Community assembly of exotic plant species across Mediterranean regions

Javier Galán Díaz

PhD Thesis 2021

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Sevilla, 2021

Estación Biológica de Doñana, CSIC

Departamento de Ecología Integrativa

Universidad de Sevilla

Facultad de Biología

Programa de Doctorado en Biología Integrada

Community assembly of exotic plant species across Mediterranean regions

Memoria presentada por el graduado en Biología Javier Galán Díaz para optar al título de Doctor por la Universidad de Sevilla

Sevilla, 2021

Fdo. Javier Galán Díaz

Firmado por GALAN DIAZ JAVIER - 52005816X el día 24/03/2021 con un certificado emitido por AC FNMT Usuarios

La Dra. Montserrat Vilà Planella, Profesora de Investigación en el Departamento de Ecología Integrativa de la Estación Biológica de Doñana (EBD – CSIC) y el Dr. Enrique García de la Riva, investigador contratado en el Departamento de Ecología de la Universidad Tecnológica de Brandenburgo Cottbus–Senftenberg, como codirectores de la tesis; y el Dr. Juan Arroyo Marín, Catedrático en el Departamento de Biología Vegetal y Ecología de la Universidad de Sevilla, como tutor

CERTIFICAN

Que Javier Galán Díaz, Graduado en Biología por la Universidad Autónoma de Madrid y Máster en Taxonomía de Hongos y Plantas, Diversidad y Conservación por la Universidad Queen Mary de Londres y el Real Jardín Botánico de Kew, ha realizado bajo su dirección la presente Memoria de Tesis Doctoral, titulada *Community assembly of exotic plant species across Mediterranean regions*, y que a su juicio reúne los méritos suficientes para optar al grado de Doctor por la Universidad de Sevilla ante el Tribunal que se designe a tal efecto. Y para que a tal manera conste, firman el presente documento en Sevilla, a 17 de marzo de 2021.

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Estación Biológica de Doñana, CSIC

Dr. Enrique García de la Riva

Universidad Tecnológica de Brandenburgo Cottbus–Senftenberg

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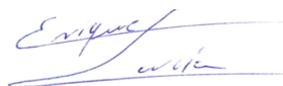
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La Comisión Académica del Programa de Doctorado en Biología Integrada de la Facultad de Biología de la Universidad de Sevilla,

CERTIFICA:

Que el doctorando **D. Javier GALÁN DÍAZ,** con D.N.I **n º 52005816-X**, ha superado positivamente las evaluaciones de los cursos académicos matriculados, y ha realizado las actividades necesarias durante todo el periodo de permanencia en este Programa de Doctorado, alcanzando la puntuación exigida para superar la *evaluación global*.

Por todo ello, se le permite la presentación de su Tesis Doctoral.

Y para que así conste, firmo la presente a 16 de marzo de 2021.

Fdo.: Susana Redondo Gómez
Coordinadora del Programa de Doctorado

Contents

Abstract

Invasions by plant species are an increasing threat which is reducing species diversity across regions, changing community composition and altering ecosystems functioning. While most investigations on impacts of exotic plants are conducted in their areas of introduction, the study of the assembly of exotic species in their native areas is emerging as a framework to better understand their roles in the invaded communities. In this regard, functional traits reflect the ecological strategy of plants and their interactions with coexistent species and the environment, therefore plant traits are a key tool to understand the role of exotic plant species in the structure of their communities.

One of the main objectives of this thesis is to identify the functional strategies of exotic species in invaded Mediterranean ecosystems and disentangle the rules that govern the assembly of invaded communities. For this, we analysed traits from several plant organs (i.e. leafs, seeds, roots) of 285 species from two vegetation types (woodlands and grasslands) at different spatial scales of resolution (i.e. Biome, environmental gradients, communities, plants). We used the Mediterranean biome as a study system because of the mostly unidirectional invasion of plants from the Mediterranean Basin to California, Chile, Australia and South Africa. Many exotic species were introduced with the arrival of the European settlers and their naturalisation was facilitated by the simultaneous intensification of agriculture and farming. Currently, these exotic species are locally very abundant and cause great impacts on the diversity and functioning of the invaded communities.

We first investigated the assembly of exotic herbaceous species in their donor and recipient grassland communities in Spain and California, respectively. We found that exotic species were more abundant than other coexisting species in communities of both the donor and recipient regions

(Chapter 1). The abundance of exotic species in California was similar to that in Spain except for invasive species which were more abundant in the introduced grasslands. Overall, this resulted in striking similarities in the taxonomic structure of Spanish and California grassland communities. We also found that productivity influences the functional composition of grassland communities by filtering traits related to resource conservation (Chapter 2). Exotic species had different traits than coexisting species in both their donor and recipient communities, but trait differences were greater in the most productive sites of the recipient communities in California. Trait differences suggest a competitive advantage of exotic species in grasslands, and supports that water and resource availability might determine niche segregation between native and exotic species in invaded California grasslands. Altogether, the results of the first two chapters indicate that the invasiveness of an exotic species could be predicted by understanding its role in its native communities.

Finally, we explored the functional strategies and trait variability of coexisting native and invasive plant species across eight highly invaded Mediterranean communities of the World (Chapter 3). Invasive species were more frequently herbaceous than natives, and had a more acquisitive resource-use strategy across the studied Mediterranean communities. Also, invasive species showed higher trait diversity in half of the communities. We also found that intraspecific variance constitutes a non-negligible source of community trait diversity accounting for 11%–27% of total trait variation. Intraspecific trait variability was on average greater in invasive than in native species, which probably reflects the ecological versatility of invasive species but also the greater susceptibility to environmental heterogeneity of herbaceous plants.

Overall, by comparing the abundance, the traits and the intraspecific variability of exotic species across communities of the Mediterranean Biome, this thesis provides insights to disentangle the assembly processes

of invaded Mediterranean communities and advances our understanding on the biogeography of plant invasions.

General introduction

Biological invasions by plant species

Exotic species are those present in a region due to human-mediated introduction (Richardson et al. 2000). We refer to exotic plant species as "naturalised", if they are able to maintain self-sustainable populations in the introduced region; and as "invasive", if they quickly reproduce and spread from the introduction area and accumulate large quantities of biomass (Richardson et al. 2000). Exotic plants are an important driver of global change (Pyšek et al. 2020) and cause many ecological impacts. For instance, exotic species decrease the fitness, abundance and richness of native plant and animal species (Vilà et al. 2011, Bradley et al. 2019), change the ecosystem properties and disturbance regimes (D'Antonio and Vitousek 1992), form novel communities replacing the native vegetation (Stotz et al. 2020), and homogenise species pools across habitats of the recipient region (La Sorte and Pyšek 2009, Arianoutsou et al. 2013).

The introduction of exotic plant species, or any taxa, has occurred for millennia (MacDougall et al. 2018), but it was the arrival of Europeans to America and the establishment of trade shipping routes that increased the rate of introduced species (Martín-Forés 2017). The rate of plant introductions has steadily increased since the eighteen century (Seebens et al. 2017), and the increase of trade and social connections over the last decades has enhanced the transport of species across the planet even more (Olden et al. 2011). Plant invasions are expected to worsen in the future as a consequence of the interaction with other agents of global change, such as habitat transformation, pollution and climate change (Kumar Rai and Singh 2020). Currently, around 4% of all known vascular plant species grow outside of their native regions due to human activity (Van Kleunen et al. 2015). Hence, it is necessary to identify the determinants of invasion by exotic species in order to develop screening tools and inform management programs.

The steps that lead to the arrival and establishment of exotic plant species in recipient communities, although highly context-dependent, can be described as plants overcoming several ecological barriers (Figure 1). First, species need to pass geographical barriers assisted by humans, either accidentally or deliberately. Then, the establishment is determined by several factors. Initially, the probability of establish successfully is directly correlated to the propagule pressure and the number of localities where the species are introduced (Kowarik 1995, Pyšek et al. 2015). Propagule pressure tends to be greater in areas with a long history of human colonisation and near urban and agricultural land (Dark 2004, Chytrý et al. 2008), and is expected to increase the genetic diversity of exotic populations, subsequently facilitating their survival and adaptation (Lockwood et al. 2005). Other evolutionary mechanisms, such as phenotypic plasticity (Funk 2008) or the ability to rapidly evolve (Dlugosch and Parker 2008), also influence the species establishment in the introduced habitat.

The establishment of exotic species and their role in the new community ultimately depend on the interaction among different abiotic and biotic filters (Kraft et al. 2015). The abiotic filter includes the climatic and physico-chemical properties of the habitat which a species need to be able to tolerate physiologically in order to thrive. Many exotic species are generalists that grow under a wide range of environmental conditions in their native range (La Sorte and Pyšek 2009, Casado et al. 2018). Climatic similarity between the native and introduced regions usually facilitates the invasion, but many exotic species thrive in habitats with very different climatic conditions to their native range (Atwater et al. 2018). Regions subjected to extreme conditions of climate and resource availability are less prone to being invaded (Sax 2001). In contrast, mesic and highly disturbed habitats, especially ruderal areas such as road margins or old fields, tend to be among the most invaded habitats (Arianoutsou et al. 2013). Therefore, disturbance is another key abiotic factor that facilitates invasion by releasing resources that may be exploited by opportunistic exotic species, however it can also reduce interspecific competition and

contribute to local exotic-native coexistence by promoting within-site abiotic heterogeneity (Kraft et al. 2015).
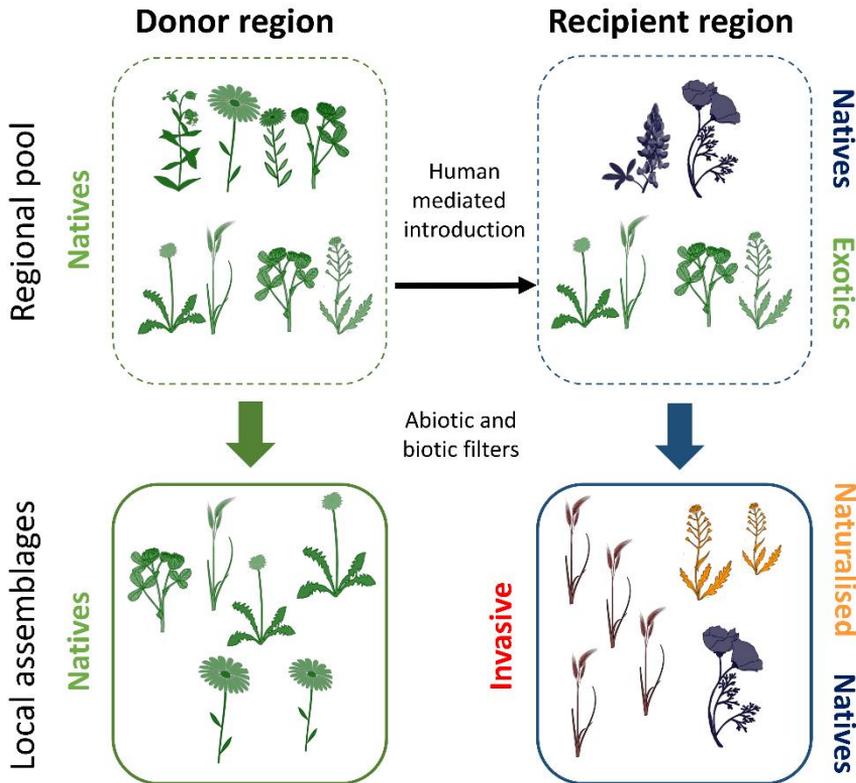
Figure 1. General framework of plant invasions. (a) Species pass geographical barriers assisted by humans. (b) Environmental abiotic and biotic filters, which operate from the regional to the local scale, facilitate or limit the establishment of species with certain characteristics. Some exotic species achieve great fitness and performance in their new ranges, and become invasive.

