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Global Distribution of Alien Mammals Under Climate Change

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ABSTRACT

The recent thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services reaffirmed biological invasions as a major threat to biodiversity. Anticipating biological invasions is crucial for avoiding their ecological and socio-economic impacts, particularly as climate change may provide new opportunities for the establishment and spread of alien species. However, no studies have combined assessments of suitability and dispersal to evaluate the invasion by key taxonomic groups, such as mammals. Using species distribution models, we estimated the potential effect of climate change on the future distributions of 205 alien mammal species by the year 2050 under three different climatic scenarios. We used species dispersal ability to differentiate between suitable areas that may be susceptible to natural dispersal from alien ranges (Spread Potential, SP) and those that may be vulnerable to alien establishment through human-assisted dispersal (Establishment Potential, EP) across 11 zoogeographic realms. Establishment Potential was generally boosted by climate change, showing a clear poleward shift across scenarios, whereas SP was negatively affected by climate change and limited by alien species insularity. These trends were consistent across all realms. Insular ecosystems, while being vulnerable to invasion, may act as geographical traps for alien mammals that lose climatic suitability. In addition, our analysis identified the alien species that are expected to spread or decline the most in each realm, primarily generalists with high invasive potential, as likely foci of future management efforts. In some areas, the possible reduction in suitability for alien mammals could offer opportunities for ecosystem restoration, particularly on islands. In others, increased suitability calls for adequate actions to prevent their arrival and spread. Our findings are potentially valuable in informing synergistic actions addressing both climate change and biological invasion together to safeguard native biodiversity worldwide.

1 | Introduction

Human activities have pervasively reshaped global ecosystems, causing unprecedented rates of species loss during the sixth mass

extinction on Earth (Barnosky et al. 2011; Cowie, Bouchet, and Fontaine 2022; Olden, Comte, and Giam 2018). Climate change and species redistribution among ecosystems are two of the major causes underlying these extinctions, as reaffirmed by the

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Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recent thematic Assessment Report on Invasive Alien Species (IPBES 2023; Schwindt et al. 2023) and the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Calvin et al. 2023). Climate change may exacerbate the effects of biological invasions by making native communities more vulnerable to the impacts of alien species (Falaschi et al. 2019; Walther et al. 2009). The joint impacts of these two stressors can be diverse and unforeseeable (Bellard et al. 2013). In light of this, the Convention on Biological Diversity has declared the management of biological invasions as a crucial target (Global Biodiversity Framework Target 6) for preserving biodiversity (CBD 2022).

Managing alien species, especially charismatic ones like mammals, can be particularly challenging (Bertolino et al. 2020; Capinha et al. 2023; Clout and Russell 2008). Mammals were among the first alien species introduced in prehistoric times (Grayson 2001), and their global spread has continued over the millennia, including several livestock, pets, game, and commensal species (Biancolini et al. 2021; Blackburn et al. 2017; Seebens et al. 2023). These alien species may have significant impacts on recipient ecosystems through predation, herbivory, and competition (Clout and Russell 2008; Seebens et al. 2023). The introduction of mammalian carnivores and rodents, for example, has led to the extinction and decline of several island endemic vertebrates (McCreless et al. 2016; Spatz et al. 2017).

Climate change is a growing concern in invasion ecology (Bellard et al. 2018; Di Febbraro et al. 2023) and is expected to increase biological invasions in the coming decades (Dehnen-Schmutz et al. 2018; Walther et al. 2009). Projections on alien species' responses to climate change can inform policy and management (Bellard et al. 2013; Dana, Jeschke, and García-De-Lomas 2014; Jiménez-Valverde et al. 2011). Recent data availability has led to the widespread use of Species Distribution Models (SDMs) for this purpose (Bellard et al. 2018; Jiménez-Valverde et al. 2011). These models use species distributions and baseline climatic conditions to project future distributions under different climate change scenarios (Guisan and Zimmermann 2000; Mod et al. 2016). SDMs are based on species' realized niches and assume constant climatic requirements over space and time (Guisan et al. 2014). Alien mammals have shown high niche conservatism between their native and alien ranges (Broennimann et al. 2021; Du et al. 2024; Strubbe, Beauchard, and Matthysen 2015), supporting the use of SDMs to identify suitable areas outside their known distribution (Liu et al. 2020).

Although several studies have used SDMs to assess invasion risk (Bellard et al. 2018; Jiménez-Valverde et al. 2011), the potential effect of climate change on the global distribution of alien mammals has been overlooked (Bellard et al. 2018; Bertolino et al. 2020). Previous research has primarily focused on specific mammals and regions, with limited multi-species studies (Bertolino et al. 2020). Furthermore, SDM studies often overlook the ability of alien species to spread, which is crucial for accurate estimates of their distributions under climate change (Miller and Holloway 2015; Wilson et al. 2009). To develop effective management strategies, it is crucial to consider the establishment and spread potential of alien mammals under changing climatic conditions.

Our objective was to investigate how climate change might affect the global distribution of 205 self-sustaining and free-ranging alien mammal species. We used SDMs and a global database of alien mammal distribution (Biancolini et al. 2021) to model alien mammals' climatic suitability. Then, we used their natural dispersal ability to distinguish between areas that may be vulnerable to establishment, potentially involving human-assisted dispersal (Establishment Potential, EP), and those that may be vulnerable to alien mammals' spread via natural dispersal (Spread Potential, SP) by 2050 under three different climate change scenarios.

2 | Methods

2.1 | Study Area

We conducted analyses on a global scale and within the 11 recognized zoogeographic realms (Holt et al. 2013) (Figure S1). To facilitate comparison and interpretation of results, we classified the Nearctic, Palearctic, Saharo-Arabian, and Sino-Japanese realms as “Northern” and the remaining seven as “Southern” based on their main geographic position and climate characteristics. All analyses were performed with a resolution of 10×10 arc-minutes (roughly 18.5×18.5 km at the equator). Islands with climatic information not classified by Holt et al. (2013) were assigned to the closest realm (Figure S1).

2.2 | Alien Species Presence

We obtained species distribution data from the Distribution of Alien Mammals (DAMA) database (Biancolini et al. 2021) and the International Union for Conservation of Nature (IUCN) Red List (IUCN 2020) for the alien and native ranges, respectively. Both sources use IUCN range mapping protocols (IUCN 2019), which rely on expert opinion, various sources (e.g., atlases, surveys, published literature), and land-cover categories to map species' presence. The DAMA database is the most comprehensive resource on alien mammal distribution available. It contains range maps of 230 mammal species with established self-sustaining alien populations, totaling 2726 range polygons, covering the period 21500 BC–AD 2020. For *Camelus dromedarius*, we obtained the native range from the Phylacine database (Faurby et al. 2018), as its native populations are extinct. Taxonomy followed both the IUCN Red List version 2020-1 (IUCN 2020) and the Phylacine database. *Bubalus arnee* and *Lama guanicoe* from the IUCN were matched with *Bubalus bubalis* and *Lama glama* from DAMA, respectively.

