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Species pool, human population, and global versus regional invasion patterns

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Abstract

Context Biological invasions are among the greatest global and regional threats to biomes in the Anthropocene. Islands, in particular, have been perceived to have higher vulnerability to invasions. Because of the dynamic nature of ongoing invasions, distinguishing regional patterns from global patterns and their underlying determinants remains a challenge.

Objectives We aim to comparatively examine global versus regional patterns of plant invasions and the possible underlying mechanisms. We also test whether there is a difference in degree of invasion and invasibility between mainland areas and islands.

Methods We compiled and analyzed data from published sources for 100 mainland areas (i.e., regions, countries, states, and provinces) and 89 islands across the globe.

Results We find that (1) the pool of exotic species available intrinsically decreases as area of the land considered increases (at global scale, all is native), thus global invasion patterns assessed by exotic fraction (proportion of exotics) are primarily determined by land area; (2) because "exotic" is defined relative to the borders of the target region, "boundary effects" can result in regional differences in invasion patterns without any ecological processes being involved; and (3) human population density is closely linked to exotic fraction within regions that are defined

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by a single administrative border.

Conclusions There were clear differences between global and regional patterns of plant invasions. We observed no difference in the exotic fraction-area relationship between mainland areas and islands, supporting what we refer to as the "island-mainland continuum concept" (i.e., no clear separation in the degree of invasion between islands and mainland area with regard to the effects of area). Because of scale-dependency in many observed patterns, future focus should be placed on the links between local, regional, and global invasion patterns.

Keywords Anthropocene · Area · Boundary effects · Comparison · Globalization · Homogenization · Human · "Island-mainland continuum"

Introduction

Human-induced exotic invasions are a major component of ongoing global change (Seebens et al. 2015). Introductions of exotic species (also referred to as nonnative, alien, or introduced species) following the spread and expansion of human populations and associated activities (e.g., trade and travel) are dramatically changing world biogeography in multiple ways. The many changes include but are not limited to: (1) shifts in elevational ranges of native and nonnative species distributions (Alexander et al. 2009), (2) alterations of regional biodiversity patterns (Williamson 1996; Mack et al. 2000), (3) acceleration of evolution or hybridization of both native and exotic species (Whitney and Gabler 2008), (4) advancement of biotic homogenization at all spatial scales (Drake et al. 1989; Mckinney 1998), and (5) alterations in ecological states due to invasion-caused landscape metamorphosis (Fei et al. 2014). Because of these often irreversible changes, understanding the mechanisms behind observed invasion patterns remains a critical subject for both basic ecological research and land management.

Like many other ecological sub-disciplines, most studies to date dealing with biotic invasions have been conducted on small scales, although those based on regional- or subcontinental-scales are increasingly popular (Winter et al. 2010; Essl et al. 2013; Liebhold et al. 2013; Iannone et al. 2015; Oswalt et al. 2015; Fei

et al. 2016), as are those making cross-continental comparisons (e.g., Guo et al. 2006). Nevertheless, efforts aiming to form a global picture of species invasions (i.e., including all major landmasses) are extremely rare (but see Seebens et al. 2015; van Kleunen et al. 2015). Such efforts, particularly those comparing large taxonomic groups, can greatly improve our understanding of the key mechanisms driving invasion patterns at smaller spatial scales. Moreover, they can help to avoid bias or misinterpretation when comparing degrees of invasion in the same type of habitats at the same spatial scale but in different regions or continents (e.g., grasslands in California versus northern Asia, deciduous forests of the eastern USA versus Europe).

The need for investigating invasions at regional and global scales is in part revealed by the cross-regional inconsistency in the way key invasion drivers affect invasion patterns. With all else being equal, the degree to which smaller areas are invaded (i.e., exotic fraction) is often determined by species interactions such as competition and predation, while exotic fraction at landscape to regional scales (i.e., county/ state/province) is primarily controlled by the history of human colonization and associated social-economic factors such as population density, trade, and travel (Mack et al. 2000; Williamson and Harrison 2002; Iannone et al. 2015). Although human-related drivers affect invasion patterns at global scales (Seebens et al. 2015), they also vary spatially in the degree to which they do so. For instance, despite the clear link between exotic fraction and human population and associated activities (e.g., Renne et al. 2003; Luck 2007), some of the most populated regions have not been as heavily invaded as less populated regions (Sax 2001). These inconsistencies indicate potential cross-regional variabilities in the degree to which other driving factors (e.g., climate and/or land use changes) impact invasions, suggesting the need to identify factors that drive invasion patterns more consistently at regional and global scales.

