

1 **Improving spatial predictions of taxonomic, functional and phylogenetic** 2 **diversity**

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26 Running head: Spatial predictions of multiple plant diversity facets

27 **Summary**

28 1. In this study, we compare two community modelling approaches to determine their ability
29 to predict the taxonomic, functional and phylogenetic properties of plant assemblages along a
30 broad elevation gradient and at a fine resolution. The first method is the standard stacking
31 individual species distribution modelling (SSDM) approach, which applies a simple
32 environmental filter to predict species assemblages. The second method couples the SSDM
33 and macroecological modelling (MEM - SSDM-MEM) approaches to impose a limit on the
34 number of species co-occurring at each site. Because the detection of diversity patterns can be
35 influenced by different levels of phylogenetic or functional trees, we also examine whether
36 performing our analyses from broad to more exact structures in the trees influences the
37 performance of the two modelling approaches when calculating diversity indices.

38 2. We found that coupling the SSDM with the MEM improves the overall predictions for the
39 three diversity facets compared with those of the SSDM alone. The accuracy of the SSDM
40 predictions for the diversity indices varied greatly along the elevation gradient, and when
41 considering broad to more exact structure in the functional and phylogenetic trees, the SSDM-
42 MEM predictions were more stable.

43 3. SSDM-MEM moderately but significantly improved the prediction of taxonomic diversity,
44 which was mainly driven by the corrected number of predicted species. The performance of
45 both modelling frameworks increased when predicting the functional and phylogenetic
46 diversity indices. In particular, fair predictions of the taxonomic composition by SSDM-MEM
47 led to increasingly accurate predictions of the functional and phylogenetic indices, suggesting
48 that the compositional errors were associated with species that were functionally or
49 phylogenetically close to the correct ones; however, this did not always hold for the SSDM
50 predictions.

51 4. *Synthesis*. In this study, we tested the use of a recently published approach that couples
52 species distribution and macroecological models to provide the first predictions of the
53 distribution of multiple facets of plant diversity: taxonomic, functional and phylogenetic.
54 Moderate but significant improvements were obtained; thus, our results open promising
55 avenues for improving our ability to predict the different facets of biodiversity in space and
56 time across broad environmental gradients when functional and phylogenetic information is
57 available.

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64 **Key words.** Assemblage modelling, vegetation, ecological assembly rules, macroecological
65 models, similarity effect, Sørensen dissimilarity index, stacked species distribution models.

66 **Introduction**

67 Significant research efforts are allocated to assessing and modelling the impact of global
68 changes on biodiversity over a wide range of scales and for different ecosystems and taxa
69 (Bellard *et al.* 2012). An integrative assessment requires the simultaneous investigation of the
70 multiple facets of biodiversity: taxonomic, functional and phylogenetic (Thuiller *et al.* 2015).
71 The most frequently considered element of biodiversity is the taxonomic facet, which is
72 associated with species richness and composition and requires the counting and identification
73 of species that co-occur in a given unit area (alpha diversity; e.g., Ferrier & Guisan 2006;
74 White & Kerr 2006; Mateo *et al.* 2012). The capacity to model functional and phylogenetic
75 diversity has been explored more recently and is an important area of research (Dubuis *et al.*
76 2013; Ndiribe *et al.* 2014; Rosauer *et al.* 2014; Chalmandrier *et al.* 2015b; Thuiller *et al.*
77 2015; Jarzyna & Jetz 2016). Phylogenetic diversity is a measure that accounts for
78 phylogenetic relationships among taxa, and it facilitates investigations into the impacts of
79 evolutionary history in the assemblage of communities (Faith 1992; Webb *et al.*, 2002).
80 Finally, functional diversity represents the variance of species functional traits within a given
81 assemblage (*sensu* Violle *et al.* 2007) and may provide insights into the processes that shape
82 local assemblages (Lavorel & Garnier 2002; McGill *et al.* 2006).

83 Biodiversity patterns can be predicted via modelling approaches of varying complexity and
84 different emphases on the processes that generate community structure (e.g., Webb *et al.*
85 2010; Mokany *et al.* 2011; Fernandes *et al.* 2013, see D'Amen *et al.* 2015c for a review). A
86 standard approach to obtaining compositional information is to reconstruct communities by
87 stacking individual species predictions obtained from species distribution models (stacked
88 species distribution models, SSDMs, Pineda & Lobo, 2009; Mateo *et al.* 2012). This strategy
89 is based on the assumption that communities originate from the coincidental assemblage of
90 individualistic ecological responses of species. Because individual species distribution models

91 (SDMs) mainly use abiotic environmental data to perform inferences regarding species range
92 limits and habitat suitability (Franklin 1995; Guisan & Zimmermann 2000; Elith & Leathwick
93 2009), the derived SSDMs can account for the effect of environmental drivers in the
94 community predictions but may not include the effects of historical factors, biotic interactions
95 and dispersal limitations (Thuiller *et al.* 2013). These models show varying abilities in
96 predicting observed species richness patterns or assemblage compositions, but for certain
97 groups they have a tendency to over-predict the number of species in a community (e.g.,
98 Guisan & Rahbek 2011; Pineda & Lobo 2012; Calabrese *et al.* 2014; but see D'Amen,
99 Pradervand & Guisan 2015b and Mateo *et al.* 2016).

100 Recently, the novel community modelling framework SESAM has been proposed to
101 reconstruct species assemblages by integrating the different drivers of the assembly process,
102 including species pool definitions, habitat filtering, macroecological constraints and
103 ecological assembly rules (Guisan & Rahbek 2011). To date, the SESAM framework has
104 been mostly implemented by applying the habitat filter through stacking simple static SDMs
105 and constraining predictions for different assemblage properties via coupling with
106 macroecological models (MEMs) (e.g., as species richness or functional limits) (D'Amen *et*
107 *al.* 2015a). A key question in such SESAM implementation is related to the species that
108 should be selected from the pool of species predicted by the SSDM to produce the MEM
109 prediction. One possible solution is to rank species by their SSDM-predicted probability at
110 each site and retain only the highest probability species in the final assemblage prediction
111 until the MEM prediction is reached (“probability ranking” rule, PRR, D'Amen *et al.* 2015a).
112 This approach can be considered a putative ecological assembly rule if the probability of
113 presence at each site can be assumed to be a good proxy for species competitive strength at
114 that site. Because our implementation only represents a part of SESAM, in the following
115 sections we will refer to it as SSDM-MEM.

