Protected Areas offer refuge from invasive species spreading under climate change

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Authors: Belinda Gallardo[1]*, David C. Aldridge[2], Pablo González-Moreno[3,†], Jan Pergl[4], Manuel Pizarro[1], Petr Pyšek[4,5,6], Wilfried Thuiller[7], Christopher Yesson[8], Montserrat Vilà[3]

[1] Pyrenean Institute of Ecology (IPE-CSIC), Biodiversity and Restoration Department, Avda. Montañana 1005, 50059 Zaragoza, Spain,

[2] Department of Zoology, University of Cambridge, The David Attenborough Building, Pembroke Street, CB2 3QZ Cambridge, UK

[3] Doñana Biological Station (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la Cartuja, 41092 Sevilla, Spain

[4] Institute of Botany, The Czech Academy of Sciences, Department of Invasion Ecology, CZ-25243 Průhonice, Czech Republic,

[5] Charles University, Faculty of Science, Department of Ecology, Viničná 7, CZ-12844 Prague, Czech Republic,

[6] Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Matieland 7602, South Africa,

[7] Univ. Grenoble Alpes, CNRS, Laboratoire d’Écologie Alpine (LECA), F-38000 Grenoble

[8] London Zoological Society, Institute of Zoology, Regent’s Park, NW1 4RY, London, UK

† CABI, Bakeham Lane, TW20 9TY, Egham, UK

*Correspondence to: belinda@ipe.csic.es; galla82@hotmail.com

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Abstract:

Protected Areas (PAs) are intended to provide native biodiversity and habitats with a refuge against the impacts of global change, particularly acting as natural filters against biological invasions. In practice, however, it is unknown how effective PAs will be in shielding native taxa from invasions under projected climate change. Here, we investigate the current and future potential distributions of 100 of the most invasive terrestrial, freshwater and marine species in Europe. We use this information to evaluate the combined threat posed by climate change and invasions to existing PAs and the most susceptible species they shelter. We found that only a quarter of Europe's marine and terrestrial areas protected over the last 100 years have been colonized by any of the invaders investigated, despite offering climatically suitable conditions for invasion. In addition, hotspots of invasive taxa and the most susceptible native species to their establishment do not match at large continental scales. Furthermore, the predicted richness of invaders is significantly lower inside PAs than outside them (by 11-18%). Invasive species are rare in long-established national parks and nature reserves, which are actively protected and often located in remote and pristine regions with very low human density. In contrast, the richness of invasive species is high in the more recently designated Natura 2000 sites, which are subject to high human accessibility. This situation may change in the future, since our models anticipate important shifts in species' ranges towards the north and east of Europe at unprecedented rates of 14-55 km/decade, depending on taxonomic group and scenario. This may seriously compromise the conservation of biodiversity and ecosystem services. This study is the first comprehensive assessment of the resistance that PAs provide against biological invasions and climate change on a continental scale, and illustrates their strategic value in safeguarding native biodiversity.

Introduction

Global species and habitat diversity are declining at unprecedented rates with no signs of abatement in spite of international efforts to halt biodiversity loss (Butchart *et al.*, 2010). Biological invasions and climate change are two key drivers behind such declines (Walther *et al.*, 2009). The proliferation of invasive species can be linked to 58% of recent species extinctions, and is currently considered a major threat for the conservation of native flora and fauna around the world (Bellard *et al.*, 2016a). This impact will be aggravated by climate change, expected to accelerate the risk of extinction for up to one in six species, depending on region (Bellard *et al.*, 2012, Urban, 2015). The problem is particularly acute in Europe, where the number of invasive species has increased four-fold in the last century (Hulme *et al.*, 2009), and is likely to continue increasing with the intensification of socioeconomic activities coupled with on-going climate changes (Seebens *et al.*, 2017, Seebens *et al.*, 2015).

Protected areas (PAs), as cornerstones of global conservation efforts, are championed as refugia for native species, locally preventing habitat degradation attributable to human activities (Rodrigues *et al.*, 2004), facilitating the adaptation of species and communities to on-going climate changes (Gaüzère *et al.*, 2016, Johnston *et al.*, 2013, Thomas *et al.*, 2012), and acting as a natural filter against invasions (Foxcroft *et al.*, 2011, Pyšek *et al.*, 2003). In practice, however, little is known about the effectiveness of PAs in shielding native taxa from biological invasions (Pyšek *et al.*, 2013).

Europe has one of the largest coordinated networks of protected areas in the world. The Natura 2000 network of protected sites, coupled with national designated areas such as national parks and nature reserves, provide crucial shelter from the damaging effects of human-related stressors to over 1,100 species listed by the Habitats (92/43/EEC) and Birds (2009/147/EC) Directives (Gaston *et al.*, 2008, Gruber *et al.*, 2012).

Several studies over recent years have documented how climate change – and associated changes in land-use and human transportation— progressively removes physiological constraints for the growth and spread of some invasive species, particularly those introduced from warm climates, facilitating their expansion into regions where they previously could not survive and reproduce (Walther *et al.*, 2009). However, no studies have explored to what extent climate change may facilitate (or constrain) the expansion of invasive species into PAs at continental scales.

Here, we investigate the current and future distribution of some of the most serious invasive species across Europe, integrating for the first time the study of the terrestrial, freshwater and marine environments at a scale of an entire continent. We use this information to evaluate the combined threat posed by climate change and biological invasions to existing PAs and the most susceptible species they harbour. To guarantee a high relevance to researchers and environmental practitioners, we focus on “100 of the most invasive species in Europe”, a representative set of invaders with different life-strategies, invaded habitats, and impacts (Vilà *et al.*, 2009). The spread of these invaders poses a serious threat to a large variety of native European taxa through competition, predation, parasitism, hybridization and indirect habitat alteration (Hulme *et al.*, 2009). For this reason, here we evaluate the effectiveness of protected areas in shielding native biota from the current and future impacts of invasive species. Findings from this study are pivotal to support the implementation of the Habitats and Birds Directives as well as the European Regulation (1143/2014) on invasive alien species, all of which prioritize the protection of native biodiversity, habitats, and related ecosystem services.

Methods

Invasive Species Occurrence

Information on the current global (i.e. native and invaded) spatial distribution of 100 of the most invasive species in Europe (see the list of species in http://www.europe-aliens.org/speciesTheWorst.do), was obtained from multiple international and regional data gateways: the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), the Biological Collection Access Service for Europe (BioCase, http://www.biocase.org/), the Ocean Biogeography Information System (IOBIS, http://www.iobis.org/), the UK's National Biodiversity Network (https://data.nbn.org.uk/), DiscoverLife (http://www.discoverlife.org/), Aquamaps (http://www.aquamaps.org/) and the Integrated Digitized Biocollections (iDigBio, https://www.idigbio.org/).

To cover gaps in the distribution of invaders (i.e. no georeferenced records in regions where the species is suspected to be present), data were checked against the global distribution of each species described in CABI-Invasive Species Compendium (CABI-ISC, http://www.cabi.org/isc/) that lists countries (or major oceanic regions) where the species has been reported (either as native or introduced). We then performed an extensive ISI Web of Knowledge literature review using a combination of keywords including the species taxonomic name and the specific data-missing region (Suppl Material, Table S1).