To date, two frequently considered factors in regional and global investigation of species invasions are human population size and the area of the landmasses being compared (Lonsdale 1999). The need for a better understanding of how human population density (a surrogate for human disturbance, invasive propagule pressure and human-mediated dispersal) relates to regional and global invasion

patterns is revealed by the previously-described inconsistencies in which this factor affects invasions. As for landmass area, this factor directly affects whether or not a given species is defined as "exotic". The generally accepted definition of exotic species (i.e., species introduced by human activity to areas outside their native species ranges) makes the classification of species as exotic area- or boundary-dependent (Richardson et al. 2000). As a result, the area of the landmasses being compared could affect the interpretation of exotic invasion patterns and drivers (e.g., Guo and Ricklefs 2010). Nonetheless, area appears to be a suitable surrogate for exotic species pool size, as evidenced by the positive relationships between land area and exotic richness (Blackburn et al. 2008). However, this positive relationship will diminish as the target area becomes larger while the remaining earth' landmass area becomes smaller (i.e., the exotic species pool for the target area becomes more depleted; Fig. 1). Consequently, with increasing land area, the proportion of native species always increases while that of exotics
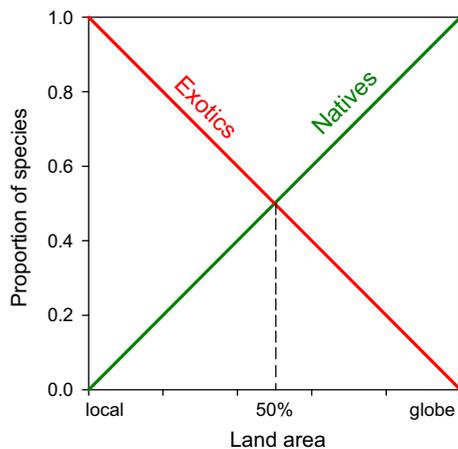
always decreases. In other words, the potential maximum exotic fraction of a given region taken from the global species pool will decrease with area. At the maximum possible area (i.e., at the global scale), no species are exotic and all species are native to the planet.

Using datasets compiled globally from prior investigations (described below and in Online Supporting Information), we aimed to better understand the factors contributing to regional and global invasion patterns, with particular emphasis on human population as the driver of species introductions and landmass area (mainland areas vs. islands). We addressed the latter by determining the size of the exotic species pool for a given area. Human population data were based on the latest available censuses and/or official estimates (or projections). When recent data were not available for a given country, we used data based on 2012 estimates made by the Population Division of the United Nations Department of Economic and Social Affairs (2013). We used population density (i.e., the number of people per square kilometer), and not population size (an attribute that depends on area, but does not account for it), because population density more accurately represents the magnitude or intensity of human activity in any given region. While there are many other indicators of the intensity of human activity such as gross domestic product (GDP) or transportation intensity, we choose population density as it is often closely correlated with other indicators (i.e., collinearity), and the data are readily available worldwide (Elvidge et al. 2001). Nevertheless, it is worthwhile to point out that patterns of species exchange and introductions across regions, such as introduction effort and pathway, can to some degree be altered by socio-economic status. For example, species introduction for ornamental purposes, which represents the major pathway for subsequent invasion in many developed countries, may be less intensive in developing countries due to a lack of resources, although this may change in the future (Seebens et al. 2015).

