- 1 Empirical modelling of trait selection by partitioning
- ² selection into direct selection and selection that is
- ³ mediated by interspecific interactions
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6 Abstract

7 Trait selection has received considerable attention in the pursuit to understand niche-based community 8 assembly processes and to generate ecological predictions. To further advance the study of trait selection, 9 a conceptual statistical model is presented that outlines and discuss the possibilities of i) estimating the 10 effect of interspecific interactions on traits rather than just testing weather selection has had an effect on 11 the observed trait distributions, ii) discriminating between environmental filtering and niche partitioning 12 processes and estimate the characteristic features and importance of both processes, and iii) predicting the 13 effect of environmental changes and gradients on trait selection. To achieve these goals a number of 14 necessary assumptions have to be specified and these assumptions are discussed and assessed. Simulated 15 plant cover data from a simple uniform environment was successfully fitted to the model and the results 16 indicates that it is possible to partition direct population growth and population growth that is mediated by 17 interspecific interaction. The data requirements of the model are modest, i.e. time series data on plant 18 species abundance and a species – trait matrix. Consequently, the model concept may be used to model 19 trait selection, including the effect of interspecific interactions, in many existing plant ecological datasets. 20 Keywords: interspecific interactions; competition; trait selection; selection model; directional selection; 21 stabilizing selection; disruptive selection; plant cover

22 Introduction

23 Interspecific interactions among neighbouring plants typically arise because the resources needed for plant 24 growth and reproduction are limited, and the plant that extracts or monopolizes most of the limiting 25 resources will grow faster and reproduce in greater numbers (e.g., Goldberg et al., 1990; Weiner, 1986). 26 The possibly important role of interspecific interactions in regulating natural plant communities and 27 determining community assembly rules (e.g., Gotelli and McCabe, 2002; Kraft et al., 2015b; Silvertown et 28 al., 1999; Weiher et al., 1998) has been investigated in a multitude of studies using different methods 29 (Damgaard, 2011). However, considering its high ecological relevance and status as a classic research 30 question in plant population ecology, it is noteworthy that only relatively few studies have measured the 31 direct effect of interspecific interactions on plant performance and its role for regulating plant communities 32 in undisturbed natural communities, and the results are still too sparse to allow much generalization across 33 different plant communities or even among years (Turnbull et al., 2004). This paradox is due to the fact that 34 the measurement of interspecific interactions in natural ecosystems is a non-trivial task (Damgaard, 2011), 35 and applicable methods for measuring interspecific interactions in natural ecosystems is needed in order to 36 make progress in understanding community assembly rules and making quantitative ecological predictions 37 on the effect of environmental changes on biodiversity.

38 An increasingly popular way of describing plant communities is to focus on the expressed phenotypes of 39 the plant species, i.e. plant traits, rather than on the species itself. The advantage is that plant traits are 40 characteristic features, which to a certain extent will determine the survival, growth and reproductive 41 strategies of the species, and are expected to respond in a more predictable way to an altered environment 42 than the observed change in species composition (Garnier et al., 2004; Garnier et al., 2016; Shipley, 2010a). 43 Furthermore, plant traits involved in resource acquisition and use at the species level will scale-up to 44 ecosystem functioning, provided that traits are weighed by the species' contribution to the community 45 (Garnier et al., 2007; Lavorel and Garnier, 2002).

Broadly speaking, a trait selection response is caused by i) environmental or biotic filtering processes where 46 47 the abiotic and biotic environment selects for a certain combination of plant traits that have a relatively 48 high adaptive value in the specific environment independent of the other plant species in the population, 49 i.e. the fundamental niche (Hutchinson, 1957), and ii) competitive or facilitative processes where the trait 50 selection response depends on the traits of the other plant species in the population, i.e. the realized niche 51 (Hutchinson, 1957). The resulting observed selection response on individual traits after both selection 52 processes has operated may be classified into either i) directional selection, where either relatively high or 53 low trait values are favored, ii) stabilizing selection, where specific intermediary trait values are favored 54 over all other trait values, or iii) disruptive selection, where extreme values for a trait are favored over 55 intermediate values.

It is important not to confuse the selection processes with the resulting observed selection response, since multiple assembly processes has been shown to lead to the same pattern of trait dispersion and the same process can lead to different patterns of trait dispersion (Herben and Goldberg, 2014). However, if would be valuable to be able to distinguish between the two types of selection processes from observed changes in the distribution of plant traits since the two different selection processes lead to different expectations of community dynamics including species coexistence and niche-based community assembly processes (e.g. Chesson, 2000; Mayfield and Levine, 2010).

