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RESEARCH ARTICLE

Time since first record and population density influence range sizes of non-native plants, but also of native plants, in a chronically overgrazed island

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Background and aims − Humans are increasingly introducing species to new regions. It is necessary to understand the processes that drive the expansion of non-native species into these new habitats across multiple spatiotemporal scales.
Material and methods − We studied the spatial distribution of the non-native flora (39 species) of Guadalupe Island (246 km^2) in the Mexican Pacific. We analyzed how residence time (time since first report in historical sources, 1875–2004) and species attributes (population density, flowering phenology, and individual height) are related with range sizes of non-native plants. To test whether the residence time – range size relationship of non-native plants can result from other factors besides time since their arrival, we compared it to the residence time – range size relationship of native plants. Range sizes were obtained using herbarium data and a systematic field sampling of 110 transects (50 × 2 m) throughout the entire island. We used beta regression to analyze the relationship of range sizes with residence time and species attributes.
Key results − Range sizes of non-natives showed a positive relationship with residence time, flower phenology, and notably with plant density, but not with individual height. However, similar relationships were found for native species, casting doubts on whether our results reflect the range expansion rates of non-native species.
Conclusions − Our results suggest that the production of large numbers of propagules, both as a result of long reproductive periods and large population sizes, determines to a large extent the rates of range size expansion of non-native species. However, the relationship we found between time since discovery and range size may arise from sampling biases, biological processes, or – most likely – both. This highlights the need for new approaches that allow us to discern the relative contributions of bias and process in our study of non-native species expansion.

Keywords − Density; grazing; non-native species; range size; residence time; sampling bias.

INTRODUCTION

Species movement beyond their natural areas of distribution into new regions is one of the global changes driven by the worldwide expansion of human activities during the last centuries (van Kleunen et al. 2015a; Pyšek et al. 2017). At least 4% of all vascular plants have established beyond their natural boundaries (van Kleunen et al. 2015a). Identifying the factors that drive geographical dynamics of neobiota in newly-invaded regions is crucial to understand this ecological phenomenom.

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Colonization of new regions by non-native (alien) species can be unwittingly associated with human activities or arise from intentional introductions for human use (Richardson et al. 2000). Their establishment and distribution are governed mainly by species characteristics (i.e. invasiveness; Baker 1965; Pyšek & Richardson 2007; van Kleunen et al. 2015b) and biotic and abiotic factors of the new region like disturbance, resource availability, population dynamics, and biotic interactions (i.e. invasibility; Elton 1958; Levine et al. 2004; Richardson & Pyšek 2006; Theoharides & Dukes 2007), which have all been considered to be key factors. Range expansion rates depend largely on long-distance dispersal events and on the intrinsic capacity of the species to produce seeds (Shigesada & Kawasaki 2002). Long-distance dispersal is rare, but, if many seeds are produced, at least some of the propagules are expected to reach distant sites. Thus, invaders that produce large amounts of seeds either because of their large density or because many of their members reproduce successfully, are expected to expand rapidly over a new habitat (Levine et al. 2006; Pachepski & Levine 2011).

Biological invasions also depend on fortuitous factors associated with the invasion process, such as residence time, i.e. the time since arrival of the non-native species (Rejmánek 2000; Wilson et al. 2007). Residence time shows a positive relationship with range size of non-native species in their new distribution regions (e.g. Castro et al. 2005; Pyšek & Jarošík 2005; Wilson et al. 2007; Williamson et al. 2009; Schmidt et al. 2017), even on a temporal scale of millenia (Sheppard & Schurr 2019). Thus, residence time should be considered in any attempt to explain species range distributions (Wilson et al. 2007). To our knowledge there are no studies directed to analyze how residence time and local factors interact to affect geographical ranges of non-native species in small regions.

Exploring the relationship between species residence time and range size poses important methodological challenges. It requires a high sampling frequency over a long period to reliably estimate species arrival dates. As these temporal sampling requirements were usually only available for large areas, the analysis of the residence time and range size relationship has been mainly performed in large regions, generally above 10^4 km^2 (e.g. Castro et al. 2005; Wilson et al. 2007; Williamson et al. 2009; Ahern et al. 2010; Sheppard & Schurr 2019). Moreover, even in the best sampling scenario, the first detection of a non-native species will also be dependent on its range size: species that have expanded rapidly may be discovered sooner than those that remain secluded in a tiny area of their new habitat. This can imply that the widely found positive relationship between species residence time and their range sizes can be the result of the residence time effect on expansion of range size, but also of earlier discovery of species with larger range sizes.

