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The importance of taxonomy in species distribution models at a global scale: the case of an overlooked alien squirrel facing taxonomic revision

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Abstract

The Siberian chipmunk is native to north-eastern Asia, but alien populations of this squirrel, introduced through the pet trade, occur in many European countries. This rodent has been listed as an invasive species of European concern, being a potential vector of ticks spreading Lyme disease. We aimed to assess its current distribution range and to identify areas of potential invasion. Two sets of species distribution models were conducted, one considering the locations of the species (n = 625 occurrences) and the other with only the occurrences of the Korean subspecies (the invasive one in Europe; n = 255 occurrences), which might be a separate species from the Siberian one. We included 19 uncorrelated predictors (two topographic, nine land cover, five bioclimatic and three anthropogenic variables), which may represent the habitat characteristics of the target species. Most of the northern hemisphere supports the establishment of the Siberian chipmunk, particularly for the invasive Korean subspecies (especially in Europe, where it is already established), mostly in urban areas. Anthropogenic food supply was found to be an important factor promoting the growth of alien populations of chipmunks, whereas the presence of the native red squirrel at the time of introduction may limit it.

Introduction

Spatial models have been thoroughly applied in conservation biology to inform both policy and management decisions (Helliwell & Chapman, 2013). Species distribution models (SDMs, also known as ecological niche models; Guisan *et al.*, 2013; Buchadas *et al.*, 2017), are correlative models, which relate species (i.e. the response variable) to environmental predictors (i.e. predictor variables). SDMs have been successfully used in studies concerning invasive species, one of the main components of the human-driven global environmental change (Jeschke *et al.*, 2014; Hulme, 2015; Dyer *et al.*, 2017). Several studies reported the high predictive accuracy of SDMs in estimating potential areas of alien species invasion (Stohlgren & Schnase, 2006; Crall *et al.*, 2013; Mori *et al.*, 2015; Taucare-Ríos, Bizama & Bustamante, 2016; but see Buchadas *et al.*, 2017). Spatially explicit models are also useful tools to investigate the response of animal species to habitat change at the population level; conversely, building them at large spatial scales or for many taxa is challenging and may produce unreliable outputs (Dunning *et al.*, 1995; Chandler & Clark, 2014).

SDMs require the collection of precise occurrences throughout the species range, both for native and introduced populations (Guisan *et al.*, 2013). Up to the early 2000s, to collect reliable species occurrence data from online datasets or platforms was quite hard (Stohlgren & Schnase, 2006) and, thus, field investigations were often necessary. Recently, the explosion of social networks and open-access online platforms has resulted in the collection of species occurrences through citizen-science, wildlife photography and expert reports, and seem to have partially overcome this issue (Dylewski *et al.*, 2017; Suzuki-Ohno *et al.*, 2017; Tiago, Pereira & Capinha, 2017). In this context, one of the main issues related to species occurrence data is their reliability and verifiability (Mori, Di Bari & Coraglia, 2018a). One of the main assumptions for producing reliable results from SDMs is that the taxonomic status of the study species should be well-defined. Different subspecies of the same species may show different distribution patterns, different habitat requirements and, thus, different establishment success after introduction (Rushton *et al.*, 2006; Cardador *et al.*, 2016; Le Gros *et al.*, 2016; Menchetti, Mori & Angelici, 2016). One of the most successful bird invaders, the ring-necked parakeet *Psittacula krameri*, occurs across a wide

range, including central Africa and the Indian subcontinent (Menchetti *et al.*, 2016), but the Asian subspecies are more adapted than African ones to European temperate to cold climates (Cardador *et al.*, 2016; Le Gros *et al.*, 2016; Luna *et al.*, 2017). Currently, molecular analyses and geometric morphometrics are redefining the taxonomic status of many species worldwide, resulting in the splitting or clumping animal taxa (e.g. Roca *et al.*, 2001; Puechmaille *et al.*, 2012; Koepfli *et al.*, 2015; Hernández-Roldán *et al.*, 2016). This is remarkably evident for small mammal species (e.g. rodents and shrews), whose conservation has been long overlooked (Bertolino *et al.*, 2015). Genetic studies have raised the potential of a number of new species by splitting those having wide geographical ranges, particularly for those taxa showing different morphological and behavioral adaptations to local environments (e.g. Mediterranean water shrews in Italy and Spain: Igea *et al.*, 2015; water voles in Italy: Castiglia *et al.*, 2016).