The biotic filter refers to the complex network of species interactions that occur in the recipient habitat. The physiological tolerance of a species shapes its potential distribution, but it is the native community of plants, herbivores, pathogens, pollinators, etc. which ultimately determines their integration to the new community. Some species have diseases and herbivores keeping them in check in their native range, but once abroad

the lack of natural enemies is key to them reaching great local abundance and spread (Keane and Crawley 2002). For instance, the prickly pear (*Opuntia ficus-indica* (L.) Mill.) is not invasive in its native range in Mexico, where it is extensively used by humans and has specialised herbivores and pathogens, but the absence of natural enemies abroad partially explains its invasion across the globe (Nobel 2002). Interspecific plant competition for resources is another key component of the biotic filter. Some exotic species establish by using empty niches. Other species use the same resources as natives but exploit them more efficiently. For example, eucalyptus outcompete native species by having higher relative growth rates and extracting large amounts of water with deep tap-roots. In a given habitat, some species have greater potential to become invasive than others. In temperate regions, species with shorter life cycles (Kowarik 1995) and efficient mechanisms of seed dispersal (Pyšek and Richardson 2007) tend to overcome the environmental barriers and become invasive quicker than others. Correctly assessing these abiotic and biotic filters is fundamental to identify vulnerable habitats, assess the invasiveness of species and prioritise management actions.

Once established, exotic species can have either similar or different roles in their donor and recipient plant communities. Over the last decade, studies have emphasised the necessity of investigating exotic species across their distribution range as the mechanisms that allow them to establish could be comparable between the native and introduced regions. This biogeographical approach allowed us to assess the relative importance of the intrinsic characteristics of a species' invasive potential versus the extrinsic ecological influences (Colautti et al. 2014). For instance, it has been shown that exotic species tend to maintain their abundance in the donor and recipient communities, whereas only a few achieve greater dominance (Firn et al. 2011, Pearson et al. 2018). Thus, some species have greater potential to dominate the recipient communities, whereas others frequently persist as less abundant. This reflects, to some extent, the importance of a species' own characteristics on invasion. In order to look

into this question, we need precise descriptors to compare plant function between native and exotic species.

Functional traits of exotic plants and assembly of invaded communities

Over the last three decades, tools from functional ecology have widened the traditional taxonomic view to allow a better understanding of the structure of natural communities. One approach in functional ecology is based on the use of species traits to understand their roles in communities, responses to environmental factors, and impacts on ecosystem properties and services (Calow 1987, Keddy 1992a). Functional traits are morphological, physiological and phenological plant attributes that relate to individual performance and fitness (Violle et al. 2007). Functional traits reflect plant ecological strategies and help us understand the relationship between plant performance with their environment, providing information about community assembly processes (Díaz and Cabido 2001, Garnier and Navas 2012). Two evolutionary closely related species might be functionally different, as well as evolutionary distant but functionally similar. Thus, traits allow overcoming the problems that arise from a taxonomic approach by characterising species by their attributes instead of using broader categories of form and function, such as life or growth forms. The use of functional descriptors of plants and communities offer a promising approach for identifying attributes that promote invasiveness (i.e. potential to invade) of exotic species, and contribute to the understanding of the processes of community assembly of invaded communities (Garnier et al. 2016).

Functional strategies are main axes of trait covariation directly related to plant growth, survival and reproduction (Díaz et al. 2016). The LHS scheme of Westoby (Westoby 1998) constitutes one of the first efforts in defining the functional strategy of a plant based on its traits. Westoby proposed that the leaf area (L), height (H) and seed mass (S) inform the

growth-rate of a species and its ability to endure disturbances. The leaf economics spectrum is key axis of functional specialisation (Wright et al. 2004), representing a trade-off (i.e. trait covariation) between relative growth rate and the conservation of resources. Species on the "quick return on investments" end of the spectrum show high photosynthetic rates and leaf nutrient concentration, whereas species toward the "slow return on investments" end show great leaf dry mass and long leaf lifespan. Studies tend to be biased toward leaf traits, as this organ is easily collected and manipulated, however each plant organ (i.e. leaf, stem, seed, roots) offers unique information on plant function and its relationship within the community and the environment. Therefore, it is necessary to measure traits from different plant organs to correctly approximate plant function and community structure (Laughlin 2014).

The functional structure of a community is defined as the diversity and composition of the functional traits of its species (Díaz and Cabido 2001). The functional diversity is a descriptor of the distribution and range of species traits in a community. On the other hand, the functional composition describes the trait values of a community. Taxonomic and functional descriptors of communities offer a useful approach to quantify and explore ecosystem properties, as well as developing better management tools (Garnier et al. 2016). In the last decades, there has been an impressive development of functional indices to characterise community functions and quantify their responses to environmental changes. The most relevant indices used in the present thesis are described below:

i. Community weighted trait mean (CWM): the mean value of a given trait across all species in a community, weighted by species abundance (Garnier et al. 2004). The concept of CWM is based on the mass ratio hypothesis, which predicts that ecosystem processes are mainly determined by the most abundant species (Grime 1998).

ii. Mean functional dissimilarity (MFD): the pairwise functional distance between all species in a community. It is a measure of functional trait diversity, unrelated to species richness, and, in this thesis, weighted by species abundances following de Bello et al. (2016).

iii. Hypervolumes: hypervolumes quantify the amount of trait space occupied by species in a community, as well as their overlap. Hypervolumes use a multidimensional kernel density estimation procedure, and, unlike other metrics of functional richness, define high-dimensional non-continuous shapes (Blonder et al. 2018).

If we examine the stages of plant invasions from a functional perspective, the habitat often constrains trait diversity. Exotic species need to possess a suite of traits to endure environmental conditions. The traits that allow to grow in a given habitat will most likely resemble those of the native residents, therefore we might expect coexisting species in an invaded community to be more functionally similar than a random sample from the regional pool (de Bello et al. 2012). In addition, the interplay between the traits of the exotic species and the native community influence its establishment (Elton 1958). It is assumed that exotic species need to be somehow different to natives, and different combinations of functional traits might allow plants to thrive in a given habitat (de la Riva et al. 2019). Attributes that confer invasive potential are very context dependent, however there are some general patterns that has emerged from previous studies, i.e. rapid resource-use strategies, tissue resistance to physical hazards, great height and clonality (Pyšek and Richardson 2007). These traits can allow exotic species to exploit resources more efficiently than natives, ultimately outcompeting them, or to occupy empty niches by showing different resource-use strategies. Yet, functional differences between exotic and native species might lead to the exclusion of native species as a result of competitive asymmetries (Godoy et al. 2014).

Exotic plant species in the Mediterranean Biome

The Mediterranean Biome includes five world regions characterised by mild wet winters and warm dry summers: California, central Chile, the Mediterranean Basin, the Cape Region, and south-western Australia (Figure 2; Olson et al. 2001). The Mediterranean Biome hosts the second world richest flora (after the wet tropics) with around 49900 species, of which 56% are unique to this Biome (Cowling et al. 1996). Mediterranean ecosystems are characterised by great environmental stability and, as a consequence, the native vegetation of these regions has converged functionally and exhibits traits of resource conservation in response to the highly seasonal climate (Rundel et al. 2016). Sclerophyllous scrublands are the most characteristic vegetation in Mediterranean regions, adapted to withstand summer drought and frequent fires.

Figure 2. The five Mediterranean-climate regions include California, central Chile, the Mediterranean Basin, the Cape Region, and south-western Australia. This map highlights the ecoregion corresponding to Mediterranean forests, woodlands and scrub, according to the World Wildlife Fund (WWF; Olson et al. 2001).

Humans have transformed 40% of the original Mediterranean ecosystems into human- dominated areas (Hoekstra et al. 2005). These changes in land use have compromised native species diversity, directly or indirectly favouring some species over others. The exotic flora of the Mediterranean Biome is mostly composed of generalist herbaceous taxa (Arianoutsou et al. 2013), which have great potential to homogenise the taxonomic composition of communities across the regions where they establish (La Sorte and Pyšek 2009, Winter et al. 2009). These species tend to accumulate in productive and/or highly disturbed habitats, such as wetlands or grasslands (Arianoutsou et al. 2013). Mediterranean ecosystems are traditionally highly managed habitats (Hoekstra et al. 2005) and undisturbed patches of Mediterranean vegetation are rare (Cowling et al. 1996).

The Mediterranean Biome includes various regions of the world with similar climates and land uses, thus it is a good study system to investigate exotic plants while also controlling key factors of the invasion process. Currently, hundreds of exotic species threaten Mediterranean ecosystems (Arianoutsou et al. 2013). The Mediterranean Basin shows the lowest number of exotic species per area (0.4 species per 10^3 km^2), whereas the other four regions accumulate an exotic pool 4.75 to 6.5 times higher (Arianoutsou et al. 2013). In fact, the Mediterranean Basin is home to many herbaceous species naturalised in other Mediterranean regions (Figure 3; Casado et al. 2018). Most of these naturalised species were unintentionally introduced after the arrival of the first Europeans settlers into these territories, and their establishment was probably facilitated by the subsequent intensification of agriculture and farming (Martín-Forés 2017).
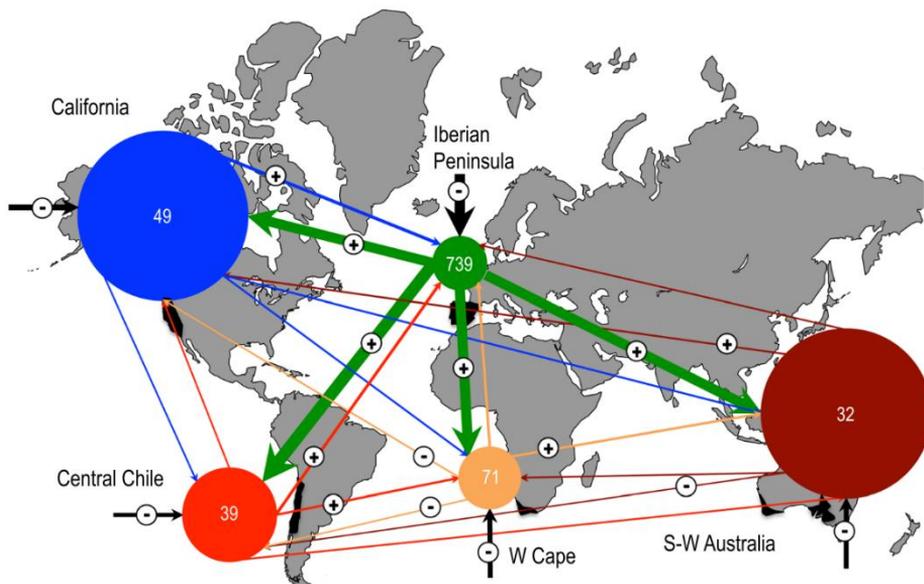
Figure 3. Regions of origin and establishment of unintentionally translocated exotic herbaceous species within the Mediterranean Biome (Casado et al. 2018).