As a result, over 1.15 million georeferenced locations were compiled from 184 countries across the globe, detailing the native and invasive distribution of candidate invasive species. Because data quality (sample size, spatial errors, spatial auto-correlation) strongly determines the performance of distribution models (Graham *et al.*, 2008, Wisz *et al.*, 2008), we applied an exhaustive cleaning protocol (see Supplementary Materials) that removes erroneous records (e.g. duplicates, misleading values, low resolution coordinates), reduces sampling bias and ultimately allows analysis of macroecological patterns (García-Roselló *et al.*, 2015). As a result, the number of georeferenced records available for this study was reduced to 238,000, with an average 2,767 per species. Species with less than 100 occurrence records were discarded for further modelling to avoid any potential influence of low sample sizes (Barbet-Massin *et al.*, 2012), so that 86 species (27 terrestrial animals, 18 terrestrial plants, 13 freshwater, and 28 marine organisms) were finally evaluated (see the complete list of species in Table S2).

Susceptible Protected Species

To identify the native protected species that may be affected by the 86 focus invaders, we consulted impact information from the Global Invasive Species Database (GISD, http://www.iucngisd.org/gisd/), CABI-ISC, the European Network on Invasive Alien Species (NOBANIS, https://www.nobanis.org/) and the European Alien Species Information Network (EASIN, http://easin.jrc.ec.europa.eu/). We restricted our analysis to species: i) considered native in Europe, ii) with published evidence of negative impact from any of the 86 focus invaders , and iii) protected under the Birds or Habitats Directives, or by other internationally relevant Conventions (e.g. Bern Convention, OSPAR Convention, Bonn Convention, Helsinki Convention and Barcelona SPA/BD Protocol). It must thus be noted that invasive species in our list may affect directly and indirectly a much larger number of native (as well as other invasive) species that do not meet our criteria for selection.

As a result, we identified 148 native protected species that may be susceptible to the expansion of our focus invaders (54 terrestrial animals, 37 semi-aquatic animals, 24 freshwater organisms, 22 terrestrial plants, and 9 marine organisms) (Table S3). Their conservation status according to the IUCN European Red List was variable: 2 Data Deficient, 22 Not Evaluated, 79 Least Concern, 13 Near Threatened, 15 Vulnerable, 9 Endangered and 8 Critically Endangered. Examples of the latter include the European eel (*Anguilla anguilla*), several bivalve freshwater mussels (*Margaritifera auricularia, M. margaritifera* and *Unio gibbus*),the berlengensis Armeria (*Armeria berlengensis*), Maltase cliff-orache (*Cremnophyton lanfrancoi*), and Maltese everlasting (*Helichrysum melitense*). The most threatening invaders in our list included the American mink (affecting 37 species), brown rat (29) and red-swamp crayfish (16), altogether posing a threat to 69 native protected species (Table S3).

Protected Areas In Europe

In this study, we investigate the potential joint threat posed by climate change and the concurrent expansion of invasive species on the conservation of protected areas and species in Europe. We restricted our analyses to PAs with area > 1 km^2 to match the resolution of information on invasive species occurrence and environmental predictors. Two sources of PAs were used (more details in Suppl. Material):

- **Nationally designated areas**. We extracted from the World Database on Protected Areas (WDPA, http://protectedplanet.net/) a map including PAs belonging to IUCN categories I and II that correspond to nature reserves and national parks respectively. Once PAs > 1km^2 in Europe were extracted, 2,038 nationally designated sites were obtained (1,882 inland covering both terrestrial and freshwater environments, 156 in marine areas). Nationally designated areas are large unmodified or slightly modified areas, without permanent or significant human habitation, which are strictly protected to preserve biodiversity and ecosystem processes. They are on average 22±16 years old (designation between 1920 and 2015) and have a size of 73±305 km^2 (area range: 1-5,551 km^2).

- **Natura 2000**. We extracted from the European Commission's repository (http://ec.europa.eu/environment) the Natura 2000 database and shapefile containing information from 11,046 inland (terrestrial and freshwater) and 2,064 marine PAs > 1km^2. Natura 2000 areas in our database have been more recently designated (11±5 years old, designation between 1940 and 2015), and are generally larger (89±317 km^2, range: 1-9,016 km^2) than nationally designated areas. As many as 90% of nationally designated areas in our database are also integrated within Natura 2000 (Fig. S1). Natura 2000 is not a system of strict nature reserves from which all human activities are excluded, but low-intensity human activities are allowed on most of the land.

These two distinct networks, totaling 15,148 PAs (18% of Europe's inland and 6% of marine surface), allow the assessment of the effectiveness of protected areas in shielding native biota from the current and future impacts of invasive species.

First, using our comprehensive database on the global occurrence of Europe's 86 most invasive species, we identified the invaders already reported from each protected area (Richness Invasive Species, RIS). We must note, however, that this is likely an underestimation since rigorous data on the continent-wide distribution and abundance of invasive species within PAs are rarely available (Pyšek *et al.*, 2013). With this information, we calculated the number of invasive species recorded per unit area protected over time. Second, we obtained the incidence of the 148 susceptible native species in each protected area from the European Nature Information System (EUNIS, http://eunis.eea.europa.eu/), which lists all protected areas with known populations of each listed species. While EUNIS is useful to identify the protected areas that shelter each native species investigated, lack of spatially-explicit information (geo-referenced locations) prevented modelling the distribution of native species under future scenarios. Finally, because EUNIS depends on information provided by member states and may underestimate the known distribution of susceptible native species; we complemented it with additional records from GBIF.

Environmental Predictors

Terrestrial and Freshwater Scenarios. Candidate environmental predictors to model the potential expansion of 58 inland invasive species (i.e. terrestrial and freshwater) included 19 bioclimatic variables extracted from WorldClim-Global Climate Data (http://www.worldclim.org/). Bioclimatic variables represent annual trends, seasonality, extremes or limiting environmental factors related to temperature and precipitation for the 1950-2000 reference period (Hijmans *et al.*, 2005), that are commonly used in species distribution models. To account for the strong human relationship usually displayed by invasive species, we incorporated an "accessibility" proxy as covariate. Produced by the European Commission (http://forobs.jrc.ec.europa.eu/products/gam/), this proxy measures the travel time to the nearest city (i.e. population > 50,000), thereby integrating both distance to urban areas and the presence of transportation networks (Nelson, 2008). This map has been used before to compensate sampling bias towards areas with high accessibility (Fourcade *et al.*, 2014), which may be particularly important in the case of invasive species.

Identifying the most appropriate variables for modelling is crucial to maximize the accuracy of distribution models and their projection in space in time. In this study, we followed a selection protocol that involved removing highly correlated and multi-collinear variables while prioritizing predictors that are ecologically meaningful to explain the large-scale distribution of flora and fauna (see Tables S4-S5). Final variables considered for modelling included: accessibility (travel time, hours), maximum annual temperature (°C), minimum annual temperature (°C), maximum annual precipitation (mm), minimum annual precipitation (mm) and precipitation seasonality (Fig. S2). For all inland predictors, we chose a high resolution of 30 arc-seconds (1x1 km aprox.), which allows a better characterization of the climatic niche of species and identification of areas most vulnerable to invasion than using coarser resolutions.

