





# Worldwide effects of non-native species on species–area relationships

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**Abstract:** Non-native species have invaded most parts of the world, and the invasion process is expected to continue and accelerate. Because many invading non-native species are likely to become permanent inhabitants, future consideration of species-area relationships (SARs) should account for non-native species, either separately or jointly with native species. If non-native species occupy unused niches and space in invaded areas and extinction rate of native species remains low (especially for plants), the resultant SARs (with both native and non-native species) will likely be stronger. We used published and newly compiled data (35 data sets worldwide) to examine how species invasions affect SARs across selected taxonomic groups and diverse ecosystems around the world. We first examined the SARs for native, non-native, and all species. We then investigated with linear regression analyses and paired or unpaired *t* tests how degree of invasion (proportion of non-native species) affected postinvasion SARs. Postinvasion SARs for all species (native plus non-native) became significantly stronger as degree of invasion increased ( $r^2 = 0.31$ ,  $p = 0.0006$ ), thus, reshaping SARs worldwide. Overall, native species still showed stronger and less variable SARs. Also, slopes for native species were steeper than for non-native species (0.298 vs. 0.153). There were some differences among non-native taxonomic groups in filling new niches (especially for birds) and between islands and mainland ecosystems. We also found evidence that invasions may increase equilibrium diversity. Study of such changing species–area curves may help determine the probability of future invasions and have practical implications for conservation.

**Keywords:** complementarity, diversity, island biogeography, natives, niche, non-natives, richness, transition

Efectos Globales de las Especies No Nativas sobre las Relaciones Especie–Área

**Resumen:** Las especies no nativas han invadido la mayor parte del mundo y se espera que el proceso de invasión continúe y se acelere. Ya que muchas especies invasoras no nativas probablemente se conviertan en habitantes permanentes, la consideración a futuro de las relaciones especie–área (REA) debería considerar a las especies no nativas, ya sea por separado o en conjunto con las especies nativas. Si las especies no nativas ocupan nichos sin usar y el espacio en las áreas invadidas y la tasa de extinción de las especies nativas permanecen bajas (especialmente para las plantas), las REA resultantes (tanto con las especies nativas como las no nativas) probablemente sean más fuertes. Usamos datos publicados y recientemente compilados (35 conjuntos de datos mundiales) para examinar cómo las invasiones de especies afectan a las REA en grupos taxonómicos selectos y en diversos ecosistemas en todo el mundo. Primero examinamos las REA para todas las especies, así como para las nativas y las no nativas. Después investigamos con análisis de regresión lineal y pruebas *t* emparejadas o no emparejadas cómo afectó el grado de invasión (proporción de la especie no nativa) a las REA post-invasión. Las REA post-invasión para todas las especies (nativas más no nativas) se volvieron significativamente más fuertes conforme incrementó el grado de invasión ( $r^2 = 0.31$ ,  $p = 0.0006$ ), remodelando así las REA en todo el mundo. En general, las especies nativas

**Article Impact Statement:** Increasingly, altered species–area relationships due to non-native species invasions affect future conservation efforts. Paper submitted December 4, 2019; revised manuscript accepted June 9, 2020.

todavía mostraron REA más fuertes y menos variables. De igual manera, las pendientes de las especies nativas fueron más pronunciadas para las especies no nativas (0.298 vs. 0.153). Hubo algunas diferencias entre los grupos taxonómicos no nativos al llenar nichos nuevos (especialmente para las aves) y entre las islas y los ecosistemas de tierra firme. También encontramos evidencias de que las invasiones pueden incrementar la diversidad equilibrada. El estudio de dichas curvas cambiantes de relación especie-área podría ayudar a determinar la probabilidad de las futuras invasiones y tener implicaciones prácticas para la conservación.

**Palabras Clave:** biogeografía de islas, complementariedad, diversidad, nativas, no nativas, nicho, riqueza, transición

**摘要:** 非本地种入侵正发生在全球的大部分地区,并且在有些地区入侵过程愈演愈烈。由于许多非本地种都有可能成为永久定居者,在解释新的物种-面积关系(SARs)时就应该单独考虑非本地种与本地种,然后综合考虑所有物种(本地种与非本地种的总和)。如果非本地种占据了入侵地区的未被利用生态位与空间,且本地种的灭绝速率保持较低,那么由此形成的所有物种的物种-面积关系会更加紧密。我们利用已发表的以及自行整合的数据(全球35个数据集),在全球尺度上对不同类群在不同生态系统中物种入侵后的物种-面积关系的影响进行了检验。我们首先检验了本地种、非本地种及所有物种的物种-面积关系。其次,我们利用线性回归分析、配对t检验、非配对t检验等方法研究了入侵度(非本地种占有物种的比例)对物种入侵后的物种-面积关系的影响。分析结果表明,随着入侵程度的增加,所有物种的物种-面积关系显著增强( $r^2 = 0.31, p = 0.0006$ ),这在全球尺度上重塑了物种-面积关系。总体而言,本地种的物种-面积关系依旧比非本地种强且更少变化。本地种的物种-面积曲线的斜率也比非本地种更高(分别是0.298和0.153)。不同非本地生物类群在入侵岛屿与大陆生态系统之间也存在着不一致的情况,但总体上增强了物种多样性与面积的平衡态。因此,研究物种-面积曲线的变化将有助于预测未来生物入侵的可能性,也对生物保护有着现实意义。

