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

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Abstract

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

Location: North America, Eurasia and Australia

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

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

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

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

Introduction

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

However, some SDMs, based on some techniques or for some species, have shown limited predictability when projected to different areas (e.g. Randin *et al.*, 2006; Broennimann *et al.*, 2007) or to past climatic conditions (e.g. Maiorano *et al.*, 2013). Failures in model transferability can result from many, possibly interrelated factors, such as violation of the niche conservatism assumption (Broennimann *et al.*, 2007; Early & Sax, 2014; Guisan *et al.*, 2014) or methodological limitations (Randin *et al.*, 2006; Peterson *et al.*, 2007; Wenger & Olden, 2012). Because the realized environmental niche fitted in SDMs is restricted to the available environmental variables (Halvorsen, 2012), the choice of predictor variables can thus have a strong effect on quantification of the realized niche and therefore on SDM transferability (Rödder *et al.*, 2009; Peterson, 2011). Three aspects, in particular, are critical to consider when building a set of predictors to project SDMs in time or space: i) *proximality*, ii) *multicollinearity* and *over-parametrization* and (iii) *analog environments*.

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

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

Over-parameterization can be the result of fitting a model with too many predictors relative to the number of available observations. It may result in modeling spurious relationships between biological and environmental variables (depending on the model algorithm) without any ecological and causal relationship, thus potentially reducing transferability (Warren & Seifert, 2011). A common solution is the empirical rule of "1 in 10" (Harrell *et al.*, 1984), i.e. the use of a maximum of one predictor for ten (but preferably 15-20) species occurrence records.

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

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

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

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

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

Methods

Data

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

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

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

Variable selection strategies

For each species, each SDM calibrated on the exhaustive set of variables (S_{all}) was compared to nine other strategies to select variables in the SDM (Table 3, Fig. S1 in Appendix S2). The variable selection strategies included increasing proximality (S_{soa}, S_{sh}), reducing multicollinearity and over parametrization (S_{unc}, S_{ran}, S_{pc8}, S_{pc2}) and/or considering climate analogy in the invaded range (S_{ana}, S_{anc}, S_{con}). Note that the performances of S_{ran} and S_{unc} were assessed with an average of 1000 replicates of variable combinations. These selection strategies based on processes expected to affect SDM transferability are not exhaustive and do not deal explicitly with purely statistical variables selection, such as backward/forward stepwise analysis or shrinkage (although such processes are included in some of the modeling techniques, see below). A full explanation of each strategy is provided in Table 3.

Modeling techniques

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

Evaluation of predictions across predictor combinations

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

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

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

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

Results

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

Comparison of strategies

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

In the Holarctic invaded range, species showed lower Se and B values than in the native range. The variable selection strategy had a significant effect on average model performance for B and Se (Kruskal-Wallis test P < 0.001 and P = 0.001 respectively), but with different trends from the native range. S_{pc2} and S_{soa} had better evaluation scores on average for both Se (0.83 ± 0.14 and 0.76 ± 0.20) and B (0.81 ± 0.26 and 0.81 ± 0.23 respectively) and smaller variance in performances with fewer poorly predicted species than the other strategies. Most notably, this was true for S_{pc2} (*A. retroflexus, A. fruticosa*; *C. stoebe*, *C. scoparius*, *R. Typhina*, *A. novi-belgii* and *H. tuberosus* had bad results with S_{soa}, whereas only *A. fruticosa*, *C. stoebe* and *A novi-belgii* had bad SDMs with S_{pc2}, Fig. 1, Table S3 and S4 in Appendix S2). This translated into negative or weak correlations between the SDMs’ evaluation obtained in the native and the invaded ranges (Table S5 in Appendix S2). The better performances of S_{pc2} and S_{soa} appear even clearer when niche-shifting species are removed (Fig. S5 in Appendix S2). SDMs for niche-shifting species showed lower performances on average in their Holarctic invaded range for both Se and B but the magnitude of this decrease depended on the variable selection strategy (Fig. S5 in Appendix S2). Among seven niche-shifting species in the Holarctic, 4 species were badly predicted with S_{soa} (*A. fruticosa*, *C. stoebe*, *C. scoparius*, *H. tuberosus*) and 2 with S_{pc2} (*A. fruticosa* and *C. stoebe* Fig. S5, Tables S2 and S3 in Appendix S2). Importantly, this pattern showing S_{pc2} and S_{soa} as better strategies for SDM transferability remains constant across the individual ensembled modeling techniques (Fig. S6 and S7 in Appendix S2).

