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1 Is prediction of species richness from Stacked Species Distribution Models biased by habitat
2 saturation?

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Author note

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13

Abstract

14 Several studies have proposed to predict Species Richness (SR) by combining the
15 predictions of independent Species Distributions Models (SDMs) (the predict first-assemble later
16 strategy). Alternative methods propose to combine outputs from SDMs differently, by either
17 summing predicted presence probabilities at each location, or summing binary presence
18 predictions after thresholding the probabilities. Species can occupy various proportions of their
19 suitable habitats (i.e, have various levels of habitat saturation), which can cause discrepancy
20 when predicting their presences through SDMs. Furthermore, these discrepancies can be
21 increased when combining the predictions of individual SDMs to predict SR. In this article, we
22 performed simulations of species distributions with varying habitat saturation (i.e., the amount of
23 suitable habitat occupied by a species), and we compared observed richness with that predicted
24 by the alternative approaches. We found that probability-based richness is not biased by the level
25 of habitat saturation, while threshold-based richness over-predicts richness at low habitat
26 saturation and under-predicts it as high habitat saturation. Probability-based richness should thus
27 be used in priority when predicting species richness locally. Nonetheless, threshold-based
28 richness represents species richness constrained by environmental filtering only and thus is a
29 useful indicator of potential species richness when species fully saturate their habitats. Thus the
30 systematic comparison of probability-based and threshold-based richness predictions can reveal
31 the importance of habitat saturation and can thus help identify community assembly mechanisms
32 at play.

33 *Keywords:* habitat saturation, species richness, stacked species distribution models,
34 predicted presence probabilities, threshold-based presence prediction

35 Word count: 2909

36 **Highlights**

- 37 • Habitat saturation impacts predictions from Species Distribution Models (SDM)
- 38 • Habitat saturation biases stacked SDMs (S-SDMs) predictions
- 39 • Probability-based richness predicts local SR without bias whatever habitat saturation
- 40 • Comparing different S-SDMs predictions can shed light on community assembly processes

41 **Introduction**

42 Species Richness is an Essential Biodiversity Variable (EBV) (Pereira et al., 2013), which
43 should be assessed, monitored and compared across space, time, and ecological contexts.

44 Different models have been proposed for richness prediction in diverse ecological contexts and at
45 large spatial scale (Dodson, 1992; Graham and Hijmans, 2006; O'Brien, 1998), with the
46 perspective of identifying biodiversity hotspots (Mazel et al., 2014; Myers et al., 2000), targeting
47 effective management practices (Chown et al., 2003), quantifying biodiversity changes (Newbold
48 et al., 2015) and predicting ecosystem functioning (Cardinale et al., 2012).

49 Several methods can be used to predict richness depending on which ecological processes
50 are at play. For example, Macro-Ecological Models (MEMs) directly predict richness at any
51 location as a function of local environmental variables. These models consider the influence of
52 environmental filtering and energy limits on richness (Hurlbert and Stegen, 2014). Because site-
53 species data are first aggregated to estimate richness and then used to predict the variation with
54 the environment, these approaches are called 'assemble first, predict later' (Ferrier and Guisan,
55 2006). Conversely, more and more global and local biodiversity databases include species

56 occurrences instead of local assemblage composition (GBIF, 2019; Sullivan et al., 2009; Tedesco
57 et al., 2017). An alternative approach has been to first model occurrences, independently for each
58 species, at any location using environmental variables through species distribution models
59 (SDMs) (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000), then to deduce potential
60 local richness by combining (=stacking) the predictions of individual SDMs (Calabrese et al.,
61 2014; D’Amen et al., 2015b; Gavish et al., 2017; Scherrer et al., 2018; Schmitt et al., 2017),
62 which is known as the ‘predict first, assemble later’ approach (Ferrier and Guisan, 2006). When
63 stacking SDMs, each SDM predicts occurrences for species independently using environmental
64 variables (Guisan and Zimmermann, 2000). Then, predictions of SDMs for different species are
65 summed to predict richness at assemblage-level. Stacked-SDMs (S-SDMs) predict observed
66 richness as well as or better than macro-ecological models (Dubuis et al., 2011; Guisan and
67 Rahbek, 2011), but there is still no consensus on the stacking method to be used so as to reliably
68 predict richness with S-SDMs (Scherrer et al., 2018).

69 Two main methods exist to stack SDMs (Dubuis et al., 2011; Pineda and Lobo, 2009;
70 Scherrer et al., 2018). Some authors suggested using thresholds to convert probabilities to binary
71 predictions (presence and absence) (Jim’enez-Valverde and Lobo, 2007; Liu et al., 2005). These
72 binary predictions are then summed to predict richness at local scale (hereafter threshold-based
73 richness). One of the main arguments for conversion of probabilities provided by SDMs to binary
74 predictions is that most of practical applications need binary maps (Jim’enez-Valverde and Lobo,
75 2007). A caveat of binary predictions is that they translate continuous responses of species along
76 environmental gradients into binary responses, which imply more abrupt shifts from presence to
77 absence between suitable and unsuitable conditions (Meynard and Kaplan, 2012). When
78 predicted probabilities are under the threshold, the model only predicts absences, while it only

79 predicts presences when predicted probabilities are above it. Close to the threshold value, a small
80 change in predicted presence probability can change the binary prediction from absence to
81 presence. Meynard et al. (2012) showed that presence predictions using thresholds fit observed
82 presences only when species has a threshold-like response, while error increases when a species
83 response is more gradual. The more species considered that have a gradual response along the
84 environment, the greater the error when predicting richness. SDMs also directly provide
85 continuous presence probabilities as outputs (Guisan and Thuiller, 2005), and threshold
86 conversion to binary predictions adds a step compared to the direct sum of individual model
87 predictions. Summing the probabilities of individual species model provides the mathematical
88 expectation of the number of species locally present, assuming that species occurrences are
89 independent (Calabrese et al., 2014; Violle et al., 2011), hereafter called probability-based
90 richness.