**关键词:** 补偿效应,多样性,非本地种,岛屿生物地理学,本地种,生态位,物种丰富度,过渡性

## Introduction

Species invasion is a rapidly growing, global problem with greater impacts on island than mainland ecosystems (Supporting Information) (Sax & Gaines 2008; Baiser & Li 2018). The theory of island biogeography has been applied mostly to native species relative to research and conservation goals (e.g. MacArthur & Wilson 1967; Warren et al. 2015). Considerable variation in the species-area relationship (SAR) across regions, ecosystems, and taxonomic groups has been reported (Rosenzweig 1995; Ricklefs & Lovette 1999; Blackburn et al. 2008). However, in the era of biotic invasions, the theory of island biogeography could have predictive power for different taxa (e.g. plants vs. birds) and for different regions (e.g. mainland vs. island) across the globe (Sax & Gaines 2003). An increasingly important question is whether the theory also applies to non-native species (e.g. Burns 2015; Baiser & Li 2018; Leihy et al. 2018). In most invaded ecosystems, naturalized non-native species are difficult to eradicate and are likely to remain as elements of the local biota (Powell et al. 2013). Thus, how non-native species influence SARs may provide key insights for conservation science, biogeography, and management and inform understanding of species' extinction and biotic resistance to future invasions (Sax & Gaines 2003; Nunez-Mir et al. 2017). For example, if non-native species invasion enhances SARs, it could mean a greater level of species saturation and continued accumulation in both richness and abundance of non-native species through time (Warren et al. 2015). In the process, more native

species could become rare, endangered, or extinct (Sax & Gaines 2008; Rouget et al. 2016).

Species invasions may also provide insights into understanding of carrying capacity, niche theory, and biotic homogenization (e.g. McKinney 1998; Lockwood & McKinney 2001). Indeed, invasions by non-native species have apparently changed some commonly observed patterns exhibited by native species across multiple scales (Sax & Gaines 2003). For example, invasions inevitably affect equilibrium conditions in a community via colonization and extinction (cf. the equilibrium theory of island biogeography) (Sax & Gaines 2011). As a result, a key biogeographical pattern—the species-area relationship—will likely shift (He et al. 2005; Storch 2016).

Closely linked to the theory of island biogeography, the SAR has long been a central topic in ecology, biogeography, and conservation (Rosenzweig, 1995, 2001; Solyomos & Lele 2012). The SAR has frequently been used to test species saturation and equilibrium conditions (Powell et al. 2013; Helmus et al. 2014). In natural settings, SARs are always positive despite their varied shapes and forms (Lomolino et al. 2006). Species invasions likely alter SARs (Sax & Gaines 2008), but how these effects vary across different spatial scales, in different settings (e.g. islands vs. mainland), and for different taxonomic groups is not clear (Rosenzweig 2001; Collins et al. 2002; Powell et al. 2013). Comparing non-native species with native species and combining both sets of species on the same sites would be useful for testing key ecological and biogeographic theories concerning competition, coexistence, and species saturation.

Although most previous work on SARs focused on native species governed by natural dynamics (Rosenzweig 1995), in the Anthropocene human activities are increasingly altering SARs. Examples of such alterations include creating disturbances that increase species richness (e.g. via the intermediate disturbance hypothesis), which could strengthen or weaken SARs; creating large-scale disturbances that cause species extinctions, leading to weakened SARs; and introducing species locally (where they fill unoccupied niche space), which may enhance SARs disproportionately at small scales (Hulme 2008).

Previous researchers have investigated specific forms of SARs, mostly for native species (MacArthur & Wilson 1967; Rosenzweig 1995) or to contrast native versus non-native species (e.g. Blackburn & Duncan 2001; Hulme 2008; Li et al. 2018). Instead of dealing with specific shapes of SARs or investigating whether species invasions affect regional or global diversity (Rosenzweig 2001), we used published data sets and newly compiled data sets to examine how species invasions have reshaped SARs in diverse ecosystems, among different taxa, and across multiple spatial scales (Hulme 2008). To do this, we included a more relevant scope for SARs: all resident species in invaded habitats including both native and non-native species. We tested three major hypotheses. First, non-native species invasion leads to new and stronger SARs (e.g. larger  $r^2$ ) than those for native species only (Supporting Information). Second, because non-native species usually occupy some unoccupied native species niches, the new SARs (native plus non-native) become stronger as degree of invasion (DI) based on richness measures increases. Third, the levels of change in new SARs are different between plants and birds and between mainland sites and islands. To address these hypotheses, we compared the SARs among native species, non-native species, and total species (native and non-native species combined). These relationships were then compared between mainland regions or sites and islands and between plants and birds (no corresponding comparisons were made for other taxonomic groups due to limited data).

## Methods

We used 35 data sets from diverse types of ecosystems and taxonomic groups from around the world (27 for islands and 8 for mainland sites) including 29 published data sets and 6 newly compiled data sets (Table 1 & Supporting Information). The 35 data sets identified through a Google Scholar search with the keywords “*species-area*” AND “*non-native*” OR “*exotic*” OR “*introduced*” OR “*alien*” OR “*native*” published before 11 August 2016. Although some of the related studies did not address SARs specifically, they included data required for

our study: native and non-native species richness and area for each site. The 35 data sets included a range of taxonomic groups including plants ( $n = 22$ ), birds ( $n = 8$ ), mixed (bird, amphibian, and mammal species;  $n = 2$ ), insects ( $n = 2$ ), and earthworms ( $n = 1$ ). The study sites included local terrestrial ecosystems, watersheds across various scales, and islands. To meet the analytical requirements of our study, we collected baseline information including area, native species richness, and non-native species richness for each mainland site and each island.