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

Best model across all combinations

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

In the best models, the most frequently included variables are, in rank order, precipitation seasonality, precipitation of the coldest quarter, annual precipitation, moisture seasonality and precipitation of the warmest quarter. Mean diurnal temperature range is included in only 5 best models and the two first principal components provided the best models for five species, all from NA. Some variables are never or rarely included in the best models of NA species, whereas they are frequently included for EU species (e.g. temperature daily range, temperature seasonality, precipitation of the wettest week, moisture of the wettest quarter, Fig. 3a, Table S8 in Appendix S2). Once they are included, temperature variables have higher contribution than the variables in other categories. This trend is also confirmed by the more important contributions of the second component of the PCA, corresponding to temperature variables, when PCA provides the best model (Fig. 3b).

Discussion

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

A starting point: niche conservatism

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

This dataset of widespread invaders with a large distribution shows no major niche expansion for more than 70% of the species (Petitpierre *et al.*, 2012), probably explaining the good overall transferability of the SDMs. However, niche conservatism may be lower for species with smaller distributions and niche breadth, potentially affecting SDM transferability (Li *et al.*, 2014; Early & Sax, 2014; Bocsi *et al.*, 2016). For such species, particular care given to variables selection may be even more important to obtain reliable predictions of species' potential distribution. For example, niche expansion may occur only at one end (low or high) of a predictor variable's gradient. Indeed, the realized niche can be more labile at one or another extremity of the gradient and it has been shown that the most stressful extremity of the gradient is more predictable by SDMs because it corresponds to physiological limits affecting the fundamental niche (Normand *et al.*, 2009; Maiorano *et al.*, 2013; Araújo *et al.*, 2013). In our dataset, this can be seen for isothermality in the case of *C. scoparius* and for moisture of the coldest quarter in the case of *H. lanatus*, which appear to be a limiting factor only at the lower side of the gradients (Appendix S3). For such species, modelling the limiting thresholds along critical variables rather than the typical bell-shaped distribution may provide more transferable models.

Proximality

It is recommended to use proximal variables, known to have direct impact on species physiology and fitness, to predict potential species distribution (Austin, 2007; Kearney & Porter, 2009; Rödder *et al.*, 2009; Buckley *et al.*, 2010). Because the variables included in the best models provide the best transferability, such variables may be assumed to have more proximal effects on species distributions. Among the 27 included variables, the analysis of variable importance shows that thermal variables are more important in the single best models and thus may be more proximal for invasive plants. This finding, comparable to Randin *et al.* (2013), provides support for forecasting plant species distributions under climate change scenarios, given that scenarios of future precipitations are more uncertain than temperature scenarios (Bosshard *et al.*, 2011). However, precipitation and moisture variables are more often included in the best model, suggesting that they are necessary for good transferability, even if they have less impact on predictions. Beyond these generalities, the fact that the best model of each species does not follow a particular strategy in most of the cases supports that proximality of variables is species specific. Additionally, the discrepancy between EU and NA in the inclusion of some variables in the best models (Fig. 3a) also suggests a possible effect of the study area in the selection of variables optimizing the transferability. Focusing on the variable set which provides the best SDM transferability among multiple combinations, as we did in this study, could precede and help in selecting variables to include in further experimental research on species' physiological response to environmental complex gradients. Only these physiological models can be used to ultimately define species' fundamental niche, a safer approach to predict all the species' potential habitats excluding competitive interactions. This is because, even if the fundamental niche may also be subject to changes, it requires evolutionary adaptations which take times to develop (Whitney & Gabler, 2008). Note that the realized niche is generally equal to or smaller than the fundamental niche (i.e. except in the case of biotic facilitations; Callaway *et al.*, 2002), and predictions based on models of the fundamental niche may overestimate species potential distribution in their native range.