In the early eighteenth century, the establishment of Spanish settlements in California led to the intensification of livestock management and decrease in fire frequency, causing great impacts in the fauna and flora of California original grasslands (Barry et al. 2006, Martín-Forés 2017). The easy accessibility and fertility of California prairies facilitated their transformation (Figure 4; D'Antonio and Vitousek 1992). California native grasslands, initially dominated by perennial bunchgrasses, such as *Nassella pulchra* or *Poa fecunda*, were invaded by deliberately or accidentally introduced European species (Stromberg and Griffin 1996). Some examples of European colonisers are some species of bromes (*Bromus* spp.) and wild oats (*Avena* spp.), medusahead (*Taeniatherum asperum*), or the Kentucky bluegrass (*Poa pratensis*).

The dominance of European species has led to a great taxonomic similarity between the regional species pools of California and European Mediterranean grasslands (Leiva et al. 1997, Casado et al. 2018). California grasslands together with oak savannahs make up to 25% of the

land and hold 90% of plant species included in the California Inventory of Rare and Endangered Species (Barry et al. 2006). Yet, in many grasslands of California, exotic species account for more than 99% of the total plant biomass (Barry et al. 2006), and exert great constraints in the functional structure of coexistent natives (Molinari and D'Antonio 2014).
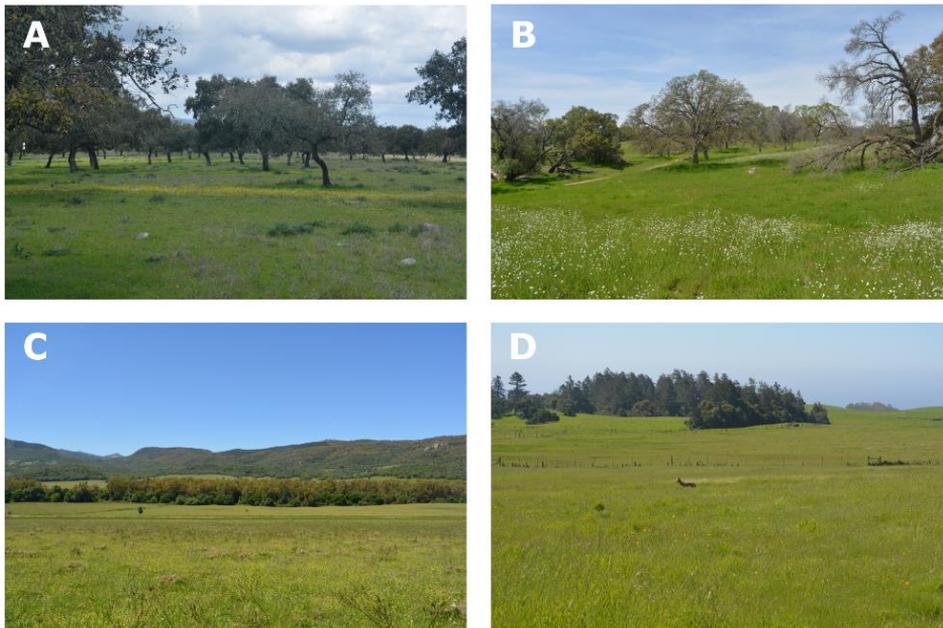
Figure 4. Photographs of grasslands in Spain (a, c) and California (b, d). These habitats are subjected to similar climatic constraints and, after the introduction of herbaceous plant species from the Mediterranean basin to California, share hundreds of species.

The success of European species in California seems to be explained by the novel plant traits of exotic species, which were most likely beneficial in the new scenario of intense herbivory regimes, fire suppression and long drought periods (D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, HilleRisLambers et al. 2010). In this context, the comparison of the functional assembly of exotic species in their donor and recipient Mediterranean grasslands offers an excellent framework to assess the importance of environmental factors and species traits in plant invasions.

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Objectives and structure of the thesis

This thesis takes a biogeographical approach on biological invasions. In particular, it compares the taxonomic and functional assembly of invaded communities across Mediterranean regions at different spatial scales: from plants, to the community and to the Biome. We leverage the historical translocation of plant species across Mediterranean communities to explore three central themes in biological invasions:

(i)   The role of exotic species in the taxonomic and functional structure of their putative donor and recipient communities.

(ii)   The importance of environmental gradients in the functional assembly of exotic species in invaded communities.

(iii) The extent of intraspecific trait variability in native and exotic assemblages of highly invaded communities.

The thesis includes a general introduction, three experimental chapters, and a general discussion and conclusions. The specific objectives of each chapter are:

-    To evaluate the similarity in the taxonomic structure in donor and recipient Mediterranean grassland communities in Spain and California, respectively (**Chapter 1**).

We sampled grasslands of Spain and California as a model system of a major unidirectional introduction of plant species from Europe to North America. In Spain, we measured species composition and abundance in grassland communities of the Parque Natural de Alcornocales near the southern coast of Spain, and the Sierra Norte de Sevilla. In California, we sampled grassland communities near the coast in La Honda and Santa Cruz, and communities of the Central Valley in San Joaquin and Merced.

Sites in both regions we located along a similar coast-inland gradient of precipitation and temperature.

- To determine how community functional structure changes across productivity gradients in donor and recipient grassland communities in Spain and California, respectively (**Chapter 2**).

In the sites described for Chapter 1, we measured eight plant traits related to resource-use and competitive hierarchy of dominant species: height, specific leaf area, leaf dry matter content, leaf nitrogen concentration, isotopic carbon fraction, specific root length, root dry matter content and seed mass. We used these traits to characterise the functional structure of Spanish and California communities and that of native and exotic assemblages across a productivity gradient.

- To analyse the functional strategies of native and invasive species, and intraspecific trait variation, in invaded communities of the five regions of the Mediterranean Biome (**Chapter 3**).

We compared eight plant traits of dominant native and invasive species in eight invaded plant communities of the five Mediterranean regions: an inland and a coastal Banksia woodland in Australia, a coastal grassland in Spain, a serpentine grassland and a coastal sage scrub in California, an acid sands fynbos and renosterveld scrubland in South Africa and a sclerophyll woodland in Chile. The traits measured were related to plant resource-use and acquisition strategies: leaf mass per area, mass-based photosynthetic rate, water-use efficiency, mass-based leaf nitrogen content, photosynthetic nitrogen-use efficiency, mass-based leaf phosphorus content, photosynthetic phosphorus-use efficiency and plant height.

Chapter 1

Plant community assembly in invaded recipient Californian grasslands and putative donor grasslands in Spain

Merced Vernal Pools & Grassland Reserve, California, United States (10th April 2019)

Abstract

The introduction of exotic species to new regions offers opportunities to test fundamental questions in ecology, such as the context-dependency of community structure and assembly. Annual grasslands provide a model system of a major unidirectional introduction of plant species from Europe to North America. We compared the community structure of grasslands in two Mediterranean regions by surveying plots in Spain and in California with similar environmental and management conditions. All species found in Spanish grasslands were native to Spain, and over half of them (74 of 139 species) are known to have colonised California. In contrast, in California, over half of the species (52 of 95 species) were exotic species, all of them native to Spain. Nineteen species were found in multiple plots in both regions (i.e., shared species). The abundance of shared species in California was either similar to (13 species) or greater than (6 species) in Spain. In California, plants considered pests were more likely than non-pest species to have higher abundance. Co-occurring shared species tended to maintain their relative abundance in native and introduced communities, which indicates that pools of exotic species might assemble similarly at home and away. These findings provide interesting insights into community assembly in novel ecosystems. They also highlight an example of startling global and local floristic homogenisation.

Introduction

The introduction and invasion of exotic species across new regions is causing biotic homogenisation of species assemblages at different spatial scales (Sax and Gaines 2003, McKinney 2004, Winter et al. 2009, Bernardo-Madrid et al. 2019). As a result, many exotic species co-occur in habitats outside their native regions (Van Kleunen et al. 2015, Stotz et al. 2020). However, to date only a few studies have assessed whether exotic species are equally abundant, and if pools of exotic species assemble similarly, in their recipient communities as in putative donor communities of their native range (see Firn et al. 2011 and Pearson et al. 2018). Because patterns may arise from local differences in species richness and diversity,

these comparisons need to consider the entire plant community, not just one focal species (Hierro et al. 2005).

Biogeographical comparisons of exotic plant species in their native and recipient communities are important and gaining interest (Hierro et al. 2005, Hejda et al. 2017, 2019, Pearson et al. 2018). A general assumption is that exotic species are more abundant in the introduced region than in the native range (Sounding et al. 2000, Hierro et al. 2005). However, this assumption is probably biased towards the worst invasive species that are known to cause great impacts (Guerin et al. 2018). For instance, many exotic species do not consistently show greater population density, abundance, and/or biomass per area in the introduced range (Parker et al. 2013). Instead, this variation in abundance across exotic species may be predictable from abundance in the native range. In two previous studies, the abundance of exotic species in the native region was positively correlated with abundance in the recipient communities (Firn et al. 2011, Pearson et al. 2018). Such results imply that species attributes might determine the success of exotic species, rather than ecological differences between the native and introduced ranges (Thompson et al. 1995, Firn et al. 2011). However, some species may benefit from ecological differences between the native and introduced regions (e.g., loss of natural enemies) and become invasive pests (Colautti et al. 2014, Pearson et al. 2018). A gap in previous studies is the lack of consideration of the entire native and recipient communities. This is necessary because changes in abundance of native and invasive species within a community are not independent of each other.

Exotic species frequently co-occur in sites with high propagule pressure such as in ruderal or riparian habitats (Arianoutsou et al. 2013), and frequently aggregate forming patches of exotic species (de Miguel et al. 2016, Stotz et al. 2020). This, in addition to individual exotic species maintaining their abundances at home and away, might suggest that pools of exotic species might assemble similarly in the native and introduced communities. A previous global analysis showed that community similarity among invaded sites increased with the number of shared exotic

species (Firn et al. 2011). However, the similarity between two plots can merely increase because of the inclusion of new shared elements. Thus, it is still unclear whether the similarity between the recipient and native communities also increased because exotic species abundances in introduced communities tend to match the abundances of their native communities as the number of shared species increase. The potential underlying hypothesis for this similarity between ranges could reflect a common evolutionary and ecological history of species interactions (MacDougall et al. 2018). In other words, synergism in the interactions among species from the same origin might cause the abundance of exotic species to be more similar to those of their native communities as their richness increase in the recipient communities. We argue that it is necessary to consider the number of shared species to fully understand the similarity between native and recipient communities.

The Mediterranean Biome constitutes an excellent study system to explore community structure and floristic homogenisation across regions, and compare assembly patterns of exotic plant species in donor and introduced communities. There has been an extensive and asymmetric introduction of species from the Mediterranean Basin to all other Mediterranean-climate regions of the world (Arianoutsou et al. 2013), especially of herbaceous species in grasslands (Casado et al. 2018). This pattern is a result of sustained propagule pressure accompanying human migration patterns together with the intensification of agrarian activities with European settlement (Martín-Forés 2017, MacDougall et al. 2018). Currently, up to the 70–80% of the exotic herbaceous flora across regions with Mediterranean-type climates is native to the Mediterranean Basin (Casado et al. 2018). It has been suggested that preadaptation to intense disturbance regimes might explain why many Eurasian coloniser species thrive when introduced to disturbed or managed habitat in new regions (MacDougall et al. 2018). In California, more than two-thirds out of the 975 exotic plant species currently registered in the region are originally from Europe (Rejmánek and Randall 1994, Cal-IPC 2019). In only two and a half centuries, Eurasian species have become so widespread and dominant in

grasslands across the state that there is much debate about the original composition of these grasslands (D'Antonio and Vitousek 1992, Minnich 2008), most probably previously covered by perennial grasslands, oak woodlands, and coastal scrub (Hamilton 1997).