Among invasive rodents, the Siberian chipmunk *Eutamias sibiricus* is the only Palaearctic chipmunk species, with a wide natural extent of occurrence, ranging from Russia to Korea through Mongolia and China (Obolenskaya, 2008). The subspecific classification, based on morphology, has not been confirmed by recent morphometric and molecular analyses (Obolenskaya *et al.*, 2009; Patterson & Norris, 2016). Genetic studies have identified only three defined and divergent clades within *E. sibiricus* (Obolenskaya *et al.*, 2009; Patterson & Norris, 2016; Lissovsky *et al.*, 2017): the Siberian chipmunk *E. s. sibiricus,* the Korean chipmunk *E. s. barberi* and the Chinese chipmunk *E. s. senescens.* These genetic distances between these clades exceed interspecific genetic distances between other chipmunk species, thus potentially they represent three species (Lissovsky *et al.*, 2017). Marked differences occur also in skull morphometrics, head and contrast of stripes, with the Chinese one having the lightest dark stripes (Obolenskaya *et al.*, 2009; Lissovsky *et al.*, 2017). These differences allowed researchers to distinguish Siberian chipmunk subspecies even by phenotype alone. Furthermore, Pisanu *et al.* (2013) showed that differences also occur in bioacoustics, including alarm calls.

The Siberian chipmunk *sensu lato* is a very popular, widely traded pet squirrel (Bertolino, 2009), which has established many alien populations in Eurasia (Mori, Zozzoli & Menchetti, 2018b). According to phenotype and genetics, alien populations in Europe belong to the Korean clade (Dal Farra, Cassol & Lapini, 1996; Pisanu *et al.*, 2013). Since August 2016, the European Regulation 1143/2014 lists it among the invasive alien species of European Union Concern, mostly because of potential health impacts of this species (Vourc'h *et al.*, 2007, 2016; Mori *et al.*, 2018b). Thus, predicting the potential distribution of the Siberian chipmunk in Europe is strictly necessary to design sound management actions to prevent the spread of alien populations.

Given that different subspecies of *E. sibiricus* experience different conditions, showing different habitat preferences (Obolenskaya, 2008; Jo, Seomun & Baccus, 2014; cf. also Rushton *et al.*, 2006), we expected that (1) model outputs can be influenced by the taxonomic level and that (2) the probability of occurrence in the invaded range can be better predicted, if locations of the only invasive subspecies are used. Thus, the aim of our research was to test whether alternative SDMs strategies (i.e. models fitted with Korean subspecies locations only vs. models based on pooled locations from the entire range of *E. sibiricus*) lead to different predictions of Siberian chipmunk invasion risk throughout the world.

Materials and methods

Data collection

Most of the native range of *E. sibiricus* is included within the Russian (former USSR) borders (Obolenskaya, 2008). Russia currently lacks an updated national biodiversity database (Ivanova & Shashkov, 2016), with the Russian database including very few species occurrences (Russian database: www.zmmu.msu.ru/rusmam/). Thus, we collected occurrence records in both native and invaded range from a number of sources: (1) online databases (i.e. iNaturalist.org, Ornitho.it, Global Biodiversity Information Facility, Waarneming.be, Waarneming.nl, Naturgucker.de, Centre Suisse de Cartographie de la Faune); (2) public photos posted on Facebook and groups dealing with free-ranging chipmunks (www.facebook.com/SiberischegrondeekhoornsinTilburg); (3) observations posted on the image-hosting website www.flickr.com; (4) scientific papers (e.g. Lissovsky *et al.*, 2017), books and gray literature; (5) contacts with local experts and research groups. Some occurrences were also obtained by a private project collecting squirrel occurrences in Italy ('SaveRedSquirrel': Mori & Menchetti, 2014). When photos of Siberian chipmunks both on Facebook and on Flickr were detected, we obtained exact coordinates and assessed data reliability by directly contacting authors and by searching for literature confirming the species presence (cf. Ancillotto *et al.*, 2016).

