Research Article

Modelling the effects of climate change on the risk of invasion by alien squirrels

Mirko Di Febbraro[1], Adriano Martinoli[2], Danilo Russo[3], Damiano Preatoni[2], Sandro Bertolino[4,*]

[1]*Environmetrix Lab, Department of Biosciences and Territory, Università degli Studi del Molise, Contrada Fonte Lappone, 86090, Pesche (Isernia), Italy.*
[2]*Unità di Analisi e Gestione delle Risorse Ambientali – Guido Tosi Research Group, Dipartimento di Scienze Teoriche e Applicate, Università degli Studi dell'Insubria, via J.H. Dunant 3, 21100 Varese, Italy.*
[3]*Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Via Università 100, 80055 Portici (Naples), Italy.*
[4]*Department of Agricultural, Forest and Food Sciences, Università degli Studi di Torino, largo Paolo Braccini 2, 10095, Grugliasco (Turin), Italy.*

Abstract

Assessing invasion risk by alien organisms implies evaluating the likelihood of successful establishment and spread once they are accidentally or deliberately introduced. The importance of implementing accurate risk–assessment procedures is further stressed by the evidence that ongoing climate change can promote invasion processes, from initial introduction through establishment and spread. Although squirrels are considered powerful invaders with well–documented negative impacts on biodiversity and human activities, there is a noticeable gap of comprehensive investigations specifically focused on this group, especially as far as the effect of climate change on worldwide invasion risk is concerned. In this study we predicted current and 2070 potential distributions of eight squirrel species with a SDM–based framework, also detecting current potential hotspots of invasion and evaluating how these could be modified by climate change in 2070. SDM predicted the eight species to potentially occur in large areas worldwide (12.12% to 39.23% of the mainland), with 70 to 129 countries vulnerable to a potential invasion. Model projections over the 2070 climate change scenarios predicted five to seven squirrel species undergoing an increase in their future potential distribution in non–native ranges. Current hotspots of potential invasion were predicted to occur in southeastern Asia, northeastern Australia, tropical Africa and South America, as well as Central and North America. Projections to 2070 showed most of the hotspots of invasion to remain substantially stable in terms of number of potential invasive species, regardless of the scenario. The most relevant increase/reduction in extent of species distribution and in the number of potential invasive species in invasiveness hotspots were predicted for 2070 under the most severe scenarios. We emphasize a strong species–specific response to climate change, which could also affect invasive species by making them less competitive, therefore potentially leading to a retreat from the invaded ranges.

Introduction

Mitigating the impacts posed by the spread of alien species requires the development of screening tools designed to predict which species can become invasive if they escape from containment or are released into the wild (Keller et al., 2007). Therefore, assessing invasion risk by alien organisms implies evaluating their possibility of enter into a country, establish viable populations and spread over large areas, producing adverse economic, environmental or social impacts (Bomford, 2008; Genovesi and Shine, 2004). The procedure should evaluate the likelihood of arrival, ability to survive and establishment of an alien species both in natural and human–made environments, as well as the speed and extent of invasion, the feasibility of eradication or spatial containment and the potential negative impacts (Genovesi and Shine, 2004). Every evaluation should be accompanied by an assessment of its confidence, from low to very high, based on the information available for the species. Data from previous introductions are therefore useful to improve the level of confidence of the evaluations and to support the assessment.

A first step in risk–assessment procedures is to evaluate the establishment likelihood of a taxon in a given geographical area if some individuals are released or escape containment. For instance, successful

invaders tend to have larger geographic distributions (i.e. higher adaptability) and are more likely to have already established exotic populations elsewhere (high propagule pressure); if introduced into areas with a climate that matches the native range, their possibility of establishment typically increases (Hayes and Barry, 2008; Jeschke and Strayer, 2006; Van Wilgen and Richardson, 2012).

The importance of implementing accurate risk–assessment procedures is further stressed by the evidence that ongoing climate change, including extreme climatic events (i.e. floods, wildfires), can promote invasion processes, from initial introduction through establishment and spread (Bellard et al., 2013; Diez et al., 2012; Walther et al., 2009). Therefore, investigating how climate change could affect the global process of biological invasions represents a crucial question for the development of nature management policies (Bellard et al., 2013).

Species Distribution Models (SDM) are a useful tool to evaluate current and future species potential distributions, therefore providing relevant information to anticipate species' invasions and controlling their spread (Broennimann et al., 2007; Jiménez-Valverde et al., 2011). Such technique has been used in several studies dealing with invasion risk of single (Di Febbraro et al., 2013; Ficetola et al., 2010; Mori et al., 2015) or large assets of species (Bellard et al., 2013; Thuiller et al., 2005).

Squirrels (Sciuridae) are considered powerful invaders: in 200 out of 248 introduction events (80.6%) considered by Bertolino (2009) the animals established viable populations. The main vector of squirrel introduction into new areas is the pet trade, with connected risk of either

*Corresponding author
Email address:* sandro.bertolino@unito.it (Sandro Bertolino)
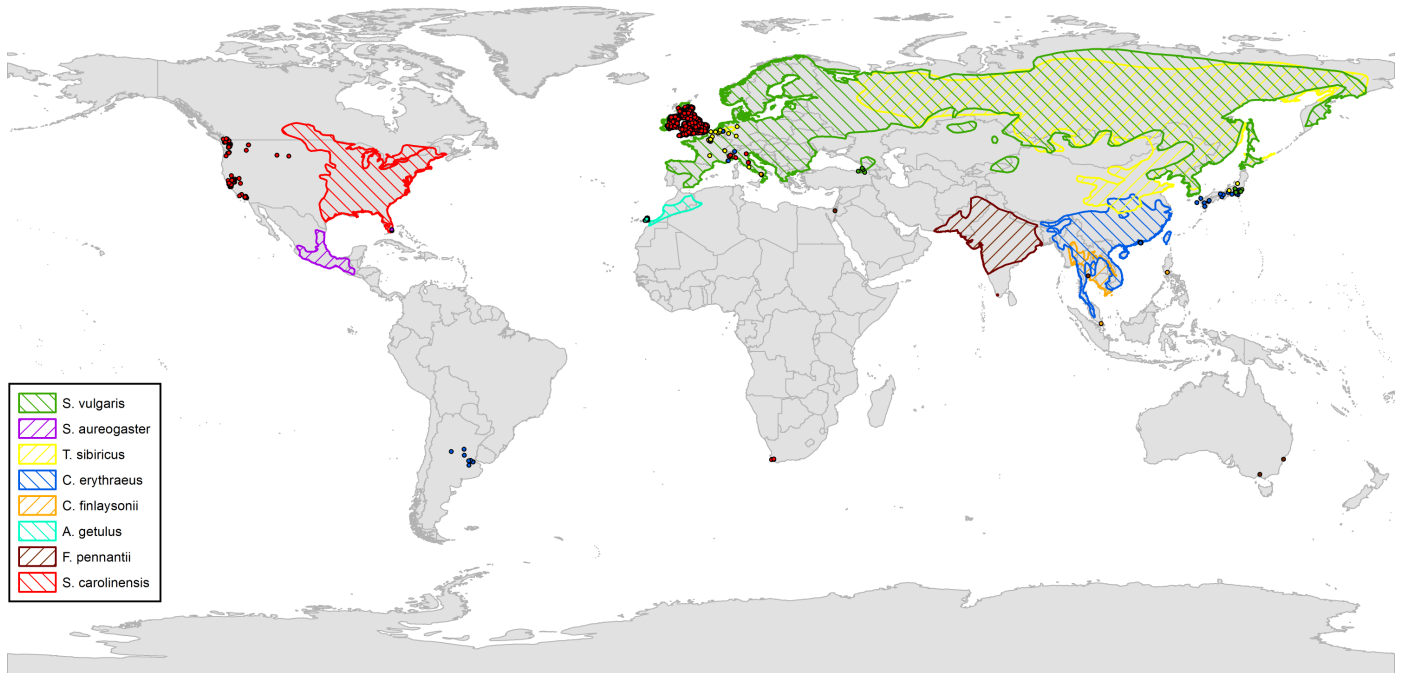
Figure 1 – IUCN range maps and occurrence records used for the model training. Species occurrences from the native ranges (continuous lines) were derived by randomly sampling the IUCN range maps and were added to those from the non–native ranges (dots of the same colors) obtained from online databases.

