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# Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks

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## ABSTRACT

**Aim** Studies of environmental niche shift/niche conservatism that are based on species distribution modelling require a quantification of niche purity and potential overlap. Although various metrics have been proposed for this task, no comparisons of their performance are available yet that express the linearity of range shifts and error-proneness. Herein, we assess the performance of six niche overlap metrics using three sister pairs of plethodontid salamanders as well as artificial species to test for linearity of overlap curves, impacts of varying potential distribution sizes and study area sizes.

**Location** North America, artificial environments.

**Methods** Species distribution models for the salamanders were performed with MAXENT, and artificial species were created in the R environment. Potential distributions of species with varying range sizes and extents of the study area were compared using the Bray–Curtis distance *BC*, Schoener's *D*, two different modifications of the Hellinger distance *I*<sub>mod</sub>, *I*<sub>cor</sub>, Pianka's *O* and Horn's *R*. Niche overlaps in ecological space were compared using linear discriminant analyses based on principal components.

**Results** Simulations of niche overlaps revealed strong variations in the performance of the niche overlap metrics. In artificial species, *BC* and *D* performed best, followed by *O*, *R* and *I*<sub>cor</sub>, but the modified Hellinger distance *I*<sub>mod</sub> showed a non-linear slope and a truncated range. Furthermore, the simulations suggest that, in proportionally small potential distributions on large grids, an inclusion of a high proportion of grid cells with low occurrence probabilities representing background noise may bias assessments of niche overlaps.

**Main conclusions** Both the salamander examples and simulations suggest that Schoener's *D* and the Bray–Curtis distance *BC* are best suited to compute niche overlaps from potential distributions derived from species distribution models. However, like all analysed metrics, both *D* and *BC* are seriously affected by the inclusion of high numbers of grid cells where the species are probably absent, i.e. with low occurrence probabilities. Therefore, pre-processing to eliminate background noise in the potential distribution grids is highly recommended.

## Keywords

Environmental space, geographic space, niche conservatism, niche evolution, niche shift, North America, salamanders, simulated environment, simulated species, species distribution model.

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## INTRODUCTION

The identification of processes that have generated, or which may threaten, biodiversity is one of the major tasks in biogeography.

In the face of intense debates on anthropogenic climate change, studies assessing possible adaptation to climate change or resulting speciation and diversification when adaptation is not possible, or only possible to a very limited extent, have

become very important. In recent years, species distribution models (SDM) have received increasing attention in many biological fields and now allow testing of different speciation scenarios and evolution of environmental niches (Kozak & Wiens, 2006; Evans *et al.*, 2009; Jakob *et al.*, 2010). They are also widely used in biodiversity research (e.g. Thuiller *et al.*, 2006), conservation biology (e.g. Guisan & Thuiller, 2005; Rödder & Schulte, 2010) and invasion biology (e.g. Peterson & Vieglais, 2001). The general idea behind correlative SDMs is to compute a model of the target species' idealized niche based on information on the species' occurrence (presence-only, presence–pseudoabsence or presence–absence data) and environmental data commonly stored as geographic information system (GIS) layers (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). The output is a map showing relative suitability (or the likelihood of occurrence, depending on the approach used) of each grid cell for the species at hand.

When applying SDMs, various assumptions are made, wherein Hutchinson's (1957, 1978) niche concept as extended by Soberón (2007) and Godsoe (2010) provides the theoretical basis for the interpretation of results. Herein, each species possesses a distinct fundamental niche comprising all environmental features in a multidimensional ecological (E)-space, which supports indefinite population existence without emigration or immigration. Commonly, the potential niche (i.e. the representation of all parts of the fundamental niche available in geographic (G)-space) (Jackson & Overpeck, 2000), dispersal limitations and biotic interactions restrict the representation of the fundamental niche in G-space defining the species' realized niche (Soberón & Peterson, 2005; Soberón, 2007; Colwell & Rangel, 2009; Soberón & Nakamura, 2009). Using SDMs, equivalents of the E-space occupied by the species' realized distribution are determined in G-space and its potential distribution is inferred (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). Note that, at least theoretically, the fundamental niche may comprise environmental features or combinations thereof which are not represented in G-space (Jackson & Overpeck, 2000; Godsoe, 2010) and that source–sink dynamics may sometimes cause species to be found outside their fundamental niche (Puliam, 2000). Furthermore, in SDMs the Grinnellian niche (Grinnell, 1917) is predominately addressed by using coarse-scale scenopoetic environmental variables such as temperature and precipitation, whereas it is in most cases very difficult to address the Eltonian niche (Elton, 1927) reflected by biotic variables (i.e. biotic interactions and resource–consumer dynamics) (Hutchinson, 1978; Soberón, 2007). However, at coarse scales the Eltonian niche may become less important (the Eltonian noise hypothesis; Soberón & Nakamura, 2009).

A necessary assumption when projecting SDMs through space and time is that a species' niche remains comparatively stable (Elith & Leathwick, 2009). Hence, niche conservatism (i.e. the tendency of closely related species to occupy more similar niches than expected by chance; Peterson *et al.*, 1999; Wiens & Graham, 2005) and patterns of niche shift (*sensu* Pearman *et al.*, 2008) have become a central topic in evolutionary research on

both inter-specific (e.g. Peterson *et al.*, 1999; Graham *et al.*, 2004; Jakob *et al.*, 2010) and intra-specific scales (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder & Lötters, 2009). Various methods have been proposed to study conservatism in Grinnellian niches (see Discussion). Hence, it is not surprising that results of studies analysing niche conservatism/niche shift are mixed, often contradictory and currently highly debated (Pearman *et al.*, 2008; Rödder & Lötters, 2010). One problem may be that strikingly different hypotheses in a continuum between 'niche similarity' and 'niche equivalency' have been tested in the past (Warren *et al.*, 2008). Since studies comparing SDM outputs to address those patterns are becoming more and more popular, standardized statistics are needed to validate results and to make comparable statements.

