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Contrasting effects of a native and an alien N-fixing species on the diversity and composition of dune plant community assemblages

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ABSTRACT

The establishment of plant species in coastal dune systems has received increasing attention in recent years due to their potential threats to the unique biotic and abiotic characteristics of these fragile ecosystems. Plants exhibiting invasive behavior, whether alien or native, merit particular focus in coastal dunes systems given their ability to form extensive, high-density populations. To address whether there are differences in the effects of a native and an alien species on dune systems, we examined the impact of two N-fixing species, one an alien invader (*Ulex europaeus*) and the other a native colonizer (*Gunnera tinctoria*), on taxonomic and functional plant diversity. In these coastal dune systems where the resident community contains a high (56 %) proportion of introduced species, invasion by the alien species *Ulex europaeus* significantly reduced the diversity of the resident community by decreasing species richness, evenness, and taxonomic complexity. In contrast, colonization by the native *Gunnera tinctoria* did not lead to significant reductions in species richness or evenness but did reduce overall species diversity and likely facilitated species turnover by altering species assemblages. We conclude that U. *europaeus* invasions exert significantly negative effects on resident coastal plant communities, whereas colonization by the native G. *tinctoria* has comparatively less impact. This study represents one of the few field experiments directly comparing the impacts of invasive alien species with those of range-expanding native species, providing evidence that alien species can exert greater ecological effects. These findings hold significant conservation and management implications, as they highlight the need to address the ecological consequences of overgrowing populations, whether native or alien, particularly in coastal dune systems.

1. Introduction

Biological invasions are one of the major drivers of global environmental change, and often lead to negative impacts on ecosystem functioning, biodiversity and human well-being (IPBES, 2023). These impacts have both time- and scale-dependent effects on key ecological processes (Rejmánek et al., 2005), that can disrupt the integrity of the native community, altering abiotic and biotic factors, and reducing biodiversity and ecosystem stability (Parker et al., 1999; Pyšek et al., 2012; Vilà et al., 2011).

Alien species are widely spread throughout all ecosystems of the world even under the most extreme environmental conditions (Chown et al., 2012; IPBES, 2023), including coastal dune systems, which seem to be highly susceptible to biological invasions (Chan and Briski, 2017; Simberloff, 1995). In the last decades, an increase in ‘greening’ due to establishment by grasses, forbs and scrub of invasive behavior, both native and alien species, have been reported in coastal areas worldwide (Jackson et al., 2019). This is somewhat surprising as the establishment of plants in these habitats is often associated with specific adaptations to salinity and water availability (Hesp, 1991). Such changes may lead to the formation of novel plant communities and modifications in several abiotic and biotic factors, including a reduction in bare soil, reduced water infiltration, nutrient enrichment, and more stable dune systems (Hodgkin, 1984; Provoost et al., 2011; Stešević et al., 2017; Vecchio et al., 2015).

Previous studies have reported that the resident plant communities

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of coastal dune systems are composed of a significant number of alien species that are characterized by a high invasiveness, potentially causing “extreme cases of species invasion” (Castillo and Moreno-Casasola, 1996; Gallego-Fernández et al., 2019). However, invasion processes are not necessarily confined to alien introductions, as establishment of native species beyond their original range (natural range expansion) could also generate populations of highly dominant individuals, adding an additional level of complexity within the resident plant communities (D’Odorico et al., 2012; Peyrat and Fichtner, 2011; Provoost and Declerck, 2020).

Plant species with invasive behavior, whether native or alien, are likely to have characteristics that enable them to outcompete species that are present in the local community, particularly, in coastal and island ecosystems. However, these habitats tend to have a lower species richness, fewer functional groups, and more unfilled niches that favour new introductions (Elton, 2020; Simberloff, 1995; Tilman, 1985). The increased cover and dominance of plant species may lead to the spatial displacement of resident communities and a reduction in land availability in the limited area of fixed dunes, decreasing plant diversity (Isermann, 2008).

Plant traits, such as the ability to fix atmospheric nitrogen (N_2) through plant-microbe symbioses, can be a strong predictor of establishment success and high primary productivity in species with invasive behavior, particularly under nutrient poor conditions like dune systems (Marchante et al., 2008). The presence of nitrogen-fixing plants in coastal ecosystems has important implications for the cycling of nutrients and the overall ecosystem dynamics. Primary production in dune systems is often limited by nitrogen availability (Sundareshwar et al., 2003), and N-fixing species can, through the enrichment of soil N, increase plant community productivity (Danin, 1991), promoting the growth of ruderal species, and ultimately influencing the taxonomic and functional diversity of the resident plant community (Guignard et al., 2017; Shumway, 2000).

Among the globally significant invasive N-fixing species, *Ulex europaeus* (Fabaceae, gorse) is listed as one of the 100 worst invasive species worldwide (Lowe et al., 2000). U. *europaeus* is an evergreen shrub that can colonize a wide range of habitats, including grasslands, shrublands, forest margins, and even coastal habitats (Hill, 2010). Whilst it is regarded as a native from the Iberian Peninsula to the UK and Ireland (Bowman, et al., 2008), it is a widespread invader in >22 countries (ISSG, 2022a). Notably, U. *europaeus* successfully invades dunes and coastal areas within its invasive range (Smith, 2020), in contrast to its relatively infrequent occurrence in coastal areas within its native range. In its native range, U. *europaeus* is primarily found in the Atlantic coastal *Calluna* and *Ulex* heath ecosystem, or is restricted to landward coastal scrub communities, although it is rare in these habitats, with recent evidence showing a reduction in both its range and population size (Tryfon, 2016).

In Chile, where U. *europaeus* was introduced around the early XIX century (Hoffmann, 2005), it is found in the mediterranean type regions of the country and is associated with significant economic losses in agriculture and forestry, with impacts on a wide range of ecosystems (MMA, 2022a; PNUD, 2016). In southern Chile, U. *europaeus* forms particularly large and extensive populations and is considered one of the most damaging and dominant alien species (Norambuena and Escobar, 2007). Despite this, it has been poorly studied, and little is known about the underlying consequences of these invasions, and the threat it poses to native plant species and communities (Altamirano et al., 2016; PNUD, 2016).

In many coastal areas of Chile, the co-occurrence of U. *europaeus* with the native *Gunnera tinctoria* (Gunneraceae, giant rhubarb) is common. Like U. *europaeus*, G. *tinctoria* is also a symbiotic N-fixing species, although this involves an association with a cyanobacterium, a unique feature of angiosperms (Osborne et al., 1992). The ability of G. *tinctoria* to achieve a large size and form extensive populations, can result in the formation of almost monospecific stands. In its native range in South America, G. *tinctoria* is often considered to be an early colonizer, and in places where it was introduced, in Europe, Oceania and North America, it is considered a problematic invasive plant species (Gioria and Osborne, 2013; ISSG, 2022b; Mantoani et al., 2020).

The challenge of addressing range-expanding native species that exhibit invasive behavior represents a significant dilemma for conservation efforts (Simberloff and Rejmanek, 2011). Native species that become overabundant can cause serious harm to ecosystems (Pivello et al., 2018). On Chiloé, *Gunnera tinctoria* is commonly found in various ecosystems across the island and on sandstone cliffs and dunes in coastal areas (Darwin, 1988). However, as a pioneer species, it continues to expand its native range, increasingly colonizing new habitats, including dune systems, where it can form dense populations (Appendix A.1). Despite this, the potential impacts on native ecosystems have not been documented, to the best of our knowledge. Nevertheless, some detrimental effects might be expected in coastal systems, like those reported in the studies conducted in its invasive range (Gioria and Osborne, 2013; Mantoani et al., 2020; Mantoani and Osborne, 2022), where G. *tinctoria* has wide ranging effects on soils properties, vegetation assemblages, soil seed banks and ecosystem productivity. Few species are found growing beneath invasive populations of G. *tinctoria*, resulting in a depauperate plant community often comprised of several alien and ruderal species (Gioria and Osborne, 2010, 2013; Hickey and Osborne, 1998; Williams et al., 2005).

Previous reports have indicated that alien species and native colonizers with invasive behavior may exert similar impacts on ecosystems (Hejda et al., 2017; Pivello et al., 2018). However, there are few field experiments comparing native and alien invasive species that can be used to evaluate the general assumption that an alien species has a greater impact than a native species (Vilà and Weiner, 2004) and this may be complicated by phylogenetic differences when comparisons are made with contrasting species. In coastal dune systems on Chiloe Island, the co-occurrence of the native *Gunnera tinctoria* and the alien *Ulex europaeus*, both of which have N-fixing capability, provides an opportunity to directly compare their ecological impacts under similar environmental conditions (Appendix A.1).