To compare plant community structure and species assembly between donor and recipient communities, we surveyed 120 grassland plots across analogous climate and land use gradients in Spain and California, respectively, to (1) compare local plant species richness, composition, and cover of native and exotic species pools between ranges; (2) test if the abundance of single exotic species in California match that of putative donor communities in Spain; and (3) determine if species within exotic assemblages maintain their abundances across Californian and Spanish communities, and whether it depends on the number of shared species.

We expect introduced species to have a dominant role in both native and recipient communities and a subsequent large community taxonomic similarity between regions. We expect most exotic species to show similar abundances in Californian and Spanish grasslands. However, based on the extensive evidence of the impact of exotic plant species on native species in California (Stromberg and Griffin 1996, Corbin and D'Antonio 2004, HilleRisLambers et al. 2010, Reilly et al. 2020), we hypothesize pest species might achieve greater abundances in the introduced than in putative donor communities. Finally, interactions among species from the same origin may cause the relative abundance of exotic species to be more similar to those of their native communities as their number in the recipient community increase. Thus, we expect community similarity to increase with the number of shared exotic species, and the relative abundance of the exotic species in the Californian plots become more similar to those of the Spanish plots as their number increases.

Methods

Grassland Surveys

From March 2018 to May 2018, we surveyed 60 plots across four grasslands in Spain, and from March 2019 to May 2019, we surveyed 60 plots across four grasslands in California (Figure 1). The four grasslands within a region were at least 6 km apart, and all eight grasslands were located in sites with similar climatic characteristics along a coastal–inland gradient (Table 1, Figure S1). Because soil disturbance influences the establishment of invasive species (D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, Corbin and D'Antonio 2004, HilleRisLambers et al. 2010, Reilly et al. 2020, Stuble and Young 2020), we sampled sites with similar land-use histories for the last 30 years. Specifically, grasslands that had been continuously grazed by wild and domestic ungulates, and avoiding sites with any recent history of burning, ploughing or planting.

In each grassland, we recorded species composition and cover in fifteen (50 by 50 cm) plots situated along a 1 km transect. Plots within a grassland were at least 50 m apart and located avoiding ecotones with adjacent habitats such as woodlands or vernal pools. Cover was visually estimated according to an adapted Braun–Blanquet scale (Martín-Fores et al. 2017): 1 = one or few individuals with cover less than 5%; 2 = one or few individuals with cover less than 25%; 3 = several individuals with cover between 25% and 50%; 4 = several individuals with cover between 50% and 75%; and 5 = several individuals with cover over 75%. Then, we calculated species relative cover abundances at the plot level by dividing the cover of each species by the total sum cover of all species present in the plot.
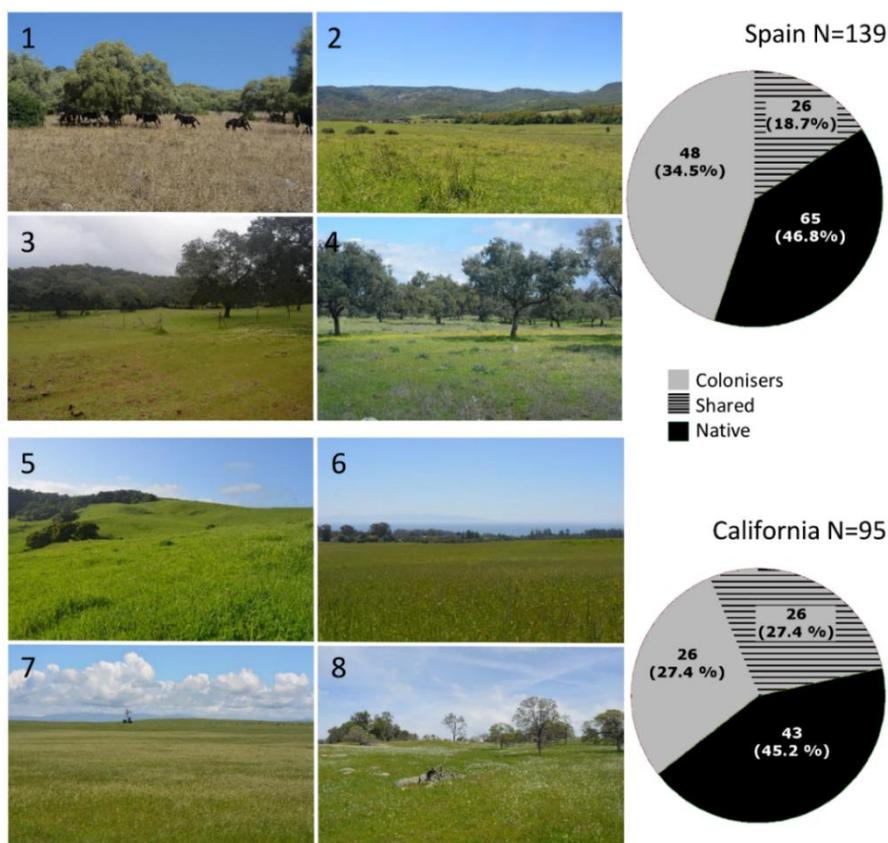
Figure 1. Study grassland sites in the native and the introduced range. Spain (native region): 1. Puerto de la Pared, 2. Montes de Propios, 3. Ventas Quemadas, 4. Navalagrulla. California (introduced region): 5. La Honda Creek, 6. University of California Santa Cruz, 7. Merced Vernal Pools and Grassland Reserve, and 8. San Joaquin Experimental Range. Pie-charts indicate the number and percentage of species in the following categories. Colonisers are Spanish origin species known to be established in California, many coloniser species found in plots of one region were not found in the plots of the other. Shared species are the subset of coloniser species observed in our plots in both regions. Natives refer to non-coloniser native species in Spain and all native species in California. The location of each grassland and species list are available in Figure S1 and Table S1, respectively.

Table 1. Characteristics of the sampled grasslands. Altitude and climate: Mean annual rainfall (MAR), mean annual temperature (MAT), and minimum temperature of coldest month (MCM), extracted from WorldClim (Fick and Hijmans 2017). Soil properties: N concentration, available phosphorus (P), carbon and nitrogen ratio (C:N), organic matter (OM) (mean ± SE), and pH. Information on measurements of soil properties can be found in Table S2. Total species richness and number of species per group. Colonisers are Spanish origin species established in California. Shared species are the subset of colonisers observed in our plots in both regions. Natives refer to non-coloniser native species in Spain and all native species in California.

Region	Grassland	Altitude (m)	MAR (mm)	MAT (°C)	MCM (°C)	N (%)	P (mg/kg)	C:N	OM (%)	pH	Richness	Natives	Colonisers	Shared
Spain	Navalagrulla	300	596	17	4	0.13 ± 0.01	10.70 ± 1.46	12.41± 0.07	2.88 ± 0.16	6–7	63	18	45	19
	Ventas	280	617	17	4	0.13 ± 0.02	7.26 ± 0.95	12.31± 0.52	2.78 ± 0.47	6–7	60	23	37	17
	Montes	180	753	17	7	0.23 ± 0.03	13.72 ± 3.92	12.18± 0.35	4.80 ± 0.77	6–7	53	23	30	11
	Puerto	245	796	16	5	0.17 ± 0.02	8.10 ± 0.79	12.32± 0.87	3.64 ± 0.49	6–7	61	28	33	14
California	San Joaquin	310	519	16	2	0.08 ± 0.01	8.86 ± 3.30	13.01± 0.94	1.80 ± 0.21	6–7	31	17	14	8
	Merced	100	375	16	2	0.23 ± 0.05	4.54 ± 1.00	10.70± 0.49	4.26 ± 1.05	6–7	32	19	13	10
	Santa Cruz	115	769	14	4	0.19 ± 0.02	4.44 ± 1.37	12.18 ± 0.63	3.99 ± 0.35	6–7	31	8	23	14
	La Honda	405	794	13	4	0.28 ± 0.03	18.66 ± 4.16	12.40± 0.68	5.82 ± 0.62	6–7	31	7	24	16

All species we found in Spanish grasslands, and all exotic species we found in California, were native to Spain (Valdés et al. 1987, Calflora 2014). We classified species as "colonisers" if they were species native to Spain and known to be introduced in California. Many coloniser species were not found in plots we surveyed in both regions. Thus, we referred as coloniser "shared" species as those common species we surveyed in both regions. (Figure 1). For statistical analyses, we only considered shared species that appeared in at least three plots per region (19 out of 26 species). Shared species were further separated according to their level of invasion in California into pests and non-pests (Cal-IPC 2019). Pest refers to non-native invasive species which once introduced, they quickly establish, reproduce, and spread, and cause economic or environmental harm (Cal-IPC 2019). The remaining species are referred to as "native," which includes all native species in California grasslands, but only the subset of non-coloniser native species in Spain.

Statistical Analyses

We assessed regional differences in total species richness and diversity (Shannon Index), as well as richness and relative cover of the three different groups of species per plot (native, coloniser, and shared). For this, we added the relative cover of native, coloniser, and shared species within each plot to obtain the proportion of shared, coloniser, and native species per plot, and fitted linear mixed models (LMM) with region as a fixed factor, and grassland as a random effect. We also compared richness and relative cover of native and coloniser species per plot within regions using LMM with origin as a fixed factor and grassland as a random effect. We ln-transformed relative cover to meet assumptions of normality and homoscedasticity of data (Pearson et al. 2018). We analysed species richness using a log link function and a Poisson distribution error.

To explore overall floristic similarities between Californian and Spanish plots, we performed a two-dimensional non-metric multidimensional scaling (nMDS) analysis with Bray–Curtis dissimilarity. We square root

transformed relative cover data to stress the importance of medium abundant and dominant species (Clarke and Green 1988).

To check for changes in the assembly of shared species between regions, we conducted two analyses. First, we compared the abundance of shared species between Californian and Spanish plots. For each shared species, we calculated Hedges'd and bias-corrected 95% bootstrap-confidence interval as a measure of effect size. Hedges'd is an estimate of the standardised mean difference and it is not biased by small sample sizes. An effect size is significantly different from zero when its 95% confidence intervals do not bracket zero. Complementarily, we tested whether regional changes in mean cover of shared species depended on the level of invasion in California (pest vs. non-pest) by fitting LLM with region and level of invasion as fixed factors, and grassland and species as random effects.