In this contribution, we aim to analyze whether species characteristics such as population density and reproduction, together with some of the attributes that may determine them, affect the range size of non-native plants that were introduced on a small island at different points in time. Guadalupe is an oceanic island in the Pacific Ocean off the Baja California peninsula, Mexico, where detailed spatial and temporal data of its non-native flora are available. It is an island without native species of terrestrial mammals, amphibians, or reptiles, and the native flora therefore lacks previous interactions with vertebrate herbivory. After the introduction of goats, the island experienced one and a half centuries of uncontrolled grazing that deeply affected plant population dynamics, including density and dispersal. It was distressingly reported that population sizes of many native plant species decreased progressively through time; some 20 of them have even been considered currently extinct from the island (Moran 1996). We use Guadalupe Island as study system to analyze how much range size distributions of non-native species in small regions are positively associated with residence time or affected by species characteristics, such as population density and reproduction, and their possible interaction with biotic characteristics of the region, in this case the ecological factor of grazing.

Livestock grazing is an extended land use worldwide (Erb et al. 2007) and a recognized driver of plant community dynamics (Milchunas & Lauenroth 1993; Adler et al. 2001; Díaz et al. 2007). One of the more direct consequences of grazing on herbaceous plants dynamics is the change of their population density (Fuhlendorf et al. 2001; Porensky et al. 2016), thus determining the chance of long-distance dispersal events. In arid lands, it has been observed that under increasing grazing intensity reproduction success of plants is related with earlier blooming and shorter duration (Tadey 2020). Finally, height of plant individuals tends to decrease with grazing intensity (Díaz et al. 2007), becoming a response to avoid grazing pressure, in the same way that low population density would be. Indeed, both functional responses to grazing, flowering phenology and height, can be correlated. Species that start growing and flowering earlier show smaller individual height than those that flower later (Sun & Frelich 2011). Combining these attributes (population density, flowering phenology, and individual height) for non-native species, we can hypothesize that their response to grazing will influence their propagule production, range sizes distribution, and their corresponding range size – time residence relationship. If this is correct, we expect to find (i) a weak relationship between species range size and residence time, and (ii) larger range sizes in those species showing, under this intense grazing scenario, higher population density, earlier flowering time, and smaller mature individual height. We also compare our results to a similar analysis using native species, to test whether the relationships between density, range size, and time since first detection may arise from sampling biases rather than from recent range expansion. We expect to find a positive relationship between range size and time since discovery and density in non-natives, but not in native plants.

MATERIAL AND METHODS

Study area

Guadalupe is an oceanic island of 246 km^2 formed about 7 Ma ago (Engel & Engel 1961), and located in the Pacific Ocean 260 km off the west coast of the Baja California peninsula, Mexico (29°00′N, 118°15′W). It has a Mediterranean

climate, with a mean monthly temperature between 12°C and 21°C, and 280 mm of annual precipitation (Moran 1996). In the mid-nineteenth century, whale hunters introduced goats, and the natural dynamics of the island changed dramatically. Uncontrolled growth of the goat population for at least one and a half centuries modified the vegetation dynamics through restriction of seedling recruitment, plant dwarfing, and soil loss. Although the island has been sporadically visited by whalers and goat hunters, it has remained uninhabited. Only in the 1940s, a small outpost of the Mexican Navy was installed on its southern tip and in the 1970s, a small fishing camp was established on the west coast. There are no permanent residents on the island. However, due to the irregular topography and the lack of vehicles, the overland activity of the temporary inhabitants has been very limited and their role in species dispersal on the island is therefore probably minimal.

