



HAL
open science

A nonlinear Bayesian model of trait selection forces

Rune Østergaard Pedersen, Anne Bonis, Christian Damgaard

► **To cite this version:**

Rune Østergaard Pedersen, Anne Bonis, Christian Damgaard. A nonlinear Bayesian model of trait selection forces. *Ecological Modelling*, 2019, 393, pp.107-119. 10.1016/j.ecolmodel.2018.12.002 . hal-02991038

HAL Id: hal-02991038

<https://hal.science/hal-02991038v1>

Submitted on 6 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Running headline: Trait selection forces

Title

A Nonlinear Bayesian model of trait selection forces

By Rune Østergaard Pedersen^a, Anne Bonis^b and Christian Damgaard^c

^a Aarhus University, Vejlsovej 25, 8600 Silkeborg, Denmark, E-mail address: rupd@bios.au.dk

^b UMR 6042 GEOLAB, CNRS - University Clermont Auvergne, Clermont-Ferrand, France

^c Aarhus University, Vejlsovej 25, 8600 Silkeborg, Denmark, E-mail address: cfd@bios.au.dk

Abstract

We model trait selection by deriving and comparing models for direct trait selection and selection that is mediated by interspecific interactions. The purpose is to model the two selection forces simultaneously, in order to account for potential trait covariance in the estimation procedure when including multiple trait values. In addition, we identify those traits most important for selection forces, and the role of flooding duration. A Bayesian modelling approach is applied and fitted to plant species cover including stochastic variable selection, to test the importance of individual traits on selection forces. We used pin-point data from wet grasslands of the French Atlantic Coast. Our results show that trait selection forces are driven by direct selection and, to a minor extent, by selection mediated by interspecific interactions. Of the tested traits leaf dry matter content (LDMC) and specific leaf area (SLA), seemed most important for selection forces. We find a significant effect of flooding on selection forces. Parameter covariance analysis revealed flooding to be most strongly correlated with direct selection forces. The method has less critical assumptions regarding the geographical limit of the ecological environment than a traditional filtering approach, and allows weighting traits simultaneously and accounting for their covariance. Inference is easy to obtain from the posterior parameter distributions of the Bayesian estimation. Thus, the Bayesian method presented is very objective. A program architecture is supplied in the R-programming language.

Keywords: Bayesian model, interspecific competition, multiple traits, plant cover, selection forces

1 Introduction

2 Local species assemblages made off local communities results from the selection of the regional species
3 pool by various filters.

4 Lortie et al. (2004) describes three filters, going from the coarse to the fine scale. The first filter is a
5 spatial/geographical filter, which provides a boundary limiting the spread of the species, for example the
6 sea or a mountain chain. The second level is a physiological filter, caused by environmental conditions
7 filtered plant species according to their respective tolerance. Finally, the biotic filter works by plant-plant
8 interaction by competition, symbiosis and facilitation. In praxis, all three levels must interact to some
9 extent, and also vary with a stochastic component, physiological and biotic filters interacted(Shipley (2010)
10 .

11 . For example, a drought intolerant plant will also compete less in a dry environment , whereas less intuitive
12 pattern of biotic interaction issues have also been find along elevation gradient (see e.g. Damgaard et al
13 2017, Oecologia. A Any modeling aiming to predict plant abundance pattern in environmental gradient
14 within their community must thus include both filters, and their effect at the adequate spatial scales.

15 Functional traits (Garnier et al., 2016) is a way to quantify the adaptative species' response to constraint ,
16 from plant community to larger levels of organization, i.e. across environmental gradients. At the same
17 time knowing the species composition on the community level they may be applied in models of spatial
18 interaction on the finest scale by traits. Thus, traits in models can work on different spatial resolutions.

19 In ecology, traits can be defined as measures of expected genetic heritable abilities of different species or
20 performance under idealized conditions having no restrains (McGill and Brown, 2007). Most often, the
21 traits refer to a pool of individuals in the environment rather than a single subject (Violle et al., 2007).

22 Traits are often applied in the study of selection forces of plant populations in a two-step process. Firstly,
23 through a survey the species of a habitat are identified, and, secondly, the distributional properties of their
24 traits are studied as a proxy for the filtering (pass through) facilitated by selection forces (Keddy, 1992,

25 Loranger et al. 2016). This is done by comparing observed trait pattern with a global species trait
26 distributional reference. If the variance of the local environment is less than expected by random sampling
27 in a null model (Bernard-Verdier et al., 2012), trait values are driven in a direction towards a common
28 stable equilibrium. If the variance is higher than at random, then the traits are selected in divergent
29 directions. The outcome of such a method depends on specification of the global trait pool and the
30 geographical area under investigation, the first of which it is critical to define properly because it serves as
31 an ecological reference model (Gotelli and Graves, 1996). The temporal stage of the area is also important,
32 since pioneering species will perform differently in different stages of succession. If the subjective
33 definition of the null model is biased relative to the “correct” one, then all successive results are influenced.
34 In addition, it can be difficult to distinguish which part of selection is due to niche partitioning and which is
35 due to interspecific competition (Adler et al., 2013), since both can result in the same trait distribution.
36 Another weakness of modelling each trait separately is that it neglects trait interaction and studies
37 selection forces of traits independently of each other. However, since traits are in fact multivariate
38 measures of potential plant performance, it seems reasonable to assume that they simultaneously will have
39 an impact on the outcome of the selection process (Garnier et al., 2016, P. 11 and 20). Studies using traits
40 often look at species diversity and its relation to trait variation (Dwyer and Laughlin, 2017). Because trait
41 variation and species richness seem not to be related in a simple linear way, covariance among trait, i.e. the
42 fact that traits express the same property or interact in a synergistic way, becomes important. Therefore,
43 new methods are required that look at traits simultaneously and integrate them in the selection process.
44 Traits are often surrogates, and initial exclusion of traits can be made e.g. by principal components analysis
45 (Bernard-Verdier et al., 2012; Johnson and Wichern, 2007), to reduce the number of model variables and
46 make parameter estimation easier. While a principal components analysis is an objective measure of
47 correlation, data variables need to be seen in a framework where the outcome of species competition
48 interaction is also included and confounding effects can be studied. Lavorel and Garnier (2002) underline
49 this point by differentiating traits that are causes/drivers of the pattern that we observe in nature (effect

50 traits) or merely a phenotype resulting from a response to affect and stress induced to the environments
51 (response traits).

52 As pointed out by Mather (1953), the selection forces may be divided into three possible outcomes:
53 directional, disruptive and stabilizing selection. If we assume that the original quantity of interest – for
54 example height of individuals over an area, is symmetrically distributed around a mean, then stabilizing
55 selection will result in the same mean, but less variance, i.e. the heights will become less dispersed.
56 Directional selection, on the other hand, will shift both the mean, but also the frequency in form of
57 skewness. The reason for this is that selection forces act differently on the extreme values of the initial
58 distribution. Disruptive selection tends to multimodality of the resulting distribution, i.e. more new optima.
59 Any model of selection forces must capture these theoretical outcomes.

60 For this purpose, Damgaard (2016) presented a method based on theoretical justifications and assumptions
61 about the competitive processes using nonlinear models. These models make it possible to:

- 62 1) Decide which of the three types of fundamental selection forces described by Mather that are
63 supported by the data.
- 64 2) Differentiate between the direct selection forces originating from traits alone and selection that is
65 mediated by interspecific interactions.

66 We make the first practical implementation of the method of Damgaard in order to study the empirical
67 process of trait selection. The models of Damgaard are essentially modifier functions made according to
68 our expectation on different types of directional selection. In addition, a term involving species interaction
69 is applied. The general form of the model is:

70 Equation 1
$$q' = q * F * C$$

71 Where q' is the quantitative outcome of selection forces collected in a survey, e.g. observed cover, and q is
72 the cover in the previous year. F is the expression of the direct trait selection forces, and C is an expression

73 of selection that is mediated by interspecific interactions. We give different examples of modifier functions
74 and put them into the context of the selection forces. Adler et al. (2013) advocate that any model of
75 competition should include spatial as well as temporal variation in the environment and its resources in
76 order to incorporate the carrying capacity of the plant species (niche differentiation) and competitive
77 pressure caused by the spatial pattern (Wyszomirski and Weiner, 2009). We therefore model the spatial
78 scale at two levels, firstly at a landscape level with a flooding gradient in order to include the effect of
79 hydrology on species interaction and the impact of change in the species ecological and physical amplitude
80 (Bernard-Verdier et al., 2012). This is a proxy variable for the realized and fundamental niche (Harper,
81 1977). Secondly, we model at a plot level where species interactions could be present. Hence, we include
82 both niche differentiation and competitive effects. The mathematical formulation is important for the
83 spatial incorporation of spatial effect, and this is done by means of the $F * C$ terms, which will be described
84 more in detail later. We apply a Bayesian framework, as it allows for inference of the model parameters
85 using their posterior distribution without dubious assumptions or mathematical approximations of the joint
86 distribution of model parameters (Montgomery et al., 2006, p. 546).

87 The objectives of the study are:

- 88 a) To develop and fit a model of the selection forces in a natural environment, which include space,
89 time and multiple traits.
- 90 b) To test whether direct selection forces and selection that is mediated by interspecific interactions
91 are important for species abundance.
- 92 c) To see whether hydrology has an impact on the selection forces.

93 **Materials and Methods**

94 **Sampling design**

95 The data was collected using the pin-point method, where a frame 25*25 cm contain points positioned
96 along the diagonal of the frame located with 4 cm apart yielding 17 pin-points per frame for 70 plots. At
97 each point, a needle was positioned vertically towards the ground and a plant species was recorded, if it
98 touched the needle. The fraction of the plant relative to all recorded species in the grid could then be
99 calculated and applied as plant cover (q).

100 Measurements in the first period took place from 23-29 October 2008 and in the second period from 19-20
101 October 2009. We made the assumption that plot cover of species between the years could be regarded as
102 paired observations, despite the fact that it was not measured exactly at the same time of the year. This
103 has previously been tested using the data in the current study and has proven to be a valid approach
104 (Damgaard et al., 2016).

105 **Study area and data**

106 The data was collected in the Marais poitevin marshland on the French Atlantic coast (46°26N, 1°13W). The
107 marshland is grazed by cattle and horse, and the plots were fenced to prevent grazing during the study
108 period. The plant community is dominated by different grass species, mainly *Agrostis Stolonifera* (L.) (51 %
109 of pinpoint observations) and *Cynosurus Cristatus* (L.) (Around 13 %). A summary is given in Figure 1 and
110 the right column of Table 1. The mean precipitation falls in the winter, with a surplus of 220 mm
111 precipitation when accounting for evapotranspiration. The summer has a deficit of 300-350 mm (Amiaud et
112 al., 1998). The average of the minimum*, and maximum** temperatures in the four seasons are
113 respectively (winter 3*,9.7**; spring 6.3*,15**, summer 13*,23.3**, autum:8.7*,17**) (taken from the
114 city La-Rochelle – France) (Climatedata.eu, 2017). Damgaard *et al.* (2016) gives a more detailed description
115 of the study site.