Given that the 'Siberian chipmunk' may be a species *complex* (Obolenskaya *et al.*, 2009), we considered two set of locations to develop SDMs, one including only occurrences of *E. s. barberi* (i.e. the invasive subspecies, from Korea and invaded range) and another with the total range of *E. sibiricus*. According to Obolenskaya *et al.* (2009), chipmunks in Hokkaido (Japan) belonged to the (sub)species *E. (s.) sibiricus*, but some photos we obtained showed that they have the phenotype of *E. (s.) barberi* (Obolenskaya *et al.*, 2009). Given that more than one introduction event may have been happened, we included occurrences from Hokkaido in both SDMs. Conversely, both genetics and morphology showed that individuals

Table 1 Number of occurrences of *E. (s.) barberi* (Dataset 1) and *E. sibiricus* (Dataset 2) collected from different sources

Source	Dataset 1	Dataset 2
Facebook	6	16
Local expert/photographers	61	102
Flickr	49	75
Online databases	102	104
Scientific papers	16	306
«SaveRedSquirrel» database	21	22

from Sakhalin island belong to *E. (s.) sibiricus* (Obolenskaya *et al.*, 2009). The first set of locations included 255 observations corresponding to 249 different locations (*E. s. barberi*, native and invaded, i.e. Dataset 1), the second one included 625 observations corresponding to 618 locations (*E. sibiricus*, native and invaded, i.e. Dataset 2: Table 1). For exploration purposes, we also tested SDMs removing all the locations collected in Hokkaido ($N = 16$; Figures S1, S2 in Appendix S1) following Obolenskaya *et al.* (2009), who ascribed the individuals present in this island to the nominal subspecies.

Predictor variables

We initially took into account a total of 36 predictors (two topographic, 11 land cover, 19 bioclimatic and four anthropogenic variables), which may represent the habitat characteristics of the target species (Obolenskaya, 2008; Jo *et al.*, 2014; Table 2). Topographic variables were derived from a digital elevation model (DEM), with a spatial resolution of 15 m (ASTER GDEM, gdem.ersdac.jspacesystems.or.jp), whereas land cover features were derived from a recently developed datasets (Tuanmu & Jetz, 2014; www.earthenv.org/landcover) at 1 km resolution. Bioclimatic predictors were collected from the WorldClim dataset (www.worldclim.org) for the current period (1950–2000 average) at 2.5 min resolution (≈5 km) and finally anthropogenic variables encompassed percentage and (Euclidean) distance to urban/built-up areas (Tuanmu & Jetz, 2014), to roads (derived from OpenStreetMap; www.openstreetmap.org) and human population density, available at the spatial resolution of 1 km (Gridded Population of the World, GPW; http://beta.sedac.ciesin.columbia.edu/data/collection/gpw-v4). All these 36 predictors were resampled at a spatial resolution of 5 km.

We calculated the Variance Inflation Factor (VIF) for all the variables and we removed predictor variables with values higher than three (i.e. highly correlated to other predictors;

Table 2 Predictor variables considered in the analysis

Variable	Units	VIF
Altitude	m a.s.l.	1.621
Slope	°	1.422
Needle-leaf forests	%	1.625
Broad-leaf forests	%	2.722
Mixed forests	%	1.699
Shrubs	%	1.626
Herbaceous Vegetation	%	1.605
Cultivated and Managed Vegetation	%	2.558
Regularly Flooded Vegetation	%	1.077
Snow/ice*	%	>3
Barren*	%	>3
Open water	%	1.358
Shannon diversity index of habitats	$H' = -\Sigma\,(p_i \times lnp_i)$	2.649
Bio 1–Annual mean temperature*	°C	>3
Bio 2–Mean diurnal range	°C	2.195
Bio 3–Isothermality [(BIO2/BIO7) × 100]*	°C × 100	>3
Bio 4–Temperature seasonality*	standard deviation *100	>3
Bio 5–Max temperature of warmest month*	°C	>3
Bio 6–Min temperature of coldest month*	°C	>3
Bio 7–Temperature annual range	°C	1.936
Bio 8–Mean temperature of wettest quarter *	°C	>3
Bio 9–Mean temperature of driest quarter*	°C	>3
Bio 10–Mean temperature of the warmest quarter*	°C	>3
Bio 11–Mean temperature of the coldest quarter*	°C	>3
Bio 12–Annual precipitation*	mm	>3
Bio 13–Precipitation of wettest month*	mm	>3
Bio 14–Precipitation of driest month*	mm	>3
Bio 15–Precipitation seasonality	coefficient of variation	1.472
Bio 16–Precipitation of wettest quarter*	mm	>3
Bio 17–Precipitation of the driest quarter*	mm	>3
Bio 18–Precipitation of the warmest quarter	mm	1.821
Bio 19–Precipitation of the coldest quarter	mm	1.699
Urban/Built-up	%	1.259
Distance to urban/Built-up*	m	> 3
Distance to roads	m	1.821
Human population density	number km^{-2}	1.251

