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The relationship between naturalized alien and native plant species: insights from oceanic islands of the south-east Pacific over the last 200 years

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Abstract

Aim: The relationship between native and naturalized alien species has been widely studied, particularly across large geographic scales. However, our knowledge of the spatial and temporal variations of their relationships is still limited, particularly for remote oceanic islands such as those of the south-east Pacific and across islands and archipelagos. In this study, we aim to assess the relationships between native and naturalized alien species by analyzing their current patterns of species-area relationships at different spatial scales, in addition to temporal variations in species richness, over the last 200 years.

Area: One island (Rapa Nui) and two archipelagos (Juan Fernandez and Desventuradas Islands) comprising a total of 11 oceanic islands of the south-east Pacific (OISEP).

Methods: We assembled the most comprehensive dataset of the vascular flora of the OISEP from currently available island flora checklists and updated with recent publications. Each plant species was classified as being native or naturalized alien. We examined temporal changes by estimating species richness, naturalization rates and naturalized-to-native ratios over time based on the first collection year of each naturalized alien species. Then, we determined the best shape of naturalized alien species richness accumulation over time by contrasting the fit of lineal, exponential, sigmoidal and Weibull regressions. Finally, we analyzed the relationships between native and naturalized species firstly at the inter-archipelagic scale by fitting island species-area relationship models and secondly at the island scale by performing ranged major axis regression analysis on residual values.

Results: The OISEP flora dataset contained 674 species of which 282 were native and 392 were naturalized alien. Native island species-area relationships were similar to those of the naturalized alien species. Naturalized alien species richness increased notably through time with two clear peaks in 1950 and 2000. A Weibull regression and an exponential shape over time were the most appropriate fits for naturalized alien species richness accumulations at the inter-archipelagic scale, which further emphasizes the notable increase in naturalized alien species richness experienced in the timeframe examined here.
Main conclusions: The relationship between naturalized alien species richness and native species richness was found to be independent of the geographic scale. The number of naturalized alien species clearly exceeded the number of native species on most islands but also for the whole OISEP. The accumulation of newly detected naturalized alien species does not show any sign of saturation and it is likely that new species will arrive in the future. Increased efforts on monitoring, prevention and biosecurity are needed to halt biological invasions on these unique island ecosystems.

Keywords
island flora, islands species-area relationship, naturalized alien species additions

Introduction

Islands have long been of considerable scientific interest for studies in ecology, biogeography and evolution thanks to their well-delimited geographic features and their high levels of biodiversity (Whittaker et al. 2017). In addition, many islands are particularly vulnerable to anthropogenic disturbances (Whittaker and Fernández-Palacios 2007; Keppel et al. 2014), with one of the major drivers of biodiversity loss being the introduction of alien biota and their subsequent naturalization (hereafter, naturalized alien species) (Caujapé-Castells et al. 2010; Leclerc et al. 2018; Fernández-Palacios et al. 2021). In this context, we referred to "naturalized alien species" as plant species deliberately or unintentionally introduced by humans that have, in turn, gone on to form self-sustaining populations – or are in the process of doing so – in an area outside their native range. Such naturalized alien species can be catalysts for biodiversity loss on oceanic islands (Tye 2006; Kueffer et al. 2010). However, the hypothesis that alien plant invasions trigger declines in native plant species populations or, indeed, lead to extinctions, is still debated (Sax et al. 2002; Gurevitch and Padilla 2004; Sax and Gaines 2008). Nevertheless, there is consensus that the number of naturalized alien species has increased distinctly during recent times (Sax et al. 2002; Sax and Gaines 2008; Seebens et al. 2017). This has drastically changed plant species diversities more so on oceanic islands than on continental islands or mainland areas (Sax et al. 2002; Denslow 2003; Sax and Gaines 2006; Castro et al. 2010; Kueffer et al. 2010; van Kleunen et al. 2015).

The combination of steep invasion rates and small island areas suggests that the number of species on oceanic islands might reach saturation as there is, first, a limited number of species that can be supported by the environmental conditions and, second, a strictly defined area within which they can establish reproducing populations. Two possible mechanisms can emerge if an island reaches the saturation point, each of which has different implications for the relationship between naturalized aliens and native species

(Sax and Gaines 2008). The first, called "extinction-based saturation" (Sax and Gaines 2008), predicts that new naturalizations will trigger subsequent species extinctions, in line with the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). The second hypothesis, termed "colonization-based saturation" (Sax and Gaines 2008), predicts that if island species richness remains constant through time, then the colonization would be suppressed without any extinction of native or established species (Tilman 2004). Signs of extinction-based saturation have been found on Alejandro Selkirk island (Juan Fernandez Archipelago; Greimler et al. 2017), while there has been no evidence of colonization-based saturation on any island worldwide (Sax and Gaines 2008; Seebens et al. 2017). In contrast, the observed increases in alien plant naturalizations have been linear on islands worldwide (Esler and Astridge 1987; Wu et al. 2003; Tye 2006; Sax and Gaines 2008). This could be interpreted as an indication of no saturation, whereby the number of naturalized alien species will continue to increase without extinctions (Seebens et al. 2017). Sax et al. (2002) put forward the idea that extinctions of native plant species on oceanic islands were not a consequence of the presence of naturalized alien species. Gaining insights into temporal variation and its relationship with native species richness is highly relevant in understanding current and future patterns of the fate of native species while also helping to define priorities in conservation planning (Tye 2006; Greimler et al. 2017); however, such insights remain limited (Sax and Gaines 2008). In this context, we examined temporal variation of naturalized alien species richness and its relationship to native species diversity at island and inter-archipelagic scales.