deliberate introduction or escape from captivity. In the past, squirrel species were also translocated into new areas by game and wildlife management agencies (Davis and Brown, 1988), yet this is no longer considered a suitable management option. After their establishment, many squirrel species produced negative impacts to biodiversity and human activities (e.g. forestry, agriculture, damage to technical installations) besides carrying diseases that may affect humans as well as native species (Bertolino, 2009; Bertolino and Lurz, 2013; Wood et al., 2007). Despite their long history of invasions, squirrels still have an innate appeal to people, and are still widely traded as pet species and imported in countries outside their native distribution (UNEP-WCMC, 2010a,b), where they continue to establish new populations (Bertolino et al., 2015; Guichón et al., 2015; Signorile et al., 2014).

Pet squirrels are usually kept in cages, from where they can escape or be freed or are directly released in estates and private parks. Since most people live in cities or in surrounding areas, it is likely that animals are released in urban parks, or reach these areas after escaping (Bertolino et al., 1999; Guichón et al., 2015; Martinoli et al., 2011). Urban parks are often good habitats for squirrels due to the presence of large trees suitable for nesting, providing seeds and other food sources in absence of competition and predation pressure (Bonnington et al., 2014; Parker and Nilon, 2012). Furthermore, squirrels in urban areas may benefit from supplemental feeding provided by citizens that could help surviving periods of food shortage (Bertolino et al., 2004; Bonnington et al., 2014; Parker and Nilon, 2012). As a result, just a few squirrels released in an urban park could originate high-density populations acting as a source of animals dispersing in surrounding natural areas (Bertolino et al., 2008; Bonnington et al., 2014; Parker and Nilon, 2012).

Given the relevance and the complex dynamics involved in the establishment and spread of invasive squirrels, along with a noticeable gap of comprehensive investigations specifically focused on this group, the objective of our work is to predict current and future global invasion risk for eight squirrel species: *Atlantoxerus getulus*, *Funambulus pennantii*, *Callosciurus erythraeus*, *C. finlaysonii*, *Sciurus aureogaster*, *S. carolinensis*, *S. vulgaris* and *Tamias sibiricus*. These species were selected considering only alien squirrels that underwent introduction events in countries other than the native ones, thus excluding those species that have been translocated outside their native range but still within the native countries. This criterion was chosen because in many cases there was a certain degree of uncertainty in considering trans-

locations within the same country as a real introduction or simply a translocation of animals of different subspecies. Specifically, we aim at: a) predicting the current potential distribution of the selected species with a SDM–based analytical framework, driven by climatic data; b) project the models to 2070 under different climate models outputs and climate change scenarios; c) individuate current potential hotspots of invasion and d) evaluate how these could be modified by climate change in 2070.

Materials and methods

Species occurrence data

Species distribution data used to train SDM were derived considering both native and non–native ranges (Broennimann and Guisan, 2008; Di Febbraro et al., 2013; Mainali et al., 2015). Specifically, we used the IUCN species' range maps (IUCN, 2012) instead of georeferenced occurrence records, as the latter, if even available, may exhibit strong spatial biases (Boakes et al., 2010). This was our case, as the georeferenced (point data) species occurrence records that we extracted from the online database Global Biodiversity Information Facility (GBIF) resulted largely incomplete when compared with non–georeferenced or aggregated data (georeferenced polygon data) on species range commonly available in the literature. In particular, an almost complete absence of data was recorded outside of western countries. Following Strubbe et al. (2015), we derived species occurrences from the known native ranges, cartographically represented as polygons, by randomly sampling the IUCN range maps (see also Yannic et al., 2013) and adding these records to those from the non–native ranges that we gathered with an extensive search in the literature and from the GBIF database (Fig. 1). Each range map was converted to grids with a resolution of 2.5 arc–minutes (≈5 km) and 1% of the resulting cells were randomly sampled, repeating the procedure 10 times and using each replicate for a model run (Innangi et al., 2015). We decided not to include all the cells as a whole in the model training in order to counterbalance the difference in sample size of the occurrence data from native and non–native ranges. The accuracy of the records gathered from online databases was assessed by including only occurrences given to at least two decimal places (0.01 decimal degrees, corresponding to 1.11 km at the equator). In addition, we filtered these data by removing duplicated records and those with unrealistic coordinates. For each species, a set of 10000 pseudoabsences were randomly sampled over a region iden-

tified by all the WWF Terrestrial Ecoregions (Olson et al., 2001) that included species records (Barve et al., 2011; Di Febbraro et al., 2015; Mateo et al., 2015).

Environmental variables

As initial set of environmental predictors for SDM training, we considered the 19 bioclimatic variables derived from the WORLDCLIM dataset at a spatial resolution of 2.5 arc–minutes ($\approx$5 km) (Hijmans et al., 2005). To take into account the pairwise correlation between the predictors, the final set of variables was subselected considering a variance inflation factor (VIF) $\leqslant$3 (Zuur et al., 2010) and included the following six predictors: Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean Temperature of Wettest Quarter (BIO8), Precipitation Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19). Models were then projected over the same predictor variables using future climate scenarios for 2070, available in the WORLDCLIM dataset as well. In particular, we chose among the 19 scenarios available in WORDCLIM two climate change model outputs that are part of the fifth assessment report (IPCC, 2013), HadGEM2 and CCSM4, for the two most impacting IPCC's climate scenarios: RCP6.0 and RCP8.5. These scenarios describe possible future trends in concentration of greenhouse gases, with RCP6.0 forecasting emissions to reach a peak around 2080, then decline substantially, and RCP8.5 a continue emissions' rise throughout the 21[st] century (IPCC, 2013). For computational reasons, all the models were projected worldwide at a resolution of 0.5°($\approx$50 km). To counter the effect of model extrapolation on values of predictor variables laying outside the training range, projections were constrained using environmental clamping (Elith et al., 2011). This procedure prescribes to treat variables outside the training range as if they were at the limit of the training range and was applied to all the cells where more than one environmental predictor was outside the limits used in model construction (Bush et al., 2014; Elith et al., 2011). All procedures were carried out with the packages `spatstat` (Baddeley and Turner, 2005), `maptools` (Bivand and Lewin-Koh, 2013)), `rgeos` (Bivand and Rundel, 2015) and `raster` (Hijmans, 2015), in the R environment (R Development Core Team, 2015).

Species distribution models

Models were generated using MaxEnt 3.3.3k (Phillips and Dudík, 2008; Phillips et al., 2006), a popular machine-learning method based on an application of the maximum entropy principle in an ecological context (Jaynes, 1957). MaxEnt has generally shown to perform better than other similar techniques (Elith et al., 2006) and has been widely used in a plenty of ecological studies (e.g. Mayol et al., 2015; Rödder and Lötters, 2009; Roscioni et al., 2014, 2013; Russo et al., 2015, 2014), including the prediction of invasive species potential distributions under current and future conditions (Di Febbraro et al., 2013; Ficetola et al., 2010, 2007; Heikkinen et al., 2006; Mori et al., 2015). MaxEnt models were trained with the package `dismo` (Hijmans et al., 2016) in the R environment (R Development Core Team, 2015). Each of the 10 replicated occurrence datasets was randomly split into a 70% sample, used for the calibration of the model, and the remaining 30%, used to evaluate model performance. All the others MaxEnt settings were kept to their default values. This choice was made as the default MaxEnt settings have been tested across a range of taxonomic groups (Phillips and Dudík, 2008) and may be useful when modelling many species simultaneously (Merow et al., 2013). In addition, MaxEnt models trained with the default settings proved more accurate than those with different setups when predicting species richness (Cao et al., 2013). Predictive performance of the model was assessed by measuring the area under the receiver operating characteristic curve (AUC) (Hanley and McNeil, 1982) and the true skill statistic (TSS) (Allouche et al., 2006).