To account for uncertainty in future scenarios, we used three different Global Circulation Models: the Community Climate System Model, version 4 (CCSM4), the Hadley Global Environmental Model – Earth System version 2 (HadGEM2-ES), and the climate model developed by the National Centre for Meteorological Research, version 5 (CNRM-CM5) (see Suppl. Materials). Within each GCM, different scenario alternatives are provided based on increasing Representative Concentration Pathways (RCPs), that is, greenhouse gas concentration trajectories. For this study we chose the 2.6 and 8.5 RCPs because they represent two extremes of the potential range of future conditions. All scenarios were downloaded for the "medium-term" (representing average conditions predicted for 2041-2060) and the "long-term" (average for 2061-2080) from WorldClim. As a result, we obtained climatic proxies for 12 different scenarios (3 GCMs x 2 RCPs x 2 time periods, see Table S6). Accessibility was considered to remain at least the same under future climate scenarios, although we may expect it to keep increasing in the future, as transportation and urban development continues, which may affect the expansion of invasive species (Seebens *et al.*, 2015).

Marine Scenarios. For modelling of the 38 marine species, nine candidate variables were obtained from Bio-Oracle (Ocean Rasters for Analysis of Climate and Environment, http://www.oracle.ugent.be/, Tyberghein *et al.*, 2012): salinity, sea surface temperature (mean, minimum, maximum and range) and air temperature (mean, minimum, maximum and range). Variables represent current conditions calculated with reference data from 1961-2010 (Tyberghein *et al.*, 2012). Bathymetry was obtained from MarSpec - Ocean Climate Layers for Marine Spatial Ecology (http://www.marspec.org). Accessibility was in this case calculated in QGIS v 2.6.1 as the Euclidean distance to commercial ports, weighted by their total cargo volume (see more details in Gallardo *et al.*, 2015). The maximum available spatial resolution for marine predictors was 5 arc-minutes (10x10 km approx.). After the selection protocol, predictors considered for modelling marine invasive species included: bathymetry (m), salinity (PSS) annual range of air temperature (°C), annual maximum and range of sea surface temperature (°C) and accessibility (km) (Fig. S3).

The range of future scenarios available for modelling the marine environment was more limited than for the inland in terms of GCM and time-frames. Thus, in this study we could only focus on a single GCM: the UKMO-HadCM3 developed by the Hadley Centre for Climate Prediction and Research (Gordon *et al.*, 2000). This model has been used extensively for climate prediction and other climate sensitivity studies in the marine environment. Three greenhouse gas emission trends are considered (IPCC, 2000): A1B, A2 and B1 (see Suppl. Materials). For each emission trend, we obtained “medium-“ and “long-term” future predictions corresponding to 2087-2096 and 2187-2196 respectively. This makes a total of 5 future marine scenarios (B1 not available for 2187-2196, see Table S7). Please note that available time-frames for the inland (2041-2060 and 2061-2080) and marine (2087-2096 and 2187-2196) environments differ, and are hereafter termed “medium-” and “long-term” future scenarios respectively to avoid confusion.

Bathymetry and accessibility were considered to remain constant under future marine scenarios, although we may expect accessibility to increase with on-going globalization (Seebens *et al.*, 2015), and sea-level rise to expand the total coastal area susceptible to marine invasions (Courchamp *et al.*, 2014, Hellmann *et al.*, 2008).

Statistical Analyses

Summary of invasion. To provide a general overview of the current state of invasion, we first obtained the total area of inland and marine Europe from the European Environment Agency repository (EEA, https://www.eea.europa.eu/). In the marine environment, the EEA uses the Economic Exclusive Zone (200NM from the coast) as reference for natural resources evaluation. We then calculated the number of spatial units (at 30 arc-second resolution ~ 1 km^2) in Europe occupied by any of our 86 invasive species. Likewise, we calculated the total surface covered by the network of protected areas (nationally designated areas and Natura 2000, excluding those smaller than 1 km^2), and the proportion occupied by our focus invaders.

Spatial correlation analysis. All correlations reported in this study were evaluated using Pearson’s correlation coefficients. The significance of correlations between spatial patterns (e.g. between the richness of invasive and susceptible species) were estimated using Dutilleul’s spatially corrected degrees of freedom (Dutilleul *et al.*, 1993). This method modifies the effective degrees of freedom by a normalization factor estimated from the degree of spatial autocorrelation in the variables. Spatial correlations and their significance were assessed using package “SpatialPack” (Osorio *et al.*, 2012) in R 3.1.3 (R Core Team, 2015).

Changes in the richness of invasive species in PAs over time. We analyzed changes in the richness of invasive species with time since designation of the protected area, using the accessibility, area and type of protected area (nationally designated areas *vs.* Natura 2000 sites) as covariates. Because the database structure (~75% of the protected areas have not been colonized by any of the invaders evaluated) we used zero-inflated negative binomial regression (ZINB). This method is used to model count data that has an excess of zero counts, and is especially suited to data with overdispersion (i.e. variance much larger than the mean). A ZINB assumes that zero outcome is due to two different processes. In our specific case, we may assume that a protected area has not been colonized because the invasive species didn't have the opportunity to invade. In this case, without any propagule pressure, the only outcome possible is zero. If there is opportunity to invade (positive propagule pressure), it is then a count process: the richness of invasive species can be 0 or higher depending on the protected area's suitability for the species establishment. ZINB were run using package "pscl" (Jackman, 2008), and plots were developed with "ggplot2" (Wickham, 2009).

Species Distribution Models. To investigate the potential consequences of climate change, an ensemble of distribution models was used to calculate climate suitability for each of the invasive species evaluated. Species Distribution Models (SDM) were performed using R package BIOMOD2 version 3.1-64 (Thuiller *et al.*, 2014). Because data quality and modelling settings determine strongly the performance of distribution models (Araújo & Guisan, 2006, Pearson & Dawson, 2003), sensitivity tests were conducted to investigate, and where possible compensate, for the influence of modelling algorithm, strategy of pseudo-absence selection, maximum number of presence records, sampling bias, and extrapolation onto novel climates (Figs. S4-S9).

For input, we used the dataset of species occurrences and the set of predictors that might affect the likelihood of species establishment. As no independent data existed to evaluate the predictive performance of the models, data were split randomly into two subsets: 70% of the original data was used for training the models, and the remaining 30% for evaluation (Araújo & New, 2007). This repeated split-sampling was repeated five times to account for the uncertainty associated to dataset partition (Thuiller, 2003). Four different algorithms (GLM, GBM, RF and GAM, see Suppl. Materials) and three independent sets of pseudo-absences were generated to contrast presences. Thus, for each species, 60 model replicates were run (4 algorithms x 3 pseudo-absence datasets x 5 split samplings).

Four criteria available in BIOMOD2 were considered for model evaluation: the area under the receiver operating characteristic (ROC) curve (AUC), the True Skill Statistic (TSS), Kappa and the success rate (i.e. percentage of correctly predicted occurrence locations, SR). However, since statistics were consistent and highly correlated, we subsequently used TSS because it is independent of prevalence (i.e. ratio of presence to pseudo-absence data) (Allouche *et al.*, 2006).

An 'ensemble model' (Thuiller *et al.*, 2014) was finally created averaging the 60 model replicates weighted by their predictive performance (TSS), with a threshold of TSS> 0.7. After calibration, ensemble models were projected onto Europe to obtain binary suitability maps, using the optimal threshold maximizing the TSS of the model, which has been consistently found to produce the most accurate predictions (Barbet-Massin *et al.*, 2012, Jimenez-Valverde & Lobo, 2007). Binary maps allow the identification of broad geographic regions where suitable climatic conditions may facilitate the successful establishment of an invasive species. Finally, all binary suitability maps were combined together to produce a composite map of Predicted Richness of Invasion (PRI, number of invasive species predicted to find suitable conditions for colonization per unit area).