Variables with a variance inflation factor (VIF) > 3 were removed (*) due to multi-collinearity with other variables.

Zuur, Ieno & Elphick, 2010; Table 2), to avoid multi-collinearity among predictors. From the initial set of 36 predictor variables, we removed 17 predictors with values of VIF > 3 and thus we finally considered a total of 19 predictors (Table 2) in the further analyses.

Moreover, we alternatively combined Dataset 1 and Dataset 2 with the non-multi-correlated predictor variables, to identify novel environments in which extrapolations based on SDMs are uncertain and should not be considered. For this purpose, instead of using the Multivariate Environmental Similarity Surface (MESS; Elith, Kearney & Phillips, 2010), we used a modified version of MESS (mMESS; Milanesi *et al.*, 2017: Appendix S2). Compared to the original MESS, mMESS is not limited by the use of the most dissimilar variable as indicator of overall similarity. In other words, in MESS, the most dissimilar variable for a given pixel is the only one having an effect in the calculation of the MESS index for this pixel, whereas in mMESS all the predictor variables are considered (Milanesi *et al.*, 2017). In mMESS, values equal or higher than one indicate that a pixel has at least one predictor variable with values outside the range of the species locations and thus it should not be considered for the SDM development (Milanesi *et al.*, 2017).

Species distribution models

We estimated the *fundamental niche* (Hutchinson, 1957) of *E. s. barberi* and *E. sibiricus* as the '*n*-dimensional hypervolume' in which every point corresponds to a state of the environment which would permit (a species) to exist indefinitely and not the *realized niche* (Hutchinson, 1957), the niche reduced because of the presence of interspecific competition or predators. Specifically, we used the average ensemble prediction (EP: Thuiller *et al.*, 2009) derived from 10 SDMs to assess species distribution, avoiding biased estimation due to single model uncertainty. In detail, we developed: (1) Artificial Neural Networks (ANN: Ripley, 2007), (2) Boosted Regression Trees (BRT: Friedman, 2001), (3) Classification Tree Analyses (CTA: Breiman *et al.*, 1984), (4) Flexible Discriminant Analyses (FDA: Hastie, Tibshirani & Buja, 1994), (5) Generalized Additive Models (GAM: Hastie & Tibshirani, 1990), (6) Generalized Linear Models (GLM: McCullagh & Nelder, 1989), (7) Multivariate Adaptive Regression Splines (MARS: Friedman, 1991), (8) Maximum Entropy algorithm (MAXENT: Phillips, Anderson & Schapire, 2006), (9) factorial decomposition of Mahalanobis distances (MADIFA: Calenge *et al.*, 2008) and (10) Random Forests (RF: Breiman, 2001). SDMs were carried out through the packages ADEHABITAT (Calenge, 2006) and BIOMOD2 (Thuiller *et al.*, 2016) for the open-source software R v. 3.3.2 (www.R-project.org).

To avoid biased estimation of species distribution due to uneven sampling effort in our study area, we derived a sampling effort map through a Gaussian kernel density analysis (considering all the locations of the species). Thus, we used the values of the resulting sampling effort map as a bias grid in MADIFA, MAXENT and in all the other SDMs as case weights (Elith *et al.*, 2010; Fourcade *et al.*, 2014; Stolar & Nielsen, 2014; Milanesi *et al.*, 2015, 2017; Balestrieri *et al.*, 2016; Jarnevich *et al.*, 2017).