To avoid using poorly calibrated models, only projections from models with AUC $\geqslant$0.7 and TSS $\geqslant$0.4 were considered in all subsequent analyses. The model averaging was performed by weighting the individual model projections by their AUC scores and averaging the results, as this method was shown to be particularly robust (Marmion et al., 2009). The final models for the present and future scenarios were transformed into presence-absence values using a threshold maximizing the sum of sensitivity (the percentage of presence correctly predicted) and specificity (the percentage of absence correctly predicted) (Fielding and Bell, 1997). Such threshold has been widely used (Algar et al., 2009; Buisson et al., 2010; Di Febbraro et al., 2015; Dubuis et al., 2011; Fitzpatrick et al., 2011) and proved one of the most accurate according to Liu et al. (2005). Extent and shift of future predicted distributions was calculated. The former was expressed as the percentage of the current predicted distributions, while the latter was expressed as the percentage overlap with the current predicted distribution (Huntley et al., 2008). The final five sets (one for the present and four for the 2070 scenarios) of 10 binarized outputs were then respectively summed and all the resulting cells with a positive value were given a value of 1. Subsequently, we summed each species' projections in non–native ranges, calculating the current potential hotspots of invasion and their predicted relative change under the future scenarios. The latter was depicted as the difference between the future and the current
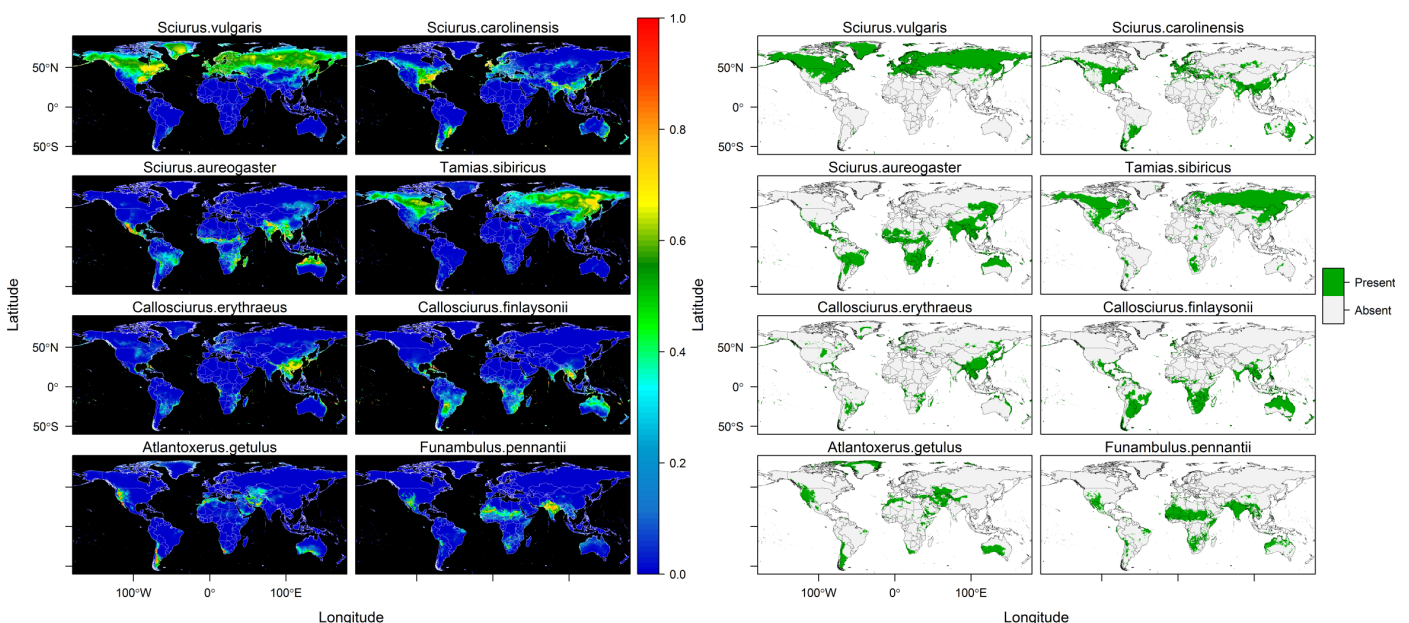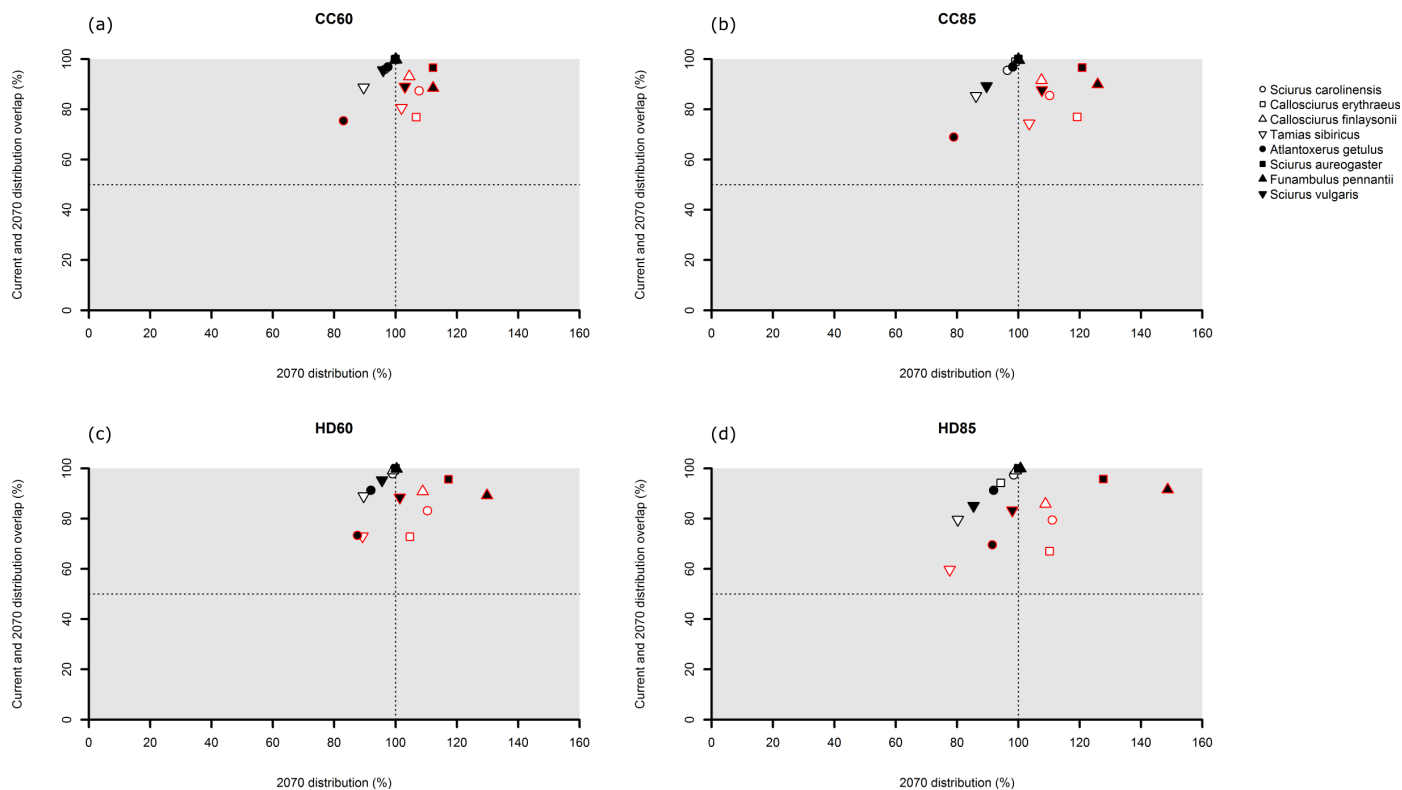

Figure 2 – Probability of presence (left) and binary maps (right) depicting the potential distribution of the invasive squirrel species for the current time.

