

 Open access • Journal Article • DOI:10.1111/GEB.12530

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**Institutions:** University of Lausanne

**Published on:** 01 Mar 2017 - Global Ecology and Biogeography (John Wiley & Sons, Ltd (10.1111))

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1 **Selecting predictors to maximize the transferability of species distribution models: lessons**  
2 **from cross-continental plants invasions**

3  
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15 **Keywords:** biological invasions, climate variables, environmental niche modeling, global change,  
16 invasive plant species, predictor selection, realized niche, species distribution models

17 **Running title:** Which predictors do increase the transferability of SDMs?

18 **Abstract's length:** 298 words

19 **Paper's length:** 5046 words

20 **Number of references:** 71

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22 **Abstract**

23 **Aim:** Niche-based models of species distribution (SDMs) are commonly used to predict impacts of  
24 global change on biodiversity but the reliability of these predictions in space and time depends on  
25 their transferability. We tested how the strategy to choose predictors impacts the SDMs'  
26 transferability at a cross-continental scale.

27 **Location:** North America, Eurasia and Australia

28 **Method:** We used a systematic approach including 50 Holarctic plant invaders and 27 initial  
29 predictor variables, considering 10 different strategies to variable selection, accounting for  
30 predictors' proximality, multicollinearity and climate analogy. We compared the average  
31 performance per strategy, some of them using a large number of predictor combinations. Next, we  
32 looked for the single best model for each species across all the predictor combinations retained in  
33 the analysis. Transferability was considered as the predictive success of SDMs calibrated in native  
34 range and projected onto the invaded range.

35 **Results:** Two strategies showed better SDM transferability on average: a set of predictors known  
36 for their ecologically-meaningful effects on plant distribution, and the two first axes of a principal  
37 component analysis calibrated on all predictor variables ( $S_{pc2}$ ). From the >2000 combinations of  
38 predictors per species across strategies, the best set of predictors yielded SDMs with good  
39 transferability for 45 species (90%). These best combinations consisted of 8 randomly-assembled  
40 (39 sp) or uncorrelated predictors (6 sp) and  $S_{pc2}$  (5 sp). We also found that internal cross-validation  
41 was not sufficient to fully inform about an SDMs' transferability to a distinct range.

42 **Main conclusion:** Transferring SDMs at the macroclimatic scale, and thus anticipating invasions, is  
43 possible for the large majority of invasive plants considered in this study, but the predictions'  
44 accuracy relies strongly on the choice of predictors. From our results, we recommend including

45 either proximal and state-of-the-art variables or a reduced and orthogonalised set to obtain robust  
46 SDMs' projections.

47

## 48 **Introduction**

49 Species distribution models (SDMs) quantify estimates of ecological niches by relating observed  
50 species occurrences to environmental variables. They rely on the realized niche concept defined  
51 from the set of environmental conditions at locations where a species is observed, i.e. accounting  
52 for the species' physiological tolerances constrained by dispersal limitations and biological  
53 interactions (Soberon & Nakamura, 2009; but see Halvorsen 2012). Projections of SDMs onto  
54 geographical space then allow predicting the potential distributions of species (Elith & Leathwick,  
55 2009), and it is frequent to project models calibrated in one area onto a different geographic area or  
56 time period, with an assumption of ecological niche transferability (Randin *et al.*, 2006; Maiorano  
57 *et al.*, 2013; Wenger & Olden, 2012). Projections in space may be used to identify the potential  
58 distribution in other distinct geographical areas that a species reached naturally (e.g. different  
59 mountain chains: Randin *et al.*, 2006) or through human activities (e.g. invasive species: Thuiller *et*  
60 *al.*, 2005). Using climate change data, SDMs can also be projected back in time (hindcasting), e.g.  
61 to depict potential glacial refugia (Maiorano *et al.*, 2013) or to the future (forecasting), e.g. to assess  
62 the impact of climate change on biodiversity (Engler *et al.*, 2011). These approaches are especially  
63 useful for supporting conservation decisions in an era where biodiversity is massively threatened by  
64 human activities (Guisan *et al.*, 2013).

65 However, some SDMs, based on some techniques or for some species, have shown limited  
66 predictability when projected to different areas (e.g. Randin *et al.*, 2006; Broennimann *et al.*, 2007)  
67 or to past climatic conditions (e.g. Maiorano *et al.*, 2013). Failures in model transferability can  
68 result from many, possibly interrelated factors, such as violation of the niche conservatism  
69 assumption (Broennimann *et al.*, 2007; Early & Sax, 2014; Guisan *et al.*, 2014) or methodological

70 limitations (Randin *et al.*, 2006; Peterson *et al.*, 2007; Wenger & Olden, 2012). Because the  
71 realized environmental niche fitted in SDMs is restricted to the available environmental variables  
72 (Halvorsen, 2012), the choice of predictor variables can thus have a strong effect on quantification  
73 of the realized niche and therefore on SDM transferability (Rödder *et al.*, 2009; Peterson, 2011).  
74 Three aspects, in particular, are critical to consider when building a set of predictors to project  
75 SDMs in time or space: i) *proximity*, ii) *multicollinearity* and *over-parametrization* and (iii)  
76 *analog environments*.

77 Using *proximal* variables, which can define species' physiological limits, is expected to bring the  
78 model closer to the real requirements of the species, thus allowing more robust predictions (Austin  
79 2007; Kearney & Porter, 2009; Rödder *et al.*, 2009). However, without *a priori* knowledge about  
80 the species' ecology and physiology, choosing the most proximal variables is not obvious as they  
81 may be confounded with other, highly correlated variables. Moreover, there is no guarantee that  
82 relevant proxies for these variables would be available as spatial GIS layers covering a wide study  
83 area.

84 *Multicollinearity* (i. e. when two or more variables are correlated) can significantly decrease the  
85 accuracy of SDM predictions if the correlation matrices of the variables differ between the  
86 calibration and projection ranges (Dormann *et al.*, 2008; Braunisch *et al.*, 2013). A common rule of  
87 thumb is to avoid correlations between variables where the Pearson's correlation  $|r|$  is higher than a  
88 fixed threshold (e.g.  $> 0.7$ ; Dormann *et al.*, 2013). When several variables are correlated, one should  
89 choose the variable most proximal to the species' ecology (Austin, 2007; Austin & Van Niel, 2011).

90 *Over-parameterization* can be the result of fitting a model with too many predictors relative to the  
91 number of available observations. It may result in modeling spurious relationships between  
92 biological and environmental variables (depending on the model algorithm) without any ecological  
93 and causal relationship, thus potentially reducing transferability (Warren & Seifert, 2011). A

94 common solution is the empirical rule of “1 in 10” (Harrell *et al.*, 1984), i.e. the use of a maximum  
95 of one predictor for ten (but preferably 15-20) species occurrence records.

96 Next, one has to take into account the distribution of environmental variables across the whole  
97 study area(s). Specific environmental conditions in distinct study areas can vary in their frequency  
98 (i.e. different *availability* between ranges, Broennimann *et al.*, 2012) or can be completely non-  
99 existent in one of the ranges (i.e. non-*analog* climate, Fitzpatrick & Hargrove, 2009). For example,  
100 the Greenhouse Frog colonized colder temperatures in its invaded ranges that do not exist in its  
101 native range (Rödder & Lötters, 2010). In such cases, models calibrated in the native range should  
102 be extrapolated with caution in the non-analog environments of the invaded range (Fitzpatrick &  
103 Hargrove, 2009; Owens *et al.*, 2013; Guisan *et al.*, 2014). Non-analog variables could be derived  
104 into more analog predictors, with the hope that they could provide more transferable SDMs.  
105 Similarly, to depict the moisture conditions in a niche comparison of arctic-alpine plant species,  
106 Wasof *et al.*, 2015) used aridity indices, more analog than the annual precipitation.