116 The SSDM-MEM approach has been shown to improve upon the SSDM approach by limiting
117 species richness over-predictions (D'Amen *et al.* 2015a). However, although many studies
118 have compared different approaches to predicting the taxonomic component of biodiversity
119 (see D'Amen *et al.* 2015a), no such comparisons have been performed for the functional and
120 phylogenetic facets. In particular, SSDM-MEM has never been tested for the prediction of
121 these components (D'Amen, Pradervand & Guisan 2015b). Here, we compare the two
122 community-modelling approaches - simple SSDM and SSDM-MEM - to determine their
123 ability to predict the three main facets of biodiversity: taxonomic, functional, and
124 phylogenetic. We use fine-resolution data of plant communities along an elevation gradient
125 and utilize a simplified concept of “community”, which we define as taxonomic assemblages
126 of species inhabiting the same plot. We also calculate and predict diversity indices for these
127 three components because they are important aggregated measures in ecology and
128 conservation biology (Corbelli *et al.* 2015; Jarzyna & Jetz 2016).

129 First, we test whether the performance of SSDMs can be improved by implementing the
130 SSDM-MEM approach. We expect taxonomic diversity to be predicted more accurately by
131 using SSDM-MEM because this method makes it possible to limit richness over-predictions
132 (D'Amen *et al.* 2015c). Functional diversity is directly linked to the response of species to the
133 environment (Thuiller *et al.* 2015); thus, we can expect here simple SSDMs that account for
134 the abiotic environmental drivers in the species sorting to show sufficient/good performances.
135 Conversely, we expect that phylogenetic diversity will be predicted with less accuracy than
136 functional diversity because it is likely to be influenced by additional processes, such as
137 evolutionary history, which are not considered here (Mouquet *et al.* 2012; Münkemüller *et al.*
138 2015).

139 Second, we test whether differences in the predictive performance of the two community
140 modelling approaches can be detected along the elevation gradient. Elevation gradients

141 include variations in several environmental factors (e.g., temperature, precipitation,
142 topography, and soil) that directly influence the presence of organisms. Therefore, these
143 gradients are useful for testing general hypotheses regarding the main drivers that shape
144 diversity patterns (e.g., Callaway *et al.* 2002; Michalet *et al.* 2014) and testing community-
145 modelling approaches (e.g., Dubuis *et al.* 2011, Mateo *et al.* 2012).

146 Finally, recent reports have indicated that the detection of diversity patterns can be influenced
147 by the different levels of the phylogenetic or functional tree when calculating functional or
148 phylogenetic indices (i.e., the “*similarity effect*” in Chalmandrier *et al.* 2015b). In fact,
149 community drivers can be applied differently across descendant clades (Vamosi *et al.* 2009).
150 Habitat filtering is primarily used when considering the assembly of distantly related lineages,
151 whereas biotic interactions have been shown to be more important for retrieving phylogenetic
152 and functional structures at the tips of the tree, i.e., among closely related taxa (Crisp *et al.*
153 2009; Ndiribe *et al.* 2013). Based on such evidence, we also test how assigning greater weight
154 to ancient or recent divergences in the functional and phylogenetic trees influences the
155 performance of the two modelling approaches in predicting diversity indices (Chalmandrier *et*
156 *al.* 2015b).

157

158 **Materials and Methods**

159 ***Species, traits, and phylogenetic data***

160 The study area covers approximately 700 km² of a mountain region located in the Western
161 Swiss Alps, and it is characterized by a large elevation gradient ranging from 375 m to 3210
162 m a.s.l. (Appendix S1 in Supporting Information). Exhaustive floristic inventories consisted
163 of a set of 613 plots of 4 m² ranging from 700 to 3000 m a.s.l., and they were distributed
164 within the study area according to a stratified-random sampling design to evenly cover the

165 range of habitat conditions (Hirzel & Guisan 2002). We did not consider the low elevation
166 band (lower than 700 m a.s.l.) to avoid areas of intense human pressure. The presence of plant
167 species in this dataset was used for to calibrate the SDM and MEM. An additional set of 298
168 plots representing the validation sites was surveyed using methods that were identical to those
169 applied to the training dataset. The validation sites were previously shown to be spatially
170 independent from the training sites and valid for model evaluation by calculating the spatial
171 correlation of the SSDM residuals between the calibration and the evaluation datasets based
172 on neighbourhood graphs and Moran's I coefficient (Pottier *et al.* 2013). A total of 241
173 vascular plant species were recorded. We considered 175 species that presented more than 30
174 occurrences and showed a low and quite uniform prevalence in the study area, with 70% of
175 the species having a prevalence ≤ 0.1 and 84% having a prevalence ≤ 0.2 (species list is
176 available in Appendix S2). No significant relationship was observed between the prevalence
177 and elevation. To build a functional tree, we also field-sampled two uncorrelated plant traits
178 associated with the performance of plant species during the persistence phase of their life
179 cycle (Westoby *et al.* 1998): vegetative height (VH in mm) and specific leaf area (SLA in
180 $\text{mm}^2 \text{mg}^{-1}$) (see Dubuis *et al.* 2013, for details on the measurements in the field). Vegetative
181 height is a stature trait associated with the plants' ability to compete for light, and specific leaf
182 area is related to the plants' ability to capture, use, and release resources to their environment,
183 thereby providing a good estimate of the position of the species along the leaf economic
184 spectrum. Each trait was log-transformed to conform to normality and scaled between 0 and
185 1. We then constructed a functional tree by calculating all of the pairwise dissimilarities
186 (Gower's distances) between observations in the data set (function `daisy {cluster}` in R). A
187 phylogenetic tree for these species is available in Ndiribe *et al.* (2013).