The studies that included the 29 published data sets used offered detailed descriptions about how the sites (or islands) were selected, and each study (or data set) had its own criteria for site selection (e.g. Southern Ocean islands in Chown et al. [2005] and Leihy et al. [2018] and Boston Harbor islands in Long et al. [2009]). Initially, we compiled a data set that was much larger (with 504 observations) than any of the other 29 data sets. This large data set was based on the same search criteria, except the sites were randomly chosen around the world (i.e. without focusing on a certain region or island group so that some data could be extracted from studies that focused on a single island or site regardless of its specific location or geopolitical boundary [Supporting Information]). To be consistent with the 29 published data sets, our large data set was subdivided into six smaller data sets based on taxa and ecosystem type (i.e. island vs. continent) (Table 1). For the islands or sites in each data set, we calculated the total species richness (native and non-native species combined) and DI (Lonsdale 1999) and then examined the native-non-native richness correlations across sites within each data set. DI was measured as the non-native fraction (or proportion) in the entire flora or fauna at each site or island (i.e.  $DI = \text{number of non-native species} / (\text{number native species} + \text{number non-native species})$ ). Because abundance data (density, biomass, or cover) were mostly unavailable across the data sets, we did not include such data in our DI measure (Guo et al. 2015).

The species-area curve is commonly described by the power function (Preston 1960) as  $S = cA^z$ , where  $S$  is the number of species,  $A$  is area,  $c$  is a constant, and  $z$  is an estimated parameter. For consistency and simplicity, we used the most common equation (simple linear regression on log-log scales) (Rosenzweig 1995):

$$\log(S) = \log(c) + z \log(A), \quad (1)$$

where  $z$  is the slope of a linear (straight line) SAR. We examined the SARs for native and non-native species separately and for all species (native + non-native) in each data set and then compared slopes, intercepts, and  $r^2$ s among the three species groups across the 35 data sets with  $t$  tests. When a normality test failed, we used the Mann-Whitney rank sum test instead.

Table 1. Results of species-area relationships examined for native, non-native, and all species (native plus non-native) and degree of invasion (DI) for each of the 35 data sets (islands and mainland).<sup>a</sup>

Location and data source	No. sites <sup>b</sup>	Taxa	Coefficient of determination ( $r^2$ ) <sup>c</sup>				Mean DI	Notes
			Native-non-native correlation ( $r^2$ ) <sup>c</sup>	Native	Non-native	All species		
<b>Island</b>								
Blackburn et al. (2008)	35	Bird	0.38 <sup>c</sup>	0.79 <sup>c</sup>	0.16	0.73 <sup>c</sup>	0.41	Worldwide
Case (1996)	72	Bird	0.01	0.71 <sup>c</sup>	0.02	0.72 <sup>c</sup>	0.23	Worldwide
Sax et al. (2002) <sup>b</sup>	23	Bird	0.27	0.47 <sup>c</sup>	0.25 <sup>c</sup>	0.62 <sup>c</sup>	0.50	Oceanic islands, Worldwide
Chown et al. (1998)	25	Bird	0.16 <sup>c</sup>	0.16 <sup>c</sup>	0.01	0.17 <sup>c</sup>	0.27	Southern Ocean Islands
Guo (2014a)	34	Bird	0.21 <sup>c</sup>	0.73 <sup>c</sup>	0.01	0.72 <sup>c</sup>	0.27	Worldwide
Blackburn et al. (2016)	68	Bird	0.40 <sup>c</sup>	0.57 <sup>c</sup>	0.33 <sup>c</sup>	0.55 <sup>c</sup>	0.24	Worldwide
This study (data set I)	41	Bird	0.11	0.72 <sup>c</sup>	0.01	0.72 <sup>c</sup>	0.16	Worldwide
This study (data set II)	125	Bird	0.003	0.64 <sup>c</sup>	0.05	0.63 <sup>c</sup>	0.22	Worldwide
Chown et al. (1998)	25	Plant	0.33 <sup>c</sup>	0.25 <sup>c</sup>	0.33 <sup>c</sup>	0.36 <sup>c</sup>	0.29	Southern Ocean Islands
Sax et al. (2002)	13	Plant	0.95 <sup>c</sup>	0.66 <sup>c</sup>	0.69 <sup>c</sup>	0.68 <sup>c</sup>	0.51	Oceanic islands, Worldwide
Moody (2000)	8	Plant	0.59 <sup>c</sup>	0.67 <sup>c</sup>	0.67 <sup>c</sup>	0.76 <sup>c</sup>	0.30	California Channel Island
Long et al. (2009)	25	Plant	0.71 <sup>c</sup>	0.29 <sup>c</sup>	0.78 <sup>c</sup>	0.75 <sup>c</sup>	0.60	Boston Harbor
Kueffer et al. (2010)	30	Plant	0.43 <sup>c</sup>	0.66 <sup>c</sup>	0.48 <sup>c</sup>	0.61 <sup>c</sup>	0.35	Atlantic, Caribbean, Pacific, and Western Indian Oceans
Guo (2014a)	44	Plant	0.68 <sup>c</sup>	0.45 <sup>c</sup>	0.14	0.36 <sup>c</sup>	0.28	Worldwide
Guo et al. (2017)	89	Plant	0.56 <sup>c</sup>	0.68 <sup>c</sup>	0.46 <sup>c</sup>	0.70 <sup>c</sup>	0.38	Worldwide islands
Denslow et al. (2009)	114	Plant	0.73 <sup>c</sup>	0.77 <sup>c</sup>	0.56 <sup>c</sup>	0.77 <sup>c</sup>	0.52	Tropical Pacific Islands
Wu et al. (2004)	20	Plant	0.52 <sup>c</sup>	0.47 <sup>c</sup>	0.26 <sup>c</sup>	0.44 <sup>c</sup>	0.31	Worldwide
Castro et al. (2010)	68	Plant	0.58 <sup>c</sup>	0.70 <sup>c</sup>	0.78 <sup>c</sup>	0.82 <sup>c</sup>	0.46	Archipelagos in Atlantic and Pacific Oceans
McMaster (2005)	22	Plant	0.88 <sup>c</sup>	0.83 <sup>c</sup>	0.85 <sup>c</sup>	0.86 <sup>c</sup>	0.45	Coast of eastern North America
Blackburn et al. (2016)	68	Plant	0.56 <sup>c</sup>	0.35 <sup>c</sup>	0.22 <sup>c</sup>	0.30 <sup>c</sup>	0.41	Worldwide
This study (data set I)	51	Plant	0.49 <sup>c</sup>	0.58 <sup>c</sup>	0.14 <sup>c</sup>	0.51 <sup>c</sup>	0.37	Worldwide
This study (data set II)	129	Plant	0.59 <sup>c</sup>	0.54 <sup>c</sup>	0.40 <sup>c</sup>	0.56 <sup>c</sup>	0.42	Worldwide