107 Fully testing the ability of SDMs to predict species’ distribution through space or time requires an  
108 independent test dataset (Bahn & McGill, 2013). The usual split-sample approach, repeatedly and  
109 randomly leaving out a certain proportion of data within the study area to evaluate models accuracy  
110 (i.e. internal cross-validation), could be insufficient in this regard (Phillips *et al.*, 2006; Randin *et*  
111 *al.*, 2006; Veloz, 2009). Independent data sets are thus optimal when they are geographically or  
112 temporally separated from the training data set (Araújo & Rahbek, 2006; Austin, 2007; Bahn &  
113 McGill, 2013). Systems with a temporal separation include ancient distribution data set such as  
114 pollen fossil data (e.g. Maiorano *et al.*, 2013). Geographical separation can be achieved between  
115 distinct study areas: e.g. different mountain ranges (Randin *et al.*, 2006), neighboring countries  
116 (Barbosa *et al.*, 2009), active subsampling disentangling spatial autocorrelation (Edwardsen *et al.*,  
117 2011), or the native and invaded ranges of invasive species (Petitpierre *et al.*, 2012). Biological

118 invasions represent one of the few opportunities to assess the predictive capacity of SDMs in a  
119 context of global change.

120 In this study, we use native and invaded ranges of 50 Holarctic plant species, to investigate the  
121 impact of variable selection on SDM transferability at a coarse macroclimatic scale. This study aims  
122 to improve our understanding of the climatic variables shaping invasive species distributions, while  
123 also assessing the validity of transferring SDMs in the context of rapid climate change, a  
124 phenomenon interconnected with invasive species distributions (Caplat *et al.*, 2013). As SDMs are  
125 currently widely used to assess global change threats to biodiversity (Guisan *et al.*, 2013), assessing  
126 their transferability is a crucial task. More specifically, we ask the following two questions:

127 - When building SDMs, how do considerations of variable proximality, collinearity and climate  
128 analogy affect model transferability?

129 - Are there general strategies for selecting variables that will optimize model cross-continental  
130 transferability?

131

## 132 **Methods**

### 133 *Data*

134 We used the same distribution data as Petitpierre *et al.* (2012) (raw distribution maps can be seen in  
135 Appendix S1 in Supporting information). The dataset consists of the distributions of 50 Holarctic  
136 plant invaders, either native in the Palearctic part of Eurasia (EU) and invading North America  
137 (NA) or vice versa. A subset of 38 of these species was introduced in Australia (AU), which was  
138 used here as a second independent invaded range outside the Holarctic (see Table 1 for the species  
139 list and their respective native and invaded ranges). In EU and NA, 10'000 background points were  
140 sampled as pseudo-absence, while 2826 background points were retained in AU (corresponding to  
141 the total number of pixels in AU).

142 Based on the conclusions of Petitpierre *et al.* (2012), we distinguished species shifting their realized  
143 niche, i.e. showing more than 10 % niche expansion (E) in analog climates, from species with stable  
144 niches. Only seven species showed niche shifts due to realized niche expansion within their  
145 Holarctic ranges comparison (*A. fruticosa*, *B. sterilis*, *C. stoebe*, *C. scoparius*, *H. lanatus*, *H.*  
146 *tuberosus* and *T. dubium*), and seven species in their Holarctic-Australian range comparison (*C.*  
147 *vulgare*, *H. radicata*, *L. vulgaris*, *M. albus*, *S. canadensis*, *S. oleraceus* and *T. dubium*). We  
148 distinguished these species because models of niche-shifting species are expected to show lower  
149 performance when projected in the invaded range, for any method of variable selection.

150 We downloaded 35 bioclimatic variables at a resolution of 10 arcminutes from the Climond  
151 database (Kriticos *et al.*, 2011, downloaded the 6.9.2012). In total, 27 variables were kept (Table 2).  
152 We did not include the solar radiation variables because they were used in the calculation of the  
153 moisture variables, the latter being more proximal for plant growth at this coarse continental scale  
154 where microhabitats and slope, two important factors affecting radiation, cannot be taken into  
155 account. Using the raster library in the R software (version 2.15.1), we aggregated these data at the  
156 same resolution as the species distribution data, i.e. 0.5°, corresponding also to the minimal distance  
157 between two occurrences.

158

### 159 *Variable selection strategies*

160 For each species, each SDM calibrated on the exhaustive set of variables ( $S_{all}$ ) was compared to  
161 nine other strategies to select variables in the SDM (Table 3, Fig. S1 in Appendix S2). The variable  
162 selection strategies included increasing proximality ( $S_{soa}$ ,  $S_{sh}$ ), reducing multicollinearity and over  
163 parametrization ( $S_{unc}$ ,  $S_{ran}$ ,  $S_{pc8}$ ,  $S_{pc2}$ ) and/or considering climate analogy in the invaded range ( $S_{ana}$ ,  
164  $S_{anc}$ ,  $S_{con}$ ). Note that the performances of  $S_{ran}$  and  $S_{unc}$  were assessed with an average of 1000  
165 replicates of variable combinations. These selection strategies based on processes expected to affect  
166 SDM transferability are not exhaustive and do not deal explicitly with purely statistical variables



167 selection, such as backward/forward stepwise analysis or shrinkage (although such processes are  
168 included in some of the modeling techniques, see below). A full explanation of each strategy is  
169 provided in Table 3.

170

### 171 *Modeling techniques*

172 For each set of predictors, we combined three of the most frequently used modeling techniques:  
173 generalized linear models (a polynomial GLM based on a stepwise predictors' selection using a  
174 Bayesian Information Criteria, McCullagh & Nelder, 1983), generalized boosted models (GBM, a  
175 synonym for boosted regression trees, with the number of trees fixed at 2500, Friedman *et al.*, 2000)  
176 and Maximum Entropy (ME with a beta-penalization analog to a Bayesian Information Criteria,  
177 Phillips *et al.*, 2006, Halvorsen *et al.*, 2015). Modeling was calibrated on the native ranges of each  
178 species using the R package biomod2 (Thuiller *et al.*, 2014) and predictions were averaged across  
179 the three modeling techniques to provide an ensemble model (Araújo & New, 2007). A preliminary  
180 analysis where all techniques were evaluated independently showed that the ensemble approach  
181 yielded predictions close to the best individual modeling technique in most cases and is quite  
182 resilient to an individual technique failing (Fig. S4 in Appendix S2). To estimate the relative  
183 contribution of individual variables, each variable was randomized while the others were kept fixed.  
184 The effect of this randomization was assessed on predictions (see Thuiller *et al.*, 2014 for more  
185 details).

186

### 187 *Evaluation of predictions across predictor combinations*

188 It is challenging to evaluate predictions of SDMs with invasive species because of the uncertain  
189 nature of the absences in the invaded range (Jiménez-Valverde *et al.*, 2011). Therefore we used two  
190 different indices to get a more insightful evaluation of SDMs. The Boyce index (B) and sensitivity

191 (Se). B measures how observed presences are distributed across the gradient of presence predictions  
192 and how it differs from the random expectation in the study area. It is analog to a Spearman  
193 correlation and varies between -1 and 1, with zero meaning no different than random. B was  
194 computed with the bin-independent approach using a moving window along continuous predictions  
195 (Hirzel *et al.* 2006). Se is the percentage of presences correctly predicted by the model. To compute  
196 Se, a threshold binarizing continuous predictions is required. We used the threshold maximizing the  
197 True Skill Statistics (TSS) in the native range (i.e. the max-TSS approach; Allouche *et al.*, 2006),  
198 where species distributions are assumed to be closer to the dispersal equilibrium than in the invaded  
199 ranges. In this manuscript we refer to bad, poor, fair, good, very good Se for values between 0 - 0.5,  
200 0.5 - 0.7, 0.7 - 0.8, 0.8 - 0.9 and 0.9 - 1 respectively. We consider SDMs to be transferable when  
201 they show  $B \geq 0.7$  and  $Se \geq 0.8$  in the invaded range.