188 ***Biodiversity modelling: taxonomic component***

189 We modelled species richness and composition using two community modelling approaches.

190 1) SSDM: individual species distribution models were fitted with climatic and
191 topographic predictors calculated from data recorded by the Swiss network of meteorological
192 stations and obtained from a digital elevation model at 25 m resolution. We selected five
193 abiotic topoclimatic variables that previous studies reported to be relevant predictors of the
194 distribution of plant species in this mountain environment (Dubuis *et al.* 2011): growing
195 degree days (above 0 °C), moisture index throughout the growing season (difference between
196 precipitation and potential evapotranspiration), solar radiation sum for the entire year, slope
197 (in degrees), and topography (indicating the ridges and valleys). We used three modelling
198 techniques: a generalized linear model (GLM), generalized additive model (GAM), and
199 generalized boosted model (GBM). We created a weighted average ensemble model of the
200 three techniques for each species and used weights from the internal cross-validation with the
201 true skill statistic (TSS, Allouche, Tsoar & Kadmon 2006) evaluation metrics. All of the
202 models and the ensemble were tested for their predictive ability on the evaluation dataset
203 using both the area under the curve (AUC) of a receiver operating characteristic (ROC) plot
204 (Swets 1988) and the TSS metric. The potential species distributions obtained for the 175
205 species were binarized (presence/absence) using two threshold approaches: *i*) the threshold
206 corresponding to equal values of sensitivity and specificity (Liu *et al.* 2005); and *ii*) the
207 threshold maximizing the TSS. The binary models were stacked to predict the assemblage
208 richness and composition in the evaluation plots (SSDM predictions). We fitted all of the
209 models in R (2.14.1) using the biomod package (Thuiller *et al.*, 2009).

210 2) SSDM-MEM: for this approach, we began with the ensemble predictions for the
211 SDMs that define the potential pool of species by abiotic (i.e., topoclimatic) drivers
212 considering the same set of 175 species. We defined macroecological drivers (MEM) by
213 modelling the observed species richness with the same environmental predictors and
214 techniques used for the SDMs and establishing a Poisson distribution (MEM). This model

215 differs slightly from the one fitted by Dubuis *et al.* (2011) due to a smaller subset of species
216 and different predictors being used in our model. We further applied the ensemble forecasting
217 approach (as described above) to obtain a final richness prediction. We then coupled the raw
218 ensemble predictions from the SSDMs and the richness predictions by applying the
219 “probability ranking” rule (PRR) (D’Amen *et al.* 2015c). Using this procedure for each site,
220 we selected a number of species equal to the MEM richness predictions based on the
221 decreasing probability of presence calculated by the SDMs, thereby obtaining the binary
222 compositional predictions.

223 ***Biodiversity modelling: functional and phylogenetic components***

224 We used the SSDM and SSDM-MEM predictions of assemblage composition to reconstruct
225 the functional and phylogenetic diversity facets of communities. The functional and
226 phylogenetic diversity patterns in the evaluation dataset were estimated based on the observed
227 and predicted assemblages. In addition, the functional and phylogenetic diversity indices were
228 calculated using the approach proposed by Chalmandrier *et al.* (2015a), which builds on a
229 multiplicative decomposition framework (Pavoine, Love & Bonsall 2009; Chao, Chiu & Jost
230 2010; Leinster & Cobbold 2012) and allows for variation in the *dominance* of species in the
231 assemblage (importance assigned to dominant vs. rare species) and the *similarity effect*
232 (effects of considering different scales in the tree from broad to more exact structures – see
233 the Introduction). However, because our analyses were not based on abundance data, we fixed
234 the first parameter in the analyses. We included and measured the strength of the *similarity*
235 *effect* in the analyses of the diversity indices by applying the δ transformation (Pagel 1997) to
236 the functional and phylogenetic trees. The parameter δ scales the overall path lengths in the
237 tree, such as the distance from the root to the species as well as the shared path lengths. We
238 considered nine δ values (0.01, 0.05, 0.1, 0.5, 1, 2.5, 5, 7.5, and 10) to assign higher
239 importance to ancient branches or recent divergences by distorting the trees. Specifically, a

240 tree that is “stretched” (i.e., distorted by the δ transformation) close to its roots assigns more
241 weight to large distances, whereas a tree stretched close to its tips assigns more weight to
242 small distances. This investigation involved nine estimations of the functional and
243 phylogenetic diversity patterns in the observed data and the SSDM and SSDM-MEM
244 predictions.

245 ***Evaluation***

246 We calculated the taxonomic, functional and phylogenetic dissimilarities between the
247 predictions by the SSDM and SSDM-MEM approaches and the evaluation data (Sørensen
248 dissimilarity index). We also disentangled the two components of the Sørensen dissimilarity
249 index, *richness difference* and *species replacement*, between the observed and predicted
250 communities using the `betapart` R package (Baselga & Orme 2012; Legendre 2014). For
251 taxonomic diversity, we calculated both the sensitivity (the proportion of species correctly
252 predicted as present among the species observed as present) and specificity (the proportion of
253 species correctly predicted as absent among the species observed as absent). Finally, we
254 evaluated the performance of the SSDM and SSDM-MEM approaches in predicting the
255 species richness and the functional and phylogenetic diversity indices by calculating i)
256 Spearman's correlation (we use the non-parametric test because the variables are not normally
257 distributed), ii) the root mean square error (RMSE, Potts & Elith 2006), and iii) the average
258 error (AVE, Potts & Elith 2006):

259

260

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{y}_i - y_i)^2}$$

261

262
$$AVE_{error} = \frac{1}{n} \sum_{i=1}^n (\hat{y}_i - y_i)$$

263

264 These formulas are based on the sample size (n) and the discrepancy between the observed
265 (y_i) and predicted (\hat{y}_i) values.