Figure 3 – Scatterplots show the extent of the 2070 predicted distributions in both native and non–native ranges against their overlap with the current distributions (both expressed as percentage of the current distributions). Along the rows are the two climate model outputs, i.e. HadGEM2 (a–b) and CCSM4 (c–d), and along the columns the two climate change scenarios, i.e. RCP6.0 (a, c) and RCP8.5 (b, d). Dotted lines indicate the "no–change" value of 100% for the extent (vertical) and a shift of 50% (horizontal) of the future distributions. Symbols with red borders refer to 2070 potential distributions in non–native ranges.

potential hotspots of invasion. Similarly, a consensus map was created showing the future relative change in invasivity hotspots predicted by all climate model outputs and climate change scenarios.

Results

SDM reached excellent predictive performances for all the species, with a mean AUC of 0.910 (SD=0.057) and a mean TSS of 0.734 (SD=0.117) (see also Tab. 1). The eight species resulted to potentially occur in large areas worldwide, covering from 12.12% (*C. erythraeus*) to 39.23% (*S. vulgaris*) of the mainland, with 70 (*A. getulus*) to 129 (*C. finlaysonii*) countries vulnerable to a potential invasion (Fig. 2). Most of the predicted suitable areas were localized in the northern hemisphere, with the exception of *C. finlaysonii*, whose potential distribution mainly concerns the southern hemisphere and *S. aureogaster* and *F. pennantii* having predicted impact areas mainly occurring around the equatorial zone (Fig. 2). Model projections over the 2070 climate change scenarios predicted five to seven squirrel species undergoing an increase in their future potential distribution in non–native ranges according to the climatic suitability of the areas (Fig. 3). On the other hand, potential distributions in native ranges were predicted to moderately reduce their extent, although not more than 20% under all the four scenarios (Fig. 3). Specifically, *S. aureogaster* and *F. pennantii* showed the highest increase in the extent of 2070 potential distribution in non–native ranges under all the four scenarios, whereas *A. getulus* showed the highest decrease under CC60, CC85 and HD60 (Fig. 3a–c) scenarios and *T. sibiricus* under HD85 (Fig. 3d). Regarding the native ranges, *T. sibiricus* exhibited the most considerable decrease (ca. 20%) in the extent of its future potential distribution under all the four scenarios, with *S. vulgaris* also showing a similar reduction under the two most impacting scenarios (i.e. CC85 and HD85) (Fig. 3b, d). Shift in future potential distribution was scarce, exceeding 20% just for few species and mainly regarding the non–native ranges. Overall, the most impacting scenarios (i.e. CC85 and HD85) seemed to predict a stronger increase/decrease (depending on the species) in the extent of future potential distributions in non–native ranges, along with a more evident

shift of potential distributions in native ranges with respect of the less impacting ones.

Current hotspots of potential invasion were predicted to occur mostly in southeastern Asia, northeastern Australia, tropical Africa and South America and in vast regions of Central and North America (Fig. 4a). Projections to 2070 showed most of the hotspots of invasion to remain substantially stable in terms of number of potential invasive species, regardless of the scenario (Fig. 4b). However, the number of cells where a relative increase in the number of invasive species was predicted in 2070 was larger than that for which a decrease was forecast (Fig. 4b). Specifically, an increase in the number of potential invasive species in 2070 was predicted for large areas of Africa, China and Australia, along with northern regions of South America and western United States, especially under the HD85 scenario (Fig. 4c–f). This scenario also showed the most evident reduction in the number of invasive species in 2070 (Fig. 4b), especially in eastern United States, continental Europe and Russia (Fig. 4f). Similarly to what highlighted for single species distributions, the more severe the climate change scenario, the higher the relative increase/reduction of the 2070 hotspots of invasion. This pattern is clearly depicted in Fig. 4b, where RCP8.5 scenarios (i.e. CC85 and HD85) predicted the highest amount of cells

Table 1 – Mean AUC and TSS scores of the SDM for the eight analyzed species. Standard deviations are reported in parentheses.

| Species	AUC	TSS
S. vulgaris	0.793 ($\pm$0.010)	0.517 ($\pm$0.012)
S. carolinensis	0.942 ($\pm$0.010)	0.790 ($\pm$0.017)
S. aureogaster	0.936 ($\pm$0.017)	0.773 ($\pm$0.052)
T. sibiricus	0.840 ($\pm$0.010)	0.598 ($\pm$0.013)
C. erythraeus	0.937 ($\pm$0.010)	0.800 ($\pm$0.029)
C. finlaysonii	0.952 ($\pm$0.014)	0.823 ($\pm$0.044)
A. getulus	0.944 ($\pm$0.033)	0.817 ($\pm$0.101)
F. pennantii	0.935 ($\pm$0.010)	0.799 ($\pm$0.029)
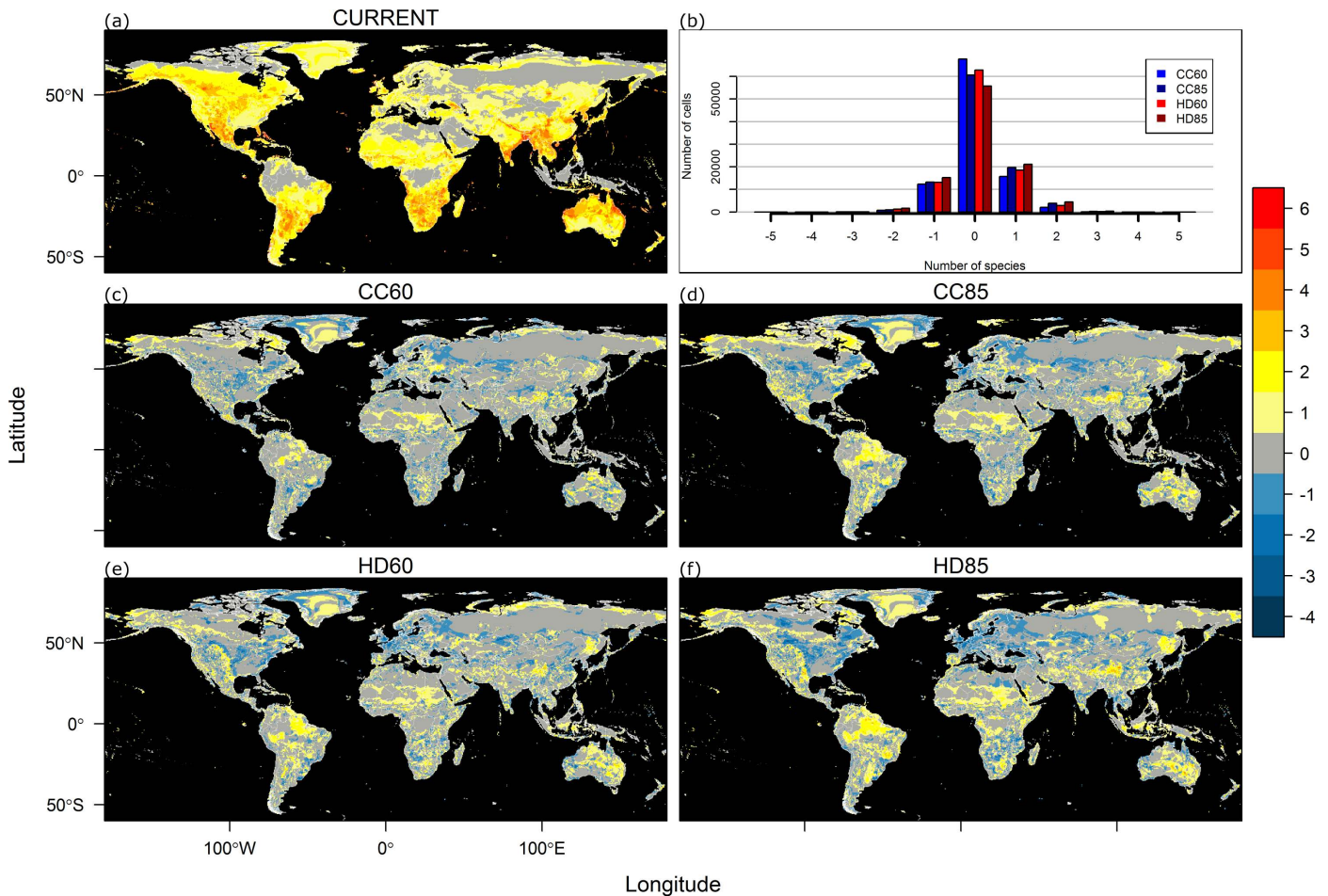
Figure 4 – Maps of current potential hotspots of invasion (a) and their predicted change under the future scenarios (c–f). The latter was depicted as the difference between the future and the current potential hotspots of invasion. Histogram in panel b shows the amount of cells (y-axis) in which the number of invasive species is predicted to increase (positive values on the x-axis), decrease (negative values) or remain stable ("0" values) in 2070, with respect of the current state.

