

ORIGINAL CONTRIBUTION

Species distribution models for the alien invasive Asian Harlequin ladybird (*Harmonia axyridis*)

K. Bidinger, S. Lötters, D. Rödder & M. Veith

Department of Biogeography, Trier University, Trier, Germany

Keywords

bioclim, fundamental niche, intraspecific niche variation, Maxent, model transferability, potential distribution, realized niche

CorrespondenceKerstin Bidinger (corresponding author),
Department of Biogeography, Trier University,
54286 Trier, Germany.
E-mail: bidi1101@uni-trier.deReceived: September 8, 2010; accepted:
November 9, 2010.

doi: 10.1111/j.1439-0418.2010.01598.x

Abstract

The Asian Harlequin ladybird (*Harmonia axyridis*) is a globally invasive alien species. We developed species distribution models (SDMs) aiming at an explanation of the observed native and invasive distributions and the prediction of the species' potential distribution. SDMs were built based on bioclim parameters with Maxent (i) on known native occurrence only (SDM_{nat}), (ii) on known European invasive occurrence only (SDM_{inv}) and (iii) by combining both previous approaches (SDM_{all}). Results indicate that SDM_{inv} match the observed European invasive range better than SDM_{nat} or SDM_{all}. The origin of Asian founders in Europe remains unknown. SDM_{inv} highlighted a restricted area in China which may represent the region of origin of the European Harlequin ladybird, leaving the possibility of within-species climate niche variation. As a result, when targeting the worldwide potential of invasiveness of *H. axyridis*, SDM_{all} may reveal maximum results uncovering the species' potential distribution. These results have to be seen in the framework of conceptual problems and pitfalls when generating SDMs including niche definition, niche shift, sampling bias, biological importance of predictors and model transferability uncertainties.

Introduction

Invasive alien species are of major concern in conservation biology, agriculture and for the human society, as they may successfully compete with native species, negatively influence crop production and cause health problems (e.g. Mack et al. 2000; Mooney and Cleland 2001; Nentwig 2008; Davis 2009). One of the 'worst' invasive alien species, in particular in North America and western Europe, is the Asian Harlequin ladybird, *Harmonia axyridis* (Pallas) (Delivering Alien Invasive Species In Europe, <http://www.europe-aliens.org/>, accessed 5 July 2010; IUCN Invasive Species Specialist Group, <http://www.issg.org>, accessed 18 August 2010). It was introduced into European greenhouses in 1982 from an unknown locality in China for biological pest control (Ongagna et al. 1993). Since the 1990s, the Harlequin ladybird has remarkably dispersed and has

established reproducing populations in the wild in at least 13 western European countries (Brown et al. 2008; Poutsma et al. 2008) (fig. 1a). Invasive *H. axyridis* are reported to negatively influence populations of native ladybirds as well as of butterflies and lacewings (Koch 2003). An economical impact has been documented for viticulture; vine can be polluted by only a few Harlequin ladybirds per litre that accidentally got into the production process. Also, human health problems caused by the beetle have been suggested including an allergic rhinoconjunctivitis to the yellow-orange body fluid of *H. axyridis* (Koch 2003 and references therein; Van Lenteren et al. 2008).

Correlation-based species distribution models (SDMs), processing ecological information at known species' presence, are a helpful tool for a better understanding and management of invasive alien species (e.g. Peterson and Vieglais 2001; Jeschke and

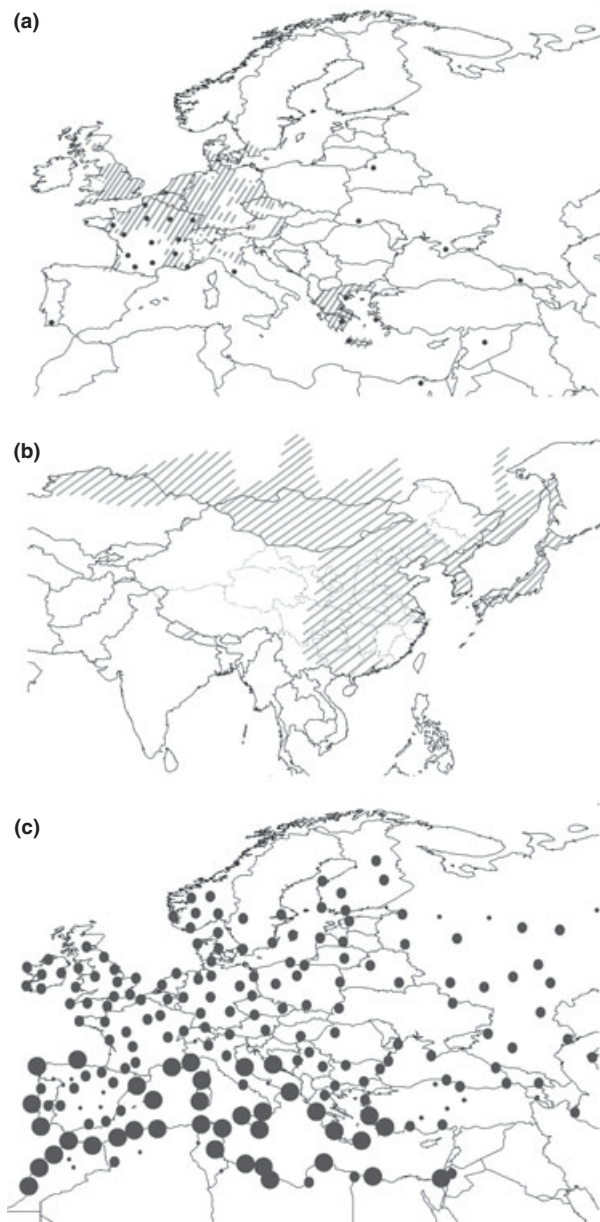


Fig. 1 Distributions of the Harlequin ladybird: (a) known invasive range in Europe (hatched) with localities of known releases (dots) (after Brown et al. 2008; Burgio et al. 2008; Poutsma et al. 2008; <http://www.gbif.org>; <http://www.europe-aliens.org/>; http://pagesperso-orange.fr/vinc.ternois/cote_nature/Harmonia_axyridis/; <http://www.harlequin-survey.org/#>; http://www.inbo.be/content/page.asp?pid=EN_FAU_INS_LAD_DIS_start; <http://www.cabi-e.ch/harmonia/deutch.html>; all accessed 15 July 2010); (b) known native range in Asia including areas of supposed occurrence, especially in the northern regions (after Koch 2003; Komai et al. 1950; Poutsma et al. 2008); (c) illustration of the results of the CLIMEX European distribution model of Poutsma et al. (2008): fig. 6) with larger items indicating higher suitability.

Strayer 2008; Bomford et al. 2009). They can be used to determine species' spatial native and invasive delimitations (i.e. the potential distribution), possible dispersal routes and overlap with native species, both in geographical and ecological space (e.g. Peterson and Vieglais 2001; Jeschke and Strayer 2008). However, their reliability depends on a detailed knowledge on the target species' ecology, as demonstrated by Rödder and Lötters (2009) and Rödder et al. (2009). Also the ecological niche concept behind SDMs, especially the distinction between the realized and fundamental niches (Hutchinson 1978; Soberón and Peterson 2005; Soberón 2007), are essential towards successful modelling. Commonly, SDMs capture only part of both the species' realized and fundamental niches and their transferability into another space may be affected by uncertainties. Furthermore, the climatic properties of a species' realized niche may locally differ due to differences in limiting ecological factors. Hence, different parts of the species' fundamental niche may be realized in different areas (Soberón and Peterson 2005; Soberón 2007; Rödder and Lötters 2010). Further difficulties may be related to uncertainties when projecting SDMs into different ecological spaces with varying correlation matrices among predictors or values outside the calibration range of the model (e.g. Peterson and Nakazawa 2008; Fitzpatrick and Hargrove 2009). Moreover, shifts of the species' niche may occur outside its native range (Broennimann et al. 2007; Fitzpatrick et al. 2007, 2008; Pearman et al. 2008; Medley 2010).

Poutsma et al. (2008) developed a worldwide climate-based SDM for the Harlequin ladybird based on climatic parameters recorded at meteorological stations within its native Asian distribution (i.e. from Russia to southern China and from the Altai mountains to Japan; fig. 1b). The derived potential invasive distribution in Europe identified highest climatic suitability in southern Europe. This does not meet the situation observed in the wild, however, as in southern European countries only few Harlequin ladybird populations have established despite multiple releases (fig. 1a). In contrast, more northern regions of western Europe, in which *H. axyridis* actually has established reproducing populations, were suggested to be less suitable in the SDM of Poutsma et al. (2008) (fig. 1c). Different 'pitfalls' may explain the mismatch including the little studied CLIMEX modelling approach used by Poutsma et al. (2008), e.g. sample bias or ecological parameter choice for model building (e.g. Rödder et al. 2009; Franklin 2010). Another problem are SDM transferability

uncertainties due to possible niche shifts during biological invasion or within-species differences in the fundamental niche among populations (Rödder et al. 2009; Franklin 2010; Rödder and Lötters 2010).