Non-analogy

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

Good at home doesn't mean good elsewhere

In contrast to recent multi-species studies investigating the importance of variable selection for SDMs (e.g. Barbet-Massin & Jetz, 2014; for birds or Ashcroft *et al.*, 2011, for plants), our study used a completely independent dataset (i.e. invaded ranges) to evaluate SDMs' transferability. Complex and highly parameterized SDMs like S_{all} can be used to depict the fine variations in the range where they are calibrated but are less robust against changes in the structure of the predictors. Therefore, the difference between the model performances in the native and invaded ranges with S_{all} and S_{pc2} demonstrates that excellent performances as determined by pseudo-independent data (native range sub-sampling) do not necessarily imply a good transferability. Spatial autocorrelation and over-parametrization can explain this apparent paradox. The usual approach by which a subsample of the calibration area is used as an independent dataset for model evaluation may be biased by spatial correlation with the calibration dataset (McPherson & Jetz, 2007; Bahn & McGill, 2013). Although fully independent dataset should always be the one and only gold standard for SDM evaluation of transferability, having such separate datasets in comparable environmental conditions is rare. Therefore, to minimize the spatial autocorrelation problem, increasing the ratio of independent data in the split-sampling evaluation, including a spatial autocorrelation term or disaggregating the calibration dataset based on a minimum distance can be alternatives (Dormann, 2007, Hijmans, 2012). Interestingly, collinearity does not show any significant negative effect on predictions in our study (e.g. when S_{unc} is compared to S_{ran}). Using Pearson's correlation to assess collinearity between variables is very common but can be subject to criticism. The threshold (here in this study $|r| \leq 0.7$) was based on a review of literature (Dormann *et al.*, 2013) and does not rely on any statistical demonstration or simulation. This approach can also be biased when non-linear relationships exist among predictors (Dormann *et al.*, 2013) and can be alternatively replaced by the use of a dissimilarity matrix based on indices such as Gower metric (Franklin, 2010), which is less sensitive to non-linearity. However, both the validity of the correlation threshold and Gower matrices require formal assessment. An independent dataset, such as a species' invasive distribution, can be useful for such purpose.

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

Recommendations

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

On average, S_{soa} performs well on the invaded range probably because it contains the major limiting predictors for the majority of the species. On the other hand, by summarizing the main regional complex gradients of the study area in only two components, S_{pc2} allowed simple and transferable SDMs for most species, presenting less variance in performance between species and yielding fewer poorly predicted species. Reducing the numerous and complex interactions between precipitation, moisture and seasonality into one component, and heat and continentality into another (Fig. S3 in appendix S2), is an efficient way to depict a simplified climatic envelop (Metzger *et al.*, 2005, Bakkestuen *et al.*, 2008, Broennimann *et al.*, 2012, Kriticos *et al.*, 2014). In addition, the fact that the maximization of the environmental variance was made across all ranges pooled together likely also contributed to make the principal components (i.e. axes) more transferable. However, these SDMs calibrated on principal components may be more problematic to interpret. Furthermore, extrapolation and climate change scenarios may change the correlation structure between parameters and thus lead to unreliable predictions when projected outside the PCA environmental space. For all these reasons, we recommend using S_{pc2} as an alternative only when limited occurrence data are available (thus avoiding SDMs overparametrization) and projecting onto predictors keeping the same correlation structure. S_{soa} may be more desirable if one is interested in ecological interpretation or in projection towards climatic scenarios where predictors may have different correlation structures. Finally, when the projection is characterized by a highly different environment relative to the calibration range (e. g. like between Eurasia and Australia), strategies maximizing climate analogy (such as S_{ana} or S_{anc}) may be considered.

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Supporting information

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

Appendix S2: Supporting material

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

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

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Table 1: Evaluation of the best models for each species with Boyce index and sensitivity in the native range, Holarctic and Australian invaded range ($B_{Nat,}$ Se_{Nat} ¸B_{Hol}, Se_{Hol}, B_{Au}, Se_{Au} respectively). 1) and 2) indicate species shifting their niche in Holarctic and Australia respectively. Strategy providing the best model is also indicated (Strat.), as well as species native origin (Nat.).