266

267 To explore variations in the predictive accuracy along the elevation gradient, all of the above
268 statistics were also calculated by grouping the evaluation plots within 500 m wide elevation
269 bands. Correlations for different bands were compared based on Z scores by applying Fisher's
270 transformation (Fisher 1921). Finally, the same statistics were calculated for each value of the
271 parameter δ to test the *similarity effect* in the predictions of functional and phylogenetic
272 diversity indices.

273

274 **Results**

275 *Accuracy of taxonomic predictions*

276 Species distribution models for most species had an AUC value higher than 0.7; therefore,
277 they can be considered useful for predictions. In particular, the mean and standard deviation
278 of the AUC scores for the different techniques were GAM: 0.803 ± 0.078 ; GLM: $0.799 \pm$
279 0.077 ; and GBM: 0.783 ± 0.081 (see Appendix S2 for the evaluation statistics for all species
280 by both AUC and TSS). The MEM prediction showed a fair correlation value between the
281 observed and predicted values of the species richness in the evaluation dataset ($\rho = 0.529$,
282 Spearman's rank correlation test), and the species richness error was centred on zero
283 (Appendix S3). The SSDM based on the two threshold approaches produced similar results (ρ
284 $= 0.504$ and 0.507 Spearman rank correlation tests); thus, we have only presented the results

285 derived from binarization using the AUC statistic. Compositional predictions from the SSDM
286 achieved higher sensitivity scores than the SSDM-MEM, whereas the opposite was observed
287 for specificity (Appendix S4). In other words, the SSDM was better for predicting the
288 presence of a species, whereas the SSDM-MEM was better for predicting the absence of a
289 species. The SSDM-MEM predictions of community composition produced a moderate but
290 significant decrease in the Sørensen dissimilarity index compared with the SSDM predictions
291 (t-test $p < 0.001$) for the entire elevational gradient (Appendix S5). The RMSE for the
292 richness component of taxonomic diversity was higher with the SSDM than the SSDM-MEM
293 (28.52 and 8.72, respectively). Moreover, the average error (AVE) was low for the SSDM-
294 MEM (1.09) but high for the SSDM (-23.94), thereby confirming the high overestimation of
295 the number of species in the latter approach without the MEM constraint.

296

297 *Accuracy of functional and phylogenetic index predictions and the similarity effect*

298 According to the Sørensen dissimilarity index, the SSDM-MEM significantly increased the
299 predictive capacity of the SSDM for the phylogenetic facet (mean of Sørensen dissimilarity
300 index: SSDM-MEM = 0.27, SSDM = 0.35; Wilcoxon signed rank test, $p < 0.001$) (Fig. 1 and
301 Appendix S5). The two components of Sørensen's dissimilarity index showed similar patterns
302 for all of the biodiversity facets and indicated that the SSDM-MEM framework provided
303 significantly improved predictions compared with the SSDM for the richness component but
304 worse predictions for species replacements in communities (Fig. 1 and Appendix S5). The
305 difference in the prediction errors of functional and phylogenetic diversity showed that the
306 former was better predicted than the latter by both modelling approaches (Wilcoxon test, $p <$
307 0.001) (Fig. 2, Appendix S6). The functional and phylogenetic diversity predictions derived
308 from the SSDM-MEM framework out-performed those derived from the SSDM. In fact, the
309 SSDM-MEM predictions obtained a lower average RMSE (functional index: mean RMSE for

310 SSDM-MEM = 2.68 and for SSDM = 6.88, phylogenetic index: mean RMSE for SSDM-
311 MEM = 3.48 and for SSDM = 9.30). According to the AVE, the predictions derived from the
312 SSDM-MEM accurately retrieved both the functional and phylogenetic diversity indices,
313 whereas the predictions derived from the SSDM produced greater errors, which were more
314 pronounced in the phylogenetic component (functional index: mean AVE for SSDM-MEM =
315 0.41 and for S-SDM = -5.76, phylogenetic index: mean AVE for SSDM-MEM = 0.02 and for
316 S-SDM = -7.81) (Fig. 2). Considering the similarity effect, assigning more weight to ancient
317 divergences ($\delta \leq 0.01$) lowered the differences in the errors between the SSDM-MEM and
318 SSDM for functional and phylogenetic diversity. Both the RMSE and AVE increased for a
319 medium to strong similarity effect, although the increase was more pronounced for the SSDM
320 predictions than for the SSDM-MEM predictions (Fig. 2; Appendix S6).

321 *Accuracy of predictions along the elevation gradient*

322 Overall, the SSDM-MEM predictions were better than the SSDM predictions across the
323 elevation gradient for the *dissimilarity* and (especially) the *richness difference* index, as
324 expected. For the SSDM-MEM predictions, the *Sørensen dissimilarity index* and its
325 components increased with elevation except for the *richness difference* component of
326 taxonomic diversity, which was low and constant across the whole gradient (Fig. 1). This
327 trend was not observed for the SSDM predictions (Fig. 1). Nevertheless, we observed the
328 reverse pattern for the *species replacement* component when considering taxonomic diversity
329 (Fig. 1). For the taxonomic component of the *Sørensen dissimilarity index*, the accuracy
330 improvement produced by the SSDM-MEM was not evenly distributed across the elevation
331 gradient. The SSDM-MEM produced a 20% improvement in performance over the SSDM in
332 the low elevation bands (up to 1500 m); however, this improving trend decreased as the
333 elevation increased to 2500 m and was no longer noticeable at higher elevations (Fig. 1). The
334 improvement produced by the SSDM-MEM for the taxonomic component considering the

335 *richness difference* index was high and ranged from 65% at lower elevations to 50% at higher
336 elevations.