91 A basic implicit assumption of SDMs is that only environmental conditions determine
92 species occurrence, depending on a species fundamental niche (Guisan and Zimmermann, 2000).
93 Additional processes should affect the realized occupancy patterns, such as dispersal limitation,
94 competitive exclusion, local extinction dynamics (Pulliam, 2000). SDM predictions and thus
95 richness predictions are likely to be biased by neglecting the contribution of processes shaping
96 realized species distributions beyond their fundamental niche requirements (Václavík and
97 Meentemeyer, 2012), thereby affecting SDM predictions and thus richness predictions. For
98 instance, due to source-sink dynamics, some species can occupy less suitable sites, and thus be
99 distributed outside the suitable habitat delimited based on presence probabilities predicted by
100 SDMs. In addition, a species that is less often present across its suitable habitat would have a
101 lower predicted presence probability than a species that is present in all its suitable habitats, even

102 though the predicted binary distribution of an SDM would be the same. We define habitat
103 saturation of a species as a parameter that affects species occurrence probability based on
104 environmental suitability. Here saturation is a species-level property and not an upper bound for
105 richness in assemblages as proposed by Mateo et al. (2017). When species display low habitat
106 saturation, their realized presence probabilities decrease, so that the predicted summed
107 probability gets lower. On the contrary, the threshold-based presence prediction is not affected,
108 by habitat saturation. Indeed, even if the determined species threshold changes with habitat
109 saturation, the prediction will still be binary (presence or absence) (Meynard and Kaplan, 2012),
110 thus we expect to observe increasing difference between threshold-based and observed richness
111 with lower (or higher) habitat saturation.

112 Predicted presence probabilities partly reflect the ability of species to saturate their niche.
113 Therefore, we expect probability-based richness to best predict actual richness. While we expect
114 threshold-based richness to over-predict actual richness. Threshold-based richness rather
115 represents a pool of species able to occur in given environmental conditions. To test these
116 expectations we simulated virtual species with varying saturation and niche requirements (Hirzel
117 et al., 2001; Meynard et al., 2019). We performed S-SDMs to predict richness given
118 environmental conditions using both threshold- and probability-based richness and compared
119 how the predictions were affected by habitat saturation. Probability-based richness followed
120 observed richness whatever the habitat saturation, while threshold-based richness only matched
121 observed richness when habitat saturation was 100%. Threshold-based richness only considered
122 the environmental requirements of species, and could thus be used as the prediction of potential
123 richness based solely on local environmental conditions. Potential richness could then be
124 compared with other richness predictions that incorporate other ecological processes.

125

Material and Methods

126 Species assemblage simulations

127 **Individual species simulation.** We simulated a linear environmental gradient of 2000
128 values, from 1 to 2000. We then used the `virtualespecies` package version 1.4-2 (Leroy et al.,
129 2016) to define 100 species independently, with quadratic environmental response $s_{i,k} = a \times$
130 $Env_k^2 + b \times Env_k$, with $s_{i,k}$ the environmental suitability of species i in assemblage k and Env_k
131 the environmental variable. a was drawn from a uniform distribution between -20 and -0.01. b
132 was chosen as $b = -m * 2 * a$ where m was drawn from a uniform distribution between 1 and
133 2000 and represents the environment of maximum suitability. The suitability was then scaled
134 between 0 and 1 by subtracting its minimum and dividing by the difference of its maximum and
135 minimum. We used the function `generateRandomSp()` in `virtualespecies` to get suitability
136 probabilities for each species and each environmental value (see Figure 1 left column).

137 **Habitat saturation and predicted assemblages.** We simulated species presences along
138 the environmental gradient by performing binomial draws based on the presence probabilities.
139 The presences probabilities $p_{i,k} = s_{i,k} \times \beta$ depend on (i) the suitability probabilities defined
140 above, $s_{i,k}$ for species i and assemblage k , reflecting fundamental niche requirements, and (ii) an
141 additional habitat saturation coefficient β representing the ability of species to occupy their
142 suitable habitat (realized niche). When saturation is below 100%, the species tend to be less often
143 present in suitable sites than species at 100% saturation (e.g., due to dispersal limitation or
144 extinction). Species can also reach a saturation over 100% when they are present in less suitable
145 conditions than according to their fundamental niche (e.g., through source-sink dynamics). We
146 simulated 8 values of β : 10%, 40%, 70%, 100%, 120%, 150% and 170%. If the weighted

147 probability of presence was greater than one, we reduced it to a maximum of one. We thus
148 simulated each species assemblage k for each value β .