The objective of this study was to compare the effects of a native colonizer, *Gunnera tinctoria* and an alien invasive *Ulex europaeus*, on plant community diversity and composition of coastal dunes on Chiloé island. This ecosystem was selected because it is a critical habitat for biodiversity conservation (Fuentes et al., 2023; Herrera et al., 2024) and is highly vulnerable to biological invasions (Daehler et al., 2004). To address this, we compared three communities: 1) resident plant communities that naturally occur and persist in the dune systems on Chiloé Island, where both the colonizer and invasive species are absent, 2) resident plant communities that are colonized by G. *tinctoria*, considered as a native pioneer species in this ecosystem, and 3) those plant communities invaded by U. *europaeus*, a highly invasive alien species on the island in general.

Our hypothesis was that both species would have negative impacts on the resident plant community of the coastal dunes. However, we expected U. *europaeus*, as an alien species, would exert a greater effect on community composition, taxonomic structure, and functional diversity, compared to the native G. *tinctoria*. Understanding the ecological effects of both species will also be critical for the conservation of these dune systems, which are often the habitats for a unique assemblage of rare and endemic species.

2. Materials and methods

2.1. Study area

The study was carried out on coastal dune ecosystems in the northwest of Chiloe Island, close to Ancud, Chile (Fig. 1). This area is characterized by dune ecosystems that are composed of mobile and fixed sand dunes with soils belonging to the Entisol order (Zhenghu et al.,

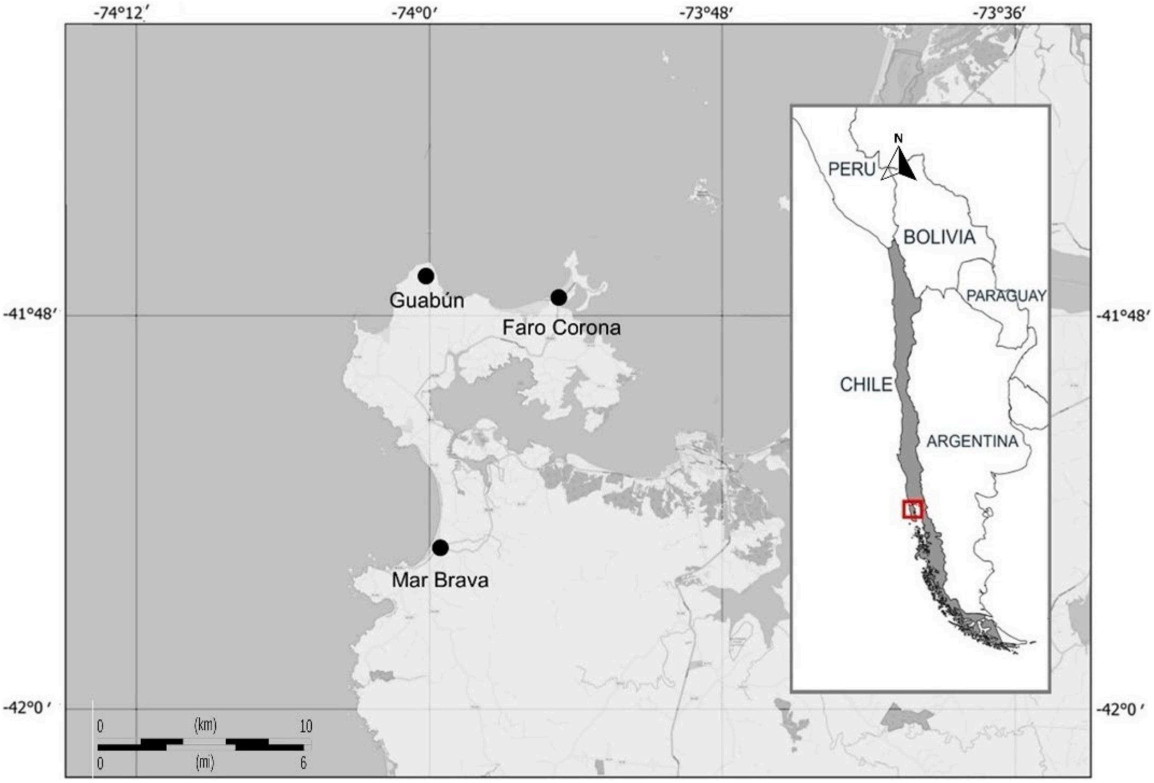

Fig. 1. Map showing the location of Chiloé island and the experimental sites (black dots).

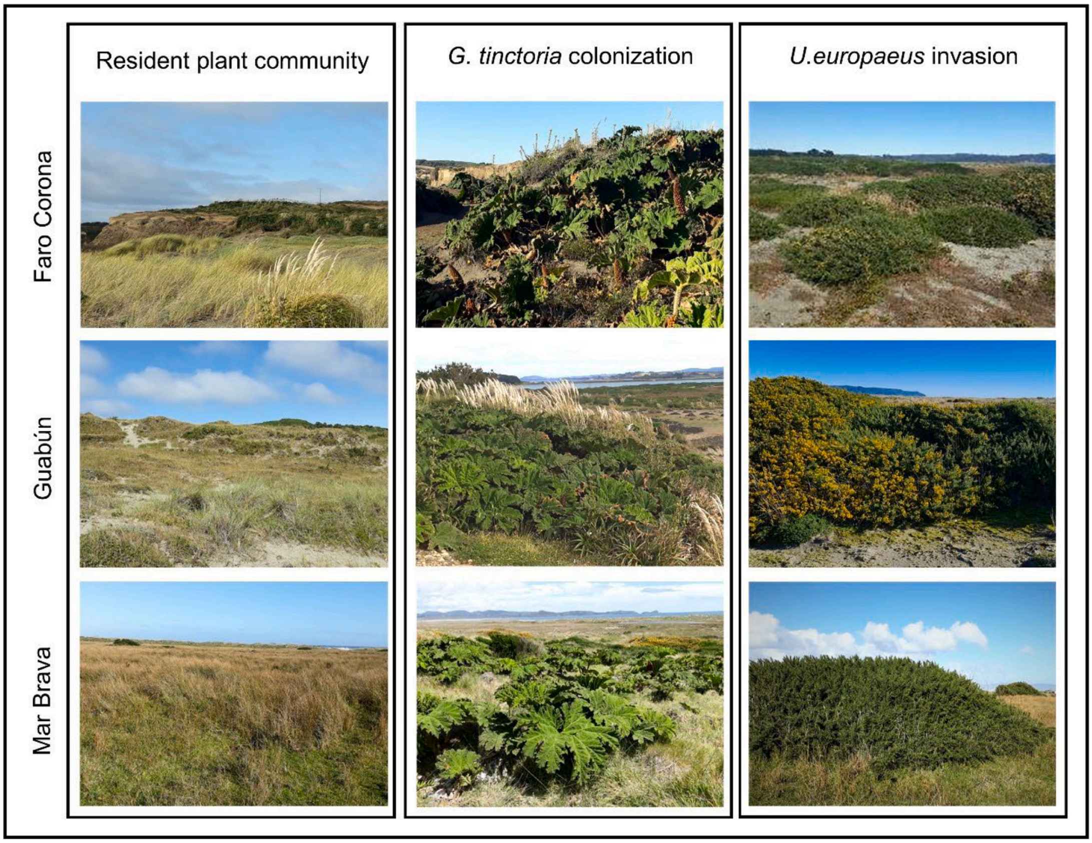

Fig. 2. Pictures of resident plant communities (left), colonization by G. *tinctoria* (center) and invasions by U. *europaeus* (right) in Faro Corona, Guabún and Mar Brava sites on Chiloe Island.

2007). The climate is humid temperate with a strong oceanic influence (Di Castri and Hajek, 1976). The meteorological records from the nearest weather station indicate an average rainfall of 2493 mm per year and an average temperature of 9.8 °C for this area (CR2, 2024). Coastal sand dunes display a psammoseric vegetation succession, with rare plant species and a unique flora and fauna of high conservation value (Carter, 1988; Nordstrom et al., 1991). Historically, human activities are common in many coastal areas of Chile and associated mainly with agricultural practices, including livestock grazing, and this has increased in recent times through urbanization, and tourism (Hidalgo et al., 2017). Despite the distinctive biodiversity and the intricate system of habitats found in coastal and dune areas, land management in Chile has contributed to the degradation of these fragile ecosystems (Barragán et al., 2005), modifying the biotic communities and facilitating the introduction of a wide number of alien species (Madrid et al., 2018).