337 The SSDM-MEM approach was better at reproducing species patterns along elevations for the
338 species richness and functional and phylogenetic diversity indices and presented the lowest
339 deviations from the observed values (Appendix S7). Comparing the accuracy across elevation
340 bands, the predictions for diversity indices in the 2000-2500 m band showed significantly
341 higher ρ correlation coefficients than the other elevation bands based on both modelling
342 approaches and all levels of the *similarity effect* (all δ values for the tree transformations)
343 (Fig. 3). The RMSE and AVE values were not significantly dissimilar across the elevation
344 bands for the SSDM-MEM predictions of the functional and phylogenetic diversity indices
345 (Fig. 3). However, the SSDM prediction errors varied for moderate to high similarity effects,
346 with the highest error in the 1500-2000 m band and a decreasing error trend observed from
347 low to high elevations (Fig. 3).

348

349 **Discussion**

350 This study is the first to compare different modelling approaches to predict the spatial patterns
351 of multiple biodiversity facets. Our results show that the SSDM coupled with the MEM
352 (SSDM-MEM) can moderately but significantly improve the predictions of the taxonomic,
353 functional, and phylogenetic diversity of plant assemblages. Moreover, the accuracy of the
354 SSDM predictions for the diversity indices varied greatly along the elevation gradient and for
355 different intensities of the *similarity effect*, whereas the SSDM-MEM predictions were more
356 stable. The predictive improvements observed via the application of the SSDM-MEM were
357 likely related to the implementation of the following two steps: 1) the correction of species
358 overestimations produced by the SSDM by imposing a limit on the number of species in each
359 site, which produced a cascade effect on the quality of the derived functional and

360 phylogenetic indices; and 2) the application of the “probability ranking” rule to sort the
361 species that can co-occur at the studied site (D’Amen *et al.* 2015c).

362 As expected, the species composition was the most difficult diversity component to predict
363 (Thuiller *et al.* 2015). Considering the direct dissimilarity in the comparison between the
364 observed and predicted assemblages, the SSDM-MEM improved the *richness difference*
365 component of the Sørensen index, which we used as a measure of the capacity of the model to
366 predict the number of species correctly (Baselga 2010; Legendre 2014). Thus, the improved
367 predictions of the taxonomic component by the SSDM-MEM were likely driven by the
368 corrected number of species predicted and the removal of the least probable species.

369 However, this removal likely also produced a degree of degradation of the *species*
370 *replacement* component, i.e., the capacity of the model to correctly predict the species present
371 in the observed community (see Baselga 2010). These results are consistent with our findings
372 regarding the sensitivity and specificity indices in the compositional predictions, with the
373 SSDM-MEM improving the specificity but producing worse scores for the sensitivity index.
374 Overall, the balance between the improved accuracy of the *richness difference* and the
375 decreased accuracy of the *species replacement* indicates that the SSDM-MEM approach can
376 produce a moderate improvement in the SSDM predictions but not for all of the components.

377 The results reported above suggest that in our study, certain species were not correctly
378 removed by the *probability ranking* rule (PPR) when attempting to control for SSDM
379 overprediction. The PPR has been assumed to represent a putative ecological assembly rule
380 that translates competitive strength as a function of environmental suitability, meaning that
381 species will be more competitive in their most favourable habitats (D’Amen *et al.* 2015a).
382 Species with the highest probability of occurrence are expected to be better adapted to the
383 environmental conditions of the site, thereby leading to higher competitive ability. A more
384 methodological justification of the PPR performance is that by removing the species with the

385 lowest probability of occurring at a site, the species with the highest probability of being
386 overpredicted by the SSDMs are also removed. A potential problem with the PPR as currently
387 implemented is that it may depend on the species prevalence in the study area. The most
388 frequent species are likely to have higher a probability of occurrence than the least frequent
389 species (pers. obs.), which may in turn affect the ranking of the species and produce
390 communities that are always composed of the most common species, although good
391 evaluation scores are still obtained. This bias should be analysed in future studies by testing
392 whether and how rescaling the probability outputs from the SSDM-MEM to correct for
393 prevalence (e.g., via changing the weighting of the presences and absences) might improve
394 the predictions. Alternative rules that also consider historical or anthropogenic factors could
395 be implemented in further developments of the SSDM-MEM framework to improve the
396 species selections from the abiotic species pool (SSDM) to match the richness predictions by
397 the MEM.

398 Upon “aggregating” the diversity components to estimate the functional and phylogenetic
399 diversity indices, the performance of the models is increased, which is likely because these
400 indices can be predicted equally well for different sets of species with similar functional or
401 phylogenetic characteristics. However, in such cases, the taxonomic diversity component
402 would lose prediction accuracy. The SSDM-MEM predictions of the species composition led
403 to accurate predictions of the functional and phylogenetic indices, suggesting that the species
404 selected incorrectly in the final community composition were at least functionally or
405 phylogenetically close to the correct ones, although this was not always true for the SSDM
406 predictions. The similarity effect (Chalmandrier *et al.* 2015b) exerted a substantial impact on
407 the detection of patterns in the functional and phylogenetic diversity indices in our plant
408 communities. The prediction errors varied with the weight assigned to large vs. small species
409 similarities when calculating diversity indices, with a much stronger variation in accuracy

410 observed for the SSDM compared with the SSDM-MEM. In particular, the predictions for the
411 phylogenetic and functional diversity indices were more accurate for a weak similarity effect.
412 The error in the SSDM predictions increased in proportion as the strength of the similarity
413 effect increased. This result can be interpreted as related to the increasing importance of biotic
414 interactions *vs.* environmental abiotic filtering when the assembly of increasingly closely
415 related lineages is considered (Ndiribe *et al.* 2013). Because the SSDM primarily accounts for
416 the effect of abiotic drivers in shaping the community structure, it performs better when
417 greater emphasis is placed on large species similarities. Conversely, the SSDM-MEM
418 framework could predict recent and profound node structures of the communities, meaning
419 that it shows good performance when a greater emphasis is placed on large or small species
420 similarities. This result is likely because of the SSDM-MEM framework's ability to set a
421 macroecological constraint on community richness. The SSDM produces considerable errors
422 when predicting phylogenetically closely related species, which may indicate that the latent
423 underlying mechanisms related to the phylogenetic community structure may not have been
424 considered in the modelling approach.