149 **Individual and Stacked Species Distribution Models**

150 We performed Species Distribution Models (SDM) based on simulated species presences.

151 **Modeling and Predicting Presences.** We modeled the presence of each species using two
152 predictors: the environmental value and the square of this value (see Figure 1 middle column) in
153 Generalized Linear Models (GLM) of the binomial family:

$$\text{logit}(p_{i,k}) = \beta_0 \text{Env}_k + \beta_1 \text{Env}_k^2, \quad (1)$$

154 with $p_{i,k}$ the presence of species i in assemblage k and Env_k its associated environmental
155 variable. We thus estimated in each assemblage the probability of finding each species. For each
156 species we determined the best threshold to get binary predictions by maximizing the True Skill
157 Statistic (TSS) (Allouche et al., 2006). The TSS balances the proportion of presences correctly
158 predicted and the proportion of absences correctly predicted.

159 **Predicting Species Richness.** We stacked SDM predictions in each assemblage to get a
160 prediction of richness, with two approaches. We first summed the predicted presence probability
161 for each species (probability-based richness, prediction (A) in Figure 1):

$$\text{pred}_{\text{rich,prob},k} = \sum_{i=1}^s p_i(k), \quad (2)$$

162 with $pred_{rich,prob,k}$ the probability-based predicted richness in assemblage k , S the total
163 number of species in the species pool, and $p_i(k)$ the predicted presence probability of species i in
164 assemblage k . Using these probabilities we determine a species-specific threshold t_i using the
165 True Skill Statistic (Allouche et al., 2006) that defines a binary function $1_i(k)$ to predict the
166 presence of the species in each assemblage:

$$1_i(k) := \begin{cases} 1 & \text{if } p_i(k) \geq t_i \\ 0 & \text{if } p_i(k) < t_i \end{cases} \quad (3)$$

167 with $p_i(k)$ the predicted presence probability of species i in assemblage k and t_i the
168 species i threshold defined using TSS. We then compared the sum of predicted presence
169 probabilities $pred_{rich,prob,k}$ to the sum of predicted presences with species-specific threshold
170 (threshold-based richness, prediction **(B)** in Figure 1):

$$pred_{rich,thresh,k} = \sum_{i=1}^S 1_i(k), \quad (4)$$

171 with $pred_{rich,thresh,k}$ the threshold-based predicted richness in assemblage k , S the total
172 number of species in the species pool and $1_i(k)$ the indicator function defined as above.

173 We examined how predicted richness fitted observed richness across the whole
174 environmental gradient, for different levels of habitat saturation. We quantified the deviation with
175 Root Mean Square Error (RMSE):

$$\text{RMSE} = \sqrt{\frac{1}{N_k} \sum_{k=1}^{N_k} (\text{pred}_{\text{rich},k} - \text{obs}_{\text{rich},k})^2}, \quad (5)$$

176 with $\text{pred}_{\text{rich},k}$ the predicted richness of a given method in assemblage k , $\text{obs}_{\text{rich},k}$, the
 177 observed richness in this assemblage, and N_k the total number of assemblages. We defined Bias
 178 and Variance components:

$$\text{Bias} = \frac{1}{N_k} \sum_{k=1}^{N_k} (\text{pred}_{\text{rich},k} - \text{obs}_{\text{rich},k}) \quad (6)$$

$$\text{Variance} = \frac{1}{N_k} \sum_{k=1}^{N_k} (\text{pred}_{\text{rich},k} - \widehat{\text{pred}}_{\text{rich}})^2 \quad (7)$$

179 with $\widehat{\text{pred}}_{\text{rich}}$ the average predicted richness of a given method across all assemblages.

180 All analyses and SDMs were performed using R version 3.5.2 (R Core Team, 2019). A
 181 version of the code used in this article is archived on Zenodo
 182 (<https://doi.org/10.5281/zenodo.3345742>).

183 **Results**

184 Binary predictions (solid segments above and below the plot) showed few differences
 185 whatever habitat saturation (Figure 2). There were the same from environment 1 to 273, then
 186 between environment 467 and 1514, and for environments greater than 1720. In total binary
 187 predictions were the same whatever habitat saturation for over 80% of the environmental values.

188 However, binary predictions changed abruptly from absences to presences and from presences to
189 absences for environment close to 500 and to 1500, respectively. On the contrary, the predicted
190 presence probabilities did vary with habitat saturation (solid curves in the center). The greater the
191 habitat saturation, the greater the maximum predicted probability. For example at 100% habitat
192 saturation, the maximum predicted probability was close to 0.95, while at 70% saturation it was
193 0.7.

194 When comparing observed richness to probability-based richness and threshold-based
195 richness (respectively green and purple points and curves on Figure 3), we observed differences
196 depending on habitat saturation. Across all habitat saturation levels, probability-based richness
197 showed consistently lower RMSE and variance than threshold-based richness (Figure 4). For
198 habitat saturation below 100%, threshold-based richness was greater than observed richness,
199 while probability-based richness followed observed richness. Observed richness against
200 probability-based richness followed the identity line closely with a slope not different from one
201 (all $p > 0.5$, H_0 being that the slope is not different from one) and an intercept not different from
202 zero, related to zero bias at all habitat saturation levels (Figure 4 middle). The relationship
203 between observed richness and threshold-based richness was not linear and did not follow the
204 identity line whatever habitat saturation. Probability-based richness showed similar RMSE at all
205 habitat saturation levels, while threshold-based richness reached its minimum RMSE when
206 habitat saturation was 80%. When species under-saturated their habitats ($\beta < 100\%$), probability-
207 based richness followed closely observed richness while threshold-richness almost always over-
208 predicted richness. Threshold-based richness lowest RMSE at 80% habitat saturation can be
209 explained by a balance between slight under-prediction when richness was smaller than 75 and
210 over-prediction when richness was greater than 75 (Figure 3). When habitat saturation reached