Thus, we generated 10 000 random points inside the minimum convex polygon estimated around native species locations, to serve as background data while considering all species occurrences (including those in the invaded range) as presence data. We found evidence of spatial autocorrelation among residuals of models and, therefore, we included X- and Y-coordinates of species locations and their interaction in SDMs (Pasinelli *et al.*, 2016). So, model residuals where no longer spatially autocorrelated (Pasinelli *et al.*, 2016).

We carried out 10-fold cross-validations (using a random subsample of 90% of the locations to calibrate the models and the remnant 10% to validate them; Thuiller *et al.*, 2009), to evaluate the predictive accuracy of SDMs through (1) the area under the receiver operating characteristic curve (AUC), (2) the true skills statistic (TSS) and (3) the Boyce index (BI). To avoid single model uncertainty, we calculated the ensemble prediction (EP) derived by the average predictions of the 10 SDMs (using all available locations of each Dataset). Thus, we converted the EP continuous map into a binary one (suitable/unsuitable), considering a threshold value estimated by maximizing the True Skill Statistics (TSS: Allouche, Tsoar & Kadmon, 2006; Thuiller *et al.*, 2016). Values higher and lower than the threshold represent suitable and unsuitable areas, respectively. Analyses were computed with the package BIOMOD2 (Thuiller *et al.*, 2016) in R v. 3.3.2 (www.R-project.org), alternatively considering Dataset 1 and Dataset 2 (see above).

Factors related to population abundance

We used GLMs to analyze the effects of (1) habitat suitability for *E. sibiricus*, (2) habitat suitability for *E. s. barberi*, (3) number of founder individuals, (4) year from first introduction, (5) absence of *Sciurus vulgaris* at the time of introduction, (6) latitude, (7) presence of food provided by humans and (8) distance from human settlements on the total population abundance in each introduction area. Variables (1) and (2) were taken from this study; all the other ones, as well as the response variable, from Mori *et al.* (2018b). In details, we obtained the number of founders from local reports or by directly asking an estimate to local researchers, based on first observations: in several cases (e.g. Dal Farra *et al.*, 1996; Mori *et al.*, 2018b), chipmunk escaped from cages or farms and, thus, we obtained the exact number of founders. Similarly, the presence of the native European red squirrels at the time of chipmunk introduction was reliably assessed by checking Mammal atlases carried out before chipmunk introduction (e.g. Bon *et al.*, 1995; Mitchell-Jones *et al.*, 1999), as well as by taking contacts with local researchers working on squirrels. Presence of 'squirrel feeders' (including intentional squirrel feeders, but also bird feeders) has been assessed through standardized questionnaires to workers and visitors of urban parks and natural areas where chipmunk populations are recorded (Mori *et al.*, 2018b; Zozzoli, Menchetti & Mori, 2018). Access to rubbish bins was not measured, thus not included in our

analysis, as it could be possible throughout the extent of occurrences of introduced populations of chipmunks.

We used subsets of uncorrelated variables (Pearson correlations $|r| > 0.7$; Dormann *et al.*, 2014) to develop GLMs in a multi-model inference approach. Specifically, we identify the best model(s) through the corrected Akaike Information Criterion (AICc; Akaike, 1974) for small sample size, considering only models with $\Delta AICc < 2$ (Burnham & Anderson, 2004). Our multi-model inference approach was developed using the R package *MuMIn* (Barton, 2009).

Results

Considering the resulting threshold value of 40.7 and 50.1 (considering Dataset 1 and Dataset 2, respectively), EP estimated the occurrence of *E. (s.) barberi* and *E. sibiricus* in total areas of 4 492 275 and 17 785 525 km^2, respectively (Figs 1 and 2; standard deviation maps of the resulting EPs are available in Appendix S1). Thus, the potential distribution of *E. sibiricus* was almost four times higher than that of *E. (s.) barberi* at global scale (Fig. 2).