425 The SSDM-MEM framework was the best technique for reproducing the observed diversity
426 patterns along elevation. A varying degree of prediction errors in species richness along
427 elevation has been previously reported for the SSDM. This variation was mainly caused by
428 the differences in the degree of overprediction along this gradient (Pottier *et al.* 2013).
429 However, we observed a different trend when considering the Sørensen dissimilarity index.
430 The SSDM-MEM index predictions showed an overall tendency towards lower accuracy with
431 increasing elevation, especially for the functional component. This trend was not noticeable
432 for the SSDM predictions.

433 According to the stress gradient hypothesis (Normand *et al.* 2009), the influence of the
434 environmental filter and biotic interactions is expected to vary with elevation. Biotic

435 interactions should be more intense or frequent under low-stress conditions (i.e., middle to
436 lower elevations), whereas the effect of the environment should be more important under
437 high-stress conditions (i.e., higher elevations; Bertness & Callaway 1994; Brooker &
438 Callaghan 1998; Pottier *et al.* 2013). The performance of the SSDMs in our study system
439 conformed to balance between the two assembly drivers, with improved performance at
440 higher elevations because of the stronger relationship between the species distribution and the
441 environment (Pottier *et al.* 2013). The decreased performance at middle elevation sites may
442 have been caused by the increased importance of biotic interactions at these sites compared
443 with the performance at higher elevation sites because the sites are generally more productive
444 at middle elevations; therefore, species interactions may occur more frequently and result in
445 the exclusion of certain of species. An alternative explanation for this result might be the
446 disequilibrium between the species distribution data and the topoclimatic data. Under mild
447 climatic conditions, other factors mediated by human-related (e.g., grazing or agricultural
448 fertilization) or stochastic processes may play a more prominent role in determining the
449 composition of the extant communities.

450 The reverse trend was observed for the SSDM-MEM predictions when considering the results
451 of the *Sørensen dissimilarity index*. We found that the SSDM-MEM had a lower performance
452 in predicting plant diversity at high elevations, where the most important community driver is
453 the environment alone. This reduction in performance was especially evident in the SSDM-
454 MEM predictions of functional diversity, which is the diversity facet that is expected to be
455 most strongly influenced by the environment. However, we may have also obtained different
456 values for the maximum species richness for each elevation band. The plots with the lowest
457 richness were located at high elevations, which might have caused the increased performance
458 of the SSDM in this band. This behaviour was not observed for the SSDM-MEM, thereby
459 supporting its more stable performance, even at different richness values. However, this

460 potential bias does not affect the comparison of the modelling methods within each elevation
461 band.

462 The patterns described above for the functional and phylogenetic diversity indices were only
463 observed when considering moderately to more closely related lineages (i.e., for a medium to
464 strong similarity effect), and stronger differences in performance were proportional to the
465 strength of the similarity effect. However, with low similarity effects, the prediction error was
466 more constant along elevation. An explanation for this result may be that an environmental
467 filter is the main assembly driver for distantly related lineages across the entire elevation
468 gradient, which also enables the SSDM approach to retrieve community patterns at middle
469 elevations.

470 Certain peculiar characteristics of the studied system and approaches could have influenced
471 the results. We focused on a simplified taxonomic assemblage of grassland species, and
472 including more complex communities, such as those with prey-predator interactions, would
473 have required a much more complex modelling strategy. Moreover, we analysed communities
474 at a very fine spatial resolution. Biotic interactions are expected to have greater importance at
475 this resolution (Pearson & Dawson 2003), which may in turn cause a stronger over-prediction
476 by the SSDMs. The accuracy of taxonomic predictions should thus improve toward lower
477 spatial resolutions for this approach (Thuiller *et al.* 2015). The influence of scale on the
478 SSDM-MEM should be assessed in future studies, specifically to ascertain whether the
479 benefits of this approach can be observed at different resolutions and extents. In addition, the
480 SSDM-MEM method can be improved by including more dynamic (e.g., Keith *et al.* 2008)
481 and/or mechanistic SDMs (e.g., Kearney & Porter 2009) when the data required to fit the
482 models are available for all species (Guisan & Rahbek 2011). Finally, concerning the SSDM
483 performance, it was shown elsewhere that the threshold selection may strongly influence the
484 reliability of the predicted richness and composition (Benito *et al.* 2013). In this paper, we

485 presented the results from two thresholding methods, but we had also calculated a large range
486 of other species-specific thresholds, none of which affected our results (unpubl. data).

487 Biodiversity integrates biotic components from genes to ecosystems. Therefore, measuring
488 such a broad concept represents a great challenge (Purvis & Hector, 2000). Here, our goal was
489 to test the capacity of a novel community modelling approach to predict three key facets of
490 biodiversity - taxonomic, functional and phylogenetic - at the alpha diversity level. The
491 approach to coupling SSDMs with richness predictions through a simple probability ranking
492 rule produced a moderate but significant improvement over the most common and simpler
493 approach of stacking individual species predictions. This result opens promising avenues
494 towards improving biodiversity predictions in space and time and across broad environmental
495 gradients using functional and phylogenetic information. However, future studies on the
496 SSDM-MEM approach could further be expanded to test additional components of
497 biodiversity. For example, when considering broader regions than our study area, the
498 collective diversity may be better determined by differences between regional species pools
499 (Guisan & Rahbek 2011) and by the turnover in biological composition between locations
500 (i.e., beta diversity) than by the site-level diversity (i.e. alpha diversity). Measuring beta
501 diversity could therefore be a critical complement to the alpha measures performed here.

502 Certain modelling approaches have already been developed to predict this component as an
503 emergent property of biodiversity (e.g., Ferrier *et al.* 2007), but often at the expense of
504 information on species identities at the local level. Recent frameworks have been proposed
505 that combine different levels of modelling to predict both alpha and beta diversities. For
506 instance the dynamicFOAM framework (Mokani *et al.* 2011) combines correlative richness
507 (alpha-diversity) models and models of compositional turnover (beta-diversity) to generate
508 compositional data for meta-communities and gamma –diversity. A comparison of the
509 performance of the SSDM-MEM method with such beta-diversity-level approaches represents

510 an interesting research perspective for improving spatial modelling research and conservation
511 applications.

