgaard, 2018). A further advantage
 175 of modelling trait selection by the change in the abundance of PFTs rather than the change in the
 176 continuous CWMs is that the class of missing values, i.e. the plant species with no or incomplete
 177 information on the trait values, is clearly defined (in this study as the rest group). Additionally, more
 178 complicated selection models than directional selection may be readily tested, e.g. stabilizing selection (the
 179 intermediary PFT is positively selected) and disruptive selection (the intermediary PFT is negatively
 180 selected).

181 The studied vegetation plots were not real permanent plots, but were only resampled with GPS-
 182 uncertainty. However, if we had access to permanent plot time-series cover data it would have been
 183 interesting to explore more sophisticated selection models, e.g. whether the observed trait selection could
 184 be partitioned into direct selection and selection that is mediated by interspecific interactions (Damgaard,
 185 2016, Pedersen *et al.*, 2019).

186

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

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

204 Tables

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

Parameter	PFTs	Mean	SD	2.5%	50%	97.5%	P(>0)
α	Thin-leaved	-0,558	0,474	-1,449	-0,572	0,626	0,068
α	Intermediary	0,255	0,386	-0,660	0,264	1,034	0,834
α	Thick-leaved	-0,710	0,712	-2,151	-0,700	0,802	0,111
$\alpha_{site_{\sigma}}$	Thin-leaved	0,691	0,042	0,613	0,690	0,777	-
$\alpha_{site_{\sigma}}$	Intermediary	0,538	0,033	0,477	0,536	0,608	-
$\alpha_{site_{\sigma}}$	Thick-leaved	1,134	0,068	1,010	1,131	1,276	-
$\alpha_{habitat_{\sigma}}$	Thin-leaved	0,744	0,653	0,225	0,537	2,934	-
$\alpha_{habitat_{\sigma}}$	Intermediary	0,659	0,541	0,207	0,488	2,365	-
$\alpha_{habitat_{\sigma}}$	Thick-leaved	1,325	0,923	0,439	1,041	3,983	-
β	Thin-leaved	-0,042	0,026	-0,086	-0,043	0,006	0,031
β	Intermediary	0,006	0,025	-0,036	0,006	0,054	0,688
β	Thick-leaved	-0,008	0,031	-0,057	-0,009	0,044	0,285
$\beta_{site_{\sigma}}$	Thin-leaved	0,027	0,008	0,012	0,027	0,043	-
$\beta_{site_{\sigma}}$	Intermediary	0,030	0,006	0,018	0,030	0,041	-
$\beta_{site_{\sigma}}$	Thick-leaved	0,044	0,009	0,026	0,044	0,063	-
$\beta_{habitat_{\sigma}}$	Thin-leaved	0,036	0,043	0,011	0,025	0,134	-
$\beta_{habitat_{\sigma}}$	Intermediary	0,032	0,036	0,010	0,021	0,119	-
$\beta_{habitat_{\sigma}}$	Thick-leaved	0,036	0,048	0,011	0,023	0,134	-

207

208 Table 2. Summary of the posterior distribution of the change in cover ($\beta_i + \beta_{habitat_{\sigma,i}} \beta_{habitat_{\epsilon,i,j}}$) for
209 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

210

211 Table 3. Summary of the posterior distribution of the degree of spatial aggregation in the different
212 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	0,100	0,103	0,107
acid grasslands	0,110	0,002	0,106	0,110	0,114
wet grasslands	0,124	0,003	0,118	0,124	0,131