With the goal to further investigate predicted potential and observed distributions of *H. axyridis* in Europe, we, instead of using climate data from meteorological stations all over the suggested native range and so ignoring regional climate conditions, developed SDMs using laminary 'bioclim' parameters. These are more suitable when creating SDMs as they are independent from latitudinal influence to climate (Busby 1991; Beaumont et al. 2005). Model building was performed with the widely used Maxent software (e.g. Elith et al. 2006; Elith and Leathwick 2009; Mateo et al. 2010), a machine-learning algorithm applying the principles of maximum entropy as described by Jaynes (1957). The reliability of the SDM results obtained via Maxent models has been confirmed by its good capacity to predict novel presence localities when geographic sampling is poor (Pearson et al. 2007) and the outcome of introductions of invasive alien species outside the native range (Peterson and Vieglais 2001; Rödder et al. 2008; Rödder 2009; Rödder and Lötters 2009, 2010). Also Maxent is a presence-only approach working with background pseudo-absence instead of observed absence. This is recommended when assessing potential distributions (Elith et al. 2010; Franklin 2010). To also address the potential problem of model transferability as a result of niche shift or within-species differences in the fundamental niche we developed different SDMs from *H. axyridis*. In this study we compare SDMs (i) based on native records only, (ii) based on invasive European records only and (iii) based on combined known native and European invasive records. In a subsequent step, we project SDMs onto the entire world to appreciate the global risk emanated from the Harlequin ladybird.

Materials and Methods

Presence records of *H. axyridis* were compiled from Burgio et al. (2008), Komai et al. (1950), Poutsma et al. (2008) and online sources (<http://www.gbif.org>; http://pagesperso-orange.fr/vinc.ternois/cote_nature/Harmonia_axyridis/; <http://www.harlequin-survey.org/#>; http://www.inbo.be/content/page.asp?pid=EN_FAU_INS_LAD_DIS_start; <http://www.cabi-e.ch/harmonia/deutch.html>; latest accessed 20 July 2010). For georeferencing, DIVA-GIS 7.1.6 (Hijmans et al. 2001; <http://www.diva-gis.org>, downloaded 1 October 2009), the Global Gazetteer, version 2.2

(<http://www.fallingrain.com/world/>, accessed 20 January to 20 February 2010) and the BioGeoMancer (<http://bg.berkeley.edu/latest/>, accessed 20 January to 20 February 2010) were used. Accuracy of coordinates was assessed with DIVA-GIS.

Of the 231 records, 60 were situated in the native range and 171 were attributed to invasive alien populations in Europe (Appendix 1); suitable New World records were not available. Likewise, the suggested Asian natural distribution (fig. 1b after Komai et al. 1950; Koch 2003; Poutsma et al. 2008) is poorly reflected within our samples. Moreover, presence records *a priori* were not spatially well concerted, leaving the problem of sample selection bias likely violating SDM assumptions (e.g. Dormann et al. 2007). To account for this, we extracted all bioclim values at records with DIVA-GIS and performed a cluster analysis based on Euclidean distances in climate space with Addinsoft XLSTAT 2009 (<http://www.xlstat.com>, downloaded 6 May 2009). The final data set comprised 40 classes for native SDMs (SDM_{nat}), 85 for the European invasive SDMs (SDM_{inv}) and 100 for the approach combining known native and invasive occurrences (SDM_{all}). When the number of records in one class was >1, a single record was randomly chosen and used for further model computation.

Using DIVA GIS, we generated 19 bioclim parameters (Beaumont et al. 2005) in the manner of Busby (1991). For this, the WorldClim version 1.4 data set was used, which is based on weather conditions recorded 1950–2000 and subsequently interpolated to a grid cell resolution of 2.5 arc minutes (Hijmans et al. 2005; <http://www.worldclim.org>, downloaded 23 October 2009).

Multicollinearity among ecological predictors may hamper the transferability of SDMs over space (Heikkinen et al. 2006). To address this issue, we computed a pair-wise Pearson correlation matrix with XLSTAT using bioclim values at all occurrences of *H. axyridis* in Asia and Europe. This way, we identified highly correlated parameters ($R^2 > 0.75$), of which the expectedly less informative one was always removed. Ten remaining bioclim parameters, best describing the availability of water and energy, were subsequently processed: 'annual mean temperature' (BIO 1), 'isothermality' (i.e. mean monthly temperature range/temperature annual range * 100) (BIO 3), 'maximum temperature of the warmest month' (BIO 5), 'minimum temperature of the coldest month' (BIO 6), 'temperature annual range' (BIO 7), 'mean temperature of the wettest quarter' (BIO 8), 'mean temperature of the driest quarter' (BIO 9),

'precipitation seasonality' (BIO 15), 'precipitation of the wettest quarter' (BIO 16) and 'precipitation of the driest quarter' (BIO 17).

To test whether *H. axyridis* populations exploit the entire available bioclim range in their native and alternatively their invasive range or if they realize just part of it, we created box plots of the 10 input bioclim parameters in three different ways based on (i) Maxent model output statistics with regard to the variable contributions for each model run; (ii) bioclim data extracted with DIVA-GIS from *H. axyridis* records in Europe and Asia; (iii) climate conditions at randomly chosen points in the background areas used for model building. For the last mentioned, bioclim values at 1 000 randomly chosen points were extracted with the Hawth's Tool for ArcMap (<http://www.spatial ecology.com/htools>, downloaded 15 September 2009).

Maxent 3.3.1 (Phillips et al. 2006; <http://www.cs.princeton.edu/~shapire/maxent>, downloaded 1 February 2010) was used for SDM processing in order to assess the worldwide potential distribution of *H. axyridis* or its particular geographic subsets. Default settings with automatic 'clamping' were used and, as suggested by Phillips and Dudík (2008), the logistic output format (suitability values ranging 0–1, i.e. unsuitable to optimal) was applied. In each model run, 10 000 random background points were automatically taken as pseudo-absence from within an area covering and including the native and invasive records, respectively (Mateo et al. 2010). Due to the sample bias in the species' native geographic range, no minimum convex polygon could be used in Asia to define the spatial extent of suitable background. Hence, for comparability in Europe and Asia, rectangular boxes were drawn around the known ranges, including the presence points, as boundaries for model backgrounds. The box in Europe was used as the background for SDM_{inv} and likewise that in Asia for SDM_{nat} . For the model generated with all known records from Asia and Europe (SDM_{all}), we used the combined backgrounds of SDM_{inv} and SDM_{nat} . Coordinates of the remaining species localities were used as presence records for model computation and the remaining bioclim parameters as climate data.

Maxent allows for model testing by calculation of the area under the curve (AUC), referring to the receiver operation characteristic curve (ROC) (Hanley and McNeil 1982; Heikkinen et al. 2006; Nemes and Hartel in press). For this purpose, 25% of the input species records were randomly set aside as test points while the remaining ones were actively involved in the modelling process for training. This

procedure was repeated 50 times and subsequently, averages of the predictions were computed for further processing. AUC as a non-parametric method is recommended in ecological studies (Pearce and Ferrier 2000). Its values range 0.5–1.0, i.e. random to perfect model prediction (Swets 1988). For further interpretation, ROC plots were generated in DIVA-GIS (note that AUC scores are slightly differently computed in Maxent and DIVA-GIS). Additionally, we present the respective sensitivity and specificity rates indicating relative omission and commission errors of the SDMs and their projections. For the calculation of the specificity rate and the ROC plots in DIVA-GIS, the Hawth's Tool was used to generate 10 000 randomly distributed pseudo-absence points within the model backgrounds, respectively. The probability values suggested by Maxent for both presence and absence points were used to compute the ratios.

Results

Exploitation of available and occupied bioclimatic ranges in SDMs

Figure 2 compares the Maxent variable contributions for each of the SDMs. Accordingly the 'precipitation of the driest quarter' (BIO17) had the highest predictive power in all SDMs, especially in the SDM_{all} . This implies that water availability during drier periods is crucial for the establishment of reproducing population in the Harlequin ladybird (see Poutsma et al. 2008). Differences in variable contributions to SDMs were related to the 'minimum temperature of the coldest month' (BIO6), the 'mean temperature of the driest quarter' (BIO9), the 'annual mean temperature' (BIO1) and 'isothermality' (BIO3).

Figure 3 shows box plots for bioclim variables generated from species localities and background points in Europe and Asia. When comparing the box plots for European invasive records to those for the native records, all of them (except BIO 17) were clearly different in value spans suggesting differences in realized niches. In addition, value spans of the native and invasive background box plots were in eight of ten cases quite different, representing different available climate conditions in Europe and Asia, respectively.