116 For each plot, the traits were measured and an average abundance was taken as a general estimate of trait
117 performance for each species in the data, though other methods using a probability weighted average
118 could also have been used (Bernard-Verdier et al., 2012). The trait values can be seen in Table 1. We
119 selected the species trait values specific leaf area (SLA), measured on one-side divided by its oven dry mass
120 (m^2/kg), leaf dry matter content (LDMC) (mg/g), calculated as the ratio between oven-dry mass of leaf
121 divided by its water saturated mass, and vegetative height (m), defined as distance between the top of the
122 species and the ground.

123 These traits are considered important measures of plant fitness (Dwyer and Laughlin, 2017) on for example
124 vegetative growth (LDMC), light competition (Vegetation height), and respirational processes (SLA). For the
125 species *Plantago major* (L.), the LDMC was missing and set to the average during the calculations.

126 Flooding impacts/constrains plant performance and plant interaction due to its role in the main plant's
127 determinant process through e.g. photo synthesis, transpiration and diffusion of gases in the root system.
128 The Sum Exceedance Value (SEV) (Swetnam et al., 1998) was applied as a proxy for flooding. It is calculated
129 by counting the number of days during the year that the water level exceeds a threshold that causes stress
130 due to aeration and multiplying these numbers by the difference in observed and threshold water levels,
131 followed by summation.

132 In the grassland, the soil conductivity peaks where the flooding is of intermediate duration. Thus, though
133 SEV is a measure of aeration and water shortage, aspects regarding salinity are also incorporated. The
134 calculations of SEV was done as specified by Damgaard et al. (2016). Because we collected cover data in
135 two periods, some species only appeared in one year, indicating ingrowth or mortality. In order to utilize
136 the collected data information and avoid bias by removing species that are rare in the area, or missing due
137 to the probabilistic nature of the sampling design, we set missing cover values close to 0 and assumed SEV
138 to be constant for those observations. A motivation for including hydrology in studies of cover from the
139 French wet grasslands can be found in Damgaard et al. (2016) and Violle et al. (2011), who found strong

140 significant correlations between observed species cover and hydrology in the same data. Selection may
141 therefore depend on hydrology.

142 **Model, estimation and evaluation**

143 A phenotype under selection may be summarized by its empirical density function. We can interpret the
144 selection forces as functions to modify this distribution. Depending on the shape of the modifying function,
145 the selection forces change the moments of the phenotype distribution (Harper, 1977, 758-760 ; Westoby,
146 1982). Also, the variance of the modifying function has an impact (Hara, 1984). For example, directional
147 selection affects the mean and skewness of this distribution, whereas stabilizing selection will affect only
148 the variance. Disruptive selection tends to affect both the mean and skewness. Damgaard (2016) made
149 functions that are capable of doing this modification, and the model applied here is an extension of these
150 methods seen in Equation 1. F is a growth function for estimation of the direct selection forces originating
151 from the x' th trait, and C an expression of the selection forces put on species with trait x from competing
152 species y . The idea is to separate direct selection from traits and the selection that is mediated by
153 interspecific interactions into two, in order to model each of them individually. This allows complex models
154 of the selection outcome. The terms q and q' are the covers in Year and Year+1. Summation was done over
155 all m plots, for k traits.

156 Equation 2

$$157 \quad q'_j = q_j \sum_{k=1}^m \left(F_k(x, SEV) \left(\sum_{y \in \Omega} C_k(x, y, SEV) q_{t_k=y} \right) \right) + \varepsilon$$

158 Because F and C are jointly estimated in a one-step model, their interaction can be studied by means of
159 the parameter correlations. The hydrology (SEV) variable was included into each of the functions F and
160 C by an easily interpretable linear term, as shown in Table 2. Also, the table contains all models tested in
161 the study, with an explanation in the most left column of the table. Spatial patterns are modelled implicitly
162 since the pin-point method is a spatial sampling procedure. Furthermore, the mathematical formulas of

163 Table 2 assumes different effect nonlinear (spatial) effects of the traits. For example Model 3 of Table 2
164 contains the expression shown in Equation 3, where Exp is the natural exponential function, H is a term
165 measuring hydrology and y and x denotes the traits observed in the pinpoint frame. The subtraction of the
166 traits put implicit assumptions about their spatial interaction, which cannot be proved, but justified by
167 statistical analysis. The other models of Table 2, put other assumptions on the spatial interaction such as a
168 fraction (Model 4). In addition H was assumed to enter as a multiple, in order to separate this term from
169 separately from the trait term, but allow potential interaction to be studied. Hydrology is modelled per plot
170 and therefore this is also a spatial measure. Inside the pinpoint frame, we made a mean-field assumption
171 (Bolker and Pacala, 1999), thus we do not apply the needle positions in our analysis.

172 **Equation 3**

173
$$C_{DIR,k}(x, y, H) = Exp(-H(y - x))$$

174 The model was estimated using the Metropolis algorithm (M) (Gelman et al., 2004, p. 289-290), a Markov
175 chain Monte Carlo procedure (MCMC). This algorithm is simple and able to fit non-linear models. Complex
176 interactions were analyzed by the joint model parameter distributions using Pearson correlations. In order
177 to apply a normal distributed probability density function (PDF) logit transformations were made on q'_j
178 and q_j . The M-algorithm requires a symmetric proposal function, hence we applied this when possible, in
179 most cases a normal distribution. Since the variance parameters cannot be negative, a normal distribution
180 with small variance was applied and, in the rare negative case, the proposal was set close to 0.

181 The priors were assumed normal distributed, except for the variance, which was gamma distributed with
182 both scale and rate parameters equal to 2, to avoid negative values. For all models, 150.000 simulations of
183 the M-algorithm were made. After removing 10.000 burn-in observations the remaining observations were
184 applied to model the joint and marginal posterior distributions.

185 Model comparison was made using the Deviance Information Criteria (DIC) (Spiegelhalter et al., 2002; Zuur
186 et al., 2009, p. 528) by application of the mean parameter of each marginal parameter distribution. To

187 evaluate the predictive performance and account for the dispersal of the marginal distributions, i.e. their
 188 variance, we made 15.000 simple random samples in the posterior distributions of the parameters,
 189 excluding the error term of the normal density describing the dependent variable. The empirical density of
 190 cover q'_j was compared to the simulated cumulative empirical distribution using the Kolmogorov-Smirnof
 191 test (Massey, 1951).

192 One assumption, which may be critical, is the additivity of the terms in Equation 2, but this can be justified
 193 by means of variable selection, which allows selecting the terms that have parameters significantly
 194 different from zero. We applied the variable selection proposed by Kuo and Mallick (KM) (1998). In short,
 195 the method of Kuo and Mallick introduces a multiplicative indicator to each model term. The indicator
 196 variable consist of two parts, a "0" part which is assumed non-stochastic and is named the spike, and a "1"
 197 part (the slab) which has Bernoulli (Owen et al., 2009, 268) prior distribution. We extend Equation 2 to
 198 include the indicator $I_1 \dots I_k$ variables as in Equation 4.

199 **Equation 4**

$$200 \quad q'_j = q_j \sum_{k=1}^m I_k \left(F_k(x, SEV) \left(\sum_{y \in \Omega} C_k(x, y, SEV) q_{t_k=y} \right) \right) + \varepsilon$$

201 The indicator variable enters the M-algorithm, and the preferred model is the one where the posterior
 202 inclusion probabilities of the indicator variable are higher than 0.5, i.e. the indicator variable enters in at
 203 least 50 % of the selected models, this is called the median probability model (Barbieri and Berger, 2004).
 204 To test the sensitivity of the Bernoulli distribution, we ran the selection including 30, 50 and 80 percent of
 205 the variables and found, using DIC, the best results with 80 % inclusion. This is due to the high number of
 206 model parameters, which seems sensitive to a sudden exclusion of a whole term, making it difficult to get
 207 acceptance in the M-algorithm. One advantage of the KM method is that it runs as an integrated part of the
 208 M-algorithm, and therefore the computation time is less than an all-possible subset test (Montgomery et
 209 al., 2006). Furthermore, contrary to the stochastic search variable selection method (SSVS) (George and

210 McCulloch, 1993) the KM method allows for priors with a mean other than 0, and no standardization of the
211 variables is needed. In order to improve the mixing properties of the chain, the chain value of the
212 individual parameters that were multiplied to I_k were retained whenever each of the terms I_k of Equation
213 4 was 0. In addition, when predictions were made from the mean parameter values we used a conservative
214 approach so that the indicator variable parameter was included in the model whenever it appeared in more
215 than 5 pct. of the MCMC simulations, i.e. I_k were statistically significant at the 5 percent level. A program
216 for model estimation and evaluation was made in R (R Development Core Team, 2016), and a flowchart of
217 the programs is available in the online Appendix A.1, which can be send on request.

218

219 **Results**

220 In Figure 1 the left side of the boxplots shows the cover for the different species in the first measurement
221 period, and the right side is the change registered in the second. We see that many species show a change
222 in cover bteewn the two periods, potentially due to selection forces, making further modelling attempts
223 reasonable. Plots of SEV versus cover for different species (see Figure A. 2 in Appendix A.2) revealed strong
224 trends and thus justify the inclusion of this variable in the model. We noticed that some species however
225 have almost the same cover.

226 The chains produced by the MC-algorithm showed good mixing properties, though at least 10.000 burn-ins,
227 were needed before the chain seemed to stabilize. Some correlations were present between the
228 parameters, and this may be of general interest due to the biological nature of the model. The time for
229 running the model seems limited by the term C_k (Equation 2), which requires looping through all species on
230 the plot level. Nevertheless, within 10 days we could compute more than 150.000 MCMC iterations on a
231 standard PC 2.4 GHz processor of even the slowest model tested, making the method applicable to most
232 practical implementations. For the more complicated models (Model 4-5), we manually calculated initial
233 guesses in order reduce the burn-in period of the MCMC. Our experience is that few model parameters set

234 near to mean trait values are a good starting point. In addition, the variances of the posterior parameter
235 histograms of Models 4 -5 seemed smaller, probably due to the formula using exponential in fractions,
236 making only a narrow number of values reasonable.