We converted range maps (which included both native and alien ranges) from polygons to rasters at a resolution of 10×10 arc-minutes, using cell centroids as occurrences (Data S1, Alien species presence section). We excluded 19 species whose introduction can be considered “benign” according to IUCN guidelines (Data S1, Alien species presence section) (Biancolini et al. 2021; IUCN 2013). Among the remaining species, 207 had at least 20 occurrences from the total range, meeting the minimum requirement for SDMs (Table S1) (Guisan, Thuiller, and Zimmermann 2017; Merow et al. 2014). The modeled species belong to 15 orders, with the most numerous being Rodentia

(54 species, 26.09%), Artiodactyla (48 species, 23.19%), and Carnivora (28 species, 13.53%), as well as 45 families, with the most numerous being Bovidae (22 species, 10.63%), Sciuridae (21 species, 10.14%), and Cervidae (18 species, 8.70%). The median number of occurrences per species was 69 for alien ranges (ranging from 1 to 116,664), 6159 for native ranges (11–283,486), and 7439 for the total ranges (22–327,360) (Table S1).

2.3 | Background Area

To develop reliable SDMs, it is important to consider the ecology and evolutionary history of the species when selecting the background area for sampling pseudo-absences (Acevedo et al. 2012; Sillero et al. 2021). We defined a species' background area as the mammal zoogeographic region(s) (Holt et al. 2013) overlapping with its native and/or alien ranges (Data S1, Background area section). These areas result from the evolutionary history of mammal communities and natural dispersal barriers, providing an adequate representation of the environments available to the species. The median number of occupied mammal regions per species was 3 (range: 1–18) (Table S1).

2.4 | Bioclimatic Variables and Climate Change Scenarios

To ensure the high reliability of SDMs, variables must be ecologically relevant to the modeled species (Sillero et al. 2021). The 19 bioclimatic variables from WorldClim (Fick and Hijmans 2017) are frequently used to generate projections of species distribution under climate change (Guisan, Thuiller, and Zimmermann 2017; Mod et al. 2016). They describe temperature and precipitation patterns at ecologically relevant times of the year and have been widely applied to both native and alien mammals (Bertolino et al. 2020; Cardillo, Skeels, and Dinnage 2023). Temperature variables can describe the windows outside which mammalian metabolism and reproductive success may suffer (Mitchell et al. 2018), whereas precipitation variables directly reflect water availability, essential for survival. Finally, both are indirect proxies for plant and prey abundance (Gillman et al. 2015). To select the most suitable variable sets, we used a species-specific approach, masking the 19 variables with each species' background and then performing a Variance Inflation Factor (VIF) analysis on the resulting rasters using the 'vifstep' function from the 'usdm' 2.1-7 R package (Naimi 2023). The VIF analysis quantifies how much the variance of a model is inflated by correlations between variables, referred to as multicollinearity (Guisan, Thuiller, and Zimmermann 2017). This analysis is particularly useful when considering multiple candidate variables, as it helps identify those that minimize multicollinearity, which can negatively affect SDM results (Guisan, Thuiller, and Zimmermann 2017). For each species, we selected only variables with VIF values below 5, a threshold generally considered adequate to avoid multicollinearity issues (Guisan, Thuiller, and Zimmermann 2017). Furthermore, maintaining low VIF values improves SDM transferability, or the ability to project species' suitability to new areas, which is critical for SDMs applied to alien species (Werkowska et al. 2017). Because VIF results can vary by region, this process produced a set of variables best suited to describe climatic conditions within

each species' background (Data S1, Bioclimatic Variables section). The median VIF value across species was 2.362 (SD 0.875) (Figshare file "Species_variables.csv"), with a median of seven variables used per species (Table S3).

To investigate variable patterns, we used the variable importance calculated with the 'biomod2' R package (see next section) as well as the percentage of species for which the variable was used. We only considered variables with a median importance greater than 0.041 (median across variables and species) and selected for at least 30% of species. To rank variables, we calculated an "Index of Relevance" as follows: $\sqrt{\text{median variable importance} \times \text{species percentage}}$. This provides a balanced measure unaffected by extreme values.

We used scenarios by 2050 from the Global Circulation Model (GCM) developed by the Institut Pierre-Simon Laplace for the 6th Intergovernmental Panel on Climate Change report (IPSL-CM6A-LR) (Boucher et al. 2020). This GCM is among the top-performing GCMs that follow the Shared Socioeconomic Pathways (O'Neill et al. 2017). SSPs represent various socioeconomic development pathways used to create the most recent scenarios (Calvin et al. 2023). We chose three SSP scenarios with increasing climate change severity: SSP1-2.6 (a mitigation scenario), SSP3-7.0 (an intermediate scenario), and SSP5-8.5 (a high-emission scenario) (O'Neill et al. 2017). All climate data were obtained from the WorldClim 2.1 database (Fick and Hijmans 2017). Finally, to investigate the possible influence of climate change on species responses, we calculated the per cell change of the six most relevant variables by subtracting the future values of each scenario from the current ones using the 'raster' 3.6-26 package in R (Figures S2–S4).

2.5 | Species Distribution Modeling

We developed SDMs using Generalized Boosted Models with 200 trees from the 'biomod2' 4.2–4 R package (Thuiller et al. 2023). This algorithm with such settings has shown low model complexity and high transferability compared to other methods, making it highly suited for modeling alien species distributions under climate change (Elith, Kearney, and Phillips 2010; Hao et al. 2020; Jiménez-Valverde et al. 2011; Werkowska et al. 2017). We trained SDMs combining occurrences from both the native and the alien range to better capture the realized climatic niche of the species (Broennimann and Guisan 2008). We randomly selected five sets of pseudo-absences, matching the number of species occurrences, in both the alien and native backgrounds. The presence and pseudo-absence data were randomly split, with 70% used for model training and 30% for testing. This allowed us to evaluate SDM performance using the Receiver Operating Characteristic (ROC) curve, a metric commonly used in species distribution modeling that indicates how well the SDM distinguishes between presences and absences, with values closer to 1 representing better performance (Guisan, Thuiller, and Zimmermann 2017). We repeated this process three times for each set of pseudo-absences, creating 15 model replicates per species. To ensure good model performance, only replicates with ROC values above 0.7 were used to make the final models (Guisan, Thuiller, and Zimmermann 2017). Multiple metrics are recommended for evaluating SDMs (Guisan, Thuiller, and

Zimmermann 2017; Sillero et al. 2021); thus, we also calculated the True Skill Statistic (TSS) and the Boyce Index using the ‘biomod2’ and ‘ecospat’ R packages, respectively. TSS is a metric that ranges from -1 to 1 and measures both sensitivity (true positive rate) and specificity (true negative rate), with higher values indicating better model performance. The Boyce Index also ranges from -1 to 1 and evaluates whether the frequency of species presences is higher in areas with greater projected suitability, making it especially useful for SDMs based on presence-only data (Di Cola et al. 2017; Guisan, Thuiller, and Zimmermann 2017). For both metrics, values close to $+1$ indicate excellent projections, while values close to or below zero indicate projections that are no better or worse than random.