The null model of invasion. A null model was designed to discard that any significant difference found in the predicted richness of invasion (PRI) inside and outside PAs is not simply a consequence of the random distribution of invaders across Europe. To that end, we first calculated the difference in PRI between a number of cells randomly located inside and outside PAs (5.000 for inland Europe, and 1.000 in marine Europe). We then randomly permuted the classification of sites into inside/outside categories, recalculated the difference in PRI, and repeated this procedure 5,000 times. If the difference between cells located inside *vs*. outside PAs is not significant when shuffling categories, then we can reject the null hypothesis that there is no difference in the predicted richness of invasion.

Range Change Under Climate Change. To quantify the potential range expansion of invasive species after climate change, we calculated the total suitable area gained and lost under each climate change scenario using R package BIOMOD2 (Thuiller, 2003). Range change indicates potential expansion/contraction of the species range of distribution, but does not assess for any migration shifts as it strictly compares the range sizes between present and future projections. Thus, we located the centroid of each binary present and future distribution and calculated latitudinal and longitudinal shifts between them (in km/decade) using R package “rgeos” (Bivand & Rundel, 2016).

Extent of Extrapolation. Distribution models sometimes extrapolate suitability in areas and times outside the training data, a pervasive problem in distribution modelling (Elith *et al.*, 2010). To measure uncertainty associated to extrapolation, we used Multivariate Environmental Similarity Surfaces (MESS) using R package “dismo” (Hijmans *et al.*, 2013). This method measures the similarity in terms of predictor variables of any given point to a reference set of points. In this study, MESS maps for each invasive species were combined into a single map reflecting the total number of species that may encounter non-analog climates to their current range. It is important to note that non-analog climates do not necessarily mean incorrect predictions, since invasive species have often shown their ability to colonize new environments, but areas were predictions may be relatively uncertain.

Results

Invasive species in Protected Areas

In this study we compiled 41,000 records for 86 of Europe’s most invasive species within the European network of protected areas (nationally designated areas and Natura 2000 sites), affecting 26% of Europe’s PAs (25% by area invaded, Table

1). Marine PAs are more frequently affected by invasive species (38%), probably because of their closeness to the coastline and thus high accessibility (Table 1). Overall, 85% of the area colonized by invaders is located outside PAs.

Tabla 1. Summary of the area affected by 86 of the most invasive species in Europe. Data are provided for the European Union (28 member states), and for the network of Protected Areas (PA), including nationally designated areas and Natura 2000 sites. Units are million hectares (Mha). Also indicated, the total number of PAs and the % affected by any of the invaders investigated.

	Inland	**Marine**	**Total**
Total EU Area	442 MHa	572 Mha	1,014 Mha
EU Area Invaded	159 Mha (36%)	40 Mha (7%)	199 Mha (19%)
Total PA Area	88 Mha	34 Mha	122 Mha
PA Area Invaded	24 Mha (27%)	7 Mha (20%)	31 Mha (25%)
Total Num. PAs	12,928	2,220	15,148
Num. Invaded PAs	3,152 (24%)	847 (38%)	3,999 (26%)

Invasive species are not evenly distributed across PAs, but concentrated in central and northwest Europe (Fig. 1a). In contrast, the most susceptible species to the establishment of our focus invaders are scattered in PAs across continental Europe (Fig. 1b). Accordingly, latitudinal patterns of invasive *vs.* susceptible species are only partially correlated (modified *t*-test of spatial association, *r*=-0.12, P<0.001, Fig. 1c).

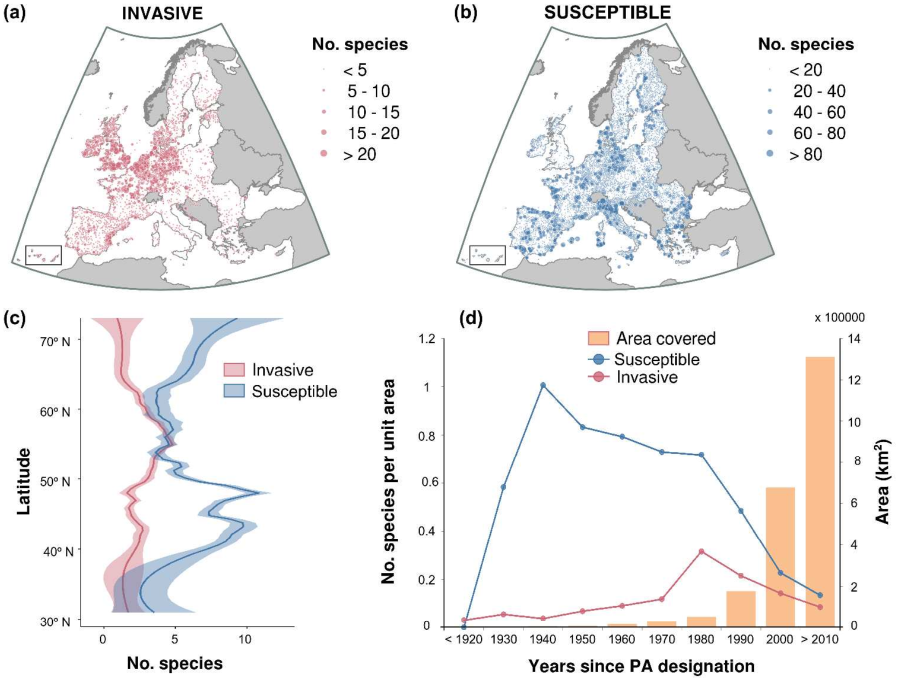

Fig. 1. Spatial patterns of invasive and susceptible species within protected areas (PAs) in Europe. The size of bubbles represents the number of invasive (a) and susceptible (b) species currently known to occur in any of the 12,928 inland and 2,220 marine PAs evaluated (total N=15,148). While 64% (9,749) of PAs host susceptible species, only a third (28%; 4,361) has been invaded. (c) Latitudinal distribution of invasive and susceptible species (spatially corrected Pearson, *r*=-0.12, P<0.001). The solid line and shaded area represent the mean and standard error of the number of species, fitted by LOESS with a 0.1 span. (d) Number of susceptible and invasive species per unit area covered by PAs designated in the last hundred years. Bars represent the cumulative area protected over time. See Fig. S1 for a map of protected areas (only those > 1 km^2 considered here).

According to a Zero-Inflated Negative Binomial regression (ZINB, Table 2), the richness of invasive species (RIS) significantly decreases with human accessibility (Fig. 2a). Interestingly, accessibility was the most important factor of the count part of the model but not of the zero part (Table 2). This means that invaded PAs are usually highly accessible, which is not the case for uninvaded PAs that show different levels of accessibility. The richness of invaders shows a unimodal response to the year of designation, peaking at those declared in the 1990s (Fig. 2b). In accordance, areas protected before the 1950s provide shelter to a large number of susceptible species but none of our focus 86 invasive species, and the richness of invaders increases rapidly in PAs designated after the 1970s (Fig. 1d). We must note that older PAs tend to be located in more inaccessible areas (correlation between accessibility and year of designation, t=-0.11, F= 10.10 on 1 and 874 DF, P=0.0015) and may thus be subject to a lower propagule pressure than newer, more accessible PAs. The response of RIS to surface of the PA followed the common species-area curve (Fig. 2c), basically reflecting the higher probability to find invasive species at larger PAs (also indicated by Fig. 1d). It is also noteworthy that the richness of invasive species is less than half in nationally designated areas than in Natura 2000 sites (Fig. 2d).

