

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 whether 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 (Damgaard et al., 2014; Garnier et al., 2004; Pellissier et  
43 al., 2014; Shipley, 2010a). Furthermore, plant traits involved in resource acquisition and use at the species  
44 level will scale-up to ecosystem functioning, provided that traits are weighed by the species' contribution to  
45 the community (Garnier et al., 2007; Lavorel and Garnier, 2002).

46 Generally, the selection response for the individual traits may be classified into either i) directional  
47 selection, where either relatively high or low trait values are favored, ii) stabilizing selection, where specific  
48 intermediary trait values are favored over all other trait values, or iii) disruptive selection, where extreme  
49 values for a trait are favored over intermediate values. Furthermore, the selection response of different  
50 plants traits may be broadly classified into either i) competitive effect traits, which are traits that reduce  
51 resource availability to neighboring plants through plant activity, e.g. plant height, where a high plant  
52 reduces the amount and quality of light that is received by shorter neighboring plants and ii) competitive  
53 response traits, which are traits that capture the response of a plant to the change in resource availability  
54 due to the activity of other plants, e.g. decreasing leaf thickness as a response to decreasing light  
55 availability (Violle et al., 2009).

56 The trait selection process has previously been described by a two-step process in a meta-community  
57 model, where plants from a regional species pool are dispersed to a local habitat, and trait filtering  
58 excludes individuals with unfit trait values, and within the local species pool, trait values may influence  
59 performance, which may lead to patterns of trait convergence or divergence (e.g. Bernard-Verdier et al.,  
60 2012; Webb et al., 2010). The selection due to performance differences in the local species pool is thought  
61 to be mediated by interspecific interactions as the difference between the fundamental niche and the  
62 realized niche of the local species (Hutchinson, 1957). Under this framework, the effect of interspecific  
63 interactions is detected from deviations of the observed trait distribution from random expectations in the  
64 local species pool. If the variance of the observed trait distribution is lower than the random expectations,  
65 this is an indication of directional or stabilizing selection (convergent trait distribution pattern). Conversely,  
66 if the variance of the observed trait distribution is higher than the random expectations, this is an indication  
67 of disruptive selection (divergent trait distribution pattern) (Bernard-Verdier et al., 2012).

68 Using such test procedures, several plant ecological studies have reported non-random trait dispersion  
69 distributions in favor of different niche-based community assembly hypotheses compared to the neutral

70 hypothesis of plant community assembly (Weiher et al., 2011). However, this test procedure has been  
71 criticized by e.g. Adler et al. (2013), who argue that trait dispersion tests have low power to detect niche  
72 partitioning, and that patterns typically interpreted as either environmental filtering or niche partitioning  
73 may be generated by the same process. Most importantly, Adler et al. (2013) note that: “The common  
74 interpretation is that species interactions play no role in the abiotic environmental filtering process, while  
75 abiotic factors play no role in the competitively driven niche partitioning process. However, the dichotomy  
76 between environmental filtering and niche partitioning can arise from an arbitrary decision about the  
77 spatial scale of analysis, not from distinct biological processes”. Furthermore, since multiple assembly  
78 processes can lead to the same pattern of trait dispersion and the same process can lead to different  
79 patterns of trait dispersion (Herben and Goldberg, 2014), it is not possible to generate ecological  
80 predictions on the effects of e.g. environmental changes on plant traits simply by comparing observed trait  
81 distributions with random expectations.

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

89 Consequently, in order to make progress in the understanding of the role and nature of niche-based  
90 community assembly processes in the structuring of plant communities, it would be beneficial to be able i)  
91 to estimate the effect of interspecific interactions on traits rather than just testing whether selection has  
92 had an effect on the observed trait distributions, ii) to discriminate between environmental filtering and

93 niche partitioning processes and estimate the characteristic features and importance of both processes,  
94 and iii) to predict the effect of environmental changes and gradients on trait selection.