Biomod2 projections initially have continuous values ranging from 0 (no suitability) to 1000 (maximum suitability) (Thuiller et al. 2023). To facilitate comparison between current and future projections, we converted these values into two classes (suitable and unsuitable) based on a species-specific threshold that maximized specificity and sensitivity (Liu, Newell, and White 2016) in the alien background with the ‘PresenceAbsence’ R package (Freeman 2023) (Table S3). We also used the clamping mask from ‘biomod2’ to identify areas with non-analogous climates, where projection uncertainty is high because climate conditions exceeded the training range of at least one variable (Data S1, EP section) (Williams and Jackson 2007).

2.6 | Establishment Potential

Biological invasions progress in a series of more or less sequential stages (Blackburn et al. 2011). In particular, introduction to a new location may be followed by establishment, and established species may then spread to other areas. EP is location-specific and is defined here as “the possible number of species for which a cell offers suitable climatic conditions outside their current native and alien range.” Dispersal to new cells can be natural or anthropogenic (or both), and EP may be interpreted as assuming “unlimited dispersal” potential for alien mammals. We excluded areas with non-analogous climates present outside of the species’ background to reduce projection uncertainty using the biomod2 clamping mask (Fitzpatrick and Hargrove 2009). We created a baseline for EP by only considering cells outside of their current native and alien ranges. To determine whether EP increased with increasing climate change severity, we used Wilcoxon rank sum tests with Bonferroni correction for each realm between each pair of climate scenarios, with a priori expectations of which should have the higher EP (alternative “greater” in Wilcoxon test). Finally, we defined hotspots of EP gain as the top 25% of grid cells holding the highest positive EP values. More information on EP methods is available in the related section of the Data S1.

2.7 | Spread Potential

SP refers to the stage of the invasion process where established and self-sustaining alien populations spread into suitable areas near the edges of their current alien range (Blackburn et al. 2011). We defined SP as “the species’ range change in a realm due to its natural dispersal ability,” following Rondinini

and Visconti (2015) and Visconti et al. (2016). The reachable distance (RD) of each species was calculated as follows:

$$RD = D \times (t/GL)$$

where D is the median dispersal distance per generation (km), t is the study period (35 years, from 2015 to 2050), and GL is the generation length (years) (Soria et al. 2021). We expanded alien ranges in accordance with the RD using the ‘sf’ 1.0-14 R package (Pebesma et al. 2023) and limited species spread to the invaded landmasses, implying that species could not reach the mainland from islands and vice versa. We excluded natural but extreme cases of jump dispersal, such as rafting. We used RD to limit the expansion to the projected 2050 climatic suitability and obtain an estimate of the species’ alien range under the three scenarios. Then we calculated the relative change in alien range extension (cells) for each realm: positive values indicated a species’ range expansion, while negative values indicated a range contraction. We established a baseline for SP by considering only suitable cells within current alien ranges (polygons from DAMA). We used a $\pm 5\%$ change in SP to categorize species based on projected range changes: species with SP changes between -5% and $+5\%$ were considered stable, species with SP declines greater than -5% were classified as declining, and species with SP gains greater than $+5\%$ were classified as expanding. Finally, we created lists of “top-spreading” and “top-declining” mammals by calculating the absolute range change across all three scenarios (using the mean value). Top-spreading species had the greatest mean range change, while top-declining species had the least mean range change, with one species from each realm. These species may be important targets for eradication and control efforts. To determine if SP differed significantly between scenarios, we used a Wilcoxon rank sum test (alternative “two-sided”) per realm with Bonferroni correction. More information on SP methods is available in the related section of the Data S1.

3 | Results

The six most relevant bioclimatic variables for alien mammals at a global scale were temperature seasonality (Worldclim code Bio4, relevance index = 3.99, modeled species = 63), mean temperature of wettest quarter (Bio8, 3.15, 108), precipitation of warmest quarter (Bio18, 3.14, 113), mean diurnal range (Bio2, 3.01, 86), isothermality (Bio3, 3.01, 68), and precipitation of coldest quarter (Bio19, 2.85, 87) (Table S2 and Figure S5).

Every evaluation metric, including ROC (median across species = 0.964, SD = 0.029), TSS (0.830, 0.085), Sensitivity (94.518%, 4.325%), Specificity (89.682%, 5.972%), and Boyce Index (0.931, 0.086), indicated that all models performed well (Table S3 and Figure S6). Due to insufficient data, models for *Macaca nigra* and *Sundasciurus juvencus* could not be developed, and these species were not included in any additional analyses.

3.1 | Establishment Potential

Across the 11 realms, the 205 species that were modeled showed distinct distribution patterns and variations in EP (Figure 1a, Table S4, Figures S7 and S8). The three most invaded realms