When comparing Grinnellian niches, two general approaches may be applied: niches can either be compared (1) in E-space using multivariate statistics such as principal components analyses (PCAs) or (2) in G-space comparing SDM outputs. However, one of the most often chosen approaches is to compare SDM outputs of two taxa (e.g. Peterson *et al.*, 1999; Warren *et al.*, 2008; Evans *et al.*, 2009; Dormann *et al.*, 2010). Various metrics have been proposed to compute niche overlaps in Eltonian niches (for details see Krebs, 1989) and their usefulness was discussed nearly 30 years ago (e.g. Bloom, 1981; Smith & Zaret, 1982). Comparisons of Grinnellian niches in G-space via niche overlap metrics are relatively new, however. Warren *et al.* (2008) proposed Schoener's *D* and a modified Hellinger distance ( $I_{\text{mod}}$ ) as metrics to compare SDMs. Both indices have been increasingly used since their establishment (e.g. Pyron & Burbrink, 2009; Rödder & Lötters, 2009; Jakob *et al.*, 2010; McCormack *et al.*, 2010; Medley, 2010; Nakazato *et al.*, 2010), and some methodological issues such as the selection of appropriate background data for SDM computation (Anderson & Raza, 2010) and issues related to SDM transferability in G-space have already been discussed (Rödder & Lötters, 2010). A detailed evaluation of the performance of different niche overlap metrics is currently lacking, however.

Various scenarios of how potential distributions of two species may be situated in G-space are conceivable. It is currently unclear how different patterns may affect analyses using one or the other index. The simplest scenario may be represented by two species with roughly equally sized potential distributions in close proximity. Two species inhabiting distinct altitudinal bands in a mountainous area could also possess distinct, narrow potential distributions. Using SDM predictions, large parts of the study areas may be characterized by low occurrence probabilities. These may artificially increase the niche overlap values, which might then characterize the high degree of similarity in those areas characterized by low occurrence probabilities rather than overlaps in those areas where the species are actually likely to be occurring. Other possibilities could include the combination of one species with a broad potential distribution, and then another species with a narrow potential distribution or with intermediate scenarios.

To allow for good comparability between different species pairs, niche overlap values should: (1) range from 0 (no overlap)

to 1 (two potential distributions are identical), (2) show a linear slope with increasing similarity of environmental niches, and (3) be insensitive to varying spatial extents of the target species' potential distributions and inclusion of huge areas characterized by very low occurrence probabilities. To provide a better understanding of possible dependences of different statistics of such patterns when pushed to extreme comparisons, we herein develop simulations of artificial species with different potential distributions and compare them with real-life examples. Furthermore, we discuss possible advantages and disadvantages when comparing species niches either in G-space or in E-space.

## METHODS

### Species distribution models

In order to provide real-life examples of the different scenarios of different potential distribution sizes formulated in the Introduction, we repeated comparisons of niche similarities among three pairs of North American salamanders of the genus *Plethodon* Tschudi, 1838 as described in Kozak & Wiens (2006). The first example illustrating two sister taxa with roughly equally sized ranges situated close to each other is represented by the two salamander species *Plethodon cylindraceus* Harlan, 1825 and *Plethodon teyahalee* Hairston, 1950. The second case of two species with distinct, narrow ranges can be found in the two salamander species *Plethodon nettingi* Green, 1938 and *Plethodon hubrichti* Thurow, 1957. Finally, *Plethodon wehrlei* Fowler & Dunn, 1917 and *Plethodon punctatus* Highton, 1972 illustrate the last case, i.e. the combination of one species with a broad range and one species with a narrow range. Species records were provided by J. Milanovich and additional records obtained through the Global Biodiversity Information Facility (<http://www.gbif.org>). All records were checked for possible bias and errors using DIVA-GIS 7.1.6 (Hijmans *et al.*, 2005b). The final data set includes 180 records of *P. cylindraceus*, 761 records of *P. teyahalee* (species pair 1), 28 records of *P. hubrichti*, 16 records of *P. nettingi* (species pair 2), 37 records of *P. punctatus* and 110 records of *P. wehrlei* (species pair 3) (see also Fig. 1).

Information on current climate was obtained from the WorldClim database (Hijmans *et al.*, 2005a; <http://www.worldclim.org>). Following Kozak & Wiens (2006), the variable set used for SDM computation comprised the 'mean annual temperature range', the 'maximum temperature of the warmest month', the 'minimum temperature of the coldest month', 'precipitation seasonality' and 'precipitation of the driest quarter'. These variables were suggested to be biologically relevant to the salamanders (Kozak & Wiens, 2006), which significantly enhance the reliability of SDM results (Rödder *et al.*, 2009).

SDMs were computed with MAXENT 3.3.2 (Phillips *et al.*, 2006; Phillips & Dudík, 2008) using the logistic output format. Being a presence–pseudoabsence method, MAXENT provides an estimate of the probability of presence of the species (Soberón & Nakamura, 2009) in a grid with values ranging linearly from 0 to 1. Furthermore, SDMs were developed using the default settings