Native species richness are also highly correlated after accounting for the area effect (i.e., by means of island species-area residuals; Lonsdale 1999; Sax and Gaines 2008). Even islands rich in native species often also harbor many naturalized alien species (Lonsdale 1999; Rojas-Sandoval et al. 2020). Through the loss of island habitats and increasing propagule pressure of alien plant species, human activity led to increases in naturalized alien species. This, in turn, can negatively influence native species richness - mostly through habitat loss - potentially leading to the extirpation of native species. However, the magnitude of these disturbances is very different across islands triggering different native-naturalized alien species richness scenarios (Caujapé-Castells et al. 2010).

On the other hand, it remains unclear whether naturalized alien species richness increases with area in the same way as native species richness. Here, island species-area relationship models (hereafter, ISAR) have played a central role as their parameters (intercept and slope) can be interpreted with a biogeographic sense (Triantis et al. 2012). ISAR parameters are sensitive to island isolation resulting in more isolated islands having steeper slopes and lower intercepts in comparison to less isolated islands (McArthur and Wilson 1967). In fact, ISAR parameters for islands have produced higher slopes and lower intercepts than for continental areas (Rosenzweig 1995) while oceanic islands showed higher slopes and lower intercepts than continental islands (Triantis et al. 2012; Patiño et al. 2014). It can also be expected that ISAR slopes and intercepts differ between native and naturalized alien species because dispersal barriers have been lowered for naturalized species, potentially resulting in higher colonization rates. Previous studies revealed that the slopes of native and naturalized alien ISAR have shown similar trends on continental islands (Long et al. 2009) and on islands of mixed origins (Chiarucci et al. 2017). On oceanic islands, the slopes of native and naturalized alien ISAR have shown conflicting patterns in slopes (Burns 2016; Blackburn et al. 2016; Chiarucci et al. 2021). One possible explanation may be that isolation could vary for naturalized alien species that are transported by humans, placing more emphasis on human connectivity over geographical proximity (Russell et al. 2017). Another explanation could be that these three studies have analyzed different area ranges influencing changes on ISAR slopes (Triantis et al. 2012). Thus, naturalized alien ISAR will see lower slopes and higher intercepts as a result of increased human transport, whereby anthropogenic activity facilitates species' arrivals independent of island isolation (McArthur and Wilson 1967; Chiarucci et al. 2021).

Oceanic islands of the south-east Pacific (hereafter, OISEP) include Rapa Nui (also known as Easter Island or Isla de Pascua), which is one of the more anthropogenically impacted islands in the region, while the Juan Fernandez Archipelago has the highest level of endemism per km^2 for an oceanic archipelago (Caujapé-Castells et al. 2010; Vargas et al. 2014). Although the origins of the naturalized alien plants varied before the arrival of Europeans, today, the dominant source pool for alien plants on OISEP islands is Chile (Castro et al. 2007). This study area is part of the Pacific region, which has, globally, experienced the most rapid increase in instances of naturalized alien plants (van Kleunen et al. 2015). Despite these trends, detailed analyses of naturalization on OISEP are scarce. Most studies focused exclusively on one island (Stuessy et al. 1997; Swenson et al. 1997; Stuessy et al. 1998; Vargas et al. 2011; Greimler et al. 2017; Vargas-Gaete et al. 2018) or a single archipelago (Sanders et al. 1982; Greimler et al. 2002; Danton et al. 2006). A very limited number of studies have focused on the whole island group (Castro et al. 2007, 2010; Castro and Jaksic 2008) albeit only the larger islands. Our study builds upon studies describing the vascular flora of smaller OISEP islands (Danton et al. 2006; Danton and Perrier 2016) and the considerable number of important botanical studies of the OISEP vascular flora (Skottsberg 1937; Sparre 1949; Hoffmann and Marticorena 1987; Hoffmann and Tellier 1991; Zizka 1991; Matthei 1995; Muñoz-Schick 1995; Mueller-Dombois and Fosberg 1998; Cuvertino 2001; Danton et al. 2006; Meyer 2008; Escobar et al. 2011; Finot et al. 2015; Danton and Perrier 2016, 2017). Thus, we aim to test the following hypotheses: (1) naturalized alien species richness has exceeded native species richness at inter-archipelagic and island scales; (2) naturalized alien species richness has linearly increased over time at the inter-archipelagic scale; (3) native and naturalized alien species are not related at island scale, likely due to the aforementioned variations in the history of human colonization; and (4) slopes and intercepts differ between native and naturalized alien ISAR.

Methods

Study Area

We examined 11 oceanic islands and islets in the south-east Pacific, each of which has well-documented native and naturalized alien flora (Fig. 1; see Suppl. material 1:

table S1 in for further details). These islands can be grouped into Desventuradas islands (Fig. 1A), Rapa Nui (Fig. 1B) and Juan Fernandez Archipelago (Figure 1C).

The Desventuradas islands are dominated by two small islands about 890 km off the north coast of Chile and about 810 km north of the Juan Fernandez Archipelago (Fig. 1). The two main islands, San Ambrosio (SA, Fig. 1A) and San Felix (SF, Fig. 1A), are separated by 18.5 km. Gonzalez Islet, at the south-eastern tip of San Felix, was excluded from our analyses because it has no documented flora. The archipelago has an oceanic, subtropical climate with annual precipitation of around 100 mm that falls mainly in winter between May and August (Hajek and Espinoza 1987), while yearly temperatures range between 10 °C and 25 °C (Hoffmann and Tellier 1991). The vegetation in San Felix reflects the arid conditions where plant cover, dominated by bushes, does not exceed 25% of the surface (Hoffmann and Tellier 1991). The more elevated nature of San Ambrosio (479 m in comparison to San Felix's 193 m) facilitates greater vegetation cover thanks to the presence of fog (Johnston 1935; Kuschel 1962) and more developed soils (González-Ferrán 1988). San Ambrosio and San Felix are uninhabited islands, but they are visited occasionally by groups of fishermen (Hoffmann and Tellier 1991).