Continued

Table 1. Continued

Location and data source	No. sites <sup>b</sup>	Taxa	Coefficient of determination (r <sup>2</sup> ) <sup>c</sup>					Notes
			Native-non-native correlation (r <sup>2</sup> ) <sup>c</sup>	Native	Non-native	All species	MeanDI	
Walsh et al. (2012)	65	Mixed <sup>d</sup>	0.03	0.55 <sup>c</sup>	0.08	0.50 <sup>c</sup>	0.40	World islands and Archipelagos
Berglund et al. (2009)	25	Mixed <sup>d</sup>	0.02	0.48 <sup>c</sup>	0.33 <sup>c</sup>	0.60 <sup>c</sup>	0.14	Single-country islands
Chown et al. (1998)	25	Insect	0.12	0.13	0.01	0.18 <sup>c</sup>	0.18	Southern Ocean Islands
Economou et al. (2017)	19	Ant	0.14	0.35 <sup>c</sup>	0.66 <sup>c</sup>	0.60 <sup>c</sup>	0.44	Pacific Island groups
Roura-Pascual et al. (2016)	102	Ant	0.08 <sup>c</sup>	0.57 <sup>c</sup>	0.46 <sup>c</sup>	NA	0.22	Worldwide
Mainland								
Guo and Ricklefs (2010)	48	Plant	0.04	0.31 <sup>c</sup>	0.05	0.15 <sup>c</sup>	0.35	48 conterminous U.S. states
Guo (2014b)	3107	Plant	0.69 <sup>c</sup>	0.17 <sup>c</sup>	0.02	0.16 <sup>c</sup>	0.16	3107 counties in 48 conterminous U.S. states
Espinosa-García et al. (2004)	32	Plant/weed	0.52 <sup>c</sup>	0.22 <sup>c</sup>	0.02	0.21 <sup>c</sup>	0.05	federal states of Mexico
Guo et al. (2017)	24	Plant	0.11	0.002	0.18 <sup>c</sup>	0.17 <sup>c</sup>	0.11	Europe (countries)
Guo et al. (2017)	28	Plant	0.29 <sup>c</sup>	0.12 <sup>c</sup>	0.11 <sup>c</sup>	0.001	0.06	China (provinces)
Mooney et al. (1986)	19	Plant	0.61 <sup>c</sup>	0.78 <sup>c</sup>	0.18	0.71 <sup>c</sup>	0.22	California
This study (data set I)	152	Plant	0.36 <sup>c</sup>	0.80 <sup>c</sup>	0.20 <sup>c</sup>	0.66 <sup>c</sup>	0.35	Worldwide (terrestrial)
This study (data set II)	6	Earthworm	0.17	0.83 <sup>c</sup>	0.17	0.79 <sup>c</sup>	0.42	Worldwide

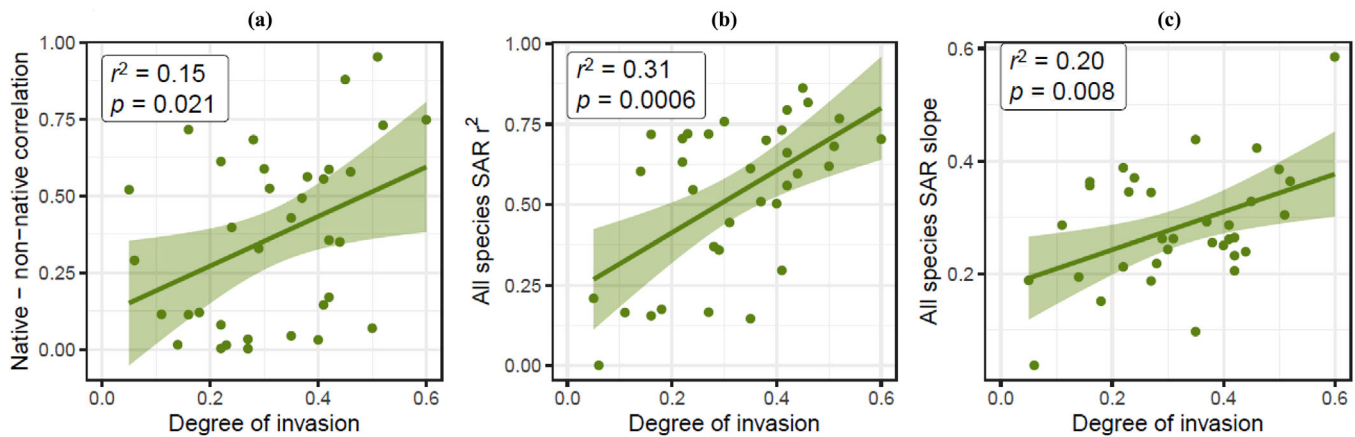
<sup>a</sup> Non-significant correlations or relationships do not have asterisks. All data were log-transformed before analyses. A list of data sources is provided in Supporting Information.