When Comparing the box plots for the bioclim parameters with the highest contributions to the model runs with the others, ranges at species records were more similar, even though the box plot ranges of the background points were quite different. This

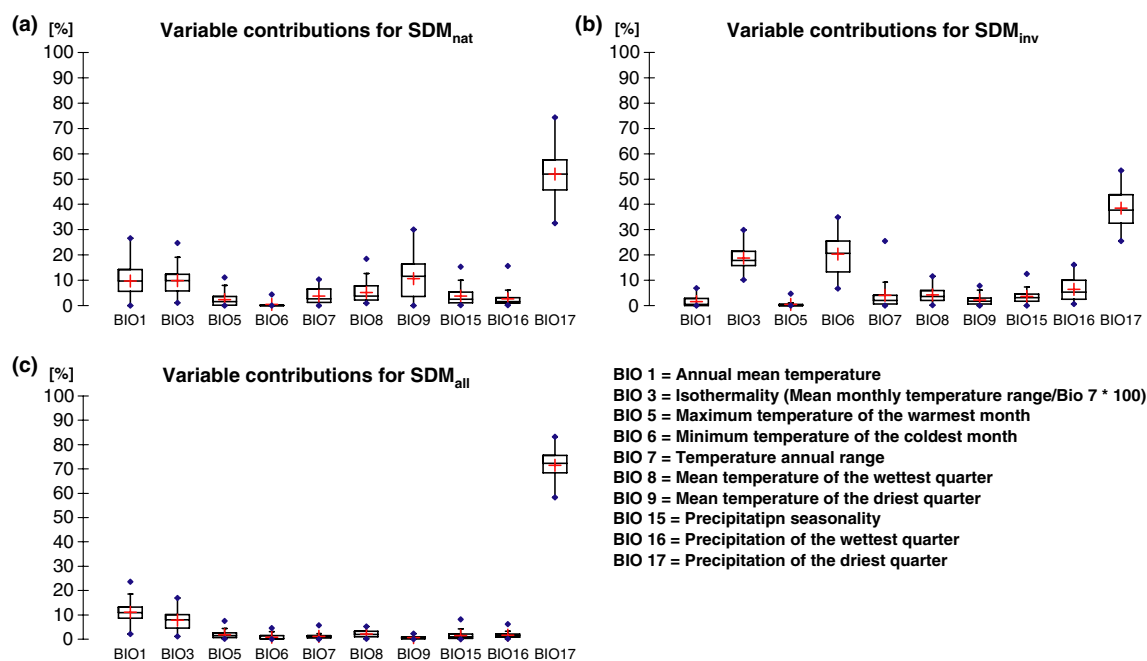


Fig. 2 Relative contributions of 10 bioclim input variables to the Maxent SDMs for (a) the model built with records from the native range in Asia (SDM_{nat}), (b) the model built with records from the invasive range in Europe (SDM_{inv}) and (c) for the model built with records from the native Asian and European invasive ranges combined (SDM_{all}).

suggests a relatively high importance of these bioclim conditions for the persistence of the Harlequin ladybird, e.g. ‘conservative’ variables (in comparison to more ‘relaxed’ variables) and active habitat choice if available climate conditions are limited (e.g. compare ‘mean temperature of the driest quarter’ (BIO9) in figs 2 and 3 for the SDM_{nat}).

In six of the ten bioclim variables, the box plots for the European invasive records fell within the range of those of the native background, but – in contrast – did not overlap with those of the native records. Furthermore, all ranges of background box plots were similar to or exceeded those of the corresponding box plots of bioclim variables at species records, despite the ‘precipitation of the driest quarter’ (BIO17). These observations reflect a bias related to the poor sampling in the Harlequin ladybird’s native Asian range, especially to the North and South-East China, as mentioned above (figs 1b and 4d).

Potential distribution in native and invasive geographic ranges based on native presence data

For the SDM_{nat} (fig. 4), we received AUCs ranging 0.82–0.99 (average 0.932) (see fig. 5 for ROC plots) and a sensitivity rate of 97.50% and a specificity rate of 25.85% (both: related to the minimum training

logistic threshold, table 1). It is noteworthy, that the known native range was not entirely predicted by the model (compare figs 1b and 4d). This is especially true for the northern parts from where exact records are sparse and hence did not influence the model building process. With regard to regions of known biological invasion, Europe was suggested to be largely suitable to *H. axyridis* (fig. 4c), including parts of the Iberian peninsula, southern Italy, some islands in the Mediterranean Sea and large parts of western Europe where the species is not invasive (fig. 1a). In North America, almost the entire invasive range was predicted as suitable (compare figs 4b and 6a), except some regions in eastern Canada, Florida, on the US West coast and Central Mexico. Regarding South-America, regions in the South-East are predicted as suitable as well as a small portion of Chile (fig. 6a).

Potential distribution in native and known invasive geographic ranges based on European invasive presence data

The SDM_{inv} (fig. 7) revealed lower AUCs as the SDM_{nat} , ranging 0.75–0.88 (average 0.82). For the corresponding ROC plots see fig. 5. A sensitivity rate of 100% and a specificity rate of 51.75%, both

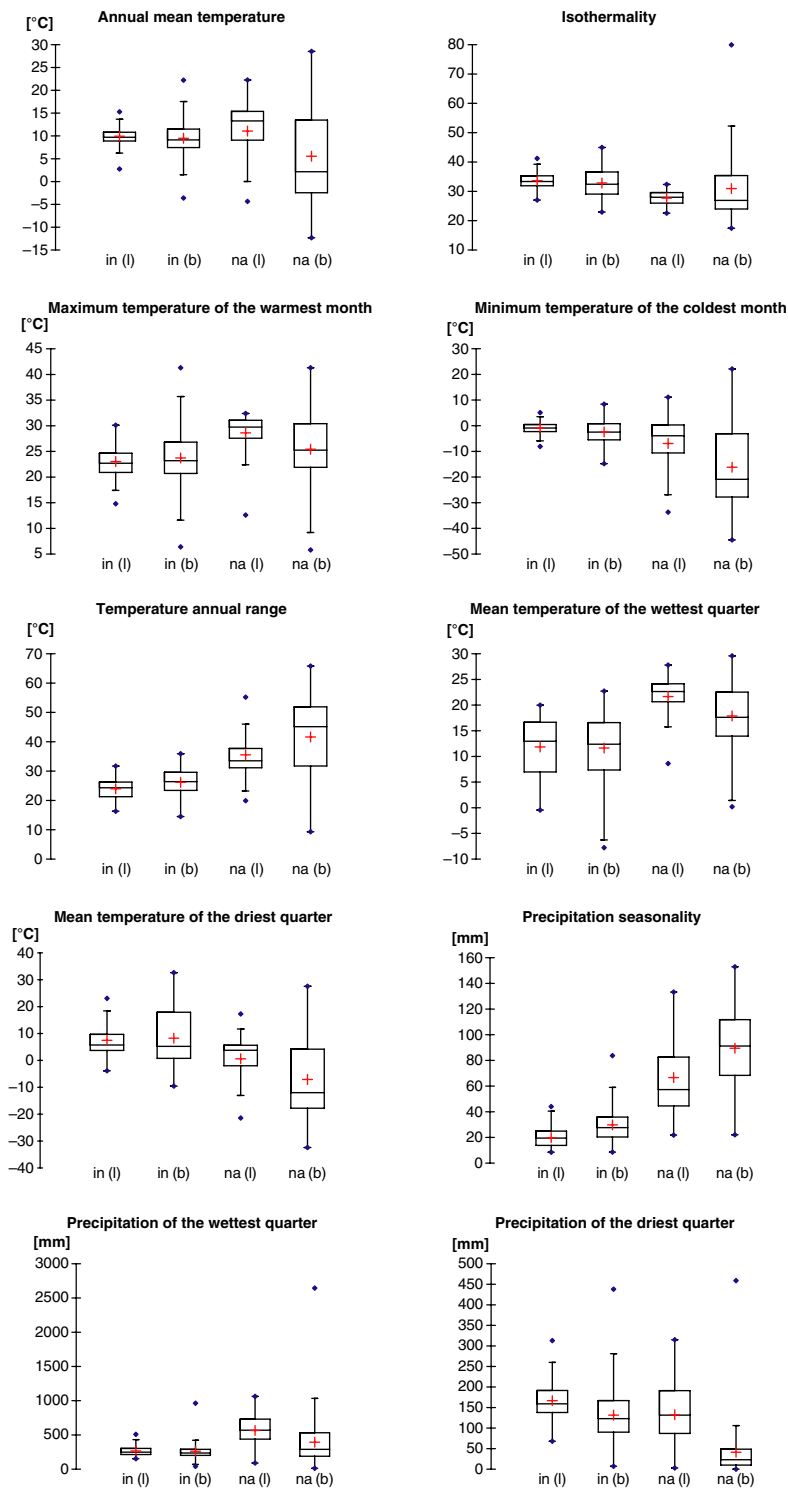


Fig. 3 Box plots for 10 bioclim input variables for SDM building based on the bioclim data extracted in DIVA-GIS, for: in (l) = invasive localities in Europe, in (b) = 1000 randomly chosen points within the European invasive background area used for model runs, na (l) = native localities in Asia, na (b) = 1 000 randomly chosen points within the Asian native background area used for model runs.