In the three localities of northern Chiloé selected for this study (Fig. 1, Mar Brava 41 ° 53S, 73 ° 59W, Guabún 41° 48S, 74° 52W and Faro Corona 41° 46S, 73° 54W), we focused on coastal dune low shrub communities. The principal vegetation association is the Margyricarpo-Gaultheria, a resident plant community composed of small native shrubs, grasses and herbs either native or naturalized aliens (Ramirez et al., 1992). The most significant species in this community are the natives *Gaultheria mucronata,* and *Margyricarpus pinnatus*, and some species of *Juncus*, and *Poa* (Fig. 2. Left). A gradual replacement of resident plant species by locally expanding N-fixing species, the native G. *tinctoria* and the alien U. *europaeus* has been identified in the area. In the north of Chiloé Island this dynamic is evident across the coastal dunes, making it easy to find colonizing populations of G. *tinctoria* and invasive populations of U. *europaeus.* This is modifying the landscape with the formation of large and well-defined stands of G. *tinctoria* and U. *europaeus* (Fig. 2. Center and right respectively). At each site, we compared the resident species community with communities colonized by G. *tinctoria* or invaded by U. *europaeus.*

2.2. *Sample collection*

To examine how U. *europaeus* invasions and G. *tinctoria* colonization affected plant community composition, floristic inventories were carried out in February 2021 (austral summer). The sampling design was based on the space-for-time substitution approach, comparing nearby colonized and invaded sites. Given that this is a long-established resident community this provides information on how these areas have changed over time (Sax et al., 2005; Thomaz et al., 2012). Study plots were selected comprising areas of 5 × 5 m colonized by G. *tinctoria* (GT) or invaded by U. *europaeus* (UE). The selection criteria included a minimum of 75 % of cover by either species to categorize the area as colonized or invaded, as studies have reported high dominance and significant impacts of invasive species at around this threshold (Rentería et al., 2012; Tererai et al., 2013). Also, the plots used were estimated to represent populations that were ~ 20 years of age. These plots were compared to areas located within ~10 m, which were representative of the resident community (G. *tinctoria* and U. *europaeus* were absent). We assumed that the spatial and temporal variation was similar in all sites and that the resident community plots represented similar conditions to those prior to colonization (see Appendix A.1).

At each site, 5 plots were sampled for each condition (invaded, colonized and resident community), resulting in a total of 45 plots sampled. We generated a list with the taxonomic identity of all vascular plant species, and using phytosociological methods based on Braun-Blanquet (1964) and Westhoff & van der Maarel (1973), recorded the presence and relative cover across the sampling plots (see Appendix A.2).

To classify the species into ecological groups, we selected eight functional traits related to community structure (Plant life form, Raunkiær life form and life span), plant fitness and environmental tolerance (shade tolerance, pH, soil N requirement, soil nutrients requirements and vegetative reproduction capacity) and conservation status. Functional ecological traits were identified using an inductive approach, based on data collected from scientific and technical reports, and the open-access plant trait database TRY (Kattge et al., 2020). The information was analyzed and generalized to transform numerical variables into categorical ones and to create a trait matrix (Appendix A.3 and A.4).

2.3. *Data analysis*

Using field data, we constructed four species matrices: relative abundance, presence-absence, taxonomic rank, and plant ecological traits, which were the basis for statistical assessments to identify taxonomic and functional diversity and taxonomic community composition. To analyze taxonomic diversity, we calculated species richness (S), Shannon diversity index (H'), and Pielou evenness index (J) (Magurran, 1988), using the *vegan* package in R software (Oksanen et al., 2020). To estimate functional diversity, we calculated the mean pairwise trait distance (pwtd), functional richness (frich) and functional divergence (fdiv), using the *picante* (Kembel et al., 2010) and *FD* packages (Laliberté et al., 2014) in R software. To analyze the vegetation composition, all plant species were classified by taxonomic ranks: family and order according to APG IV (2016), as well as origin, according to the national inventory of species of Chile (MMA, 2022b). The statistical significance of the effects of U. *europaeus* and G. *tinctoria* on taxonomic diversity and community composition was evaluated using Moran's I test, using the *spdep* package (Bivand, 2022) to account for spatial autocorrelation. To further analyze differences between communities, generalized linear mixed models (GLMM) were implemented incorporating a spatial autocorrelation structure, using the *lme4* (Bates et al., 2015) and *spaMM* (Rousset and Ferdy, 2014) packages. When significant differences were detected, pairwise comparisons of predicted means with Bonferroni corrections were conducted using *emmeans* (Lenth et al., 2024).

To evaluate similarities and dissimilarities between vegetation composition and the functional traits of the species in the invaded, colonized and resident community, non-metric multidimensional scaling (NMDS) methods were used, based on Bray-Curtis similarity matrices. The analysis was carried out excluding the target species *Gunnera tinctoria* and *Ulex europaeus* to avoid the effects of their dominance. Statistical differences were tested using the ANOSIM nonparametric test.

Prior to the statistical analysis, each variable was assessed by multivariate and individual normality tests (Shapiro and Wilk, 1965), and homoscedasticity, using the Fligner-Killen test. All statistical analyses were performed using R version 4.1.3 (R Development Core Team, 2020).

3. Results

3.1. *Taxonomic diversity*

A total of 37 vascular plant species were recorded, belonging to 15 orders and 17 families (Appendix A.2). We observed a significant decrease in species richness in U. *europaeus* (UE) sites compared to the resident (RC) community (on average 4 species lower, ($P < 0.01$) (Table 1). In addition, we found a significant decrease in species richness

Table 1
Taxonomic diversity results comparing resident plant communities.

	RC	GT	UE
Richness (S)	15.7 (± 3.6) ^{a}	15.1 (± 3.9) ^{a}	11.7 (± 4.6) ^{b}
Diversity (H')	2.1 (± 0.5) ^{a}	1.9 (± 0.2) ^{b}	1.4 (± 0.3) ^{c}
Evenness (J)	0.29 (± 0.04) ^{a}	0.28 (± 0.05) ^{a}	0.25 (± 0.06) ^{b}

Data are the mean ± SE. Means followed by different letters are significantly different ($P < 0.05$). RC: resident community, UE: invasion by U. *europaeus* and GT: colonization by G. *tinctoria.*

between the UE and G. *tinctoria* (GT) plots ($P = 0.03$), while no significant differences were found between the RC and GT plots.

The Shannon diversity index (H') showed significant differences among treatments. The resident community exhibited a significantly higher diversity compared to plots colonized by *Gunnera tinctoria* ($P < 0.01$) and invaded by *Ulex europaeus* ($P < 0.001$). Additionally, the diversity in G. *tinctoria* plots was significantly greater than in U. *europaeus* plots ($P < 0.001$) (Table 1).

The Pielou evenness index (J') ranged from 0.17 to 0.36. The lowest J' values were associated with U. *europaeus* invasions, which were significantly lower than those of the RC ($P < 0.01$) and GT ($P = 0.02$) plots. No significant differences in J' were found between the GT and RC plots.

3.2. *Functional diversity*

The functional traits of the 37 identified species are presented in Appendix A.3. Estimates of functional diversity revealed significant effects of G. *tinctoria* colonization and U. *europaeus* invasion on the resident plant communities of the coastal dunes in Chiloé Island. Functional richness did not exhibit significant variation among treatments, with comparable values observed across GT, UE, and RC ($P = 1$). However, when accounting for species abundance, indices such as the pairwise trait distance (pwtd) ranged from 1.1 to 2.7, with RC plots displaying significantly higher pwtd values than GT ($P < 0.001$) and UE ($P < 0.001$) plots. Similarly, there were significant differences in functional divergence (fDiv) across the treatments ($P < 0.001$), with values ranging from 0.38 to 0.97. The highest fDiv values were observed in areas invaded by U. *europaeus*, followed by the GT and RC plots, respectively (Table 2).

3.3. *Plant community composition*

Taxonomic Rank

In terms of the taxonomic composition of the plant communities, the UE plots had a significantly lower taxonomic rank than the RC and GT ones (Table 3). Plant establishment, by either the native or alien species, was associated with structural changes in the taxonomic rank of the resident community (Fig. 3). Orders such as the *Orchidales* and *Caryophyllales* were exclusively associated with the RC plots. Other taxa, such as the *Asparagales, Athyriales* and *Gunnerales* were present solely in the colonized communities, whilst the *Apiales, Ranunculales* and *Geraniales* were found either in the invaded or colonized communities. No exclusive taxa were found in the UE communities.