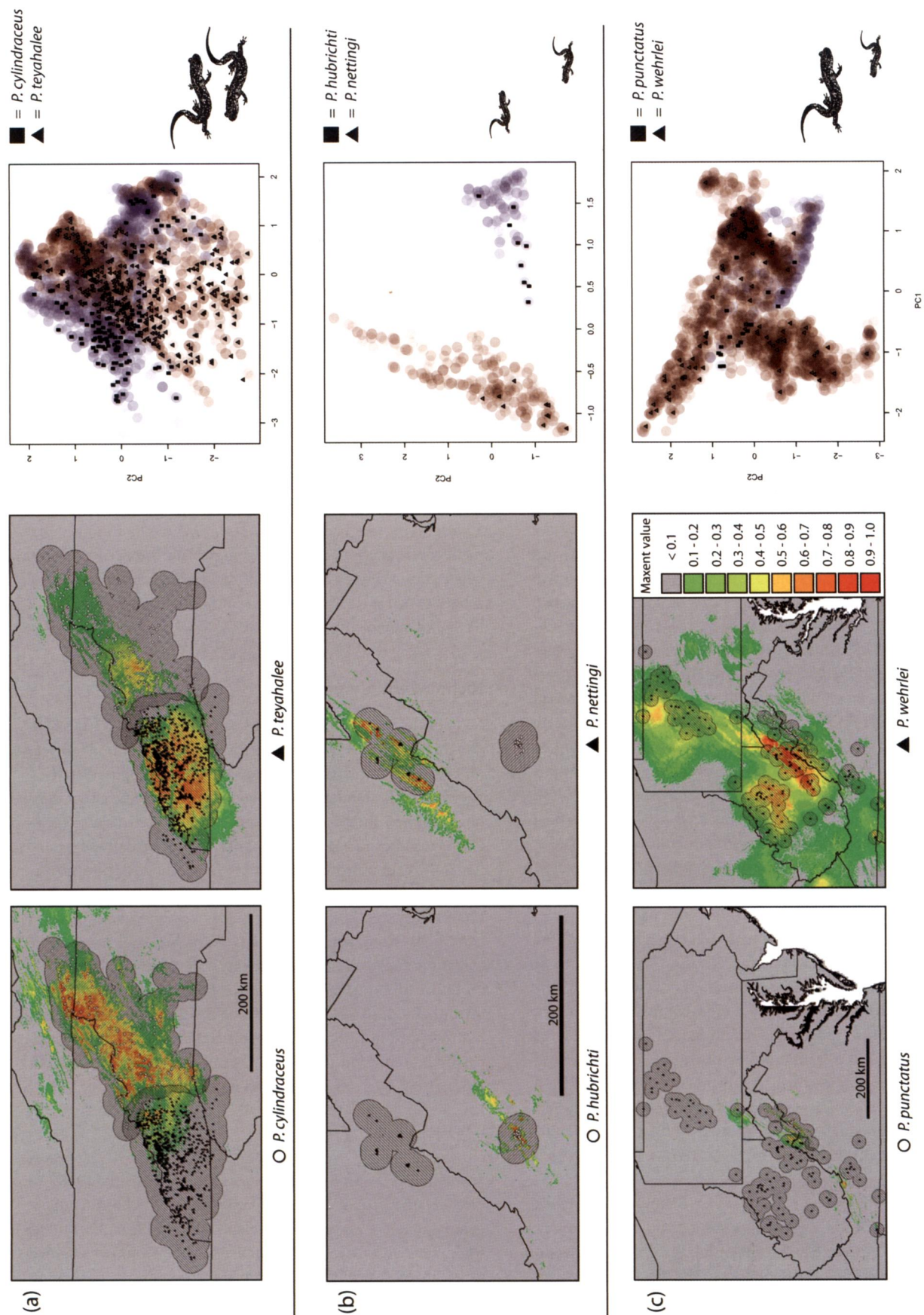
but splitting the species records 10 times into 70% used for training the model and 30% to test model performances via the area under the receiver operating curve (AUC), which is recommended for ecological applications as it is nonparametric (e.g. Pearce & Ferrier, 2000; Manel *et al.*, 2001). This measure of model performance was recently criticized by Lobo *et al.* (2008), but correctly applied and interpreted it is still state-of-the-art (Elith & Graham, 2009). Subsequently, averages of all models per species were computed for further processing. Various thresholds have been proposed to transform continuous probability surfaces into presence–absence maps (Liu *et al.*, 2005). Herein, we chose two of them to distinguish those areas which are likely to be suitable for the species from unsuitable sites, i.e. the 'minimum training presence' and the 'lowest 10th percentile training omission'. Note that the probability surfaces were reclassified into grids maintaining the probability of occurrence in those areas above a certain presence–absence threshold, which were transformed into a novel probability distribution summing up to 1, and setting those areas below the threshold to 0. This procedure allowed us to maintain the probability information in a reasonable estimate of the potential distribution of the species but excluding huge areas with low occurrence probabilities reflecting background noise. This method implies that niche overlap assessments are biologically more meaningful when comparing environmental conditions within the actual ranges of the species rather than in those areas which are most likely not suitable for the species.

### Niche overlap metrics

It is not the focus of the present study to provide a comprehensive review of niche overlap indices, which can be found in Krebs (1989), for example. Out of a huge number of proposed metrics, we selected six standard niche overlap metrics being either most often applied in the past to compare Eltonian niches (Bray–Curtis distance *BC*, Horn's *R*, Pianka's *O*) or recently suggested for SDM comparisons (Schoener's *D*, modified Hellinger distance  $I_{\text{mod}}$ ; for formulae and ranges see Table 1). Warren *et al.* (2008) suggested *D* and  $I_{\text{mod}}$  for niche overlap analyses between two SDMs. Note that, recently, a typographic error has become evident in the formula of the Hellinger distance *H* subsequently modified to  $I_{\text{mod}}$  given in Warren *et al.* (2008). The erroneous formula was also used in ENM-tools 1.0 and previous versions but corrected in version 1.1 and subsequent releases (D. Warren, personal communication). The correct formula for the Hellinger distance ( $I_{\text{cor}}$ ) is given in Table 1, wherein

$$I_{\text{cor}} = 1 - 2(1 - I_{\text{mod}})^2.$$

Schoener's *D* was first introduced by Renkonen (1938) to measure the proportional similarity of two niches making it comparable to a percentage overlap (Kohn & Riggs, 1982). The second metric, the Hellinger distance *H*, was previously assumed to be an ecologically meaningful measurement in ordination methods (Legendre & Gallagher, 2001). Warren's retransformation of the original formula of *H* aimed to create a value range



**Figure 1** Potential distributions of three pairs of salamander sister taxa and corresponding niche overlaps in E-space. In maps, warmer colours correspond to higher occurrence probabilities. Grey hatching indicates 0.16° circular buffers per record sampled using random points for E-space principal components analyses (PCAs). Blue and brown areas in PCA plots illustrate the environmental space available for the corresponding species within downward and upward hatched areas, respectively, in the maps.



**Table 1** Niche overlap indices compared in this study. In each formula  $p_{X,i}$  and  $p_{Y,i}$  denote the probability assigned in a species distribution model computed for species  $X$  and  $Y$  to grid cell  $i$ .