In 1875, the naturalist Edward Palmer visited Guadalupe Island and made the first botanical collections of its flora. He collected about 1,200 specimens of vascular plants corresponding to 113 species, among them the first ten non-native species recorded for the island (Moran 1996). Between 1875 and 2004, there were at least 36 trips to Guadalupe Island led by several botanists who made botanical collections. Reid Moran (San Diego Natural History Museum) deserves special mention as he visited the island more than 20 times between 1948 and 1988 and published "The flora of Guadalupe Island, Mexico" in 1996 (Moran 1996). Overall, the extant flora in 2004 comprised 193 species, 154 native and 39 non-native species (Moran 1996; Junak et al. 2005). Another 27 species, 21 native and six non-native species (*Anagallis arvensis* L., *Avena fatua* L., *Brassica nigra* (L.) W.D.J.Koch, *Bromus tectorum* L., *Festuca bromoides* L., and *Triticum aestivum* L.) were considered extinct in 2004 (Moran 1996; Junak et al. 2005). After 2004, when goat eradication began, the long-time transformation of Guadalupe Island by grazing came to a halt and the vegetation dynamics returned to natural drivers. However, new players, non-native plants, had been (and are still being) added to this ecological theater.

Data

We compiled a list of the 39 non-native species (92% annuals or biennials) recorded on Guadalupe Island between 1875 and 2004, and for each species we estimated: (i) distribution range, (ii) residence time, (iii) population density, and assigned (iv) two attributes related to tolerance to grazing: flower phenology and minimal height at first reproduction.

Distribution range – Range size of each non-native plant species on the island was estimated using two sources: (i) systematic field sampling made along the entire island in 2004, and (ii) historical records of the Guadalupe flora present in regional herbaria. Since botanists have preferentially collected native species during historical expeditions, this has resulted in a bias towards native species (as compared to non-native species) in collections (Garcillán & Ezcurra 2011). We therefore only used the systematic field sampling as a source for range sizes when comparing native and non-native species.

Residence time – It is difficult to get an accurate determination of the first arrival date of new non-native species; therefore, the time of the first collection or reliable bibliographic reference (i.e. time since discovery) has been used as proxy (Rejmánek et al. 2005). The length of time since discovery is denominated minimum residence time for non-native species (Rejmánek 2000). Besides residence time, probability of first species detection is also partially dependent on its range size. We explored these dependences by comparing the relationship of range size and time since discovery of native and non-native species. We established the year of first record of native and non-native species based on Moran (1996) and subsequent floristic updates of the island (Rebman et al. 2002; León de la Luz et al. 2003; Junak et al. 2005; Vanderplanck et al. 2018). We calculated the time since the first record up to 2004 of each native and non-native species. In the case of the non-native *Cenchrus setaceus* (Forssk.) Morrone, discovered in 2004, we assigned it the minimum value of time since discovery of one year.

Field sampling − In spring 2004, just before goat eradication began, we did a systematic sampling of the island flora (Garcillán et al. 2008). The island was divided into 46 cells of 1.5′ latitude × 1.5′ longitude (~ 7 km^2) and in each cell, three 50 × 2 m transect plots were established, one in the cell centre and the other two at approximately 350 m north and south of the centre. Once discarding some transects due to difficult access, a total of 110 transects were done in 40 cells. In each transect, we recorded all the plant species, both natives and non-natives (supplementary file 1A & B).

Herbarium records − In 2006, we checked the main regional herbaria with Guadalupe Island records (CAS, DS, SD, and UC) and updated this information in 2020 through the revision of BajaFlora (www.bajaflora.org), an online consortium of regional herbaria of Mexico and US (BCMEX, HCIB, POM, RSA, SD, SBBG, SDSU, UCR). We defined non-native species range size as the number of cells in which a species was present from field observations or from herbarium records. Population density was calculated as the number of field transects where the species was recorded divided by the number of grid cells of the geographic range of the species. For each non-native species, we obtained data on two functional traits related to tolerance to grazing (FNA 1993+; CalFlora 2020; Jepson Flora Project 2020): minimal height at first reproduction and flower phenology (first month and duration).

Analysis

Because the start of the reproductive period and its duration were correlated ($r = -0.50$, $p = 0.001$), both variables can be summarized into a single one by means of PCA after standardizing both variables. The first principal component accounted for 75.3% of the variation, supporting the idea that phenology can be represented by a single variable. Positive phenology scores over this new axis correspond to species that start flowering earlier and do so for longer. We will refer to this new value as the phenology index. Moreover, using a single variable solves collinearity problems in statistical analyses.