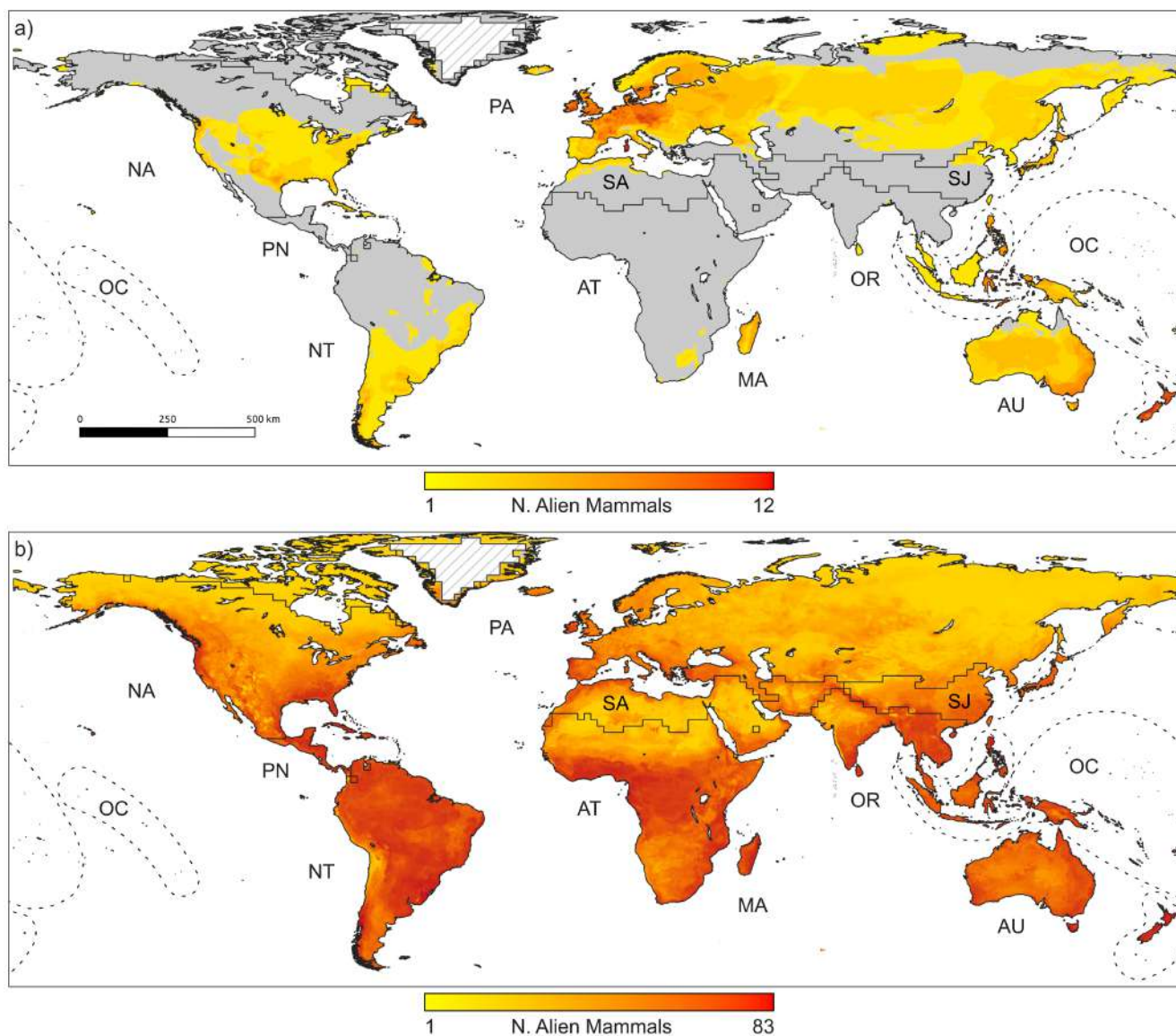


FIGURE 1 | (a) Alien mammal richness, baseline for Spread Potential, and (b) Establishment Potential (EP) baseline in current climatic conditions for the Afrotropical (AT), Australian (AU), Madagascan (MA), Nearctic (NA), Neotropical (NT), Oceanian (OC), Oriental (OR), Palearctic (PA), Panamanian (PN), Saharo-Arabian (SA), and Sino-Japanese (SJ) realms.

are the Australian (Max species number = 12, mean species per cell = 2.72, SD = 1.71), Palearctic (12, 1.33, 1.50), and Oriental (9, 0.47, 1.22) realms, while the Afrotropical realm was the least invaded (2, 0.02, 0.15) (Table S9). High levels of alien mammal richness were found in the insular regions of the Sino-Japanese, Oriental, and Panamanian realms.

Every realm may see an increase in the number and distribution of alien species under the current conditions, leading to high EP in the majority of the world's regions (Figure 1b, Table S4, Figures S7 and S8). The highest current mean EP was found in the Panamanian realm (mean = 54.67, SD = 7.52), followed by the Madagascan (53.09, 7.57) and Neotropical (49.60, 9.35) realms. The Saharo-Arabian (22.21, 10.73) and Palearctic (15.26, 9.19) realms showed the lowest EP.

Under all scenarios, EP change was generally lower in the southern realms (SSP1-2.6 mean EP = 0.77, SSP3-7.0 = 0.90,

SSP5-8.5 = 0.92) and higher in the northern ones (SSP1-2.6 = 1.66, SSP3-7.0 = 1.89, SSP5-8.5 = 2.09) (Figure 2a,b, Table S4, Figures S7 and S8). EP trends intensified from SSP1-2.6 to the SSP3-7.0 and SSP5-8.5 scenarios. The Madagascan realm experienced the greatest decrease in mean EP of all realms (SSP1-2.6 = -1.24, SSP3-7.0 = -1.60, SSP5-8.5 = -1.86) and was followed by the Panamanian (-0.02, -0.21, -0.32) and Saharo-Arabian (-0.09, -0.06, -0.13) realms (Figure 2a,b, Table S4, Figures S7 and S8). In the Northern Hemisphere, the Palearctic (+1.98, +2.27, +2.45), Nearctic (+1.80, +2.00, +2.36), and Afrotropical (+1.05, +1.29, +1.48) realms experienced the greatest gains in mean EP in every scenario (Figure 2a,b, Table S4, Figures S7 and S8). The increase in EP was significantly higher under the SSP5-8.5 scenario in comparison to the SSP1-2.6 for seven realms, according to the Bonferroni-corrected Wilcoxon test (Figure 2c, Table S5, Figures S7 and S8). Every realm showed hotspots of EP gain; however, their extent was greater in the Northern Hemisphere, particularly in the Palearctic