The Juan Fernandez Archipelago is composed of three islands and multiple islets about 784 km off the coast of Chile (Fig. 1B). The three main islands are Robinson Crusoe (RC), Alejandro Selkirk (AS) and Santa Clara (SC). The archipelago also includes the five islets of Morro Juamango (MJ), Morro Verdugo (MV), Morro Vinilo (Mvi), Morro Sin Nombre (Msn) and Morro Spartan (MS), whose flora has been described by Danton et al. (2006) and Danton and Perrier (2016). The climate is subtropical oceanic with an annual precipitation of around 1100 mm while temperatures range from 15 °C to 25 °C (Hajek and Espinoza 1987). Robinson Crusoe and Alejandro Selkirk islands are home to a greater diversity of vegetation thanks to their larger size (both ~50 km^2) and higher elevation (1320 m and 915 m, respectively). Meanwhile, the considerably smaller Santa Clara (2.2 km^2, 367 m a.s.l.) has predominantly herbaceous vegetation (Hoffmann and Marticorena 1987). Only Robinson Crusoe contains a permanent human settlement with 927 inhabitants, of which 35–50 move to Alejandro Selkirk during the period of increased fishing activity (October-May; Gobierno Regional de Valparaiso, 2016).

Rapa Nui (IP) is the easternmost island of Polynesia, about 3510 km off the north coast of Chile (Fig. 1C). Nearby are the three islets of Motu Iti, Motu Nui and Motu Kao Kao, while Salas y Gomez Island lies about 390 km to the northeast. The flora of these islands has not been documented. The climate is subtropical-oceanic with annual precipitation of 1365 mm (Mueller-Dombois and Fosberg 1998) and yearly temperatures range between 15 °C and 25 °C (Hajek and Espinoza 1987). The vegetation is predominantly herbaceous grassland consisting mainly of introduced grass species (Etienne et al. 1982; Zizka 1991). There are some small, dense forests composed of introduced tree species. The vegetation less impacted by humans is located on inaccessible coastal habitats, the upper parts of Maunga Terevaka and on Rano Kao zones (Zizka 1991). Rapa Nui contains a permanent human settlement with 7750 inhabitants (Instituto Nacional de Estadísticas de Chile 2017).

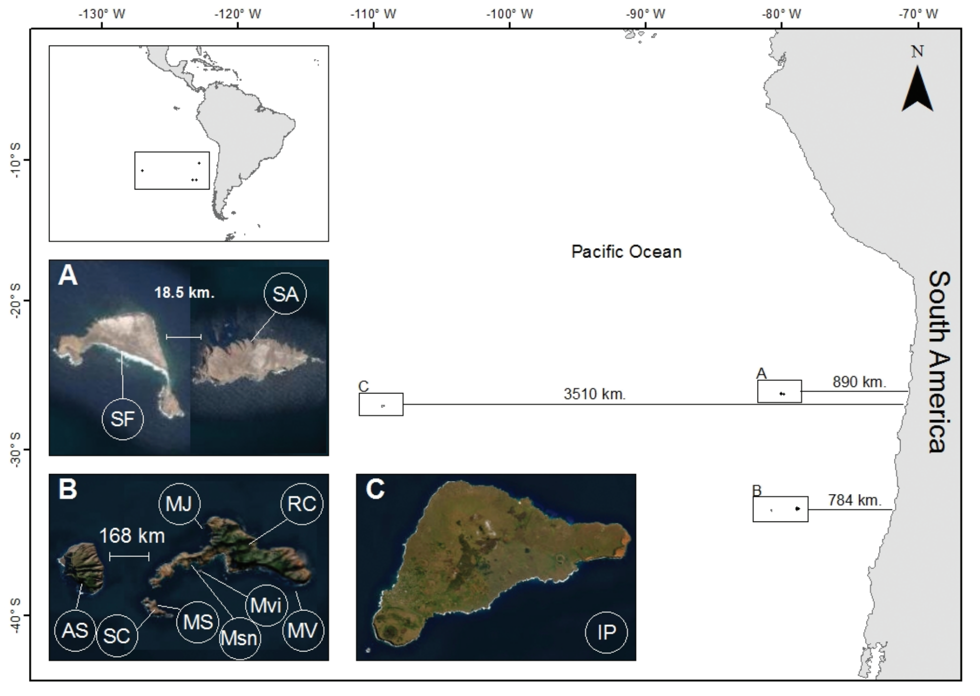

Figure 1. Map of the study area **A** Desventuradas islands, composed of San Felix (SF) and San Ambrosio (SA) **B** Juan Fernandez Archipelago, composed of Robinson Crusoe (RC), Alejandro Selkirk (AS), Santa Clara (SC), Morro Spartan (MS), Morro Sin Nombre (Msn), Morro Verdugo (MV), Morro Juamango (MJ) and Morro Vinilo (Mvi) and **C** Rapa Nui (IP).