202 To evaluate SDMs in the native range, models were calibrated on a random sample of 70% of the  
203 data and evaluated with the remaining 30%. The evaluation was averaged through 5 repeated splits-  
204 samples. On the other hand, SDMs calibrated on 100% of the native dataset were projected to the  
205 invaded ranges. Hence, we considered Se and B as indices of SDMs transferability in the invaded  
206 range and examined how they differ between different variable selection strategies. Strategies  
207 providing both high Se and B on the average were considered as the best strategies providing the  
208 most transferable SDMs.

209 Finally, among all the predictor combinations generated for each species across strategies, including  
210 all the replicates for  $S_{ran}$  and  $S_{unc}$  (1000 for each strategy), we identified for each species the single  
211 best combination that maximized both B and Se in the Holarctic and Australian invaded ranges  
212 (hereafter called *best model*). For species not present in AU, we considered only the Holarctic  
213 invaded range to find the best model. The aim was twofold: first, to test if the best transferability  
214 depends of a particular predictor selection strategy and second, to test if some particular variables  
215 were more closely associated with better transferability.

## 216 **Results**

217 Across all strategies, 2011 predictor combinations were examined for 38 species present in the three  
218 study areas (EU, NA and AU), while 2008 predictor combinations were examined for the 12 species  
219 not present in AU, resulting in a total of 100'514 ensemble SDMs to evaluate how variable  
220 selection affects SDM transferability.

221

### 222 *Comparison of strategies*

223 In each species' native range, Se varied between 0.81 and 0.99 whereas B was between 0.75 and 1,  
224 corresponding to good to excellent predictive power for most SDMs, except for *M. albus* which had  
225 a lower but still fair Se and *A.novi-belgii* with a lower B (Fig. 1, Table S1 and S2 in Appendix S2).  
226 Selection strategy had a significant effect on Se and B (Kruskal-Wallis test  $P < 0.001$  and  $P = 0.027$   
227 respectively), with  $S_{all}$  showing better Se than other strategies and  $S_{pc2}$  having lower B on average.

228 In the Holarctic invaded range, species showed lower Se and B values than in the native range. The  
229 variable selection strategy had a significant effect on average model performance for B and Se  
230 (Kruskal-Wallis test  $P < 0.001$  and  $P = 0.001$  respectively), but with different trends from the native  
231 range.  $S_{pc2}$  and  $S_{soa}$  had better evaluation scores on average for both Se ( $0.83 \pm 0.14$  and  $0.76 \pm$   
232  $0.20$ ) and B ( $0.81 \pm 0.26$  and  $0.81 \pm 0.23$  respectively) and smaller variance in performances with  
233 fewer poorly predicted species than the other strategies. Most notably, this was true for  $S_{pc2}$  (*A.*  
234 *retroflexus*, *A. fruticosa*; *C. stoebe*, *C. scoparius*, *R. Typhina*, *A. novi-belgii* and *H. tuberosus* had  
235 bad results with  $S_{soa}$ , whereas only *A. fruticosa*, *C. stoebe* and *A novi-belgii* had bad SDMs with  
236  $S_{pc2}$ , Fig. 1, Table S3 and S4 in Appendix S2). This translated into negative or weak correlations  
237 between the SDMs' evaluation obtained in the native and the invaded ranges (Table S5 in Appendix  
238 S2). The better performances of  $S_{pc2}$  and  $S_{soa}$  appear even clearer when niche-shifting species are  
239 removed (Fig. S5 in Appendix S2). SDMs for niche-shifting species showed lower performances on

240 average in their Holarctic invaded range for both Se and B but the magnitude of this decrease  
241 depended on the variable selection strategy (Fig. S5 in Appendix S2). Among seven niche-shifting  
242 species in the Holarctic, 4 species were badly predicted with  $S_{\text{soa}}$  (*A. fruticosa*, *C. stoebe*, *C.*  
243 *scoparius*, *H. tuberosus*) and 2 with  $S_{\text{pc2}}$  (*A. fruticosa* and *C. stoebe* Fig. S5, Tables S2 and S3 in  
244 Appendix S2). Importantly, this pattern showing  $S_{\text{pc2}}$  and  $S_{\text{soa}}$  as better strategies for SDM  
245 transferability remains constant across the individual ensembled modeling techniques (Fig. S6 and  
246 S7 in Appendix S2).

247 In the Australian invaded range, SDMs showed good performance on average. Although strategy  
248 did not show a significant effect, we observed that  $S_{\text{pc2}}$  and  $S_{\text{soa}}$  had the best B ( $0.79 \pm 0.23$  and  $0.76$   
249  $\pm 0.28$  respectively) and Se along with  $S_{\text{ana}}$  ( $0.81 \pm 0.25$ ,  $0.82 \pm 0.26$  and  $0.83 \pm 0.19$ , Fig. 1, Tables  
250 S6 and S7 in Appendix S2). Niche-shifting species had a significantly lower Se in Australia (Fig. S5  
251 in Appendix S2).

252

### 253 *Best model across all combinations*

254 When focusing on the model maximizing both B and Se, screening all the replicates of  $S_{\text{ran}}$  and  $S_{\text{unc}}$ ,  
255 we found 45 species with a transferable SDM (i.e.  $\text{Se} \geq 0.8$  and  $\text{B} \geq 0.7$ ) and 5 species with bad or  
256 poor predictive SDMs in the invaded range (Fig. 2, Table 1): *A. novi-belgii* (Se = 0.40 in EU and B  
257 = 0.69 in AU), *C. stoebe* (Se = 0.48 in NA), *S. oleraceus* (Se = 0.76 in NA), *A. retroflexus* (Se =  
258 0.76 in EU) and *H. tuberosus* (B = 0.67 in AU). We observed that the single best models are  
259 achieved by the random ( $S_{\text{ran}}$ : 39 species), the random/uncorrelated ( $S_{\text{unc}}$ : 6 species) or with the two  
260 first components of the PCA ( $S_{\text{pc2}}$ : 5 species) strategies (Table 1).

261 In the best models, the most frequently included variables are, in rank order, precipitation  
262 seasonality, precipitation of the coldest quarter, annual precipitation, moisture seasonality and  
263 precipitation of the warmest quarter. Mean diurnal temperature range is included in only 5 best

264 models and the two first principal components provided the best models for five species, all from  
265 NA. Some variables are never or rarely included in the best models of NA species, whereas they are  
266 frequently included for EU species (e.g. temperature daily range, temperature seasonality,  
267 precipitation of the wettest week, moisture of the wettest quarter, Fig. 3a, Table S8 in Appendix  
268 S2). Once they are included, temperature variables have higher contribution than the variables in  
269 other categories. This trend is also confirmed by the more important contributions of the second  
270 component of the PCA, corresponding to temperature variables, when PCA provides the best model  
271 (Fig. 3b).

272

## 273 **Discussion**

274 Our results show that variable selection significantly impacts predictions of the SDMs in the  
275 invaded ranges and that across the numerous predictor sets screened for each species, there is at  
276 least one that can provide a reliably transferrable model for 45 invasive species out of 50. Among  
277 the different strategies used to select predictors, a standard set of variables ( $S_{\text{soa}}$ ) and a reduced and  
278 orthogonalized set ( $S_{\text{pc2}}$ ) yield the highest SDMs transferability in the Holarctic. When projecting  
279 into a more different environment such as Australia, although  $S_{\text{soa}}$  remains robust, the analogy of  
280 specific predictors between native and invaded ranges should be taken in account (as in  $S_{\text{ana}}$ ), as the  
281 analog variables set provides better SDMs for species shifting their niches in Australia. Overall,  
282 these findings favor using proximal variables and simpler, more parsimonious models for spatial  
283 projections. This systematic approach including many of the most widespread Holarctic plant  
284 invaders offers strong support to previous discussions raised from more case-specific review  
285 (Jiménez-Valverde *et al.*, 2011). Beyond the particular case of invasive species, it is reasonable to  
286 assume that such recommendations for building transferrable SDMs in space can be extended more  
287 generally to projecting species' potential habitats under rapid climate changes scenarios, where  
288 variable selection can also affect predictions (Synes & Osborne, 2011). Hereafter we discuss the

289 factors involved in the success or the failure of the transferability of SDMs and how to optimize  
290 model performance when predicting distributions in space and time.