The taxonomic ranking of species is presented in Fig. 3, illustrating variations in the relative cover of orders and families within the RC, GT, and UE plots. The cover of the families *Fabaceae* and *Gunneraceae* significantly increased ($P < 0.01$), as expected, due to the dominance of U. *europaeus* and G. *tinctoria*, respectively. In addition, three plant families were significantly affected by invasion and colonization. For the *Ericaceae* family, the only species present in the study area, *Gaultheria mucronata*, exhibited a marked reduction in cover, decreasing from 29.2 % in the RC to 4.6 % in the GT and 3.1 % in the UE ($P < 0.01$). Similarly, for the *Rosaceae* family, *Margyricarpus pinnatus* showed a significant decline in cover from 10.25 % in the RC to 1.5 % in the GT and 1 % in the UE ($P < 0.01$). The *Poaceae* family also displayed significant differences in cover, with reductions observed between the RC and GT ($P < 0.01$) and between the GT and UE ($P < 0.01$), although no significant difference was found between the RC and UE ($P = 0.2$). Conversely, an increase in cover for several species within the *Poaceae* family was observed in the GT plots. For example, *Holcus lanatus* increased in cover from 1.1 % in the RC to 2.6 % in the GT plots, while remaining relatively unchanged in areas dominated by UE at 1.2 %.

Table 2
Functional diversity results comparing among plant communities.

	RC	GT	UE
Pairwise trait distance (pwtd)	2.4 (± 0.4) ^{a}	2 (± 0.2) ^{b}	1.7 (± 0.3) ^{c}
Functional richness (frich)	0.09 (± 0.03) ^{a}	0.1 (± 0.03) ^{a}	0.09 (± 0.05) ^{a}
Functional divergence (fdiv)	0.71 (± 0.13) ^{a}	0.79 (± 0.05) ^{b}	0.93 (± 0.03) ^{c}

Data are the mean ± SE. Means followed by different letters are significantly different ($P < 0.05$). RC: resident community, UE: invasion by U. *europaeus* and GT: colonization by G. *tinctoria*.

Table 3
Summary of taxonomic ranks.

	RC	GT	UE
Order	8.3 (± 1.9) ^{a}	8.3 (± 1.8) ^{a}	6.3 (± 2.4) ^{b}
Family	9.4 (± 2.1) ^{a}	9.5 (± 2.1) ^{a}	7.5 (± 2.5) ^{b}

Data are the mean ± SE. Means followed by different letters are significantly different ($P < 0.05$). RC: resident community, UE: invasion by U. *europaeus* and GT: colonization by G. *tinctoria.*

Plant origin

Regarding the origin of the species, we found that of the 37 vascular plants described in this study, 20 were identified as aliens and 17 as native species. In the resident community 56 % of the species present were aliens with a relative cover of 39.2 %; in plots colonized by G. *tinctoria* the percentage of alien species was 61 % with a relative cover of 34 % and in areas invaded by U. *europaeus,* they represented 70 % of the species present with a relative cover of 83 %. There was a significant difference in the number of native species between the UE and RC communities, whilst there was little difference between the GT and RC communities (Fig. 4.A). In contrast, the richness of alien species did not differ among the different communities (Fig. 4. B).

Community assemblage

The plant community composition of the resident community showed distinct clusters from the areas colonized by U. *europaeus* or G. *tinctoria* (Fig. 5). Nevertheless, there are some species, such as *P. annua* and *P. pratensis, A. capillaris*, L. *saxatilis, P. lanceolata,* among others that are common in the three communities, producing a resemblance to the resident community in terms of species composition (ANOSIM, $R = 0.3$, $P < 0.01$).

Multivariate analysis showed differences in trait assemblages among the communities (ANOSIM $R = 0.5$, $P < 0.01$) (Fig. 6,Appendix A.5). Some traits tend to be more related to the different communities, such as the Raunkiær life forms, particularly a reduction in the occurrence of chamaephytes in both the GT and UE communities ($P < 0.001$). For example, the presence of M. *pinnatus* declined notably in colonized and invaded communities. Additionally, plants with moderately alkaline soil requirements decreased significantly in the UE community and were entirely absent in the GT community ($P < 0.001$), such as *Ambrosia chamissonis*. In contrast, traits associated with fern growth form and moderately acidic soil pH requirements increased in the GT communities compared to RC and UE ($P = 0.03$), reflected by the higher occurrence of species like *Blechnum chilense*, H. *lanatus, Libertia chilensis*, and *Rubus ulmifolius*. A notable finding was that *Rumex obtusifolius*, the only species with a high nitrogen demand, was primarily found in the resident communities rather than in the GT or UE communities ($P < 0.05$). Additionally, no significant differences were detected among the evaluated traits, including plant lifespan, nutrient requirements, growth form, shade tolerance, or regeneration characteristics.

4. Discussion

4.1. *Effects of colonization and invasion on plant taxonomic diversity*

Comparisons of the effects of the native colonizer *Gunnera tinctoria* and the alien invader *Ulex europaeus* on plant community diversity and composition in the coastal dunes of Chiloé Island consistently demonstrated that alien invasion has a significantly greater impact on plant

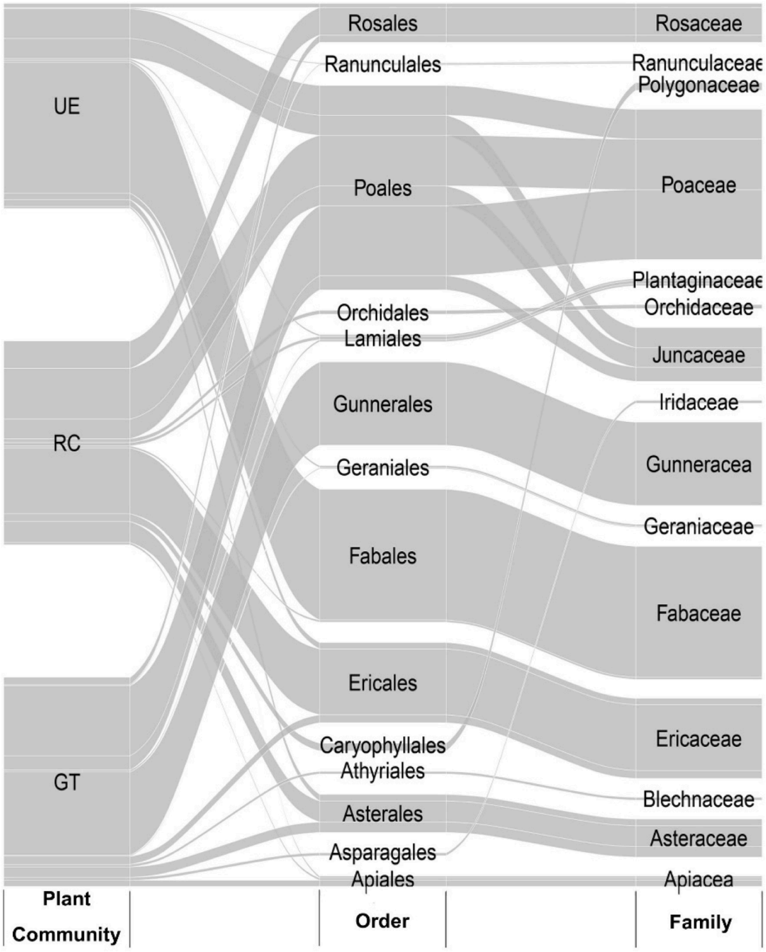

Fig. 3. Sankey diagram showing the taxonomic ranking of species in the *Ulex europaeus* (UE) resident (RC) and *Gunnera tinctoria* (GT) plant communities. Line thickness is related to the relative cover of the taxa within the community.