Data assembly

We assembled data on the vascular native and naturalized alien flora for the entire OI-SEP (Fig. 1). The many scientific expeditions to the islands over the past two centuries have ensured a comprehensive insight into their flora. We assembled the flora of the Desventuradas islands based on the works of Skottsberg (1937), Sparre (1949), Hoffmann and Marticorena (1987), Hoffmann and Tellier (1991), Muñoz-Schick (1995), Mueller-Dombois and Fosberg (1998), Cuvertino (2001) and Escobar et al. (2011). The flora of the Juan Fernandez Archipelago was gathered using Danton et al. (2006), Danton and Perrier (2016), Danton and Perrier (2017) and Stuessy et al. (2018b). The works of Zizka (1991), Matthei (1995), Meyer (2008) and Finot et al. (2015) provided data for Rapa Nui. Species that have subsequently proved to be misidentified and those for whom there remains reasonable doubt over their identification were excluded (Danton and Perrier 2017). Taxa were standardized according to the Global Biodiversity Information Facility (GBIF) taxonomic backbone using TAXADB package (Norman et al. 2020) of the statistical environment R (R Core Team 2020). Synonyms, heterotypic and homotypic synonyms were changed to the accepted names while the Catalog of the Vascular Plants of Chile (Rodriguez et al. 2018) was used as back-up source of information for more problematic taxa.

The original sources facilitated the classification of the assembled flora into native and naturalized alien species from which the species richness for each island and the whole OISEP was determined. We excluded cultivated or occasional species from the naturalized alien species lists (Tye 2006).

Data analysis

Native and naturalized alien species relationships through time

For the analysis of plant diversity changes over time, we obtained the year of the first record or reference available of each alien plant that became naturalized alien on each island. If multiple first records for one naturalized alien species were provided for different islands (because they have different arrival dates), the earlier first record was selected for the entire study area. On the larger islands of Rapa Nui, Alejandro Selkirk, Robinson Crusoe, Santa Clara, San Ambrosio and San Felix, confidence in the early records is high due the frequent and detailed botany studies carried out throughout time. For the smaller islands of Morro Juamango, Morro Spartan, Morro Sin Nombre, Morro Verdugo, and Morro Vinilo, the first records were gathered during the first expeditions, in 1998 and 2008, respectively (Danton et al. 2006; Danton and Perrier 2016). Altogether, 1410 native and naturalized alien species occurrences and 731 first records were analyzed. This allowed us to investigate the naturalized alien species richness accumulation and the naturalization rate over time at both island and inter-archipelagic scales.

We examined how naturalized alien diversity changed over time by applying a regression model using the naturalized alien species richness from 1810 to 2021 for the entire OISEP. This was done by fitting three functions: linear ($y = a + bx$), exponential ($y = a\ (\exp)^{bx} + c$) and sigmoidal ($y = a\ (x^b/(x^b + c^b))$). In addition, we fitted a Weibull function ($y = c+(d-c)\exp\{-\exp[b(\log(x)-\log(e))]\}$) to test for potential stabilization in the observed naturalized alien richness in recent years. Model fits were compared using Akaike's Information Criterion (AIC), whereby the lowest AIC value was considered to be the best.

Finally, to determine whether and when naturalized alien species richness could have surpassed native species richness, we calculated the naturalized-to-native species ratio over time. This was achieved by examining the naturalized alien species richness at 20-year intervals over the past 200 years at two scales: the individual island level and the entire OISEP. Following that, we obtained the naturalized-to-native species ratio by dividing naturalized alien by native species richness at both scales. Native species richness was assumed to be constant through time as it had not changed notably during the analyzed period (Castro et al. 2007; Sax and Gaines 2008).

Current island native and naturalized alien species relationships

To investigate native and naturalized alien species richness, we used the SARS package (Matthews et al. 2019) of the statistical software environment R to fit two species-area relationship models for the 11 islands studied. To describe the relationship between species richness and area, we employed the commonly-used Arrhenius power function (Arrhenius 1921) in a log-log transformed space:

$$\log_{10}(S) = c + z \log_{10}(A) \quad (1)$$

where S is species richness, A is island area and c and z are two fitted parameters that correspond to the intercept and the slope, respectively. We tested for significant differences between native and naturalized alien ISAR intercepts and slopes using multiple linear regressions. Here, the response variable was species richness (n = 22; 11 native and 11 naturalized alien) and the explanatory variables were area, a categorical variable (entitled status) describing if the response variable corresponds to native or naturalized alien species richness, and the interaction between area and status. Significant differences between intercepts and slopes were verified when the interaction (status*area) and the status variable were, respectively, significant (p-value < 0.05) (Gelman and Stern 2006).

To further analyze how species are responding to local island factors such as habitat heterogeneity, productivity, etc. (Stark et al. 2006; Hulme 2008), we extracted the ISAR model residuals, which denote deviations of predicted values from those that were observed. These residuals helped to assess the importance of island area, allowing a comparison of the influence of islands of varying size on species richness (Lonsdale 1999). For this purpose, we extracted naturalized alien and native ISAR residuals and carried out a regression analysis (naturalized alien ISAR residuals against native ISAR residuals) using type II regression (ranged major axis) (Sokal and Rohlf 1995; Legendre and Legendre 2012). In this way, we tested if naturalized alien species richness is influenced by the same island factors that are promoting native species richness. If this is true, then ISAR residuals of both naturalized alien and native species will be strongly correlated with a positive slope of close to 1. The type II regression was run using the LMODEL2 package (Legendre 2018).