Although both exotic richness and biomass should ideally be used to assess habitat invasibility and degree of invasion (Guo et al. 2015). However, data on invader biomass are usually not available across large spatial scales (e.g., continental, regional). Instead, most large-scale studies use the number of exotic species or exotic fraction in the entire flora as an

Fig. 1 A local to global overview of relationships between species proportions (including exotic fraction) and land area for native and exotic species. On the global scale and following the definitions of native and exotic, the proportion of established or possible invading exotics will decrease with increasing area, while both the number and proportion of natives will always increase with area, resulting in a negative relationship between the proportions of natives and exotic species. The definition of "exotics" and global perspective control the upper bound value of the proportion of exotic species although the actual values could vary with time but still be anywhere below the theoretical limit. These patterns emerge because when all of the globes land areas are considered, all species are defined as both native and endemic, while no species are defined as exotic

indicator of degree of invasion or of invasibility (Elton 1958; Lonsdale 1999; Moore et al. 2001). We relied on exotic fraction as our measure of degree of invasion because it helps to standardize cross-regional and cross-scale comparisons (Hamil et al. 2016).

We used the most updated data that we had access to during our data gathering period of 2013–2015. For the comparisons among the three regions, we used data from Biota of North America Program (BONAP) for the USA (48 states); the exotic richness data (Jiang et al. 2011) at the province level for China (25 provinces); Essl et al.'s (2013) data which was based on the Delivering Alien Invasive Species Inventories for Europe (DAISIE) project for Europe (23 countries), accompanied by Weber (1997), Lambdon et al. (2008) for a few locations where DAISIE did not cover (Fig. S1). The majority of the islands' data were from Guo (2014). In addition, we compiled data from other individual countries and islands that are not included in the aforementioned main sources based on individual studies that cover a single or few areas and the related papers as listed below. Detailed information about the data and a full list of data sources are provided in online Supporting Information (Appendix S1). The comparative analyses among the three

regions used the data from the administrative units within each region, and the analyses for global patterns excluded the three continent regions (Europe, USA, and China) to ensure data independency. All analyses for this investigation were conducted using SAS 9.3 (SAS Institute, Cary NC).

Global patterns are influenced by land area and exotic species pools

To examine the relationship between exotic fraction and both landmass area and human population size, we compiled data from published sources for 189 sites worldwide (Fig. S1) from studies on mainland areas (region/countries/states/provinces; N = 100), as well as on islands (N = 89).

At the global scale, the numbers of native and exotic plant species within a given landmass are positively related to the area of that landmass (Fig. 2a). This relationship was stronger, however, for natives than it was for exotic species. These positive relationships agree with those previously found for native and exotic birds (Blackburn et al. 2008), and suggest land area to be a suitable surrogate
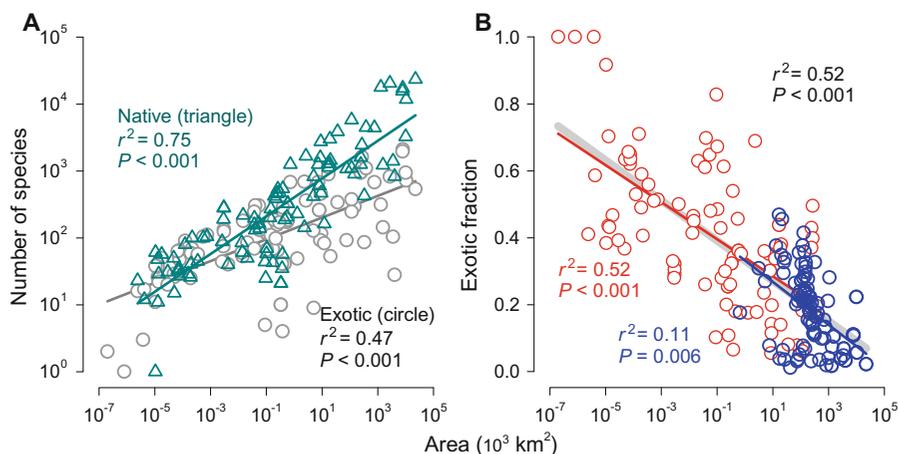