with an increase/decrease in the number of potential invasive species, than RCP6.0 scenarios. The final consensus map in Fig. 5 depicts the hotspots of invasion predicted by all climate model outputs and climate change scenarios. The hotspots of invasion with an increase in the number of potential invasive species in 2070 — which represent the areas with the most serious climate change–enhanced risk of invasion by alien squirrels — are mostly located in western China, Australia, Brazil, Greenland and Sub–Saharan Africa (Fig. 5). On the other hand, the widest areas where climate change might somehow mitigate the future invasion risk related to alien squirrels are located in continental Europe, Russia and western regions of United States and Canada (Fig. 5).

Discussion

Our analyses showed that invasive squirrels could adapt worldwide to the climatic conditions of large areas, covering up to 10–40% of mainland. Current hotspots of potential squirrel invasion were predicted for southeastern Asia, northeastern Australia, tropical Africa and South America and in parts of central and North America. Some of these areas, i.e. southeastern Asia, Central America, Brazil and eastern Australia, were already identified as potential hotspots for the 100 of the world's worst invasive species (WWIS) (Bellard et al., 2013), suggesting invasive squirrels to follow the same geographic patterns of global invasion risk. By contrast, although the hotspots at WWIS's highest invasion risk were predicted to occur in eastern United States and northeastern Europe (Bellard et al., 2013), we found that only a moderate–low potential number of invasive squirrel species would occur in such regions. Similarly, areas that we found to be at highest invasion risk for invasive squirrels were predicted to host potentially a moderate–low WWIS number (Bellard et al., 2013). Regarding the climate

change effects predicted for 2070, invasivity hotspots for alien squirrels showed a substantial stability in their geographic pattern, and did not follow the WWIS predicted global trends, which showed important geographic variations (Bellard et al., 2013). Such discrepancy is further confirmed considering that areas where a decrease in the number of invasive squirrel species was predicted for 2070 by all the scenarios, i.e. eastern United States and continental Europe, emerged as those with the highest increase in the WWIS number (Bellard et al., 2013). The divergences in the predicted effects of climate change on the invasivity hotspots of alien squirrels and WWIS are likely related to the different scope of the study by Bellard et al. (2013), which analyzed a broader list of taxa (from micro–organisms to mammals) than we did, thus including a wider spectrum of species–habitat relationships that drove the final definition of the invasivity hotspots. Overall, unlike other studies (Bradley et al., 2011; Walther et al., 2009), our analyses did not indicate a generalized increase in the invasion risk by alien squirrels following climate change and substantially confirmed what was highlighted by Bellard et al. (2013) and Bradley et al. (2009). In fact, the number of cells with a predicted increase in the number of potential invasive squirrel species was just slightly higher than that with a potential predicted decrease. In addition, a differential effect of climate change on range size and position clearly emerged among the species, with some of them (i.e. *T. sibiricus* and *A. getulus*) that were predicted to seriously shrink and shift their invasive ranges. These results are in agreement with other evidences (Bradley et al., 2009; Pyke et al., 2008) that suggested how a reduced climatic suitability on currently invaded areas could affect invasive species by making them less competitive, therefore potentially leading to their decline. Rather than a generalized increase in the invasion risk, our analyses seemed to support a relationship between the severity of climate change and the mag-

5
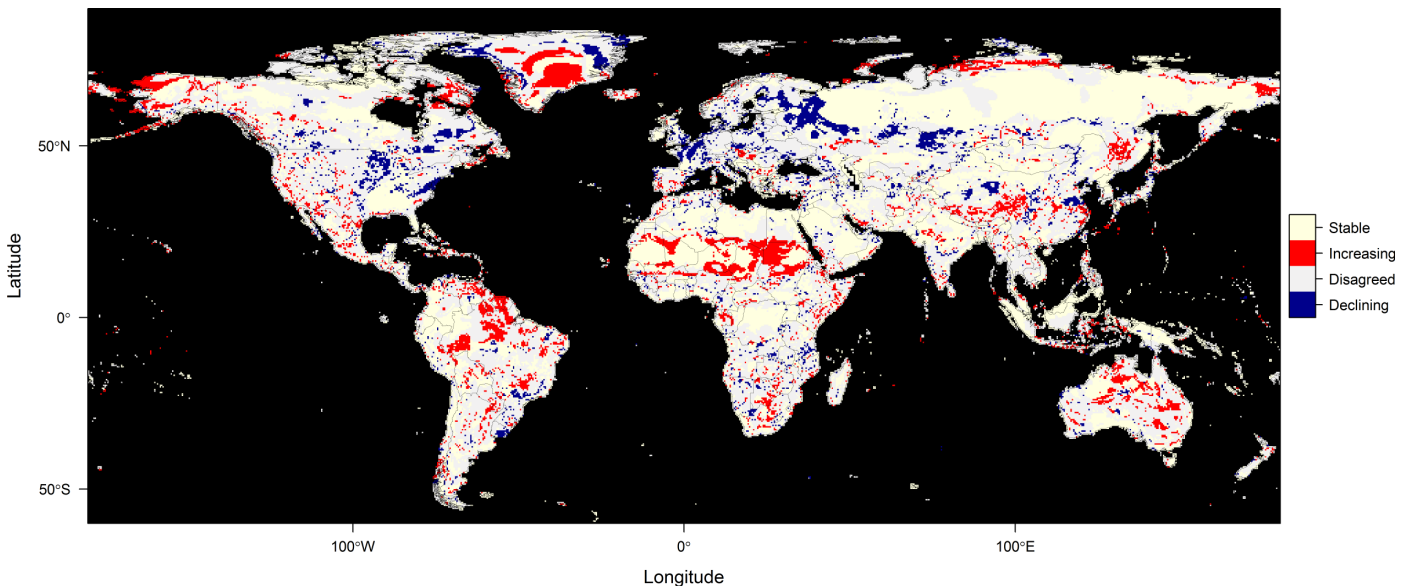
Figure 5 – Final consensus map showing the hotspots of invasion with a predicted increase (red) – decrease (blue) in the number of invasive species in 2070 predicted by all the four scenarios.

nitude of the predicted effects on the distribution of invasive squirrels, i.e. both range expansion and contraction. Effectively, the highest expansions/reductions and shifts of invasive ranges were predicted under the RCP8.5 scenario. Moreover, the number of cells where the species number was predicted to remain stable in 2070 was higher under the less severe scenario (i.e. RCP6.0), as well as more cells with an increase/decrease in the number of species were predicted under the RCP8.5 scenario.