Results

Island native and naturalized alien species relationships through time

At the island-scale, 52 alien plant species had already been naturalized on Robinson Crusoe before 1870 (Fig. 2A). The naturalized alien species richness of Robinson Crusoe and Rapa Nui islands increased gradually between 1870 and 1990, surpassing the 1:1 ratio in the late 1980s (Fig. 2A, F). Santa Clara showed two peaks of alien naturalization rates; the first was from 1890 until 1930 (surpassing the 1:1 ratio) and the sec-

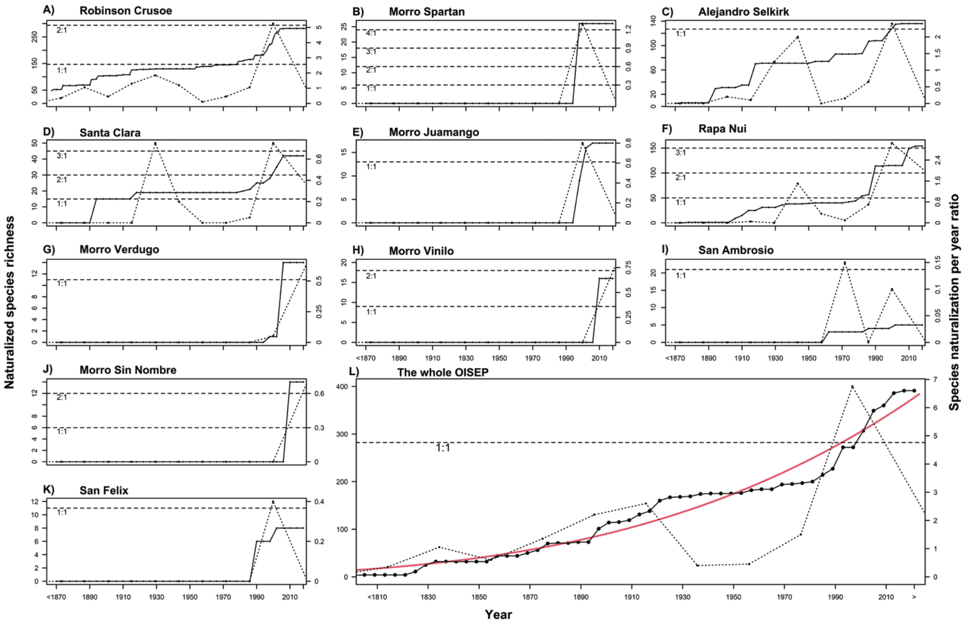

Figure 2. Naturalized alien species richness (left y-axis, black solid lines) and naturalization rates (right y-axis, black dashed lines) from <1870 to 2021. Red solid line represents the best adjusted regression (Weibull) naturalized alien species richness over time. The horizontal dashed lines represent the thresholds of the naturalized-to-native ratios.

ond was between 1990 and 2010, where it surpassed the 2:1 ratio (Fig. 2D). The other smaller islands (Morro Spartan, Morro Juamango, Morro Verdugo, Morro Vinilo, San Ambrosio, Morro Sin Nombre and San Felix) showed an increase in naturalized alien species richness from 1990 to 2010 (Fig. 2). The islands of Morro Juamango, Morro Verdugo and Morro Vinilo surpassed the 1:1 ratio (Fig. 2E, G, H), while Morro Sin Nombre and Morro Spartan surpassed the 2:1 and 4:1 ratios, respectively (Fig. 2J, B). At no point did San Ambrosio or San Felix surpass the 1:1 ratio (Fig. 2I, K). The average naturalized-to-native ratio for the islands over the entirety of the timeframe examined is 1.91, while the current ratio for the OISEP is 1.39 (see Suppl. material 1: table S2).

The 200-year dataset showed that, at present, 13% of the total naturalized alien species richness was introduced and naturalized before 1870, the majority of which occurred on Robinson Crusoe. The greatest increase in naturalized alien species descriptions occurred between 1990 and 2010. Thus, 40% of the current naturalized alien species (156 species) was observed in those 20 years. Proportionally, the naturalized alien species richness continued to increase through time, culminating in the entire OISEP surpassing the 1:1 ratio in 2000 (Fig. 2L). The most notable increases in naturalized alien species richness – overall for the OISEP and on most islands – were observed after 1990 (Fig. 2; see Suppl. material 1: table S2 for further details). Fig. 2L shows the best fit Weibull distribution for the increase in naturalized alien species (AIC = 843.9), followed by the exponential, sigmoidal and linear regression curves with increasing AIC values (848.5, 858.1 and 1076.7, respectively) (see Suppl. material 1: tables S3–S6 for details of each model). The alien naturalization rate was very variable over time on the OISEP, showing two peaks: the first in 1920 and the second in 2000 (Fig. 2L).

Current plant biodiversity in the OISEP

Analyses of the OISEP dataset revealed 1410 species occurrences of a total of 674 species, of which 392 were naturalized aliens and 282 were native (Table 1). In absolute terms, Robinson Crusoe island contained the largest number of native species (147), representing 52% of all OISEP species. The next most populous islands in terms of native species were Alejandro Selkirk with 127 species (45%) and Rapa Nui with 50 species (18%) (Table 1). Meanwhile, Robinson Crusoe was also home to the majority of naturalized alien species (282), representing 72% of the total recorded on the OISEP. This was followed by Rapa Nui (157, 40%) and Alejandro Selkirk (136, 35%), while the smaller islands were host to considerably fewer naturalized alien species (Table 1).

Assemblages of native and naturalized alien species varied notably at both inter-archipelagic and island scales (see Suppl. material 1: tables S7A, B for details). Juan Fernandez and all OISEP produced the highest Sorensen's index values (native = 0.86; naturalized alien = 0.86). Of the Juan Fernandez Archipelago, Robinson Crusoe islands and all OISEP produced the most dominant index value (native = 0.68; naturalized = 0.84; see Suppl. material 1: tables S7A, B for details). On the other hand, the Desventuradas islands and the OISEP produced the lowest Sorensen's similarity index values (native = 0.14; naturalized alien = 0.05). The Desventuradas islands also produced the lowest Sorensen similarity index with Rapa Nui Island (natives = 0; naturalized = 0.04; see Suppl. material 1: tables S7A, B for details).

