Empirical modelling of trait selection by partitioning
selection into direct selection and selection that is
mediated by interspecific interactions

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Abstract

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

Keywords: interspecific interactions; competition; trait selection; selection model; directional selection; stabilizing selection; disruptive selection; plant cover
Introduction

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

An increasingly popular way of describing plant communities is to focus on the expressed phenotypes of the plant species, i.e. plant traits, rather than on the species itself. The advantage is that plant traits are characteristic features, which to a certain extent will determine the survival, growth and reproductive strategies of the species, and are expected to respond in a more predictable way to an altered environment than the observed change in species composition (Damgaard et al., 2014; Garnier et al., 2004; Pellissier et al., 2014; Shipley, 2010a). Furthermore, plant traits involved in resource acquisition and use at the species level will scale-up to ecosystem functioning, provided that traits are weighed by the species' contribution to the community (Garnier et al., 2007; Lavorel and Garnier, 2002).
Generally, the selection response for the individual traits may be classified into either i) directional selection, where either relatively high or low trait values are favored, ii) stabilizing selection, where specific intermediary trait values are favored over all other trait values, or iii) disruptive selection, where extreme values for a trait are favored over intermediate values. Furthermore, the selection response of different plants traits may be broadly classified into either i) competitive effect traits, which are traits that reduce resource availability to neighboring plants through plant activity, e.g. plant height, where a high plant reduces the amount and quality of light that is received by shorter neighboring plants and ii) competitive response traits, which are traits that capture the response of a plant to the change in resource availability due to the activity of other plants, e.g. decreasing leaf thickness as a response to decreasing light availability (Violle et al., 2009).

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 (Hutchinson, 1957). 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) (Bernard-Verdier et al., 2012).

Using such test procedures, several plant ecological studies have reported non-random trait dispersion distributions in favor of different niche-based community assembly hypotheses compared to the neutral
hypothesis of plant community assembly (Weiher et al., 2011). However, this test procedure has been
criticized by e.g. Adler et al. (2013), who argue that trait dispersion tests have low power to detect niche
partitioning, and that patterns typically interpreted as either environmental filtering or niche partitioning
may be generated by the same process. Most importantly, Adler et al. (2013) note that: “The common
interpretation is that species interactions play no role in the abiotic environmental filtering process, while
abiotic factors play no role in the competitively driven niche partitioning process. However, the dichotomy
between environmental filtering and niche partitioning can arise from an arbitrary decision about the
spatial scale of analysis, not from distinct biological processes”. Furthermore, 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 (Herben and Goldberg, 2014), it is not possible to generate ecological
predictions on the effects of e.g. environmental changes on plant traits simply by comparing observed trait
distributions with random expectations.

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
(Bastrup-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, which is the
main objective of this study.

Consequently, in order to make progress in the understanding of the role and nature of niche-based
community assembly processes in the structuring of plant communities, it would be beneficial to be able i)
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.

To meet these objectives, I present a method for estimating the effect of species trait values on observed
population growth in a plant community by estimating parameters in two complementary population
growth functions that model both environmental filtering processes (in the following denoted direct
population growth) and niche partitioning processes (in the following called population growth that is
mediated by interspecific interaction). The underlying idea of the method is to mathematically partition the
effect of traits on direct population growth and population growth that is mediated by interspecific
interaction by two complementary functions. The resulting model is a one-step trait selection process that
operates locally and thus is conceptually simpler than the two-step process 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 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.

The aim of this paper is to present a model where the effects of plant traits on population growth is
estimated from simple longitudinal plant cover data and where the effect of traits is partitioned into direct
population growth and population growth that is mediated by interspecific interaction.

Model

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

The local abundance of the plant species is measured by their relative abundance measured by either
biomass or cover at time 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.