The 10-fold cross-validations showed significant values for all the evaluation methods of all distribution models (Table 3), with values ranging between 0.872 and 0.998 for AUC, 0.821 and 0.998 for TSS and from 0.806 to 0.997 considering Dataset 1 and between 0.848 and 0.998 for AUC, 0.803 and 0.899 for TSS and from 0.909 to 0.999 for BI considering Dataset 2 (Table 3).

Food-provisioning by humans and habitat suitability for *E. (s.) barberi* were highly correlated (Pearson correlations $r = 0.9$) and thus we developed a set GLMs using alternatively one of these two variables in combination with the remnants. These resulted in a total of 96 GLMs and only two of them showed $\Delta AICc < 2$. Specifically, the two best models to estimate population abundance in each introduction area encompassed the presence of food provided by humans (in both the best models) while only Model 2 included the absence of *Sciurus vulgaris* at the time of introduction (Table 4).

Discussion

Understanding pathways and processes of biological invasions is crucial for their control, and mandatory to identify and anticipate potential invasion landscapes (Wonham, 2006; Mutascio *et al.*, 2018). Taxonomic revisions and subsequent range redefinitions are currently continuing for many mammalian taxa (e.g. Rueness *et al.*, 2011; Nater *et al.*, 2017), thus resulting in different patterns of species distribution. This is particularly relevant for invasive alien species (Beaumont *et al.*, 2009), as SDMs represent one of the most reliable tools to identify areas at risk of future invasions (Peterson, 2003; Mori *et al.*, 2015; Tingley *et al.*, 2018). Compared to other squirrel species (e.g. Bertolino *et al.*, 2015; Mazzamuto *et al.*, 2017), very little ecological information is available for the Siberian chipmunk in the introduced range (Marmet, Pisanu & Chapuis, 2009, 2011). In our study, we have developed SDMs to quantify and identify the global patterns of distribution of the Siberian chipmunk and of its Eastern-Asiatic subspecies, the 'Korean chipmunk', which is invasive in Europe. We found significant differences in the patterns of global distribution of these two groups (i.e. developing SDMs with occurrences of all subspecies and with only occurrences of the Korean subspecies) both in the native and in the invaded ranges, thus fulfilling our expectation (1). The invasive (sub) species *E. (s.) barberi* showed a wider area of potential invasion in Europe with respect to the species as a whole. Conversely, North America, where no invasive populations are present, but where this species is kept as pet, shows the highest suitability for *E. sibiricus*. Thus, our expectation (2) was also fulfilled. Accordingly, well-supported models using occurrences only of *E. (s.) barberi* better predicted the potential distribution of invasive chipmunks compared to similarly well-supported models using the whole set of collected occurrences for the species as a whole. This finding emphasizes the importance of starting from a strong and well-supported taxonomic base to develop reliable SDMs.

Most populations of introduced Siberian chipmunks in Europe occur in urban parks and suburban landscapes (Benassi

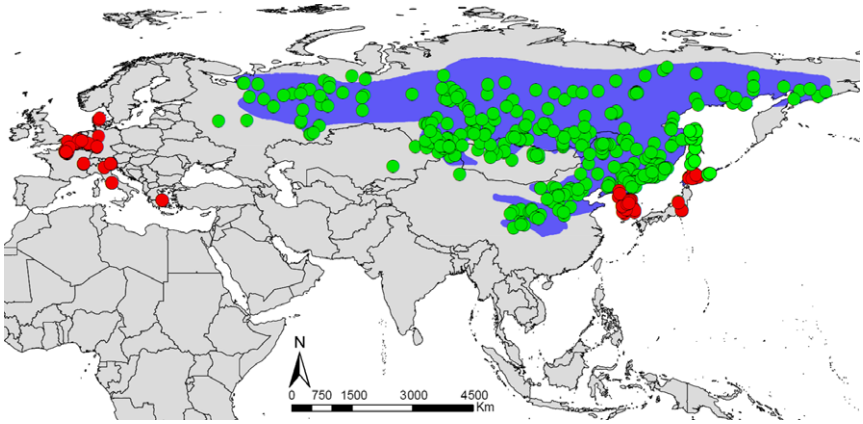

Figure 1 Records used for our analysis: red dots refer to the subspecies *Eutamias sibiricus barberi*. In blue, the natural distribution of the Siberian chipmunk from www.iucnredlist.org (accessed on 27.11.2017). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