291

292 *A starting point: niche conservatism*

293 Niche conservatism between native and invaded range is a pivotal assumption to project SDMs  
294 through space and time (Pearman *et al.*, 2008; Peterson, 2011). Niche shifts have commonly been  
295 measured from SDM predictions, i.e. the predictive ability of SDMs calibrated on one range when  
296 projected to the other range (Guisan *et al.*, 2014). Our results show that the degree of niche  
297 conservatism, when assessed through such SDMs' predictions, can thus arise independently from  
298 ecological or evolutionary processes affecting species fitness (see Pearman *et al.*, 2008 for a review)  
299 and may simply result from non-proximal variables confounded with important variables for the  
300 delimitation of species distribution or from climatic non-analogy in the native range. It is thus  
301 important to understand the nature of apparent niche shifts across the variables used to depict the  
302 species' realized niche (Rödder *et al.*, 2009; Peterson, 2011; Guisan *et al.*, 2014).

303 This dataset of widespread invaders with a large distribution shows no major niche expansion for  
304 more than 70% of the species (Petitpierre *et al.*, 2012), probably explaining the good overall  
305 transferability of the SDMs. However, niche conservatism may be lower for species with smaller  
306 distributions and niche breadth, potentially affecting SDM transferability (Li *et al.*, 2014; Early &  
307 Sax, 2014; Bocsi *et al.*, 2016). For such species, particular care given to variables selection may be  
308 even more important to obtain reliable predictions of species' potential distribution. For example,  
309 niche expansion may occur only at one end (low or high) of a predictor variable's gradient. Indeed,  
310 the realized niche can be more labile at one or another extremity of the gradient and it has been  
311 shown that the most stressful extremity of the gradient is more predictable by SDMs because it  
312 corresponds to physiological limits affecting the fundamental niche (Normand *et al.*, 2009;  
313 Maiorano *et al.*, 2013; Araújo *et al.*, 2013). In our dataset, this can be seen for isothermality in the

314 case of *C. scoparius* and for moisture of the coldest quarter in the case of *H. lanatus*, which appear  
315 to be a limiting factor only at the lower side of the gradients (Appendix S3). For such species,  
316 modelling the limiting thresholds along critical variables rather than the typical bell-shaped  
317 distribution may provide more transferable models.

318

### 319 *Proximal variables*

320 It is recommended to use proximal variables, known to have direct impact on species physiology  
321 and fitness, to predict potential species distribution (Austin, 2007; Kearney & Porter, 2009; Rödder  
322 *et al.*, 2009; Buckley *et al.*, 2010). Because the variables included in the best models provide the  
323 best transferability, such variables may be assumed to have more proximal effects on species  
324 distributions. Among the 27 included variables, the analysis of variable importance shows that  
325 thermal variables are more important in the single best models and thus may be more proximal for  
326 invasive plants. This finding, comparable to Randin *et al.* (2013), provides support for forecasting  
327 plant species distributions under climate change scenarios, given that scenarios of future  
328 precipitations are more uncertain than temperature scenarios (Bosshard *et al.*, 2011). However,  
329 precipitation and moisture variables are more often included in the best model, suggesting that they  
330 are necessary for good transferability, even if they have less impact on predictions. Beyond these  
331 generalities, the fact that the best model of each species does not follow a particular strategy in most  
332 of the cases supports that proximality of variables is species specific. Additionally, the discrepancy  
333 between EU and NA in the inclusion of some variables in the best models (Fig. 3a) also suggests a  
334 possible effect of the study area in the selection of variables optimizing the transferability. Focusing  
335 on the variable set which provides the best SDM transferability among multiple combinations, as  
336 we did in this study, could precede and help in selecting variables to include in further experimental  
337 research on species' physiological response to environmental complex gradients. Only these  
338 physiological models can be used to ultimately define species' fundamental niche, a safer approach

339 to predict all the species' potential habitats excluding competitive interactions. This is because,  
340 even if the fundamental niche may also be subject to changes, it requires evolutionary adaptations  
341 which take times to develop (Whitney & Gabler, 2008). Note that the realized niche is generally  
342 equal to or smaller than the fundamental niche (i.e. except in the case of biotic facilitations;  
343 Callaway *et al.*, 2002), and predictions based on models of the fundamental niche may overestimate  
344 species potential distribution in their native range.

345

#### 346 *Non-analogy*

347 Extrapolating complex SDMs to novel climates may lead to unreliable predictions as there is no  
348 guarantee that interactions between the predictors remain constant in the novel climates (Fitzpatrick  
349 & Hargrove, 2009; Peterson, 2011; Owens *et al.*, 2013; Guisan *et al.*, 2014). In our study, strategies  
350 based on climate analogy did not show better performances in the Holarctic invaded ranges.  
351 However, considering climate analogy did lead to a better average Se in AU where climate is more  
352 different from the native ranges (see Fig. S8 in Appendix S2). Additionally, the difference between  
353 Se for shifting- and non-shifting species in AU is strongly reduced with  $S_{ana}$  (Fig. S5 in Appendix  
354 S2), suggesting that the nature of these niche shifts in AU could be linked with the climate non-  
355 analogy with the native range (Rödder & Lötters, 2010). Therefore, species growing in a globally  
356 different climate and thus presenting an apparent niche shift may paradoxically provide information  
357 about species' niche conservatism along the few environmental predictors that do not differ  
358 between the two ranges.

359

#### 360 *Good at home doesn't mean good elsewhere*

361 In contrast to recent multi-species studies investigating the importance of variable selection for  
362 SDMs (e.g. Barbet-Massin & Jetz, 2014; for birds or Ashcroft *et al.*, 2011, for plants), our study



363 used a completely independent dataset (i.e. invaded ranges) to evaluate SDMs' transferability.  
364 Complex and highly parameterized SDMs like  $S_{all}$  can be used to depict the fine variations in the  
365 range where they are calibrated but are less robust against changes in the structure of the predictors.  
366 Therefore, the difference between the model performances in the native and invaded ranges with  $S_{all}$   
367 and  $S_{pc2}$  demonstrates that excellent performances as determined by pseudo-independent data  
368 (native range sub-sampling) do not necessarily imply a good transferability. Spatial autocorrelation  
369 and over-parametrization can explain this apparent paradox. The usual approach by which a  
370 subsample of the calibration area is used as an independent dataset for model evaluation may be  
371 biased by spatial correlation with the calibration dataset (McPherson & Jetz, 2007; Bahn & McGill,  
372 2013). Although fully independent dataset should always be the one and only gold standard for  
373 SDM evaluation of transferability, having such separate datasets in comparable environmental  
374 conditions is rare. Therefore, to minimize the spatial autocorrelation problem, increasing the ratio of  
375 independent data in the split-sampling evaluation, including a spatial autocorrelation term or  
376 disaggregating the calibration dataset based on a minimum distance can be alternatives (Dormann,  
377 2007, Hijmans, 2012). Interestingly, collinearity does not show any significant negative effect on  
378 predictions in our study (e.g. when  $S_{unc}$  is compared to  $S_{ran}$ ). Using Pearson's correlation to assess  
379 collinearity between variables is very common but can be subject to criticism. The threshold (here  
380 in this study  $|r| \leq 0.7$ ) was based on a review of literature (Dormann *et al.*, 2013) and does not rely  
381 on any statistical demonstration or simulation. This approach can also be biased when non-linear  
382 relationships exist among predictors (Dormann *et al.*, 2013) and can be alternatively replaced by the  
383 use of a dissimilarity matrix based on indices such as Gower metric (Franklin, 2010), which is less  
384 sensitive to non-linearity. However, both the validity of the correlation threshold and Gower  
385 matrices require formal assessment. An independent dataset, such as a species' invasive  
386 distribution, can be useful for such purpose.