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

$$q'_j = q_j \sum_{k=1}^{m} \left( F_k(x) \left( \sum_{y \in \Omega(t_k)} C_k(x, y) q_{t_k=y} \right) \right) + \epsilon$$

(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 $k$ with a distance function between trait value $x$ and $y$,

where $\Omega(t_k)$ is all trait values for plant trait $k$ in the community, and where $C_k(x, x) = 1$. The effects of the

$m$ traits on plant population growth were in this simple analysis assumed to be additive; but see the later
discussion on the possibilities of relaxing this important assumption. The predicted cover of plant species is

not bounded between zero and one and, consequently, the predicted cover was fitted to the observed
cover using a normal distribution, where the standard deviation was scaled by the observed cover times

one minus the observed cover, i.e. $\epsilon \sim N(0, q_j(1 - q_j)\sigma)$ . Most importantly, the parameter, $\epsilon$ , estimates

the structural variance in the change in cover, which is the variance that is not explained by the model (1),

and may consequently be used to get an estimate on the quantitative importance of the simplifying

assumptions used in the modelling process.

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, but here two simple
directional selection functions are chosen in order to illustrate the method,

$$F_k(x) = a_k x + b_k$$

(2a),
After inserting (2a) and (2b) into (1), the resulting model may be fitted to $N$ observed plots with cover data from two consecutive years, i.e. the parameters of interest may be estimated by the likelihood function,

$$L(a, b, c, \sigma) = \prod_{i=1}^{N} \prod_{j=1}^{n} \frac{1}{\sqrt{2\pi}q_{j,t+1}(1-q_{j,t+1})\sigma} \exp\left(-\frac{(q_{j,t} - q_{j,t+1})^2}{(q_{j,t+1}(1-q_{j,t+1})\sigma)^2}\right)$$

(3).

**Example data**

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 an ecological realistic data type.

An arbitrary species-trait matrix with ten species and three traits, $T_{10,3}$, was constructed with random integer values (Table 1) and using an arbitrary directional selection scheme of the population growth based on the values of the three traits, $5(x_1 - \bar{x}_1) + 3(x_2 - \bar{x}_2) - 2(x_3 - \bar{x}_3) + 100$, where $x_k$ is the trait value of trait $k$.

The initial cover of ten species was generated for a hundred plots using a Dirichlet distribution with all parameters set to one.

The selection scheme was used on the generated initial covers of the hundred plots and afterwards normalized to obtain resulting cover values that sum up to one for each plot.

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 $i$ ($i = 1, \ldots, 100$) were used in the further analysis, thus resembling the conditions in a real plant ecological study.
Estimation

The joint posterior distribution of the parameters in likelihood function (3) was simulated using a Bayesian MCMC algorithm (Metropolis-Hastings), where the parameters were assumed to have a uniform prior distribution, except for $\sigma$, 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 posterior distributions.

All calculations were done using Mathematica version 10 (Wolfram, 2015).

Results and Discussion

The generated cover data was successfully fitted by likelihood function (3) 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.

The covariance matrix of the joint posterior distribution and the graphs of the parameter iterations (not shown) showed almost no covariance between $a_k$ and $c_k$. This generally indicates that it is possible to partition direct population growth and population growth that is mediated by interspecific interaction.

Most importantly, a number of quite specific assumptions on the nature of selection and how the different traits interact (eqn. 1 and 2), is needed to set up the model and to meet the objectives of the empirical
modelling, i.e. to estimate the selection forces on traits while at the same time to discriminate between environmental filtering and niche partitioning processes. Such a modelling approach is in sharp contrast to the more simple and elegant maximum entropy models, where it is not necessary to specify detailed models on selection forces and how the different traits interact (Shipley, 2010a; Shipley, 2010b).

Consequently, in the modelling approach presented in this study it is critical to assess or test the different 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. Regarding the used assumption on the nature of selection, the cover data in the presented case-study were generated using a directional selection model and, consequently, analysed using directional selection models (2). However, if there is prior knowledge that indicates either stabilizing or disruptive selection is occurring for a subset of the traits, then the selection models (2) may be replaced by more relevant selection models for these traits. For example, the following model may be relevant in the case of stabilizing selection,

\[ F_k(x) = a_k (x - z_k)^2 + b_k \]  (4a),

\[ C_k(x, y) = \exp(-c_k (y - z_k)^2)/\exp(-c_k (x - z_k)^2) \]  (4b),
where $z_k$ is an optimum intermediary trait value. Likewise the following model may be relevant in the case
of disruptive selection,

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

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

where $z_k$ is a minimum intermediary trait value with fitness $m_k$.