<sup>b</sup> For island, number of islands or island groups.

<sup>c</sup> Significance: \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

<sup>d</sup> Including bird, amphibian, and mammal species.

<sup>e</sup> Mixed mainland and island sites due to small sample size.



**Figure 1.** Effects of degree of invasion measured as non-native species fraction of the (A) native-non-native richness correlation, (B) coefficients of determination ( $r^2$ ), and (C) slopes ( $z$ ) of the species-area relationships for all species across selected sites around the world (shading, SD estimates).

To examine how species invasions altered SARs, we used  $t$  tests to compare the slopes ( $z$ ) and intercepts ( $c$ ) among native, non-native, and in combination; between mainland and islands; and between plants and birds (other taxonomic groups were not compared separately due to their small sample sizes). Because similar intercepts and slopes may be observed among the three groups of species (i.e. native species, non-native species, and combined), we focused on the coefficients of determination ( $r^2$ ) in SARs. Because of the lack of comparable data for non-native birds on the mainland, we did not perform a comparative analysis between mainland and island data for birds.

There is no commonly accepted approach to estimate community saturation, so we assessed the possibility of its occurrence for each island or mainland site by examining the response of non-native species richness to the residuals derived from a regression of the native SARs based on the data set we compiled in this study. We assumed that positive residuals (sites above the regression line of a native species' SAR) indicated a higher probability of species saturation and that negative residuals indicated that more niches were available for non-native species to invade.

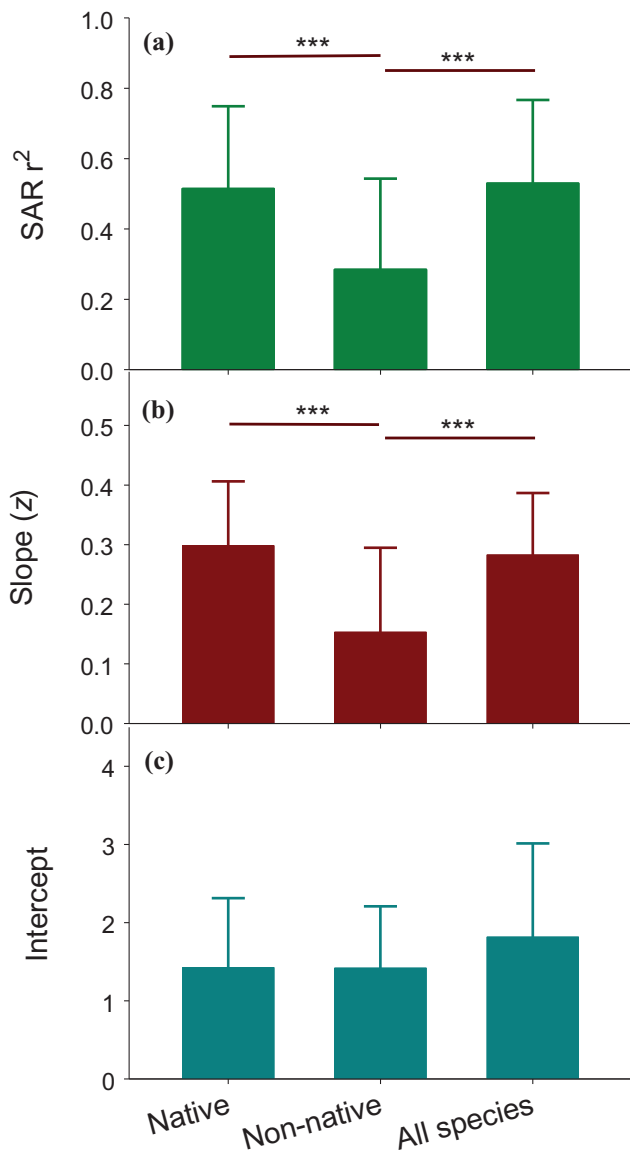
Because our focus was the postinvasion, SARs for all resident species, and both native and non-native species were sampled from the same mainland sites or islands at the same time. We did not attempt to examine the possible contributions of other factors such as isolation, latitude, elevation, and soil, to SARs. In cases where the number of either non-native or native species was 0, we log transformed ( $\log [n + 1]$ ) richness data before analysis.

## Results

Across the 35 data sets, the average DI ranged from 0.05 to 0.60 and the mean was 0.32 (SD: 0.14). The non-native and native richness correlations and the  $r^2$  and slopes in SARs for combined species (native plus non-native species) increased significantly as DI increased (Fig. 1), although the intercepts did not change as DI increased ( $r^2 = 0.04$ ,  $p > 0.05$ ).