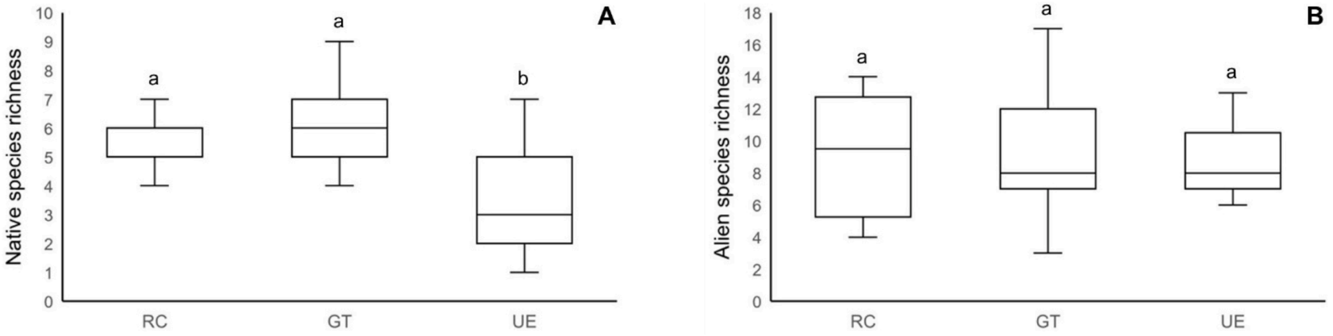

Fig. 4. **(A)** Native species richness, and **(B)** alien species richness in the resident plant communities (RC), communities invaded by U. *europaeus* (UE), and communities colonized by G. *tinctoria* (GT). Different letters indicate significant differences ($P < 0.05$).

diversity. Previous studies conducted in the invasive ranges of both species, *Gunnera tinctoria* and *Ulex europaeus,* have reported significant ecological impacts and a decrease in the functional and taxonomic diversity of the resident communities (Isern, 2007; Mantoani et al., 2020). In contrast, G. *tinctoria* did not significantly affect species richness in its native range on Chiloé Island. However, there were notable shifts in community assemblage with dissimilarity values exceeding 70 %, suggesting that G. *tinctoria* may promote species turnover despite no changes in overall richness. However, some family-related differences in the response to G. *tinctoria* dominance was found. For example, the presence of *Ericaceae* and *Rosaceae* declined, while the *Poaceae* significantly increased in communities dominated by G. *tinctoria*. This indicates that certain species within the resident community can be replaced by newcomers after G. *tinctoria* colonization, likely due to a filtering process that favors species that can adapt to the altered conditions and facilitates positive interactions with other plant species (Shumway, 2000).

The relatively small impact of *Gunnera tinctoria* colonization on species richness may be attributed to several factors. Despite the high dominance of this species in colonized areas, its deciduous nature, shedding its leaves on an annual basis, creates periods at the beginning and end of the growing season when competitive interactions are likely

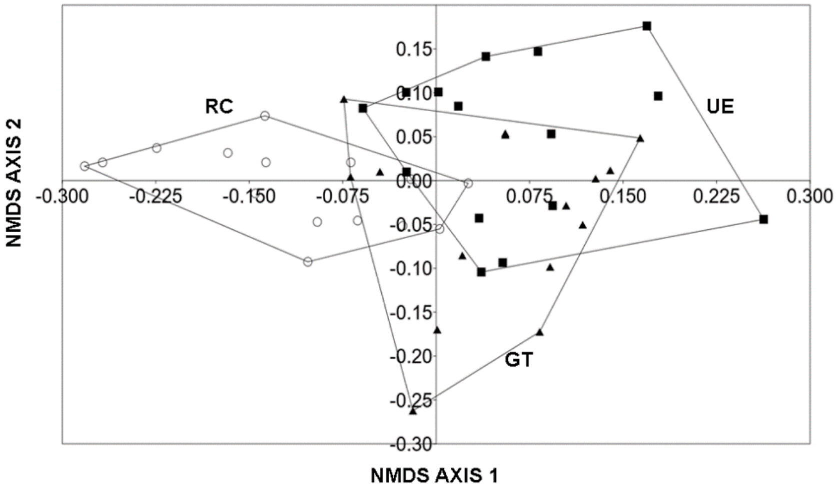

Fig. 5. NMDS plot for the different plant species assemblages. The polygons identify different groups associated with the resident community (circles) or those colonized by U. *europaeus* (filled squares), or G. *tinctoria* (filled triangles). The ordination stress factor was 0.2, which corresponds to a sample configuration showing a good significance for a 2D representation of the underlying data matrix.

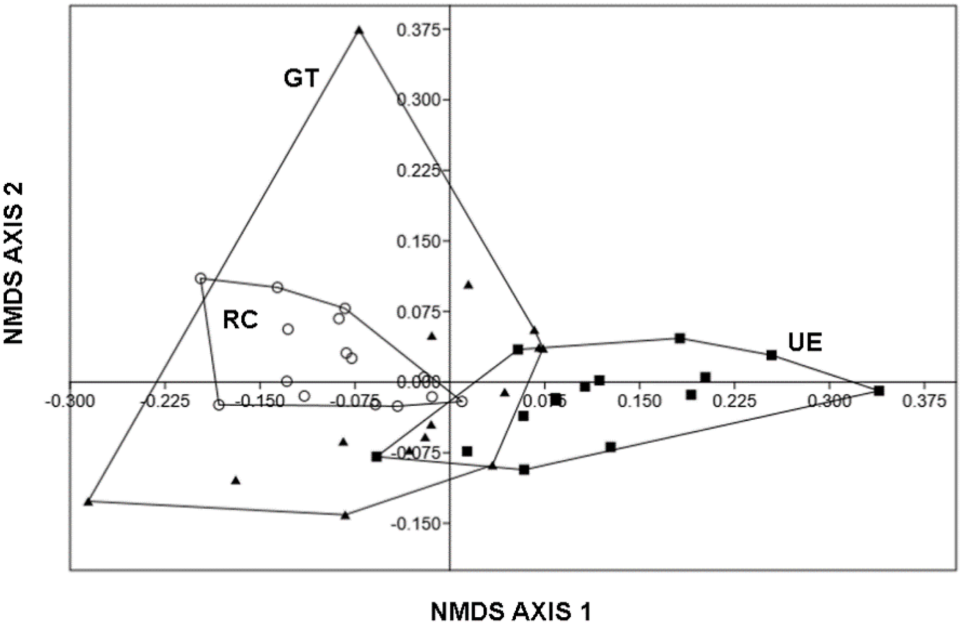

Fig. 6. NMDS plot for the different plant trait assemblages. The ordination stress factor was < 0.01, which corresponds to a sample configuration showing a good significance for a 2D representation of the underlying data matrix.

reduced, allowing opportunities for the establishment of other plant species (Gioria and Osborne, 2014; Mantoani et al., 2020). Additionally, G. *tinctoria* may exhibit a higher fitness in its introduced, compared to its native range because of localized selection and population differentiation (Colautti et al., 2017), or the absence of natural enemies (Keane and Crawley, 2002). For example, *Lysathia atrocyanea*, an endemic beetle found in Chile that feeds on *Gunnera* leaves (Jerez, 2000), may limit plant productivity and exert some control over the growth and expansion of native populations. *Eupithecia horismoides,* the leaf-stalk borer, has also been found in association with G. *tinctoria* on Chiloé (Ibarra-Vidal and Parra, 1993).

In contrast to the results for G. *tinctoria*, U. *europaeus* invasions were associated with marked changes in community composition, including a reduction in taxonomic diversity (richness, diversity and evenness). Our results are consistent with previous studies such as those by Harris et al. (2004) on shrubland in New Zealand and León-Cordero et al. (2016) in a subtropical forest-grassland in Brazil, both of which reported a decrease in species richness and a reduction in native species due to U. *europaeus* invasions. These findings could be explained by the high cover and abundance of U. *europaeus* and a negative diversity-productivity relationship. This theory suggests that high ecosystem productivity tends to be dominated by a single or few species, resulting in a lower diversity, reduced richness and uneven dominance (Cox, 2013; Guo, 2007). Another factor is the development of a dense and persistent canopy that significantly decreases light availability (Hill et al., 1996; Roberts and Florentine, 2021), thereby restricting the establishment and growth of shade-intolerant species. Furthermore, putative allelopathic effects associated with U. *europaeus* cannot be ruled out (COSEWIC, 2008; Duhart, 2012), although such a mechanism remains to be unequivocally confirmed (Barrera, 2015).

In contrast to these results previous work has shown that U. *europaeus* stands in the middle or advanced stage of invasion can provide a suitable habitat for several ruderal species, as described in a high Andean Forest in Colombia (Amaya-Villarreal and Renjifo, 2010), in montane grasslands, *Leptospermum* scrub and low forest communities (Lee et al., 1986) and in a native podocarp forest (Wilson, 1994), both in New Zealand. Establishment time and the growth of different canopy layers are key factors that shape patterns of abundance and diversity in the understory vegetation (Brosofske et al., 2001). In more advanced stages of stand development, less resource demanding species may be able to establish beneath or alongside U. *europaeus*, due to the increased availability of growing space and resources (Su et al., 2019). The time scale of the invasion can be a critical factor in identifying any potential impacts associated with alien or colonizer species and further work would be required to assess the applicability of the current results to the longer-term effects of U. *europaeus* invasions or colonization by G. *tinctoria* on these dune systems.