Squirrels are widely traded as pets, for example in Europe (UNEP-WCMC, 2010a,b), so the propagule pressure represented by animals that are released or escape from captivity could be high. Considering that for many squirrel species even few animals could establish populations (Bertolino, 2009; Bertolino and Lurz, 2013; Wood et al., 2007), the existence of large suitable areas is particularly worrying. Two of the squirrels considered in this work, *S. carolinensis* and *C. erythraeus*, were included in the list of "invasive alien species of EU concern" that will be banned from Europe. However, such a restriction in trade does not consider other possible invasive squirrels and is lacking in most of the world regions, so countries within hotspots of possible invasions should carefully target potential alien squirrels with strategies avoiding species introduction. Climate change seems to have a moderate effect on the species distribution in their native ranges, with significant reduction only under the most extreme scenario; therefore, temperature alone will probably constitute a limited threat for the conservation of these squirrel species. However, the raise of the temperature could increase the future potential distribution of squirrel species in the non–native ranges. For instance, *S. vulgaris* is predicted to undergo a relevant reduction in the extent of its native distribution under the two most impacting scenarios (i.e. CC85 and HD85), while *S. carolinensis*, a species introduced in Europe where it threatens *S. vulgaris* (Bertolino, 2008; Bertolino et al., 2008; Gurnell et al., 2014), is predicted to increase the extent of its potential non–native range under all scenarios. Therefore, climatic change could be an additive effect, exacerbating competition between the two species; hence, it is important to prevent the spread of the American species in Europe (Bertolino et al., 2015, 2014).

Prioritization to support cost–effective allocation of resources is part of decision–making in the management of invasive alien species (McGeoch et al., 2015). The main pathway of squirrels' introductions is the pet trade, connected with risk of either deliberate releases or escape from captivity. This has resulted in the worldwide introduction of about 20 species, most of them successful invaders (Bertolino, 2009). While the best strategy based on a precautionary approach would require the ban of all squirrel species from the pet market, or at least of the

genera that already proved to be invasive, legislation usually requires species being evaluated individually in their likelihood of invasiveness through a detailed risk assessment (Genovesi et al., 2015). Our results could help to identify squirrel species most likely to be invasive in large part of the world and areas at highest risk of invasion, allowing their assessment against local pathways importance (McGeoch et al., 2015).

Among the main limitations of our approach, it must be considered that we integrated two different kinds of spatial data to train our SDM, i.e. point locations and distribution maps. Specifically, these two elements are sensitive to different sources of spatial error, with point locations resulting often spatially biased and discontinuous (i.e. omission error), and distribution maps commonly overestimating species presence within the range (i.e. commission error, Boitani et al., 2011). If, on one hand, such methodological choice may represent a shortcoming of our study, on the other hand it allowed to incorporate the highest amount of available spatial information on both native and invasive ranges of the investigated species. Besides, it is important to note that SDM do not take into account factors describing the establishment probability of an invasive species (i.e. probability to entry in a country and reach natural habitats, breeding success, interactions with native species, etc.). Therefore, the simple occurrence of suitable environments for an invader in a new area does not imply per se a successful establishment, leading to a possible overestimation of the predicted invasion risk. Notwithstanding, this shortcoming may be acceptable in a risk–assessment context, where a precautionary approach to evaluate and prevent possible invasion events is desirable. Another limitation could derive by the fact that invasive species may have the physiological potential to colonize new areas with climate conditions they did not experienced in the native range. In fact, an invader could have portions of its fundamental niche not expressed in the realized one (Hutchinson, 1957), potentially undergoing to niche shift events during the invasion process and thus leading to an underestimation/mismatch of the potentially suitable areas predicted with an SDM approach. The effect of niche shift during invasion events on SDM predictions has been investigated (Broennimann et al., 2007; Di Febbraro et al., 2013; Guisan et al., 2014) and the use of occurrences from both native and invasive ranges for the model training has been suggested as a way to reduce the potential bias that could arise (Broennimann and Guisan, 2008). Finally, a shortcoming may derive by the fact that we applied a single modelling algorithm instead of an ensemble approach. If, on one hand, we are aware that the great variability in the predictions obtained from different modelling algorithms advocate using an ensemble approach (Araújo and New, 2007), we are confident to have partially by-passed this limitation by using one of the most performing algorithms

(Elith et al., 2006), as similarly done by a number of recent studies (Pardi and Smith, 2015; McCune, 2016; Morán-Ordóñez et al., 2016; Wauchope et al., 2016).

The application of SDM helped to evaluate present and future matching between the climate niche of squirrel species, trained considering both native and invaded ranges (Broennimann and Guisan, 2008; Di Febbraro et al., 2013; Mateo et al., 2015; Mainali et al., 2015), and the climatic characteristics of worldwide mainland. Our approach allowed investigating how climate change could affect the potential distribution of invasive squirrels, suggesting for these species strong invasive potentialities for the current time and both a detrimental and favorable effect of climate change depending on the species. Given that climate represents the most important predictor of the distribution of some of the worst invasive alien species at global scale (Bellard et al., 2016), our approach could be improved at a local scale, by including other variables, such as landscape composition coupled with land–use change scenarios (Bellard et al., 2013), to better focus evaluations to real world and consider where an introduced species could spread without being stopped by insurmountable barriers. ✍

References

Algar A.C., Kharouba H.M., Young E.R., Kerr J.T., 2009. Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. Ecography 32: 22–33.

Allouche O., Tsoar A., Kadmon R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43: 1223–1232.

Araújo M.B., New M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22: 42–47.

Baddeley A., Turner R., 2005. spatstat: An R Package for Analyzing Spatial Point Patterns. Journal of Statistical Software 12(6): 1–42. Available at http://www.jstatsoft.org/v12/i06/

Barve N., Barve V., Jiménez-Valverde A., Lira-Noriega A., Maher S.P., Peterson A.T., Soberón J., Villalobos F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222: 1810–1819.

Bellard C., Thuiller W., Leroy B., Genovesi P., Bakkenes M., Courchamp F., 2013. Will climate change promote future invasions? Glob. Chang. Biol. 19: 3740–3748.

Bellard C., Leroy B., Thuiller W., Rysman J.F., Courchamp F., 2016. Major drivers of invasion risks throughout the world. Ecosphere 7(3): e01241. doi:10.1002/ecs2.1241

Bertolino S., 2009. Animal trade and non-indigenous species introduction: the world-wide spread of squirrels. Divers. Distrib. 15: 701–708.

Bertolino S., 2008. Introduction of the American grey squirrel (*Sciurus carolinensis*) in Europe: a case study in biological invasion. Curr. Sci. 95: 903–906.

Bertolino S., Colangelo P., Mori E., Capizzi D., 2015. Good for management, not for conservation: an overview of research, conservation and management of Italian small mammals. Hystrix 26(1): 25–35. doi:10.4404/hystrix-26.1-10263

Bertolino S., Currado I., Mazzoglio P.J., 1999. Finlayson's (variable) squirrel *Callosciurus finlaysoni* in Italy. Mammalia 63: 522–525.

Bertolino S., Di Montezemolo N.C., Preatoni D.G., Wauters L.A., Martinoli A., 2014. A grey future for Europe: *Sciurus carolinensis* is replacing native red squirrels in Italy. Biol. Invasions 16: 53–62.

Bertolino S., Lurz P.W.W., 2013. *Callosciurus* squirrels: worldwide introductions, ecological impacts and recommendations to prevent the establishment of new invasive populations. Mamm. Rev. 43: 22–33.