Table 2. Results from a Zero-Inflated Negative Binomial model (ZINB) between the Richness of Invasive Species (RIS) and the year of designation, area, accessibility, and type (nationally designated areas or RN 2000) of protected areas. N=15,142 marine and terrestrial protected areas considered.

Factors	**Estimate**	**SE**	**CI (5/95%)**	**z-value**	**P-value**
Count model coefficients (Poisson with log link)					
Intercept	0.57	0.04	0.50/0.68	12.57	***
Year	-0.25	2.21	-4.59/4.08	-0.11	n.s.
Year^2	-19.12	2.65	-24.34/-13.93	-7.21	***
Area	11.42	0.56	10.32/12.51	20.38	***
Area^2	-4.93	0.61	-6.13/-3.73	-8.04	***
Accessibility	-41.36	5.90	-52.93/-29.79	-7.01	***
Accessibility^2	19.54	5.93	7.92/31.17	3.29	***
Type: RN 2000	0.26	0.04	0.17/0.35	5.78	***
Zero-inflation model coefficients (binomial with logit link):					
Intercept	1.10	0.10	0.90/1.30	10.92	***
Year	31.75	4.44	23.04/40.45	7.15	***
Year^2	41.71	5.29	31.34/52.08	7.88	***
Area	-384.11	19.13	-421.62/-346.60	-20.07	***
Area^2	171.69	9.99	152.10/191.29	17.17	***
Accessibility	20.88	8.83	-3.57/38.19	0.02	*
Accessibility^2	-9.36	8.01	-25.07/6.33	-1.17	n.s.
Type: RN 2000	-0.70	0.09	-0.89/-0.51	-7.20	***
Log-likelihood: -1.62x10^4 on 16 DF					

***:significant at P<0.001; *:significant at P<0.05; n.s.: not significant

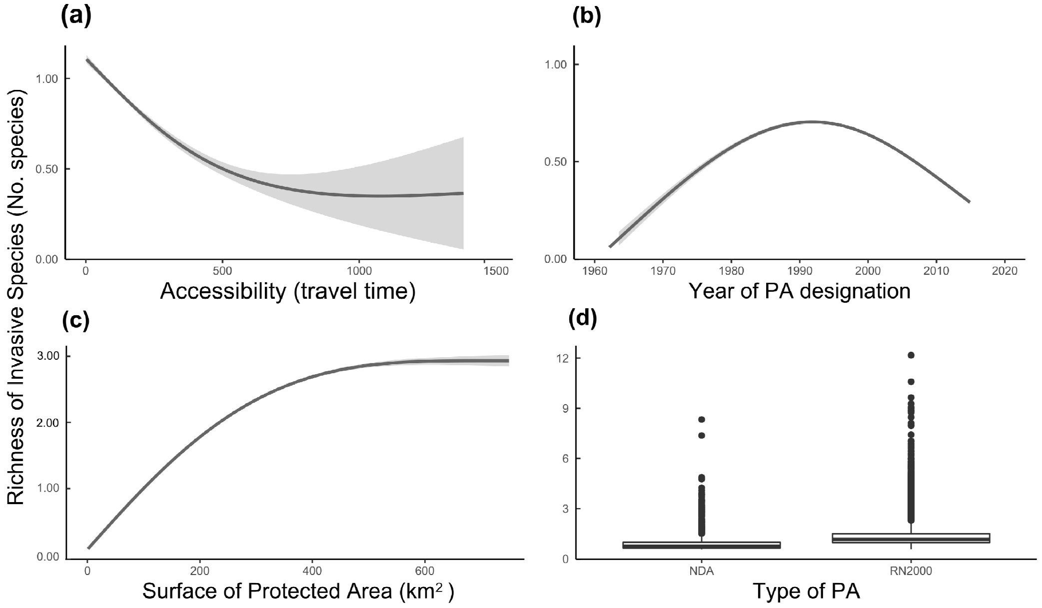

Fig. 2. Response of the Richness of Invasive Species (RIS, number of species) registered in protected areas (PA) to: (a) Accessibility measured as travel time to major cities, (b) the year of designation of the PA, please note zero RIS projected for PAs designated before the 1960s, (c) the total surface of the PA, and (d) the type of PA (Nationally Designated Areas vs. Natura 2000 sites). The solid blue line and shaded area represent the mean and standard error of the richness of species, fitted by LOESS with a 0.1 span. Statistics from a zero-inflated negative binomial model can be consulted in Table 2.

Invasive species under climate change

We used the complete database of >200,000 records reflecting the global distribution of our focus invaders to model their potential expansion across Europe under current conditions, and in the medium- and long-terms. Model evaluation indicated excellent performance (AUC of globally-calibrated models range 0.87 to 0.99, TSS 0.61–0.97, see Table S8). Most important predictors included minimum annual temperature and accessibility for terrestrial and freshwater species; and bathymetry for marine invaders (Fig. S10). Overall, 57–74% of terrestrial and freshwater invaders showed range expansion (i.e. positive range change) in the medium-term, and 62–69% in the long-term, depending on the future scenario investigated (Table S9). In contrast, fewer marine organisms are predicted to expand

(43–54% of species in the medium-, and 39–43% in the long-term, Table S10). Species particularly favoured by climate change include the knotgrass (*Paspalum paspalodes* L.), the coypu (*Myocastor coypu* Molina, 1782), the tree of heaven (*Ailanthus altissima* (Mill.) Swingle), and the American bullfrog (*Lithobates catesbeianus* Shaw, 1802) showing over a 20% expansion in their current distribution (Table S9). The spatial distribution of some invaders is predicted to contract, with examples like the rugose rose (*Rosa rugosa* Thunb.) and the raccoon dog (*Nyctereutes procyonoides* Gray, 1834), expected to lose more than 20% of their current climate suitability (Table S9).

Predictions of single-species invasion potential were overlaid to create a heat-map of Predicted Richness of Invasion (PRI, Fig. 2). Under the reference present scenario, which may represent the potential for short-term expansion, PRI is highest in the northwest of Europe, covering the Atlantic biogeographic region, the North & Celtic Seas, and Bay of Biscay (Fig. 2a, see Fig. S11 for the biogeographic regions considered). The uncertainty associated with this scenario was highest at high latitude (Artic) and altitude (Alpine) biogeographic regions, and relatively low in the rest of Europe (Fig. 2b). Under future conditions, the uncertainty associated to the Artic and Alpine regions declines, probably because of the general increase in temperatures anticipated for these areas (Table S11, Fig. S12). By contrast, uncertainty increases in the Mediterranean and Pannonian biogeographic regions, where future scenarios anticipate unprecedented warm and dry conditions (Gibelin & Déqué, 2003, Giorgi & Lionello, 2008). Uncertainty in the marine environment was highest in the Red and Mediterranean Seas and the Canary Current (Table S12 and Fig. S13).

Table 3: Summary of range changes expected for five major groups of invasive species in Europe. N= total number of invasive species considered in each group. Range Change: % area change relative to the present reference scenario according to species distribution models (see Tables S9 and S10). Lat. shift: latitudinal shift in the centroid of the distribution of invasive species relative to the present reference scenario with indication of direction (North or South). Long. shift: longitudinal shift in the centroid of the distribution of invasive species relative to the present reference scenario with indication of direction (East or West).