211 100%, both types of predictions were close to observed richness (Figure 3). At this habitat
212 saturation, threshold-based richness showed slight over-prediction in richer communities
213 (predicted richness around 90 species for sites containing 80 species) and slight under-prediction
214 in poorer sites (predicted richness of around 30 for sites containing 45 species), and an average
215 under-prediction (negative bias). At this habitat saturation, the RMSE of both methods was close
216 to the one at 80% habitat saturation, but the variance in prediction increased for probability-based
217 richness. When species over-saturated their habitats ($\beta > 100\%$), threshold-based richness
218 strongly under-predicted richness in poorer communities (negative bias) while probability-based
219 richness showed no bias on average (Figure 4 middle). For example at 150% habitat saturation,
220 for sites with observed richness around 75, threshold-based richness was around 30 while
221 probability-based richness was 75.

222 **Discussion**

223 We designed a virtual experiment of species occurrences along an environmental gradient
224 and performed binomial GLM-based species distribution modeling on these data. The binary
225 threshold-based presence prediction represented the potential habitat of each species based on its
226 fundamental niche (Guisan and Zimmermann, 2000), whatever its actual habitat saturation. On
227 the contrary, the range and average values of predicted presence probabilities depended on
228 habitat saturation, for a given fundamental niche. When summing the individual species
229 predictions, the summed presence probabilities well fitted actual richness, as expected, while
230 habitat saturation strongly affected the threshold-based richness. We thus recommend summing
231 stacked-SDMs probabilities to predict richness. Still, threshold-based richness can also be a

232 useful predictor of potential richness, as species threshold-based binary predictions can be used
233 as a reference species pool for hypothesis testing and modeling of biodiversity dynamics.

234 In our simulations, probability-based richness on average followed observed richness
235 whatever habitat saturation. This is in line with the fact that probability-based richness should
236 provide the mathematical expectation of richness at a given site (Calabrese et al., 2014). Our
237 results also showed that probability-based richness had a consistently lower RMSE than
238 threshold-based richness, mostly because of its absence of bias. However, both methods had
239 higher variance with higher habitat saturation, as a consequence of a mean-variance relationships.
240 Thus at high habitat saturation, both methods predict an unreliable richness.

241 Much emphasis has been put in species distribution modeling on providing binary
242 occurrence prediction. Methods to define thresholds for reliable occurrence prediction have been
243 extensively debated and alternative options have been proposed (Allouche et al., 2006; Freeman
244 and Moisen, 2008; Liu et al., 2005, 2013). However, such a prediction does not grasp the
245 inherently gradual response of species to environmental gradients (Hutchinson, 1957; Meynard
246 and Kaplan, 2012), and tends to generate an artificial dichotomy. This “binarization” has two
247 major caveats. First, it does not acknowledge the gradual variation of performance along the
248 gradient, which increases under-prediction below the threshold and over-prediction above the
249 threshold. Furthermore, the closer to the threshold the higher the prediction bias: just over/below
250 the threshold, there is a greater chance to find a species present/absent than further away from the
251 threshold. Second, it predicts only presences above the threshold and only absences below the
252 threshold, which does not acknowledge the influence of habitat saturation irrespective of habitat
253 suitability. In other words, threshold-based richness will always estimate richness as if species
254 habitat saturation was 100%. Because threshold-based richness over-predicts richness for habitat

255 saturation under 100% (or under-predicts when habitat saturation is over 100%), its accuracy
256 regarding the prediction of species turnover may be low (D'Amen et al., 2015b; Dubuis et al.,
257 2011). At coarser and larger scales, because niche preferences dominate the distribution of
258 species (Pearson and Dawson, 2003), we expect a more deterministic response to the
259 environment in a threshold-like fashion (Guisan and Thuiller, 2005). Species response to
260 environmental gradients is thus highly scale-dependent, specific at local and fine scales and
261 threshold-like at large and coarse scales (Meynard and Kaplan, 2013). The assumption that
262 species distribution at large and coarse scales is in a threshold fashion (Guisan and Thuiller,
263 2005) has been difficult to prove (Boucher-Lalonde et al., 2014, 2012). Instead in birds,
264 mammals and North American trees, a Gaussian distribution best explained the occurrence-
265 environment relationship for most species (Boucher-Lalonde et al., 2014, 2012), while the
266 threshold model was selected only 5% of the time. Only a fraction of species responds to broad
267 environmental gradients in a binary way. Meynard et al. (2013) also argued that threshold
268 response of species observed in many datasets could be the results of data aggregation over
269 various spatial and temporal scales.