387 Evaluating SDM predictions in the invaded range requires particular attention to the choice of the  
388 performance statistic, especially the weight given to the absences. Models predicting a wider  
389 species potential distribution and apparently increasing the rate of false positives (Type I error) may  
390 be underrated if too much weight is given to the predictions of absences because dispersal non-  
391 equilibrium prevails in the invaded range. Focusing more on the rate of predicted presences may be  
392 more insightful to assess the transferability of SDMs. To do that, using presence-oriented evaluators  
393 in the invaded range such as sensitivity or Boyce may be helpful to select more transferable models.

394

### 395 *Recommendations*

396 For a majority of species and from a purely predictive perspective, the best model is found using an  
397 iterative random approach (i.e. no strategy) to select the predictor dataset. Therefore, the variable  
398 selection providing the best model is species-specific, meaning that the final combination of  
399 predictors should be carefully chosen, based on its performance to explain the distribution of each  
400 individual species on independent data. However, when such data are not available or in cases  
401 where many species niches are modeled and a standardized set of predictors is required (e.g. to  
402 reduce computing requirements), the state-of-the-art variables used to build SDMs ( $S_{soa}$ ) or a set  
403 based on fewer and orthogonalized variables ( $S_{pc2}$ ) are the best alternatives among the numerous  
404 strategies to select predictors.

405 On average,  $S_{soa}$  performs well on the invaded range probably because it contains the major limiting  
406 predictors for the majority of the species. On the other hand, by summarizing the main regional  
407 complex gradients of the study area in only two components,  $S_{pc2}$  allowed simple and transferable  
408 SDMs for most species, presenting less variance in performance between species and yielding fewer  
409 poorly predicted species. Reducing the numerous and complex interactions between precipitation,  
410 moisture and seasonality into one component, and heat and continentality into another (Fig. S3 in  
411 appendix S2), is an efficient way to depict a simplified climatic envelop (Metzger *et al.*, 2005,

412 Bakkestuen *et al.*, 2008, Broennimann *et al.*, 2012, Kriticos *et al.*, 2014). In addition, the fact that  
413 the maximization of the environmental variance was made across all ranges pooled together likely  
414 also contributed to make the principal components (i.e. axes) more transferable. However, these  
415 SDMs calibrated on principal components may be more problematic to interpret. Furthermore,  
416 extrapolation and climate change scenarios may change the correlation structure between  
417 parameters and thus lead to unreliable predictions when projected outside the PCA environmental  
418 space. For all these reasons, we recommend using  $S_{pc2}$  as an alternative only when limited  
419 occurrence data are available (thus avoiding SDMs overparametrization) and projecting onto  
420 predictors keeping the same correlation structure.  $S_{soa}$  may be more desirable if one is interested in  
421 ecological interpretation or in projection towards climatic scenarios where predictors may have  
422 different correlation structures. Finally, when the projection is characterized by a highly different  
423 environment relative to the calibration range (e. g. like between Eurasia and Australia), strategies  
424 maximizing climate analogy (such as  $S_{ana}$  or  $S_{anc}$ ) may be considered.

425

426 **Acknowledgments:** We thank R. Halvorsen, A. Jiménez-Valverde and one anonymous reviewer  
427 for their meticulous and insightful comments on an earlier version of the manuscript. The  
428 computations were performed at the Vital-IT (<http://www.vital-it.ch>) Center for high-performance  
429 computing of the SIB Swiss Institute of Bioinformatics. AG, OB and BP received main support  
430 from the National Center for Competence in Research « Plant Survival » and from the Swiss  
431 National Science Project grant nr 31003A-1528661. CD and CK received support from the USDA  
432 National Institute of Food and Agriculture, Biology of Weedy and Invasive Species Program Grant  
433 no. 2006-35320-17360.

434

435

436 **Supporting information**

437 **Appendix S1:** Coarse species distribution and projections of the best SDMs

438 **Appendix S2:** Supporting material

439 **Appendix S3:** Response curves of the variables included in the best model for each species

440

441 **Biosketch:** Blaise Petitpierre is a biologist, specialized in spatial ecology and environmental niche  
442 modelling, whose work focuses on invasive species in the context of global change.

443

444

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640

641

642 **Table 1:** Evaluation of the best models for each species with Boyce index and sensitivity in the  
643 native range, Holarctic and Australian invaded range ( $B_{\text{Nat}}$ ,  $Se_{\text{Nat}}$ ,  $B_{\text{Hol}}$ ,  $Se_{\text{Hol}}$ ,  $B_{\text{AU}}$ ,  $Se_{\text{AU}}$   
644 respectively). <sup>1)</sup> and <sup>2)</sup> indicate species shifting their niche in Holarctic and Australia respectively.  
645 Strategy providing the best model is also indicated (Strat.), as well as species native origin (Nat.).