		Middle-term			Long-term		
Group	**N**	**Range Change (% area)**	**Lat. shift (km/dec)**	**Long. Shift (km/dec)**	**Range Change (% area)**	**Lat. shift (km/dec)**	**Long. shift (km/dec)**
TERRESTRIAL PLANTS	18	2.34±4.69	54±31 (N)	16±41 (E)	1.97±8.30	71±49 (N)	13±40 (E)
TERRESTRIAL VERTEBRATES	15	4.39±4.61	15±36 (N)	32±37 (E)	4.26±7.28	20±44 (N)	23±31 (E)
TERRESTRIAL INVERTEBRATES	12	4.85±4.94	35±43 (N)	29±33 (E)	4.68±7.78	47±56 (N)	22±27 (E)
FRESHWATER ORGANISMS	13	2.44±4.22	41±40 (N)	15±53 (E)	0.98±6.73	56±60 (N)	9±41 (E)
Summary inland species	58	3.41±4.61	37±40 (N)	22±42 (E)	2.90±7.58	50±55 (N)	17±36 (E)
MARINE ORGANISMS	28	0.92±0.78	22±34 (N)	16±47 (W)	1.30±0.63	14±19(N)	8±24 (W)

Rather than an increase in total area suitable to invaders, we found a shift in species' ranges. The core suitable distribution for inland invasive species is predicted to shift at an average rate of 37-50 km per decade towards the north, and 17-22 km per decade towards the east of Europe (Table 3, Fig. 2c and 2d).

The direction and magnitude of niche shifts was highly variable for marine invaders: those species currently distributed in the eastern part of the Mediterranean Sea are generally predicted to move north- and westwards (e.g. *Saurida undosquamis,* Table S12). In contrast, species currently distributed in the northern seas of Europe are predicted to shift further towards the Northeast (Fig. 2c and 2d). Species with widespread populations in both seas, showed multi-directional shifts with no clear trends (Table S13). Consequently, average centroid shifts for marine invaders at 14-22 km/decade northwards, and 8-16 km/decade westwards, are considerably slower than those predicted for inland species (Table 3).

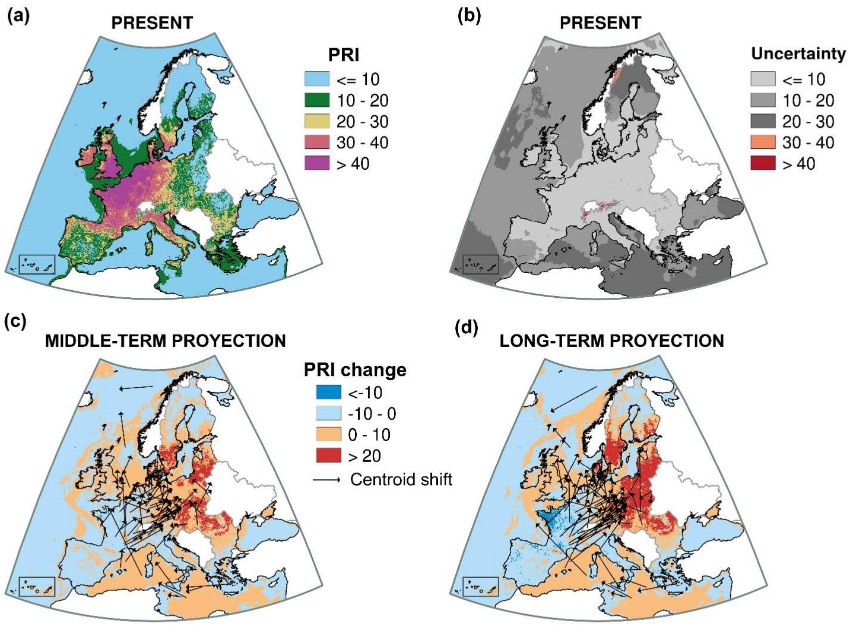

Fig. 3. Predicted Richness of Invasion (PRI) for 86 of the most invasive species in Europe. (a) PRI according to the present reference scenario. Values represent the total number of invasive species with suitable climate conditions for establishment. (b) Uncertainty associated to the present reference scenario. Values represent the number of species that encounter non-analog climates to their current global distribution. (c) and (d): Predicted changes in PRI in the medium and long term respectively. Arrows link the centroid of the species predicted distribution under present and future conditions. Inland projections correspond to the CNRM-CM5 pessimistic scenario for 2050 (c) and 2070 (d). Marine projections correspond to the HadCM3-A1b scenario for 2100 (c) and 2200 (d). Results for other scenarios can be consulted in Figures S14 and S15.

Invasive species under climate change in Protected Areas

The predicted richness of invasion (PRI) under the current reference scenario is 18% lower inside inland protected areas than outside them (Welch Two Sample t-test between 5,000 random cells located inside and outside inland PAs, t=-15.42, df= 8674, P<0.001). The null model assuming random distribution of PAs across Europe further allowed us to reject the null hypothesis of equal PRI inside and outside inland PAs (<5% probability of significant difference at random). This is likely related to the 67% lower density of human population and transportation networks inside PAs (accessibility inside *vs*. outside inland PAs, Welch Two Sample t-test: t=19.6, df=

8674, P<0.001). Under future climate change scenarios, PRI is predicted to remain 19-22% lower inside inland PAs than outside them.

In the marine environment, PRI under the current reference scenario is 11% lower inside marine PAs than outside them (Welch Two Sample t-test between 1,000 random cells located inside and outside marine PAs, t= -4.44, df= 1404, P<0.001). This difference is maintained under future scenarios (8-11% lower PRI inside PAs than outside them depending on scenario). This may again be related to the proximity of marine protected areas to the coast and thus higher human accessibility (accessibility inside *vs*. outside marine PAs, Welch Two Sample t-test: t=9.9, df= 1404, P<0.001). The null model, showing a probability <5% to find significant differences between randomly allocated marine PAs, further confirms our findings.

Discussion

Invasive species in Protected Areas

Protected areas (PAs) are championed as refugia for some of the world's most threatened organisms, but little is known about their potential to resist the damaging effects of biological invasions. While the presence (or absence) of invasive species is not specifically considered during designation, we may expect protected areas, particularly those established earlier and limiting human activities, to enjoy a good conservation status and therefore to host relatively few invasive species. In this study, we find that only a quarter of terrestrial and marine protected areas have been colonized by Europe's most invasive species, even though PAs are largely climatically suitable for invasion. Remarkably, areas protected before the 1950s provide shelter to a large number of susceptible native species, but none of our focus invaders (Fig. 1). What's more, hotspots of biological invasions and their most susceptible native taxa do not match at large scales (Fig. 1). This mismatch agrees with Bellard *et al.* (2016b), showing how the worldwide distribution of species threatened by biological invasions, and concentrated in the Americas, India, Indonesia, Australia and New Zealand, overlap only partially with hotspots of invasion in Europe, Asia and South-America. Our results can be explained by the low human accessibility of protected areas generally, and especially those protected in the early 20th century, often located in remote and pristine regions with very low human density and limited economic value, usually high mountains (Gaston *et al.*, 2008). In addition, active management of human impacts may also explain the low number of invasive species found in nationally designated areas that are usually controlled to ensure protection of the conservation values.