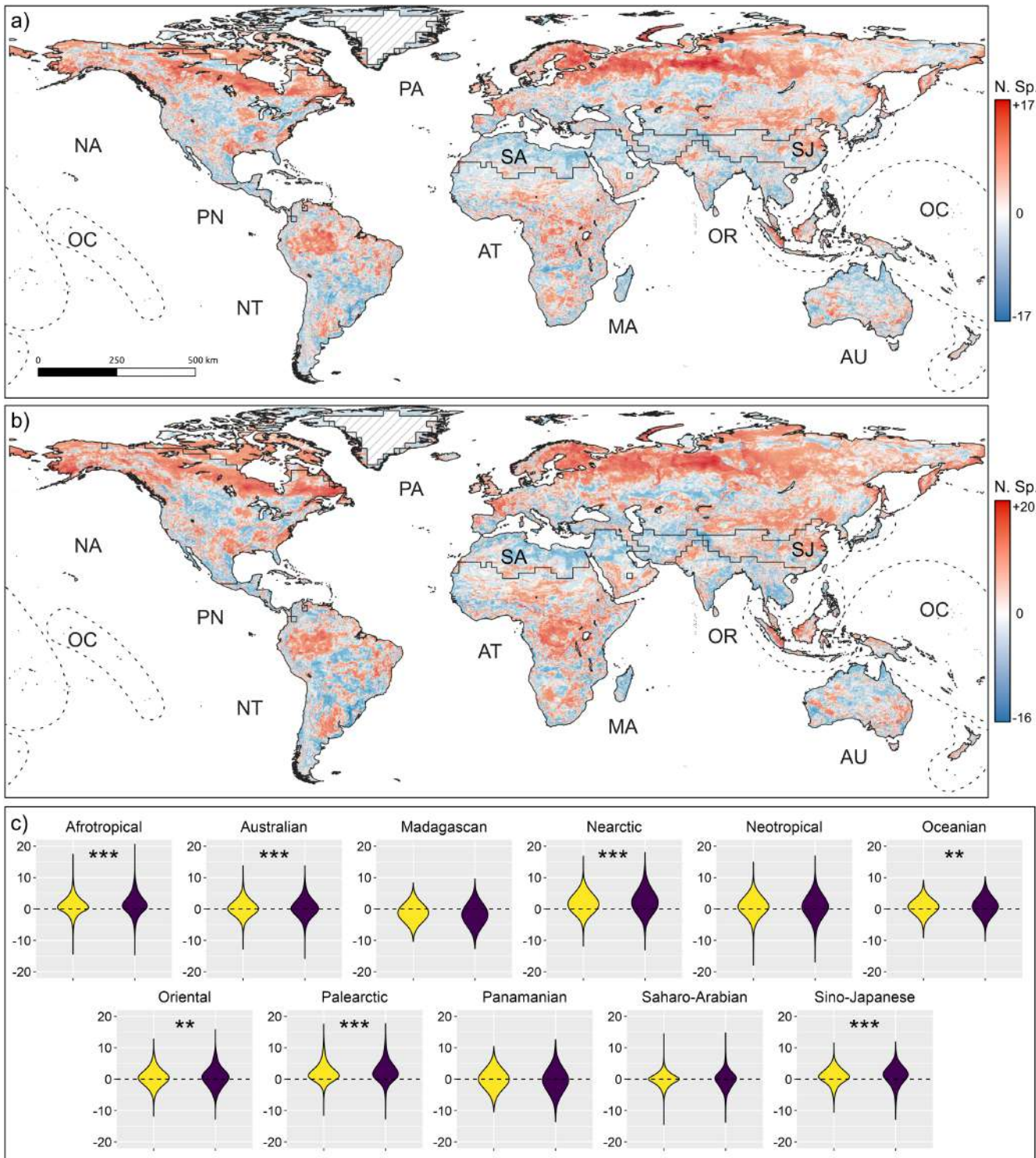


FIGURE 2 | Changes in Establishment Potential (EP) between current conditions and 2050 under (a) the mitigation scenario (SSP1-2.6) and (b) the high-emission scenario (SSP5-8.5) (for SSP3-7.0, see Figure S7). (c) Plots of EP change per realm under SSP1-2.6 (yellow) and SSP5-8.5 (dark purple) (for SSP3-7.0, see Figure S8). Significance levels from the Wilcoxon rank sum test (alternative: Greater) with Bonferroni correction, comparing SSP5-8.5 against SSP1-2.6, are indicated by asterisks: ** $p < 0.01$ and *** $p < 0.001$.

and Nearctic realms (Figure S9). In the Southern Hemisphere, the largest EP hotspots were observed in the Afrotropical and Neotropical realms. In all the realms, EP hotspots were larger under SSP3-7.0 and SSP5-8.5, compared to SSP1-2.6, with the exception of the Madagascar realm, where they remained nearly identical.

3.2 | Spread Potential

SP did not differ across climate scenarios, as the Bonferroni-corrected Wilcox test performed for each realm consistently showed $p > 0.05$ (Table S10). Thus here we focus on the results from the SSP5-8.5 scenario, as they are largely equivalent to

results from the other scenarios. Increases of alien mammal richness due to natural dispersal from already established alien ranges were concentrated in the mainland parts of the Palearctic, Nearctic, Neotropical, Australian, and Afrotropical realms (Figure 3a, Table S9 and Figure S10). Since SP was limited to invaded landmasses, realms with numerous islands, such as Madagascar, Oceanian, and Oriental realms, had lower SP values than other realms (Figure 3b, Table S6 and Figure S11). Furthermore, the percentage of species showing SP declines was higher in these island-rich realms than in realms with large mainland areas (Figure 3c, Table S8 and Figure S12).

We identified eight top-spreading species across scenarios (Figure 3a and Table S7), with two species shared between realms: *Bubalus bubalis* between the Panamanian and Neotropical realms, and *Suncus murinus* between the Saharo-Arabian and Sino-Japanese realms. No top-spreading mammal was found for the Madagascar realm, where no species showed a positive SP in all three scenarios. Artiodactyla accounted for five of the eight top-spreading species across scenarios, with Eulipotyphla, Primates, and Rodentia accounting for one each. We identified nine top-declining species across scenarios (Figure 3a and Table S7), with two species shared between realms: *Ovibos moschatus* between the Nearctic and Palearctic