237 Generally, all models showed that direct selection forces were the most dominant, as adding the C_k term
238 (Equation 2) did not seem to offer much improvement, which can be seen by looking at the DIC values of
239 Table 3. One interpretation of this result is that the model does not capture selection that is mediated by
240 interspecific interactions, nor the potential nonlinearity of the cover. However, the model overall assumes
241 linearity (q'_j times model terms), and a scatter plot of the covers in the two observed years revealed a
242 linear tendency in the nonparametric Lowess-estimator with a strongly significant Pearson correlation
243 ($R=0.78$) (see the upper left subplot of Figure 2). However, if the models are suitable, their predictions
244 should mimic that of the original data. The remaining subplots of Figure 2 show predictions against the
245 independent variable (q'_j) based on the mean parameter of the posterior MCMC -distributions. The
246 header of the subplot identifies the different models.

247 Notice that the full model and the KM-selected model are plotted in the same subplot, as shown in the
248 Figure 2 legend. When looking at the trend lines, and residual plots (Appendix A.4), Model 3 (directional
249 selection) gives the best predictions. The R^2 ranges from -0.2 (model 5) to 0.77 (Model 3), showing that the
250 best model gives R^2 similar to the original data. Though model 5 with variable selection gave lower AAB and
251 DIC, Model 3 seems to give the most reasonable predictions when looking at the subplot (Figure 2).

252 For all models, the variable selected models gave less variation in the output, though judging from the DIC
253 and AAB, and were sometimes better than the full model (Table 3). However, when looking at the actual
254 predictions, it became clear that in many cases this was due to reductions in variance (many 0 and 1
255 predictions) and not due to effective better models. Especially the near to 0 predictions can give high DIC
256 values because the raw data contains many near to 0 observations.

257 The predictive simulation using the Kolmogorow-Smirnow test is good supplement to the DIC and AAB, as
258 the variation in prediction cover is tested against the observed cover. In Figure 3, boxplot of test-values
259 confirms that Model 3 is the best model that includes selection that is mediated by interspecific
260 interactions (C_k term,) because it has the lowest test value. It can be seen that the simpler version of Model
261 3 (Model 1) excluding the C_k term is the best according to the Kolmogorow-Smirnow test. This indicates
262 that directional selection is important driver for species cover. Also, the grey boxplots show the same test
263 results based on significant variable selected terms. There is a big difference between the original models
264 and the variable selected models and, in most cases, it looks like the full models are better. Notice,
265 however, that in all cases p-values obtained from the test were not significant (not shown), due to the
266 sensitivity of the Kolmogorow-Smirnow test.

267 In Figure 4, the results of the variable selection procedure on the different I_k terms of Equation 4 are
268 shown. For each model we see the proportion of times that the MCMC procedure retains the trait value, to
269 the total number of iterations excluding burn-ins. Thus if the bar has value 1, the trait is always retained,
270 indicating that it is an important predictor, and the closer to 0 the less important. We see that for all
271 models except Model 5, vegetation height is important, whereas LDMC and SLA are often not retained and,
272 in many cases close to not significant at the 5 percent level. The fact that traits perform differently for
273 different models shows that the competitive process can be driven by different traits in different ways. The
274 best model (Model 3), contrary to other models, ranked LDMC as important. However, if we consider
275 model performance as a conclusive tool, then we must trust the model that performs the best according to
276 DIC and AAB. To this respect, the bars from Model 3 in Figure 4 is showing that all traits have some
277 importance, but that LDMC and SLA are most important, followed by vegetation height. It is interesting that
278 vegetation height for Model 3 seems slightly less important than for all other models. It shows that relying
279 on a single model and not covering all three types of selection forces may lead to wrong conclusions.

280 The Table 4 (lower half) showed the Pearson correlation coefficient between the parameters of Model 3.
281 The t-test in the upper half shows that the parameters seem to be significantly correlated at the five
282 percent level. The high correlations between parameters of the direct selection forces for the different
283 traits indicate that they mimic the same property of plant performance.

284 The results are showing that hydrology seems important, since the parameters of the H term ($H =$
285 $a_{0k} + a_k SEV$) are significantly different from 0. Interestingly, when looking at the parameter estimates and
286 their range in Table 5, we see that the terms a_{kF} and a_{0Fk} are higher than their counterparts in the
287 selection trait interaction term (a_{kC} and a_{0Ck}). This indicates that the direct trait selection seems to be a
288 more important driver for selection forces over a hydrological gradient than selection that is mediated by
289 interspecific interactions, and they have a combined impact on cover, which is in agreement with
290 Damgaard et al. (2016). The signs of the slope of the H term a_k indicate that vegetation height and SLA
291 have a small positive impact on cover when including hydrology, whereas LDMC has a small negative
292 impact. The less flooded the area becomes, the more important the direct selection forces are, which was
293 also found by Merlin et al. (2015). But, as can be seen from Table 5, the 50th percentiles are close to 0 and
294 results should not be over interpreted. When looking at the similar terms from a_C , we see that hydrology
295 has a negative impact on the selection that is mediated by interspecific interactions for vegetation height
296 and SLA and no impact for LDMC.

297 **Discussion**

298 The model presented here are in line with community based models where environmental variables
299 sometimes latent affect the selection favoring certain characteristics of plants. Certainly the study of
300 environmental variables such as the role of hydrology on succession is not new (Kikuzawa, 1991), and traits
301 may enter categorical classification as done in the Ellenberg numbers and CSR databases along ecological
302 gradients using statistical measures of correlation (Franzaring et al., 2007). The filter approach is a model
303 based extension of these explorative methods, and tends explain the actual trait distribution by

304 environmental/habitat filters that reduces the species pool followed by a limit to similarity filter. The latter
305 ensures that each plant in the community have resources to live on, and no species becomes completely
306 dominant (Garnier et al., 2016). Our approach is less subjective in estimation of the impact of traits on
307 selection forces than a traditional filtering process, and does not require classification (numeric classes) as
308 does for example the Ellenberg indicator. This is due to the simultaneous estimation, which “weights” the
309 trait contributions to selection by means of parameters in the nonlinear models applied. As such, the
310 method has some similarities with the much used structural equation modelling SEM (Weiher et al., 2011),
311 since both account for contemporary correlations among the residuals/parameters of the models. The
312 posterior parameter distribution may be applied to statistical inferences, and the correlation among
313 parameters may be seen in a biological context. Furthermore, our method does not require any subjective
314 definition of a null model. We cover all theoretical outcomes of selection a priori (see Table 2). This is,
315 however, also a weakness because such assumptions cannot be proven correct in a mathematical sense,
316 but only falsified by empirical testing (Chalmers, 1999) in the spirit of the philosopher Popper (Collin, 2003).
317 However, if we believe that the models represent expressions for directional, disruptive and stabilizing
318 selection, then we can say that one selection process explains data better, and most likely this conclusion is
319 valid on a broader scale. One way to minimize the risk of misinterpretations is by means of a flexible model
320 that can take many forms. Generalized additive models (GAM) (Wood, 2006) allow for flexible modelling of
321 the selection forces and are an alternative to this approach that remain to be tested. Our model can be
322 characterized as a classical nonlinear model (Seber and Wild, 2003), with an assumed stochastic error
323 component (normal). It therefore fit into a broad range of community based ecological models, with a
324 customized deterministic term (Bolker, 2008) in form of the nonlinear expressions of Table 2. In future
325 applications incorporation of spatial information inside the pinpoint dataframe could be tested. A
326 conditional autoregressive model (CAR) model is an obvious candidate for such a model and also works in
327 the Bayesian setting (Besag, 1974).

328 As pointed out in the literature (Damgaard and Weiner, 2017; Harper, 1977), selection forces needs to be
329 seen simultaneously in spatio-temporal scale, as competition pressure changes over time, as does the
330 spatial pattern due to succession in the plant cover. The importance of considering spatial and temporal
331 patterns is also evident when studying the literature on community growth as well as individual growth
332 models (Schabenberger, 1994; Schabenberger and Pierce, 2002). We only have two temporal
333 measurements, while a longer time-series is preferred. However, the data applied as model input includes
334 plots of plant communities at similar stages of succession, and therefore the concern of looking at only two
335 periods is minor. In addition, if needed, in future the model can be extended to having more than one
336 measurement period. This can, for example, be done by assuming that the observed change in paired
337 observations collected in different periods can be pooled and used to increase the number of observations.
338 This allows us to apply the basic model in Equation 1, but requires an assumption that the temporal
339 development does not have a trend, since the pairs applied as input comes from different time periods.
340 This assumption may be reasonable in permanent grasslands dominated by perennial plant species (80 % of
341 the species), which exist for centuries and are not submitted to disturbances. In some cases, this
342 assumption is less plausible, for example in areas with human disturbance. The studied marshlands are
343 actually grazed every year and grazing cessation over several years may lead to substantial and directional
344 temporal change (Marion et al. 2010). The data collection required the studied area to be fenced for two
345 years, but this is probably too short a duration to affect species interaction, though it cannot be concluded
346 that this is not the case. The fact that the area has been grazed prior to the experiment may influence the
347 results. For example height as a proxy for species competitive ability becomes less prominent, as grazing
348 tend to minimize the height contrast between species (Diaz et al 2007). Also, the selective browsing by
349 horses and cows will favor some species over others (Marion et al. 2010, Saatkamp et al. (2010), with some
350 species-specific response according to their tolerance ability. The traits themselves are probably selected
351 for or against. For example thornes' avoidance and preferred taste, as well as nutrient content may be
352 drive non-random consumption of plants' species by livestock and wild fauna (Milchunas and Noy-Meir,

353 2002). In addition to browsing, livestock may spread nitrogen from excrements in a clustered way affecting
354 nitrogen sensitive vegetation. In the positioning of the pinpoint frame, areas with visible excrements were
355 avoided, to minimize such source of habitat heterogeneity.

356 If data allows for temporal classification, i.e. we can make a common point in time as reference start point
357 of the plant community, then time (t) can be added as a predictor (Equation 5). In addition, while our
358 model additively includes several traits simultaneously, their covariance can be included in the future. This
359 may e.g. be done by means of multiplication of two or more trait values, which can then enter the terms
360 denoted x and y of Equation 5. The Bayesian approach allows for inclusion of many parameters even for
361 small datasets, since the estimation procedure does not lose a degree of freedom such as a frequentist
362 statistical estimation does. Due to running time of the MCMC, it may be advisable to make an initial
363 reduction in the pool of traits available prior to MCMC.