The analysis of geographic ranges is based on the recognition that such data are bound by zero, because areas must be positive, and a maximum determined by the geographic limits of the study system: no species on Guadalupe Island can be distributed over an area larger than the island itself (Williamson & Gaston 1999; Sheppard & Schurr 2019). Thus, range size is envisaged statistically as the fraction of the available area occupied. In our case, the size of the geographic range was defined as the number of grid cells in which a species was present out of a total of 46 cells on the island. The natural error distribution for data that represent the number of successes (occupied cells) out of a fixed total (46 cells on the island) is a binomial distribution. However, because variance increased with time since discovery, and because of overdispersion, we resorted to a beta regression model. In essence, beta regression is the same as any other regression model but assumes that the error follows a beta distribution rather than, for instance, a normal

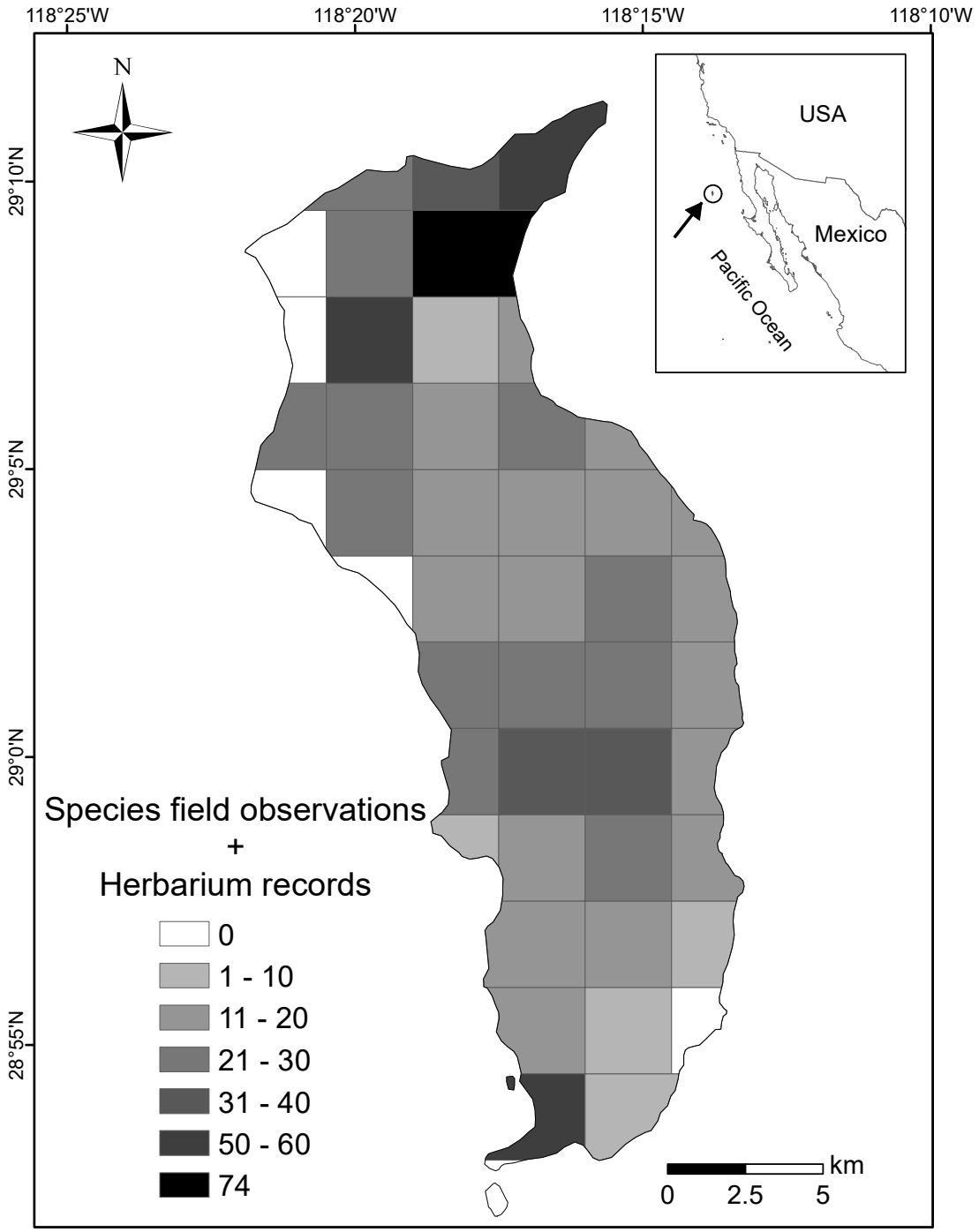

Figure 1 − Spatial pattern of the number of herbarium records between 1875 and 2004 combined with field sampling observations from 2004 for the 39 non-native plant species found on Isla Guadalupe. Cell size: 1.5′ latitude × 1.5′ longitude (~ 7 km^2).

or a binomial distribution. As the binomial distribution, beta distribution is appropriate for values that bounded both at zero and one, as is the case for the fraction of grid cells occupied. However, beta regression allows the simultaneous modelling of the mean and the variance, determined by a parameter ϕ.