related to the minimum training logistic threshold, were reached for this SDM (table 1). As shown in fig. 7c, this SDM characterized a large portion of western lowland Europe as most suitable to the

Harlequin ladybird including much of Britain, Ireland, Benelux, France, Switzerland, Italy, Germany and adjacent parts of Czech Republic, Austria and northern Spain. In addition, the region adjacent to

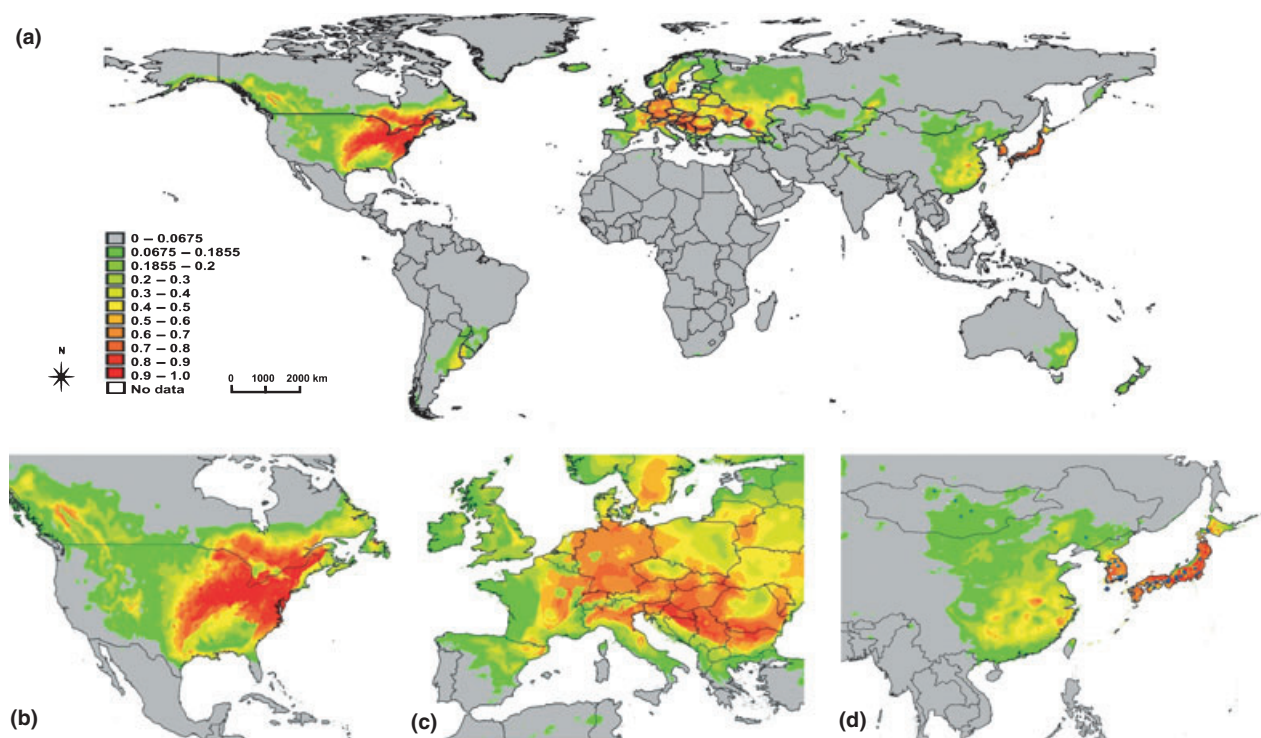


Fig. 4 (a) Mapped global output of the Maxent SDM_{nat} for the Harlequin ladybird based on bioclim parameters at records from the native Asian range, with (b) North America, (c) Europe and (d) Asia enlarged. Warmer colours suggest higher suitability to the modelled species (Phillips et al. 2006). The legend includes 'grey', indicating unsuitable areas and 'dark green' giving the value range between the minimum and the 10% training presence logistic threshold for the average input presence data; after that the modelled suitability gives 10% steps up to the value of 1 ('dark red'). Records of the study organism in the native distribution are indicated by dots; blue ones indicate the 40 residual localities used for model building after cluster analysis (see text).

the East coast of the Adriatic Sea and small areas adjacent to the Black Sea tended to be suitable to Harlequin ladybird invasions. In North America, only the East Coast was predicted to be suitable to *H. axyridis* (fig. 7b) and in South-America only parts in Uruguay. Regarding the native range in Asia, only small areas in southern China and Japan (fig. 7d) were suggested as suitable for the beetle.

Worldwide potential distribution based on all presence data

The SDM_{all} gathered AUCs with range 0.81–0.96 (average = 0.92). The related ROC plots are shown in fig. 5. This SDM uncovered a sensitivity rate of 99.00% and a specificity rate of 31.24%, which are both related to the minimum training logistic threshold (table 1). The suggested worldwide potential geographic range, i.e. spatial invasive potential, of *H. axyridis* is illustrated in fig. 8. All regions identified as suitable to the study organism in SDM_{nat} and SDM_{inv} were mapped likewise as suitable to it. Furthermore, additional regions in North America

(compare figs 4b and 7b with 8b), southern Europe and parts of northern Africa (compare Figs 4c and 7c with 8c) were identified as suitable to the Harlequin ladybird. Moreover, the area which is very likely naturally inhabited by the species in the North of Asia (Fig. 1b) and not predicted by SDM_{nat} and SDM_{inv} was included as part of its potential distribution (Fig. 8d).

Crosswise comparison of the ROC plots

Figure 5 presents the ROC plots for SDM_{nat} , SDM_{inv} and SDM_{all} including a crosswise comparison between the models. When comparing the ROC plots, it becomes obvious that the ROCs for models, evaluated with presence and absence points other than those trained with, become closer to the 'random-performance'. This is especially true for those ROCs generated for SDM_{nat} with records and background points from the invasive range. The comparative 'best' ROC plots reached the models SDM_{nat} and SDM_{all} evaluated with records and background points from the native range.

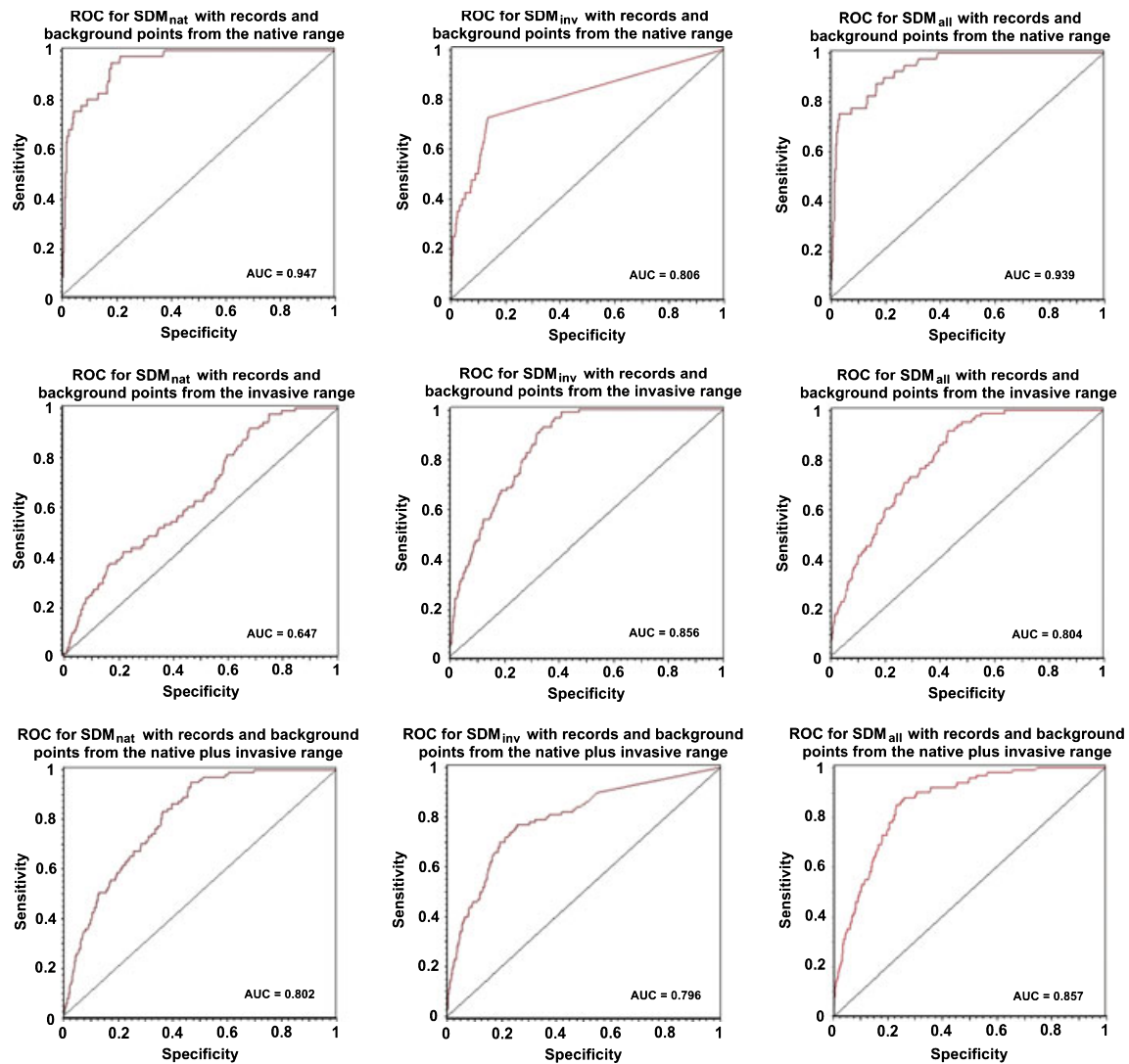


Fig. 5 Crosswise ROC plots for SDM_{nat} , SDM_{inv} and SDM_{all} based on presence (native, European-invasive and native plus European-invasive, respectively) and 10 000 pseudo-absence background points, respectively. Curves close to the diagonal line indicate a model performance close to random and curves approximating the upper left corner of the plot indicate a higher predictive power of the model.