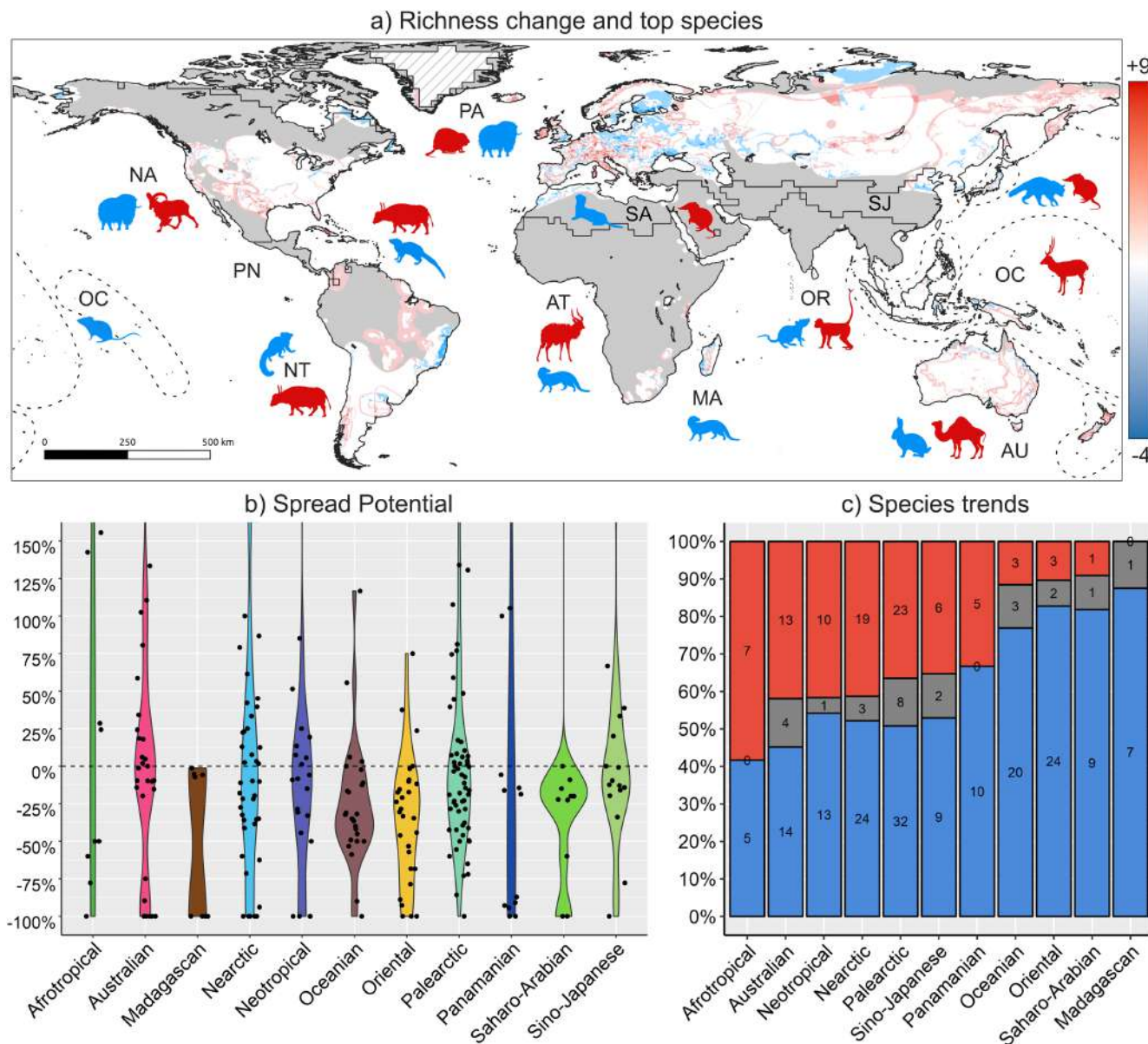


FIGURE 3 | (a) Alien mammal richness based on Spread Potential, with top-spreading (red silhouettes) and top-declining (blue silhouettes) alien mammals per zoogeographic realm; (b) plots of Spread Potential per realm; and (c) the percentage of species showing an expanding (red), declining (blue), or stable (gray) alien range under SSP5-8.5. For other scenarios, see Figures S10–S12. Top-spreading species were: AT = *Tragelaphus angasii*, AU = *Camelus dromedarius*, MA = no species, NA = *Ammotragus lervia*, NT and PN = *Bubalus bubalis*, OC = *Rusa timorensis*, OR = *Semnopithecus entellus*, PA = *Ondatra zibethicus*, SA, and SJ = *Suncus Murinus*. Top-declining species were: AT and MA = *Civettictis civetta*, AU = *Oryctolagus cuniculus*, NA and PA = *Ovibos moschatus*, NT = *Callithrix jacchus*, OC = *Rattus exulans*, OR = *Rattus tanezumi*, PN = *Herpestes auropunctatus*, SA = *Mustela nivalis*, and SJ = *Procyon lotor*.

realms, and *Viverricula indica* between the Afrotropical and Madagascan realms. Carnivora accounted for four of the nine top-declining species across scenarios, while Rodentia accounted for two and Artiodactyla, Lagomorpha, and Primates for one each.

4 | Discussion

In this study, we investigated the effect of climate change on the distribution of 205 alien mammals under different future scenarios. Using bioclimatic SDMs and species' dispersal, we were able to distinguish between areas that may be at risk of alien mammals establishment, possibly through human activities (EP), and those that may be susceptible to the natural spread of alien mammals from their current alien ranges (SP), under three different scenarios by 2050. Our findings reveal a clear poleward shift in EP across all scenarios, implying that suitable climatic conditions for alien mammal establishment may increase in the majority of realms while expanding to higher latitudes. In contrast to EP, SP decreased across all scenarios, particularly in island-rich realms.

Climate change may increase the risk of alien mammal establishment in some areas, particularly in the north, with a positive relationship between EP and climate change severity (SSP1-2.6 to SSP5-8.5). The majority of realms had the highest EP values under the high emissions scenario (SSP5-8.5), with the exception of the Madagascan, Panamanian, Saharo-Arabian and Neotropical realms. The first three even exhibited a decrease in EP. These findings appear to support the hypothesis that climate change may favor alien species establishment (Essl et al. 2020; Hulme et al. 2023; Walther et al. 2009). EP, on the other hand, does not take into account species dispersal ability because it is an unlimited dispersal projection. When dispersal is taken into account, a new picture emerges.

Mammals may struggle to track suitable climates in their native ranges under climate change (Estrada et al. 2016; Pacifici et al. 2017; Visconti et al. 2016). Our SP projections, which account for dispersal, suggest that this could also apply to their alien ranges. Climate change had a negative impact on SP for the majority of species and realms, with some differences depending on their geography. The realms with the greatest mainland area (such as Afrotropical and Nearctic) had the highest percentage of expanding species, whereas the realms with the most islands (such as Oriental and Oceanian) had a high percentage of declining species. We found no significant differences in SP change across scenarios, implying that the effect of climate change within their current alien range and potential area of expansion is similar regardless of its severity.

Numerous species are expected to move to more suitable climates toward the poles as their primary survival strategy (Scheffers et al. 2016), however, range shifts may be limited by sea barriers (Bellard et al. 2018; Gary and Parmesan 2003; Pacifici et al. 2015). Islands are known to be more susceptible to biological invasions, and they may become geographical traps for alien species, offering no escape from the loss of climatic suitability. This same factor may contribute to the SP declines observed in species within the Madagascan, Saharo-Arabian,

Oceanian, Oriental, Palearctic, Panamanian, and Sino-Japanese realms, all of which have a large number of alien mammals on islands. We identified nine "top-declining" mammals that experienced the greatest loss in SP (across scenarios) among the modeled species (Figure 3a and Table S7). The majority of these species were island invaders determining severe ecological consequences on invaded areas, such as *Herpestes auropunctatus* and *Oryctolagus cuniculus*, which rank among the 100th of the world's worst invasive alien species (Luque et al. 2014). Management should take advantage of this novel opportunity, as climate change-induced loss of suitability may increase the efficacy of control and eradication actions for these species.