We thus modelled range size of non-native species as a function of time since discovery, population density, minimum plant height at first reproduction, and phenology index using beta regression. Because we have relatively few data, we did not include interactions in this analysis. Allowing ϕ to change with the logarithm of plant height solved the problem that species with larger predicted ranges had larger standardized weighted residuals (Cribari-Neto & Zeileiss 2010). Moreover, the term relating ϕ to plant height was significant ($p = 0.010$). Beta regressions were conducted using package betareg (Cribari-Neto & Zeileiss 2010) for R v.3.5.1 (R Core Team 2018).

To test whether the relationships between time since discovery, density, and geographic range could arise from sampling bias and not from the recent expansion of geographic ranges hypothesized for non-native species, we compared natives and non-natives. If there is a trend for widely-distributed species with large densities to be discovered earlier, it should be observed in all species, irrespective of their status as natives or non-natives. Because historical records were not considered in this analysis, we excluded the species that were not observed in the field, leaving 52 natives and 27 non-natives. Morphological and phenological data were also excluded from the analysis because they were unavailable for many natives. The fitted model thus included density and time since discovery, altogether with their interactions with plant origin (native or non-native) as predictors of geographic range. We deleted non-significant terms via step-wise deletion (see R code and databases in supplementary file 2).

RESULTS

We obtained 692 field observations and 267 herbarium records for the 39 non-native species, distributed over 41 of the total 46 cells; and for natives, we got a total of 520 field observations for 53 of the 175 native species, which occupied 38 cells (supplementary file 1A–C). Combined field and herbarium data of non-natives show some areas of higher value in the northern, centre, and southern tip of the island (fig. 1). They probably reflect two points where landing is possible (northeast and south), major human presence (south), and botanists preference for some areas (northern part, where tree species are located, and an alluring mountain in the centre).

On average, one new non-native species was found every four years between 1875 and 2004. However, the number of known native species also increased through time, at a mean rate of one species every three years (fig. 2).

On an initial fit, plant height of non-natives seemed to have a significant effect on range size ($p = 0.040$), but this was mainly due to a single species (*Nicotiana glauca* Graham) that had a large influence on the regression. This species is much taller than the others, which formed a comparatively tight cluster over the plant height axis. Under such circumstances, the regression line tends to pass through the outlier, regardless of the trend observed for the remaining species. This is because the regression line tends to join the outlier and the cluster of the remaining data. If *Nicotiana* was removed, height had clearly no effect on geographic range ($p = 0.685$; supplementary file 3A). The

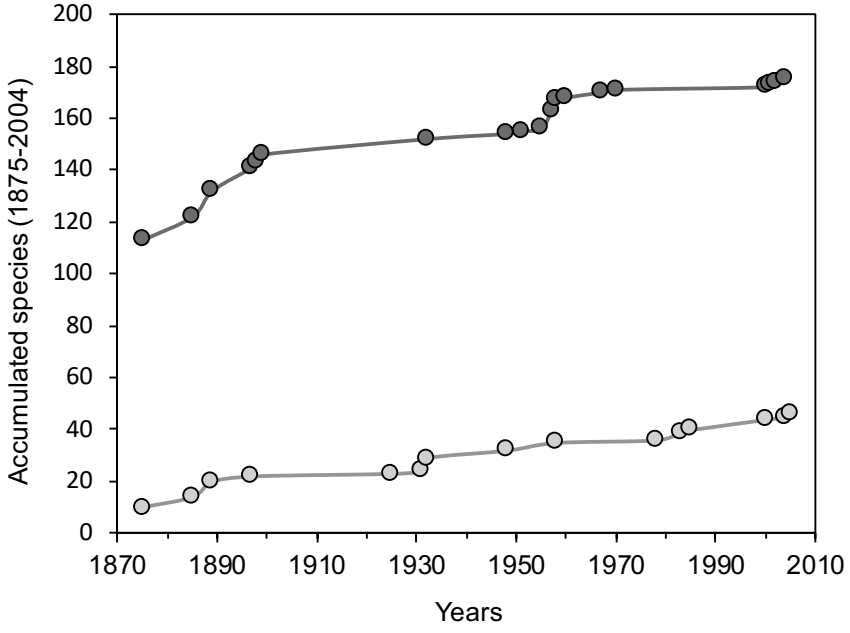

Figure 2 − Temporal pattern of new plant species accumulation recorded on Guadalupe Island, Mexico, between the first collection in 1875 until 2004. Dark grey: native species, light grey: non-native species.