512

513

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708

709 Author's Contributions

710 MD, RGM, JP, and AG developed the concept of the study, with further
711 contributions by WT, LP and LM, and all contributed to the final design of the analyses.
712 AG provided the plant distribution data and CN and NS developed the phylogenetic tree.
713 MD, RGM, JP analysed the data. MD, RGM, AG drafted the manuscript. All authors
714 contributed to the interpretation of results and to revise the manuscript critically.

715

716 **SUPPORTING INFORMATION**

717 Additional supporting information can be found in the online version of this article:

718 **Appendix S1:** Map of the study area with sampling plots.

719 **Appendix S2:** SDM evaluation results for each species.

720 **Appendix S3:** Macroecological model results.

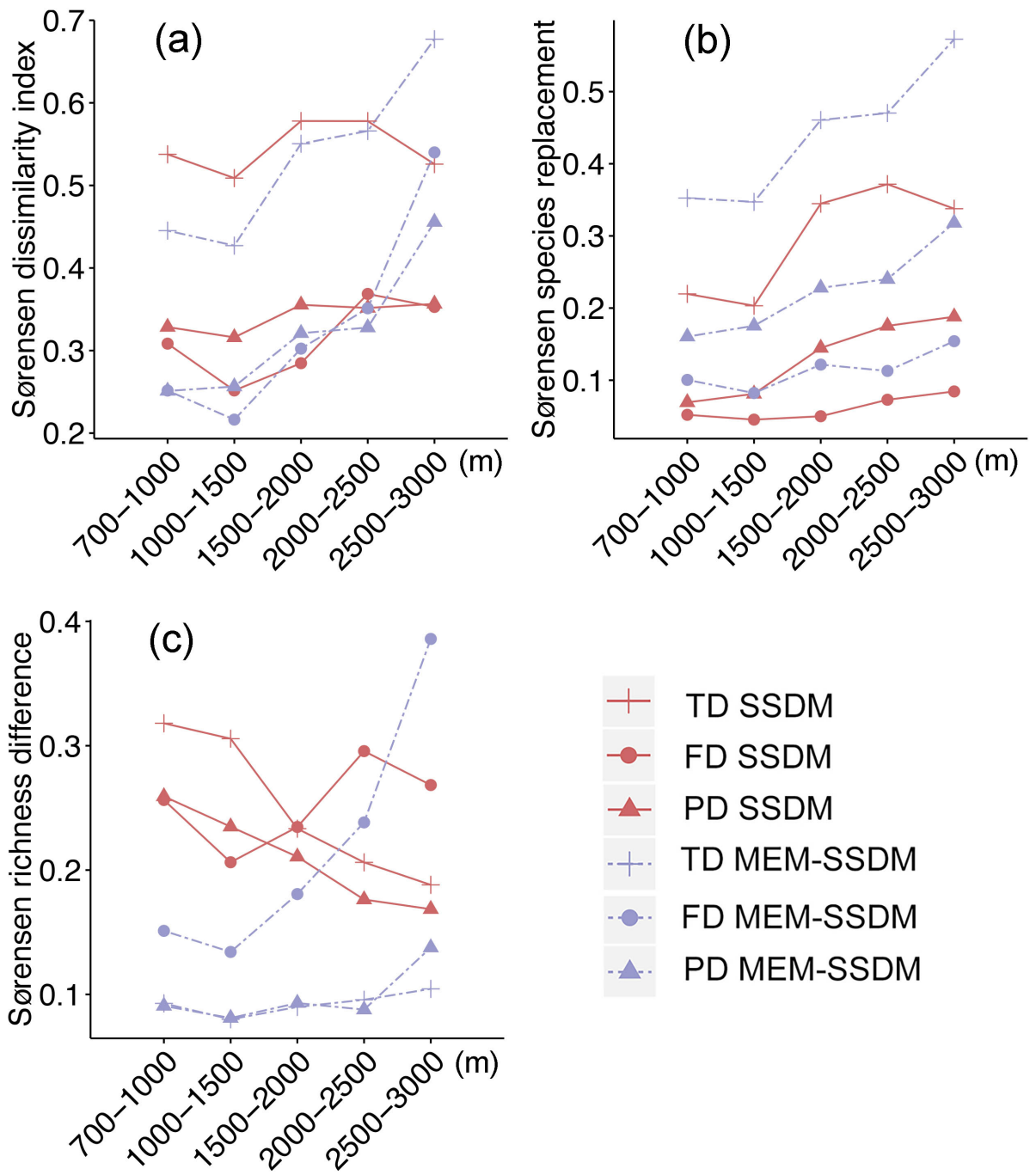
721 **Appendix S4:** Comparison of the SSDM and SSDM-MEM predictions based on the
722 sensitivity and specificity indices.

723 **Appendix S5.** Comparison of the SSDM and SSDM-MEM predictions for the three diversity
724 components based on the Sørensen dissimilarity index and its components.

725 **Appendix S6.** Variation of the root mean square error for model predictions for the FD and
726 PD indices at different similarity δ values.

727 **Appendix S7:** Values of Spearman's correlation between the observed and predicted FD and
728 PD indices for the SSDM-MEM and SSDM approaches at each similarity parametrization.

729 **Figure 1:** Mean values for the Sørensen dissimilarity index and its two components (Sørensen
 730 richness difference and Sørensen species replacement) calculated for the predictions of
 731 taxonomic (TD), functional (FD), and phylogenetic (PD) diversity from the SSDM and
 732 SSDM-MEM models for each elevation band.