Metric	Formula	Range
Schoener's $D$	$D(p_X, p_Y) = 1 - \frac{1}{2} \sum_i  p_{X,i} - p_{Y,i} $	0 to 1
Modified Hellinger distance $I_{\text{mod}}$	$I_{\text{mod}}(p_X, p_Y) = 1 - \frac{1}{2} \sqrt{\sum_i (\sqrt{p_{X,i}} - \sqrt{p_{Y,i}})^2}$	$1 - \frac{\sqrt{2}}{2}$ to 1
Corrected Modified Hellinger distance $I_{\text{cor}}$	$I_{\text{cor}}(p_X, p_Y) = 1 - \frac{1}{2} \left( \sqrt{\sum_i (\sqrt{p_{X,i}} - \sqrt{p_{Y,i}})^2} \right)^2$	0 to 1
Horn's $R$	$R(p_X, p_Y) = \frac{\sum_i (p_{X,i} + p_{Y,i}) \log(p_{X,i} + p_{Y,i}) - \sum_i p_{X,i} \log p_{X,i} - \sum_i p_{Y,i} \log p_{Y,i}}{2 \log 2}$	0 to 1
Pianka's $O$	$O(p_X, p_Y) = \frac{\sum_i p_{X,i} p_{Y,i}}{\sqrt{\sum_i p_{X,i}^2 \sum_i p_{Y,i}^2}}$	0 to 1
Bray–Curtis distance $BC$	$BC(p_X, p_Y) = \frac{\sum_i 2 \min(p_{X,i}, p_{Y,i})}{\sum_i (p_{X,i} + p_{Y,i})}$	0 to 1

from 0 to 1 (unmodified range 0 to 2), which makes it more comparable to other niche overlap metrics. The third metric,  $R$ , is based on information theory (Horn, 1966), which was emphasized to be very useful because it is comparatively fail-safe (Ricklefs & Lau, 1980; Smith & Zaret, 1982). The fourth index,  $O$  (Pianka, 1973), is one of several overlap metrics that are mathematically identical (e.g. to the modified Morisitas index). Therefore the others will not be considered herein (see Bloom, 1981, for details). Finally,  $BC$  (Bray & Curtis, 1957) was chosen because previously it was assumed to be an ecologically meaningful distance measure (e.g. Legendre & Legendre, 1998).

Applying each of the six metrics, we compared niche overlaps in the three salamander species pairs and computed different simulations to test their performance (see below). As niche overlap indices ideally range linearly from 0 (no overlap) to 1 (identical potential distributions), we suggest the following classes to facilitate the interpretation of results: 0–0.2 = no or very limited overlap, 0.2–0.4 = low overlap, 0.4–0.6 = moderate overlap, 0.6–0.8 = high overlap, 0.8–1.0 = very high overlap.

In order to illustrate the relative positions of the sister species in E-space as well as the potential niche available for each of them, we computed PCAs. For PCAs, available E-space was sampled using random points in a circular buffer per record of  $0.16^\circ$  (c. 14 km radius) with  $0.004^\circ$  minimum distance between points and an equal density per species as previously suggested (Anderson & Raza, 2010). Only those principal components were selected which had eigenvalues  $\geq 1$ . To assess the niche overlaps in E-space, we subsequently performed linear discriminant analysis (LDA). In LDA a priori defined groups (i.e. both sister species) with equal prior probabilities were compared through a set of explanatory variables, representing the E-space spanned by principal components. A randomly selected subset of 70% of the dataset was used to construct the discriminant model and validated with the rest of the data. Total overlaps in

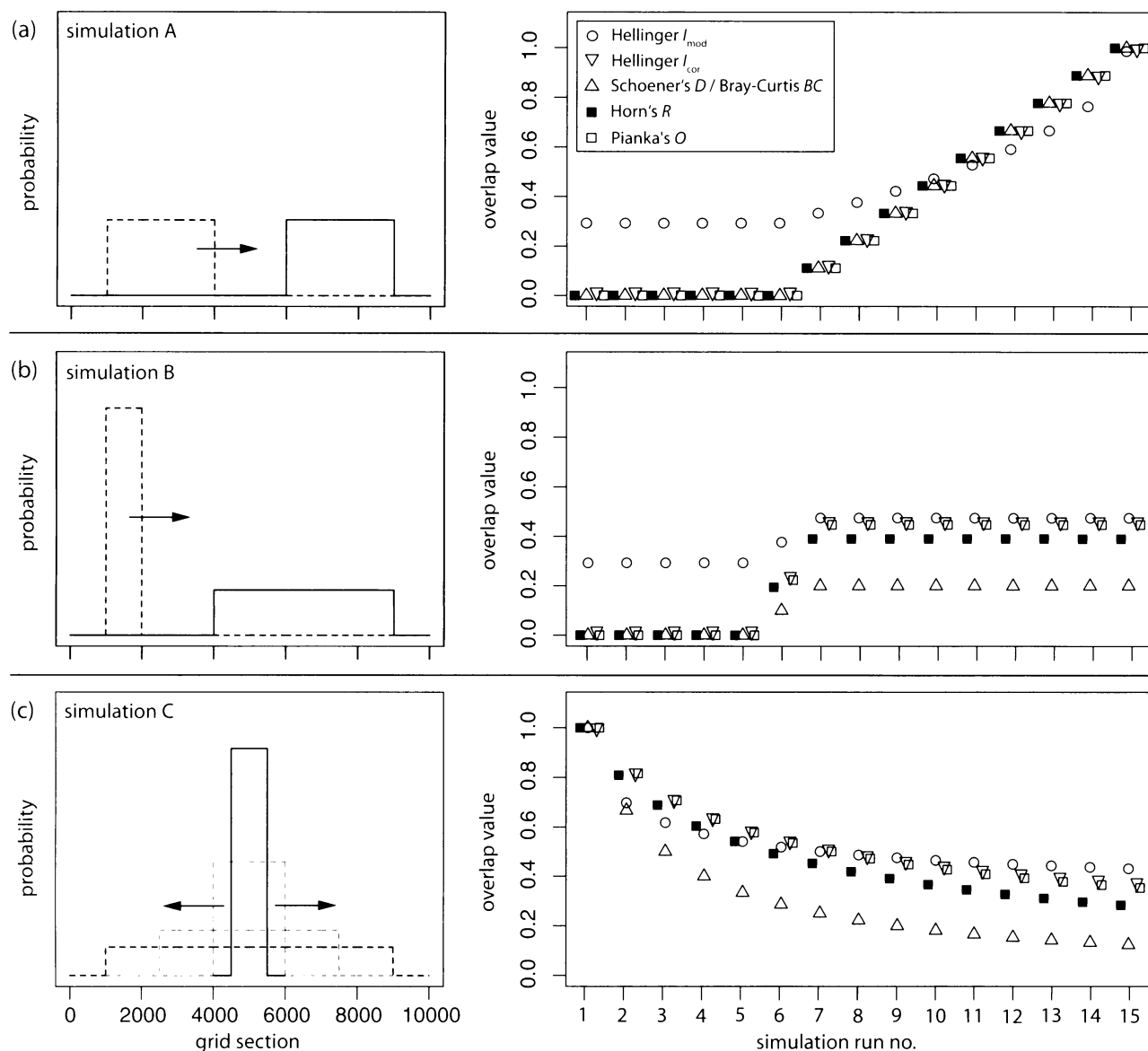
E-space were derived by summing all falsely classified values and dividing them by the total of all values. Accounting for possible variations caused by data splits, this procedure was repeated 1000 times. Computations were conducted using ArcGIS 9.3 with the Hawth's Tools extension (Beyer, 2004), and R 2.11.1 (R Development Core Team, 2010).