Bertolino S., Lurz P.W.W., Sanderson R., Rushton S.P., 2008. Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: A call for a co-ordinated European approach. Biol. Conserv. 141: 2564–2575.

Bertolino S., Mazzoglio P., Vaiana M., Currado I., 2004. Activity budget and foraging behavior of introduced *Callosciurus finlaysonii* (Rodentia, Sciuridae) in Italy. J. Mammalogy 85: 58–63.

Bivand R., Lewin-Koh N., 2013. maptools: Tools for reading and handling spatial objects. R package version 0.8-23. Available from http://CRAN.R-project.org/package=maptools

Bivand R., Rundel C., 2015. rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-13. Available from http://CRAN.R-project.org/package=rgeos

Boakes E.H., McGowan P.J.K., Fuller R.A., Chang-qing D., Clark N.E., O'Connor K., Mace G.M., 2010. Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. PLoS Biol. 8(6): e1000385. doi:10.1371/journal.pbio.1000385

Boitani L., Maiorano L., Baisero D., Falcucci A., Visconti P., Rondinini C., 2011. What spatial data do we need to develop global mammal conservation strategies? Philos. Trans. R. Soc. Lond., B, Biol. Sci. 366: 2623–2632.

Bomford M., 2008. Risk assessment models for establishment of exotic vertebrates in Australia and New Zealand. Invasive Animals Cooperative Research Centre. Canberra, Australia.

Bonnington C., Gaston K.J., Evans K.L., 2014. Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. Urban Ecosyst. 17: 533–546.

Bradley B.A., Blumenthal D.M., Early R., Grosholz E.D., Lawler J.J., Miller L.P., Sorte C.J.B., D'Antonio C.M., Diez J.M., Dukes J.S., 2011. Global change, global trade, and the next wave of plant invasions. Front. Ecol. Environ. 10: 20–28.

Bradley B.A., Oppenheimer M., Wilcove D.S., 2009. Climate change and plant invasions: restoration opportunities ahead? Glob. Chang. Biol. 15: 1511–1521.

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 U., Müller-Schärer H., Thuiller W., Peterson A.T., Guisan A., 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10: 701–709.

Buisson L., Thuiller W., Casajus N., Lek S., Grenouillet G., 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Chang. Biol. 16: 1145–1157.

Bush A., Nipperess D., Duursma D.E., Theischinger G., Turak E., Hughes L., 2014. Continental-scale assessment of risk to the Australian odonata from climate change. PLoS ONE 9(2): e88958. doi:10.1371/journal.pone.0088958

Cao Y., DeWalt R.E., Robinson J.L., Tweddale T., Hinz L., Pessino M., 2013. Using Maxent to model the historic distributions of stonefly species in Illinois streams: The effects of regularization and threshold selections. Ecol. Modell. 259: 30–39.

Davis R., Brown D.E., 1988. Documentation of the transplanting of Abert's squirrels. Southwest. Nat. 33: 490–492.

Di Febbraro M., Lurz P.W.W., Genovesi P., Maiorano L., Girardello M., Bertolino S., 2013. The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: a case with the American Eastern Grey Squirrel. PLoS ONE 8(7): e66559. doi:10.1371/journal.pone.0066559

Di Febbraro M., Roscioni F., Frate L., Carranza M.L., De Lisio L., De Rosa D., Marchetti M., Loy A., 2015. Long-term effects of traditional and conservation-oriented forest management on the distribution of vertebrates in Mediterranean forests: a hierarchical hybrid modelling approach. Divers. Distrib. 21: 1141–1154.

Diez J.M., D'Antonio C.M., Dukes J.S., Grosholz E.D., Olden J.D., Sorte C.J.B., Blumenthal D.M., Bradley B.A., Early R., Ibáñez I., Jones S.J., Lawler J.J., Miller L.P., 2012. Will extreme climatic events facilitate biological invasions? Front. Ecol. Environ. 10: 249–257.

Dubuis A., Pottier J., Rion V., Pellissier L., Theurillat J.P., Guisan A., 2011. Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. Divers. Distrib. 17: 1122–1131.

Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A, Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J.McC.M., Peterson A.T., Phillips S.J., Richardson K., Scachetti-Pereira R., Schapire R.E., Soberon J., Williams S., Wisz M.S., Zimmermann N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.

Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E., Yates C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17; 43–57.

Ficetola G.F., Maiorano L., Falcucci A., Dendoncker N., Boitani L., Padoa-Schioppa E., Miaud C., Thuiller W., 2010. Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. Glob. Chang. Biol. 16: 528–537.

Ficetola G.F., Thuiller W., Miaud C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species — the American bullfrog. Divers. Distrib. 13: 476–485.

Fielding A., Bell J., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24: 38–49.

Fitzpatrick M.C., Sanders N.J., Ferrier S., Longino J.T., Weiser M.D., Dunn R., 2011. Forecasting the future of biodiversity: a test of single- and multi-species models for ants in North America. Ecography 34: 836–847.

Genovesi P., Carboneras C., Vilà M., Walton P., 2015. EU adopts innovative legislation on invasive species: a step towards a global response to biological invasions? Biol. Invasions 17: 1307–1311.

Genovesi P., Shine C., 2004. European Strategy on Invasive Alien Species: Convention on the Conservation of European Wildlife and Habitats (Bern Convention). Nature and Environment, Vol 137. Council of Europe Publishing, Bern, Switzerland.

Guichón M.L., Benitez V.V., Gozzi A.C., Hertzriken M., Borgnia M., 2015. From a lag in vector activity to a constant increase of translocations: invasion of *Callosciurus squirrels* in Argentina. Biol. Invasions 17: 2597–2604.

Guisan A., Petitpierre B., Broennimann O., Daehler C., Kueffer C., 2014. Unifying niche shift studies: insights from biological invasions. Trends Ecol. Evol. 29: 1–10.

Gurnell J., Lurz P., Bertoldi W. 2014. The changing patterns in the distribution of red and grey squirrels in the North of England and Scotland between 1991 and 2010 based on volunteer surveys. Hystrix 25(2): 83–89. doi:10.4404/hystrix-25.2-9988

Hanley J.A., McNeil B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143: 29–36.

Hayes K., Barry S., 2008. Are there any consistent predictors of invasion success? Biol. Invasions 10: 483–506.

Heikkinen R.K., Luoto M., Araújo M.B., Virkkala R., Thuiller W., Sykes M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog. Phys. Geogr. 30: 751–777.

Henderson W., Bomford M., 2011. Detecting and preventing new incursions of exotic animals in Australia. Invasive Animals Cooperative Research Centre.

Hijmans R.J., 2015. raster: Geographic Data Analysis and Modeling. R package version 2.4-20. Available from https://CRAN.R-project.org/package=raster

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.J., Jarvis A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hijmans R.J., Phillips S.J., Leathwick J., Elith J., 2016. dismo: Species Distribution Modeling. R package version 1.0-15. Available from https://CRAN.R-project.org/package=dismo

Huntley B., Collingham Y.C., Willis S.G., Green R.E., 2008. Potential impacts of climatic change on European breeding birds. PLoS ONE 3(1): e1439. doi:10.1371/journal.pone.0001439

Hutchinson G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22: 66–77.

Innangi M., D'Alessandro F., Fioretto A., Di Febbraro M., 2015. Modeling distribution of Mediterranean beech forests and soil carbon stock under climate change scenarios. Clim. Res. 66: 25–36.

IPCC, 2013. Climate change 2013: the physical science basis. Cambridge University Press, Cambridge, United Kingdom.

IUCN, 2012. IUCN Red List of Threatened Species. Version 2012.1.

Jaynes E.T., 1957. Information Theory and Statistical Mechanics. II. Phys. Rev. 108, 171–190.

Jeschke J.M., Strayer D.L., 2006. Determinants of vertebrate invasion success in Europe and North America. Glob. Chang. Biol. 12: 1608–1619.