Species	Nat.	Strat.	$B_{\text{Nat}}$	$Se_{\text{Nat}}$	$B_{\text{Hol}}$	$Se_{\text{Hol}}$	$B_{\text{AU}}$	$Se_{\text{AU}}$
<i>Alliaria petiolata</i> (M.Bieb.) Cavara & Grande	EU	$S_{\text{ran}}$	0.99	0.95	0.98	1.00	-	-
<i>Amaranthus retroflexus</i> L.	NA	$S_{\text{pc}2}$	0.98	0.92	0.93	0.76	0.71	1.00
<i>Ambrosia artemisiifolia</i> L.	NA	$S_{\text{pc}2}$	0.97	0.88	0.94	0.92	0.90	1.00
<i>Amorpha fruticosa</i> L. <sup>1)</sup>	NA	$S_{\text{ran}}$	0.91	0.91	0.71	0.84	-	-
<i>Anagallis arvensis</i> L.	EU	$S_{\text{ran}}$	0.99	0.93	0.97	1.00	0.99	1.00
<i>Anthoxanthum odoratum</i> L.	EU	$S_{\text{ran}}$	0.97	0.92	0.95	1.00	0.97	0.98
<i>Arabidopsis thaliana</i> (L.) Heynh	EU	$S_{\text{ran}}$	1.00	0.94	0.99	0.98	0.90	1.00
<i>Bromus sterilis</i> L. <sup>1)</sup>	EU	$S_{\text{ran}}$	0.97	0.97	0.94	0.84	0.79	0.91
<i>Bromus tectorum</i> L.	EU	$S_{\text{ran}}$	0.99	0.95	0.97	0.81	0.81	0.96
<i>Carduus nutans</i> L.	EU	$S_{\text{ran}}$	0.99	0.93	0.96	0.97	0.91	1.00
<i>Centaurea stoebe</i> L. <sup>1)</sup>	EU	$S_{\text{ran}}$	0.96	0.96	0.91	0.48	-	-
<i>Cirsium vulgare</i> (Savi) Ten. <sup>2)</sup>	EU	$S_{\text{ran}}$	0.99	0.96	0.98	0.96	0.98	0.87
<i>Conyza canadensis</i> (L.) Cronquist	NA	$S_{\text{ran}}$	0.96	0.94	0.99	0.94	0.94	1.00
<i>Cytisus scoparius</i> (L.) Link <sup>1)</sup>	EU	$S_{\text{ran}}$	0.98	0.97	0.97	0.89	0.97	1.00
<i>Dactylis glomerata</i> L.	EU	$S_{\text{ran}}$	0.99	0.89	0.99	0.97	0.95	0.99
<i>Echinocystis lobata</i> (Michx.) Torr. & A. Gray	NA	$S_{\text{ran}}$	0.97	0.95	0.97	0.96	-	-
<i>Erigeron annuus</i> (L.) Pers.	NA	$S_{\text{unc}}$	0.96	0.96	0.97	0.94	-	-
<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton	EU	$S_{\text{ran}}$	0.99	0.94	0.98	0.94	0.97	0.98
<i>Euphorbia esula</i> L.	EU	$S_{\text{ran}}$	0.99	0.92	0.93	0.81	-	-
<i>Holcus lanatus</i> L. <sup>1)</sup>	EU	$S_{\text{ran}}$	0.97	0.97	0.97	0.88	0.97	0.97
<i>Hypochaeris radicata</i> L. <sup>2)</sup>	EU	$S_{\text{ran}}$	0.98	0.98	0.99	0.92	1.00	0.93
<i>Juncus tenuis</i> Willd.	NA	$S_{\text{ran}}$	0.99	0.91	0.98	0.98	0.93	1.00
<i>Linaria vulgaris</i> Mill. <sup>2)</sup>	EU	$S_{\text{ran}}$	1.00	0.89	0.99	0.97	0.86	1.00
<i>Lythrum salicaria</i> L.	EU	$S_{\text{ran}}$	0.99	0.96	0.91	0.95	0.95	0.97
<i>Medicago lupulina</i> L.	EU	$S_{\text{ran}}$	0.99	0.89	0.98	0.97	0.95	1.00
<i>Melilotus albus</i> Medik. <sup>2)</sup>	EU	$S_{\text{ran}}$	0.99	0.82	1.00	0.93	0.97	0.94
<i>Phytolacca americana</i> L.	NA	$S_{\text{ran}}$	0.92	0.91	0.94	0.98	0.92	1.00
<i>Plantago lanceolata</i> L.	EU	$S_{\text{ran}}$	0.99	0.94	0.97	0.94	1.00	0.98
<i>Plantago major</i> L.	EU	$S_{\text{ran}}$	1.00	0.90	1.00	0.94	0.95	0.97
<i>Poa annua</i> L.	EU	$S_{\text{ran}}$	0.99	0.85	0.99	0.92	0.98	0.95
<i>Potentilla recta</i> L.	EU	$S_{\text{ran}}$	0.99	0.93	1.00	0.99	0.93	1.00
<i>Prunus serotina</i> Ehrh.	NA	$S_{\text{ran}}$	0.97	0.96	0.99	1.00	-	-
<i>Rhus typhina</i> L.	NA	$S_{\text{pc}2}$	0.91	0.96	0.86	1.00	-	-
<i>Robinia pseudoacacia</i> L.	NA	$S_{\text{pc}2}$	0.97	0.93	0.99	0.98	0.97	0.98
<i>Rumex acetosella</i> L.	EU	$S_{\text{ran}}$	0.97	0.92	0.99	0.95	0.95	0.95
<i>Solidago canadensis</i> L. <sup>2)</sup>	NA	$S_{\text{unc}}$	0.99	0.92	0.96	0.90	0.93	0.90
<i>Solidago gigantea</i> Aiton	NA	$S_{\text{ran}}$	0.98	0.96	0.98	0.99	-	-
<i>Sonchus oleraceus</i> L. <sup>2)</sup>	EU	$S_{\text{ran}}$	0.99	0.95	0.89	0.76	0.99	0.96
<i>Trifolium arvense</i> L.	EU	$S_{\text{ran}}$	0.99	0.95	0.99	0.98	0.93	0.98
<i>Trifolium dubium</i> Sibth. <sup>1) 2)</sup>	EU	$S_{\text{ran}}$	0.98	0.98	0.97	0.91	0.97	0.95
<i>Trifolium repens</i> L.	EU	$S_{\text{ran}}$	0.99	0.85	0.99	0.91	0.98	0.98

<i>Verbascum thapsus</i> L.	EU	S <sub>ran</sub>	0.99	0.92	0.99	0.94	0.93	0.96
<i>Vicia sativa</i> L.	EU	S <sub>ran</sub>	0.99	0.93	0.97	0.93	0.99	0.99
<i>Acer negundo</i> L.	NA	S <sub>ran</sub>	0.99	0.93	0.93	0.97	0.83	1.00
<i>Asclepias syriaca</i> L.	NA	S <sub>unc</sub>	0.95	0.96	0.95	0.99	-	-
<i>Aster novi-belgii</i> L.	NA	S <sub>unc</sub>	0.79	0.97	0.78	0.40	0.69	0.80
<i>Bidens frondosa</i> L.	NA	S <sub>ran</sub>	0.98	0.92	0.97	0.97	-	-
<i>Epilobium ciliatum</i> Raf.	NA	S <sub>unc</sub>	0.98	0.88	0.97	0.97	0.94	1.00
<i>Helianthus tuberosus</i> L. <sup>1)</sup>	NA	S <sub>pc2</sub>	0.97	0.93	0.81	0.92	0.67	0.91
<i>Rudbeckia laciniata</i> L.	NA	S <sub>unc</sub>	0.99	0.95	1.00	0.97	-	-

**Table 2:** Description of climatic variables (available in the Climond, Kriticos *et al.*, 2011)

Number	Abbreviation	Description
1	Tmean	Annual mean temperature (°C)
2	Tdrange	Mean diurnal temperature range (mean(period max-min)) (°C)
3	IsoT	Isothermality (Bio02 ÷ Bio07)
4	Tvar	Temperature seasonality (C of V)
5	Tmaxw	Max temperature of warmest week (°C)
6	Tcoldw	Min temperature of coldest week (°C)
7	Tarange	Temperature annual range (Bio05-Bio06) (°C)
8	Twetq	Mean temperature of wettest quarter (°C)
9	Tdryq	Mean temperature of driest quarter (°C)
10	Twarmq	Mean temperature of warmest quarter (°C)
11	Tcoldq	Mean temperature of coldest quarter (°C)
12	Pa	Annual precipitation (mm)
13	Pwetw	Precipitation of wettest week (mm)
14	Pdryw	Precipitation of driest week (mm)
15	Pvar	Precipitation seasonality (C of V)
16	Pwetq	Precipitation of wettest quarter (mm)
17	Pdryq	Precipitation of driest quarter (mm)
18	Pwarmq	Precipitation of warmest quarter (mm)
19	Pcoldq	Precipitation of coldest quarter (mm)
20	Ma	Annual mean moisture index
21	Mwetw	Highest weekly moisture index
22	Mdryw	Lowest weekly moisture index
23	Mvar	Moisture index seasonality (C of V)
24	Mwetq	Mean moisture index of wettest quarter
25	Mdryq	Mean moisture index of driest quarter
26	Mwarmq	Mean moisture index of warmest quarter
27	Mcoldq	Mean moisture index of coldest quarter



28-35	PC	Principal components calibrated on the 27 climate variables
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- 1 **Table 3:** List, abbreviation, number of replicates (# rep., i.e. number of different predictor combinations) and description of each strategy used to
- 2 select the predictors included in the SDMs. Note that for species present in Australia, there are two datasets for strategies optimizing climate
- 3 analogy ( $S_{ana}$ ,  $S_{anc}$  and  $S_{con}$ ): one optimized for climate analogy with the Holarctic invaded range and one for the Australian invaded range.