Second, we assessed whether pools of shared species assembled similarly (i.e., exotics species maintain their relative abundances within the assemblage) in Californian and Spanish communities, and whether this depends on the richness of the shared pool. We included pairs of plots in Spain and California with two or three species in common (n = 46, only one pair of plots had four species in common). For each pair, we first calculated their similarity as 1−Bray–Curtis Dissimilarity Index (hereafter, observed similarity) as follows:

$$\text{Observed similarity}_{ab} = 1 - \frac{\sum_{j=1}^{J}|n_{aj} - n_{bj}|}{n_{a+} + n_{b+}} \qquad (1)$$

where *a* and *b* refer to a pair of plots. *j* refers to each of the shared species. n_{aj} and n_{bj} depicts the abundance of species *j* in plots *a* and *b*, respectively. n_{a+} and n_{b+} depicts the total cover of species in plots *a* and *b*, respectively. Following Firn et al., we square root transformed the relative cover data prior to calculate the observed similarities to emphasize dominant and medium abundant species (Clarke and Green 1988, Firn et al. 2011).

We later used this information to check two points. First, we calculated the probability of detecting the observed similarities by chance, and whether

it decreased from two to three species. Just for the Californian plot, we created 99 null communities by reshuffling the abundance of its present species, and computed the similarity of the Spanish plot with each of its null Californian pairs (hereafter, null similarity). Then, we calculated the proportion of times that the observed similarity was higher than the null similarities. This value indicates the probability that the observed similarity may be random and that there is no similar assembly mechanism between the Californian and Spanish plots. Our null model is based on the general and global evidence that there are always "abundant" and "rare" species (Calatayud et al. 2020). Thus, we assumed that coloniser species occupy the role of any pre-existing species (i.e., its abundance) and become an abundant or rare species, i.e., new exotic species in a recipient community do not disturb the general and global pattern of species assemblages. To check our assumption, we performed, on our communities, the same analyses as Calatayud et al. (2020) and found the same pattern. Secondly, we assessed whether the similarity between the plots in California and Spain also increases when the plots change from sharing two to three species, but correcting for the fact that the similarity between two plots can merely increase because of the inclusion of new shared species. The goal is to shed light on the presence of synergic effects among coloniser species when assembling in non-native communities. To this end, for each pair of plots with three species in common, we recalculated their similarity after removing each of the shared species from the Californian plot one at a time. We did this by removing the abundance of the given shared species from the numerator of the Bray–Curtis index, but not from the denominator. In that way, we simulate that the focal species is not shared, but it still exists in the community. We later averaged the recalculated similarities in each pair of plots, and compared the resulting values with the observed similarities of pairs of plots that shared two species with an ANOVA. If the average similarity after removing one shared species at a time is greater than the observed similarity of pairs of plots with two species in common, it would suggest that the more species they share, the more similar their relative abundances are compared to their native range.

All statistical analyses were performed with the software R v3.6.1 (R Core Team 2019).

Results

We recorded 139 species in Spain and 95 in California. In Spain, all species were native, of which 74 are known to be naturalized in California, i.e., colonisers (Figure 1). In California, we found 43 native species and 52 exotic species, all of which are native to Spain. Twenty-six species were found in plots of both regions: 15 are classified as non-pest and 11 as pest species (Cal-IPC 2019). Of these 26 shared species, there were 7 grasses (Poaceae) and 19 forbs, most commonly of the families Asteraceae (7 species) and Fabaceae (4 species).

Similarities of Californian and Spanish Grassland Communities

Spanish plots were significantly richer and more diverse than Californian plots (Table 2). In both regions, there were on average five more colonisers than native species per plot (California, native = all native species: $F_{1,115} = 96.98$, $p < 0.001$; Spain, native = non-coloniser: $F_{1,115} = 103.26$, $p < 0.001$). In Californian plots, Spanish coloniser species had four times greater cover than native species ($F_{1,115} = 202.38$, $p < 0.001$); whereas in Spain, coloniser species had twice greater cover than other native species (Spain: $F_{1,118} = 92.65$, $p < 0.001$). In Spain, even without including native coloniser species, there were three more native species per plot than in California, and these other species had twice as much cover per plot in Spain than native species in California (Table 2). The richness and cover of coloniser species was similar between Californian and Spanish plots. There were on average five shared species per plot in both Spain and California, but their cover was twice as high in California as in Spain (Table 2).

Table 2. Results of linear mixed models (LMM) on native and exotic species diversity, richness, and total relative cover (model estimate ± SE) between grassland plots in California and Spain. Colonisers are Spanish origin species established in California. Shared species are the subset of colonisers observed in our plots in both regions. Natives refers to non-coloniser native species in Spain and all native species in California.

Variable (per plot)	California	Spain	df	F	*p*
Total Shannon diversity	2.09 ± 0.07	2.51 ± 0.11	1,6	15.38	0.007
Total richness	11.05 ± 1.05	16.65 ± 1.07	1,6	32.11	< 0.001
Richness natives	2.62 ± 1.25	5.69 ± 1.36	1,6	6.44	0.01
Richness colonisers	7.53 ± 1.13	10.71 ± 1.20	1,6	3.17	0.08
Richness shared species	5.39 ± 1.19	4.89 ± 1.28	1,6	0.16	0.69
Cover natives	17.64 ± 15.54	33.47 ± 23.39	1,6	7.49	0.03
Cover colonisers	81.11 ± 8.03	61.69 ± 11.43	1,6	5.75	0.05
Cover shared species	59.20 ± 11.15	26.57 ± 11.67	1,6	26.89	0.002

Communities segregated between regions (Figure 2). Interestingly, plots in La Honda Creek (California) were more similar to plots from Puerto (Spain) than to plots from San Joaquin and Merced. Communities within each region segregated in the nMDS plots according to their geographic distance (Figure 2).
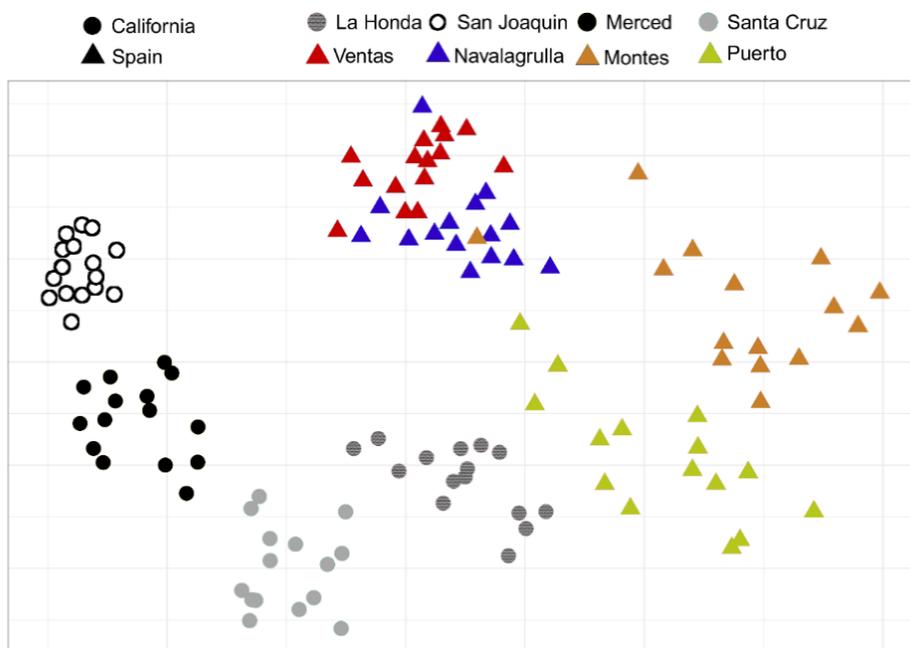

Figure 2. Non-metric multidimensional scaling (nMDS) analysis with species composition and abundance in grassland plots in California (circles) and Spain

(triangles). Analysis was done using Bray–Curtis dissimilarity. Relative cover was square root transformed. Two-dimensional stress was set to 0.17.

Assembly of Shared Species in Californian and Spanish Grasslands

Of the 19 shared species included in these analyses, 6 were more abundant (i.e., mean cover per occupied plot) in Californian plots compared to Spanish plots. These were *Hedypnois rhagadioloides*, *Hypochaeris glabra*, *Bromus hordeaceus*, *Avena barbata*, *Geranium dissectum*, and *Festuca perennis* (Figure 3a). For the other 13 species the effect size was not significantly different from zero, i.e., they were equally abundant in Californian and Spanish plots (effect size estimates in Figure S2). Interestingly, when grouped by their level of invasion in California, shared species categorized as pests had a mean cover nearly two times greater in California, whereas non-pest species had similar mean relative cover in both regions ($F_{3,39.9} = 7.33$, $p < 0.001$; Figure 3b). Within regions, pest and non-pest species had similar relative cover (Figure 3b).

In total, 46 pairs of Californian and Spanish plots met the requirements to be included in the analyses of the assembly of pools of shared species in California and in Spain: 38 plot pairs shared two species (4 Californian plots/15 Spanish plots) and eight pairs shared three species (4/5). Pairs sharing three species were 5% more similar than pairs sharing two species ($F_{1,43} = 18.66$, $p < 0.001$; Figure 4a). The observed similarity between pairs sharing two species was 58.46% ± 36.17% (mean ± SE) greater than expected by chance, while the observed similarity between pairs of plots sharing three species was 86.13% ± 12.98% greater than expected by chance (Figure 4b). When corrected by the number of shared species, the similarities between pairs which shared two or three species were not significantly different ($F_{1,43} = 0.27$, $p = 0.61$; Figure 4c).
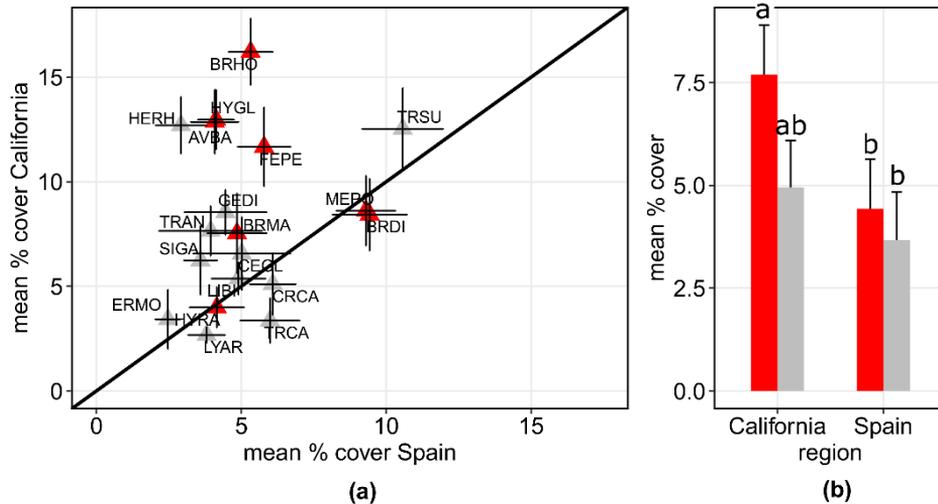
Figure 3. (a) mean relative cover per plot of shared species in grassland plots in California and Spain, with indication of their level of invasion in California: Non-pest (grey) and pest (red). The 1:1 line indicates equal abundance between regions. (b) relative cover of shared species grouped by their level of invasion in California. Different letters on bars indicate significant differences ($p < 0.05$) according to LMM with region and level of invasion as a fixed factor and grassland and species as random factors. Error bars indicate SE. AVBA: *Avena barbata*, BRDI: *Brachypodium distachyon*, BRHO: *Bromus hordeaceus*, BRMA: *Bromus madritensis*, CEGL: *Cerastium glomeratum*, CRCA: *Crepis capillaris*, ERMO: *Erodium moschatum*, FEPE: *Festuca perennis*, GEDI: *Geranium dissectum*, HERH: *Hedypnois rhagadioloides*, HYGL: *Hypochaeris glabra*, HYRA: *Hypochaeris radicata*, LIBI: *Linum bienne*, LYAR: *Lysimachia arvensis*, MEPO: *Medicago polymorpha*, SIGA: *Silene gallica*, TRAN: *Trifolium angustifolium*, TRCA: *Trifolium campestre*, and TRSU: *Trifolium subterraneum*.
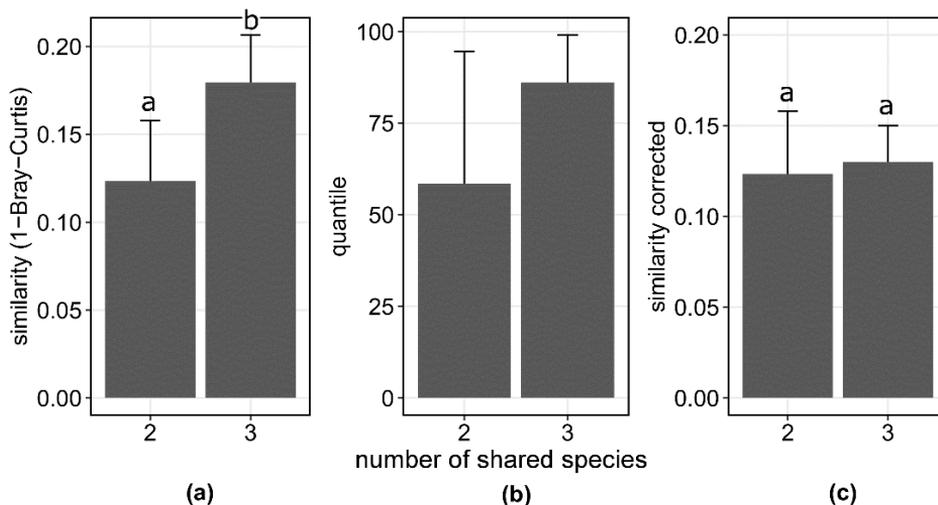
Figure 4. (a) averaged observed similarities between pairs of Californian and Spanish plots grouped by the number of shared species. (b) proportion of null communities with similarities (1–Bray–Curtis) smaller than the observed similarity. (c) comparison of the averaged observed similarities of pairs of plots with two shared species (same as 4a), with the similarity of plots with three shared species, corrected by the number of shared species. Error bars indicate SE. Different letters on bars indicate significant differences ($p < 0.05$).