Table 1 Sensitivity and specificity rate, e.g. omission and commission errors, for the model build with records from the native range in Asia (SDM_{nat}), the model build with records from the invasive range in Europe (SDM_{inv}) and the model build with records from the native Asian and European invasive ranges combined (SDM_{all}). Sensitivity is defined as the ratio of positive sites correctly predicted over the total number of positive sites in the sample, while specificity is the ratio of negative sites correctly predicted over the total number of negative sites

	Sensitivity (%)			Specificity (%)		
	SDM_{nat}	SDM_{inv}	SDM_{all}	SDM_{nat}	SDM_{inv}	SDM_{all}
Min	97.50	100.0	99.00	25.85	51.75	31.24
10%	82.50	87.06	88.00	86.94	68.48	70.54

The rate of specificity is based on 10 000 pseudo-absence points, generated within the background areas, respectively. The probability that this area covers locations of occurrence of the beetle is therefore not reduced to zero, leading to the opportunity that a probably higher rate of specificity may occur, which does not correspond to the quality of model output.

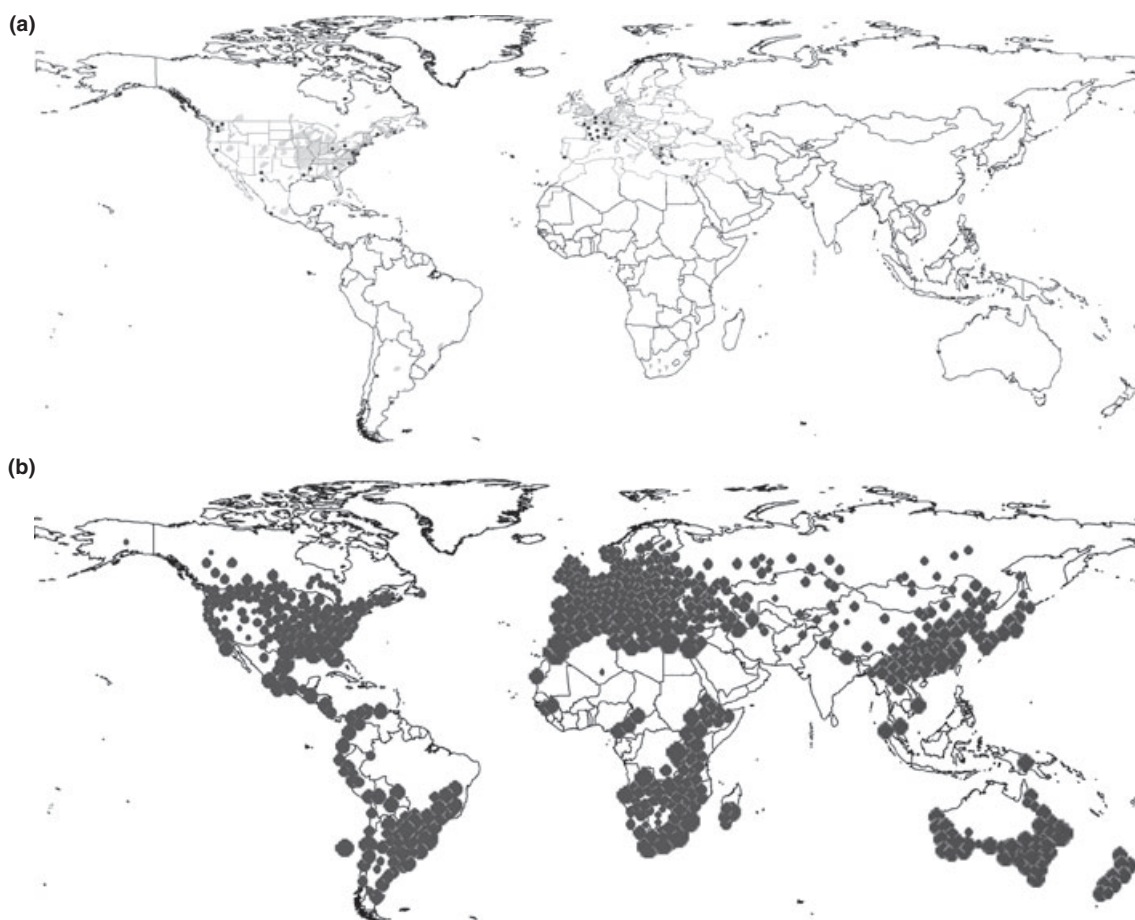


Fig. 6 (a) Worldwide invasive distribution of the Harlequin ladybird: known range (hatched), possible range (question marks) and localities plus areas of known releases (dots) (after Brown et al. 2008; Burgio et al. 2008; Poutsma et al. 2008; <http://www.gbif.org>; <http://www.europe-aliens.org/>; http://pagespersoorange.fr/vinc.ternois/cote_nature/Harmonia_axyridis/; <http://www.harlequin-survey.org/#>; http://www.inbo.be/content/page.asp?pid=EN_FAU_INS_LAD_DIS_start; <http://www.cabi-e.ch/harmonia/deutch.html>; all accessed 15 July 2010); (b) reproduction of the results of the CLIMEX global distribution model of Poutsma et al. (2008): fig. 3) with larger items indicating higher suitability.

Discussion

Our Maxent SDM_{nat} (fig. 4c) better explained the observed European invasive distribution of the Harlequin ladybird (fig. 1a) than the CLIMEX model (fig. 1c) of Poutsma et al. (2008). However, likewise to the CLIMEX approach, Maxent did not provide convincing predictions. Also the native range in Asia and the invasive North America distribution were not entirely predicted by the SDM_{nat} . Comparing the recognized European distribution of *H. axyridis* with SDM_{nat} , one may argue that the model mismatch may result from 'incomplete' biological invasion. This remains unknown. However, there is evidence that at least some regions in eastern and partly southern Europe suggested to be (highly) suitable to

the target species and SDM_{nat} in fact are unsuitable for its permanency. Here, the Harlequin ladybird had been introduced to the wild, e.g. in southern France, Belarus and Ukraine, but has not established reproducing populations (Brown et al. 2008).

In the SDM_{inv} , compared to SDM_{nat} , the known European invasive distribution was better explained leaving mismatches in middle Italy and southern France (compare figs 1a and 7c). Here, the beetle has been introduced and regions were highly suitable according to our model, but wild populations remain unknown (Brown et al. 2008). Certainly, it can be expected that a SDM for any region performs better when trained with matching regional input data than from an outside region. However, probably the explanation even goes beyond. This is discussed below.