364 **Equation 5**

365
$$q'_j = q_j \sum_{k=1}^m \left(F_k(x, SEV, t) \left(\sum_{y \in \Omega} C_k(x, y, SEV, t) q_{t_k=y} \right) \right) + \varepsilon$$

366 The model architecture explicitly includes interspecific competition because it involves traits, but it ignores
367 intraspecific competition. From a logical point of view, we cannot know if intraspecific competition will
368 have an impact on the selection forces, and the model is therefore a simplification of reality. However, it
369 has been recognized for long that the maintenance of species diversity in plant communities where the
370 fundamental niches of several species overlap, required that interspecific competition to be less intense
371 than the intraspecific competition (e.g. Chesson 2000). Thus, intraspecific competition is significant, and
372 other models combining these two effect can be developed. Models involving intraspecific competition
373 have often the weakness that the huge number of model parameters makes inference from the model
374 difficult. This can be one justification to ignore this effect and broadly focus on the outcome of selection.

375 Another argument is that trait contrasts are mainly expected to occur between species, which is then the
376 main contrasts to focus on for predicting their effects along environmental gradients.

377 **Conclusion**

378 The model developed allows to investigate the importance of direct trait selection and selection that is
379 mediated by interspecific interactions. It was tested using pin-point cover data from grasslands of the
380 French Atlantic Coast. We tested 5 main models, in addition to 5 sub models, using variable selection. With
381 reference to the objectives of the study, we conclude that:

- 382 a) All models can be fitted within reasonable time and are capable of using spatial as well as temporal
383 effects. Many (in our case 3) trait values may be included, and their potential interaction can be
384 modelled simultaneously and confounding statistical effects may be accounted for. The Bayesian
385 approach allows for inferences to be made without assumptions of residual independence. The
386 best model gave very similar predictions to the raw data, though some systematic residual patterns
387 could be seen. Problems with observations of cover value 0 may have an impact on the model
388 performance.
- 389 b) The direct selection forces seem to dominate in the current data, which can be seen from the
390 model predictions, indicating that selection is driven towards a new mean optimum value.
- 391 c) Hydrology has an impact, most strongly in interaction with the direct trait selection forces and, to a
392 minor extent, on the species interaction component. The forces of direct trait selection on the
393 species cover are increasing with the reduction of the flooding duration/intensity.

394 The model can be extended to include one or more interaction terms among trait values, thus including
395 covariance among traits in the model output.

396

397 **Acknowledgements**

398 The study was made as a part of the project “From vegetation patterns to ecological processes”, supported
399 by The Danish Council for Independent Research. We are grateful to the Parc Naturel regional du Marais
400 poitevin and the Etablissement public du Marais poitevin for their support in maintaining the experimental
401 setting in the Magnils-Reigniers common (France). The authors thank the mairie des Magnils-Reigniers for
402 granting permission to work in the common.

403

404

405 **References**

- 406 Adler, P.B., Fajardo, A., Kleinhesselink, A.R., Kraft, N.J.B., 2013. Trait-based tests of coexistence
 407 mechanisms. *Ecology Letters* 16, 1294-1306.
- 408 Amiaud, B., J-B., B., Tournade, F., Bonis, A., 1998. Spatial patterns of soil salinities and old embanked
 409 marshlands in western France. *Wetlands* 18, 482-494.
- 410 Barbieri, M.M., Berger, J.O., 2004. Optimal Predictive Model Selection. *The Annals of Statistics* 32, 870–897.
- 411 Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A., Garnier, E., 2012. Community
 412 assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a
 413 Mediterranean rangeland. *Journal of Ecology* 100, 1422-1433.
- 414 Besag, J.E., 1974. Spatial interaction and the statistical analysis of lattice systems *Journal of the Royal*
 415 *Statistical Society Series B (Methodological)* 36.
- 416 Bolker, B.M., 2008. *Ecological Models and Data* In R. Princeton University Press, Princeton.
- 417 Bolker, B.M., Pacala, S.W., 1999. Spatial Moment Equations for Plant Competition: Understanding Spatial
 418 Strategies and the Advantages of Short Dispersal. *The American Naturalist* 153, 575-602.
- 419 Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and*
 420 *Systematics* 31, 343-366.
- 421 Chalmers, A.F., 1999. *What is this thing called science?* Open University Press, Buckingham XXII, 266 s. pp.
- 422 Climatedata.eu, 2017. Climatedata.eu, <https://www.climatedata.eu>.
- 423 Collin, F., 2003. *Engelsk og amerikansk filosofi: videnskab og sprog*. Politikens Forlag, København 599 s. pp.
- 424 Damgaard, C., 2016. Empirical modelling of trait selection by partitioning selection into direct selection and
 425 selection that is mediated by interspecific interactions. *bioRxiv*.
- 426 Damgaard, C., Merlin, A., Bonis, A., 2016. Plant colonization and survival along a hydrological gradient:
 427 demography and niche dynamics. *Oecologia*, 201-210.
- 428 Damgaard, C., Weiner, J., 2017. It's About Time: A Critique of Macroecological Inferences Concerning Plant
 429 Competition. *Trends in Ecology & Evolution* 32, 86-87.
- 430 Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpes, C., Rusch, G.,
 431 Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W. Clark, H., Campbell, B.D. 2007. Plant trait responses to
 432 grazing- a global synthesis. *Global Change Biol.* 13, 313-341.
- 433 Dwyer, J.M., Laughlin, D.C., 2017. Selection on trait combinations along environmental gradients. *Journal of*
 434 *Vegetation Science* 28, 672-673.
- 435 Franzaring, J., Fangmeier, A., Hunt, R., 2007. On the consistencies between CSR plant strategies and
 436 Ellenberg ecological indicator values. *Journal of Applied Botany and Food Quality* 81, 86 - 94.
- 437 Garnier, E., Navas, M.-L., Grigules, k., 2016. *Plant functional diversity. Organism traits, community structure*
 438 *and ecosystem properties.* , 1 ed. Oxford University Press.
- 439 Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis* Second ed. Chapman &
 440 Hall/CRC United States of America.
- 441 George, E.I., McCulloch, R.E., 1993. Variable Selection via Gibbs Sampling. *Journal of the American*
 442 *Statistical Association* 88, 881-889.
- 443 Gotelli, N.J., Graves, G.R., 1996. *Null models in ecology*. Smithsonian Institution Press United States of
 444 America.
- 445 Hara, T., 1984. Dynamics of stand structure in plant monocultures *Journal of Theoretical Biology* 110, 223-
 446 239.
- 447 Harper, J.L., 1977. *Population biology of plants*. Academic Press, London.
- 448 Johnson, R.A., Wichern, D.W., 2007. *Applied multivariate statistical analysis*. Pearson Prentice Hall, Upper
 449 Saddle River, N.J. XVIII, 773 s. pp.
- 450 Loranger J, Violle C, Shipley B, Lavorel S, **Bonis A**, Cruz P, Louault F, Loucougaray G, Mesléard F, Yavercovski
 451 N, Garnier E. 2016. Recasting the dynamic equilibrium model through a functional lens: the interplay of
 452 trait-based community assembly and climate. *J. Ecology* 104 (3): 781-791

453 Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of*
454 *Vegetation Science* 3, 157-164.

455 Kikuzawa, K., 1991. A Cost-Benefit Analysis of Leaf Habit and Leaf Longevity of Trees and Their Geographical
456 Pattern. *The American Naturalist* 138, 1250-1263.

457 Kuo, L., Mallick, B., 1998. Variable Selection for Regression Models. *Sankhy*; The Indian Journal of
458 *Statistics, Series B (1960-2002)* 60, 65-81.

459 Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning
460 from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–556.

461 Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I., Callaway, R.M., 2004.
462 Rethinking plant community theory. *Oikos* 107, 433-438.

463 Massey, F.J., 1951. The Kolmogorov-Smirnov Test for Goodness of Fit. *J. Am. St. Ass.* 46, 68-78.

464 Mather, K., 1953. The genetical structure of populations in: Brown, R., Danielli, J.F. (Eds.), *Symposia of the*
465 *Society for Experimental Biology*, pp. 66-95.

466 McGill, B.J., Brown, J.S., 2007. Evolutionary Game Theory and Adaptive Dynamics of Continuous Traits.
467 *Annual Review of Ecology, Evolution, and Systematics* 38, 403-435.

468 Marion B., Bonis A. & Bouzillé JB. 2010. How much grazing-induced heterogeneity impact plant diversity
469 and richness in wet grasslands ? *Ecoscience* 17: 229-239.

470 Merlin, A., Bonis, A., Damgaard, C., Mesléard, F., 2015. Competition Is a Strong Driving Factor in Wetlands,
471 Peaking during Drying Out Periods. *PLoS ONE* 10.

472 Milchunas, D.G., Noy-Meir, I., 2002. Grazing Refuges, External Avoidance of Herbivory and Plant Diversity.
473 *Oikos* 99, 113-130.

474 Montgomery, D.C., Peck, E.A., Vining, G.G., 2006. *Introduction to linear regression analysis.*, 4th ed. Wiley,
475 Hoboken, New Jersey XVI, 612 s. pp.

476 Owen, J., Maillardet, R., Robinson, A., 2009. *Scientific Programming and Simulation Using R.* CRC Press,
477 Taylor & Francis Group, New York.

478 R Development Core Team, 2016. *R: A language and environment for statistical computing*, in: R
479 *Foundation for Statistical Computing (Ed.)*, Vienna, Austria.

480 Schabenberger, O., 1994. Nonlinear mixed effect growth models for repeated measures in ecology,
481 *Proceedings of the Section on Statistics and the Environment. Annual Joint Statistical Meetings Toronto,*
482 *Canada*

483 Schabenberger, O., Pierce, F.J., 2002. *Contemporary statistical models for the plant and soil sciences.* CRC
484 *Press, Boca Raton, Florida XXII, 738 s. pp.*

485 Seber, G.A.F., Wild, C.J., 2003. *Nonlinear regression.* Wiley, Hoboken, New Jersey.

486 Shipley, B., 2010. *From plant traits to vegetation structure* Cambridge, UK.

487 Spiegelhalter, D.J., Carlin, B.P., Van der Linde, A., 2002. Bayesian measures of model complexity and fit (with
488 discussion). *Journal of the Royal Statistical Society Series B (Methodological)* 64, 583-639.

489 Swetnam, R.D., Mountford, J.O., Armstrong, A.C., Gowing, D.J.G., Brown, N.J., Manchester, S.J., Treweek,
490 J.R., 1998. Spatial relationships between site hydrology and the occurrence of grassland of conservation
491 importance: a risk assessment with GIS. *Journal of Environmental Management* 54, 189-203.

492 Saatkamp, A., Römermann, C., Dutoit, T., 2010. Plant Functional Traits Show Non-Linear Response to
493 Grazing. *Folia Geobotanica* 45, 239-252.