Fig. 2 a The numbers of native and exotic plants increase with area across the 189 mainland and island sites worldwide but exotics increase at a slower rate. Panel-a only represents the positive portion of the native-exotic correlations across the globe in Fig. 1 as the area of each largest continental site is still <20% of earth's land area and at this scale, both native and exotic species increase with area. A negative relationship will emerge if area continues to increase (to be >50% of earth's land area) and the exotic richness and exotic species pool is reduced as indicated by the steeper slope for native than for exotic

species in Fig. 2a. b The decline in exotic fraction with landmass area (see also Fig. 1). *Red dots* and *regression line* represent this relationship for islands ($r^2 = 0.52$, $P < 0.001$), *blue dots* and *regression line* represent this relationship for mainland areas excluding the three continental regions (Europe, USA, and China; $r^2 = 0.11$, $P = 0.006$), and the *gray regression line* represents this relationship for all data points across both mainlands and islands (data sources are listed in Appendix S1 of Supporting Information)

for both native and exotic species pool size. The ability of landmass area to act as a surrogate for exotic species pool, i.e., larger landmasses have fewer potential exotic species, explains why exotic fraction was so strongly and negatively related to land area (Fig. 2b). In fact, land area alone explained more than 50% of the variation in observed exotic fraction across various mainland areas and islands of the globe ($r^2 = 0.52$, $P = 0.001$).

We performed analyses of covariance (ANCOVA) to examine whether relationship between landmass area and exotic fraction differed between islands and mainland areas, and found no statistically significant difference ($F = 2.21$, $df = 191$, $P = 0.14$). This lack of difference, together with results from other recent studies (e.g., Sol 2000; Guo and Ricklefs 2010), supports what we refer to as the "island-mainland continuum concept" in terms of species invasions or invasibility (Fig. 2). That is, islands may not be more susceptible to invaders than continents, but rather, due to their smaller size, have more species defined as exotic and therefore have a larger exotic species pool (Lonsdale 1999; Guo 2014). These results are consistent with those of an increasing number of authors who

draw the same or similar conclusions (e.g., Simberloff 1995; Sol 2000). However, it is also important to point out that degree of invasion changes over time. Therefore, future studies that include more island and mainland sites are needed to confirm our findings.

We also performed linear regressions to examine the relationship between exotic fraction and human population density at the global scale. Although human population density has been identified as a driver of large-scale invasion patterns (see also Liebhold et al. 2013), human population density was not significantly related to degree of invasion at the global scale, i.e., when considering data from the 189 geographical units worldwide (Fig. 3a, $r^2 = 0.003$, $P = 0.28$). The absence of a clear effect of human population density on exotic fraction at the global scale makes sense considering that exotic fraction remains low in many highly-populated areas, particularly those in tropical zones such as south and southeast Asia (e.g., India, Malaysia, China; Jiang et al. 2011). On the continental scale, Asia comprises 30% of earth's land area and contains roughly 60% of the world-human population, yet is less invaded (exotic fraction = 0.07) than Europe (exotic frac-
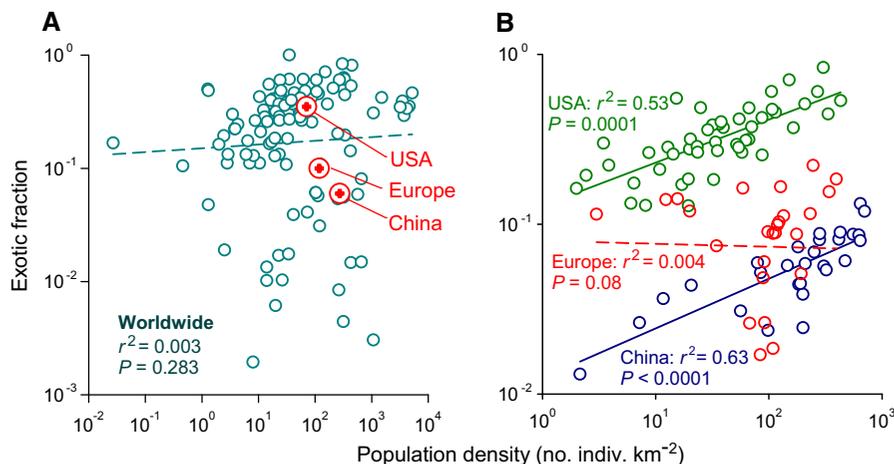