270 We defined habitat saturation as a coefficient (β) that affects environmental suitability of
271 species: it increases ($\beta > 1$) or decreases ($\beta < 1$) habitat suitability. It has been shown in diverse
272 taxa that most species do not saturate their habitat: they occupy less habitat than their potential
273 habitat (Boucher-Lalonde et al., 2012; Munguia et al., 2008; Svenning and Skov, 2004). Several
274 mechanisms can explain why a species under-saturates its habitat. For example, dispersal
275 limitation due to slow recolonization of European trees from glacial refugia has led to habitat
276 under-saturation (Svenning and Skov, 2004). Biotic interactions are often cited as an additional
277 factor explaining habitat under-saturation (Svenning and Skov, 2004), as species close in traits

278 can experience limiting similarity and competitively exclude one another. On the contrary,
279 positive biotic interactions as well as source-sink dynamics can cause habitat over-saturation
280 (Eriksson, 1996; Pulliam, 2000; Pulliam and Danielson, 1991). Positive interactions such as
281 facilitation make facilitated species occupy less suitable habitat thanks to the presence of other
282 species (Bertness and Callaway, 1994; Stachowicz, 2001). Source-sink theory explains how a
283 species can be present in unsuitable habitat (sink) by continuously immigrating from a suitable
284 habitat (source) (Pulliam and Danielson, 1991). Here we considered a single habitat saturation
285 coefficient (β) used for all species across all assemblages. This coefficient does not take into
286 account the variability of habitat saturation that may exist between species, where some species
287 saturate more their habitat than others. Furthermore, the habitat saturation coefficient cannot take
288 into account biotic interactions as it is not conditional to the presence of other species; nor that
289 we expect source-sink dynamics to occur only close to the sources, which should lead to a
290 context-dependent habitat saturation. Habitat saturation is also influenced by the extent to which
291 it is measured. In very small areas (e.g., a single quadrat), species tend to fully saturate their
292 suitable habitat, because they occupy the only micro-habitat available for them. For larger areas
293 (e.g., several plots), the occurrence of species should be more stochastic due to dispersal
294 limitation, limiting similarity and biotic interactions as stated above. For even larger areas (e.g.,
295 regional, continental or global), habitat saturation should increase again with the dominance of
296 deterministic processes that influence occurrence. As such, we could use a species habitat
297 saturation profile at different areas whose variation would show the change in main assembly
298 processes. Further research is needed regarding habitat (un-)saturation to understand its causes
299 and consequences.

300 A recent study mentions a different but related concept of saturation (Mateo et al., 2017).
301 Mateo et al. (2017) defined saturation as “environmental constraints [that] limit the number of
302 species that can coexist in a community”. Here, we defined habitat saturation as a species-level
303 pattern: it represents the proportion of suitable habitat that a species occupies, it is a species-level
304 property not a community-level property. Community saturation, i.e. saturation *sensu* Mateo et
305 al. (2017), depends on habitat saturation of species. If species have a limited habitat saturation, it
306 imposes an upper bound to species richness. In our model, there are no strict limits on species
307 richness, but on each species’ capacity to saturate its habitat. The neutral theory imposes a limit
308 on the number of individuals in any community (Hubbell, 2001), it is a subset of the
309 individuals/species present in the species pool that encompasses a larger area. Changes in
310 number of individuals per community, species regional abundances and/or immigration
311 probability m from the species pool can cause changes in species habitat saturation. By choosing
312 these three parameters, we can obtain a stable richness that can be interpreted as an upper bound,
313 as if saturation was community-level process. However, in this case there is no direct bound on
314 species richness. Richness results from the dynamic extinction-colonization equilibrium and
315 fluctuates over time, it is not a property of the community *per se*. Mateo et al. (2017) focused
316 mostly on S-SDMs that can be constrained with an explicit constraint on richness. As stated
317 above, species richness is unlikely to be directly constrained and thus modeling explicitly a
318 richness constraint may not underline the true community assembly mechanisms that affect
319 community composition.

320 Our model, while an interesting basis to test assumptions regarding SDM stacking,
321 represents an ecologically idealistic situation that uses virtual species. We used a single linear
322 environmental gradient, which is an over-simplification of environmental gradients. Indeed,

323 species occurrences are jointly affected by multi-dimensional environmental gradients, which can
324 be non-linear and lead to observed trait syndromes (Laughlin and Messier, 2015). In our
325 simulations, all species have a single trait with a single optimum, however with multi-
326 dimensional environmental gradients we could also expect multi-dimensional optima (Oksanen
327 and Minchin, 2002). Our simulations do not consider biotic interactions, as we simulated the
328 presence of species independently, while, as stated above, biotic interactions can strongly
329 influence species habitat saturation (Pulliam, 2000). We used a species pool containing species
330 with optima on the whole range of the environmental gradient. However, the distribution in
331 species optima among the species pool can be asymmetrically distributed, which in turn can
332 affect local community assembly dynamics (Patrick and Brown, 2018). Furthermore, because of
333 the way the species were simulated, most species niche breadth covered around one third of the
334 range of the environment. While real communities contain a mix of species with narrow and wide
335 niches, with many of species having narrow niches and a few having wide niches (Brown, 1984).
336 Thus, we could determine a ratio between species with wide and narrow environmental niches,
337 based on observed communities, and simulate virtual communities accordingly. We also assumed
338 that species' suitabilities had a quadratic response to the environment, while more complex
339 relationships exist (Oksanen and Minchin, 2002) and could be used in our model. Our simulation
340 setup can thus be made more complex for more investigations on factors that may influence S-
341 SDMs richness predictions. Still, our simplified model can help gain insights about S-SDMs.

342 Depending on the scales considered, we can expect different shapes of species occurrence-
343 environment relationships. At local scale, we expect many stochastic processes (e.g.,
344 demographic stochasticity, competitive exclusion, biotic interactions, microclimatic variations,
345 etc.) to be at play and drive community assembly (Chase and Myers, 2011). Dominance of

346 stochastic processes leads to blurred response to environmental variables, because species
347 occurrence is then not only determined by environmental variables. Predicted presence
348 probability can account for these processes, because they predict the parameter that governs the
349 stochastic process leading to species occurrence such as a binomial trial (Pottier et al., 2013).
350 Indeed, probability-based richness have been shown to estimate the richness of local assemblages
351 well (Calabrese et al., 2014; D'Amen et al., 2015a, 2015b; Guisan and Rahbek, 2011; Pellissier et
352 al., 2013).