There is an uneven distribution of species across the islands with 67% of the OISEP native species restricted to just one island. Of those, Robinson Crusoe is home to 24.5%, 22.7% are on Alejandro Selkirk, 14.9% are on Rapa Nui, 3.9% are on San Ambrosio, while San Felix and Santa Clara are each home to 0.35% (Table 1). In comparison, 57.9% of the naturalized alien species are restricted to just one of four islands: 32.4% are on Robinson Crusoe, 22.5% on Rapa Nui, 2.5% on Alejandro Selkirk and 0.5% on San Felix (Table 1).

Current island native and naturalized alien species relationships

The ISAR for native species had a better fit and lower *p*-values for its adjusted parameters than those for the naturalized alien species (adj. $R^2 = 0.7$ and 0.32; intercept *p*-values = $10^{-8} \times 4.5$ and $10^{-6} \times 2.1$, respectively; slopes *p*-values = $10^{-4} \times 7.7$ and $10^{-2} \times 4.1$ respectively). ISAR parameter comparisons revealed no significant differences for parameters c and z between native and naturalized alien ISARs (*p*-value = 0.303 and 0.697, respectively; Fig. 3A).

Native and naturalized alien residuals were significantly correlated ($r = 0.64$; *p*-value < 0.05). The regression analysis for ISAR residuals for native and naturalized

Table 1. Native and naturalized alien species richness and their island exclusivity. Total SR indicates the total species richness (native + naturalized alien species); % Natives and % Naturalized aliens are the proportions of island native or naturalized alien species richness; Ex-Natives and Ex-Natu represent the amount of native or naturalized alien species exclusively present; % Ex-Natives and % Ex-Natu are the proportions of native or naturalized alien species exclusively present.

Island	Natives	Naturalized aliens	Total SR	% Natives	% Naturalized aliens	Ex-Natives	% Ex-Natives	Ex-Natu	% Ex-Natu
Alejandro Selkirk	127	136	263	45.0	34.7	64	22.70	10	2.55
Rapa Nui	50	157	207	17.7	40.1	42	14.89	88	22.45
Morro Juamango	13	17	30	4.6	4.3	0	0	0	0
Morro Spartan	6	26	32	2.1	6.6	0	0	0	0
Morro Sin Nombre	6	14	20	2.1	3.6	0	0	0	0
Morro Verdugo	11	14	25	3.9	3.6	0	0	0	0
Morro Vinilo	9	16	25	3.2	4.1	0	0	0	0
Robinson Crusoe	147	282	429	52.1	71.9	69	24.47	127	32.40
San Ambrosio	21	5	26	7.4	1.3	11	3.90	0	0
Santa Clara	15	42	57	5.3	10.7	1	0.35	0	0
San Felix	11	8	19	3.9	2.0	1	0.35	2	0.51
Total	282	392	674	100	100	188	66.67	227	57.91

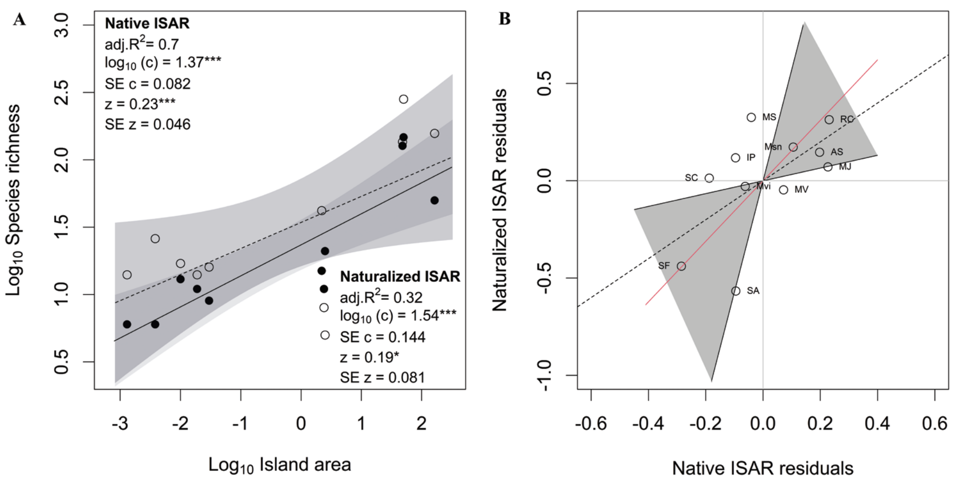

Figure 3. Island species-area and its residuals for native and naturalized alien species **A** ISAR fitted for both native (black circles; solid line; dark gray bands represent the 95% confidence interval) and naturalized alien species (white circles; dashed line; light gray bands represent the 95% confidence interval); SE: Standard error. Significance levels are denoted by * (0.01), ** (0.001) and *** (< 0.0001). **B** Type II regression of native and naturalized alien ISAR residuals (solid red line). Dashed line represents the perfect regression with intercept = 0 and the slope = 1; dark-grey band represents the 95% confidence interval.

alien species yielded a slope parameter not significantly different to 1 (estimated slope = 1.71; 0.54–4.97, 2.5%–95% confidence interval; *p*-value = 0.015, Fig. 3B). As Fig. 3B shows, four different island scenarios could be identified: a) islands with a high naturalized alien ISAR residual and a low native ISAR residual (Rapa Nui, Santa Clara and Morro Spartan islands); b) islands with similar naturalized alien and native species residuals (Morro Juamango, Morro Verdugo, Morro Vinilo and Morro Sin Nombre islands); c) islands with high naturalized alien and native ISAR residuals (Robinson Crusoe and Alejandro Selkirk islands); and d) islands with low native and naturalized alien ISAR residuals (San Felix and San Ambrosio islands).