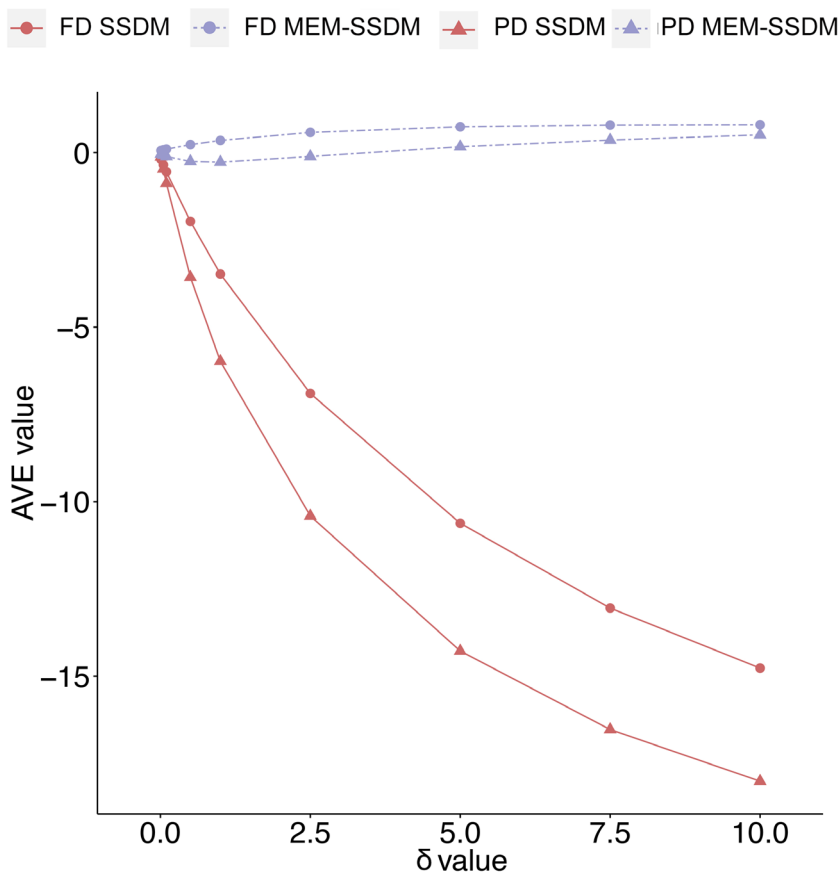
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735 **Figure 2:** Variation of the average error (AVE) for the SSDM and SSDM-MEM predictions
736 for the functional and phylogenetic diversity indices for different intensities of the similarity
737 effect (different values of the δ parameter transform the functional and phylogenetic trees:
738 values closer to 0 indicate that a greater importance is assigned to ancient branches, whereas
739 values closer to 10 indicate that the transformation assigns more weight to recent
740 divergences).

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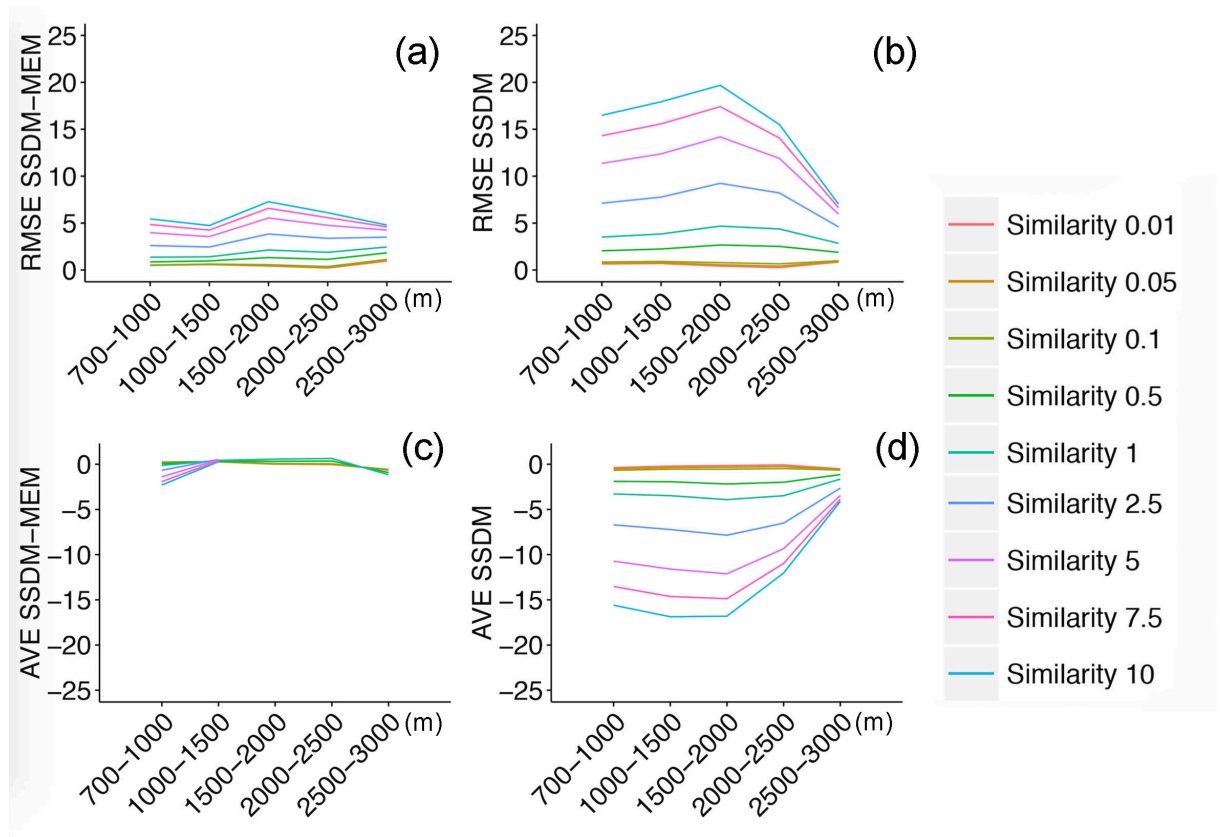


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746 **Figure 3:** Evaluation statistics (root mean square error, RMSE; and average error,
 747 AVE) across elevation bands for the functional diversity index and all similarity δ values,
 748 derived from the SSDM and SSDM-MEM predictions.



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750