Species	**Nat.**	**Strat.**	**B_{Nat}**	**Se_{Nat}**	**B_{Hol}**	**Se_{Hol}**	**B_{AU}**	**Se_{AU}**
Alliaria petiolata (M.Bieb.) Cavara & Grande	EU	S_{ran}	0.99	0.95	0.98	1.00	-	-
Amaranthus retroflexus L.	NA	S_{pc2}	0.98	0.92	0.93	0.76	0.71	1.00
Ambrosia artemisiifolia L.	NA	S_{pc2}	0.97	0.88	0.94	0.92	0.90	1.00
Amorpha fruticosa L.1)	NA	S_{ran}	0.91	0.91	0.71	0.84	-	-
Anagallis arvensis L.	EU	S_{ran}	0.99	0.93	0.97	1.00	0.99	1.00
Anthoxanthum odoratum L.	EU	S_{ran}	0.97	0.92	0.95	1.00	0.97	0.98
Arabidopsis thaliana (L.) Heynh	EU	S_{ran}	1.00	0.94	0.99	0.98	0.90	1.00
Bromus sterilis L.1)	EU	S_{ran}	0.97	0.97	0.94	0.84	0.79	0.91
Bromus tectorum L.	EU	S_{ran}	0.99	0.95	0.97	0.81	0.81	0.96
Carduus nutans L.	EU	S_{ran}	0.99	0.93	0.96	0.97	0.91	1.00
Centaurea stoebe L.1)	EU	S_{ran}	0.96	0.96	0.91	0.48	-	-
Cirsium vulgare (Savi) Ten.2)	EU	S_{ran}	0.99	0.96	0.98	0.96	0.98	0.87
Conyza canadensis (L.) Cronquist	NA	S_{ran}	0.96	0.94	0.99	0.94	0.94	1.00
Cytisus scoparius (L.) Link1)	EU	S_{ran}	0.98	0.97	0.97	0.89	0.97	1.00
Dactylis glomerata L.	EU	S_{ran}	0.99	0.89	0.99	0.97	0.95	0.99
Echinocystis lobata (Michx.) Torr. & A. Gray	NA	S_{ran}	0.97	0.95	0.97	0.96	-	-
Erigeron annuus (L.) Pers.	NA	S_{unc}	0.96	0.96	0.97	0.94	-	-
Erodium cicutarium (L.) L'Hér. ex Aiton	EU	S_{ran}	0.99	0.94	0.98	0.94	0.97	0.98
Euphorbia esula L.	EU	S_{ran}	0.99	0.92	0.93	0.81	-	-
Holcus lanatus L.1)	EU	S_{ran}	0.97	0.97	0.97	0.88	0.97	0.97
Hypochaeris radicata L.2)	EU	S_{ran}	0.98	0.98	0.99	0.92	1.00	0.93
Juncus tenuis Willd.	NA	S_{ran}	0.99	0.91	0.98	0.98	0.93	1.00
Linaria vulgaris Mill.2)	EU	S_{ran}	1.00	0.89	0.99	0.97	0.86	1.00
Lythrum salicaria L.	EU	S_{ran}	0.99	0.96	0.91	0.95	0.95	0.97
Medicago lupulina L.	EU	S_{ran}	0.99	0.89	0.98	0.97	0.95	1.00
Melilotus albus Medik.2)	EU	S_{ran}	0.99	0.82	1.00	0.93	0.97	0.94
Phytolacca americana L.	NA	S_{ran}	0.92	0.91	0.94	0.98	0.92	1.00
Plantago lanceolata L.	EU	S_{ran}	0.99	0.94	0.97	0.94	1.00	0.98
Plantago major L.	EU	S_{ran}	1.00	0.90	1.00	0.94	0.95	0.97
Poa annua L.	EU	S_{ran}	0.99	0.85	0.99	0.92	0.98	0.95
Potentilla recta L.	EU	S_{ran}	0.99	0.93	1.00	0.99	0.93	1.00
Prunus serotina Ehrh.	NA	S_{ran}	0.97	0.96	0.99	1.00	-	-
Rhus typhina L.	NA	S_{pc2}	0.91	0.96	0.86	1.00	-	-
Robinia pseudoacacia L.	NA	S_{pc2}	0.97	0.93	0.99	0.98	0.97	0.98
Rumex acetosella L.	EU	S_{ran}	0.97	0.92	0.99	0.95	0.95	0.95
Solidago canadensis L.2)	NA	S_{unc}	0.99	0.92	0.96	0.90	0.93	0.90
Solidago gigantea Aiton	NA	S_{ran}	0.98	0.96	0.98	0.99	-	-
Sonchus oleraceus L.2)	EU	S_{ran}	0.99	0.95	0.89	0.76	0.99	0.96
Trifolium arvense L.	EU	S_{ran}	0.99	0.95	0.99	0.98	0.93	0.98
Trifolium dubium Sibth.1) 2)	EU	S_{ran}	0.98	0.98	0.97	0.91	0.97	0.95
Trifolium repens L.	EU	S_{ran}	0.99	0.85	0.99	0.91	0.98	0.98