Discussion

Overall, Spanish grassland communities had greater species richness and diversity than Californian grasslands, as previously reported (Leiva et al. 1997). We show this result is primarily driven by a greater richness and cover of additional native non-coloniser species in Spain, in comparison to the abundance of native grassland species in California. It has been suggested that the cultural landscape of Europe may have promoted high levels of biodiversity through human-mediated niche construction (Eriksson 2013). On the other hand, the low number of native plants in California grasslands may well reflect an impoverished flora relative to its pre-invasion state (Minnich 2008). It is unknown how many native species in California grasslands were locally (even globally) extirpated with the introduction and invasion of exotic plants and grazers from Spain starting in the 1700s (D'Antonio and Vitousek 1992). Grasslands dominated by

annual grasses can be considered a "novel ecosystem" in California; native-dominated perennial grasslands may have been poorly adapted to continuous grazing by livestock (Hamilton 1997, Corbin and D'Antonio 2004). Interestingly, in Spain we did not find introduced plants from California or elsewhere. It has been hypothesized that exotic species might fail to establish in grasslands of the Mediterranean Basin because the herbaceous native flora is highly adapted to intense grazing and management regimes (La Sorte and Pyšek 2009, MacDougall et al. 2018).

As we expected, we found a notable floristic similarity at the regional level. Half of the species found in Spain are colonisers, persisting as introduced species in California. Overall, these findings highlight the marked influence of the Mediterranean Basin as a donor of herbaceous exotic species to other Mediterranean regions (Casado et al. 2018). In line with our results, Martín-Forés et al. also found that coloniser species accounted for half of the total species richness in surveys of Spanish grasslands, and that only a subset of the coloniser species were found in surveys of Mediterranean Chilean grasslands (Martín-Forés et al. 2015). They suggest that this points to failures to establish after translocation. At the plot level, we also found that communities were strongly dominated by coloniser species in terms of both richness and cover. This translated into a high community similarity between regions. For example, La Honda Creek grasslands (California) were more similar in species composition to Puerto, Spain than to other California grasslands. La Honda Creek is close to San Francisco Bay, which is the California bioregion with the greatest number of exotic plant species (Dark 2004). In general, urban and agricultural landscapes are known to be positively correlated to propagule pressure (Chytrý et al. 2008). The success of coloniser species in California grasslands is probably related to several interacting factors, such as a strong propagule pressure since the establishment of Spanish settlements in the 18th century (Rejmánek and Randall 1994), and the simultaneous introduction of agricultural practices traditionally in place in Europe (MacDougall et al. 2018).

Our results support the hypothesis that the abundance of exotic species in their native grasslands is a good indicator of their abundance in the introduced communities (Firn et al. 2011), but that this is also determined by the level of invasion of the exotic species in the introduced range (Pearson et al. 2018). Whereas non-pest species had similar relative cover in California and Spain, pest species were significantly more abundant in California. Interestingly, none of the species was more abundant in Spain. Overall, exotic species in Mediterranean grasslands might maintain their hierarchies, which suggests that they might be equally competitive in their native and introduced ranges (Thompson et al. 1995, Sutherland 2004, Van Kleunen et al. 2010). This emphasizes the role of species attributes, in contrasts to external ecological factors, in influencing their establishment (Colautti et al. 2014, Pearson et al. 2018). However, some species (i.e., pest species) might benefit from the biogeographical translocation and thrive under the ecological characteristics of the introduced region, becoming more abundant (Parker et al. 2013, Colautti et al. 2014). There is extensive evidence of the competitive dominance of these pest species in California grasslands, such as the grasses *Bromus hordeaceus*, *B. madritensis*, *Brachypodium dystachyon*, *Avena barbata*, and the forbs *Hypochaeris* spp. and *Medicago polymorpha* (D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, Leiva et al. 1997, Corbin and D'Antonio 2004, HilleRisLambers et al. 2010, Molinari and D'Antonio 2014, Stuble and Young 2020).

These analyses support our hypothesis that pools of exotic species might assemble more similarly in their native and recipient communities than expected by chance, i.e., species tend to maintain their relative abundances within home and away communities. We also observed that the average similarity between plots increased as they went from sharing two to sharing three species. However, the assembly of shared species in Spain and California was not more similar as the richness of the pool of shared species increased. This lack of evidence is most probably related to our limited sample size. Firn et al. observed that similarities between communities were higher as shared species increased from 10, even

without correcting for shared species richness (Figure S1 in Firn et al. 2011). The absence of a strong effect in our study may be explained by the low numbers of shared species overall and how similarity is calculated. Note that a similarity value of two hypothetical communities sharing one species is higher if the exotic species is more abundant than rare. Because the abundant species has a higher influence on the similarity estimate, it is expected that for communities with the same number of shared species, their similarities will fluctuate less if they have more abundant species (i.e., assuming that species have similar relative cover in the native and recipient communities, as in our system). In addition, if species are introduced stochastically, the probability of containing more abundant species is positively correlated with the number of shared species. We thus expect that communities sharing fewer species will have more variation associated with stochastic processes, making it difficult to detect clear patterns. We encourage future studies comparing communities with a wider range of shared species to better understand exotic species assemblage in the introduced range (Stotz et al. 2020).

Conclusions

Our results are among the first to compare the assembly of plant species in native and recipient communities, using the unidirectional flow of grassland species from Spain to California as a model system. We show that there are consistent differences in species richness and diversity at the regional and plot scale between Spain and California, which underscores the importance of community context when comparing exotic species between their native and introduced ranges (Hierro et al. 2005). Our study supports the claim that exotic species perform in a similar way in a given habitat type regardless the biogeographical region (Firn et al. 2011), and that only the subset that become invasive pests are consistently more abundant (Pearson et al. 2018). Furthermore, exotic species may maintain hierarchies of abundances when they co-occur together outside their native range, an interesting finding in the context of novel ecosystems.

Acknowledgments and funding

Supplementary Material

Table S1. Species found in the surveys. We recorded 139 species in Spain and 95 in California. In Spain, all species were native. Colonisers are Spanish origin species established in California. In California, we found 43 native species, and all exotic species were native to Spain (i.e., colonisers).

species	family	origin	level of invasion in California
Achryrachaena mollis	Asteraceae	Californian native	-
Aegilops geniculata	Poaceae	Exotic	non-pest
Aegilops triuncialis	Poaceae	Exotic	pest
Agrostis pourretii	Poaceae	Spanish native	-
Aira caryophyllea	Poaceae	Exotic	non-pest
Amsinckia menziesii	Boraginaceae	Californian native	-
Anacyclus radiatus	Asteraceae	Spanish native	-
Andryala integrifolia	Asteraceae	Spanish native	-
Anthoxanthum odoratum	Poaceae	Exotic	pest
Arisarum simorrhinum	Araceae	Spanish native	-
Asphodelus ramosus	Xanthorrhoeaceae	Spanish native	-
Avena barbata	Poaceae	exotic	pest
Bellis annua	Asteraceae	Spanish native	-
Bellis perennis	Asteraceae	exotic	non-pest
Beta vulgaris	Quenopodiaceae	exotic	non-pest
Biscutella sp	Brassicaceae	Spanish native	-
Biserrula pelecinus	Fabaceae	Spanish native	-
Brachypodium distachyon	Poaceae	exotic	pest
Briza maxima	Poaceae	exotic	pest
Briza minor	Poaceae	exotic	non-pest
Bromus diandrus	Poaceae	exotic	pest
Bromus hordeaceus	Poaceae	exotic	pest
Bromus madritensis	Poaceae	exotic	pest
Bromus tectorum	Poaceae	exotic	pest
Calandrinia ciliata	Montiaceae	Californian native	-
Calandrinia menziesii	Montiaceae	Californian native	-
Calandrinia sp	Montiaceae	Californian native	-
Carduncellus caeruleus	Asteraceae	Spanish native	-