The observed patterns in EP and SP may be explained by considering which variables were most relevant to the modeled species and their ecology (Figure S5). Tropical and subtropical mammals in the southern realms evolved with stable climates, whereas temperate and continental mammals in the northern realms are able to tolerate greater climatic variability (Figure S13) (Osland et al. 2021; Sheldon 2019). In fact, indicators of climate variability such as mean diurnal range (Bio2), isothermality (Bio3), and temperature seasonality (Bio4) were among the most relevant variables (Figure S5). Furthermore, precipitation and temperature can influence resource availability in occupied ecosystems for both herbivores and carnivores (Gillman et al. 2015). We found that the precipitations of warmest (Bio18) and coldest (Bio19) quarters, as well as the mean temperature of wettest quarter (Bio8), are among the most relevant variables, most likely because they have direct effects on primary productivity during the overwintering and growing seasons (Gillman et al. 2015; Mod et al. 2016). Resources are not stable throughout the year, and their fluctuations can be described by temperature seasonality (Bio4), as they follow seasonal patterns across latitudes (Sheldon 2019; Williams et al. 2017). Finally, mammals' survival depends on having access to water during the warmest quarter (Bio18), particularly in drought-prone climates.

In the future, the most relevant variables showed clear patterns of change potentially linked to projected changes in EP and SP (Figures S2–S4). In the northern realms, increased mean temperature of the wettest quarter (Bio8), precipitation of the warmest quarter (Bio18), and precipitation of the coldest quarter (Bio19) combined with decreases in mean diurnal range (Bio2), isothermality (Bio3), and temperature seasonality (Bio4) may result in more warm, humid, and stable climates suitable for tropical and subtropical mammals. Currently, only a relatively small number (28) of alien mammals have been introduced from the Southern realms to the Northern realms (Biancolini et al. 2021); however, it is expected that many species from warm climates may be able to expand poleward in the coming decades due to decreases in extreme cold events in the higher latitudes (Osland et al. 2021). The Palearctic and Nearctic realms are expected to become more similar in climate to other realms under climate change, especially under SSP5-8.5 (Hubbard, Drake, and Mandrak 2024). In the southern realms, increased temperature seasonality (Bio4), precipitation of warmest quarter (Bio18), and precipitation of coldest quarter (Bio19) combined with decreases in mean diurnal range (Bio2), isothermality (Bio3), and mean temperature of wettest quarter (Bio8) all point to great alterations of tropical and subtropical climates, where seasonal fluctuations are mainly related to precipitation rather than

temperature (Sheldon 2019). A conspicuous number of alien mammals (127) have been introduced from the southern realms into the same group of realms (Biancolini et al. 2021). Indeed, climate matching has been shown to have an important impact on alien mammal establishment (Broennimann et al. 2021; Du et al. 2024; Strubbe, Beauchard, and Matthysen 2015). Tropical species are expected to be more vulnerable to climate change because of their restricted niches (Sheldon 2019), and alien mammals from these regions may be no exception, as evidenced by *Callithrix jacchus*, native and introduced to the Neotropical realm and one of the top-declining species. Among the species possibly favored by climate change and showing high SP, we identified eight “top-spreading” mammals. These species had the highest mean increase (across scenarios) in SP among the modeled species (Figure 3a and Table S7). They belong to the orders Artiodactyla (5), Eulipotyphla, Primates, and Rodentia (1 species each), all of which are known to contain successful mammal invaders due to their ecological generalism, dispersal ability, and propagule pressure (Blackburn et al. 2017; Clout and Russell 2008; Long 2003). The majority have well-known impacts (e.g., overgrazing and competition with native herbivores for artiodactyls and *Ondatra zibethicus*, predation and competition for *Suncus murinus*), but no current studies have addressed the alien ecology of *Semnopithecus entellus* (Long 2003; Biancolini et al. 2021).

Without prevention and control measures, the top-spreading mammals may invade a broad portion of the nearby suitable areas, possibly causing unforeseeable damage to the recipient ecosystems. Since the magnitude of ecological impacts is correlated with the extent of the invaded area (Latombe et al. 2022; Pagad et al. 2018), these eight species may be considered strong candidates for management strategies. However, a conservation paradox emerges for the ones that are threatened in their native range (Gibson and Yong 2017; Tedeschi et al. 2024). The Aoudad (*Ammotragus lervia*) and the Javan Deer (*Rusa timorensis*) are classified as vulnerable by the International Union for Conservation of Nature (IUCN) due to habitat loss and over-hunting (IUCN 2020). Moreover, *Bubalus arnee*, the wild ancestral species of *Bubalus bubalis*, is classified as endangered, while *Camelus dromedarius* is Extinct in the wild (IUCN 2020). Although classified as Least Concern, *Ovibos moschatus*, one of the top-declining species in the Palearctic and Nearctic realms, is threatened by the rapid warming of the Arctic due to changes in forage, increased exposure to pathogens and parasites, and heat stress (IUCN 2020). The alien populations of these species may hold conservation value, and management may carefully consider strategies to maintain them “ecologically sustainable,” aiming to prevent both their extinction and the loss of native biodiversity (Gibson and Yong 2017; Tedeschi et al. 2024).

Managing alien mammals can indeed pose diverse challenges (Bertolino et al. 2020; Clout and Russell 2008; Latham et al. 2017), although the decline of alien mammals on islands may present opportunities for management programs, particularly in the Australian and Oceanian realms. These have the most distinctive vertebrate fauna in the world, with high levels of endemism and unique phylogenetic lineages (Longman, Rosenblad, and Sax 2018; McCreless et al. 2016; Woinarski, Burbidge, and Harrison 2015). In these realms, alien mammals have caused significant declines in native biodiversity since

human arrival (McCreless et al. 2016; Woinarski, Burbidge, and Harrison 2015). The loss of suitability for alien mammals on islands could facilitate eradication programs (Bellard et al. 2018) which should be coupled with climate change mitigation strategies to preserve native communities (Russell and Kueffer 2019).