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

Table 3: List, abbreviation, number of replicates (# rep., i.e. number of different predictor combinations) and description of each strategy used to select the predictors included in the SDMs. Note that for species present in Australia, there are two datasets for strategies optimizing climate 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 *et al.*, 2010, Hill *et al.*, 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 *et al.*, 2005, Broennimann *et al.*, 2007, Petitpierre *et al.*, 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 *et al.*, 2007) and can be used in a hierarchical way (e.g. Roura-Pascual *et al.*, 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 *et al.*, 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 *et al.*, 2007, Bakkestuen *et al.*, 2008, Zhang & Zhang, 2012, Kriticos *et al.*, 2014). Moreover, it has been shown to be the most accurate way to build an environmental space to assess niche overlap (Broennimann *et al.*, 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.

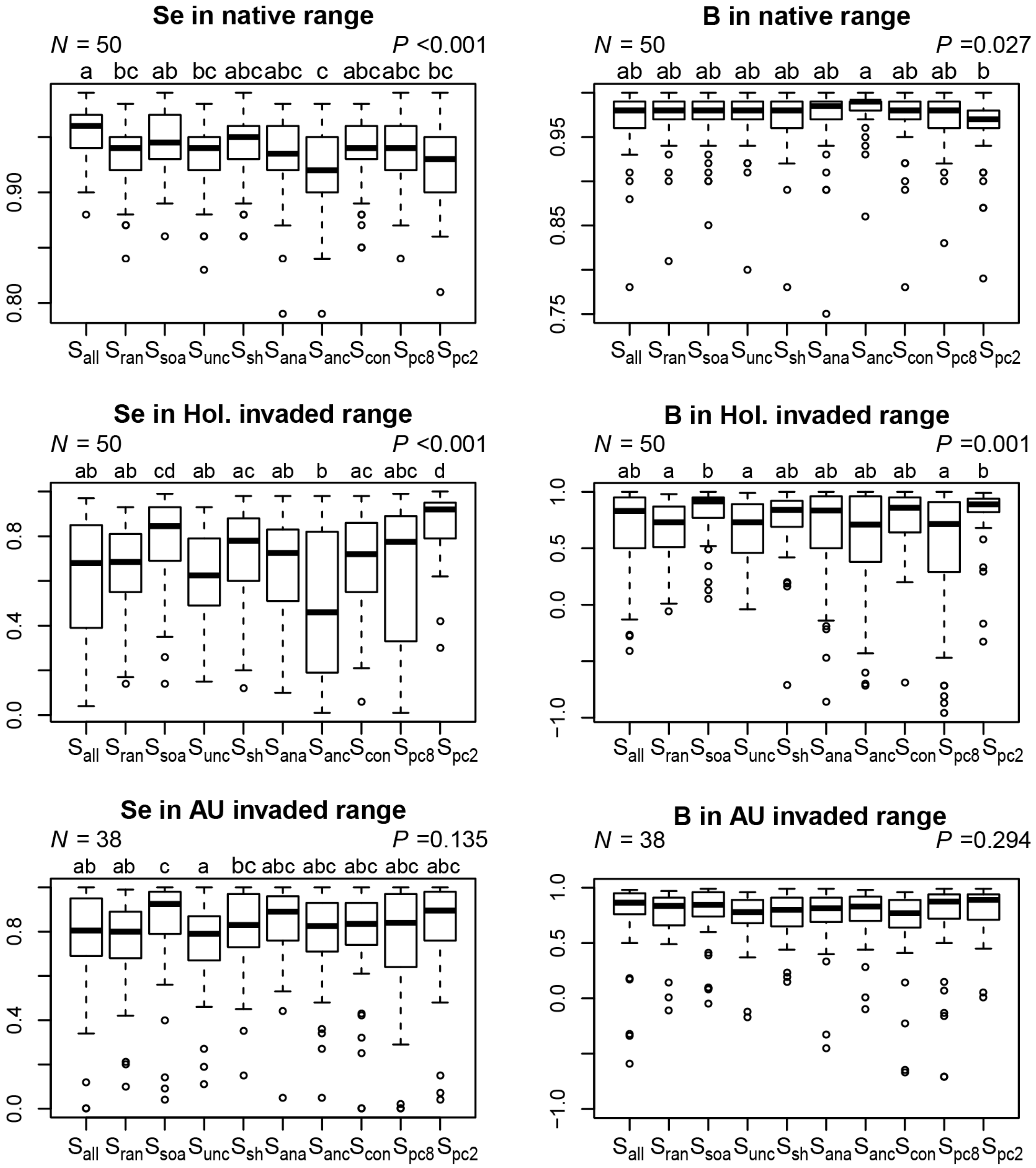
Se in native range
N = 50
P <0.001
a bc ab bc abc abc c abc abc bc
0.80
0.90
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}
B in native range
N = 50
P =0.027
ab ab ab ab ab ab a ab ab b
0.75
0.85
0.95
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}
Se in Hol. invaded range
N = 50
P <0.001
ab ab cd ab ac ab b ac abc d
0.0
0.4
0.8
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}
B in Hol. invaded range
N = 50
P =0.001
ab a b a ab ab ab ab a b
−1.0
0.0
0.5
1.0
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}
Se in AU invaded range
N = 38
P =0.135
ab ab c a bc abc abc abc abc abc
0.0
0.4
0.8
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}
B in AU invaded range
N = 38
P =0.294
−1.0
0.0
0.5
1.0
S_{all} S_{ran} S_{soa} S_{unc} S_{sh} S_{ana} S_{anc} S_{con} S_{pc8} S_{pc2}