494 Violle, C., Bonis, A., Plantegenest, M., Cudennec, C., Damgaard, C., Marion, B., Le Cœur, D., Bouzillé, J.-B.,
495 2011. Plant functional traits capture species richness variations along a flooding gradient. *Oikos* 120, 389-
496 398.

497 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of
498 trait be functional! *Oikos* 116, 882-892.

499 Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., Bentivenga, S., 2011. Advances, challenges and a
500 developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal*
501 *Society B: Biological Sciences* 366, 2403-2413.

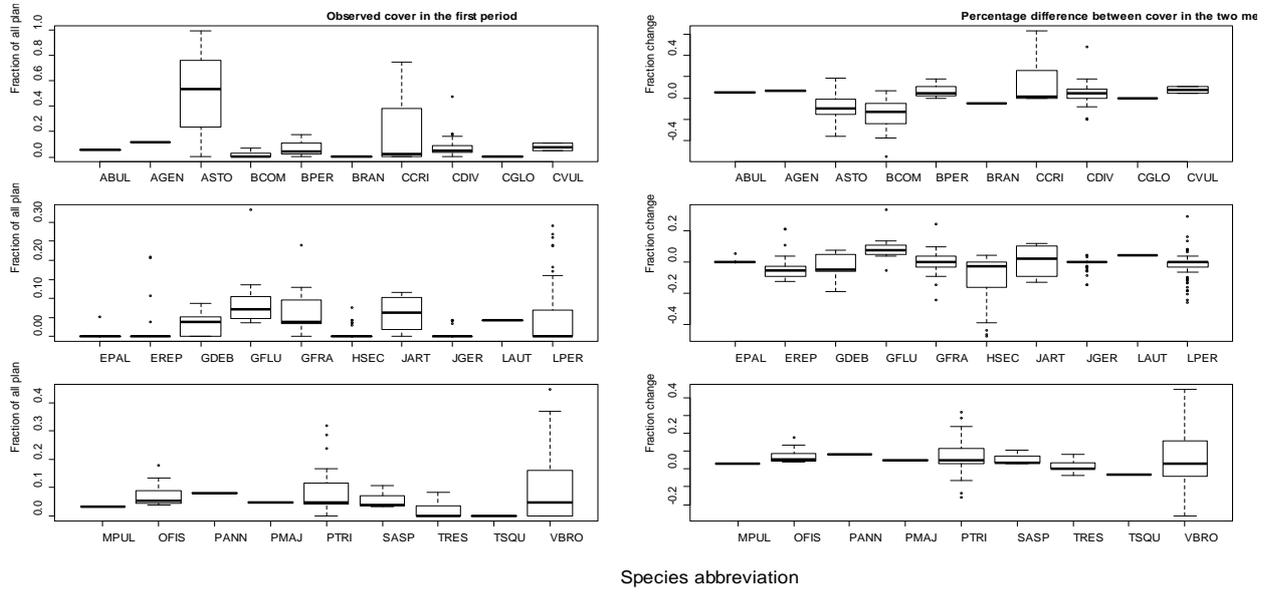
502 Westoby, M., 1982. Frequency distributions of plant size during competitive growth of stands: the
503 operation of distribution-modifying functions. *Ann. Bot.* 50, 733-735.
504 Wood, S.N., 2006. *Generalized additive models : an introduction with R*. Chapman & Hall/CRC, Boca Raton,
505 Florida. xvii, 392 s., ill. pp.
506 Wyszomirski, T., Weiner, J., 2009. Variation in Local Density Results in a Positive Correlation between Plant
507 Neighbor Sizes. *The American Naturalist* 173, 705-708.
508 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions*
509 *in Ecology with R* Springer Science+Business Media, LLC New York, USA.

510

511

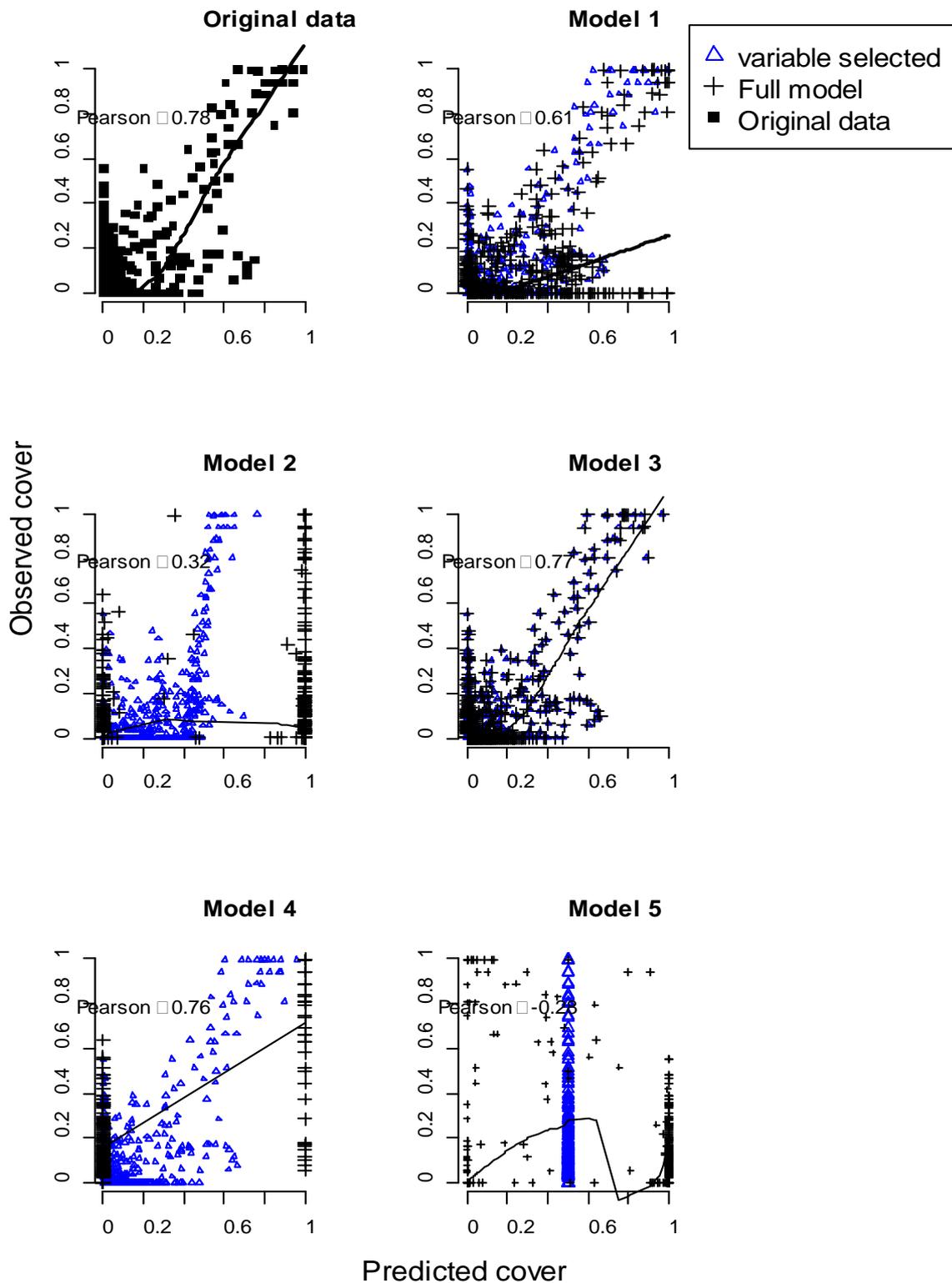
512

513 **Figures**



514

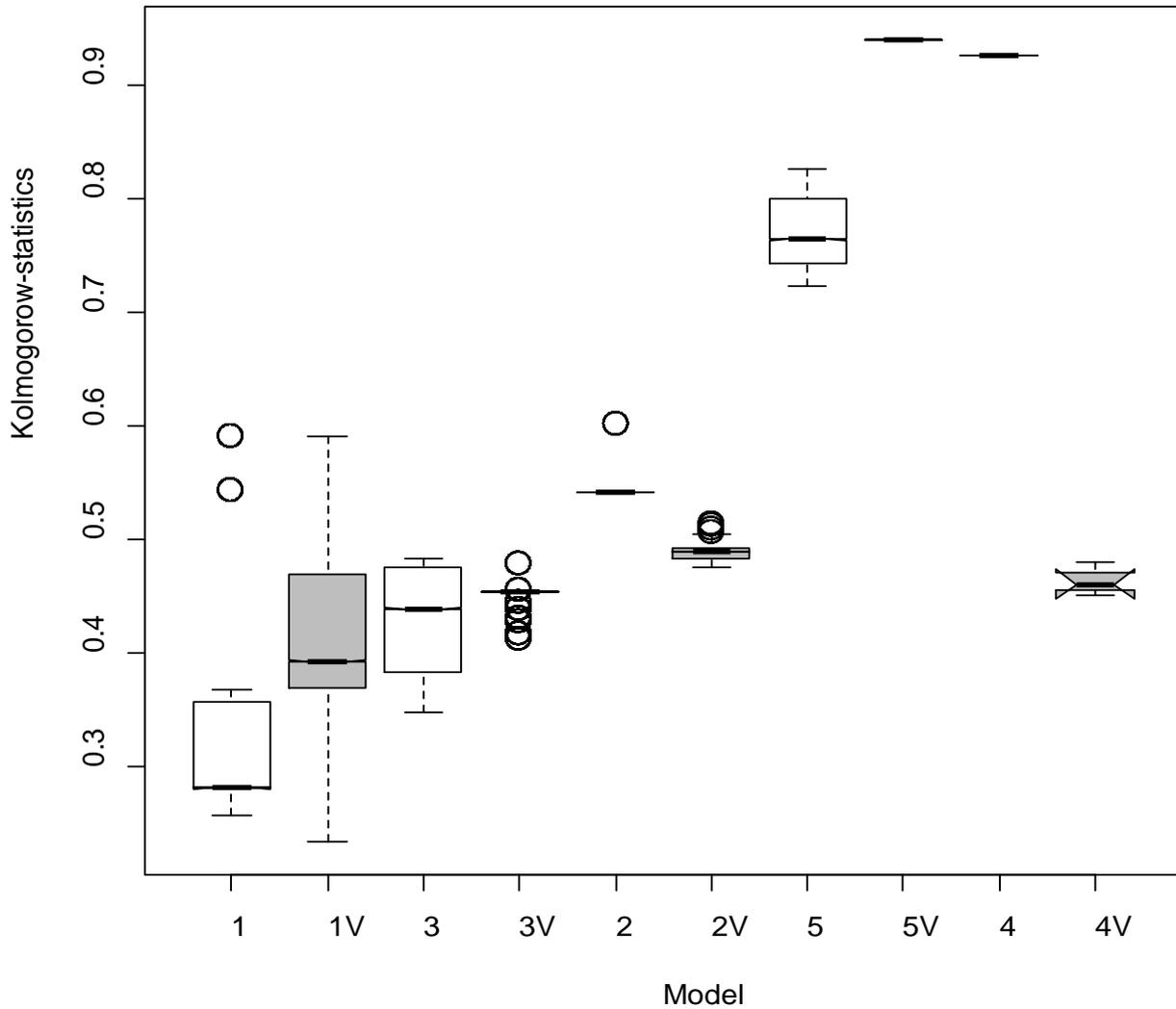
515 **Figure 1. Histograms on the left side are showing the cover in percent for the different species in the first**
516 **year of measurement. On the right side is the percentage change in cover between the two years of**
517 **measurement for the same species. The abbreviation refers to the species abbreviation in Table 1.**



518

519 **Figure 2.** Top left: The cover data entering the model as independent and dependent variable, with the
 520 nonparametric Lowess-estimator and the Pearson correlation. The remaining subplots: Cover data
 521 against the predicted values using means of the multivariate parameter distributions from MCMC of the

522 models in the subplot header (Table 2). The Lowess-estimators are based on the predictions of the full
523 models.