Carduus bourgeanus	Asteraceae	Exotic	pest
Carduus tenuifolius	Asteraceae	Spanish native	-
Carlina corymbosa	Asteraceae	Spanish native	-
Carlina sp	Asteraceae	Spanish native	-
Carthamus lanatus	Asteraceae	exotic	pest
Castilleja attenuata	Orobanchaceae	Californian native	-
Castilleja campestris	Orobanchaceae.	Californian native	-
Centaurea pullata	Asteraceae	Spanish native	-
Centaurium maritimum	Gentianaceae	Spsnish native	-
Cerastium glomeratum	Caryophyllaceae	exotic	non-pest
Chaetopogon fasciculatus	Poaceae	Spanish native	-
Chamaemelum mixtum	Asteraceae	Spanish native	-
Chlorogalum pomeridianum	Asparagaceae	Californian native	-
Cichorium endivia	Asteraceae	Exotic	non-pest
Clarkia sp	Onagraceae	Californian native	-
Coleostephus myconis	Asteraceae	Spanish native	-
Convolvulus meonanthus	Convolvulaceae	Spanish native	-
Crassula connata	Crassulaceae	Californian native	-
Crepis capillaris	Asteraceae	exotic	non-pest
Croton sp	Euphorbiaceae	Californian native	-
Cynara humilis	Asteraceae	Spanish native	-
Cynodon dactylon	Poaceae	exotic	pest
Dactylis glomerata	Poaceae	exotic	pest
Danthonia californica	Poaceae	Californian native	-
Daucus muricatus	Apiaceae	Spanish native	-
Daucus pusillus	Apiaceae	Spanish native	-
Dichelostemma capitatum	Asparagaceae	Californian native	-
Diplotaxis catholica	Brassicaceae	Spanish native	-
Diplotaxis sp	Brassicaceae	Spanish native	-
Drimia maritima	Asparagaceae	Spanish native	-
Echium plantagineum	Boraginaceae	Exotic	pest
Erodium aethiopicum	Geraniaceae	Spanish native	-
Erodium botrys	Geraniaceae	Exotic	non-pest
Erodium brachycarpum	Geraniaceae	Exotic	non-pest
Erodium cicutarium	Geraniaceae	Exotic	pest
Erodium moschatum	Geraniaceae	Exotic	non-pest
Eryngium tricuspidatum	Apiaceae	Spanish native	-

Eschscholzia californica	Papaveraceae	Californian native	-
Eschscholzia lobbii	Papaveraceae	Californian native	-
Euphorbia akenocarpa	Euphorbiaceae	Spanish native	-
Euphorbia exigua	Euphorbiaceae	Exotic	non-pest
Fedia cornucopiae	Caprifoliaceae	Spanish native	-
Festuca bromoides	Poaceae	Exotic	non-pest
Festuca microstachys	Poaceae	Californain native	-
Festuca perennis	Poaceae	Exotic	pest
Galactites tomentosa	Asteraceae	Spanish native	-
Galium parisiense	Rubiaceae	exotic	non-pest
Galium sp	Rubiaceae	Spanish native	-
Gaudinia fragilis	Poaceae	exotic	non-pest
Geranium dissectum	Geraniaceae	exotic	non-pest
Geranium molle	Geraniaceae	exotic	non-pest
Gilia tricolor	Polemoniaceae	Californian native	-
Gladiolus italicus	Iridaceae	Exotic	non-pest
Hedypnois rhagadioloides	Asteraceae	Exotic	non-pest
Hedysarum coronarium	Fabaceae	Spanish native	-
Hordeum marinum	Poaceae	Exotic	pest
Hordeum murinum	Poaceae	Exotic	pest
Hymenocarpos lotoides	Fabaceae	Spanish native	-
Hypochaeris glabra	Asteraceae	Exotic	pest
Hypochaeris radicata	Asteraceae	Exotic	pest
Juncus bufonius	Juncaceae	Cosmoppolitan native	-
Juncus sp	Juncaceae	Spanish native	-
Lamarckia aurea	Poaceae	exotic	non-pest
Lathyrus angulatus	Fabaceae	exotic	non-pest
Leontodon salzmannii	Asteraceae	Spanish native	-
Leontodon taraxacoides	Asteraceae	exotic	non-pest
Lepidium nitidum	Brassicaceae	Californian native	-
Linum bienne	Linaceae	exotic	non-pest
Logfia gallica	Asteraceae	exotic	non-pest
Lotus conimbricensis	Fabaceae	Spanish native	-
Lotus corniculatus/tenuis	Fabaceae	Exotic	non-pest
Lotus strigosus	Fabaceae	Spanish native	-
Lotus subbiflorus	Fabaceae	Spanish native	-
Lupinus bicolor	Fabaceae	Californian native	-

Lupinus sp	Fabaceae	Californian native	-
Lysimachia arvensis	Primulaceae	Exotic	non-pest
Matricaria discoidea	Asteraceae	Californian native	-
Medicago doliata	Fabaceae	Spanish native	-
Medicago orbicularis	Fabaceae	Exotic	non-pest
Medicago polymorpha	Fabaceae	Exotic	pest
Medicago scutellata	Fabaceae	Exotic	non-pest
Misopates orontium	Plantaginaceae	Exotic	non-pest
Molineriella minuta	Poaceae	Spanish native	-
Muilla transmontana	Themidaceae	Californian native	-
Nassella pulchra	Poaceae	Californian native	-
Ononis sp	Fabaceae	Spanish native	-
Ornithogalum narbonense	Asparagaceae	Spanish native	-
Ornithopus compressus	Fabaceae	Spanish native	-
Ornithopus pinnatus	Fabaceae	Exotic	non-pest
Othospermum glabrum	Asteraceae	Spanish native	-
Petrorhagia velutina	Caryophyllaceae	exotic	non-pest
Phalaris aquatica	Poaceae	exotic	pest
Plagiobothrys fulvus	Boraginaceae	Californian native	-
Plagiobothrys greenei	Boraginaceae	Californian native	-
Plagiobothrys nothofulvus	Boraginaceae	Californian native	-
Plantago bellardii	Plantaginaceae	Spanish native	-
Plantago coronopus	Plantaginaceae	exotic	non-pest
Plantago lagopus	Plantaginaceae	Spanish native	-
Plantago lanceolata	Plantaginaceae	exotic	pest
Plantago serraria	Plantaginaceae	Spanish native	-
Poa sp	Poaceae	Spanish native	-
Polycarpon tetraphyllum	Caryophyllaceae	exotic	non-pest
Ranunculus californicus	Ranunculaceae	Californian native	-
Ranunculus paludosus	Ranunculaceae	Spanish native	-
Raphanus raphanistrum	Brassicaceae	exotic	non-pest
Raphanus sativus	Brassicaceae	exotic	pest
Rapistrum rugosum	Brassicaceae	exotic	non-pest
Rumex acetosella	Polygonaceae	exotic	pest
Rumex bucephalophorus	Polygonaceae	exotic	non-pest
Rumex conglomeratus	Polygonaceae	exotic	non-pest
Rumex pulcher	Polygonaceae	exotic	non-pest

Scolymus hispanicus	Asteraceae	exotic	pest
Scorpiurus vermiculatus	Fabaceae	Spanish native	-
Senecio vulgaris	Asteraceae	exotic	non-pest
Serapias parviflora	Orchidaceae	Spanish native	-
Sherardia arvensis	Rubiaceae	exotic	non-pest
Silene colorata	Caryophyllaceae	Spanish native	-
Silene gallica	Caryophyllaceae	exotic	non-pest
Silybum marianum	Asteraceae	exotic	pest
Sisymbrium officinale	Brassicaceae	exotic	non-pest
Sisyrinchium bellum	Iridaceae	Californian native	-
Sonchus asper	Asteraceae	Exotic	non-pest
Spergularia rubra	Caryophyllaceae	Exotic	non-pest
Stachys arvensis	Lamiaceae	Exotic	non-pest
Stachys ocymastrum	Lamiaceae	Spanish native	-
Stegia trimestris	Malvaceae	Spanish native	-
Stellaria media	Caryophyllaceae	Exotic	non-pest
Stipa capensis	Poaceae	Exotic	pest
Taeniatherum caputmedusae	Poaceae	Exotic	pest
Tetragonolobus maritimus	Fabaceae	Spanish native	-
Thysanocarpus curvipes	Brassicaceae	Californian native	-
Tolpis barbata	Asteraceae	exotic	non-pest
Tragopogon sp	Asteraceae	Spanish native	-
Trifolium angustifolium	Fabaceae	exotic	non-pest
Trifolium arvense	Fabaceae	exotic	non-pest
Trifolium bocconei	Fabaceae	Spanish native	-
Trifolium campestre	Fabaceae	exotic	non-pest
Trifolium cherleri	Fabaceae	Spanish native	-
Trifolium depauperatum	Fabaceae	Californian native	-
Trifolium dubium	Fabaceae	exotic	non-pest
Trifolium fragiferum/hybridum	Fabaceae	exotic	non-pest
Trifolium glomeratum	Fabaceae	exotic	non-pest
Trifolium hirtum	Fabaceae	exotic	pest
Trifolium microcephalum	Fabaceae	Californian native	-
Trifolium obtusiflorum	Fabaceae	Californian native	-
Trifolium pratense	Fabaceae	exotic	non-pest
Trifolium scabrum	Fabaceae	Spanish native	-
Trifolium sp	Fabaceae	Californian native	-

Trifolium squarrosum	Fabaceae	Spanish native	-
Trifolium stellatum	Fabaceae	exotic	non-pest
Trifolium striatum	Fabaceae	exotic	non-pest
Trifolium subterraneum	Fabaceae	exotic	non-pest
Trifolium tomentosum	Fabaceae	exotic	non-pest
Trifolium variegatum	Fabaceae	Californian native	-
Trifolium willdenovii	Fabaceae	Californian native	-
Triteleia laxa	Themidaceae	Californian native	-
Tuberaria guttata	Cistaceae	exotic	non-pest
Vicia benghalensis	Fabaceae	exotic	non-pest
Vicia lutea	Fabaceae	exotic	non-pest
Vicia sativa	Fabaceae	exotic	non-pest
Viola sp	Violaceae	Spanish native	-
Vulpia geniculata	Poaceae	Spanish native	-
Vulpia myuros	Poaceae	exotic	non-pest
Vulpia sp	Poaceae	Spanish native	-

Table S2. Soil properties of studied sites.

We characterised soil nutrient in each grassland by measuring N concentration, ratio C:N ratio, available phosphorus and organic matter. To this end, we collected five soil cores per grassland, of the top 20 cm of soil where nutrient uptake by plants mostly occurs. Then, we dried the samples in the oven, grounded and sieved to 2 mm. We estimated total nitrogen by Kjeldahl digestion, organic matter by the Walkley and Black method, and available phosphorus by the Olsen method. We evaluated if there were differences in soil C:N, P and OM between regions by fitting linear mixed models with region and site as fixed and random factors, respectively. The results did not show any regional significant difference in these soil characteristics between Spain and California. Instead, most variability was explained by differences among grassland plots within the sites.

	Fixed effect	Random effect	Df	F	p	California	Spain
C:N	Region	Grassland	1,6	0.22	0.65	12.07±0.35	12.30±0.49
P	Region	Grassland	1,6	0.05	0.83	9.13±2.58	9.93±3.64
OM	Region	Grassland	1,6	0.22	0.66	3.97±0.67	3.43±0.95
N	Region	Grassland	1,6	0.38	0.56	0.19±0.03	0.17±0.05

Figure S1. Location of sites considered in this study.

Figure S2. Hedges'd for comparison of shared species abundance in Spanish and Californian plots. Pest species are in red, and non-pest species in blue according to CAL-IPC. We indicate mean relative cover per occupied plot ± SE.