square-root of time since discovery provided a slightly better fit than the untransformed variable, and was therefore used in all analyses. However, there was no difference in the conclusions or qualitative results.

The size of the geographic range was larger for non-native species with longer time since discovery ($p < 0.001$), greater density ($p < 0.001$), and that had earlier and longer flowering periods ($p = 0.019$; fig. 3). The pseudo R^2 of the full model was 0.822 (supplementary file 3B). When comparing natives and non-natives, the interactions of density and time since discovery with native status were not significant ($p > 0.28$). After removing these interaction terms, it was observed that geographic range increased with density ($p = 0.003$) and time since discovery ($p = 0.001$), and, although both trends did not differ significantly between natives and non-natives, the latter had larger geographic ranges ($p < 0.001$; fig. 4). This model had a pseudo $R^2 = 0.301$ (supplementary file 3C).

DISCUSSION

In this study, we wanted to know if the range size of non-native species in small regions, like Guadalupe Island, is related to time since discovery, as has been observed for larger regions, or if it is more related to species attributes as population density and reproduction. We also wanted to found out if time since discovery, as an estimate of residence time, can be affected by the influence of species range size in their detection probability. For this goal, we compared the relationship of range size with time since discovery and density between native and non-native species.

Range sizes were larger for non-native species, but also for native species, with longer time since discovery. In the case of non-natives, this relationship was affected by species attributes. For any value of time since discovery, non-natives with higher densities show larger range sizes, suggesting that the expansion of such species through time was faster than that of low-density species. Consequently, range size differences between high- and low-density species got wider through time. Also, in accordance with our hypothesis, plants that flower earlier and for a longer period show a positive relationship with range size. However, the possibility that sampling bias results in false relationships between time since discovery, density, and range size in non-native species cannot be discarded.

The widely found positive relationship between residence time and range size of non-native species in large regions (e.g. Castro et al. 2005; Pyšek & Jarošík 2005; Ahern et al. 2010; Sheppard & Schurr 2019) seems to also be present in small regions; despite that local ecological factors are the main drivers of species distribution in them (Richardson & Pyšek 2012). We found that in small areas, like Guadalupe Island, residence time can show a positive relationship with the range sizes of the non-native species.