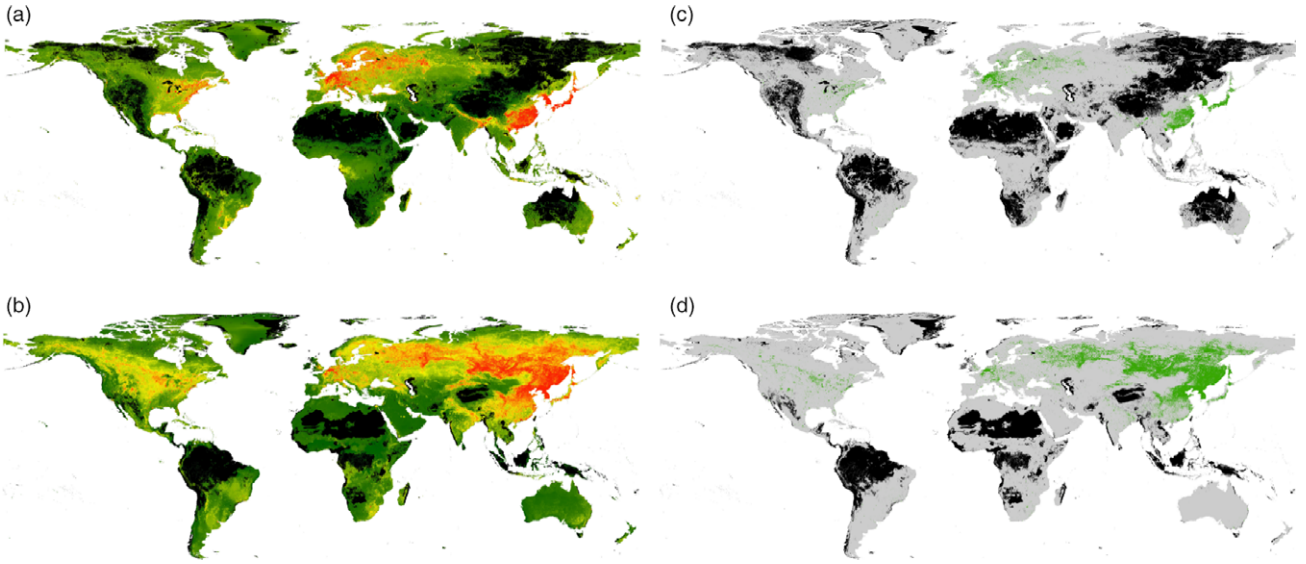

Figure 2 (a) Probability of occurrence of the Siberian chipmunk estimated using locations in Japan, Korea and the invaded range in Europe and (b) estimated using locations of all of Asia and the invaded range in Europe (red-green scale indicates higher-lower probability values, respectively) derived by the ensemble prediction of 10 species distribution models, (c) distribution of the species (in green) estimated using a threshold value of 40.7 (using locations in Japan, Korea and the invaded range in Europe) and (d) estimated using a threshold value of 50.1 (using locations of all of Asia and the invaded range in Europe). Relative areas of uncertain prediction identified by mMESS are shown in black. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

Table 3 Model evaluation with 10-fold cross-validation of the 10 species distribution methods and their ensemble prediction (EP). Average values are shown

	Korea-Japan + invaded			Asia + invaded		
Model	AUC	TSS	BI	AUC	TSS	BI
ANN	0.962	0.881	0.997	0.848	0.804	0.998
BRT	0.998	0.979	0.943	0.965	0.803	0.999
CTA	0.991	0.967	0.996	0.968	0.882	0.988
FDA	0.978	0.845	0.806	0.929	0.808	0.997
GAM	0.997	0.998	0.988	0.964	0.821	0.909
GLM	0.991	0.931	0.833	0.941	0.832	0.952
MADIFA	0.932	0.821	0.997	0.887	0.871	0.988
MARS	0.991	0.934	0.894	0.941	0.851	0.998
MAXENT	0.872	0.835	0.877	0.915	0.871	0.955
RF	0.999	0.998	0.964	0.998	0.899	0.998
EP	0.999	0.984	0.959	0.982	0.876	0.998

Area Under the Curve (AUC) ranges between 0 and 1 (worse than a random model and best discriminating model, respectively). True Skill Statistic (TSS) and Boyce's Index (BI) ranges between −1 and 1 (higher values indicate a good predictive accuracy, while 0 indicates random prediction). Average values are shown (*$P < 0.001$).