Paired  $t$  tests did not show differences in SARs between native and all species combined (Fig. 2A). In almost all cases, the  $r^2$  and slopes of the SARs for native species in all taxonomic groups (i.e. birds, plants, insects, and earthworms) were higher than that for non-native species (Table 1, Figs. 2A-B, Supporting Information). In 43% (35 total) of the cases, species introductions and successful invasions led to stronger SARs (Table 1). The slopes of SAR did not differ between only native species and all species combined (Fig. 2B). Intercepts of SARs did not differ among native, non-native, and all species combined (Fig. 2C).

We observed both similarities and differences in SARs between islands and mainland sites when all taxonomic groups were combined (Supporting Information). On both islands and mainland sites, native species had stronger SARs (with respect to both  $r^2$  and slopes) than non-native species (Supporting Information). The SAR slopes did not differ between islands and mainland sites for native ( $t = 0.131$ ,  $p = 0.45$ ), non-native ( $t = 0.95$ ,  $p = 0.18$ ), and all species ( $t = 0.37$ ,  $p = 0.36$ ), despite the higher DIs on islands than on mainland sites ( $t = 1.94$ ,  $p = 0.033$ ). Islands had steeper slopes ( $t = 2.738$ ,  $p = 0.01$ ) and higher DIs ( $t = 2.21$ ,  $p = 0.023$ ) than sites on the



**Figure 2.** Comparison of (A) coefficient of determination ( $r^2$ ), (B) slope, and (C) intercept of the species-area relationships (SARs) for native, non-native, and all species across all study sites from both islands and mainlands around the world (error bars, SE).

mainland for non-native plants. This analysis could not be done for non-native birds due to limited data. Intercepts increased significantly on mainland sites after invasion (native species vs. all species combined; Wilcoxon signed rank test,  $w = 325$ ,  $z = 4.372$ ,  $p < 0.001$ ), but not on islands (Supporting Information). When islands and mainland sites were combined, no difference was detected.

Across the 35 data sets, the fits of the SARs and their slopes for non-native species increased as DI increased (Figs. 3A-B). The intercepts for non-native species SARs

showed no significant correlation with DI (Fig. 3C). The  $r^2$ s in SARs of both native and non-native species were positively related to  $r^2$ s for all species (Supporting Information). Coefficients of determination of the SARs were not correlated between native and non-native species when all taxonomic groups were included ( $r^2 = 0.052$ ,  $p = 0.168$ ) (Supporting Information).

Major similarities and differences in non-native SARs were also evident between birds and plants. Other groups did not have large enough samples for testing. (Supporting Information). For example, in all cases for birds, the slopes were shallower and  $r^2$  was lower for non-native species than for native species. The opposite was true for plants (Table 1). The differences in SAR slopes were not statistically significant between native plants and birds (0.328 vs. 0.300,  $t = 0.736$ ,  $df = 27$ ,  $p = 0.551$ ) and  $r^2$  values (0.598 vs. 0.491,  $t = 1.083$ ,  $df = 27$ ,  $p = 0.288$ ). Similarly, for non-native species only, birds and plants showed no difference in slopes (0.085 vs. 0.189,  $t = -1.707$ ,  $df = 27$ ,  $p = 0.099$ ). Finally, combining native and non-native species produced no difference in slopes (0.330 vs. 0.283,  $t = -1.059$ ,  $df = 27$ ,  $p = 0.202$ ).

Contrary to our predictions regarding community saturation based on native SARs, the positive native versus non-native correlation (Table 1) and positive residuals in Supporting Information indicated lack of community saturation, especially at larger scales (i.e., islands and large mainland sites), at least in the short term.

## Discussion

Our results show that species invasions have reshaped SARs around the world. This can be seen in the differences between SARs of all species combined (native and non-native) compared with those for native species only. In some cases, species invasion indeed altered SARs or led to new SARs (for all species) that were different from the original SARs (for native species only) across the globe (Supporting Information). Furthermore, the change in original SARs depended on DI. Increased DI was associated with strong SARs (higher  $r^2$  and steeper slope) for all species combined (i.e., supporting our second hypothesis). This change in SARs was not readily apparent in paired comparisons (i.e.,  $t$  tests) between SARs of native species and those of all species (native plus non-native) (Fig. 2). This is because such paired comparisons between native and all species did not take proportional non-native richness into account, and when an area is not heavily invaded (small DIs), overall SARs may not change significantly. The positive effect of DI on SARs for all species may also have been reflected in the increasing native versus non-native species richness correlations as DI increased (Fig. 1A). Therefore, to test whether invasion has reshaped SARs, comparing invaded with uninvaded areas is inadequate and DI needs to be considered.