Figure 1.

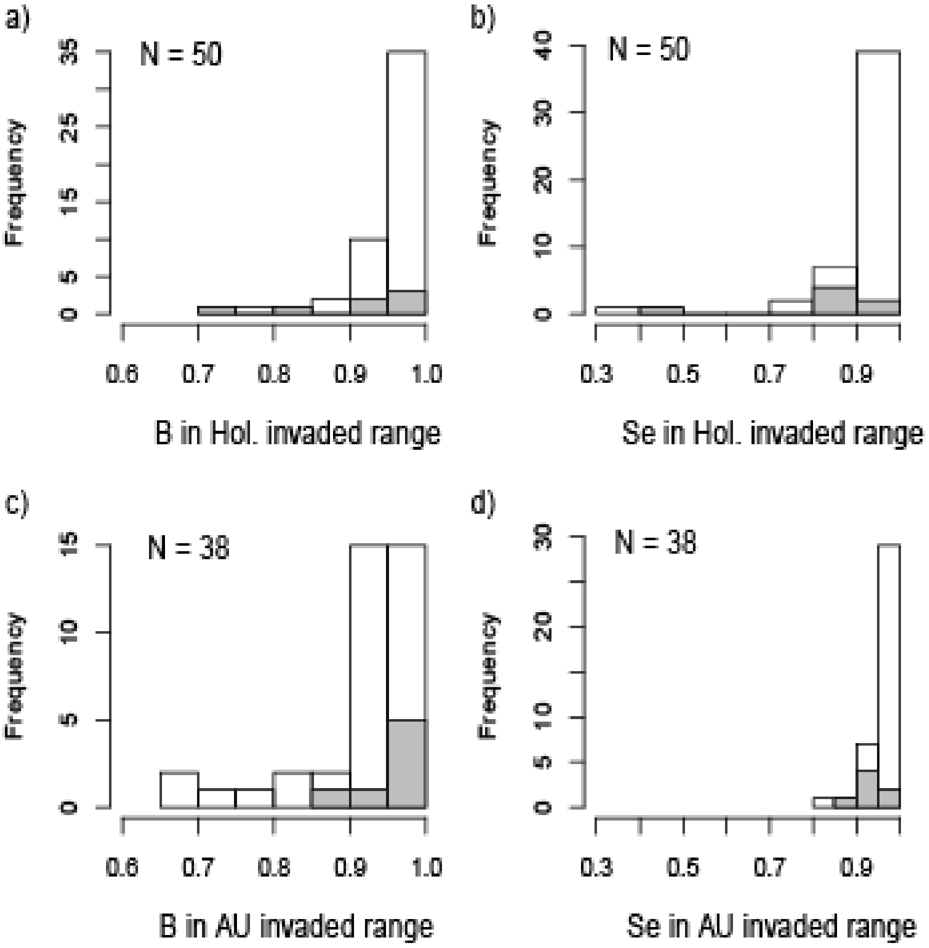
a)
N = 50
Frequency
0
5
15
25
35
0.6
0.7
0.8
0.9
1.0
B in Hol. invaded range
b)
N = 50
Frequency
0
10
20
30
40
0.3
0.5
0.7
0.9
Se in Hol. invaded range
c)
N = 38
Frequency
0
5
10
15
0.6
0.7
0.8
0.9
1.0
B in AU invaded range
d)
N = 38
Frequency
0
5
10
20
30
0.3
0.5
0.7
0.9
Se in AU invaded range

Figure 2.