Nevertheless, we identified large areas across all realms that could gain suitability for numerous alien mammals (Figure S9). Hotspots of EP gain were similar across scenarios, however, more extended under SSP5-8.5 than SSP1-2.6 and widely distributed globally, including regions where many native mammals are expected to decline in the future. Alien species often impact native species synergistically with other major threats such as climate and land-use change (Munstermann et al. 2022). The greatest losses of habitat for native mammals caused by these two stressors are expected in the Southern Hemisphere, specifically in South America, Central and Southern Africa, Southeast Asia, and Oceania, especially under SSP5 (Baisero et al. 2020; Pacifici, Visconti, and Rondinini 2018). These same regions showed extensive hotspots of EP gain (Figure S9) and could thus experience a turnover between declining native species, adversely affected by climate and land-use change, and alien species, which may benefit from both (Liu et al. 2023; Walther et al. 2009). This could finally result in the biotic homogenization of unique tropical and subtropical ecosystems (Capinha et al. 2015; Olden, Comte, and Giam 2018). In the Northern Hemisphere, habitat loss for native mammals due to climate and land-use change is expected to be mitigated by a poleward shift in their climatic suitability and the renaturalization of agropastoral land (Baisero et al. 2020; Scheffers et al. 2016). However, drastic environmental alterations could still favor alien mammals over natives, which showed the greatest hotspots of EP gain in the Nearctic and Palearctic realms (Figure S9). Higher latitudes are expected to harbor more alien species under all scenarios, aligning with previous research indicating a poleward shift for both native and alien species (Bellard et al. 2018; Scheffers et al. 2016). The Nearctic, Palearctic, and Sino-Japanese realms contain several countries with high gross domestic product and human population density, both positively associated with alien richness (Bellard et al. 2016; Dawson et al. 2017), putting them at high risk of mammal introduction. Despite lower levels of EP increase in the southern realms than in the northern realms, the number of alien mammals that could find suitable areas remains high under all scenarios. The contraction of currently established species may be offset by new introductions in these regions, as low- and middle-income countries are often under-equipped to tackle biological invasions (Early et al. 2016).

Projecting the future distribution of alien species is challenging due to knowledge gaps in their distribution, fundamental niche, phenotypic plasticity, rapid evolution, and biotic interactions (Cosner 2014; Whitney and Gabler 2008). It has been suggested that IUCN range maps overestimate species distributions by including unsuitable conditions (Ramesh et al. 2017); however, a certain degree of overestimation may be acceptable in the case of alien species, as it can motivate greater caution in preventing their arrival. Furthermore, alien species may be able to colonize new environments through phenotypic or genetic adaptation (Whitney and Gabler 2008) or adapt to new climates (Hällfors et al. 2016). Our estimation of the possible natural spread of alien mammals allowed us to project changes in alien range

size. However, species dispersal ability may be modulated by environmental connectivity, biotic interactions, and rapid evolutionary changes (Whitney and Gabler 2008; Wilson et al. 2009). Biotic interactions, such as competition, predation, and mutualism, have a significant impact on both native and alien distributions; however, their inclusion is an outstanding challenge for species distribution modeling due to their inherent complexity and lack of data (Yates et al. 2018). Furthermore, human action is the primary cause of species introduction and is especially challenging to anticipate (Dehnen-Schmutz et al. 2018). New introductions may involve mammals native to regions that could become accessible in the future, rather than the modeled species (Seebens et al. 2018). The 205 species introduced by humans here considered are a small subset (3.27%) of the 6264 mammals that are currently known to exist on Earth (Soria et al. 2021). Some mammal groups, such as artiodactyls, have been found to be more likely to have been introduced than expected, while others, such as rodents, are far less likely (Blackburn et al. 2017). When compared to mammals in general, alien mammals have significantly larger body masses (and consequently dispersal ability, median 2.39 km versus 0.60 km) (Blackburn et al. 2017; Soria et al. 2021). This could explain the high SP estimated for Artiodactyla, which had the highest positive SP values of any major group (Figure S14) and five of the “top spreading” species. Furthermore, conspicuous and charismatic species such as artiodactyls receive more research attention, whereas smaller, less charismatic species may go undetected, resulting in distribution bias (Troudet et al. 2017). Species’ traits, national biosecurity protocols, and shifting pathways can result in varying degrees of natural and anthropogenic dispersal. These factors were not considered when estimating EP, which is a “worst-case” scenario of unrestricted dispersal, useful for assessing the influence of climate change on alien species and prioritizing areas to prevent their arrival.

We have identified several avenues for future research on the invasion ecology of alien mammals. While our study used the entire niche of alien mammals to model their potential response to climate change, the native and alien niches may have different weights in determining this response. Niche analysis could offer further insights on the observed patterns and climatic requirements of alien mammals from various regions. Although identifying areas climatically suitable for alien mammals provides a solid basis, future research should focus on modeling factors that may influence anthropogenic dispersal to provide a comprehensive risk assessment. Incorporating biotic interaction with native fauna is also fundamental to estimating the probability of the establishment of alien mammals. Lastly, while our study provided a global perspective, regional analyses at higher resolutions could offer crucial information for local-scale conservation efforts, particularly if focused on overlooked alien mammals.

Despite the limitations of our methodological approach, our projections rely on the most comprehensive data on alien mammals, and SDMs remain among the best tools for assessing the effects of climate change on species distributions (Jiménez-Valverde et al. 2011; Pacifici et al. 2015). SDMs have been proven to accurately capture range shifts using historical data (Araújo et al. 2005; Rapacciuolo et al. 2012) and are widely used to guide management and policy decisions (IPBES 2016, 2023). Our

findings may assist with two aspects of alien species management: EP could help guide biosecurity measures like blacklisting, early detection, and rapid response frameworks to prevent further human-assisted dispersal, whereas SP could inform eradication and control efforts in alien ranges. To prevent the spread of alien mammals, strict policies should be implemented on known introduction pathways (Clout and Russell 2008; Seebens et al. 2023). Where alien species could experience a loss in climatic suitability, opportunities for restoration could emerge (Bellard et al. 2018; Finch et al. 2021). However, these efforts may not be sufficient to improve the conservation status of native species, as climate change will most likely have an impact on them as well (Baisero et al. 2020; Pacifici, Visconti, and Rondinini 2018). Management of alien mammals under climate change poses several challenges and must be planned proactively within future biodiversity loss mitigation strategies to anticipate change and promote thoughtful adaptation.

Author Contributions

Dino Biancolini: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Michela Pacifici:** methodology, validation, visualization, writing – review and editing. **Mattia Falaschi:** methodology, validation, writing – review and editing. **Céline Bellard:** methodology, validation, writing – review and editing. **Tim M. Blackburn:** methodology, validation, writing – review and editing. **Gentile Francesco Ficetola:** methodology, validation, writing – review and editing. **Carlo Rondinini:** conceptualization, funding acquisition, methodology, project administration, resources, supervision, validation, visualization, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code supporting the findings of this study are openly accessible on Figshare at <https://doi.org/10.6084/m9.figshare.25195628>. Species range maps and traits are available from the DAMA on Figshare at <https://doi.org/10.6084/m9.figshare.13014368.v1>, IUCN at <https://www.iucnredlist.org/search?permalink=244328c08a554921a8601b70ef673f95> and COMBINE on Figshare at <https://doi.org/10.6084/m9.figshare.13028255.v4>. Bioclimatic variables and climate scenarios were obtained from WorldClim at <https://worldclim.org/data/>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.