In contrast, the richness of invasive species increases rapidly in PAs designated after the 1970s (Fig. 1), which may reflect the intense proliferation of invaders in Europe registered after a five-fold increase in global trade over the last decades (Butchart *et al.*, 2010, Seebens *et al.*, 2015). Concurrently, the number and size of European PAs has experienced an exponential growth since the 1990s (Gruber *et al.*, 2012), explaining the increase in both susceptible and invasive species found in PAs by a simple species/area relationship (i.e. the larger total area protected, the more probabilities to find both native and invasive species). The larger number of invasive species registered in Natura2000 in comparison to nationally designated areas can be related to their recent designation, large area, high human accessibility and variable management (Fig. 2). Actually, while Natura 2000 includes strictly protected nature reserves, low-intensity human activities are allowed on most of the land, which can reasonably explain their higher levels of invasion.

Altogether, these observations suggest that the early establishment and restriction of human activities within PAs provide an effective barrier against biological invasions (Pyšek *et al.*, 2003). The difficulty for invasive species to colonize protected areas can be attributed to a combination of factors including: natural biotic resistance of taxonomically-rich resident communities promoted by the relatively pristine conditions of protected areas (Foxcroft *et al.*, 2011), restriction of human activities and intensive conservation management (Pyšek *et al.*, 2003), low human accessibility and thus low propagule pressure, and the time lag between a species' initial colonization of disturbed areas and its wider expansion towards more natural –and typically more diverse—landscapes (González-Moreno *et al.*, 2015). In this sense, Hiley *et al.* (2014) cautioned that while PAs do not facilitate the colonization of invasive species at their initial stage, they are more susceptible to invasion as populations establish and spread. Understanding the relative contribution of these factors to explain PAs susceptibility to biological invasions is beyond the objectives of this study, but fundamental to optimize PA's design and management for the conservation of native species and habitats undergoing global changes.

Invasive species under climate change

Predictions extracted from distribution models match the empirical evidence that the level of invasion in the Atlantic biogeographic region (6,600 non-native species according to Zieritz *et al.*, 2014), is among the highest in the world. This pattern has been attributed to several colluding factors: the presence of several large ports such as Antwerp and Hamburg, which rank among the top 20 ports with the highest invasion risk (Seebens *et al.*, 2013), mild temperate conditions (Béllard *et al.*, 2013), high habitat disturbance, dense human population and transportation networks, and high degree of economic activity (Gallardo *et al.*, 2015). Such concurrence of risk factors may also explain the concentration of invasive species in protected areas around the British Channel observed in Figure 1. Furthermore, our results match observations of climate-related increases in fish richness in the North Sea over the last two decades (Hiddink & Ter Hofstede, 2008), and of the northward expansion of invaders from the southern (Levant Sea) towards the northern (Adriatic and Liguarian Seas) coasts registered in the Mediterranean Sea (Bianchi & Morri, 2000).

As temperature increases across inland habitats, our models predict invasive species to shift northwards at an average pace of 37 (middle-term) to 55 (long-term) km/decade (Table 3), which is two to nine times faster than previously predicted for native terrestrial species (17.6±2.9 km/decade, Chen *et al.*, 2011, 6.1±2.4

km/decade, Parmesan & Yohe, 2003). Multidirectional shifts in the marine environment, with important differences among species currently located in the Mediterranean, the northern Seas, or both, lead to lower average centroid shift rates of 14 (middle-term) to 22 (long-term) km/decade (Table 3). Indeed, rapid range changes have been documented for invasive species in terrestrial and marine environments (see examples in Hellmann *et al.*, 2008, Walther *et al.*, 2009), often associated to their competitive ecological traits (Estrada *et al.*, 2016). However, more research is still needed to allow direct comparison of realized range shifts between native species and their invasive counterparts.

Not all invasive species are predicted to expand their distribution as a response to climate change, but 33-48% of the invasive species are predicted to loose areas climatically suitable across Europe. Reduced climate suitability may indeed impair the performance of some invaders, eventually increasing their vulnerability to other factors, including management (Béllard *et al.*, 2013, Bezeng *et al.*, 2017). It is nevertheless reasonable to expect invasive species to adapt and persist under increasing temperatures, particularly in the case of rapidly reproducing taxa (Thomas *et al.*, 2004). Furthermore, global warming is facilitating the migration of new invasive species from lower latitudes that will increase the pressure of biological invasions in southern Europe. As way of example, the Mediterranean Sea is currently experiencing the massive migration of Lessepsian invaders from the Red Sea via the Suez Canal (Por, 2012), and mosquito-borne tropical diseases like malaria, dengue or the West Nile Virus are under-going rapid expansion towards northern latitudes in continental Europe (Lafferty, 2009).

Large and rapid distributional shifts reported in this study derive from a wide diversity of species-specific responses, as evidenced by the large overdispersion of range change and centroid shift metrics reported in Table 3 (extended in Tables S9-S12). The realized shift of each species will ultimately depend on biological characteristics of its populations, including the interaction with other species, as well as on how they cope with the drivers of change. In this sense, most of the species investigated here are highly fertile and/or fecund, have a broad diet, mobile adult or juvenile forms, and are habitat generalists able to persist under unfavourable conditions (DAISIE, 2009). All of these characteristics have been linked to the extraordinary ability of invasive species to circumvent geographical barriers profiting from the intense transportation of people and commodities across the world (Capinha *et al.*, 2015, Seebens *et al.*, 2015), and consequently with the potential to occupy all of their climatically suitable habitats (Estrada *et al.*, 2016). Nevertheless, some taxonomic groups that are difficult to detect such as parasites, fungi and algae, may have been underrepresented here, a pervasive taxonomic bias in the invasive species literature. Finally, species are distressed to different extents by non-climatic factors (e.g. landscape structure, human-induced disturbances, habitat characteristics) and by multispecies interactions, which themselves depend on a variety of environmental drivers. However, these factors are more likely to affect local and regional distributions of species rather than the continental patterns investigated here (Pearson & Dawson, 2003).

Invasive species under climate change in Protected Areas

Biological invasions constitute one of the most important threats associated with species extinction (Bellard *et al.*, 2016a), both via direct impacts on resident species and through synergies with other extinction drivers (Walther *et al.*, 2009). Here we show that range expansion is likely to prevail over contraction for many environments, taxonomic groups, life-history strategies and future scenarios. Our results suggest that climate change could not only drive protected species out of the boundaries of static protected areas (Araújo *et al.*, 2011), but also facilitate the colonization by invasive species (Pyšek *et al.*, 2013), thereby increasing the pressure posed upon native populations. As temperature increases, species are largely predicted to shift northwards at a much faster pace than previously envisioned for native species (Chen *et al.*, 2011, Parmesan & Yohe, 2003), which may seriously compromise the conservation of biodiversity and ecosystem services. Considering the successful history of invasion of the species investigated, their biological traits and human-related dispersal, our projections indicate a worrying increase in invasion intensity in Europe. Fortunately, this trend is somewhat tempered by our analyses that reveal that the observed and expected intensity of invasion are less pronounced within the network of inland and marine protected areas. While the static nature of PAs has been largely questioned (Hannah *et al.*, 2007), studies have highlighted their essential role to protect species shifting their ranges as a response to climate change (Araújo *et al.*, 2004), and to facilitate the adaptation of resident communities (Gaüzère *et al.*, 2016, Johnston *et al.*, 2013, Thomas *et al.*, 2012). We conclude that protected areas have the potential to provide strategic refugia to native species from the expansion of invasive species spreading under climate change. Understanding the mechanisms underlying such potential is crucial in facilitating the identification of areas of future conservation concern as well as opportunities for restoration.