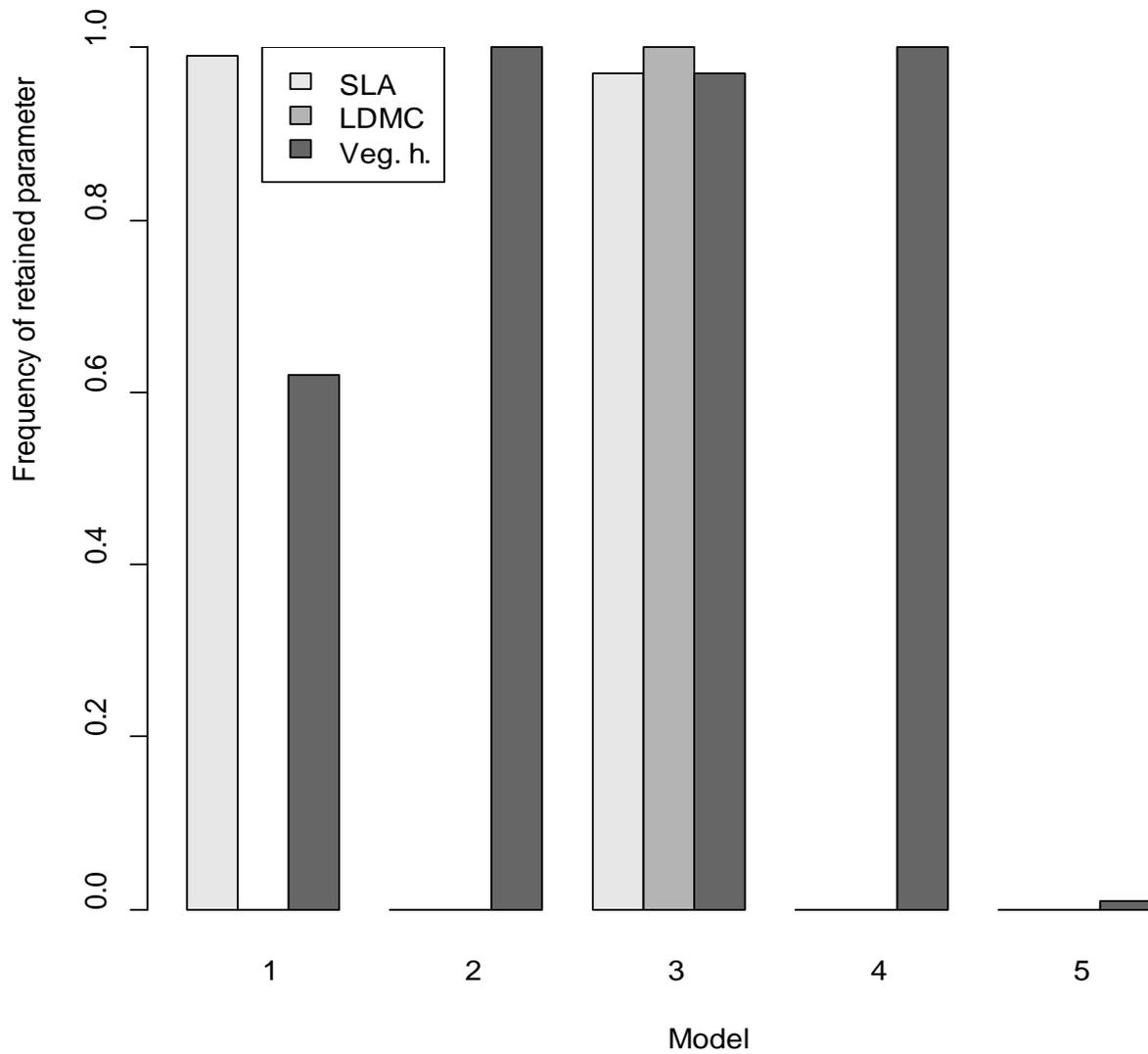


524

525 **Figure 3.** The test values of the Kolmogorow-Smirnow statistics when comparing the predicted cover
526 distribution for each model with the observed empirical cover distribution. The full model is identified by
527 its number and the variable selected model by the suffix "V" (gray color). Model numbers refer to Table
528 2.

529

530



531

532 **Figure 4.** Barplot of the fraction of times that the indicator variable (trait) was included in the model
 533 **(Equation 4), to the total number of MCMC iteration excluding burn-in. SLA, LDMC and Veg. h.**
 534 **(Vegetation height) shown in the legend, refers to the traits applied in the model.**

535

536

537

538 **Tables**

539 **Table 1. The species trait values used in the study. Specific leaf area (SLA), Vegetative height (Veg. h),**
 540 **Leaf dry matter content (LDMC), Percent recorded of all pin-point recordings on the study area (%).**

541

Species	SLA (m ² /kg)	Veg. h. (m)	LDMC (mg/g)	%
<i>Alopecurus bulbosus</i> (Abul)	28.6	0.28	215.1	0.06
<i>Alopecurus geniculatus</i> (Agen)	27.55	0.3	211.95	0.13
<i>Agrostis stolonifera</i> (Asto)	29.3	0.11	309.9	51.53
<i>Bromus commutatus</i> (Bcom)	28.6	0.5	253.9	1.67
<i>Bellis perennis</i> (Bper)	27.9	0.045	131	0.25
<i>Baldellia ranunculoides</i> (Bran)	27.48	0.13	98.46	0.03
<i>Cynosurus cristatus</i> (Ccri)	22.3	0.55	248.5	13.45
<i>Carex divisa</i> (Cdiv)	13.5	0.49	230.2	3.84
<i>Cerastium glomeratum</i> (Cglo)	35.07	0.15	576.3	0.00
<i>Cirsium vulgare</i> (Cvul)	15.7	0.9	140.72	0.09
<i>Eleocharis palustris</i> (Epal)	8.5	0.53	265.1	0.07
<i>Elymus repens</i> (Erep)	21.5	0.75	301.2	1.67
<i>Galium debile</i> (Gdeb)	39.6	0.21	197.7	0.85
<i>Gaudinia fragilis</i> (Gfra)	31.28	0.28	235.35	1.73
<i>Glyceria fluitans</i> (Gflu)	36.7	0.5	218.7	0.72
<i>Hordeum secalinum</i> (Hsec)	29.3	0.33	269.1	6.90
<i>Juncus articulatus</i> (Jart)	11.86	0.19	193.85	0.31
<i>Juncus gerardi</i> (Jger)	10.2	0.33	256	1.04
<i>Leontodon automnalis</i> (Laut)	25.91	0.07	157.74	0.03
<i>Lolium perenne</i> (Lper)	26.7	0.13	227	7.15
<i>Mentha pulegium</i> (Mpul)	33.9	0.17	136.5	0.03
<i>Oenanthe fistulosa</i> (Ofis)	36.6	0.43	140	0.85
<i>Poa annua</i> (Pann)	35.28	0.14	262	0.06
<i>Plantago major</i> (Pmaj)	28.8	0.07	222.03 ¹	0.03
<i>Poa trivialis</i> (Ptri)	30.1	0.25	257.2	2.67
<i>Sonchus asper</i> (Sasp)	24.7	0.18	123.67	0.16
<i>Trifolium resupinatum</i> (Tres)	35.9	0.14	146.8	0.26
<i>Trifolium squamosum</i> (Tsqu)	35.5	0.4	158.6	0.03
<i>Vulpia bromoides</i> (Vbro)	30.5	0.1	254.4	4.37

542

543 ¹The data is the mean of traits since no data is available for the species.

544
545
546
547
548

Table 2. The different kinds of selection models considered denoted by suffix s in the model. F is the function that capture selection forces due to the trait. C is a function to model selection that is mediated by interspecific interactions for traits x (subject) and y (competitor) for the k 'th trait. H is the hydrology measure (SEV). a_0, a, b_0, b, d, m and z are model parameters, and their suffix (k) indicates the trait they are made for. DIR is directional selection, SS is stabilizing selection, DIS is disruptive selection. Exp is the natural exponential.