### Simulations of varying distribution patterns

In order to assess possible influences of varying potential distribution patterns, simulations were constructed in R. Along a one-dimensional (1-D) grid with 10,000 sections (i.e. grid cells), potential distributions of fictitious species were created (occurrence probability inside range = 0.8, outside = 0) and subsequently transformed into probability distributions for overlap calculations. This approach results in 1-D grids that are conceptually equal to those obtained by SDMs in a two-dimensional (2-D) context (Phillips *et al.*, 2006; Phillips & Dudík, 2008).

**Simulation A.** Two species with two identical, spatially restricted potential distributions (range size = 3000 sections) were generated. Starting at the opposite ends of the 10,000-section grid, the potential distribution of one species was stepwise moved towards the potential distribution of the second (fixed) species resulting in a decreasing isolation between both species until complete overlap in G-space (16 steps with shifts of 333 grid cells per step; Fig. 2a). This simulation assesses range constancy and linearity in different metrics.

**Simulation B.** The restricted potential distribution of a species (range size = 1000 sections) was moved towards a fixed, broader potential distribution of a second species (range size = 5000 sections) located at the opposite end of the grid (17 steps with shift of 500 grid cells per step; Fig. 2b), to test for differences caused by varying range sizes.



**Figure 2** Simulations of niche overlap in different artificial species compared with Bray–Curtis distances  $BC$ , Schoener's  $D$ , Hellinger's  $I$  as modified by Warren *et al.* (2008), Horn's  $R$  and Pianka's  $O$  in three different scenarios. Schematic illustrations of the simulations, which were run on linear grids with 10,000 grid cells, are given in the left column and the results in the right column. (a) Two species (dashed versus solid lines) occupying narrow potential distributions interacting by decreasing isolation. (b) One species occupying a narrow potential distribution and one species occupying a broad potential distribution moving towards each other. (c) One species increased its potential distribution within the optimum of a species with a narrow, fixed potential distribution. Arrows indicate moving directions of the potential distribution of one artificial species towards the potential distribution of a second species fixed in space.

**Simulation C.** A species posing a fixed, relatively restricted potential distribution (range size = 1000 grid cells) located in the middle of the grid was compared with a second species, which increased the size of its potential distribution (increasing range size from 1000 to 8000 grid cells in 15 steps) starting also in the middle of the grid (Fig. 2c). This simulation allowed us to test for possible effects of varying grid occupancy patterns.

#### Simulation of varying grid sizes

In *Simulation D*, we tested for effects of background noise expressed in very low occurrence probabilities in a high propor-

tion of grid cells when potential distributions occupy only small parts of large grids. Therefore, we 'created' two species with distinct ranges and equal small range sizes of 1000 sections fixed left and right from the middle of the grid with 5000 grid cells between them. The simulation starts with a 1-D grid length of 10,000 grid cells, which was subsequently increased in steps of 50,000 grid cells up to a final length of 1,010,000 grid cells. Using three different settings, only the magnitude of the background noise in areas which can be classified as absence (e.g. applying the minimum training presence threshold) was changed (first run: median value of absence in salamander species pair 2 = 0.00018; second run: values randomly extracted from the pool of

**Table 2** Model performance in terms of test area under the receiver operating characteristic curve (AUC), presence-absence thresholds and fraction of the study area characterized as unsuitable in three sister pairs of plethodontid salamanders. The corresponding models are shown in Fig. 1.

Species	AUC <sub>test</sub>	Min train	% unsuitable	10% train	% unsuitable
<i>Plethodon cylindraceus</i>	0.947	0.031	68.6	0.254	91.9
<i>P. teyahalee</i>	0.940	0.005	37.8	0.220	91.4
<i>P. hubrichti</i>	0.987	0.071	98.0	0.375	99.6
<i>P. nettingi</i>	0.993	0.133	95.7	0.252	97.6
<i>P. punctatus</i>	0.990	0.086	98.6	0.210	99.5
<i>P. wehrlei</i>	0.870	0.042	38.9	0.177	75.0

Min train = minimum training presence; 10% train = lowest 10th percentile training omission.

**Table 3** Niche overlaps of three sister species pairs of salamanders in geographic (G-) space computed with Bray–Curtis distances *BC*, Schoener's *D*, a modified Hellinger distance *I*, Pianka's *O* and Horn's *R* and in environmental (E-) space determined in 1000 replications of a linear discriminant analysis (LDA) based on a principal components analysis (PCA). In the LDA, 70% of the records were used for model training and 30% for model evaluation. As presence-absence thresholds, the minimum training presence (min train) and the lowest 10th percentile training omission (10% train) were used. For threshold values see Table 2.

Species pair	Threshold	Overlap metric (G-space)						PCA/LDA overlap (E-space)	
		<i>BC</i>	<i>D</i>	<i>I<sub>mod</sub></i>	<i>I<sub>cor</sub></i>	<i>O</i>	<i>R</i>	Mean	SD
Pair 1	None	0.4052	0.4052	0.6084	0.6823	0.4465	0.6137	0.3763	0.0253
	Min train	0.3546	0.3546	0.5425	0.5825	0.4228	0.5327		
	10% train	0.2250	0.2250	0.3999	0.2799	0.2537	0.2758		
Pair 2	None	0.0588	0.0588	0.3799	0.2310	0.0360	0.1447	0.0000	0.0000
	Min train	0.0004	0.0004	0.2931	0.0004	0.0002	0.0004		
	10% train	0.0000	0.0000	0.2929	0.0000	0.0000	0.0000		
Pair 3	None	0.2175	0.2175	0.4886	0.4769	0.2653	0.3816	0.3178	0.1092
	Min train	0.0440	0.0440	0.3657	0.1953	0.2013	0.1229		
	10% train	0.0254	0.0254	0.3487	0.1516	0.1551	0.0828		

the same absence values). This allowed us to simulate small probability variations as present in areas of low occurrence probabilities in SDMs. In the last run, the outside occurrence probability was set to zero to create a null model.