95 To meet these objectives, I present a method for estimating the effect of species trait values on observed  
96 population growth in a plant community by estimating parameters in two complementary population  
97 growth functions that model both environmental filtering processes (in the following denoted *direct*  
98 population growth) and niche partitioning processes (in the following called population growth that is  
99 *mediated by interspecific interaction*). The underlying idea of the method is to mathematically partition the  
100 effect of traits on direct population growth and population growth that is mediated by interspecific  
101 interaction by two complementary functions. The resulting model is a one-step trait selection process that  
102 operates locally and thus is conceptually simpler than the two-step process meta-community model that  
103 previously has been used (e.g. Bernard-Verdier et al., 2012; Webb et al., 2010). Furthermore, a one-step  
104 trait selection response is probably a more realistic model of the selection process, since there are no  
105 compelling reasons for why the processes of environmental filtering and niche partitioning should not  
106 operate simultaneously.

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

## 110 **Model**

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

114 The local abundance of the plant species is measured by their relative abundance measured by either  
115 biomass or cover at time  $t$ , where  $\sum_{j=1}^n q_{j,t} = 1$ . The plants grow, die and reproduce  $q_j$  under the influence of

116 interspecific interactions at a given environment where certain combinations of plant traits have a positive  
117 effect on growth and reproduction and other combinations of plant traits have a negative effect on growth  
118 and reproduction.

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

$$120 \quad q'_j = q_j \sum_{k=1}^m \left( F_k(x) \left( \sum_{y \in \Omega(t_k)} C_k(x, y) q_{t_k=y} \right) \right) + \varepsilon \quad (1),$$

121 where  $F_k(x)$  is the direct population growth function of plant species with trait value  $x$  for plant trait  $k$ ,  
122 and  $C_k(x, y)$  is a function that models the effect of interspecific interactions on population growth of plant  
123 species with trait value  $x$  for plant trait  $k$  with a distance function between trait value  $x$  and  $y$ ,  
124 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  
125  $m$  traits on plant population growth were in this simple analysis assumed to be additive; but see the later  
126 discussion on the possibilities of relaxing this important assumption. The predicted cover of plant species is  
127 not bounded between zero and one and, consequently, the predicted cover was fitted to the observed  
128 cover using a normal distribution, where the standard deviation was scaled by the observed cover times  
129 one minus the observed cover, i.e.  $\varepsilon \sim N(0, q_j(1 - q_j)\sigma)$ . Most importantly, the parameter,  $\varepsilon$ , estimates  
130 the structural variance in the change in cover, which is the variance that is not explained by the model (1),  
131 and may consequently be used to get an estimate on the quantitative importance of the simplifying  
132 assumptions used in the modelling process.

133 The population growth functions  $F_k(x)$  and  $C_k(x, y)$  may vary according to plant life forms, habitat type,  
134 and existing prior knowledge of e.g. the type of selection on the different traits, but here two simple  
135 directional selection functions are chosen in order to illustrate the method,

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

137  $C_k(x, y) = \text{Exp}(-c_k (y - x))$  (2b).

138

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

141 
$$L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \sigma) = \prod_{i=1}^N \prod_{j=1}^n \frac{1}{\sqrt{2\pi} q_{j,t+1} (1-q_{j,t+1}) \sigma} \text{Exp} \left( -\frac{(q'_{j,t} - q_{j,t+1})^2}{(q_{j,t+1} (1-q_{j,t+1}) \sigma)^2} \right)$$
 (3).

## 142 Example data

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

146 An arbitrary species-traits matrix with ten species and three traits,  $\mathbf{T}_{10,3}$ , was constructed with random  
147 integer values (Table 1) and using an arbitrary directional selection scheme of the population growth based  
148 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  
149 of trait  $k$ .

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

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

154 Only the species-trait matrix,  $\mathbf{T}_{10,3}$ , and the initial cover data,  $\mathbf{q}_{i,1}$ , and resulting cover data,  $\mathbf{q}_{i,2}$ , at plot  $i$   
155 ( $i = 1, \dots, 100$ ) were used in the further analysis, thus resembling the conditions in a real plant ecological  
156 study.