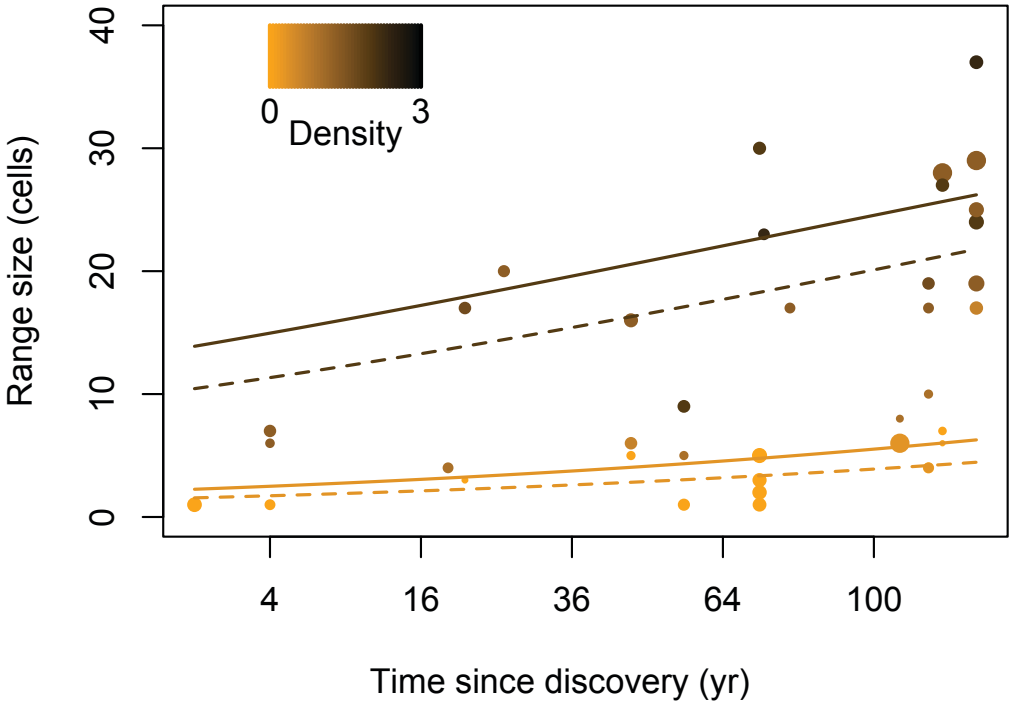

Figure 3 − Relationship between range size, time since discovery, density, and phenology index of non-native plants on Guadalupe Island. The circle size corresponds to species with a larger phenology index, i.e. species that flower earlier and for longer periods, and colours represent density. We show the estimated relationship between time since discovery and range size for four combinations of density and phenology indices. Solid lines: early flowering species (phenology index = 1.226); dashed lines: species that flower late and for shorter periods (phenology index = -1.226). Brighter lines: low-density species (density = 0.153); dark lines: high-density species (density = 1.673). The selected density and phenology values were obtained as the mean ± 1 sd of each variable.

Residence time, more than a simple variable, should be conceptualized as a temporal axis that integrates the effects of multiple ecological factors on species ranges (Catford et al. 2009). Residence time has been interpreted as an expression of species propagule pressure, because the longer a species is established, the higher its propagule production will be (Rejmánek et al. 2005; Richardson & Pyšek 2006). The positive relationship observed between range size and propagule production (Gassó et al. 2009) would be produced by the temporal dynamics of propagule pressure.

The two factors that were found positively related with range sizes, i.e. population density and phenology index, are intimately associated with propagule production. If we consider that the majority of non-natives are annual species, an increase in seed production would enlarge the probability of population renewal next year (spatial population maintenance) and also its dispersal capacity (spatial population expansion). This is also in line with the probabilistic expectation that some long-distance dispersal becomes unavoidable, even if it occurs in a very small fraction of the propagules, when large numbers of seeds are dispersed (Levine et al. 2006; Pachepski & Levine 2011).

Conversely to what we expected, minimum individual height, as an expression of faster life cycle and lower detectability by goats, did not show a relationship with range size. Probably, the plant height data we used may not well reflect the real variability of individual height of these species on Guadalupe Island, not only because of differences in abiotic conditions with respect to California, the region where the height database was constructed, but also due to the effect on plant biomass of the intense grazing by goats on the island for a long time period. It is also possible that non-native species that have successfully invaded Guadalupe are highly tolerant to grazing, and thus that differences in height, and thus exposure to goats, have little effect on their populations. Non-native species showed larger range sizes with respect to time since discovery than native species. We think that the long-term grazing has reduced the range sizes of native plants, who lacked historical interaction with grazers, and increased range sizes of non-native species, better adapted to grazing.

Our analysis is based on the assumption that the date of first record of a non-native species is a good proxy of its arrival time, although we realise this approach may be flawed. On Guadalupe Island, the discovery rates of natives and non-native species were similar for the periode 1875–2004. It could be that some of the newly recorded, putative native species are instead recent colonizers from the nearby continental mass. Indeed, Moran (1996) already suggested the existence of about 15 such species on Guadalupe Island. However, Fuentes et al. (2008) also found similarity in rates of species accumulation of native and non-native species in Chile between 1900 and 2000. Besides that, we also found a positive relationship between the range size of native plants and their time since discovery and density. This suggests that time of discovery of native plants depends on their detectability: smaller range size and density result in later discovery. Consequently, a similar potential effect