## RESULTS

### Salamander SDMs

On average we received 'good' to 'excellent' test AUC values in our models (Table 2). Predicted potential distributions match the known ranges of the species (Fig. 1) when applying the 'minimum training presence' or the 'lowest 10th percentile training omission' as presence-absence thresholds. It classified a varying but generally high proportion of the grids as unsuitable (Table 2). The two sister species *P. cylindraceus* and *P. teyahalee*, and with roughly equal-sized potential distributions, showed a remarkable overlap in E-space (Fig. 1a, Table 3). Applying the six niche overlap indices, the results suggest a moderate (*O*, *D*, *BC*) to high (*I<sub>mod</sub>*, *I<sub>cor</sub>*, *R*) niche overlap in G-space (Table 3). The second species pair *P. hubrichti* and *P. nettingi* occupying distinct, not overlapping, potential distributions is well separated in E-space (Fig. 1b) which was correctly identified by most

metrics indicating no to very low overlaps (Table 3). Only the modified Hellinger distance *I<sub>mod</sub>* suggested a much higher overlap. Niche overlap metrics performed differently in our third example, comprising one species posing a large potential distribution and one with a small potential distribution. Values of three metrics were rather alike (*O*, *D*, *BC*) wherein three suggest high to much higher values (*R*, *I<sub>mod</sub>*, *I<sub>cor</sub>*; Table 3). Application of presence-absence thresholds reduced the niche overlap in G-space across all metrics in all species (Table 3).

### Simulations of varying distribution patterns

In order to detect possible performance differences between niche overlap metrics, we simulated varying degrees of overlaps of potential distributions in G-space using artificial species. In Simulation A varying degrees of niche overlap were illustrated in two species with identical niche breadths. Five (*BC*, *D*, *I<sub>cor</sub>*, *O*, *R*) of the six indices correctly suggested overlap values of 0 when the potential distributions were not overlapping at all. The overlap values computed with the modified Hellinger distance were higher (*I<sub>mod</sub>* = 0.29), however (Fig. 2a). With increasing spatial overlap of the simulated potential distributions, values computed with all overlap indices increased and reached a value



of 1 at complete overlap. However, while  $BC$ ,  $D$ ,  $I_{\text{cor}}$ ,  $O$  and  $R$  values linearly increased, a nonlinear increase was detected when using the modified Hellinger distance  $I_{\text{mod}}$  (Fig. 2a).

When comparing niche overlaps among one species with a spatially restricted potential distribution and one exhibiting a spatially more extended potential distribution (Simulation B), a similar picture becomes evident as in Simulation A (Fig. 2b). Again, in the absence of relevant spatial overlap, all except the modified Hellinger distance  $I_{\text{mod}}$  indicate a niche overlap of 0. However, different maximum niche overlap values with increasing spatial overlap were detected ( $BC_{\text{max}} = 0.31$ ,  $D_{\text{max}} = 0.31$ ,  $R_{\text{max}} = 0.39$ ,  $O_{\text{max}} = 0.45$ ,  $I_{\text{mod, max}} = 0.53$ ,  $I_{\text{cor, max}} = 0.47$ ).

When two potential distributions are nested but one species differs in the absolute size of the potential distribution (Simulation C), maximum overlap values decrease differently with increasing potential distribution sizes using the five niche overlap indices (Fig. 2c). With increasing spatial extent of the species' potential distribution,  $I_{\text{mod}}$  suggested the highest niche overlap among the five indices and  $D$  the lowest.

### Simulation of varying grid sizes

Artificial extension of the grid size had varying impacts on niche overlaps computed with the six metrics (Fig. 3). Pianka's  $O$  was most error prone by constantly producing values near 0 when introducing both constant background noise and a random selection of background values (Fig. 3a,b). As in the former simulations,  $D$  revealed exactly the same results as  $BC$ , and fairly similar results to  $R$  in the first run but considerably lower values in the second run. Niche overlaps computed with  $I_{\text{mod}}$  were never lower than 0.29 and were moderately affected by increasing grid size. With the exception of  $I_{\text{mod}}$ , all metrics correctly suggested no overlap when assigning a value of 0 outside the potential distributions (Fig. 3c). This means that the derived niche overlaps actually measure the overlap of the likely occupied Grinnellian niches.

## DISCUSSION

### Performances of metrics

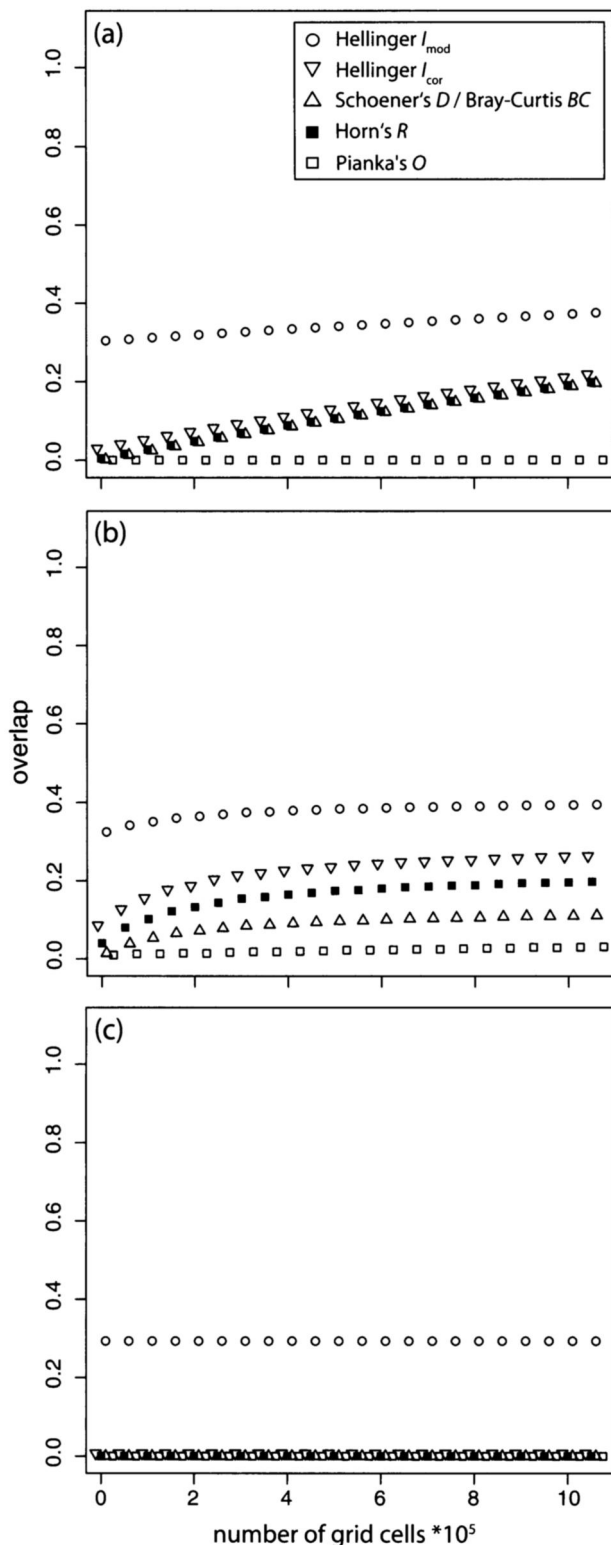
Our results revealed varying performances of niche overlap metrics when applied to real or simulated species pairs. Quality criteria for niche overlap metrics were an easily interpretable range from 0 (no overlap) to 1 (two potential distributions are identical) with a linear slope. Simulations A and B suggested that all metrics except one fulfil the former criterion. Only the range of  $I_{\text{mod}}$  is restricted to a fraction of the optimal 0 to 1 range as evident in all our simulations (Figs 2 & 3). Similar patterns are detectable when comparing the salamander species and in other previously published studies (e.g. Warren *et al.*, 2008; Rödder & Lötters, 2009, 2010; Jakob *et al.*, 2010). Mathematically,  $I_{\text{mod}}$  does not reach the zero minimum since the term  $\sum_i (\sqrt{p_{x,i}} - \sqrt{p_{y,i}})^2$  cannot exceed 2 when both potential distributions are completely distinct in G-space. Hence,  $I_{\text{mod}}$  can only reach a minimum of 0.2928932.