Fig. 3 a The relationship between human population density and degree of invasion (exotic fraction) across sites at the global scale. This dataset includes exotic plants on both islands and mainlands (i.e., countries, states/provinces, and regions) around the world for which data are available in literature. **b**: Despite the general positive relationships between human population and exotic plant richness in three regions (relationship not shown), positive population density-exotic fraction

relationships were evident only in USA (across states) and China (across provinces) but not in Europe (across countries). The ranked order of both population size and density is China > Europe > USA but the reverse order is true for exotic fraction (i.e., USA > Europe > China). Such regional patterns may reflect regional and historical differences in native plant richness and species introductions, and the effects of geopolitical boundaries in counting exotics

tion = 0.09) and North America (exotic frac-tion = 0.19) (data from Lonsdale 1999). Conversely, regions with relatively low population densities, such as North America and Australia, are heavily invaded (van Kleunen et al. 2015).

Region-specific effects of human-population density

To investigate the effects of human population density and area on invasion patterns at regional scale, we focused our analyses only on native and exotic plant species for the United States of America (USA), China, and Europe. We chose these three continental-level regions because data for these regions were readily available and more reliable relative to those for other large regions of the world.

Although human population density cannot explain global invasion patterns, it appears to be relevant to invasion patterns within individual regions, as it was found to be positively related to exotic fraction in two of the three regions. Positive associations between human population density and exotic fraction are clear within the USA and China, but not within Europe (Fig. 3b). This pattern may be explained by the size of the political sub-units within each investigated region. Within large countries that use a national border to define exotic species (e.g., China, Russia, USA, Mexico, etc.), exotic fraction within administrative sub-regions (e.g., states and provinces in USA and China, respectively) is often highly correlated with population density. However, in regions such as Europe, in which countries are smaller and each country defines exotics within the context of its own borders rather than for the entire region (e.g., European Union), this relationship is weak (Fig. 3).

In contrast to global patterns in which land area explained more than 50% of the variation in observed exotic fraction, land area of political sub-regions (e.g., states and provinces) explained less variability in exotic fraction in the USA ($r^2 = 0.39$, $P < 0.0001$) and in China ($r^2 = 0.30$, $P = 0.004$). However, similar to the effect of population density, land area also explained very little variability in exotic fraction for Europe ($r^2 = 0.003$, $P = 0.94$; Fig. S2). Multiple regression analyses indicate that area and population density together account for 74% ($F = 31.86$, d.f. = 24, $P < 0.0001$, VIF = 1.553), 74% ($F = 29.54$, d.f. = 47, $P < 0.0001$, VIF = 1.306), and 16% ($F = 1.96$, d.f. = 22, $P = 0.167$, VIF = 1.111) of total variation in exotic fraction for China, USA, and Europe, respectively (Fig. S3). The low amount of variation explained for Europe relative to China and the USA was expected given that exotic fraction was not related to area or population density in Europe (Fig. S4). These patterns were consistent with the observed population density-exotic fraction relationships in each region (as described above and in Fig. 3b).

Other influential factors

Regional differences in invasibility and propagule pressure

Despite the strong area-exotic fraction relationship that we found, variability among regions still exists. Inspection of plant species data revealed notable differences among regions in exotic fraction. Mean exotic fraction across sub-regions was considerably higher for the USA (across states; mean ± standard deviation: 0.35 ± 0.15) than it was for either Europe (across countries, 0.1 ± 0.06) or China (across provinces, 0.06 ± 0.03). These mean values were also significantly different from one another based on Student's t-tests (USA vs. Europe $T = 7.96$, $df = 72$, $P < 0.0001$; USA vs. China, $T = 9.68$, $df = 74$, $P < 0.0001$; Europe vs. China, $T = 2.98$, $df = 52$, $P = 0.004$). These observed differences in exotic fraction could be confounded by differences among these regions in disturbance levels (e.g., eastern Asia has a larger population, but less intense human land use than North America) and by asymmetrical flow of exotic propagules (Guo et al. 2006).