The trait selection process has previously been described by a two-step process in a meta-community model, where plants from a regional species pool are dispersed to a local habitat, and trait filtering excludes individuals with unfit trait values, and within the local species pool, trait values may influence performance, which may lead to patterns of trait convergence or divergence (e.g. Bernard-Verdier et al., 2012; Webb et al., 2010). The selection due to performance differences in the local species pool is thought to be mediated by interspecific interactions as the difference between the fundamental niche and the realized niche of the local species. Under this framework, the effect of interspecific interactions is detected from deviations of the observed trait distribution from random expectations in the local species pool. If the variance of the observed trait distribution is lower than the random expectations, this is an indication of directional or stabilizing selection (convergent trait distribution pattern). Conversely, if the variance of the observed trait distribution is higher than the random expectations, this is an indication of disruptive selection (divergent trait distribution pattern).

75 Using such test procedures, several plant ecological studies have reported non-random trait dispersion 76 distributions in favor of different niche-based community assembly hypotheses compared to the neutral 77 hypothesis of plant community assembly (Weiher et al., 2011). However, this test procedure has been 78 criticized by e.g. Adler et al. (2013), who argue that trait dispersion tests have low power to detect niche 79 partitioning, and that patterns typically interpreted as either environmental filtering or niche partitioning 80 may be generated by the same process. Most importantly, Adler et al. (2013) note that: "The common 81 interpretation is that species interactions play no role in the abiotic environmental filtering process, while 82 abiotic factors play no role in the competitively driven niche partitioning process. However, the dichotomy 83 between environmental filtering and niche partitioning can arise from an arbitrary decision about the 84 spatial scale of analysis, not from distinct biological processes".

In a seminal work using maximum entropy models Shipley (2010a; 2010b) estimated the selection response
from change in plant abundance. The maximum entropy models have the large advantage that it is not
necessary to specify detailed models on selection mechanisms or how the different traits interact
(Baastrup-Spohr et al., 2015; Shipley, 2010a; Shipley, 2010b), but this advantage is also their main
drawback, since the method does not allow for discriminating between different selection models or
whether selection is occurring due to environmental filtering or niche partitioning processes.

91 Consequently, in order to make progress in the understanding of the role and nature of niche-based
92 community assembly processes in the structuring of plant communities, it would be beneficial to be able i)
93 to estimate the effect of interspecific interactions on traits rather than just testing whether selection has

had an effect on the observed trait distributions, ii) to discriminate between environmental filtering and
niche partitioning processes and estimate the characteristic features and importance of both processes,
and iii) to predict the effect of environmental changes and gradients on trait selection.

97 To meet these objectives, I present a method for estimating the effect of species trait values on observed 98 population growth in a plant community by estimating parameters in two complementary population 99 growth functions, which partition the observed change in trait distribution of plant population into i) a 100 direct selection process that is independent of the trait distribution of the plant population, which mainly is 101 assumed to arise from environmental filtering processes, and ii) a selection process mediated by 102 interspecific interaction that depend on the trait distribution of the plant population, which mainly is 103 assumed to arise from the niche partitioning processes of competition and facilitation. The resulting model 104 is a one-step trait selection process where the effects of plant traits on population growth is estimated 105 from simple longitudinal plant cover data in an approach that is similar to the approach suggested by Lande 106 and Arnold (1983) to measure selection on correlated characters, but where the effect of traits on 107 population growth is partitioned into direct population growth and population growth that is mediated by interspecific interaction (also see Laughlin et al., 2015; Laughlin et al., 2012). The model operates locally 108 109 and is conceptually simpler than the two-step meta-community model that previously has been used (e.g. Bernard-Verdier et al., 2012; Webb et al., 2010). Furthermore, a one-step trait selection response is 110 111 probably a more realistic model of the selection process, since there are no compelling reasons for why the processes of environmental filtering and niche partitioning should not operate simultaneously. 112

The modest aim of this paper is only to present the model concept and for demonstration purposes to apply it on a toy example. As explained later there are a multitude of possible selection processes, that may be modelled using the model concept and it is meaningless to explore the fitting properties of all the different combinations; except in the context of a genuine plant ecological example.

117 Model

118 A plant community has *n* plant species that are characterized by *m* species-specific plant traits, which are 119 known to be important for plant growth and demography. The plant traits are stored in a species-trait 120 matrix, $T_{n,m}$, with *n* rows and *m* columns.