Model	explanation	Trait selection	Trait selection interaction	Hydrology	Explanation
1.	Only subject trait, no interaction (directional selection)	$F_{DIR_k}(x, SEV) = Hb_0x + b_k$	None	$H = a_{0ks} + a_{ks}SEV$	Relative high or low trait values are selected.
2.	Only subject traits, no interaction (stabilizing selection)	$F_{SS_k}(SEV) = H(x - z_k)^2 + b_k$	None	$H = a_{0ks} + a_{ks}SEV$	Intermediate trait values will be selected, reducing the variance around the mean.
3.	Directional selection	$F_{DIR_k}(x, SEV) = Hb_0x + b_k$	$C_{DIR_k}(x, y, SEV) = Exp(-H(y - x))$	$H = a_{0ks} + a_{ks}SEV$	Either high or low trait values are selected.
4.	Stabilizing selection	$F_{SS_k}(x, SEV) = H(x - z_k)^2 + b_k$	$C_{ST_k}(x, y, SEV) = \frac{Exp(H(y - d_k)^2)}{Exp(H(x - d_k)^2)}$	$H = a_{0ks} + a_{ks}SEV$	Intermediate trait values are selected. The mean of the frequency will remain unchanged, and the variance will decrease
5.	Disruptive selection	$F_{DIS_k}(x, SEV) = H(x - z_k)^2 + b_k$	$C_{DIS_k}(x, y, SEV) = ((1 - m_k) \frac{1 - Exp(H*(y - z_k)^2)}{1 - Exp(H*(x - z_k)^2)} + m_k)$	$H = a_{0ks} + a_{ks}SEV$	Extreme intermediate trait values are selected. Change the trait frequency from uni to bimodal

549

550

551 **Table 3. The suffixes are DG= Direct growth, SS= Stabilizing selection, DIS= Disruptive selection. DIC = Deviance Information Criteria (smaller is**
552 **better). AAB = Average absolute bias. The model numbers refer to Table 2. In [] the best model including at least 1 of the terms for the three traits.**
553 **In () the average model performance is given including all traits.**

	DIC	AAB
1) $Cover_{year} = Cover_{year-1} * F_{DIR}(x, SEV)$	[5.96e+06](1.4e+08)	[4.31](4.51)
2) $Cover_{year} = Cover_{year-1} * F_{SS}(x, SEV)$	[1.95e+05](1.02e+12)	[2.76](57.85)
3) $Cover_{year} = Cover_{year-1} * F_{DIR}(x, SEV) * C_{DIR}(x, y, SEV)$	[1.88e+04](1.93e+04)	[4.33](4.57)
4) $Cover_{year} = Cover_{year-1} * F_{ST}(x, SEV) * C_{ST}(x, y, SEV)$	[5.62e+04](1.34e+24)	[4.24](1285553.44)
5) $Cover_{year} = Cover_{year-1} * F_{DIS}(x, SEV) * C_{DIS}(x, y, SEV)$	[8.45e+03](8.38e+05)	[0.10](-84.25)

554

555

556 **Table 4. In the lower half, the Pearson correlations between the parameters of the best performing model. In the upper half the p-value of a t-test**
 557 **testing the correlation. The suffix refers to the traits of Table 1, and the parameters are referring to Model 3 of Table 2.**

	a_{0SLA}	a_{0FLDMC}	a_{0Fvegh}	a_{FSLA}	a_{FLDMC}	a_{Fvegh}	b_{0FSLA}	b_{0FLDMC}	b_{0Fvegh}	b_{FSLA}	b_{FLDMC}	b_{Fvegh}	a_{0CSLA}	a_{0CLDMC}	a_{0Cvegh}	a_{CSLA}	a_{CLDMC}	a_{Cvegh}	σ
a_{0SLA}	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{0FLDMC}	-0.05	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{0Fvegh}	-0.77	0.45	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{FSLA}	0.58	0.44	-0.50	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{FLDMC}	0.28	0.47	-0.22	0.66	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{Fvegh}	0.76	0.10	-0.65	0.86	0.58	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{0FSLA}	0.21	-0.25	0.15	-0.51	-0.57	-0.23	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{0FLDMC}	-0.57	-0.09	0.69	-0.87	-0.31	-0.77	0.47	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{0Fvegh}	0.70	0.29	-0.63	0.97	0.60	0.92	-0.39	-0.90	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{FSLA}	0.33	0.58	-0.19	0.67	0.89	0.51	-0.49	-0.30	0.59	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{FLDMC}	-0.58	-0.60	0.36	-0.95	-0.78	-0.82	0.43	0.71	-0.92	-0.78	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
b_{Fvegh}	-0.67	-0.29	0.58	-0.96	-0.58	-0.93	0.41	0.89	-0.95	-0.53	0.89	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{0CSLA}	-0.59	0.32	0.88	-0.49	-0.46	-0.56	0.42	0.57	-0.58	-0.46	0.41	0.49	1.00	0.00	0.00	0.00	0.00	0.00	0.00
a_{0CLDMC}	0.68	0.36	-0.40	0.81	0.70	0.88	-0.15	-0.57	0.80	0.59	-0.85	-0.87	-0.30	1.00	0.00	0.00	0.00	0.00	0.00
a_{0Cvegh}	0.54	-0.47	-0.36	-0.25	-0.04	0.14	0.65	0.29	-0.12	-0.04	0.18	0.12	-0.24	0.16	1.00	0.00	0.00	0.00	0.00
a_{CSLA}	-0.27	-0.11	0.36	-0.70	-0.06	-0.60	0.36	0.87	-0.70	0.03	0.51	0.75	0.14	-0.46	0.49	1.00	0.00	0.00	0.00
a_{CLDMC}	-0.83	-0.01	0.49	-0.50	-0.22	-0.73	-0.30	0.45	-0.56	-0.12	0.50	0.67	0.20	-0.79	-0.50	0.38	1.00	0.00	0.00
a_{Cvegh}	0.68	-0.09	-0.61	0.71	0.22	0.89	-0.04	-0.80	0.81	0.09	-0.60	-0.84	-0.36	0.73	0.08	-0.79	-0.77	1.00	0.00
σ	0.69	-0.41	-0.47	0.10	-0.24	0.47	0.64	-0.23	0.25	-0.32	-0.05	-0.31	-0.08	0.42	0.66	-0.25	-0.84	0.67	1.00

558

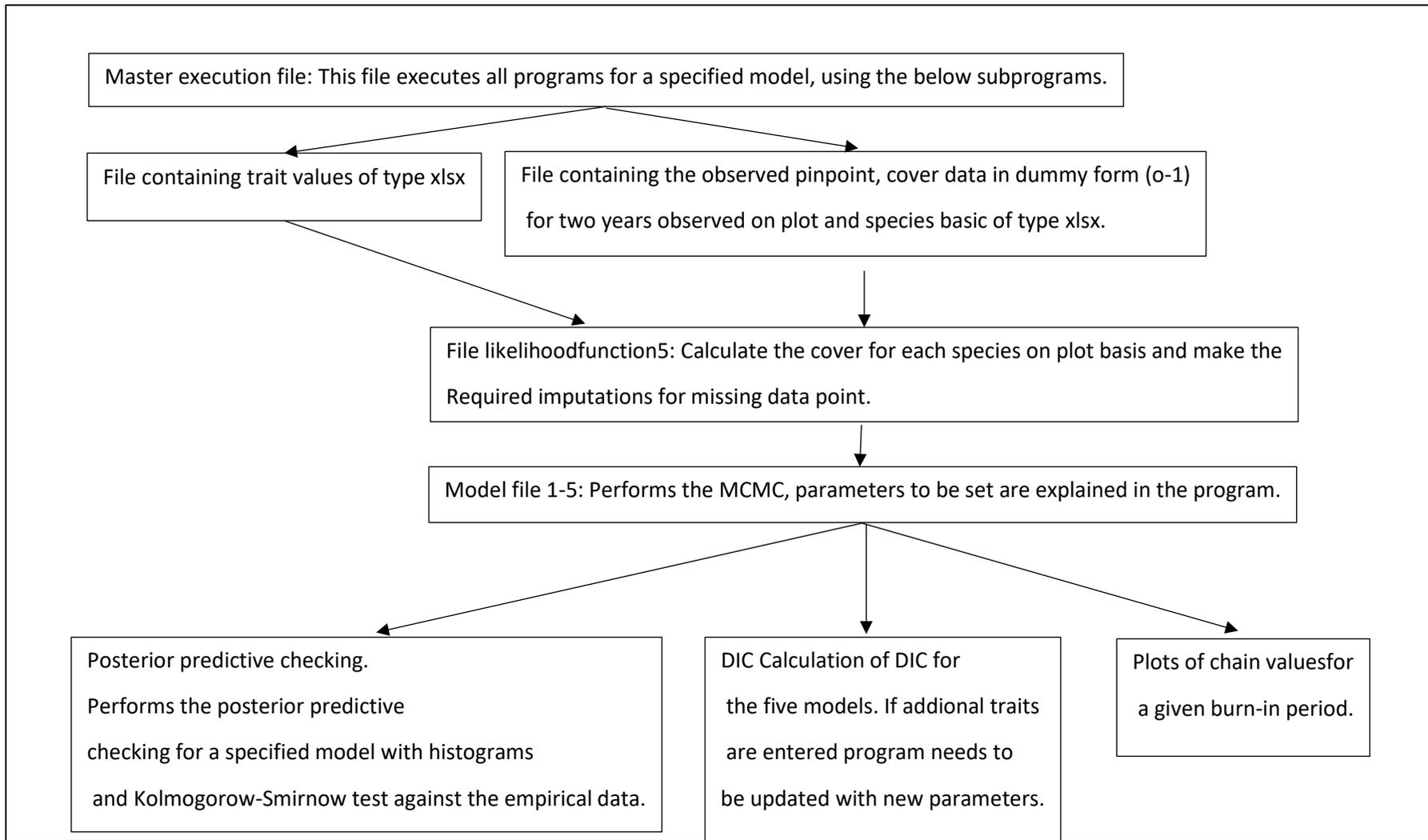
559

560

561 **Table 5. The quantiles of the parameters for Model 3 of Table 2, and the probability of the parameter**
 562 **being larger than 0. In [] the estimates from the variable selected model.**

Paramete	2.5%	50%	97.5%	P(X>0)
a_{0SLA}	0.017	0.063	0.074	1
a_{0FLDMC}	0.03	0.037	0.069	1
a_{0Fvegh}	-0.036	-0.011	0.002	0.16
a_{FSLA}	-0.027	-0.009	0.008	0.07
a_{FLDMC}	0.001	0.001	0.002	0.99
a_{Fvegh}	0	0	0.001	1
b_{0FSLA}	0.009	0.009	0.009	1
b_{0FLDMC}	0.001	0.001	0.002	1
b_{0Fvegh}	-0.006	-0.006	-0.002	0
b_{FSLA}	0[]	0.004	0.004	1
b_{FLDMC}	0.003	0.005	0.005	1
b_{Fvegh}	0.003	0.004	0.004	1
a_{0CSLA}	0.006	0.009	0.009	1
a_{0CLDMC}	-0.005	-0.004	0.001	0.07
a_{0Cvegh}	-0.002	-0.001	0	0.02
a_{CSLA}	-0.001	-0.001	-0.001	0
a_{CLDMC}	0	0	0	0.01
a_{Cvegh}	-0.001	0.001	0.001	0.72
σ	1.004	1.012	1.012	1