213

214 Electronic Supplements

215 A: Species list (Excel file)

216 B: STAN model (text file)

References

- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P. & Riddell, A. (2017) Stan: A Probabilistic Programming Language. *2017*, **76**, 32.
- Clark, J.S. (2016) Why species tell more about traits than traits about species: predictive analysis. *Ecology*, **97**, 1979-1993.
- Craine, J.M. (2009) *Resource strategies of wild plants*. Princeton University Press.
- Cruz, P., De Quadros, F.L.F., Theau, J.P., Frizzo, A., Jouany, C., Duru, M. & Carvalho, P.C.F. (2010) Leaf Traits as Functional Descriptors of the Intensity of Continuous Grazing in Native Grasslands in the South of Brazil. *Rangeland Ecology & Management*, **63**, 350-358.
- Damgaard, C. (2009) On the distribution of plant abundance data. *Ecological Informatics*, **4**, 76-82.
- Damgaard, C. (2012) Trend analyses of hierarchical pin-point cover data. *Ecology*, **93**, 1269-1274.
- Damgaard, C. (2013) Hierarchical and spatially aggregated plant cover data. *Ecological Informatics*, **18**, 35-39.
- Damgaard, C. (2015) Modelling pin-point cover data of complementary vegetation classes. *Ecological Informatics*, **30**, 179-184.
- Damgaard, C. (2016) Empirical modelling of trait selection by partitioning selection into direct selection and selection that is mediated by interspecific interactions. *bioRxiv*.
- Damgaard, C. (2018) The joint distribution of pin-point plant cover data: a reparametrized Dirichlet - multinomial distribution. *arXiv e-prints*.
- Damgaard, C. (2019) A Critique of the Space-for-Time Substitution Practice in Community Ecology. *Trends in Ecology & Evolution*, **34**, 416-421.
- Damgaard, C. & Irvine, K.M. (2019) Using the beta distribution to analyze plant cover data. *Journal of Ecology*.
- Damgaard, C., Jensen, L., Frohn, L.M., Borchsenius, F., Nielsen, K.E., Ejrnæs, R. & Stevens, C.J. (2011) The effect of nitrogen deposition on the species richness of acid grasslands in Denmark: A comparison with a study performed on a European scale. *Environmental Pollution*, **159**, 1778-1782.
- Douma, J.C., de Haan, M.W.A., Aerts, R., Witte, J.-P.M. & van Bodegom, P.M. (2012) Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. *Journal of Ecology*, **100**, 366-380.
- Ellermann, T., Bossi, R., Nygaard, J., Christensen, J., Løfstrøm, P., Monies, C., Grundahl, L., Geels, C., Nielsen, I.E. & Poulsen, M.B. (2019) Atmosfærisk deposition 2017. *Videnskabelig rapport fra DCE – Nationalt Center for Miljø og Energi* (ed D. N. C. f. M. o. E. Aarhus Universitet), pp. 84. Aarhus University.
- EU (2013) Interpretation manual of European Union habitats. . European Commission, DG Environment, Nature and Biodiversity, Bruxelles.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) PLANT FUNCTIONAL MARKERS CAPTURE ECOSYSTEM PROPERTIES DURING SECONDARY SUCCESSION. *Ecology*, **85**, 2630-2637.
- Garnier, E., Fayolle, A., Navas, M.-L., Damgaard, C., Cruz, P., Hubert, D., Richarte, J., Autran, P., Leurent, C. & Violle, C. (2018) Plant demographic and functional responses to management intensification: A long-term study in a Mediterranean rangeland. *Journal of Ecology*, **106**, 1363-1376.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theua, J.-P., Thébault, A., Vile, D. & Zarovali, M.P. (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, **99**, 967–985.

- Garnier, E., Navas, M.L. & Grigulis, K. (2016) *Plant functional diversity. Organism traits, community structure, and ecosystem properties*. Oxford University Press, Oxford, UK.
- Herben, T., Hadincová, V., Krahulec, F., Pecháčková, S. & Skálová, H. (2019) Two dimensions of demographic differentiation of species in a mountain grassland community: An experimental test. *Functional Ecology*, **33**, 1514-1523.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266-1274.
- Laliberté, E., Shipley, B., Norton, D.A. & Scott, D. (2012) Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology*, **100**, 662-677.
- Levy, E.B. & Madden, E.A. (1933) The point method of pasture analyses. *New Zealand Journal of Agriculture*, **46**, 267-279.
- Lindquist, B. (1931) Den skandinaviska bokskogens biologi. *Svenska Skogsvårdsföreningens Tidskrift*, **3**.
- Nielsen, K.E., Bak, J.L., Bruus, M., Damgaard, C., Ejrnæs, R., Fredshavn, J.R., Nygaard, B., Skov, F., Strandberg, B. & Strandberg, M. (2012) NATURDATA.DK - Danish monitoring program of vegetation and chemical plant and soil data from non-forested terrestrial habitat types. *Biodiversity & Ecology*, **4**, 375.
- Nygaard, B., Damgaard, C., Nielsen, K.E., Bladt, J. & Ejrnæs, R. (2016) Habitatdirektivets naturtyper. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi.
- Nygaard, B., Ejrnæs, R., Baattrup-Pedersen, A. & Fredshavn, J. (2009) Danske plantesamfund i moser og enge – vegetation, økologi, sårbarhed og beskyttelse. *Faglig rapport fra DMU*. DMU, Aarhus.
- Pedersen, R.Ø., Bonis, A. & Damgaard, C. (2019) A nonlinear Bayesian model of trait selection forces. *Ecological Modelling*, **393**, 107-119.
- Pellissier, L., Wisz, M.S., Strandberg, B. & Damgaard, C. (2014) Herbicide and fertilizers promote analogous phylogenetic responses but opposite functional responses in plant communities. *Environmental Research Letters*, **9**, 024016 (9pp)
- Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275-301.
- Shipley, B. (2010) *From plant traits to vegetation structure*. Cambridge University Press, Cambridge.
- Smart, S.M., Thompson, K., Marrs, R.H., Duc, M.G.L., Maskell, L.C. & Firbank, L.G. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2659-2665.
- Stegen, J.C. & Swenson, N.G. (2009) Functional trait assembly through ecological and evolutionary time. *Theoretical Ecology*, **2**, 239-250.
- Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science*, **303**, 1876-1881.
- Svenning, J.-C. & Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, **100**, 1–21.
- Timmermann, A., Damgaard, C., Strandberg, M.T. & Svenning, J.-C. (2015) Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers than winners and a shift towards competitive, tall-growing species. *Journal of Applied Ecology*, **52**, 21-30.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, **33**, 125-159.
- Zheng, S., Li, W., Lan, Z., Ren, H. & Wang, K. (2015) Functional trait responses to grazing are mediated by soil moisture and plant functional group identity. *Scientific reports*, **5**, 18163-18163.