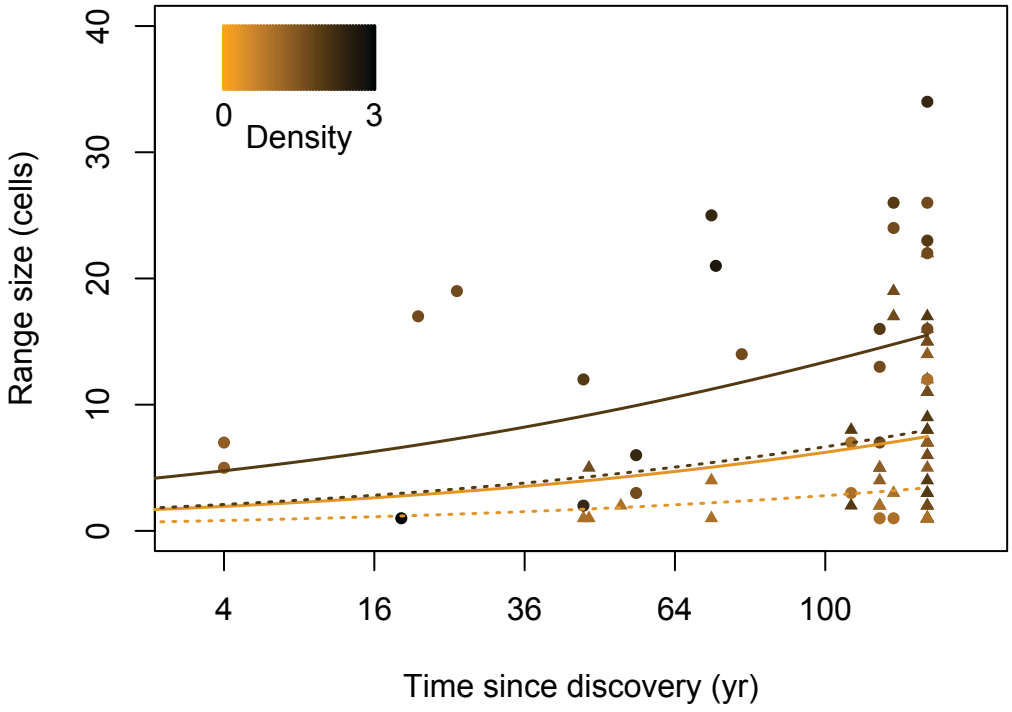

Figure 4 − Relationship between range size, time since discovery, density, and species origin of native and non-native plants on Guadalupe Island. Natives: triangles and dotted lines; non-natives: circles and solid lines. Dark lines: high-density species; brighter lines: low-density species.

of detectability in non-native plants first record cannot be discarded (Gassó et al. 2009). This advises to consider the first recording date of non-native plant as a proxy of their arrival time with some precaution. An analogous discovery rate of natives and non-natives would be expected in regions where knowledge of the native flora is less complete and discovery rates of both groups are affected by sampling bias. Thus, studies such as ours, conducted in regions whose native floras are not yet completely known and presences of new natives keep being added, provide a unique opportunity for documenting the possible circularity in the residence time – range size relationship in non-native species when time since the first record is used as an estimation of residence time.

Residence time determines the temporal dimension of species spatial dynamics. From this perspective, species range sizes would contain the ecological legacy of time across the entire spectrum of spatial scales of species display, from the priority effects in community assembly at small (Chase 2003; Fukami 2015) and large spatial extension (Hortal et al. 2011), to invasion debts (Essl et al. 2011; Rouget et al. 2016), and residence time effects in species distributions (Castro et al. 2005; Pyšek & Jarošík 2005; Williamson et al. 2009; Ahern et al. 2010; Sheppard & Schurr 2019) and community assembly (Hui et al. 2013; Latombe et al. 2018) at medium and large regions. The current species movement to new regions beyond their original distribution ranges that we are witnessing represents an extraordinary natural experiment to explore the role of time in the ecological dynamics that govern the spatial display of non-native species at different spatial scales. However, we should be cautious with the potential circularity between range size and residence time estimation. We can conclude that the patterns that we found can be result of ecological processes, sampling effects or, more likely, both. Biases in residence time estimation due to species detectability seem unavoidable in studies on non-native species, and surely contribute to a greater or lesser degree to the patterns that are observed in the data. The challenge remains on how to disentangle the effects of sampling bias from those of relevant biological processes.

SUPPLEMENTARY FILES

Supplementary file 1 – Attributes of native and non-native species used in the analyses (A & B) and herbarium records of non-native species used to estimate their range sizes (C).

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Supplementary file 2 – R code and databases used in the beta regression analyses.

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Supplementary file 3 – Additional details on beta regression model fitting.

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