Strategy	Abbreviation	# rep.	Description
All variables	$S_{all}$	1	All the 27 variables available, as a “no-strategy” to deal with the dilemma of variable selection. Used to predict species invasion (e.g. Giovanelli <i>et al.</i> , 2010, Hill <i>et al.</i> , 2012), as some statistical methods (e.g. Random Forest, Maxent, Stepwise GLM, GBM) are supposed to select automatically those variables with best discriminatory power.
Uncorrelated sets	$S_{unc}$	1000	We sampled eight non-correlated variables 1000 times. The maximal number of variables resulting in a Pearson’s correlation $ r  \leq 0.7$ was seven in North America (NA) and nine in Eurasia (EU), so that we defined eight equidistant clusters of variables on dendrograms where variables were clustered according to their pairwise correlations (Fig. S2 in Appendix S2) and randomly selected 1000 combinations including one variable in each cluster.
Random sets	$S_{ran}$	1000	We randomly sampled a subset of eight variables 1000 times to disentangle the possible effect of reducing the number of variables from 27 to 8 from the effect of removing correlation.
State-of-the-art	$S_{soa}$	1	Eight variables that are commonly used in SDMs for plant species (Thuiller <i>et al.</i> , 2005, Broennimann <i>et al.</i> , 2007, Petitpierre <i>et al.</i> , 2012): Tmean, Tvar, Tcoldq, Twarmq, Pvar, Pwetq, Ma, Mvar.

Stepwise hierarchical	$S_{sh}$	1	For each species, eight statistically most important and uncorrelated variables. Using statistical algorithms to select the most relevant variables is common in ecology (Mac Nally, 2002, Cutler <i>et al.</i> , 2007) and can be used in a hierarchical way (e.g. Roura-Pascual <i>et al.</i> , 2009). For each species, SDMs were built based on each cluster of the correlation dendrogram. Then, only the most important variable of each cluster was retained so that in the end we obtained the eight most important and uncorrelated variables. When only one variable was included in a cluster (e.g. Twetq in EU), we automatically included it in the predictors set for the final model.
Most analog	$S_{ana}$	1 or 2	Eight variables presenting the highest climate analogy between calibration and projection ranges. A Multivariate Environmental Similarity Surface (MESS, Elith <i>et al.</i> , 2010) was computed for each climate layer (instead of using composite MESS layers) to select eight variables with the lowest number of non-analog sites in the invaded range (based on all individual MESS layers). To our knowledge, this approach has never been applied despite several calls to take into account such variables' analogy in variables selection (e.g. Rödder & Lötters, 2010)
Analog-uncorrelated	$S_{anc}$	1 or 2	Eight uncorrelated and analog variables. A similar hierachical approach (as for $S_{sh}$ ) was used to select the most analog variables (as for $S_{ana}$ ) within each variables cluster of the correlation dendrogram.
Consensus	$S_{con}$	1 or 2	For each species, a consensual selection of 8 uncorrelated, analog and important variables. For each cluster of the correlation dendrogram, two scores were assigned to each variable based on its rank compared to the other variables within the same cluster: one score based on climate analogy in the invaded range and one score based

			on variable importance determined as in $S_{sh}$ . Within each cluster, variables with the lowest averaged rank between the analogy and variable importance scores were selected.
8-axes PCA	$S_{pc8}$	1	Eight variables corresponding to the 8 first component of a principal component analysis (PCA) calibrated on the 27 climate variables across EU, NA and AU (Fig. S3 in Appendix S2). PCA can be used to reduce the number of parameters in the model and to decrease collinearity because components are orthogonal (e.g. Peterson <i>et al.</i> , 2007, Bakkestuen <i>et al.</i> , 2008, Zhang & Zhang, 2012, Kriticos <i>et al.</i> , 2014). Moreover, it has been shown to be the most accurate way to build an environmental space to assess niche overlap (Broennimann <i>et al.</i> , 2012)
2-axes PCA	$S_{pc2}$	1	Same as $S_{pc8}$ but keeping only the first 2 components. The first two components explain 73% of the total climatic variation (Fig. S3 in Appendix S2) while the first eight components explain 98%

**Figure 1:** SDMs evaluated with the sensitivity (Se) and the Boyce index (B) following different variable selection strategies (see Table 3 for abbreviations' description) in the native range, the Holarctic invaded range (Hol.) and the Australian invaded range (AU). Number of species included in the analysis (N) and P-value (*P*) of a Kruskal-Wallis test is provided in each case. When a significant effect was detected, strategies were labelled with a, b and c corresponding to different groups after a pairwise-Wilcoxon test.

**Figure 2:** Performance distribution of the *best models* with the highest combination of the Boyce index (B, a and b) and the sensitivity (Se, c and d) in Holarctic (a and b) and Australian (when available, c and d) ranges. N is the number of species included in the analysis and grey area represents scores for niche-shifting species.

**Figure 3:** Importance of different variables in the best models: Number of times that variables are included in the best models (a) and average importance of variables included in the best models (b). The variables are ranked in the same order as in Table 2. T, P, M and PCA represent temperature, precipitation, moisture and principal component variables, black and grey colors indicate species native Eurasia and North America, respectively.

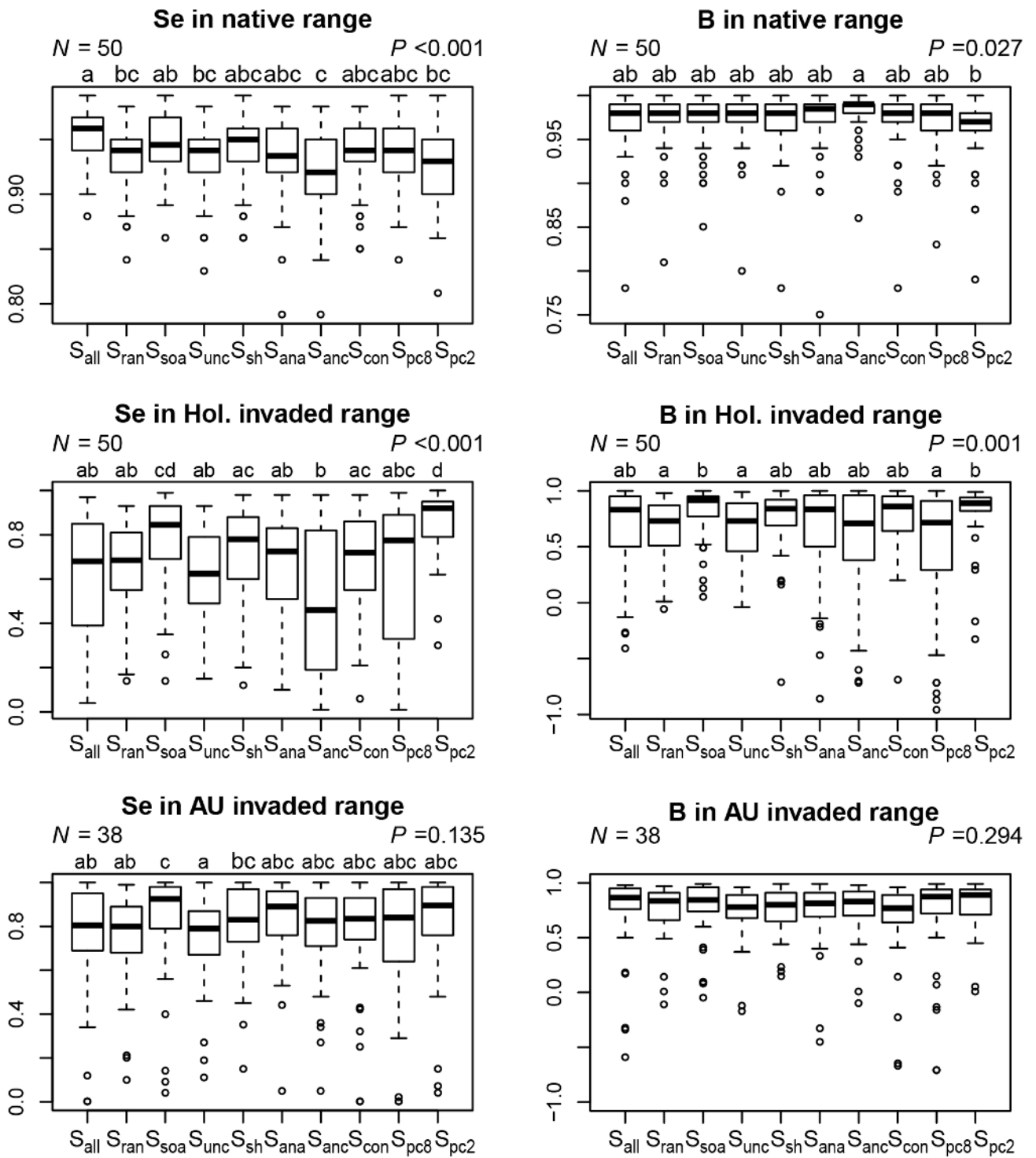


Figure 1.