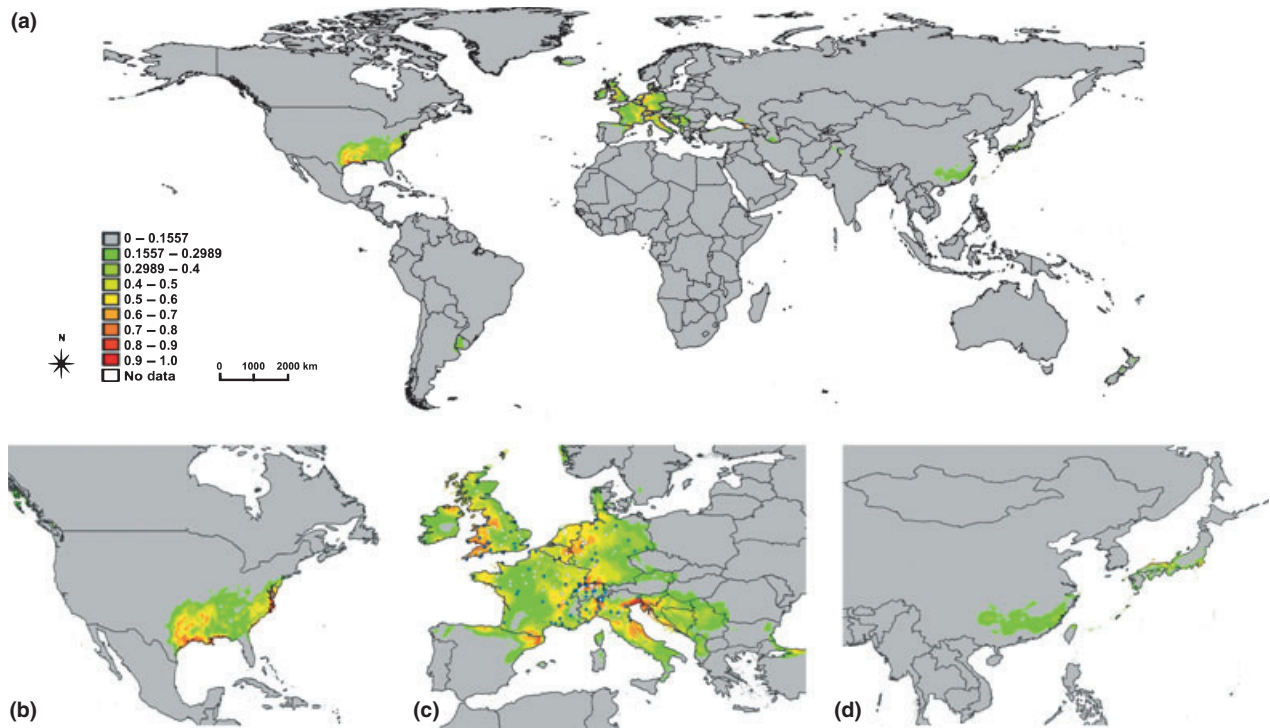


Fig. 7 (a) Mapped global output of the Maxent SDM_{inv} for the Harlequin ladybird based on bioclim parameters at records from the European invasive range, with (b) North America, (c) Europe and (d) Asia enlarged. For legend see fig. 4. Records of the target species in the European invasive distribution are represented by dots; blue indicates the 85 residual localities used for model building after cluster analysis (see text).

Sample bias (e.g. Peterson et al. 2003) may explain the mismatch between predicted and observed European distributions in both SDM_{inv} and SDM_{nat} . The realized niche of *H. axyridis* in its native distribution may not be entirely covered by the limited sample availability. At least, this may be responsible for the failure of SDM_{nat} (fig. 4d) to predict the species' northern natural range (fig. 1b). Likewise, ecological parameter choice is a crucial point steering SDM performance (Rödder et al. 2009). This is a 'chink' here, because so little is known about the biology of the Harlequin ladybird (e.g. Koch 2003). Nevertheless, a molecular genetic study by Lombaert et al. (2010), suggested that invasive alien populations in Europe originate from somewhere in Asia and eastern North America, which implies that SDM_{inv} performed well. The New World distribution of the sampling by Lombaert et al. (2010) is well predicted (fig. 3a–d). However data on the sampling localities within the native range is too vague to make reliable comparisons with our SDM attempts.

Another aspect to be taken into account is the discrepancy between a species' fundamental niche and the portion of it which it realizes (Franklin 2010). A

species may be able to realize a wider or another part of its fundamental niche outside its native distribution, e.g. there may be relaxed and conservative variables responsible for the species' distribution (Broennimann and Guisan 2008; Beaumont et al. 2009). This may explain why SDM_{all} , which incorporated information from both native and invasive ranges, had a higher predictive power than SDM_{inv} ; SDM_{nat} . This might be due to its accounting for the probability of exceeding of the fundamental niche by the Harlequin ladybird in its European invasive distribution (Rödder and Lötters 2010). The potential distribution of *H. axyridis* resulting from SDM_{all} (fig. 7) goes beyond that of SDM_{nat} or SDM_{inv} alone and well predicts worldwide regions from which this invasive alien species has been reported, e.g. from near Los Angeles or Cairo (e.g. Brown et al. 2008). However, South American occurrence is not entirely predicted by SDM_{all} (fig. 6a; Poutsma et al. 2008). This may be explained by a still limited 'image' of the beetle's fundamental niche. Additionally, SDM_{all} identified regions as suitable to *H. axyridis* from which it is currently unknown (e.g. Brown et al. 2008; Poutsma et al. 2008), i.e. southern Chile,

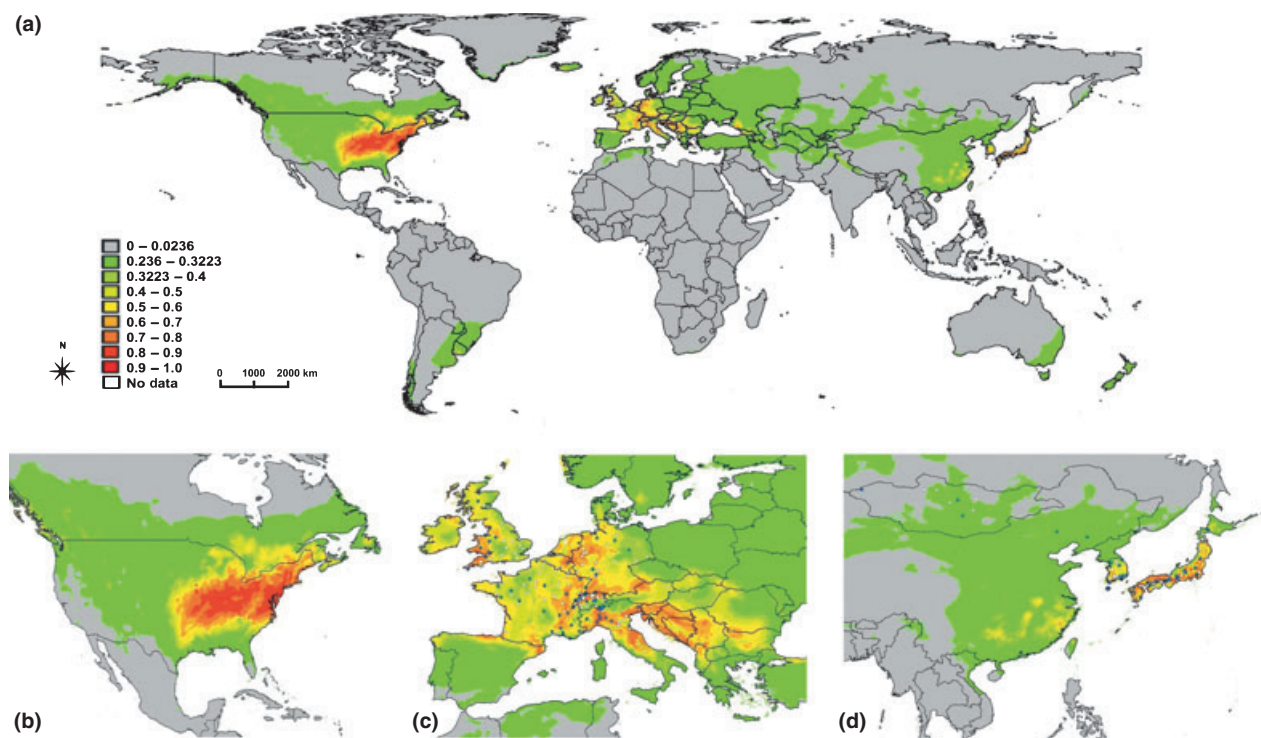


Fig. 8 (a) Mapped global output of the Maxent SDM_{all} for the Harlequin ladybird based on bioclim parameters at records from the Asian native and European invasive ranges, with (b) North America, (c) Europe and (d) Asia enlarged. For legend see fig. 4. Records of the target species in the European invasive distribution are represented by dots; blue indicates the 100 residual localities used for model building after cluster analysis (see text).

northernmost Africa, South-East Australia and Tasmania and New Zealand and large portions in central Eurasia (fig. 8a).

Is model reliability hampered when the model is projected outside the training region due to niche shift?

Niche shift during biological invasion and its influence on SDM building has been discussed by various approaches. It has been suggested that species undergo such shifts rather in the realized niche within the fundamental niche than a shift in the fundamental niche itself (e.g. Broennimann and Guisan 2008; Broennimann et al. 2007; Rödder and Lötters 2009, 2010). The available and realized climate spaces of *H. axyridis* presence in Asia and Europe showed pronounced differences in the variables which least contributed to the models. At the same time those variables which were more important for model building were also more similar (figs 2 and 3). Hence, the differences of occupied and available climate space may support the assumption that the Harlequin ladybird has shifted its niche during invasion in Europe which may be attributed to differences in the available climate space.

Is model transferability hampered due to within-species niche variation?