The linear slope quality requirement was fulfilled when using five (i.e.  $BC$ ,  $D$ ,  $I_{\text{cor}}$ ,  $R$ ,  $O$ ) of the six indices, but violated when applying the modified Hellinger distance  $I_{\text{mod}}$  (Fig. 2a). This may especially cause problems when using niche overlap values for further analyses. For example, Diniz-Filho *et al.* (2010) proposed a local version of Mantel tests among niche overlap matrices and phylogenetic distance matrices to test for varying patterns of niche conservatism. For such tasks, a linear slope of niche overlap values and an insensitivity of the metric used towards varying potential distribution sizes are most important to derive comparable overlap values for different species pairs. As our Simulations B and C indicate, the latter requirement is not met using all of the tested metrics. This means that when using these metrics, the results of any niche conservatism analyses can be affected by the bias.

As indicated by Simulation B (Fig. 2b),  $I_{\text{mod}}$ ,  $I_{\text{cor}}$ ,  $R$  and  $O$  deviate from the percentage overlap of two potential distributions, probably leading to problems when interpreting results. While  $I_{\text{mod}}$ ,  $I_{\text{cor}}$  and  $R$  strictly overestimate the extent to which two potential distributions with different sizes overlap,  $O$  may switch from overestimation to underestimation when percentage overlap becomes very small (e.g. as evident in salamander species pair 2; Fig. 1b, Table 3). These patterns were also described in previous studies, e.g. by Bloom (1981) analysing the modified Morisita index, which is mathematically similar to  $O$ . Therefore, the same result also becomes evident for  $O$  (Bloom, 1981). The application of either of these indices in comparing SDM outputs may therefore cause biased results.

The observed performance differences of the algorithms may also affect statistical tests. In the past, using the randomization tests for 'niche identity' and 'niche similarity' as implemented in the ENM-tools introduced by Warren *et al.* (2008)'s application of  $D$  and  $I_{\text{mod}}$  sometimes resulted in contradictory results (e.g. Rödder & Lötters, 2009, 2010; Jakob *et al.*, 2010). In these tests null distributions are created by either pooling the species records of two species (niche identity test of Warren *et al.*, 2008) or replacing the records of one species by random records within the general extent of its distribution (background test of Warren *et al.*, 2008). Our Simulations B and C suggest that differences in suggested overlap values among algorithms may occur when comparing potential distributions exhibiting large size differences. In extreme cases, these randomizations may lead to largely varying sizes of potential distributions translating in biased overlap estimates. This probably affects the null distributions of the significance tests when using inappropriate metrics.

Two metrics,  $D$  and  $BC$ , both reflect accurately the extent to which the potential distributions of two species overlap in G-space and show at the same time the best resolution, allowing us to distinguish even small differences (Fig. 2). However, both indices have been criticized because they may be sensitive to bias when sample sizes available for two species are different (Kohn & Riggs, 1982; Smith & Zaret, 1982). Fortunately, these formerly detected pronounced differences can be ignored herein due to the equal extents of output grids in SDMs. According to our results, both metrics are best suited for quantitative comparisons of SDM predictions.



**Figure 3** Impact of varying grid sizes on niche overlap measurements. Background noise outside the potential distribution of an artificial species delimited by application of presence-absence thresholds was simulated either by the median occurrence probability outside the potential distributions of salamander species pair 2 throughout all grid cells (a) or values were randomly extracted from the pool of these occurrence probabilities (b). In panel (c), all grid cells outside the potential distribution of the artificial species were set to zero.

### Impacts of varying grid sizes

Extending the size of the study area had moderate to very strong impacts on niche overlaps computed with the six metrics (Fig. 3). Our simulations indicate that all overlap metrics may suggest higher overlap values when increasing the number of grid cells with very low probability values. Using the absolute differences of the probability values, the metrics correctly classify these grid cells as 'very similar'. This is because the actual probabilities in the cells are very close to each other. However, this effect strongly depends on the variation in the background noise in both samples compared, with lower variation leading to higher overlap values (compare Fig. 3a and b). The problem here is that higher overlap values are derived from regions where the species are most likely absent. By excluding these regions, it is possible to compare only those parts where the species are likely to occur and, hence, only those environmental conditions which they are likely to be exposed to. Applying the minimum training presence, or the lowest 10th percentile training omission, as presence-absence thresholds and setting the corresponding grid cells to 0 eliminates the described bias (Fig. 3c). This was previously suggested by Liu *et al.* (2005) and Phillips *et al.* (2006). These overlaps do more correctly reflect the similarity of occupied niches than comparisons of those areas where both species are most likely absent. Therefore, a pre-processing of SDM outputs as proposed above before computing niche overlaps is highly recommended.