A critical related question remains to be answered in future endeavors: With the same history and level of human assistance (i.e., trade/travel), is it more likely for invaders to move from species-rich regions, such as eastern Asia (EA) or the tropics, to species-poor regions, such as North America (NA) or temperate zones, than the other way around (Sax 2001)? Much like natural species invasions that occurred without human intervention, which likely reflected the natural flow of species from species-rich regions to species-poor regions or which followed unidirectional ocean currents (Vermeij 1991), modern species invasions are also asymmetrical (e.g., van Kleunen et al. 2015). In

general, it appears that the number of species invading from species-rich regions to species-poor regions is far more than the other way around. Modern movement along this species-poor to species-rich gradient, however, differs from natural species movement in that it coincides with human activities including population migration, intentional species introductions, and unintentional introductions associated with trade and travel (Kerr and Currie 1995; Luck 2007). This movement could also be due to a greater release from competition experienced by species in species-rich areas, relative to that of species from less species-rich areas (Grace and Tilman 1990; Iannone et al. 2016). Alternatively, exotic species may have experienced lower degrees of selection pressure in what would be their new, more optimum environment (Sax 2001; Williamson and Harrison 2002). These conjectures need further investigation to confirm.

Despite the asymmetrical nature of species introduction and invasions, the regions donating most exotics are also receiving many exotic species (Guo et al. 2006). This may be at least partly due to the two-way traffic in global and cross-regional trade and travel, especially during modern times when human activities have created more open niches for exotic species establishment. However, symmetrical flow of species occurs more often across the political sub-units within larger regions (e.g., states and provinces) rather than among larger regions. For example, states such as Florida (USA) and provinces such as Guangdong (China) are both big donors and recipients of exotic species. In contrast, eastern Asia is a major donor of invaders, whereas North America is a major recipient, but not the other way around. Correspondingly, for species introductions between Europe and North America, relative to their overall species richness, the former is a major donor and the latter is a bigger receiver, largely reflecting the history of European colonization across North America. However, as new data show (van Kleunen et al. 2015), major flows in species exchange can also switch direction over time due to the changing nature of human activities.

Importance of unit for spatial inference, i.e., boundary effects

The strong relationship between area and exotic fraction that we found has important implications for the interpretation of global and regional invasion patterns. Essentially, it indicates that spatial patterns of invasions are strongly linked to how the spatial units in an investigation define an "exotic" species (Guo and Ricklefs 2010). Thus, greater than 50% of the variability in global patterns can be explained without invoking any ecological mechanism. This "boundary effect" may lead to the biased interpretations of invasion patterns. For instance, the perception that smaller islands are more invasible than mainland areas (Fig. 2; Simberloff 1995; Guo and Ricklefs 2010) may be due to nothing more than islands having more species defined as "exotic" than larger mainland areas (Guo 2014).

Boundary effects may also affect interpretations at regional scales. For example, within the USA and China, exotic fractions and human population densities are both negatively related to state and province areas (Fig. S2). This is not the case, however, for countries within Europe (Figs. 3, S3). This contradiction between Europe and both the USA and China is largely due to the differences among these studies in how "exotic" is defined. Studies of invasion in Europe define exotic separately for each observational unit, i.e., each country, contained within the continent (Weber 1997), whereas most previously published studies on invasion in USA and China define exotic relative to the entire nation, not relative to states or provinces, which have areas more similar to those of European countries. The domestic exotic richness in some large countries is likely underestimated because the monitoring efforts directed toward species introductions among internal units such as states or provinces are minimal or nonexistent. For example, exotic fraction increases substantially when species exotic to specific region within a country are considered versus only those that are exotic to the entire country (Guo and Ricklefs 2010). For this reason, caution must be used when comparing studies of invasion for Europe, the USA, and China. These patterns reveal that in order to avoid misinterpretations of global and regional invasion patterns, results of investigations must be interpreted in light of potential boundary effects.

Island vs. mainland habitats and long-term trends toward global homogenization

Because islands tend to have fewer native species than comparable mainland areas, the exotic fraction and the

invasibility of island ecosystems appear to be higher. Data presented in this study also show that the human population density tends to be higher within smaller regions or administrative units, including islands, thus increasing the propagule pressure. Our data and analyses support the "island-mainland continuum" concept (i.e., no clear cut-off in exotic fraction between island and mainland habitats as shown in Figs. 2, 3) as, in general at both global and regional levels, exotic fraction declines with increasing area, regardless of whether the target habitat is on an island or continent. It is important to note, however, that island ecosystems are likely to experience greater impacts than those of mainland areas with the same exotic fraction (Sol 2000).

