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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Abstract

6

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

Introduction

22

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.

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, $\boldsymbol{T}_{n,m}$, 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 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    $$q'_j = q_j \sum_{k=1}^{m} \left(F_k(x) \left(\sum_{y \in \Omega(t_k)} C_k(x,y)\, q_{t_k=y} \right) \right) + \varepsilon \qquad (1),$$

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, ε , 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    $$F_k(x) = a_k\, x + b_k \qquad (2a),$$

137     $C_k(x, y) = Exp\big(-c_k\,(y - x)\big)$ (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     $L(\boldsymbol{a}, \boldsymbol{b}, \boldsymbol{c}, \sigma) = \prod_{i=1}^{N} \prod_{j=1}^{n} \frac{1}{\sqrt{2\pi} q_{j,t+1}\,(1 - q_{j,t+1})\sigma}\, Exp\left(-\frac{\left(q'_{j,t} - q_{j,t+1}\right)^2}{\left(q_{j,t+1}\,(1 - q_{j,t+1})\sigma\right)^2}\right)$ (3).

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, $\boldsymbol{T}_{10,3}$, 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, $5(x_1 - \overline{x_1}) + 3(x_2 - \overline{x_2}) - 2(x_3 - \overline{x_3}) + 100$, 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, $\boldsymbol{T}_{10,3}$, and the initial cover data, $\boldsymbol{q}_{i,1}$, and resulting cover data , $\boldsymbol{q}_{i,2}$, 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.

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 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

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

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 (Shipley, 2010a; Shipley, 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    $$F_k(x) = a_k \, (x - z_k)^2 + b_k \tag{4a},$$

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

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

205 $$C_k(x,y) = (1 - m_k) \left(1 - Exp(-c_k \, (y - z_k)^2)\right)/\left(1 - Exp(-c_k \, (x - z_k)^2)\right) + m_k \qquad (5b),$$

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

Tables and figures

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

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
σ	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, $C(x,y)$.
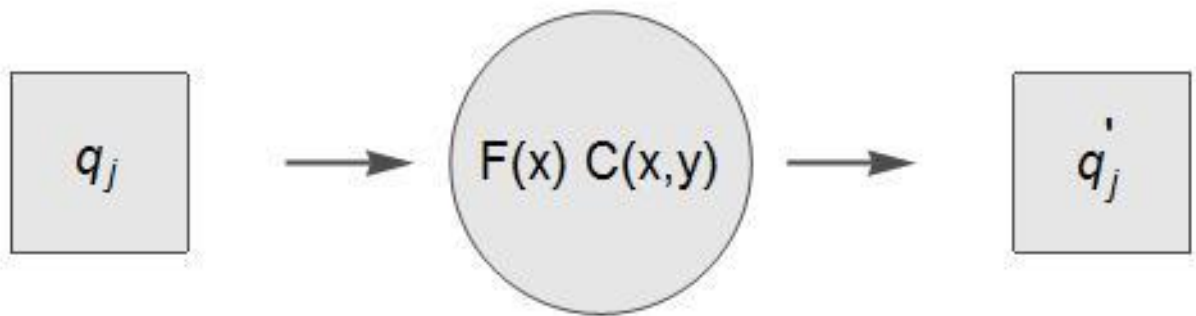
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