The relative local abundance of the plant species is measured by either biomass or cover at time *t*, $q_{j,t}$, where $\sum_{j=1}^{n} q_{j,t} = 1$. The plants grow, die and reproduce under the influence of interspecific interactions at a given environment where certain combinations of plant traits have a positive effect on growth and reproduction, and other combinations of plant traits have a negative effect on growth and reproduction (compare with Lande and Arnold, 1983).

126 The predicted cover the following year of plant species j with trait values $t_k = x$ is determined by (Fig. 1),

127
$$q'_{j} = q_{j} \sum_{k=1}^{m} \left(F_{k}(x) \left(\sum_{y \in \Omega(t_{k})} C_{k}(x, y) q_{t_{k}=y} \right) \right) + \varepsilon$$
(1),

where $F_k(x)$ is the direct population growth function of plant species with trait value x for plant trait k, and $C_k(x, y)$ is a function that models the effect of interspecific interactions on population growth of plant species with trait value x for plant trait k, where the interspecific interaction of plant species with trait value x and y is modelled by a distance function, i. e. the effect of species interaction between two species on population growth is determined by the difference in trait values between the two species.

The population growth functions $F_k(x)$ and $C_k(x, y)$ may vary according to plant life forms, habitat type, and existing prior knowledge of e.g. the type of selection on the different traits. For example, if there is prior information that suggest that directional selection may be operating then this model may be relevant,

136
$$F_k(x) = a_k x + b_k$$
 (2a),

137
$$C_k(x,y) = Exp(-c_k(y-x))$$
 (3a),

and the following model may be relevant in the case of stabilizing selection,

139
$$F_k(x) = a_k (x - z_k)^2 + b_k$$
 (2b)

140
$$C_k(x,y) = Exp(-c_k(y-z_k)^2)/Exp(-c_k(x-z_k)^2)$$
 (3b),

where z_k is an optimum intermediary trait value. Likewise the following model may be relevant in the case of disruptive selection,

143
$$F_k(x) = a_k (x - z_k)^2 + b_k$$
 (2c),

144
$$C_k(x,y) = (1-m_k) \left(1 - Exp(-c_k (y-z_k)^2) \right) / \left(1 - Exp(-c_k (x-z_k)^2) \right) + m_k$$
(3c),

where z_k is a minimum intermediary trait value with fitness m_k . But generally a number of different $F_k(x)$ and $C_k(x, y)$ functions may be conceived depending on the specific plant ecological case. Alternatively, if limited or no prior information of the selection forces exists then model (1) may be fitted using e.g. spline functions (also see Laughlin et al., 2015).

149 The effects of the *m* traits on plant population growth is here assumed to be additive; but see the later

- discussion on the possibilities of relaxing this important assumption.
- 151 The different selection models may be fitted to longitudinal plant relative abundance data by specifying the 152 relevant likelihood function. Since the predicted cover of plant species *j* in eq. 1 is not bounded between
- 153 zero and one, the predicted cover was fitted to the observed cover using a normal distribution, where the
- 154 standard deviation was scaled by the observed cover times one minus the observed cover, i.e.

155 $\varepsilon \sim N(0, q_j(1 - q_j)\sigma)$. For example, in the case of fitting the directional selection, models (2a) and (3a) are 156 inserted into (1) the resulting likelihood function is,

157
$$L(\boldsymbol{a}, \boldsymbol{b}, \boldsymbol{c}, \sigma) = \prod_{i=1}^{N} \prod_{j=1}^{n} \frac{1}{\sqrt{2\pi}q_{j,t+1}(1-q_{j,t+1})\sigma} Exp\left(-\frac{\left(q_{j,t}'-q_{j,t+1}\right)^{2}}{\left(q_{j,t+1}(1-q_{j,t+1})\sigma\right)^{2}}\right)$$
(4).

158 Most importantly, the parameter, σ , estimates the structural variance in the change in cover, which is the 159 variance that is not explained by the model (1), and may consequently be used to get an estimate on the 160 quantitative importance of the simplifying assumptions used in the modelling process.

161 Demonstration with a toy example

In order to present and discuss the nature of the underlying assumptions and illustrate the possible use of
 the model, the above-outlined method was applied on a simple toy example of a realistic data type.