Generally, using model selection techniques, it will be possible to test what type of selection (directional
selection, stabilizing selection, or disruptive selection) is best supported by the data and, consequently, to
generate and test hypothesis on trait based assembly rules and possible mechanisms underlying plant
species coexistence. Furthermore, if plant abundance of perennial plants is measured several times during
a growth season, e.g. in spring and autumn (Damgaard, 2011; Damgaard et al., 2013; Damgaard et al., in
press), then the trait selection processes during summer growth may be estimated independently from the
trait selection processes during over-wintering and, consequently, allows the generation and testing of
temporal coexistence mechanisms (storage effects, Chesson, 2000).

Regarding the used assumption on the interactions between traits, model (1) assumes additivity among the
traits in regulating population growth. Generally, little information exists on the interaction among traits
(Kraft et al., 2015b), but perhaps it will be beneficial to aggregate co-varying traits into higher-order traits.
For example, it could be relevant to construct a compound leaf trait function that takes both SLA and LDMC
as arguments, which is established from prior knowledge. Again, the above-discussed model selection
techniques may be used to discriminate between different hypotheses, and in the case that some modes of
interactions are not supported by data it may be concluded that new ecological insight has been
established.
Quite generally, I would argue that only if you risk the neck and make specific assumptions on the nature of different ecological processes, it will be possible to falsify some of those assumptions that are not supported by data, which ultimately will lead to an increased understanding of the ecological processes.

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.

The outlined trait selection model is a one-step trait selection process that only operates locally and is, thus, conceptually simpler than the two-step process meta-community model that previously has been used (e.g. Bernard-Verdier et al., 2012; Webb et al., 2010). One of the advantages of this simpler model is 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 data on plant species abundance and a species – trait matrix. Consequently, the model may be used to model trait selection, including the effect of interspecific interactions, in many existing plant ecological
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.

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., in press), 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
(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

Acknowledgement

Thanks to Zdeněk Janovský for valuable comments on a previous version of the manuscript
## Tables and figures

Table 1. The used species-trait matrix with ten species and three traits, $T_{10,3}$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trait 1</th>
<th>Trait 2</th>
<th>Trait 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>1</td>
<td>6</td>
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<td>6</td>
<td>3</td>
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</tr>
<tr>
<td>10</td>
<td>5</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>
Table 2. The marginal distribution of the parameters of likelihood function (4) summarized by their 2.5%, 50%, 97.5% percentiles and the probability that the parameter is larger than zero.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2.5%</th>
<th>50%</th>
<th>97.5%</th>
<th>P(X &gt; 0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_1$</td>
<td>0.0911</td>
<td>0.0952</td>
<td>0.1011</td>
<td>1</td>
</tr>
<tr>
<td>$a_2$</td>
<td>0.0907</td>
<td>0.0957</td>
<td>0.1003</td>
<td>1</td>
</tr>
<tr>
<td>$a_3$</td>
<td>0.0615</td>
<td>0.0658</td>
<td>0.0696</td>
<td>1</td>
</tr>
<tr>
<td>$b_1$</td>
<td>0.0019</td>
<td>0.0038</td>
<td>0.0063</td>
<td>1</td>
</tr>
<tr>
<td>$b_2$</td>
<td>0.0001</td>
<td>0.0012</td>
<td>0.0032</td>
<td>0.986</td>
</tr>
<tr>
<td>$b_3$</td>
<td>0.0033</td>
<td>0.0052</td>
<td>0.0070</td>
<td>1</td>
</tr>
<tr>
<td>$c_1$</td>
<td>-0.0894</td>
<td>-0.0817</td>
<td>-0.0740</td>
<td>0</td>
</tr>
<tr>
<td>$c_2$</td>
<td>-0.2092</td>
<td>-0.1968</td>
<td>-0.1818</td>
<td>0</td>
</tr>
<tr>
<td>$c_3$</td>
<td>-0.3053</td>
<td>-0.2933</td>
<td>-0.2820</td>
<td>0</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>0.0941</td>
<td>0.0984</td>
<td>0.1029</td>
<td>1</td>
</tr>
</tbody>
</table>
Fig. 1. Conceptual figure of the 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, $C(x,y)$. 

$q_j \rightarrow F(x) \rightarrow C(x,y) \rightarrow q'_j$
References


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