### Comparisons with other approaches

#### E-space versus G-space

Various methods have been suggested to quantify niche overlaps in both E- and G-space. Next to niche overlap analyses via SDM approaches (e.g. Peterson *et al.*, 1999; Warren *et al.*, 2008) or niche occupancy profiles derived from SDM predictions (Evans *et al.*, 2009), species niches can be compared in E-space (i.e. using PCA; Knouft *et al.*, 2006; Broennimann *et al.*, 2007), the outlying mean index (OMI) derived from multivariate analyses (Dolédec *et al.*, 2000) or multidimensional convex hulls (Dormann *et al.*, 2010). Both general strategies have advantages and disadvantages.

Comparing species niches in E-space allows us to consider each combination of niche dimensions only once. This may provide an unbiased estimation of niche overlap with regard to the representation of niche properties in the potential niche (Dormann *et al.*, 2010) being close to Hutchinson's (1957, 1978) original definition of the niche as a multidimensional hypercube in E-space. On the other hand, it can also be argued that exactly these multiple representations of unique combinations of niche axes in geographic space would allow a quantification of the number of grid cells possessing specific selective conditions. Hence, from an evolutionary point of view, inclusion of the relative numbers of grid cells exhibiting certain environmental properties as a weighting factor may help to quantify the spatial extend of those conditions affecting most of the populations of the studied species.

Comparisons of environmental niches in E-space giving an equal weight to each combination of environmental features greatly increase the importance of outliers. Theoretically, species records that are situated outside the fundamental niche of the target species due to source–sink dynamics (see Pulliam, 2000) may cause a much stronger bias in analyses in E-space than they would in G-space using SDM predictions as proxies. An extreme scenario illustrating this potential error source would be a determination of overlaps via minimum convex polygons enclosing each species' records in E-space using a PCA as proposed by Knouft *et al.* (2006). This approach may be especially sensitive to such bias, since polygons may be greatly increased when including outliers. Note that overlap assessments in E-space were also criticized, as some variable combinations thinkable in E-space may actually not occur in G-space (Warren *et al.*, 2008). Using SDM predictions as proxies for niche overlap analyses, the impact of outliers would be reduced by assigning low occurrence probabilities to them.

Dormann *et al.* (2010) proposed to project a SDM onto a regular multidimensional raster in E-space, which is clipped to contain only those climatic combinations which are actually available in G-space, and to subsequently compute overlaps of the resulting multidimensional convex hulls. This method addresses possible problems caused by spatial clamping of records in E-space. This becomes clear by considering that, although the number of elements of both G-space and E-space may be the same given that each grid cell is characterized uniquely, both spaces may have a vastly different topology. Imagine a geographic grid with each element (i.e. grid cell) being uniquely characterized by environmental dimensions. Although each grid cell in G-space corresponds to one element in E-space, the density of elements may show spatial aggregations representing more common environments in G-space. Hence, although grid cells in G-space are regularly spaced, the E-space may be very anisotropic leading to similar over-representations of certain environmental combinations as when assessing overlaps directly in G-space. This will create major differences in measures of niche properties and niche overlaps when performed in E-space or in G-space.

In a similar vein to Dormann's approach, PCs of the environmental data can be used independently from SDMs for the calculation of overlaps in E-space through the application of a constrained ordination procedure like linear discriminant analysis, as shown herein. These two approaches overcome previous shortcomings, wherein the latter approach is much less computationally insensitive than the former. However, to reach a final conclusion, studies explicitly assessing differences in niche overlaps computed in E- and G-space are needed.

#### *Univariate versus multivariate comparisons*

Overlaps in environmental niches can be assessed in univariate (Evans *et al.*, 2009; Rödder & Lötters, 2009, 2010) or multivariate space (Warren *et al.*, 2008; Medley, 2010). The clear advantage of the latter approach is that multidimensionality can be reduced, facilitating the identification of patterns. On the other

hand, the influence of each niche axis cannot be as easily extracted as in the former approach. This requires that the selection of predictors with focus on those being biologically important for the target species has been carefully made (Rödder *et al.*, 2009). Furthermore, comparisons of SDMs developed with multiple parameters bear the risk that models become too complex (Elith *et al.*, 2010), hampering their transferability in G-space (Rödder & Lötters, 2010). This results in artefacts when assessing the degree of niche overlap due to extrapolation errors when projecting outside the calibration range or possible changes in the correlation matrix among predictors in G-space (Heikkinen *et al.*, 2006; Anderson & Raza, 2010; Rödder & Lötters, 2010).

#### **Conclusions and future challenges**

Concluding, our results imply that Schoener's *D* and the Bray–Curtis distance *BC* may be best suited to compute niche overlaps in G-space based on SDM results, wherein pre-processing with elimination of low occurrence probabilities is highly recommended to achieve unbiased results. Integration of niche overlaps with phylogenetic data covering large species groups will remain a delicate task, however. Several methodological issues will require additional attention in the future, especially the question whether niches are better compared in E- or G-space. Using SDM predictions for comparison questions of model transferability in G-space needs to be addressed, because projections onto conditions outside the calibration ranges are pivotal with increasing sizes of the study area. This may cause severe problems using one or other of the algorithms (Heikkinen *et al.*, 2006; Anderson & Raza, 2010; Rödder & Lötters, 2010). It makes the selection of appropriate algorithms a pivotal task. Uncertainties related to model selection can also be reduced when using ensemble forecasts as suggested by Araújo & New (2007) and selecting predictors describing physiologically relevant parameters for the species at hand (Rödder *et al.*, 2009).

Furthermore, when interpreting niche overlaps, it should be assessed whether overlaps of fundamental niches, realized niches or something intermediate is being measured. Depending on the question at hand, the identification of these different possibilities will be pivotal for deriving valid conclusions. As previously stated, the part of the niche captured by SDMs depends on the methods and data analysed (Jiménez-Valverde *et al.*, 2008; Soberón & Nakamura, 2009): presence–absence methods are likely to capture a species' realized niches by incorporating indirectly effects of both dispersal limitations and biotic interactions, presence-only and presence–pseudoabsence methods tend to characterize the species' potential distribution. The latter group of algorithms, including MAXENT among others, may therefore be the best choice for assessing patterns of niche conservatism.

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