353 Threshold-based richness can be thought as the potential richness expected considering
354 only abiotic deterministic processes. It can be a useful baseline to compare to models that
355 consider a broader set of processes (Pouteau et al., 2019; Violle et al., 2011). Threshold-based
356 richness defines a reference pool against which null models or hierarchical analyses can be
357 performed. It can be considered as an additional method to define species pool (Carstensen et al.,
358 2013; Lessard et al., 2012). Indeed, threshold-based richness would represent a species pool
359 (Lessard et al., 2015) that considers only the response to environmental filtering for a large area.
360 Without explicitly considering functional traits, threshold-based richness can also represent a
361 functional species pool as species traits are filtered by the environment (de Bello et al., 2012).
362 Threshold-based richness is nested in a hierarchy of models similar to the hierarchy of scales and
363 processes that shape community assembly (Keil et al., 2013; Mackey and Lindenmayer, 2001;
364 Mertes and Jetz, 2018; Meyer, 2007; Pearson and Dawson, 2003). Threshold-based predictions,
365 because they consider environmental filtering only, are representative of coarse and large scales
366 in this hierarchy of models. In the SESAM framework (D'Amen et al., 2015a; Guisan and
367 Rahbek, 2011), threshold richness is a reference richness before applying a cutoff in species
368 presences to account for local variations. The use of threshold-based predictions can thus be

369 compared to more mechanistic models, to know to what extent observed communities are mostly
370 shaped by environmental filtering. Other models, to which they can be compared, can incorporate
371 other important community assembly factors such as dispersal limitation, limiting similarity or
372 biotic interactions (Chase and Myers, 2011; Munoz et al., 2017; Pouteau et al., 2019; van der Plas
373 et al., 2015). In summary, using both threshold-based richness and probability-based richness in
374 succession —first threshold-based richness as a pure environmental prediction then compare it to
375 probability-based richness— can shed light on community assembly processes. When both agree,
376 environmental filtering dominates community assembly. If not, habitat saturation can strongly
377 change threshold-based richness and/or other processes may affect community assembly.
378 Threshold-based richness and probability-based can further be compared to other predictions
379 using process-based models that consider additional processes. Essential Biodiversity Variables
380 can be measured using multiple methods (Pereira et al., 2017), and there is no clear
381 recommendation on which method should be prioritized to predict EBVs. Probability-based
382 species richness could be used as a reliable method to predict taxonomic diversity in the EBV
383 framework, while threshold-based richness can be a useful tool to assess community assembly
384 processes (Pouteau et al., 2019).