Harmonia axyridis encompasses a remarkably large natural distribution covering different biomes (fig. 1b). However, the climatic variation within different geographic entities (e.g. the Korean peninsula) is remarkably smaller than within its entire distribution. This leads us to hypothesize that not only the realized but also the fundamental climate niche of the Harlequin ladybird may be a subject to intraspecific variation and that regional entities (e.g. populations, subspecies) only partly contribute to the fundamental niche of the species. A problem resulting from these considerations, so far not addressed in SDMs (see Jeschke and Strayer 2008; Beaumont et al. 2009; Rödder and Lötters 2010), is that the incorporation of information from records not equally scattered all over a species' native distribution neglects effects of intraspecific niche variation. Hence, this may lead to an erroneous or over-estimation of the potential distribution suitable for a particular within-species entity. Certainly, although this is an appealing new aspect in SDMs, it is difficult to access and cannot be solved here with regard to *H. axyridis*. However, what

is interesting is that when projecting SDM_{inv} into Asia only a restricted area within the natural distribution (i.e. in China and Japan) is identified as suitable (fig. 7d). This may actually correspond to an assumed within-species entity as ‘founders’ of the invasive European populations, which have been imported from a hitherto unknown locality in China (<http://www.inra.fr>, accessed 18 June 2010; Brown et al. 2008). Support comes from the observation that merely three of the genetically driven colour variants of *H. axyridis* are known from Europe (i.e. f. *succinea*, f. *spectabilis* and f. *conspicua*; e.g. Brown et al. 2008). Another point of potential relevance is that Majerus et al. (1998) found differences among *H. axyridis* populations with regard to prevalence of inherited male-killing microorganisms which significantly varies among populations.

Also uncertainties may arise when transferring models in areas outside of the training region of the model, due to non-analogous climate conditions compared to the training region (fig. 3). The reason for this is that climate variables may be correlated to each other or novel parts of the climate space may require extrapolation of the model beyond training conditions (e.g. Heikkinen et al. 2006; Fitzpatrick and Hargrove 2009; Rödder and Lötters 2010). Maxent allows for the quantification and subtraction of very high values which may result from projections onto non-analogous climate by the function ‘clamping’ (Phillips et al. 2006). However, generating multiple repeated SDMs, Maxent provides in addition an output map showing the standard deviation (SD) for the created SDM in those regions with projected suitability for the species. The SD is increasing in projection areas outside the model background area in all our three SDMs, particularly for the SDM_{nat} . This may affect predictions of our SDMs, as they are linked with uncertainties when projecting them into areas like North-America, where the available climate space was not sampled during model building, and may be responsible for missing suitability projections in areas where the species is actually known to occur.

Conclusions

Our approach for the alien invasive *H. axyridis* shows, that: (i) for species with a large native area, spanning various climatic conditions, the introduced invasive founder specimens may only be representative for part of the entire fundamental climate niche of the species. (ii) To estimate the species’ invasive

niche for local risk assessments, it is therefore necessary to run additional models solely based on the invasive records. (iii) In case specific information is lacking for the native range, records from the invasive range may fill occurrence gaps for model generation. Focussing on the species’ fundamental niche should help identifying the globally invasive potential of the species.

Acknowledgements

We are grateful to Eric Lombaert and Thomas Guilenmaud of INRA (France) for communication and discussion of the topic and two anonymous referees, whose suggestions improved this manuscript. The first author is grateful to the IUTR-‘Graduiertenkolleg’ at the University of Trier, with financial support by the German Science Foundation, DFG.

Appendix 1

Localities of *Harmonia axyridis* used for SDM building (longitude, latitude; figs 2–4): native range – China: 123.4327778, 41.7922222; 118.9155556, 42.6727778; 114.4703, 22.59556; Japan: 141.3538889, 43.0547222; 141.5380556, 42.9194444; 141.5666667, 42.9166667; 140.0666667, 39.7166667; 140.1166667, 39.7166667; 140.3374939, 38.252779; 139.6166667, 36.7499962; 140.1999969, 36.0833333; 139.7514038, 35.6849995; 138.1333333, 36.0333333; 137.9666667, 36.2333333; 137.4999924, 35.4833374; 137.0166667, 34.8333333; 136.9166667, 35.1666667; 136.7499924, 35.4166667; 135.7499924, 34.9999962; 135.6000061, 34.4999962; 135.4999924, 34.6666667; 135.4166667, 34.7166667; 134.9833333, 34.6333333; 133.9166667, 34.6499977; 133.7666667, 34.5833333; 133.1999969, 34.4166667; 132.4499969, 34.3999977; 133.5500031, 33.5499992; 132.7530556, 33.8363889; 130.3999939, 33.5833333; 131.4333344, 31.9000006; 150.7384797, 46.7310524; Mongolia: 102.8667, 47.4; 104.8333, 45.25; 106.383333, 46.133333; 89.7, 49.5333333; 99.1566667, 49.5008333; 100.8894444, 49.4783333; 106.9166667, 47.9166667; 104.05, 47.85; Russia: 92.8252716, 56.0058327; South-Korea: 126.9997222, 37.5663889; 127.1247, 36.4556; 129.2948, 35.5338; 128.3236111, 34.9727778; 127.8733, 35.41562; 126.5219444, 33.5097222; 128.2611111, 35.3191667; 128.5891, 34.86641; 128.0847222, 35.1927778; 128.7488889, 35.4933333; 126.6892, 34.7995; 127.5891667, 34.9752778; 128.2119444, 37.1361111; 128.6207, 38.07325; 127.9452778, 37.3513889; 126.7530556, 34.3141667; 127.3858333, 35.41; 127.7341667, 37.8747222; 126.56, 33.2497222;

invasive range – Austria: 16.3611, 48.2081; Belgium: 4.8449, 51.3942; 4.5226, 51.4569; 3.542, 51.2688; 2.5973, 51.0718; 3.654, 50.4898; 4.7151, 50.1361; 5.7046, 49.6749; 5.5792, 50.6017; England: –5.1932, 49.9892; –5.2853, 50.2585; –4.6192, 50.3364; –3.7404, 50.2443; –3.5491, 50.3789; –3.8184, 50.7262; –3.2869, 51.1726; –5.0585, 51.7325; –3.8184, 52.101; –2.9184, 51.6758; –2.479, 50.6128; –2.642, 50.9246; –4.0026, 53.2136; –3.3436, 53.3341; –3.0672, 53.5608; –2.805, 54.064; –0.7924, 54.5246; –1.5011, 54.5104; 0.0155, 53.6884; –2.1814, 53.1285; –2.8688, 52.7388; –1.3026, 52.8238; 0.4974, 52.8734; 1.7163, 52.5829; –0.0554, 51.5128; –1.2105, 50.6482; 0.4336, 52.2852; 1.3903, 51.364; 0.0934, 51.123; 0.7241, 51.9805; –0.431, 52.7175; –1.0353, 52.1007; –1.4743, 51.3952; –3.9672, 57.5256; –3.3871, 56.3497; –4.0927, 56.7103; France: 1.3671, 50.0503; 1.5697, 50.6845; 2.2656, 50.799; 3.1113, 50.7462; 2.8822, 50.3234; 4.829, 50.1032; 4.2916, 49.9006; 2.5475, 49.6451; –1.3283, 49.6011; –1.4428, 48.6497; –2.0682, 47.531; –1.5838, 47.1875; –1.1609, 43.7609; 4.3709, 43.6728; 5.0756, 43.6992; 5.8331, 43.1179; 7.2954, 43.7345; 6.8726, 43.8138; 3.904, 43.7697; 4.8554, 44.1309; 4.7232, 45.4169; 5.6305, 45.6283; 6.0093, 44.4392; 5.2342, 45.7605; 6.2471, 46.1921; 6.4057, 46.9056; 6.8814, 47.5663; 7.5156, 47.5839; 5.4456, 47.5134; 5.058, 46.5709; 2.9967, 45.8045; 0.3894, 46.8351; 0.1956, 46.5356; 3.0496, 46.9761; –0.5091, 47.8481; 0.865, 48.4207; 1.5081, 49.0285; 2.1423, 48.7819; 3.1025, 48.359; 4.6087, 48.5; 7.9384, 49.0197; 5.516, 49.3808; 7.5508, 48.1652; –0.4923, 47.443; 1.1794, 47.6359; 2.0924, 48.2403; 3.134, 48.3303; 4.1756, 47.2502; 5.7187, 48.4469; 6.9532, 48.9733; –1.9294, 48.2918; Germany: 8.3184, 49.9468; 8.5401, 49.3215; 8.3052, 49.9757; 8.8254, 49.8309; 8.6749, 49.4171; 7.1844, 50.4275; 8.6984, 50.5929; 10.7809, 50.7923; 12.9432, 50.7903; 7.2923, 51.9665; 7.6381, 51.63; 7.3616, 51.5356; 7.1881, 51.2622; 12.2496, 51.8898; 14.2, 51.1858; 9.8184, 52.408; 10.6901, 52.8264; 8.695, 53.8868; 8.5811, 53.541; 8.7643, 53.0593; 10.9063, 53.3185; 6.6333, 49.75; Ireland: –6.0055, 54.5466; Italy: 13.21391, 46.2136; 9.451275, 46.19521; 9.239625, 46.02001; 9.390069, 45.85298; 9.011833, 45.4024; 11.95118, 45.35331; 9.720833, 45.16222; 9.132997, 45.07889; 11.6064, 44.89884; 10.33738, 44.83075; 8.780455, 44.73875; 11.13157, 44.5114; 12.21527, 44.35127; 12.42296, 43.98332; 7.853969, 43.83413; 7.6666665, 45.0499992; 11.09996, 44.72372; 11.10187, 44.47372; 11.11937, 44.43608; Switzerland: 7.0487, 47.4782; 6.9437, 47.3875; 7.5977, 47.5736; 7.0917, 47.3493; 7.4211, 47.4304; 7.6025, 47.4782; 7.3782,