## 157 Estimation

158 The joint posterior distribution of the parameters in likelihood function (3) was simulated using a Bayesian  
159 MCMC algorithm (Metropolis-Hastings), where the parameters were assumed to have a uniform prior  
160 distribution, except for  $\sigma$ , where the prior was assumed to have an inverse gamma distributed with the  
161 parameters 0.001 and 0.001. The MCMC iterations had fair mixing properties and were judged to have  
162 converged to a stable joint posterior distribution after a lag phase of 50.000 iterations (results not shown).  
163 The joint posterior distribution was estimated from 50.000 iterations after the lag phase.

164 Statistical inferences on the individual parameters were based on the 95% credible intervals of the marginal  
165 posterior distributions.

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

## 167 Results and Discussion

168 The generated cover data was successfully fitted by likelihood function (3) and the marginal posterior  
169 distributions of the parameters are summarized in Table 2. There were significant differences among  
170 several of the growth parameters and all nine growth parameters differed significantly from zero (Table 1).  
171 This indicates, although by using artificially generated plant cover data, that it is possible to estimate the  
172 effect of traits on population growth with an acceptable signal-to-noise relationship when fitted to hundred  
173 plots, which is a realistic number of replicates in ecological studies.

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

177 Most importantly, a number of quite specific assumptions on the nature of selection and how the different  
178 traits interact (eqn. 1 and 2), is needed to set up the model and to meet the objectives of the empirical

179 modelling, i.e. to estimate the selection forces on traits while at the same time to discriminate between  
180 environmental filtering and niche partitioning processes. Such a modelling approach is in sharp contrast to  
181 the more simple and elegant maximum entropy models, where it is not necessary to specify detailed  
182 models on selection forces and how the different traits interact (Shiple, 2010a; Shiple, 2010b).  
183 Consequently, in the modelling approach presented in this study it is critical to assess or test the different  
184 necessary assumptions using either prior knowledge or model selection techniques.

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

194 Regarding the used assumption on the nature of selection, the cover data in the presented case-study were  
195 generated using a directional selection model and, consequently, analysed using directional selection  
196 models (2). However, if there is prior knowledge that indicates either stabilizing or disruptive selection is  
197 occurring for a subset of the traits, then the selection models (2) may be replaced by more relevant  
198 selection models for these traits. For example, the following model may be relevant in the case of  
199 stabilizing selection,

$$200 \quad F_k(x) = a_k (x - z_k)^2 + b_k \quad (4a),$$

$$201 \quad C_k(x, y) = \text{Exp}(-c_k (y - z_k)^2) / \text{Exp}(-c_k (x - z_k)^2) \quad (4b),$$

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

$$204 \quad F_k(x) = a_k (x - z_k)^2 + b_k \quad (5a),$$

$$205 \quad C_k(x, y) = (1 - m_k) (1 - \text{Exp}(-c_k (y - z_k)^2)) / (1 - \text{Exp}(-c_k (x - z_k)^2)) + m_k \quad (5b),$$

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

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

215 Regarding the used assumption on the interactions between traits, model (1) assumes additivity among the  
216 traits in regulating population growth. Generally, little information exists on the interaction among traits  
217 (Kraft et al., 2015b), but perhaps it will be beneficial to aggregate co-varying traits into higher-order traits.  
218 For example, it could be relevant to construct a compound leaf trait function that takes both SLA and LDMC  
219 as arguments, which is established from prior knowledge. Again, the above-discussed model selection  
220 techniques may be used to discriminate between different hypotheses, and in the case that some modes of  
221 interactions are not supported by data it may be concluded that new ecological insight has been  
222 established.

223 Quite generally, I would argue that only if you risk the neck and make specific assumptions on the nature of  
224 different ecological processes, it will be possible to falsify some of those assumptions that are not  
225 supported by data, which ultimately will lead to an increased understanding of the ecological processes.