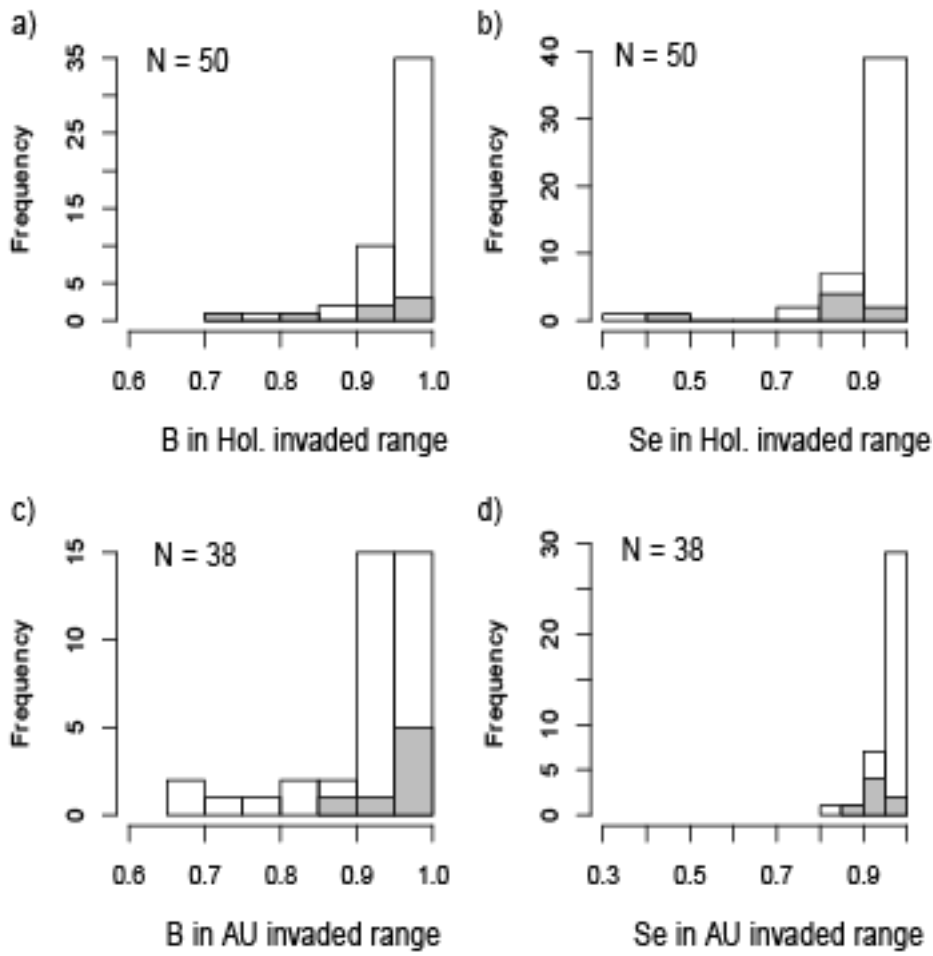
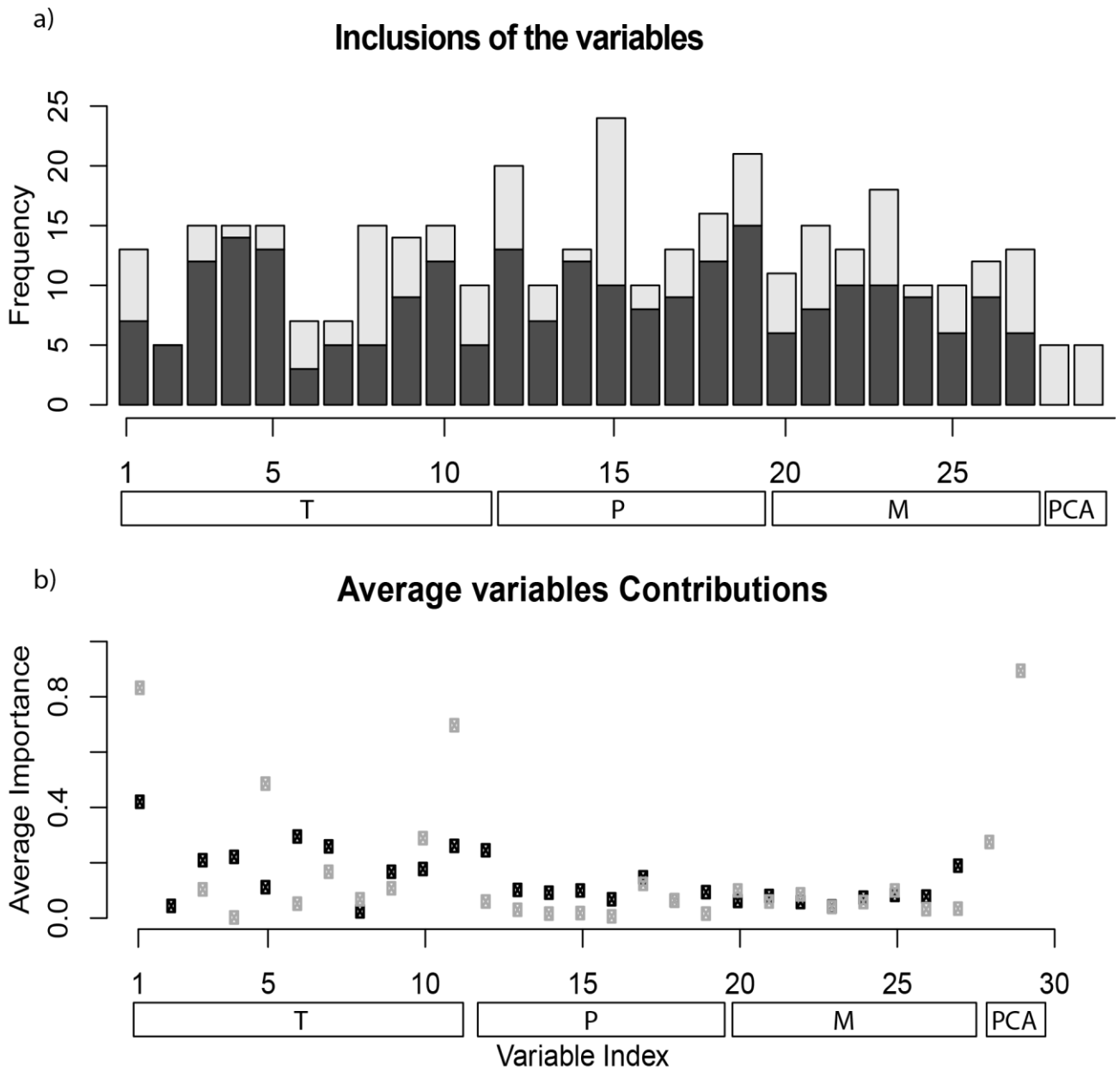


Figure 2.



**Figure 3.**