Jiménez-Valverde A., Peterson A.T., Soberón J., Overton J.M., Aragón P., Lobo J.M., 2011. Use of niche models in invasive species risk assessments. Biol. Invasions 13: 2785–2797.

Keller R.P., Lodge D.M., Finnoff D.C., 2007. Risk assessment for invasive species produces net bioeconomic benefits. Proc. Natl. Acad. Sci. 104: 203—207.

Liu C., Berry P., Dawson T., Pearson R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 3: 385--393.

Mainali K.P., Warren D.L., Dhileepan K., McConnachie A., Strathie L., Hassan G., Karki D., Shrestha B.B., Parmesan C., 2015. Projecting future expansion of invasive species: Comparing and improving methodologies for species distribution modeling. Glob. Chang. Biol. 21: 4464--4480.

Marmion M., Parviainen M., Luoto M., Heikkinen R.K., Thuiller W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15: 59--69.

Martinoli A., Bertolino S., Preatoni D., Balduzzi A., Marsan A., Genovesi P., Tosi G., Wauters L.A., 2011. Headcount 2010: the multiplication of the grey squirrel populations introduced to Italy. Hystrix 21(2): 127–136. doi:10.4404/hystrix-21.2-4463

Mateo R.G., Broennimann O., Petitpierre B., Muñoz J., van Rooy J., Laenen B., Guisan A., Vanderpoorten A., 2015. What is the potential of spread in invasive bryophytes? Ecography, 38: 480--487.

Mayol M., Riba M., González-Martínez S.C., Bagnoli F., Beaulieu J.L., Berganzo E., Burgarella C., Dubreuil M., Krajmerová D., Paule L., 2015. Adapting through glacial cycles: insights from a long-lived tree (*Taxus baccata*). New Phytol. 208: 973--986.

McCune J.L., 2016. Species distribution models predict rare species occurrences despite significant effects of landscape context. J. Appl. Ecol. (Early View) doi:10.1111/1365-2664.12702

McGeoch M.A., Genovesi P., Bellingham P.J., Costello M.J., McGrannachan C., Sheppard A., 2015. Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion. Biol. Invasions 18(2): 299—314.

Merow C., Smith M.J., Silander J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36: 1058—1069.

Morán-Ordóñez A., Whitehead A.L., Luck G.W., Cook G.D., Maggini R., Fitzsimons J.A., Wintle B.A., 2016. Analysis of trade-offs between biodiversity, carbon farming and agricultural development in northern australia reveals the benefits of strategic planning. Conserv. Lett. (Early View) doi:10.1111/conl.12255

Mori E., Mazza G., Marchetti M., Panzeri M., Gager Y., Bertolino S., Di Febbraro M., 2015. The masked invader strikes again: the conquest of Italy by the Northern raccoon. Hystrix 26(1): 47–51. doi:10.4404/hystrix-26.1-11035

Olson D.M., Dinerstein E., Wikramanayake E.D., Burgess N.D., Powell G.V.N., Underwood E.C., D'Amico J.A., Itoua I., Strand H.E., Morrison J.C., Loucks C.J., Allnutt T.F., Ricketts T.H., Kura Y., Lamoreux J.F., Wettengel W.W., Hedao P., Kassem K.R., 2001. Terrestrial Ecoregions of the World: a new map of life on Earth. Bioscience 51: 933.

Pardi M.I., Smith F.A., 2015. Biotic responses of canids to the terminal Pleistocene megafauna extinction. Ecography 39: 141--151.

Parker T.S., Nilon C.H., 2012. Urban landscape characteristics correlated with the synurbization of wildlife. Landsc. Urban Plan. 106: 316—325.

Phillips S.J., Anderson R.P., Schapire R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190: 231—259.

Phillips S.J., Dudík M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 2005–2010.

Pyke C.R., Thomas R., Porter R.D., Hellmann J.J., Dukes J.S., Lodge D.M., Chavarria G., 2008. Current practices and future opportunities for policy on climate change and invasive species. Conserv. Biol. 22: 585--592.

R Development Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/

Rödder D., Lötters S., 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). Glob. Ecol. Biogeogr. 18: 674—687.

Roscioni F., Rebelo H., Russo D., Carranza M.L., Di Febbraro M., Loy A., 2014. A modelling approach to infer the effects of wind farms on landscape connectivity for bats. Landsc. Ecol. 29: 891—903.

Roscioni F., Russo D., Di Febbraro M., Frate L., Carranza M.L., Loy A., 2013. Regional-scale modelling of the cumulative impact of wind farms on bats. Biodivers. Conserv. 22, 1821--1835.

Russo D., Di Febbraro M., Cistrone L., Jones G., Smeraldo S., Garonna A.P., Bosso L., 2015. Protecting one, protecting both? Scale-dependent ecological differences in two species using dead trees, the rosalia longicorn beetle and the barbastelle bat. J. Zool. 297: 165—175.

Russo D., Di Febbraro M., Rebelo H., Mucedda M., Cistrone L., Agnelli P., De Pasquale P.P., Martinoli A., Scaravelli D., Spilinga C., Bosso L., 2014. What story does geographic separation of insular bats tell? A case study on Sardinian Rhinolophids. PLoS ONE 9(10): e110894. doi:10.1371/journal.pone.0110894

Signorile A.L., Wang J., Lurz P.W.W., Bertolino S., Carbone C., Reuman D.C., 2014. Do founder size, genetic diversity and structure influence rates of expansion of North American grey squirrels in Europe? Divers. Distrib. 20: 918--930.

Strubbe D., Beauchard O., Matthysen E., 2015. Niche conservatism among non-native vertebrates in Europe and North America. Ecography 38: 321--329.

Thuiller W., Richardson D.M., Pyšek P., Midgley G.F., Hughes G.O., Rouget M., 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob. Chang. Biol. 11: 2234--2250.

UNEP-WCMC, 2010a. Review of the Grey Squirrel *Sciurus carolinensis*. Cambridge.

UNEP-WCMC 2010b. Review of *Callosciurus erythraeus* and S*ciurus niger*. Cambridge.

Van Wilgen N.J., Richardson D.M., 2012. The Roles of Climate, Phylogenetic Relatedness, Introduction Effort, and Reproductive Traits in the Establishment of Non-Native Reptiles and Amphibians. Conserv. Biol. 26: 267--277.

Walther G.R., Roques A., Hulme P.E., Sykes M.T., Pyšek P., Kühn I., Zobel M., Bacher S., Botta-Dukát Z., Bugmann H., Czúcz B., Dauber J., Hickler T., Jarošík V., Kenis M., Klotz S., Minchin D., Moora M., Nentwig W., Ott J., Panov V.E., Reineking B., Robinet C., Semenchenko V., Solarz W., Thuiller W., Vilà M., Vohland K., Settele J., 2009. Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24: 686--693.

Wauchope H.S., Shaw J.D., Varpe Ø., Lappo E.G., Boertmann D., Lanctot R.B., Fuller R.A., 2016. Rapid climate-driven loss of breeding habitat for Arctic migratory birds. Glob. Chang. Biol. (Early View) doi:10.1111/gcb.13404

Wood D.J.A., Koprowski J.L., Lurz P.W.W., 2007. Tree squirrel introduction: a theoretical approach with population viability analysis. J. Mammal. 88: 1271—1279.

Yannic G., Pellissier L., Ortego J., Lecomte N., Couturier S., Cuyler C., Dussault C., Hundertmark K.J., Irvine R.J., Jenkins D.A., Kolpashikov L., Mager K., Musiani M., Parker K.L., Røed K.H., Sipko T., Þórisson S.G., Weckworth B.V., Guisan A., Bernatchez L., Côté S.D., 2013. Genetic diversity in caribou linked to past and future climate change. Nat. Clim. Chang. 4: 132--137.

Zuur A.F., Ieno E.N., Elphick C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3—14.

Associate Editor: L. Maiorano