4.2. Modifications in plant functional diversity

Analysis of functional diversity is ecologically relevant because this considers key characteristics among species that are involved in ecosystem functions (Poos et al., 2009). Our result about functional diversity suggests that functional richness is similar among the resident community, G. *tinctoria* and U. *europaeus* communities. Nevertheless, plant abundance is not considered in the calculation of this index, ruling out the importance represented by vegetation cover when studying invasive species (Legras and Gaertner, 2018).

Pairwise trait distance decreased in areas invaded by U. *europaeus* or colonized by G. *tinctoria*, indicating that the community plant traits are less diverse and differ from the traits of the resident community. In contrast, the calculated functional divergence represents a significative negative effect in both invaded and colonized communities. This index is mainly affected by the high abundance of individual species, so the high cover and dominance of U. *europaeus* and G. *tinctoria* may also have subsequent effects not only on functional traits at the community level but also supports evidence of ecosystem level effects (Cadotte et al., 2010).

The results of this study indicate a relationship between specific plant traits and the distinct plant communities dominated by *Gunnera tinctoria* and *Ulex europaeus*. For instance, chamaephytes, including the native species *Gaultheria mucronata* and *Muehlenbeckia pinnatus*, are negatively affected by both G. *tinctoria* and U. *europaeus*. Chamaephytes, which are characterized by their low growth habit, appear to be particularly vulnerable to the dense canopies formed by G. *tinctoria* and U. *europaeus*. These dense canopies significantly reduce light availability to low-lying plants, resulting in decreased cover and growth (Hall et al., 2010). Additionally, the establishment of G. *tinctoria* and U. *europaeus*, both of which are perennials, likely contributes to increased organic matter deposition and stabilization of dune systems. This stabilization reduces sand movement, which may hinder the regeneration of disturbance-adapted species (McIntyre et al., 1995). The presence of plants that prefer moderately acidic soils, as well as ferns, was associated with G. *tinctoria*-dominated communities. This pattern suggests that G. *tinctoria* may promote promotespromotes conditions that are more favourable to certain species through, for instance, soil modifications, such as a higher nitrogen availability, a lower soil pH, disruption of disrupteddisrupted microbial mutualisms, or microhabitat alterations (Gioria and Osborne, 2014; Mantoani et al., 2020; Santoro et al., 2011). Also, communities dominated by U. *europaeus* were waswas associated with biannual plants, that are tolerant to moderately acidic soils, as well as those that are shade intolerant. This suggests that the effects of U. *europaeus* also include an ability to shade out light-demanding species (Brosofske et al., 2001).

The reduction in functional trait diversity indicated that U. *europaeus* and G. *tinctoria* occupy distinct functional niches and use complementary resources, overcoming the need for competition within the community (MacArthur, 1970; McGill et al., 2006). Given that some plant traits can vary with life stage, they tend to be highly time scale-dependent (Yin et al., 2021). In this investigation, however, we disregarded the structure of plant traits in time, so the results must be interpreted within these limitations.

4.3. Origin of the species associated with the colonized and invaded communities

Coastal dune systems, characterized by complex vegetation assemblages, are rarely pristine due to disturbances from human activity, wind, and water dispersal, and this can facilitate the introduction of alien or colonizer species (Hesp, 2004; Chapman, 1976). The temperate coastal ecosystems of Chiloé, which are comparable to many Mediterranean dune systems, are highly variable and often exposed to major environmental perturbations, that are compounded by human activities (Cascone et al., 2021). Although the abiotic conditions have often been thought to be the major factor limiting establishment by all but the most specialized plant species, they are now considered some of the most susceptible habitats to plant invasions (Chytry et al., 2008; Smith, 2020). Environmental changes, including climate change, greater habitat heterogeneity, and increased propagule pressure may have exacerbated this susceptibility (Muñoz-Vallés and Cambrollé, 2015).

In this study, the reference community was the resident plant community (RC), which includes native species, naturalized alien plants and alien invasive species. Although a strictly native reference community was not available as a reference for this study, the evidence indicates that the current community comprises a stable assemblage of species that represents the plant community prior to invasion by U. *europaeus* or colonization by G. *tinctoria.* Whilst we acknowledge the importance of understanding the effects of plant invasions on the native flora, we also need to recognize that these novel plant assemblages, which include both native and alien species are also susceptible to invasion or colonization.

Our study revealed a remarkably high number of alien species in the coastal dune systems of Chiloé Island. We found that 70 % of the species present in communities invaded by U. *europaeus* were alien. Even in areas where the two co-dominants, G. *tinctoria* and U *europaeus* were absent, there was a high proportion (56 %) of alien plants. Although limited research has focused on the composition and origin of plant communities in coastal dune ecosystems in the Southern Hemisphere, studies conducted in Europe and Asia have documented fewer alien species than those recorded in Chile (see Appendix A.6). This disparity may be attributed to more extensive coastal and dune management practices in Chile, which have facilitated the introduction of numerous aliens as well as native species (Madrid et al., 2018). The Law Decree No 701–1974 promoted several land reforms in areas susceptible to degradation, including coastal regions and sand dunes (Vivanco, 2019). Following the enactment of this law, over 40 % of Chilean dunes were affected by activities such as nitrogen fertilization, the planting of cover crops and alien species, such as *Ammophila arenaria, Lupinus arboreus,* and *Pinus radiata*, among others (FAO, 2011).

5. Conclusions

The juxtaposition of the native species G. *tinctoria,* and the alien U. *europaeus* in several coastal dune systems of Chiloe Island provided a unique opportunity to conduct, for the first time, an analysis of the effects of two N-fixing plants of contrasting origins with invasive behavior on plant community diversity and composition. Utilizing a multiple-indices and functional approach, we found relatively small effects of the native colonizer on resident plant communities, while invasion by the alien species had a significant negative effect on plant community diversity.

The effect of invasions by U. *europaeus*, included a decrease in the taxonomic and functional diversity of resident communities. This impact was particularly evident in the reduction of native species richness, leading to subtle shifts in plant community composition. While the native colonizer, G. *tinctoria,* had less of an impact on plant community composition than the alien invader, this study highlights that native species with invasive behavior, such as G. *tinctoria*, can still disrupt the functional diversity of resident communities. In this regard, probably more emphasis should be placed on monitoring range expanding native species given that they don't receive the same attention as alien invasive species (Pivello et al., 2018). Whilst they are often not perceived as a significant threat to native ecosystems, increasing evidence indicates that native species may be as harmful as alien invaders over relatively short time periods (Marrs and Watt, 2006; Muñoz-Vallés and Cambrollé, 2015).

In summary, our research emphasizes the complex and often underestimated impacts of both native colonizers and alien invasive species on the taxonomical and functional diversity of resident plant communities. While reports of alien species impacts on resident communities are increasing, the broader effects on other ecosystem properties remain largely unexplored and warrant further investigation. Future research is essential if we are to enhance our understanding of the ecological implications of range expanding plant populations whether alien or native if we are to develop effective management strategies for sensitive ecosystems, such as coastal dune systems.

CRediT authorship contribution statement

Liliana Vasquez-Garcia: Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Bruce Arthur Osborne:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jorge F. Perez-Quezada:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices

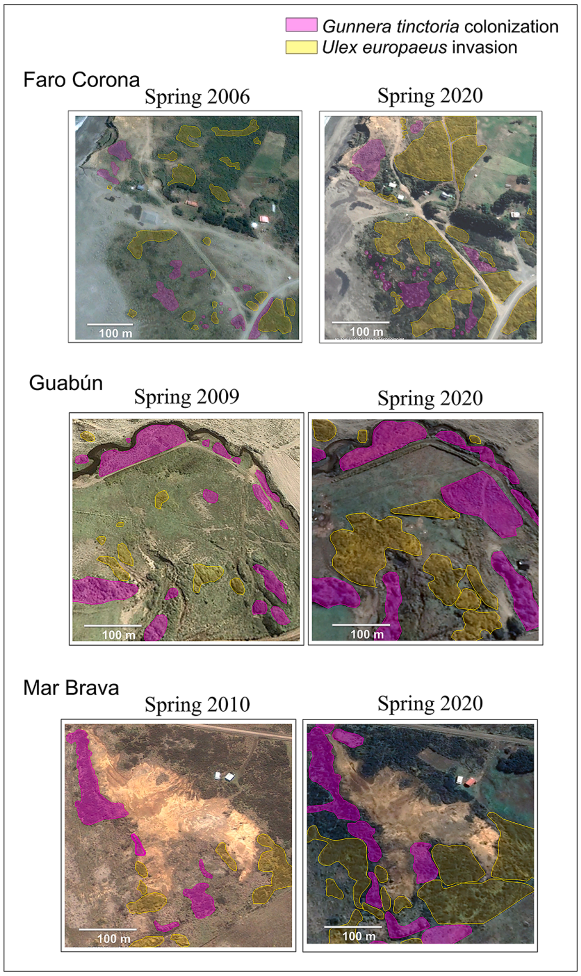

Fig. A.1. Invasion and colonization process in the study sites.
Source: Google, 2023.