Discussion

Island native and naturalized alien species relationships through time

We can accept our first hypothesis based on the evidence that naturalized alien flora achieved greater species richness than the native flora on OISEP. These results indirectly reflect the history of the whole OISEP area, including anthropogenic disturbances and the pressure placed upon native species richness by invasive alien plant species, domestic herbivores, habitat loss, etc. (Gurevitch and Padilla 2004; McKinney 2004; Sax and Gaines 2008; van der Wal et al. 2008; Caujapé-Castells et al. 2010; Wohlwend et al. 2021). Our results provide evidence of an accelerated level of alien plant naturalization when compared with Sax and Gaines's (2008) estimation that the naturalized-to-native ratio for oceanic islands was 1:1 and that the predicted ratio for 2060 will be 3:2. Considering the rapid increases in naturalized alien species numbers, the already high naturalized-to-native ratios – particularly for Morro Spartan, Robinson Crusoe and Rapa Nui – and the high propagule pressure from non-established plants (Castro and Jaksic 2008) in Robinson Crusoe and Rapa Nui (Zizka 1991; Meyer 2008; Finot et al. 2015; Danton et al. 2006), we can expect a much higher ratio in the future.

The difficulty associated with accessing San Felix and San Ambrosio means that they have been subjected to fewer human impacts when compared to other islands. Instead, only fishers and shellfish gatherers landed sporadically from Robinson Crusoe island (Bahamonde 1987; Hoffman and Teillier 1991; Castro and Jaksic 2008). This provides a plausible explanation for the lower naturalized-to-native ratios in contrast to the rest of the OISEP. However, Aguirre et al. (2009) noted a lack of concern for terrestrial conservation on Desventuradas islands. They reported that the San Ambrosio forests – hosts to a diverse collection of endemic plants (Kuschel 1962) – have disappeared due to the presence of goats. Therefore, more up-to-date inventories for San Felix and San Ambrosio may record higher naturalized alien species numbers.

Our study reveals a notable increase in naturalized alien species richness and diversity overall through time for the OISEP. This increase was better described using a Weibull function as opposed to an exponential function, likely due to the decline in naturalization rate from 1940–1960 and 2010–2021 in conjunction with the absence of flora descriptions for the same time period. Therefore, due to the fact that the Weibull fit (and the second best fit) show that the number of naturalized alien species is increasing exponentially, we can reject the idea that a saturation point has been reached (Sax and Gaines 2008). Although some other studies identified similar patterns (see Tye 2006; Seebens et al. 2017), we must interpret this result with caution due, for example, to the absence of more recent flora descriptions and the limited knowledge of the flora's temporal variation on smaller islands in Juan Fernandez Archipelago (cf. Tye 2006).

Current native and naturalized alien species relationships

Native and naturalized alien species richness in the OISEP region are positively correlated. This result is in line with other studies that have been interpreted as evidence that native species are not better competitors than naturalized alien species (Lonsdale 1999; Sax et al. 2002; Rojas-Sandoval et al. 2020). Moreover, the resulting type II regressions suggest rejecting our third hypothesis. Here, both naturalized alien and native species richness are responding in a similar way at the island scale (Lonsdale 1999; Stark et al. 2006; Hulme 2008) with at least four island scenarios identifiable. The first (scenario labelled "a" in the results) could be defined as islands that have been considerably disturbed by humans through fire, wood exploitation and introduced fauna such as rabbits, goats and horses, but still retain a rich native species pool. In this context, islands such as Robinson Crusoe and Alejandro Selkirk are exclusively home to the majority of plant biodiversity in the OISEP. The second island scenario ("b") categorizes the smaller islands that surround Robinson Crusoe (Morro Juamango, Morro Verdugo, Morro Vinilo and Morro Sin Nombre islands). Their proximity to Robinson Crusoe has seen these islands suffer from the influence of human activity, with naturalized alien species arriving by means of anemochory (mainly Asteraceae species) and zoochory (mainly Poaceae species). This, in turn, increased the naturalized alien plant species richness in the area (Danton et al 2006; Danton and Perrier 2016). However, these islands have kept their expected native species richness, with the islands of Morro Juamango, Morro Verdugo and Morro Sin Nombre having native standardized residuals near to 0. In comparison, rabbits introduced to Morro Vinilo island mean there is a limited number of native species found there (Danton and Perrier 2016).

The third island scenario ("c") applies to islands that have an impoverished native species pool. This is due to their geographic features in combination with a lower naturalized alien species pool as a result of recent anthropogenic disturbances, such as on San Felix and San Ambrosio islands (Hoffman and Marticorena 1987). Finally, the fourth scenario ("d") is not in line with our general resulting pattern, whereby native and naturalized alien species richness are correlated and respond in a similar way at the island scale. While islands such as Rapa Nui, Santa Clara and Morro Spartan have suffered notable anthropogenic disturbances (scenario "a"), they have also experienced a decrease in their native plant diversity (Zizka 1991; Danton et al 2006; Danton and Perrier 2016). For islands such as Santa Clara and Morro Spartan, this is likely to be due to extirpation, while extinction of possibly seven species has been recorded on Rapa Nui (Zizka 1991).

At the inter-archipelagic scale, that is, the entire OISEP, we showed that native and naturalized alien ISARs do not significantly differ in their fitted parameters leading to a rejection of our fourth hypothesis. Overall, our results follow the same trends identified by others for continental islands (Nichols and Nichols 2008; Long et al. 2009; Burns 2016; Chiarucci et al. 2017) and oceanic islands (Burns 2016) as well as Baiser and Li's (2018) more general assessment of plants for mixed origins. In comparison, our results differed to those revealed for Aeolian Islands (Chiarucci et al. 2021) as well a more global-scale analysis (Blackburn et al. 2016). A potential explanation for the observed differences might be our low sample size (n = 11). A different native and naturalized alien ISAR, as is in line with the findings of Blackburn et al. (2016), Chiarucci et al. (2021; when these ISARs are log-log transformed) and Burns (2016) (i.e., higher slope for native ISAR compared to naturalized alien ones) would support the hypothesis that naturalized alien species have reduced barriers to their dispersal relative to natives (Patiño et al. 2014). However, a higher sample size is required to test this more robustly.