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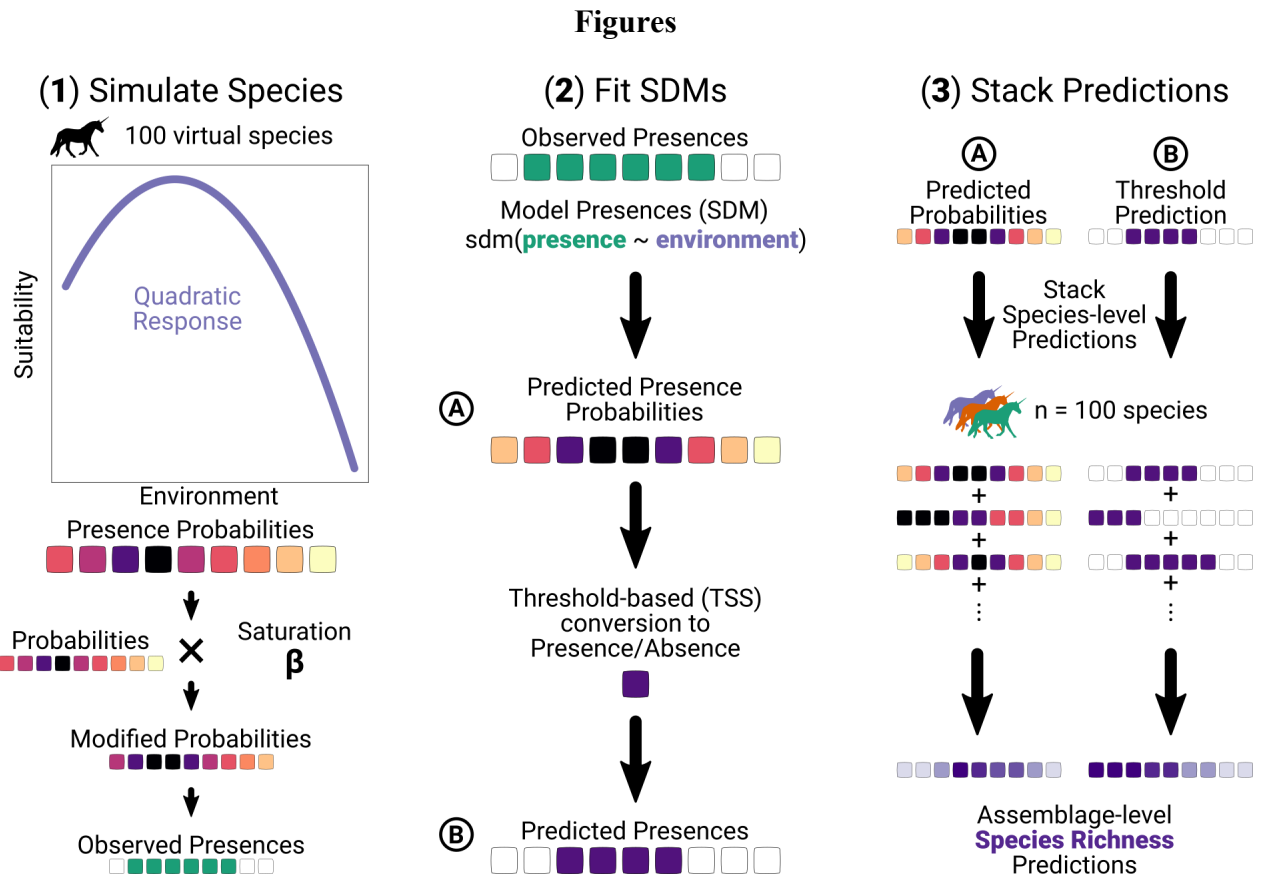
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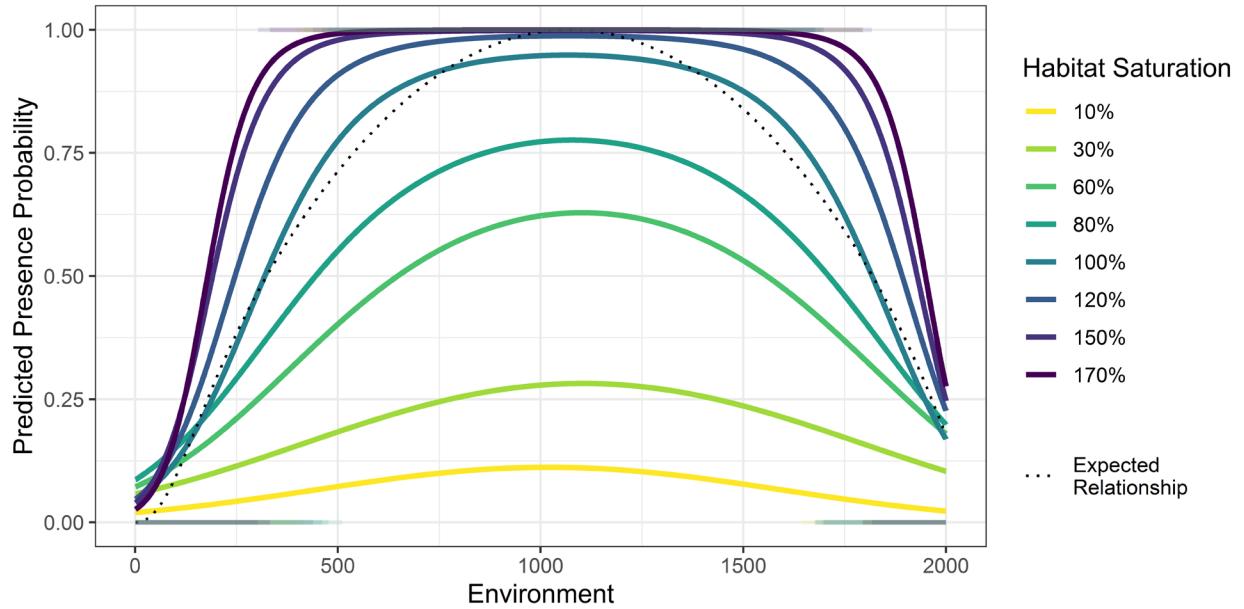
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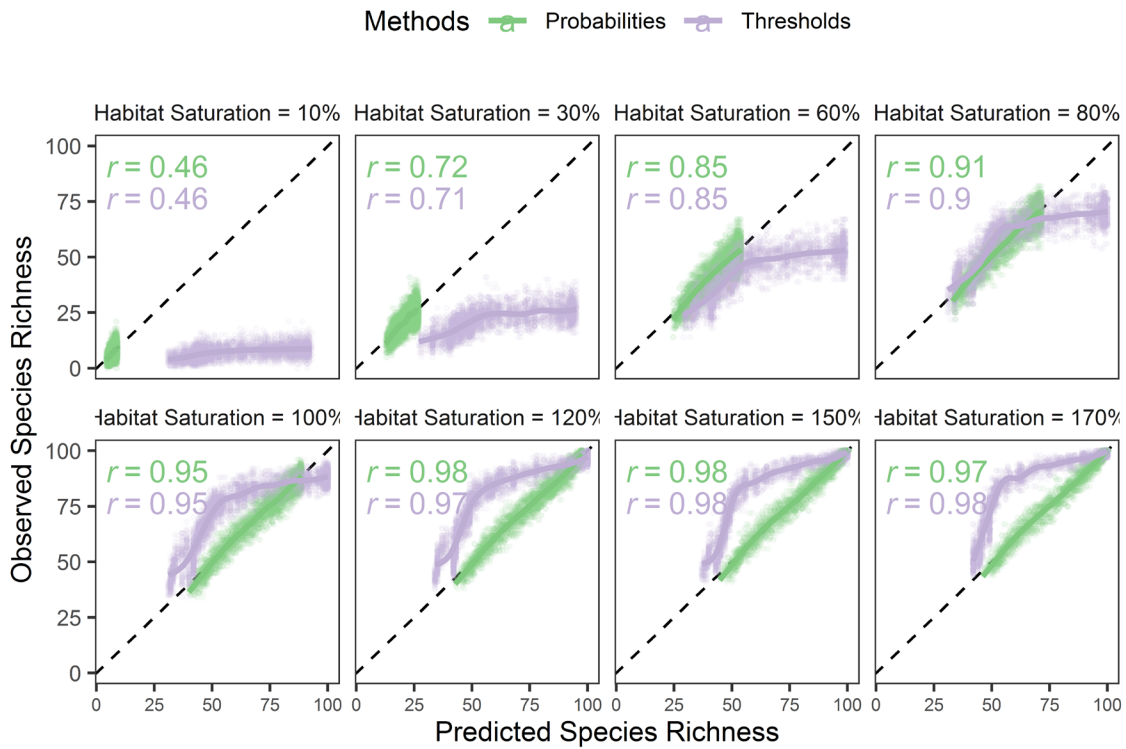