Table A2
List of species with their relative abundance (%) within plots of resident species (RC), plots colonized by G. *tinctoria (GT),* and plots invaded by *U. europaeus* (UE).

	RC	GT	UE	Impact of alien species	Year of first report in Chile
Acaena magellanica	0.5	0.8	0.9	-	
Agrostis capillaris	1.6	0.7	0.5	3	1914
Ambrosia chamissonis	3.7	0.0	0.2	3	1894
Baccharis sphaerocephala	1.1	1.3	1.0	-	
Blechnum chilense	0.0	1.2	0.1	-	
Brachystele unilateralis	1.9	0.0	0.1	-	
Chusquea quila	0.1	2.0	0.0		
Cirsium vulgare	0.0	0.1	0.2	2	1850
Cortaderia araucana	0.3	0.9	0.2	-	
Cytisus scoparius	0.5	0.1	0.4	1	1847
Erodium cicutarium	0.5	0.6	0.8	3	1846
Eryngium paniculatum	0.9	3.4	0.9	-	
Eupatorium salvium	0.2	1.3	0.2	-	
Fragaria chiloensis	2.5	0.0	0.1	-	
Gaultheria mucronata	29.2	4.6	3.1	-	
Gunnera tinctoria	0.0	40.6	0.1	-	
Hieracium pilosella	2.8	1.1	0.9	3	1951
Holcus lanatus	1.1	2.6	1.2	3	1869
Hypochaeris radicata	0.7	0.6	0.5	-	1880
Juncus procerus	8.3	5.5	7.3	-	
Juncus stipulatus	1.4	1.7	1.8		
Leontodon saxatilis	2.6	1.0	1.0	3	1930
Libertia chilensis	0.3	1.2	0.0	-	
Lotus uliginosus	0.3	0.4	0.3	4	1847

(*continued on next page*)

Table A2 (*continued*)

	RC	GT	UE	Impact of alien species	Year of first report in Chile
Lupinus arboreus	0.0	0.4	0.1	4	1881
Margyricarpus pinnatus	10.2	1.5	1.0	-	
Nolana paradoxa	0.1	0.0	0.0		
Plantago lanceolata	1.7	1.0	0.8	2	1860
Poa annua	10.4	11.4	6.1	3	1864
Poa pratensis	10.4	11.4	6.1	4	1854
Prunella vulgaris	0.3	0.3	0.1	2	1859
Ranunculus repens	0.5	0.6	0.5	2	1875
Rubus ulmifolius	0.6	1.3	0.4	1	1859
Rumex acetosella	0.5	0.0	0.0	1	1851
Rumex obtusifolius	3.8	0.4	0.0	3	1924
Trifolium repens	1.0	0.2	0.3		1897
Ulex europaeus	0.0	0.0	62.7	1	1847

Impact of alien species in Chile: 1. High, 2. Medium, 3. Low, 4. Naturalized. (Matthei, O., 1995).

Table A3

Scientific names, families, origin (O), life forms (LF), Raunkiær's life forms (RF), lifespan (LS), shade tolerance (ST), soil nitrogen requirements (NR), Soil pH requirements (pH), soil nutrient requirements (SNR), vegetative reproduction capacity (VR) and conservation status (CS) of the flora of coastal grasslands in the northwest of Chiloe Island-Chile.

Scientific name	Family	O	LF	RF	LS	ST	NR	pH	SNR	VR	CS	Source
APIALES												
Eryngium paniculatum	Apiacea	N	dl	hf	pa	it	ln	nph	oc	lv	NE	(Chichizola et al., 2019; Ramirez et al., 1991; Ramírez et al., 2018; Riedermann et al., 2014)
ASPARAGALES												
Libertia chilensis	Iridaceae	N	ml	hf	pa	it	ln	aph	oc	hv	NE	(Fundación Philippi, 2022a; Ramirez et al., 1991; Ramírez et al., 1989)
ASTERALES												
Ambrosia chamissonis	Asteraceae	A	dl	cf	pa	it	–	kph	oc	hv	NE	(Kattge et al., 2020; Kohler and Weisser, 1966; Ramírez et al., 2018)
Baccharis sphaerocephala	Asteraceae	N	dl	pf	pa	lt	–	nph	oc	lv	NE	(Ramírez et al., 2018; Riedermann et al., 2014)
Cirsium vulgare	Asteraceae	A	dl	hf	ba	lt	an	nph	ec	lv	NE	(Kattge et al., 2020)
Eupatorium salvium	Asteraceae	N	dl	pf	pa	lt	–	–	mc	lv	NE	(Fundación Philippi, 2022b; Kattge et al., 2020; Madrid et al., 2018)
Hieracium pilosella	Asteraceae	A	dl	hf	pa	it	ln	aph	oc	hv	NE	(Bishop and Davy, 1994; Kattge et al., 2020)
Hypochaeris radicata	Asteraceae	A	dl	hf	pa	it	ln	aph	oc	mv	NE	(Kattge et al., 2020)
Leontodon saxatilis	Asteraceae	A	dl	hf	pa	it	ln	aph	mc	lv	NE	(Kattge et al., 2020)
ATHYRIALES												
Blechnum chilense	Blechnaceae	N	fl	hf	pa	tt	ln	nph	mc	lv	NE	(Hoffmann, 2005; Ramirez et al., 1991; Stoll et al., 2006)
CARYOPHYLLALES												
Rumex acetosella	Polygonaceae	A	dl	hf	pa	it	ln	nph	oc	hv	LC	(Kattge et al., 2020)
Rumex obtusifolius	Polygonaceae	A	dl	hf	pa	lt	en	nph	ec	mv	NE	(Kattge et al., 2020)
ERICALES												
Gaultheria mucronata	Ericaceae	N	dl	pf	pa	lt	–	nph	oc	mv	NE	(Mansilla, 2004; Novoa, 2019; Teillier and Escobar, 2013)
FABALES												
Cytisus scoparius	Fabaceae	A	sl	pf	pa	it	an	nph	ec	lv	NE	(Kattge et al., 2020)
Lotus uliginosus	Fabaceae	A	dl	hf	pa	it	an	aph	–	mv	NE	(Kattge et al., 2020; Ramirez et al., 1991)
Lupinus arboreus	Fabaceae	A	sl	pf	pa	it	ln	nph	oc	lv	NE	(Kattge et al., 2020)
Trifolium repens	Fabaceae	A	dl	hf	pa	lt	an	nph	mc	hv	NE	(Kattge et al., 2020)
Ulex europaeus	Fabaceae	A	sl	pf	pa	it	ln	nph	oc	mv	LC	(Kattge et al., 2020)
GERANIALES												
Erodium cicutarium	Geraniaceae	A	dl	tf	aa	it	an	nph	ec	lv	NE	(Kattge et al., 2020)
GUNNERALES												
Gunnera tinctoria	Gunneracea	N	dl	hf	pa	lt	ln	aph	–	hv	NE	(Gioria and Osborne, 2013; Osborne et al., 1991, 1992; Promis et al., 2013)
LAMIALES												
Plantago lanceolata	Plantaginaceae	A	dl	hf	ta	it	an	nph	oc	mv	NE	(Kattge et al., 2020)
Prunella vulgaris	Lamiaceae	A	dl	hf	pa	lt	an	nph	mc	hv	LC	(Kattge et al., 2020)
ORCHIDALES												
Brachystele unilateralis	Orchidaceae	N	ml	gf	pa	lt	–	–	mc	lv	NE	(Novoa et al., 2006; Riedermann et al., 2014; Rodríguez et al., 2018)
POALES												
Agrostis capillaris	Poaceae	A	ml	hf	pa	lt	an	nph	mc	hv	LC	(Kattge et al., 2020)
Cortaderia araucana	Poaceae	N	ml	hf	pa	it	–	–	oc	mv	NE	(Luebert et al., 2007; Riedermann et al., 2014; Rodríguez et al., 2018)
Chusquea quila	Poaceae	N	ml	pf	ta	tt	–	aph	oc	hv	NE	(Gonzalez, 2001; Ramírez et al., 1989; Sotomayor, 2013)
Holcus lanatus	Poaceae	A	ml	hf	pa	lt	an	aph	ec	hv	NE	(Kattge et al., 2020)
Juncus procerus	Juncaceae	N	ml	hf	pa	lt	an	aph	oc	hv	NE	(Balslev, 1996)
Juncus stipulatus	Juncaceae	N	ml	hf	pa	it	an	aph	oc	hv	NE	(Balslev, 1996)
Poa annua	Poaceae	A	ml	hf	aa	lt	an	nph	oc	mv	LC	(Kattge et al., 2020)
Poa pratensis	Poaceae	A	ml	hf	pa	lt	an	nph	oc	hv	LC	(Kattge et al., 2020)
RANUNCULALES												