164 An arbitrary species-traits matrix with ten species and three traits, $T_{10.3}$, was constructed with random 165 integer values (Table 1) and using an arbitrary directional selection scheme of the population growth based on the values of the three traits, $5(x_1 - \overline{x_1}) + 3(x_2 - \overline{x_2}) - 2(x_3 - \overline{x_3}) + 100$, where x_k is the trait value 166 167 of trait k. The initial cover of ten species was generated for a hundred plots using a Dirichlet distribution 168 with all parameters set to one. The selection scheme was used on the generated initial covers of the 169 hundred plots and afterwards normalized to obtain resulting cover values that sum up to one for each plot. 170 Only the species-trait matrix, $T_{10,3}$, and the initial cover data, $q_{i,1}$, and resulting cover data, $q_{i,2}$, at plot i (i = 1, ..., 100) were used in the further analysis, thus resembling the conditions in a real plant ecological 171 172 study.

The joint posterior distribution of the parameters in likelihood function (4) was simulated using a Bayesian
MCMC algorithm (Metropolis-Hastings), where the parameters were assumed to have a uniform prior
distribution, except for *σ*, where the prior was assumed to have an inverse gamma distributed with the
parameters 0.001 and 0.001. The MCMC iterations had fair mixing properties and were judged to have
converged to a stable joint posterior distribution after a lag phase of 50.000 iterations (results not shown).
The joint posterior distribution was estimated from 50.000 iterations after the lag phase.
Statistical inferences on the individual parameters were based on the 95% credible intervals of the marginal

180 posterior distributions. All calculations were done using *Mathematica* version 10 (Wolfram, 2015).

The generated cover data was successfully fitted by likelihood function (4) and the marginal posterior
distributions of the parameters are summarized in Table 2. There were significant differences among
several of the growth parameters and all nine growth parameters differed significantly from zero (Table 1).
This indicates, although by using artificially generated plant cover data, that it is possible to estimate the
effect of traits on population growth with an acceptable signal-to-noise relationship when fitted to hundred
plots, which is a realistic number of replicates in ecological studies.

187 The covariance matrix of the joint posterior distribution and the graphs of the parameter iterations (not

- 188 shown) showed almost no covariance between a_k and c_k . This generally indicates that it is possible to
- 189 partition direct population growth and population growth that is mediated by interspecific interaction.

190 **Discussion**

- 191 Most importantly, a number of quite specific assumptions on the nature of selection and how the different
- traits interact (eqn. 1, 2 and 3), is needed to set up the model and to meet the objectives of the empirical
- 193 modelling, i.e. to estimate the selection forces on traits while at the same time to discriminate between
- 194 environmental filtering and niche partitioning processes. Such a modelling approach is in sharp contrast to
- 195 the more simple and elegant maximum entropy models, where it is not necessary to specify detailed
- 196 models on selection forces and how the different traits interact (Shipley, 2010a; Shipley, 2010b).
- 197 Consequently, in the modelling approach presented in this study it is critical to assess or test the different
- 198 necessary assumptions using either prior knowledge or model selection techniques.

As an additional tool in the model selection process valuable information may be obtained by estimates the structural variance, which is the variance that is not explained by the model and the underlying assumptions. If the structural variance is relative small then this is indirect evidence that the underlying assumptions to a certain degree are supported by the data. In the presented simple case-study the median estimate of the structural standard deviation was 0.0984 (Table 2), which should be compared with the expected cumulative cover changes of ten species with three traits. However, more worked-out empirical
examples of real data are needed in order to assess the importance of this level of structural variation.
Finally, the conclusions of the model should of course be compared with independent information or
hypotheses on the nature of trait selection.

208 For simplification it is assumed in model (1) that there is no significant intra-specific trait variation (but see 209 Laughlin et al., 2012) or intra-specific variation in population growth rate. Generally, using model selection 210 techniques, it will be possible to test what type of selection (directional selection, stabilizing selection, or 211 disruptive selection) is best supported by the data and, consequently, to generate and test hypothesis on 212 trait based assembly rules and possible mechanisms underlying plant species coexistence. Furthermore, if 213 plant abundance of perennial plants is measured several times during a growth season, e.g. in spring and 214 autumn, then the trait selection processes during summer growth may be estimated independently from 215 the trait selection processes during over-wintering and, consequently, allows the generation and testing of 216 temporal coexistence mechanisms (storage effects, Chesson, 2000).