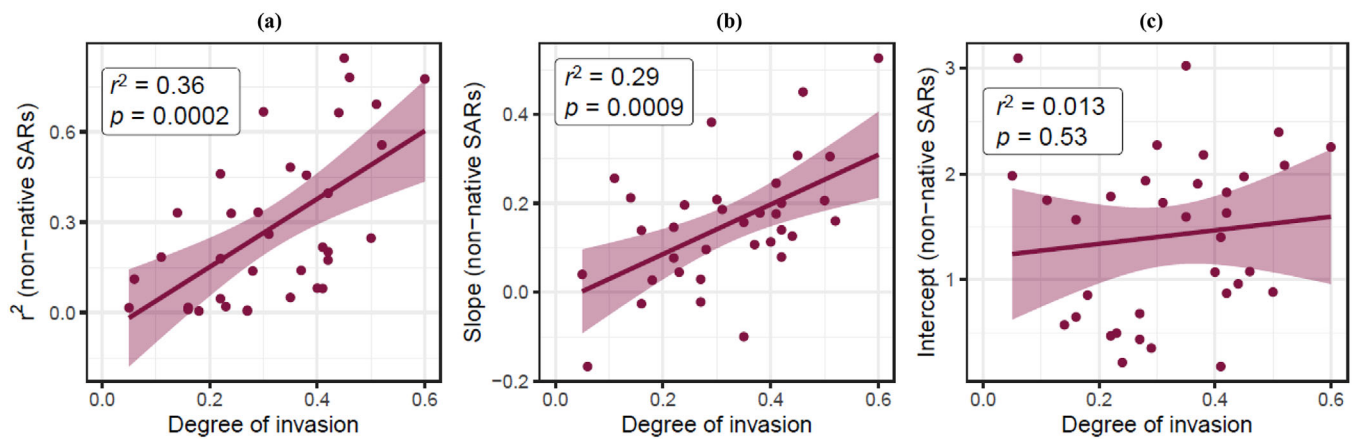


Figure 3. Effects of degree of invasion on (A)  $r^2$ , (B) slope ( $z$ ), and (C) intercept ( $c$ ) of the non-native species-area relationships across the 35 data sets (shading, SD estimates).

That  $r^2$  values and slopes of SARs increased as DI increased for all species implies that (across the sites and scales we examined and at the current level of invasion) presence of non-native species led to generally higher overall species diversity, especially for plants. Thus, ecological space appeared to have been available for non-native species to invade, especially at large scales (i.e. there is no species saturation, at least in the short term). This is indicated by the positive responses of non-native species richness to the positive residuals derived from a regression of the native SARs and negative responses to the negative residuals (Supporting Information). This observation on the richness-residual relationship is consistent with the many reported positive native versus non-native richness relationships at large scales. At small scales, the two groups may have stronger interactions (e.g. competition) and thus be negatively related. Such patterns, which are consistent among many large-scale studies, confirm the notions that “diversity begets diversity” (Palmer & Maurer 1997) and “the rich get richer” (Rejmánek 2003).

We found that, at the present level of invasion, non-native species usually had weaker and more variable SARs than native species across the globe. The weaker SARs of non-native species could be due partly to the generally lower non-native richness than native richness and partly to uneven species introductions and invasions across regions and ecosystems. This spatial variation in SARs could be expected to increase stochasticity in distributions of both native and non-native species. The shallower slope for non-native species than native species implies that non-native species increased proportionately more in number at small spatial scales (higher DI) than at large scales (lower DI) because at large scales they have had less time to disperse throughout their potential range (McKinney 2004). The stronger SARs for native than for non-native species also suggest greater dependency of native species on habitat area (i.e. loss of

the same amount of habitat may have more negative effects on native than non-native species [Niflè & Mangel 2000]). The result of no difference in the intercepts of SARs among native, non-native, and all species combined was somewhat surprising. One possible reason could be that, in certain ecosystems, especially at small scales, some native species may have been replaced by non-native species due to competition.

Native versus non-native species SAR differences may also arise from differences in, for example, dispersal ability, adaptability, and variation within taxa (Baiser & Li 2018). For example, non-native birds had shallower regression slopes and lower  $r^2$  than native birds. This pattern of low SAR slopes in non-native birds was also found in a data set compiled by Baiser and Li (2018) and in data from 250 national parks (Li et al. 2018). Such reduced slopes for non-native birds could result, for example, from higher dispersal ability relative to native birds or extensive, intentional human introductions of non-native species. It is also possible that non-native species, as a group, tend to respond differently to environmental variables, including human disturbance, as documented by Li et al. (2018).

In contrast to birds, we found that plants exhibited the opposite pattern (Table 1), which is consistent with our third hypothesis that the levels of change in SARs are different for plants and birds. Baiser and Li (2018) also found differences in native versus non-native SAR patterns between plants and birds. Studies on small sets of islands or mainland sites, however, show inconsistent results. Blackburn et al. (2016) examined richness data on non-native plants and birds from 90 of the world’s oceanic islands. They found that for non-native plant and bird richness slopes are similar, whereas slopes of non-native species are lower ( $z = 0.24$  for plants and  $z = 0.27$  for birds) than slopes for native species ( $z = 0.39$  for plants and  $z = 0.36$  for birds). Guo et al. (2017) found that across selected sites around the globe,



non-native plants ( $r^2 = 0.47$ ) have weaker SARs than native plants ( $r^2 = 0.75$ ). Because birds and plants showed similar slopes, the lower intercepts for native, non-native, and all birds, respectively, may simply reflect the generally lower bird species richness across the sampled sites. This is despite the obvious differences in dispersal capacity and propagule pressure among these groups (Simberloff 2009). For example, relative to plants, proportionally more birds have been introduced by humans, especially to remote islands (Blackburn et al. 2008).

We acknowledge that different approaches to SAR analysis may yield results different from ours. Powell et al. (2013) used the abundance of individual dominant invasive plant species to assess changes in SARs for native species. In contrast, we used non-native species richness and DI to investigate changes in SARs for native and all resident species, respectively. Use of different measures of DI such as non-native species richness and abundance (e.g. density or biomass) of dominant or all non-native species or both richness and abundance (Guo et al. 2015), could naturally lead to different invasion patterns affecting the final SARs of native and non-native species.