616
 617 Figure 1: Full Simulation routine. **(1)** We first simulated 100 virtual species with quadratic
 618 environmental suitability curves with randomly sampled coefficients. We multiplied each
 619 predicted presence probability by the habitat saturation level then use these probabilities to draw
 620 realized presences (see Material and Methods for details). Then, using the modified probabilities
 621 we drew presences in each assemblage following a binomial distribution. **(2)** We analyzed the
 622 realized presences with a binomial Generalized Linear Model (GLM), independently for each
 623 species, which provided predicted presence probability of each species in each assemblage **(A)**.
 624 We defined a threshold based on True Skill Statistic (see Material and Methods for details,
 625 Allouche et al. , 2006). This gave the second set of predictions: **(B)** binary predictions. **(3)**
 626 Finally, we summed individual predictions in each assemblage for all the species to get two
 627 richness predictions.

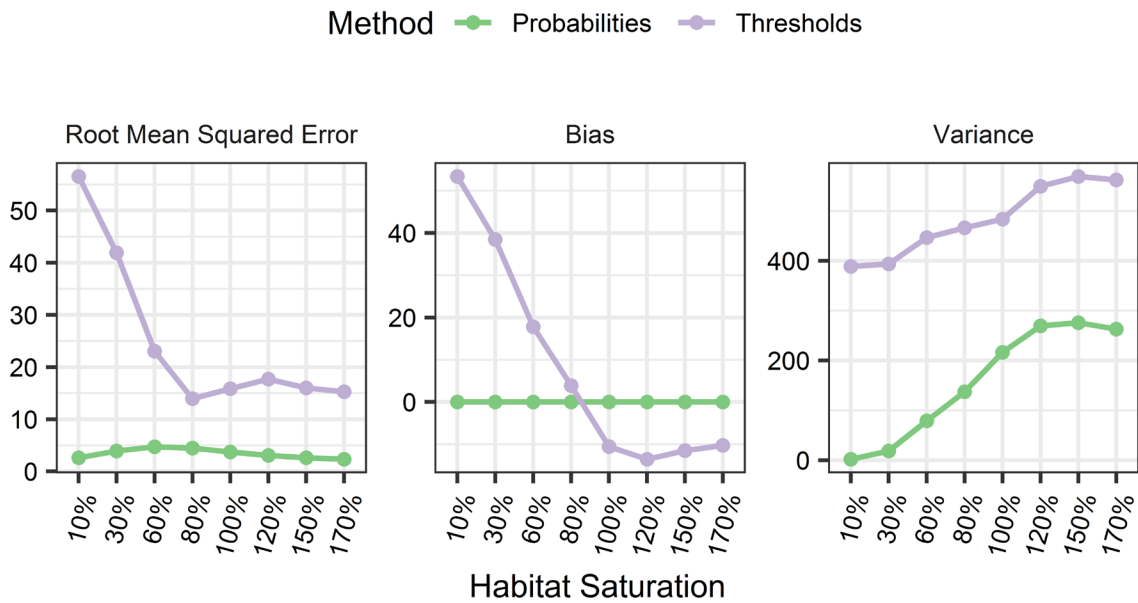


628

629 Figure 2: Species expected and predicted presence probability with and without threshold. The
 630 solid curves are the predicted presence probabilities by the GLM used to model the presence of
 631 species. The dotted curve is the expected relationship given by the parameters of the species.
 632 Segments above and below respectively show predicted presences and absences using species-
 633 specific threshold.



634
 635 Figure 3: Observed vs. predicted richness between two prediction methods as a function of
 636 habitat saturation. Each facet shows different species habitat saturation (see Material and
 637 Methods). The dashed line is the identity line ($y = x$), indicating perfect predictions. Green points
 638 are probability-based richness predictions; Purple points are threshold-based richness predictions.
 639 The corresponding colored lines are cubic splines smoothers trend lines. Spearman correlation
 640 coefficients are shown in the top left corner of each facet.



641
 642 Figure 4: Prediction accuracy of probability-based and threshold-based richness predictions in
 643 function of habitat saturation. Green points and lines: probability-based richness; purple points
 644 and lines: threshold-based richness. **(left)** Root Mean Square Error (RMSE) of predicted richness,
 645 the average error of richness prediction; **(middle)** Bias, the average difference across all
 646 assemblages between predicted and observed richness; **(right)** Variance, the variance of richness
 647 predictions across all assemblages.