217 Regarding the used assumption on the interactions between traits, model (1) assumes additivity among the 218 traits in regulating population growth. Generally, little information exists on the interaction among traits 219 (Kraft et al., 2015b), but the covariance matrix of the estimated selection coefficients a_k and c_k may give 220 important insight on the selection forces operating on a suite of correlated plant traits, e.g. specific leaf 221 area and leaf dry matter content, as previously demonstrated by e.g. Lande and Arnold Lande (1983). Again, the above-discussed model selection techniques may be used to discriminate between different 222 223 hypotheses, and in the case that some modes of interactions are not supported by data it may be 224 concluded that new ecological insight has been established.

In the presented simple demonstration case, the used cover data were generated assuming a uniform
environment, but if the cover data had been sampled along an environmental gradient, then the selection
models (2) can be made dependent on the environmental gradient; and the effect of traits on population

growth can then be estimated as functions of the environmental gradient. In similar ways, the selection
models (2) can be modified to fit many different ecological circumstances and the demonstrated model in
this paper is only one possibility of a large class of models that may be fitted using the outlined
methodology. The model is currently being used to examine the effect of plant competition on trait
selection along a hydrological gradient (Damgaard et al, in prep.)

Generally, it will be possible to generate ecological predictions with a known degree of uncertainty from
the outlined trait selection model by inserting values from the joint posterior distribution of the parameters
into numerical iterations or a numerical solution of equation (1). Such ecological predictions may be used
directly in applied plant ecological questions, e.g. effects of climate change, pesticides, or nitrogen
deposition on plant communities.

238 The outlined trait selection model is a one-step trait selection process that only operates locally and is, 239 thus, conceptually simpler than the two-step process meta-community model that previously has been 240 used (e.g. Bernard-Verdier et al., 2012; Webb et al., 2010). One of the advantages of this simpler model is 241 that it allows ecological predictions to be generated without knowledge on meta-community dynamics which, typically, is unknown. The data requirements of the presented model are modest, i.e. time series 242 243 data on plant species abundance and a species - trait matrix. Consequently, the model may be used to 244 model trait selection, including the effect of interspecific interactions, in many existing plant ecological 245 datasets. Naturally, the method is extendable so that time series longer than two years or time series data with irregular sampling intervals also may be fitted. 246

In the used modelling approach interspecific interactions are measured directly using time series plant
abundance data as the effect neighboring plants have on growth (Damgaard, 2011; Damgaard et al., 2009;
Damgaard et al., 2013; Damgaard et al., 2014), and this allows us to model the underlying ecological
processes. In my opinion, the filter analogy has been overused in empirical plant ecological trait literature,
e.g. when loosely referring to a "competitive filter" or "biotic filter" without specifying the details of the

- underlying ecological processes (Kraft et al., 2015a). Since multiple assembly processes can lead to the
- same pattern of trait dispersion and the same process can lead to different patterns of trait dispersion
- 254 (Herben and Goldberg, 2014), it is a clear advantage of the outlined model that it operates on the process
- level and that it is possible to mathematically describe the details of different ecological processes within
- the framework.

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260 Tables and figures

Species	Trait 1	Trait 2	Trait 3
1	3	2	3
2	2	4	2
3	4	1	6
4	7	5	3
5	2	3	8
6	9	4	4
7	2	3	6
8	4	6	5
9	6	3	1
10	5	1	5

261	Table 1. The used	species-traits	matrix with ten	species and	three traits, $T_{10.3}$.
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Table 2. The marginal distribution of the parameters of likelihood function (4) summarized by their 2.5%,

Parameter	2.5%	50%	97.5%	P(X > 0)
<i>a</i> ₁	0.0911	0.0952	0.1011	1
a_2	0.0907	0.0957	0.1003	1
<i>a</i> ₃	0.0615	0.0658	0.0696	1
b_1	0.0019	0.0038	0.0063	1
b_2	0.0001	0.0012	0.0032	0.986
b ₃	0.0033	0.0052	0.0070	1
<i>c</i> ₁	-0.0894	-0.0817	-0.0740	0
<i>C</i> ₂	-0.2092	-0.1968	-0.1818	0
<i>C</i> ₃	-0.3053	-0.2933	-0.2820	0
σ	0.0941	0.0984	0.1029	1

265 50%, 97.5% percentiles and the probability that the parameter is larger than zero.

266

267

268

- Fig. 1. Conceptual figure of the one-step selection model, where q_j is the cover of plant species j with trait
- values $t_k = x$, q'_j is the predicted cover of plant species *j* the following year under the influence of both
- direct selection forces, F(x), and selection forces mediated by interspecific interactions, C(x, y).



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