At the current level of invasion, island biogeography theory still has great predictive power. This is not surprising given that native species generally outnumber non-native species at most locations, especially at large spatial scales. Species richness on islands is in part a function of both immigration and extinction rates related to island area and island isolation. Invasion by non-native species could alter extinction rates, which could provide a more mechanistic explanation of our results (Warren et al. 2015). For example, non-native species could increase immigration, thus, shifting the immigration curve upward and increasing species richness. Or, non-native species could increase native species extinctions, which would decrease species richness. However, the increase in extinctions may take longer to be seen than an increase in immigration because of extinction debts (Warren et al. 2015). Also, this framework may explain differences among taxa and types of location. For example, a mainland area would likely have much higher immigration rates than islands, which would shift the immigration curve upward. Indeed, our results showed that island biogeography theory has different predictive power for different taxa (e.g. birds vs. plants) and different ecosystems or regions (e.g. island vs. mainland), as reflected in postinvasion SARs.

Whether our observed patterns are robust depends on how many non-native species persist, how many will spread, and how many new non-native species invade in the future. The stronger postinvasion SARs due to non-native species could be just a transient phenomenon from extinction debts not yet paid (Warren et al. 2015). The response of native plant species to non-native plant species can play out over decades, although sometimes

the geographic expansion and population growth of non-native species is extensive and rapid (Rouget et al. 2016). Non-native plant species could well be prone to an “invasion debt” of many decades before they spread to their full spatial distribution (Rouget et al. 2016). But our results call for caution in generalizing SAR patterns affected by species invasions because different data sets with differing degrees of invasion could lead to divergent conclusions (Guo 2014a).

Our results suggest a series of critical questions, many with practical conservation applications. The regions and islands with positive residuals (Supporting Information) had high native species richness and more non-native species than those with negative residuals. In such regions and islands, more management may be needed to reduce the population size of invasive species if complete eradication is not feasible. In contrast, those regions and islands with negative residuals (Supporting Information) had few non-native species, indicating that prevention and early detection and eradication may be more effective. Based on the altered SARs in our findings, a key issue for future research is whether increased diversity in many ecosystems improves resistance to further invasions by non-native species. Specifically, how many unoccupied niches are still available for further invasion (Lomolino et al. 2006)? How do ongoing species invasions (Supporting information Fig. S1), especially intentional species introductions (which often have greater success rates) and regional non-native species pools affect future SARs and future invasion potential (Vilà et al. 2010; Guo et al. 2017)?

Fully answering these questions will take more research, but previous work suggests that gap filling occurs more frequently at large scales than at small scales. When a community is relatively intact, available resources are often limited unless localized areas are moderately disturbed and competition is thereby reduced (Davis et al. 2000). In such cases, extinction may not be inevitable because dominant invasive species may reduce the abundance of some native (resident) species and thus open up space for a greater number of native and non-native species to coexist. A tighter SAR may, therefore, indicate a higher degree of species saturation. This observation is consistent with the reported scale-dependent switch in native and non-native species richness relationships from positive at large scales to negative or no relationship at small scales (Burns 2016).

Finally, several environmental factors besides area (e.g. climate, soil, habitat diversity, and isolation) in island systems can affect SARs (Ricklefs & Lovette 1999; Ricklefs 2009). Because we compared native and non-native species sampled from the same ecosystem types or sites, these factors may be considered constants (Ibáñez et al. 2006). One limitation of our work is the lack of information regarding preinvasion (native species only) SARs, especially when so many bird extinctions have

occurred on many islands due to human influence (Sax & Gaines 2008). However, it might be reasonable to view the SARs for native species as a baseline reference because there seems to be little evidence thus far of invasion-caused extinction, especially for plants, except at very small plot-size scales (Sax & Gaines 2008). This may change in the future if there is a significant extinction debt that will cause a decrease in species richness in the future (Gilbert & Levine 2013). However, for immediate conservation purposes, we argue that current SARs for native species are still highly relevant and useful.

In formulating general theories in ecology and biogeography (Wu and Vankat 1995), and for better invasion management, it is necessary to take both native and non-native species into account. By doing so, our results supported our main hypothesis that species invasion reshapes and forms new SARs that are different from native SARs across the globe. However, due to the highly dynamic nature of human-caused species introductions and naturalizations, it remains to be seen whether increased local and regional diversity (especially for plants) is transitory (i.e. owing to high debts of extinction or invasion) or will be sustained (Sax and Gaines 2003; Hulme 2008). It also remains to be seen how new hybrids between native and non-native species may affect postinvasion SARs (Guo 2014b). Thus, reexamining these changing species–area curves in the future is required to validate our findings and to predict invasions and subsequent equilibrium species diversity for the upcoming Homogeocene (McKinney, 1998, 2004; Rosenzweig 2001).

## Acknowledgments

We are grateful to E. Main, R. Ricklefs, L. Valente, and J. Wu for constructive comments and thank the many individuals, including T. Blackburn, J. Long, and several students at the National Environmental Modeling and Analysis Center (NEMAC), the University of North Carolina, Asheville, who kindly provided data throughout this research.

## Supporting Information

The species-area relationships (SARs) for native, non-native, and all species across the 35 data sets around the globe (Appendix S1); examples of non-native plant accumulation on islands, hypothetical local-regional postinvasion SARs, and results showing SARs for native, non-native, and all species based on newly compiled data, and residual analysis (Appendix S2); and data used in the residual analyses (compiled for this study) (Appendix S3) are available online. The authors are solely responsi-

ble for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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