226 In the presented simple demonstration case, the used cover data were generated assuming a uniform  
227 environment, but if the cover data had been sampled along an environmental gradient, then the selection  
228 models (2) can be made dependent on the environmental gradient; and the effect of traits on population  
229 growth can then be estimated as functions of the environmental gradient. In similar ways, the selection  
230 models (2) can be modified to fit many different ecological circumstances and the demonstrated model in  
231 this paper is only one possibility of a large class of models that may be fitted using the outlined  
232 methodology. The model is currently being used to examine the effect of plant competition on trait  
233 selection along a hydrological gradient (Damgaard et al, in prep.)

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

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

246 datasets. Naturally, the method is extendable so that time series longer than two years or time series data  
247 with irregular sampling intervals also may be fitted.

248 In the used modelling approach interspecific interactions are measured directly using time series plant  
249 abundance data as the effect neighboring plants have on growth (Damgaard, 2011; Damgaard et al., 2009;  
250 Damgaard et al., 2013; Damgaard et al., in press), and this allows us to model the underlying ecological  
251 processes. In my opinion, the filter analogy has been overused in empirical plant ecological trait literature,  
252 e.g. when loosely referring to a “competitive filter” or “biotic filter” without specifying the details of the  
253 underlying ecological processes (Kraft et al., 2015a). Since multiple assembly processes can lead to the  
254 same pattern of trait dispersion and the same process can lead to different patterns of trait dispersion  
255 (Herben and Goldberg, 2014), it is a clear advantage of the outlined model that it operates on the process  
256 level and that it is possible to mathematically describe the details of different ecological processes within  
257 the framework.

## 258 **Acknowledgement**

259 Thanks to Zdeněk Janovský for valuable comments on a previous version of the manuscript

260 **Tables and figures**

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

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

262

263

264 Table 2. The marginal distribution of the parameters of likelihood function (4) summarized by their 2.5%,  
265 50%, 97.5% percentiles and the probability that the parameter is larger than zero.

Parameter	2.5%	50%	97.5%	$P(X > 0)$
$a_1$	0.0911	0.0952	0.1011	1
$a_2$	0.0907	0.0957	0.1003	1
$a_3$	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
$c_1$	-0.0894	-0.0817	-0.0740	0
$c_2$	-0.2092	-0.1968	-0.1818	0
$c_3$	-0.3053	-0.2933	-0.2820	0
$\sigma$	0.0941	0.0984	0.1029	1

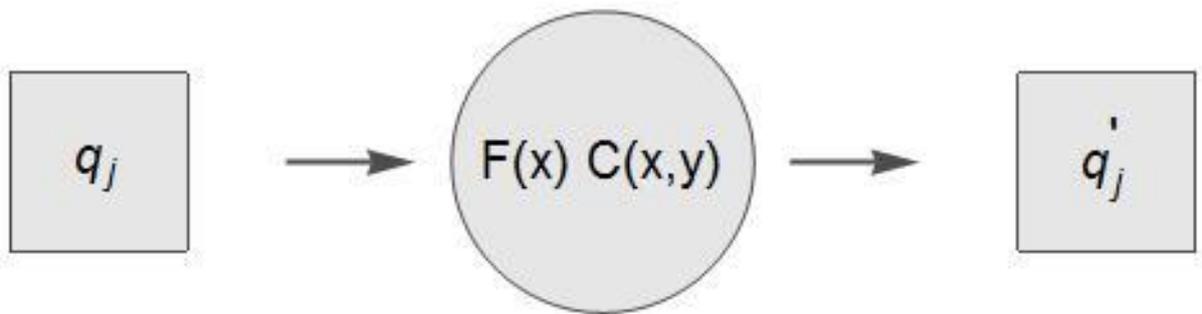
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270 Fig. 1. Conceptual figure of the selection model, where  $q_j$  is the cover of plant species  $j$  with trait  
271 values  $t_k = x$ ,  $q'_j$  is the predicted cover of plant species  $j$  the following year under the influence of both  
272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



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