47.2877; 7.7044, 47.3896; 8.1257, 47.4848; 8.282, 46.9649; 8.4043, 46.8324; 8.231, 47.2571; 8.632, 47.6784; 9.5324, 47.4814; 9.478, 47.1586; 9.7227, 46.6999; 8.9684, 45.8675; 8.6014, 46.3058; 8.829, 47.2266; 7.0079, 47.0057; 6.8618, 46.8664; 6.6511, 46.8392; 6.1143, 46.2242; 6.4099, 46.479; 7.0826, 46.1019; 6.8889, 46.4383; 7.6738, 46.7679; 9.0091, 46.2208; 9.6003, 46.9989; 8.6354, 46.897; 7.667, 46.3024; 7.2831, 47.0804; 8.3975, 47.41.

References

- Beaumont LJ, Hughes L, Poulsen M, 2005. Predicting species distributions: use of climate parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol. Model.* 186, 250–269.
- Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L, 2009. Different climate envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.* 15, 409–420.
- Bomford M, Kraus F, Barry SC, Lawrence E, 2009. Predicting establishment success for alien reptiles and amphibians: a roll for climate matching. *Biol. Invas.* 11, 1387–1397.
- Broennimann O, Guisan A, 2008. Predicting current and future biological invasions: both native and invaded ranges matter. *Biol. Lett.* 4, 585–589.
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A, 2007. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10, 701–709.
- Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A, Hägg T, Kenis M, Klausnitzer BEM, Kovář I, Loomans AJM, Majerus MEN, Nedved O, Pedersen J, Rabitsch W, Roy HE, Ternois V, Zakharov IA, Roy DB, 2008. *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *Biocontrol* 53, 5–21.
- Burgio G, Santi F, Lanzoni A, Masetti A, De Luigi V, Melandri M, Reggiani A, Ricci C, Loomans AJM, Maini S, 2008. *Harmonia axyridis* recordings in northern Italy. *Bull. Insectol.* 61, 361–364.
- Busby JR, 1991. BIOCLIM: a bioclimate analysis and prediction system. In: *Nature conservation: cost effective biological surveys and data analysis*. Eds by. Margules CR, Austin MP, CSIRO, Canberra, Australia, 64–68.
- Davis MA, 2009. *Invasion biology*. Oxford University Press, New York.
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R, 2007. Methods to account for spatial autocorrelation in the analysis of

- species distributional data: a review. *Ecography* 30, 609–628.
- Elith J, Leathwick J, 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. S.* 40, 677–697.
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Lohmann JLLG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Shapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE, 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Elith J, Kearney M, Phillips S, 2010. The art of modelling range-shifting species. *Meth. Ecol. Evol.* 1, 330–342.
- Fitzpatrick MC, Hargrove WW, 2009. The projection of species distribution models and the problem of non-analog climate. *Biodivers. Conserv.* 18, 2255–2261.
- Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR, 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Glob. Ecol. Biogeogr.* 16, 24–33.
- Fitzpatrick MC, Dunn RR, Sanders NJ, 2008. Data sets matter, but so do evolution and ecology. *Glob. Ecol. Biogeogr.* 17, 562–565.
- Franklin J, 2010. Mapping species distributions: spatial inference and prediction (ecology, biodiversity and conservation). Cambridge University Press, New York.
- Hanley J, McNeil B, 1982. The meaning of the use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143, 29–36.
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT, 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geog.* 30, 751–777.
- Hijmans RJ, Cruz M, Rojas E, Guarino L, 2001. Computer tools for spatial analysis of plant genetic resources data: 1. DIVA-GIS. *Plant Genet. Res. Newsl.* 127, 15–19.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A, 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hutchinson GE, 1978. An introduction to population ecology. Yale University Press, New Haven.
- Jaynes ET, 1957. Information theory and statistical mechanics. *Phys. Rev.* 106, 620–630.
- Jeschke JM, Strayer DL, 2008. Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. NY Acad. Sci.* 1134, 1–24.
- Koch RL, 2003. The multicolored Asian Lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *J. Insect. Sci.* 3, 1–16.
- Komai T, Chino M, Hosino Y, 1950. Contributions to the evolutionary genetics of the Lady-beetle, *Harmonia*. I. Geographic and temporal variations in the relative frequencies of the elytral pattern types and in the frequency of the elytral ridge. *Genetics* 35, 589–601.
- Lombaert E, Guillemaud T, Cornuet JM, Malausa T, Facon B, Estoup A, 2010. Bridgehead Effect in the Worldwide Invasion of the Biocontrol Harlequin Ladybird. *PLoS ONE* 5, e9743. doi: 10.1371/journal.pone.0009743.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA, 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Majerus TMO, Majerus MEN, Knowles B, Wheeler J, Bertrand D, Kuznetzov VN, Ueno H, Hurst GDD, 1998. Extreme variation in the prevalence of inherited male-killing microorganisms between three populations of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Heredity* 81, 683–691.
- Mateo RG, Croat TB, Felicísimo AM, Munoz J, 2010. Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Divers. Distrib.* 16, 84–94.
- Medley KA, 2010. Niche shifts during the global invasion of the Asian Tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Glob. Ecol. Biogeogr.* 19, 122–133.
- Mooney HA, Cleland EE, 2001. The evolutionary impact of invasive species. *PNAS* 98, 5446–5451.
- Nemes S, Hartel T, in press. Summary measures for binary classification systems in animal ecology. *North-West. J. Zool.* (in press).
- Nentwig W, 2008. Biological invasions. *Ecological Studies* 193, Springer, Berlin, Heidelberg.
- Ongagna P, Giuge L, Iperiti G, Ferran A, 1993. Life-cycle of *Harmonia axyridis* (Col, Coccinellidae) in its area of introduction – South-Eastern France. *Entomophaga* 38, 125–128.
- Pearce J, Ferrier S, 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecol. Model.* 128, 128–147.
- Pearman PB, Guisan A, Broennimann O, Randin CF, 2008. Niche dynamics in space and time. *TREE* 23, 149–158.
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT, 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34, 102–117.
- Peterson AT, Nakazawa Y, 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecol. Biogeogr.* 17, 135–144.

- Peterson AT, Vieglais DA, 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience* 51, 363–371.
- Peterson AT, Papes M, Kluza DA, 2003. Predicting the potential invasive distributions of four alien plant species in North America. *Weed Sci.* 51, 863–868.
- Phillips SJ, Dudík M, 2008. Modeling of species distributions with Maxent: new extensions and comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips SJ, Anderson RP, Schapire RE, 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Poutsma J, Loomans AJM, Aukema B, Heijerman T, 2008. Predicting the potential geographical distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX model. *Biocontrol* 53, 103–125.
- Rödder D, 2009. ‘Sleepless in Hawaii’ – does anthropogenic climate change enhance ecological and socioeconomic impacts of the alien invasive *Eleutherodactylus coqui* Thomas, 1966 (Anura: Eleutherodactylidae)? *North-West. J. Zool.* 5, 16–25.
- Rödder D, Lötters S, 2009. Niche shift versus niche conservatism? Climatic characteristics within the native and invasive ranges of the Mediterranean Housegecko (*Hemidactylus turcicus*) *Glob. Ecol. Biogeogr.* 18, 674–687.
- Rödder D, Lötters S, 2010. Explanative power of variables used in species distribution modelling: an issue of general model transferability or niche shift in the invasive Greenhouse frog (*Eleutherodactylus planirostris*). *Naturwissenschaften* 97, 781–796. doi: 10.1007/s00114-010-0694-7.
- Rödder D, Solé M, Böhme W, 2008. Predicting the potential distribution of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-West. J. Zool.* 4, 236–246.
- Rödder D, Schmidlein S, Veith M, Lötters S, 2009. Alien invasive Slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? *PLoS ONE* 4, e7843. doi: 10.1371/journal.pone.0007843.
- Soberón J, 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* 10, 1115–1123.
- Soberón J, Peterson AT, 2005. Interpretation of models of fundamental ecological niches and species’ distributional areas. *Biodivers. Inform.* 2, 1–10.
- Swets K, 1988. Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.
- Van Lenteren JC, Loomans AJM, Babendreier D, Bilger F, 2008. *Harmonia axyridis*: an environmental risk assessment for Northwest Europe. *Biocontrol* 53, 37–54.