(*continued on next page*)

Table A3 (*continued*)

Scientific name	Family	O	LF	RF	LS	ST	NR	pH	SNR	VR	CS	Source
Ranunculus repens	Ranunculaceae	A	dl	hf	pa	it	an	aph	mc	hv	LC	(Kattge et al., 2020)
ROSALES												
Acaena magellanica	Rosaceae	N	dl	hf	pa	lt	ln	nph	mc	hv	NE	(Madrid et al., 2018; Marticorena and Cavieres, 2000; Ramirez et al., 1991)
Fragaria chiloensis	Rosaceae	N	dl	hf	pa	lt	ln	nph	oc	hv	NE	(Lavín and Maureira, 2002; Ramirez et al., 1991; Ramírez et al., 1989)
Margyricarpus pinnatus	Rosaceae	N	dl	cf	pa	lt	–	–	oc	mv	NE	(Cordero et al., 2017; Ramírez et al., 2018)
Rubus ulmifolius	Rosaceae	A	dl	pf	pa	lt	–	aph	ec	hv	NE	(Monasterio-Huelin and Webert, 1996; Quiroz et al., 2009)
SOLANALES												
Nolana paradoxa	Solanaceae	N	dl	pf	pa	it	–	–	oc	lv	NE	(Luebert et al., 2007; St Andrews Botanic Garden, 2017)

Table A4
Categories and codes used in Table A3.

Traits	Categories	Traits	Categories
Plant growth form	Fern (fl) Herbaceous monocot (ml) Herbaceous dicot (dl) Shrub (sl)	pH requirements	Moderately acidic (aph) Moderately acidic or alkaline (nph) Moderately alkaline (kph)
Raunkiær’s life forms	Chamaephytes (cf) Geophyte (gf) Hemicryptophyte (hf) Phanerophyte (pf) Therophyte (tf)	Species nutrient requirements	Oligotrophic (oc) Mesotrophic (mc) Eutrophic (ec)
Plant lifespan	Annual (aa) Biannual (ba) Triannual (ta) Perennial (pa)	Plant vegetative regeneration capacity	Low (lv) Medium (mv) High (hv)
Shade tolerance	Light intolerant (it) Light tolerant (lt)	**Other information**	**Categories**
Nitrogen requirements	Least (ln) Average (an) Excessive supply (en)	Origin Conservation status	Native (N) Alien (A) Least concernation (LC) Not evaluated (NE)

Table A5
Mean frequency of plant traits and comparison between the communities: resident species (RC), *Gunnera tinctoria* (GT) and *Ulex europaeus* (UE).

	RC		GT		UE	
Plant lifespan						
Annual	1,20 (± 0,35)	a	1,47 (± 0,23)	a	1,47 (± 0,5)	a
Biannual	0,00 (± 0,00)	a	0,13 (± 0,12)	a	0,20 (± 0,35)	a
Triannual	0,93 (± 0,12)	a	0,87 (± 0,12)	a	0,53 (± 0,23)	a
Perennial	13,60 (± 1,40)	a	12,60 (± 3,29)	a	9,53 (± 3,11)	a
Raunkiær’s life forms						
Chamaephytes	1,87 (± 0,12)	a	0,20 (± 0,35)	b	0,47 (± 0,12)	b
Geophyte	0,73 (± 0,31)	a	0,00 (± 0,00)	a	0,13 (± 0,23)	a
Hemicryptophyte	10,60 (± 0,35)	a	12,13 (± 3,52)	a	8,53 (± 2,80)	a
Phanerophyte	2,13 (± 0,81)	a	2,27 (± 0,23)	a	2,13 (± 0,76)	a
Therophyte	0,40 (± 0,00)	a	0,47 (± 0,23)	a	0,47 (± 0,50)	a
Species nutrient requirements						
Eutrophic	2,13 (± 0,90)	a	2,13 (± 0,83)	a	1,33 (± 0,90)	a
Mesotrophic	3,53 (± 0,58)	a	3,73 (± 2,50)	a	2,73 (± 1,72)	a
Oligotrophic	9,80 (± 0,53)	a	7,73 (± 0,83)	a	7,40 (± 1,25)	a
Plant growth form						
Fern	0,00 (± 0,00)	a	0,40 (± 0,35)	a	0,07 (± 0,12)	a
Herbaceous dicot	11,00 (± 1,64)	a	9,73 (± 2,83)	a	6,53 (± 3,51)	a
Herbaceous monocot	4,47 (± 1,01)	a	4,60 (± 0,60)	a	3,93 (± 0,23)	a
Shrub	0,27 (± 0,46)	a	0,27 (± 0,31)	a	1,20 (± 0,35)	a
Shade tolerance						
Light intolerant	6,67 (± 1,51)	a	6,27 (± 2,47)	a	5,60 (± 2,82)	a
Light tolerant	9,07 (± 0,90)	a	8,80 (± 1,40)	a	6,13 (± 1,33)	a

(continued on next page)

Table A5 (*continued*)

	RC		GT		UE	
pH requirements						
Moderately acidic	4,67 (± 1,10)	a	6,93 (± 1,72)	b	4,07 (± 1,27)	a
Moderately acidic or alkaline	8,13 (± 0,23)	a	7,27 (± 1,86)	a	6,80 (± 2,84)	a
Moderately alkaline	0,93 (± 0,12)	a	0,00 (± 0,00)	b	0,13 (± 0,12)	b
N requirements						
Average	6,20 (± 0,20)	a	6,93 (± 2,50)	a	6,00 (± 2,11)	a
Hight	0,87 (± 0,12)	a	0,20 (± 0,20)	b	0,00 (± 0,00)	b
Least	4,13 (± 0,61)	a	5,73 (± 1,10)	a	4,07 (± 1,50)	a
Regeneration capacity						
High	7,13 (± 0,70)	a	7,40 (± 2,51)	a	5,20 (± 1,25)	a
Low	3,27 (± 0,50)	a	3,80 (± 1,06)	a	2,40 (± 2,31)	a
Medium	5,33 (± 0,31)	a	3,87 (± 0,95)	a	4,13 (± 0,76)	a
Not informed traits	6,80 (± 0,20)	a	4,53 (± 0,83)	b	2,67 (± 1,51)	b

Data are the mean ± SE. Means followed by different letters are significantly different ($P < 0.05$). RC: resident community, UE: invasion by *U. europaeus* and GT: colonization by G. *tinctoria*.

Table A6

Estimates of the proportion of aliens and native plant species in coastal dunes of different countries.

Report	**Country**	**% aliens**	**% natives**	**Source**
A preliminary field trial to compare control techniques for invasive Berberis aquifolium in Belgian coastal dunes	Belgium	5 % 20 %	–	(Adriaens et al., 2019)
La flora de las dunas chilenas y sus adaptaciones morfológicas	Chile	33.3 %	66.7 %	(San Martin et al., 1992)
Contribución al conocimiento de la flora y vegetación de las dunas de concón	Chile	86 %	14 %	(Luebert and Muñoz-Schick, 2005)
De análisis de flora y vegetación de las dunas de Cachagua, región de Valparaíso	Chile	43.3 %	56.7 %	(Montenegro et al., 2016)
Flora y vegetación de las dunas de la playa grande de Cartagena, una playa urbana en chile central	Chile	61 %	39 %	(Madrid and Teillier, 2021)
Plant species diversity and habitat conditions in a protected large coastal dune area of western Japan	Japan	27 %	73 %	(Iwasato and Nagamatsu, 2018)
Mexican coastal dunes: recipients and donors of alien flora	Mexico	8.7 %	–	(Martínez et al., 2021)
Exploring temporal trends of plant invasion in mediterranean coastal dunes	Spain	25 %	–	(Cascone et al., 2021)

Data availability

Data will be made available on request.

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