Acknowledgments

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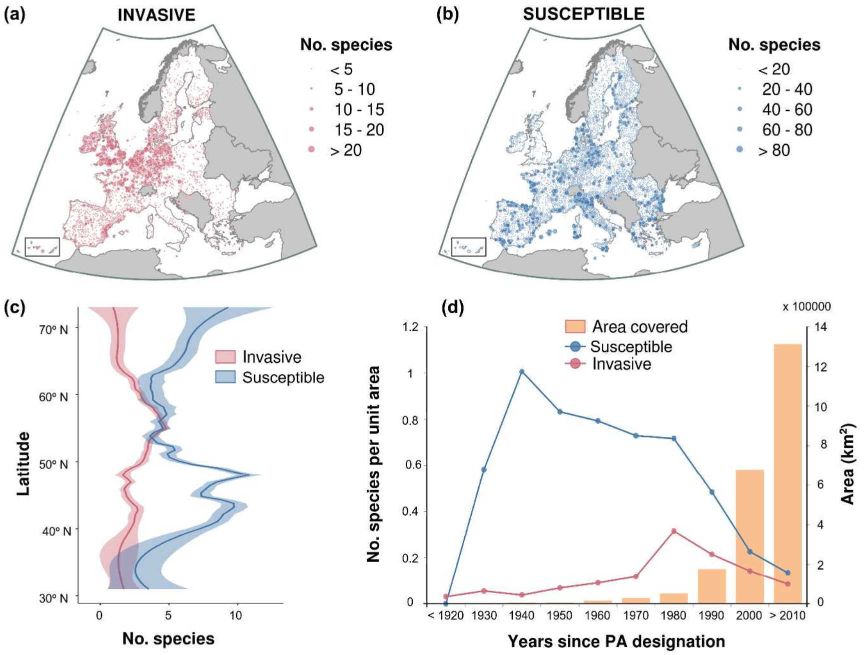

Spatial patterns of invasive and susceptible species within protected areas (PAs) in Europe. The size of bubbles represents the number of invasive (a) and susceptible (b) species currently known to occur in any of the 12,928 inland and 2,220 marine PAs evaluated (total N=15,148). While 64% (9,749) of PAs host susceptible species, only a third (28%; 4,361) has been invaded. (c) Latitudinal distribution of invasive and susceptible species (spatially corrected Pearson, r=-0.12, P<0.001). The solid line and shaded area represent the mean and standard error of the number of species, fitted by LOESS with a 0.1 span. (d) Number of susceptible and invasive species per unit area covered by PAs designated in the last hundred years. Bars represent the cumulative area protected over time. See Fig. S1 for a map of protected areas (only those > 1 km2 considered here).

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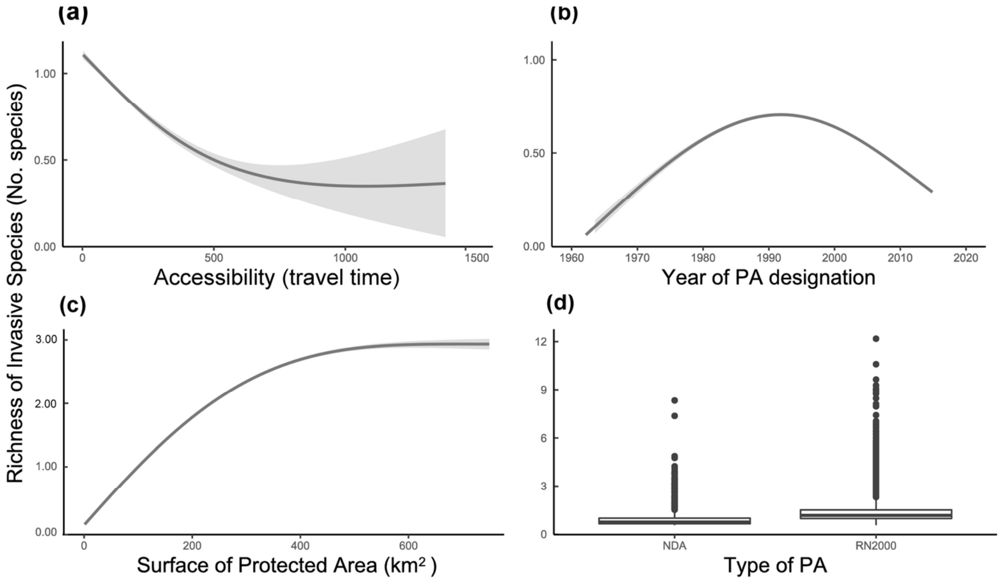

Response of the Richness of Invasive Species (RIS, number of species) registered in protected areas (PA) to: (a) Accessibility measured as travel time to major cities, (b) the year of designation of the PA, please note zero RIS projected for PAs designated before the 1960s, (c) the total surface of the PA, and (d) the type of PA (Nationally Designated Areas vs. Natura 2000 sites). The solid blue line and shaded area represent the mean and standard error of the richness of species, fitted by LOESS with a 0.1 span. Statistics from a zero-inflated negative binomial model can be consulted in Table 2.

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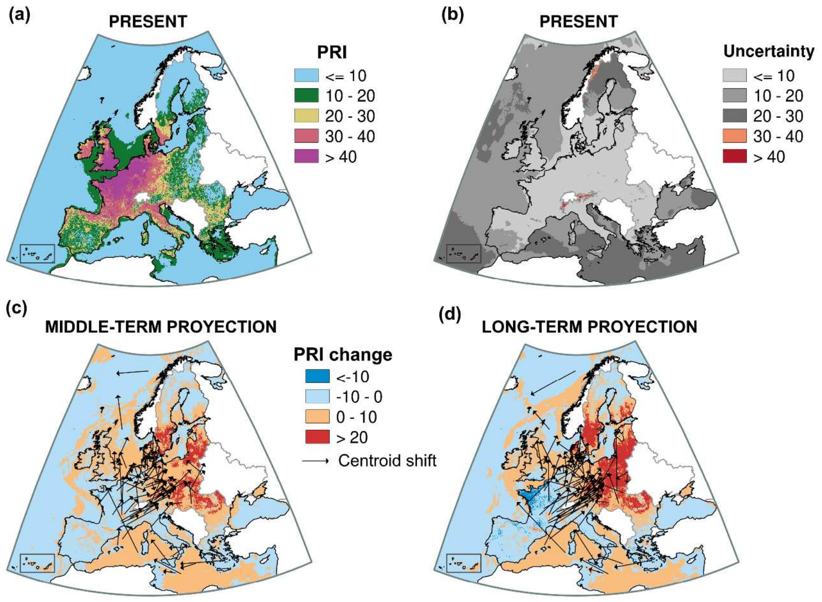

Predicted Richness of Invasion (PRI) for 86 of the most invasive species in Europe. (a) PRI according to the present reference scenario. Values represent the total number of invasive species with suitable climate conditions for establishment. (b) Uncertainty associated to the present reference scenario. Values represent the number of species that encounter non-analog climates to their current global distribution. (c) and (d): Predicted changes in PRI in the medium and long term respectively. Arrows link the centroid of the species predicted distribution under present and future conditions. Inland projections correspond to the CNRM-CM5 pessimistic scenario for 2050 (c) and 2070 (d). Marine projections correspond to the HadCM3-A1b scenario for 2100 (c) and 2200 (d). Results for other scenarios can be consulted in Figures S14 and S15.

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