The strong negative relationship that we found between area and exotic fraction suggests, as do former studies (e.g., Moore et al. 2001; Williamson and Harrison 2002), that the exotic fraction in a given target region at the global scale could be strongly influenced by: (1) the size of the potential exotic species pool and (2) the proximity to exotic species pools; i.e., with all else equal, the habitats closer to the exotic species pools will show greater "invasibility", becoming invaded more quickly over time (Williamson 1996). However, if we assume that with human assistance each species has a chance to be introduced anywhere around the world given enough time, the importance of the distance factor becomes significantly diminished (i.e., the residual values in Fig. 2b would decrease and the area-exotic fraction relations would become stronger with time). Therefore, given enough time, all regions with similar climatic and physiographic conditions would eventually attain similar exotic fractions, and become more similar with regards to species composition, thus increasing the already noted global homogenization.

To predict future exotic fraction and its relationship with area, all resident species (i.e., both natives and nonnatives), varying habitat suitability (e.g., due to climate extremes; Isbell et al., 2015), and socio-economic development (especially in "emerging economies"; Seebens et al. 2015) must be taken into account. These components of global change can cause extinctions of native species, thereby promoting biological invasions by creating open niches for exotic species (Vitousek et al. 1997; Mack et al. 2000; Joyce et al. 2013) unless such processes are limited by dispersal and/or management and policy actions

(Williamson 1996). Consequently, over the long-term and given the current rate of species introductions, exotic fraction may continue to increase in many regions and habitats while the negative area-exotic fraction relationship (Fig. 2) will likely become stronger. North America is a good example, given the recent, intense disturbance it has undergone as a result of European colonization. Nevertheless, the number of exotic species that could still successfully invade this continent in the future remains an interesting and important question to explore.

While our results show that greater than 50% of the total variation in present degrees of invasion could be explained at the global scale by the size of a given region (which acts as a surrogate for external species pool), and that human population density can largely explain variability at the regional scale, much variability across all scales still needs explanation. Identifying other drivers of this variability including possible sampling biases or limitations, i.e., the residuals in Figs. 2 and 3, is needed to better understand the mechanisms by which future invasion patterns will emerge. Additionally, the role of more concentrated or asymmetrical travel and trade among some continents such as North America, Europe, and Asia (Halpern et al. 2008) in both current and future patterns of species exchange and introduction remains to be explored. Furthermore, similar to the situation in many other ecological studies that involve data from multiple locations, our results could be influenced by the limitations in data coverage, environmental variability inherent to this dataset, and possible bias in sampling intensity. Therefore, how our findings here might be compared with the patterns and mechanisms based on future studies that include more study sites on both islands and mainland areas remains to be seen.

Conclusions

Due to human activities, many species are overcoming natural dispersal barriers at unprecedented rates, resulting in the increased homogenization of the earth's biotas. At the current rate of species invasions, it is likely that the increased exotic fraction occurring across regions will lead to higher native species extinctions across multiple spatial scales, and thus will reduce global biodiversity. At the global scale and with enough time for further invasions, the definition

of *"exotics"* (which relates to the area of the region receiving the invading species) alone could lead to some of the patterns of exotic fraction observed among regions without invoking any of the frequently cited ecological mechanisms of species invasion. Although native richness always increases with land area, the positive relationships between exotic richness and area and between native and exotic richness only exist until a threshold at which land area becomes too large and the exotic species pool becomes exhausted. At the regional level, i.e., within common administrative borders, human population density largely determines observed invasion patterns. Although invasibility may fluctuate over time, due to growing human populations and associated activities (e.g., travel/trade) and global change (e.g., climate and land use change), exotic fraction is likely to increase at local and regional scales until the species that could establish in new environments have mostly been introduced or until highly effective management is in place. Because of scale-dependency in many observed patterns, more focus should be placed on the links between local, regional, and global invasion patterns (e.g., Dawson et al. 2013; Hamil et al. 2016), and on links between current (a snapshot) and future, long-term projections of invasion patterns (Wu 2013).

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