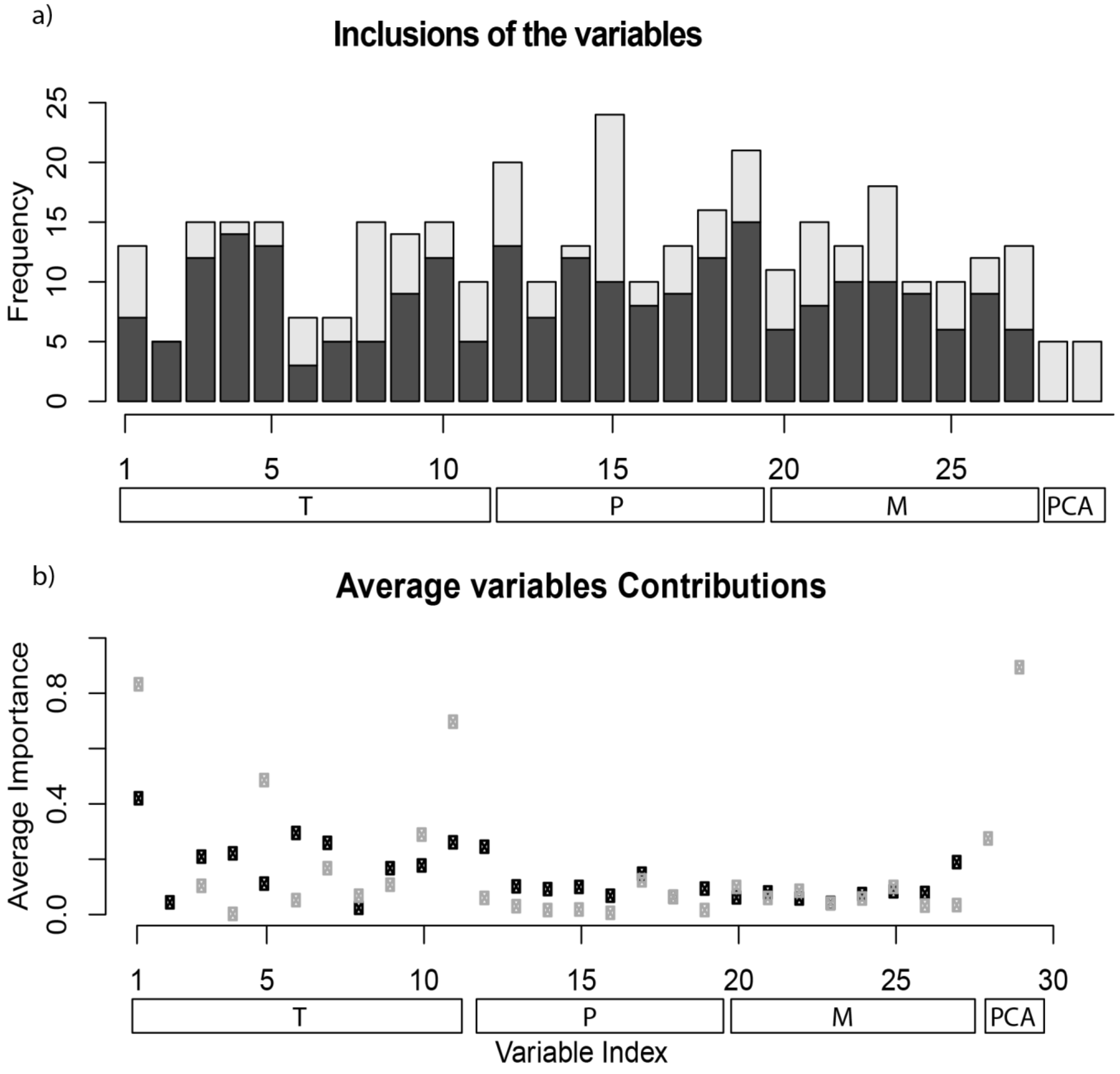
a)
Inclusions of the variables
Frequency
0
5
10
15
20
25
1
5
10
15
20
25
T
P
M
PCA
b)
Average variables Contributions
Average Importance
0.0
0.4
0.8
1
5
10
15
20
25
30
T
P
M
PCA
Variable Index

Figure 3.