& Bertolino, 2011; Mori, Zozzoli & Mazza, 2018c; Mori *et al.*, 2018b). The fruit- and seed-based diet of this squirrel may have promoted its successful establishment in temperate areas, particularly where a great diversity of plant species occurs (e.g. in urban areas: Clergeau & Vergnes, 2011; Mori *et al.*, 2018c). Furthermore, our models suggested that the largest populations of this invasive squirrel occur where supplemental food is provided by humans (i.e. urban parks). Although European suburban areas often show high densities of invasive predators of Siberian chipmunks (e.g. feral cats *Felis catus* and American mink *Neovison vison*), public parks appeared to be important for the establishment of this euryphagous species (Forstmeier & Weiss, 2004; Jo *et al.*, 2014). Mori *et al.* (2018c) suggested that the range expansion of the larger-sized native Eurasian red squirrel may displace established populations of invasive smaller-sized chipmunks, forcing them to move in the opposite direction of the expansion front of the native species. Results of GLMs shown in this study provided statistical evidence to support this suggestion. Accordingly, the presence of the native species may have limited the establishment and spread of the alien one.

Table 4 Factors affecting population abundance of introduced Siberian chipmunk, estimated with multi-model inference through generalized linear models

Model	AICc	R^2	ΔAICc	Intercept	β (presence of food provided by humans)	β (absence of *Sciurus vulgaris* at the time of introduction)
Model 1	333.653	0.667	0	−101.575	531.013*	/
Model 2	334.726	0.693	1.073	−375.131	686.028*	291.793**

*$P < 0.001$, **$P < 0.05$.

Our study shows that a large part of the northern hemisphere may support the establishment and the spread of the Siberian chipmunk, both considering the species and, mostly, the Korean subspecies (particularly in Europe). As a precautionary principle, we suggest to focus on the model with the Korean (sub)species, which seems to be the only one currently recorded with alien populations in Europe (Pisanu *et al.*, 2013). This is in line with the results of our SDMs, which generally showed a higher predictive accuracy for the Korean taxon in Europe, and a higher invasive potential for this taxon with respect to '*Eutamias sibiricus*' as a whole.

Our linear models also suggested that food provided by urban park visitors is an important factor promoting the establishment of alien populations of Siberian chipmunks, as observed for other naturalized invasive species (e.g. Le Louarn *et al.*, 2018; Wauters & Martinoli, 2018). Considering the experiences from France, where the chipmunk is considered to be responsible for an increased spread of the Lyme disease (Vourc'h *et al.*, 2016), food-provisioning by humans in urban parks should be avoided to limit population growth. Furthermore, in line with the European Regulation 1143/2014, small and isolated populations should be rapidly removed to avoid range expansion and consequent impacts on local biodiversity and human health (Carboneras *et al.*, 2018; Nentwig *et al.*, 2018). At the same time, given that the Siberian chipmunk is still common as a pet despite the European trade ban, a response system with the immediate removal of new free-ranging individuals detected in the environment should be mandatorily activated (cf. Genovesi & Shine, 2004).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Figure S1. (A) Probability of occurrence of the Siberian chipmunk estimated using locations in Korea and the invaded range in Europe and (red-green scale indicates higher-lower probability values, respectively) derived by the ensemble prediction of 10 species distribution models, (B) distribution of the species (in green) estimated using a threshold value of 48.1. Relative areas of uncertain prediction identified by mMESS are shown in black. Figure S2. Standard deviation maps of the probability of occurrence of the Siberian chipmunk derived by the ensemble prediction of 10 species distribution models estimated using locations collected (A) in Japan, Korea and the invaded range in Europe, (B) in all of Asia and the invaded range in Europe and (C) in Korea and the invaded range in Europe (red-green scale indicates higher-lower absolute values, respectively). Relative areas of uncertain prediction identified by mMESS are shown in black.
Appendix S2. Description of the mMESS method