563



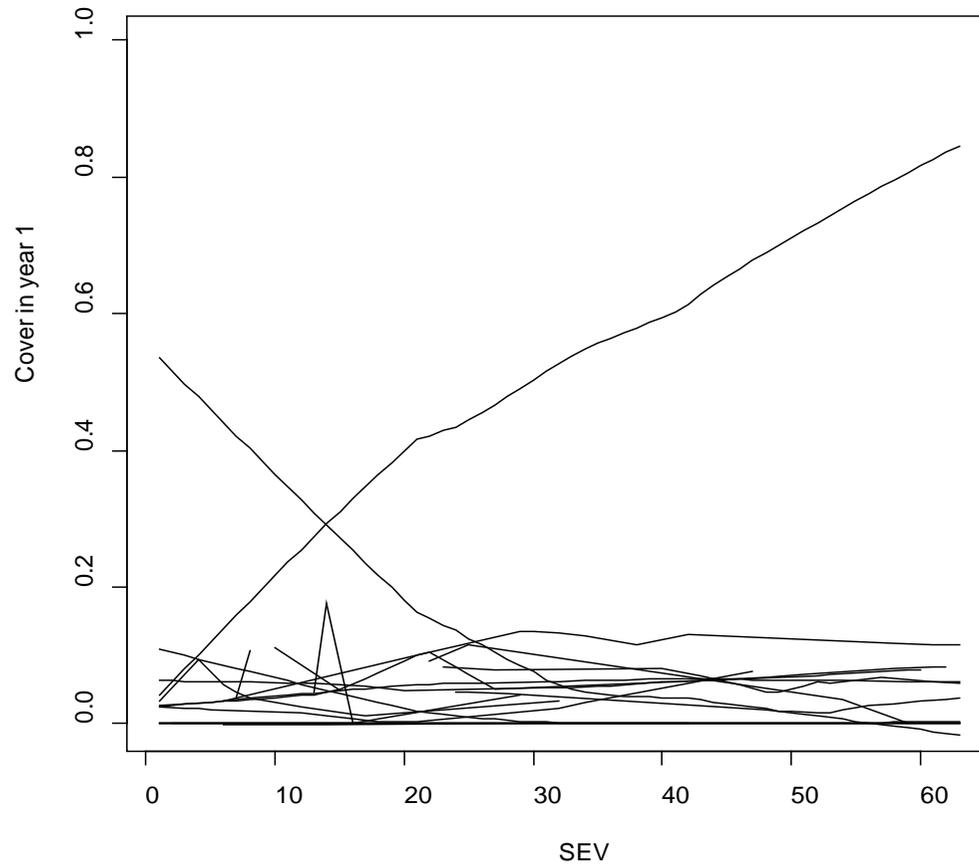
565

566

567 **Figure A. 1. Flowchart of the program architecture made in the study.**

568

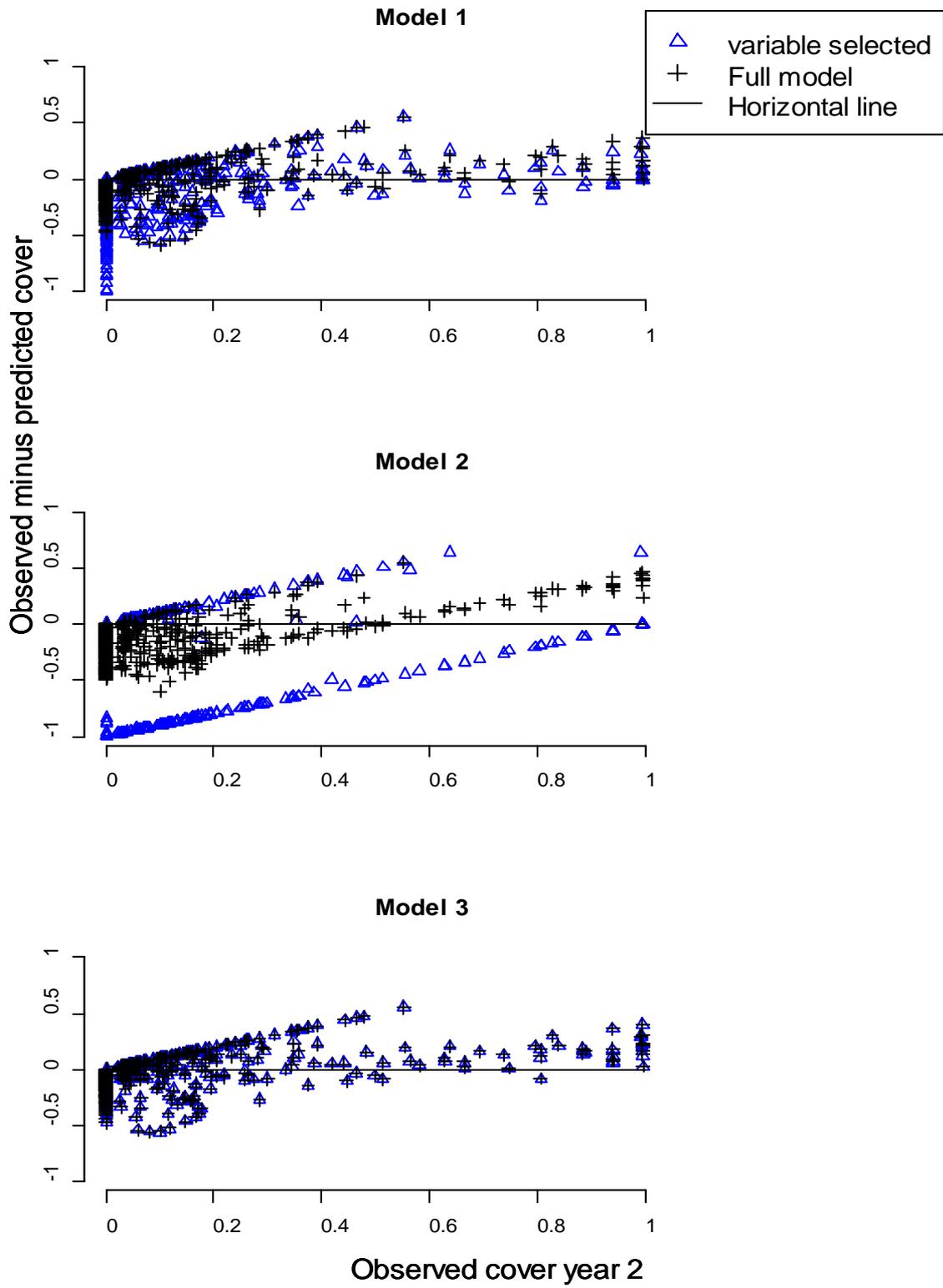
569 **Appendix A.2**



570

571

572 **Figure A. 2. The Lowess estimate of the SEV for different cover values. Each line represent a species, with different color.**

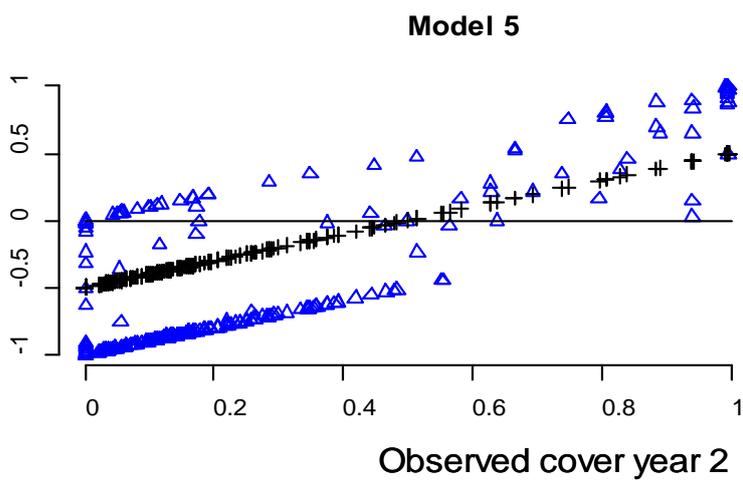
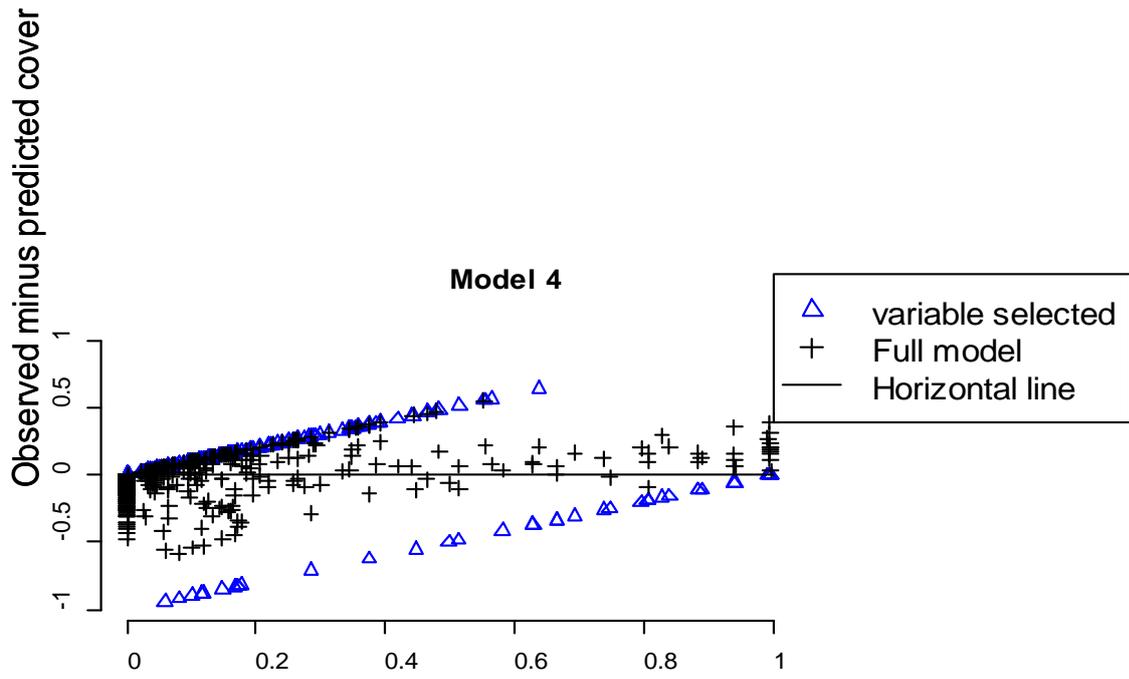


575 **Figure A.3 1. Residual plots of the models shown in Table 2 identified by the title of the subplots. The**
576 **horizontal line is corresponding to a complete match between model observed cover. Continues in Figure**
577 **A.3 2.**

578 **Appendix A.4**

579

580



582 **Figure A.3 2. Residual plots (continued from Figure A.3 1) of the models shown in Table 2 identified by**
583 **the title of the subplots. The horizontal line is corresponding to a complete match between model**
584 **observed cover.**

585