Although there were no differences between the *c* and *z* parameters, the fit of each model did differ. The native ISAR fit well (adj. $R^2 = 0.7$), which indicates that native species richness follows the typical dynamics reported in other studies; that is, species richness can be explained to a large extent by island area as the species in question have had time to adapt to and establish permanent communities in the diverse island habitats (Long et al. 2009; Sax and Gaines 2006; Burns 2016; Chiarucci et al 2021). On the other hand, naturalized alien ISAR had a poorer model fit than that of native species. As mentioned previously, this may be because islands such as San Felix, San Ambrosio and Santa Clara have similar sizes and native species richness, but have different island contexts in terms of naturalized alien species richness (D'Antraccoli et al. 2019). Thus, the dynamics for naturalized alien plants differ in comparison to native species; the entire naturalized alien species pool is not well distributed across the diverse island habitats in the OISEP. Exceptions to this are species such as *Hypochaeris radicata*, *Rumex acetosella*, *Briza minor* and *Plantago lanceolata*. However, although the low number of sample units – that is, OISEPs – available to examine is a factor that is likely to have limited our results, our study still helps to address the notable scarcity of empirical evidence available to investigate and assess naturalized alien and native SARs on oceanic islands.

Ecological and biogeographic implications

This study revealed a dramatic increase in naturalized alien species richness on OISEP, which has major implications for both island ecology and biogeography. Overall, oceanic island species richness has increased more than has been identified elsewhere on continental islands and mainland areas (Sax and Gaines. 2006; Castro et al. 2010; Kueffer et al. 2010; van Kleunen et al. 2015). This is due to the many alien plant species that have become naturalized, while few native species have become extinct (Sax et al. 2002; Sax and Gaines 2006). Whereas studies by Sax et al. (2002) and Sax and Gaines (2006) have estimated that species richness increased by ~106.5% on oceanic islands, our study of OISEPs showed that there was an increase of, on average, 84.5%

on islands and an increase of 32.1% for the entire OISEP. Proportionally, other oceanic islands and archipelagos with a similar area to the OISEP (268.7 km^2) harbor a lower species richness (that is < 674 natives and naturalized alien species); for example, El Hierro island (268.7 km^2, Canary islands) has ~550 species (Stierstorfer and von Gaisberg 2006), Tristan da Cunha (207 km^2, in the Tristan da Cunha archipelago) has ~124 species (Sax et al. 2002) while Lana`i island (364 km^2 in the Hawaii archipelago) has ~787 species (Wagner et al. 2005). When compared to continental areas, our study site has higher species richness than Weddell island – the third largest continental island of the Falklands islands – where there are ~155 species in an area of 265.8 km^2 (Upson 2012), while the estimated species richness for Futangue National Park on mainland Chile is ~400 species in 125 km^2 (Moreno et al. 2013).

Although this study has highlighted distinct richness of species in the study sites, many of these native species across the OISEP have become threatened (from the total, 18.8% are critically endangered, 30.4% are endangered and 10.6% are vulnerable; Danton et al. 2006; Stuessy et al. 2018a; MMA 2023). Due to time lags in the extinction of species, it is likely that the number of threatened species will increase further even without further alien species naturalizations (Tilman et al. 1994; Sax and Gaines 2008; Greimler et al. 2017).

Therefore, it is of the utmost importance to both prevent the introduction of alien plant species and control the most impactful naturalized alien plant species on islands such as Rapa Nui, Santa Clara, Robinson Crusoe and Alejandro Selkirk (Danton et al. 2006; Lenz et al. 2022). The existing procedures to prevent the entry of alien plant species to, for example, Rapa Nui are limited only to safeguard the forest and agricultural productive sector (COCEI 2014). More recently, formal procedures to control and prevent the movement of alien plant species between islands in the Juan Fernandez Archipelago have been established; however, controls from continental South America remain voluntary (MMA 2017). It is also important to control anthropogenic disturbances, including the introduction of herbivorous fauna on islands such as Desventuradas islands where there is low naturalized alien species richness (Wohlwend et al. 2021). A further positive move would be to restore heavily disturbed islands in the study region, in particular Santa Clara, Morro Spartan, Robinson Crusoe, Alejandro Selkirk, Rapa Nui and Morro Vinilo. This could improve the conservation status of endangered plants and maintain focus on the conservation of native plant species across the OISEP (Stuessy et al. 2018a). Additionally, it is necessary to assess the effects of native plant species restoration on the extinction debt process and generate novel evidence on plant conservation research (Downey and Richardson 2016).

Conclusions

By assembling an updated dataset for 11 oceanic islands of the south-east Pacific (OISEP), our study reveals that there has been a dramatic increase of naturalized alien plant species richness in the last 200 years, and that naturalized alien species richness has become dominant over native plant species richness on most of the islands. Native and naturalized alien species richness, ISAR residuals and ISAR shapes are very much related and, by consequence, independent of the geographic scale. Relevant ecological and biogeographic implications for native and naturalized alien plant species diversity by means of different temporal and spatial scale patterns include similar levels of species richness between island and continental systems. There could be a possible increment of the extinction debt as there are currently no signs that alien plant invasion is reaching a saturation point soon.

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Supplementary material 1

Tables with general information

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