Species	Hedges'd	Cover Spain	Cover California
TRCA		5.99 ± 1.02	3.36 ± 1.09
LYAR		3.8 ± 0.64	2.67 ± 0.39
CRCA		6.09 ± 0.79	5.11 ± 1.48
BRDI		9.43 ± 1.29	8.43 ± 1.72
MEPO		9.3 ± 1.02	8.61 ± 1.68
HYRA		4.15 ± 0.94	3.99 ± 0.96
LIBI		4.9 ± 0.93	5.37 ± 0.77
TRSU		10.57 ± 1.4	12.53 ± 1.97
CEGL		5.02 ± 1.67	6.56 ± 1.76
BRMA		4.85 ± 1.02	7.54 ± 1.91
ERMO		2.47 ± 0.44	3.42 ± 1.42
TRAN		3.94 ± 1.79	7.65 ± 1.19
SIGA		3.59 ± 0.57	6.24 ± 1.66
FEPE		5.79 ± 0.91	11.67 ± 1.9
GEDI		4.45 ± 1.41	8.54 ± 1.08
AVBA		4.08 ± 0.82	12.86 ± 1.53
BRHO		5.32 ± 0.77	16.21 ± 1.6
HYGL		4.13 ± 0.62	12.97 ± 1.44
HERH		2.92 ± 0.87	12.7 ± 1.38

< Spain   < California

Chapter 2

Functional assembly of grassland plant species in donor communities in Spain and recipient communities in California

Popcorn flower (*Plagiobothrys* sp.) at San Joaquin Experimental Range, California, United States (2nd April 2019)

Galán Díaz, J., M. Vilà, I. M. Parker and E.G. de la Riva. Functional assembly of grassland plant species in donor communities in Spain and recipient communities in California. (Submitted)

Abstract

A major aim in biological invasions is to understand the role of exotic species in natural communities. So far, most studies have explored the traits of exotic species in the context of the introduced community. Yet functional comparisons of entire assemblages of exotic species in their native and introduced communities have rarely been analysed. This study investigates the functional assembly of exotic species in their native and introduced grassland communities to elucidate the relative importance of traits, environmental factors, and biogeography in determining their establishment. We measured functional structure along coast-inland gradients in the donor and recipient Mediterranean grassland communities in Spain and California respectively. Traits were related to resource use in above- and belowground organs, and reproductive strategy. We explored the relationship between environmental constraints and community function, and we investigated how habitat filtering and niche segregation operate along environmental gradients in native and introduced assemblages as compared to their co-occurring species. There were clear differences in the functional structure of Mediterranean grassland communities both between and within regions related to the environmental gradient. Paradoxically, the most acquisitive communities occurred in less productive sites, highlighting that rapid acquisition and use of resources permit species to cope with environmental stress. In addition, in Spain, trait differences between coloniser and non-coloniser species were mostly absent, and they did not change along the gradient. This might reflect preadaptation of the entire species pool to the agricultural practices that have taken place in Europe for millennia. In California, exotic coloniser species were more acquisitive in their use of resources under favourable conditions, but functionally converged with natives in less productive sites. This indicates that niche differentiation between native and exotic species is subject to the influence of abiotic filters. Our results show that trait comparisons are context dependent and that a correct interpretation of filtering processes in community assembly requires a regional perspective. The comparison of exotic species in their native and introduced

communities emerges as an interesting framework to test the importance biogeographical factors facilitating or limiting plant invasions.

Introduction

Biological invasions by exotic plant species are causing worldwide homogenisation of species pools by reducing variation in species composition across habitats and regions (La Sorte and Pyšek 2009, Arianoutsou et al. 2013). Exotic species that achieve dominance in their introduced ranges may substantially change species interactions, shifting in the functional structure of the recipient plant communities and, consequently, altering community assembly patterns and ecosystem processes (Pyšek et al. 2012, de la Riva et al. 2019). Therefore, a current challenge in ecology is to understand the role of exotic species in community assembly (Gallien and Carboni 2017, Hulme and Bernard-Verdier 2018a). This question requires a comparative biogeographical study of community assembly across donor and recipient communities (Firn et al. 2011).

Species assemble into communities as a consequence of environmental and biotic filters that operate from the regional to the local scale, favouring species that tolerate the environment, find suitable resources, and thrive along with the indigenous organisms (Keddy 1992b, Grime 2006, Kraft and Ackerly 2014). Descriptors of the functional structure of communities (i.e. trait composition and diversity) inform our understanding of these filters because they define the characteristics of species and assemblages that establish under the given ecological constraints (Grime 2006; Kraft and Ackerly 2014). It is frequently assumed that abiotic filtering limits establishment to those species that possess attributes similar to native species (Tecco et al. 2010, Funk et al. 2016). On the other hand, several studies have shown that exotic species as compared to natives tend to display traits related to rapid resource uptake and growth, which points towards functional differences as a primary mechanism of invasion (Pyšek and Richardson 2007, Ordonez et al. 2010, Galán Díaz et al. 2021). Thus, exotic species could establish in a community by excluding functionally

similar competitors; or by exploiting an "empty niche" from the resident species (Macarthur and Levins 1967, Herbold and Moyle 1986). As ecological conditions change from the native to the introduced range, we might expect shifts in the functional structure of plant communities after the introduction of exotic species (Molinari and D'Antonio 2014, de la Riva et al. 2019), revealing the strength and nature of the ecological filters.

Niche differentiation between native and exotic species cannot be assessed in isolation from the environmental constraints of their distributional range because climate, soil fertility and disturbance determine the relative importance of limiting similarity versus abiotic filtering in the assembly of exotic species in recipient communities (Gallien and Carboni 2017, Hulme and Bernard-Verdier 2018a).Within regional climatic and productivity gradients, native and exotic species tend to show similar traits in colder and nutrient-limited sites, but exotics show more acquisitive attributes than natives (taller, higher relative growth rate) in warm and productive sites (Burns 2006, Gross et al. 2013, Henn et al. 2019, El-Barougy et al. 2020). This suggests that, depending on the environmental constraints, attributes that make exotic species successful may either overlap with those of the recipient community or increase the variation in the functional structure of the recipient communities (de la Riva et al. 2019). However, many of these assertions remain speculative. We argue that a comparative approach of the assembly patterns of exotic species in their donor and recipient communities is crucial to understand and even predict their performance in the introduced areas.

Mediterranean grasslands are an excellent study system to explore this biogeographical framework of functional community assembly. Over the last four centuries, there has been a mostly unidirectional introduction of herbaceous species from the Mediterranean Basin to other Mediterranean regions (Leiva et al. 1997, Casado et al. 2018). In California, herbaceous species from the Mediterranean Basin account for 672 out of the 975 exotic plant species established in the region (Rejmánek and Randall 1994). Here, we leverage this historical introduction of plants to assess the degree to which exotic species assemble in recipient communities in parallel to their

putative donor communities. We measured eight functional traits for 208 herbs in grassland communities along coastal-inland transects in California and Spain to (i) compare how the environment conditions shape the functional structure (i.e. trait composition and diversity) of donor and recipient communities; and (ii) quantify the relative contribution of abiotic filtering and niche differentiation on community assembly between exotic coloniser species and coexisting species in both ranges. Because in grassland communities, exotic species tend to maintain similar abundance hierarchies between native and introduced ranges (Firn et al. 2011, Pearson et al. 2018, Galán Díaz et al. 2020), we first hypothesize that similar functional structure will be observed between communities in Spain and California along the environmental gradient. In addition, the extensive influence of thousands of years of agrarian and farming practices in Spain likely led to suites of traits in Spanish species related to rapid resource-use strategies that confer a competitive advantage in productive and disturbed ecosystems (MacDougall et al. 2018). Consequently, our second hypothesis is that in recipient communities in California, the functional structure of exotic and native species will likely differ because native species are not as adapted to intense farming and grazing; whereas in donor communities in Spain, coloniser species that invaded California are expected to have a similar functional structure to the non-coloniser species, reflecting adaptation to the same disturbance regimes.

Methods

Grassland vegetation surveys

From March 2018 to May 2018, we sampled 60 vegetation plots across 4 sites in Spain; and from March 2019 to May 2019, we sampled 60 vegetation plots across 4 sites in California (Table S1). Sites were located along a coast-inland transect which reflected a gradient of mean annual rainfall (MAR) and temperature annual range (TAR). MAR and TAR are key drivers in the assembly of herbaceous communities in Mediterranean regions (Martín-Forés et al. 2015). Because soil disturbance, fire and restoration treatments alter the ratio of native and exotic species in

Mediterranean grasslands (Stromberg and Griffin 1996), we selected grasslands that had been moderately grazed by wild and domestic ungulates, but had not been burned, ploughed or planted, at least during the last 30 years. Additionally, we quantified soil properties by collecting five cores of the top 20 cm of soil along the vegetation transect. Samples were dried in the oven, then ground and sieved to 2 mm. We estimated percentage total nitrogen (N) by Kjeldahl digestion, organic matter (OM) by the Walkley and Black method, and available phosphorus (P) by the Olsen method. We averaged the soil variables within sites.

In each site, we collected plant species composition and cover in fifteen plots (0.25 m^2) situated along a 1 km transect. Plots within a site were at least 50 m apart. Species cover was visually estimated using five classes: 1: cover $< 5\%$; 2: cover between 5% - 25%; 3: 25% - 50%; 4: 50% - 75%; 5: $> 75\%$. These values were scaled into relative cover abundances. We classified species as "colonisers" if they were species native to Spain and known to be introduced in California (Galán Díaz et al. 2020). In California, all the exotic species we found were colonisers from Spain (Calflora 2014). In Spain, all the species we found were native to Spain (Valdés et al. 1987), and we refer to them as coloniser or non-coloniser species depending on whether they are established as exotics in California.

Functional traits measurements

We identified the species that contributed to 90% of cumulative cover of plots (ranging from 31 to 63 species per site) and measured 8 plant traits for each species (Table 1). Each trait was estimated from a sample of randomly collected 10 individuals per species per site, and measured according to the handbook for standardised measurement of plant functional traits (see Figure S1). The chosen above and below-ground traits reflect orthogonal axes of plant functioning related to resource acquisition, and reproductive potential (Garnier et al. 2016). In total, traits were measured in 127 species in Spain and 81 species in California, 248 species-site combinations in Spain and 120 species-site combinations in California. Some physiological and root attributes were missing from the final

database (5.47% of the cells) due to the difficulty of collecting enough material to obtain reliable measurements. Missing data reduces sample size and introduces bias (Divíšek et al. 2018), thus, if the missing trait was available for the same species in other sites, we used the mean trait value for that species across sites; and if the missing trait belonged to a site specific species, we used the mean trait value of that genus or family.

Table 1. Traits measured in plant species from Spanish and California grasslands with indication of their related function.

Trait	Abb.	Units	Related function
Specific Leaf Area	SLA	cm^2/g	Resource acquisition rate and conservation, photosynthetic rate, relative growth rate
Leaf Dry Matter Content	LDMC	mg/g	Leaf tissue density, resistance to physical hazards, stress tolerance
Leaf Nitrogen Content	LNC	%	Photosynthetic rate
Isotopic Carbon Fraction	$\delta^{13}C$	‰	Integrated water use efficiency
Specific Root Length	SRL	cm/mg	Resource acquisition rate and conservation, relative growth rate
Root Dry Matter Content	RDMC	mg/g	Root tissue density, resistance to physical hazards, drought resistance
Height		cm	Dispersal distance, position in the light gradient
Seed Weight		g	Seedling survival and establishment

Statistical analyses

We compared the functional structure of Spanish and California plots, and coloniser / non-coloniser and exotic / native species assemblages, with two complementary metrics: community weighted trait means (CWM) and mean functional dissimilarity (MFD). CWM is the average value of a trait across all the species present in the plot and weighted by their abundances (Garnier et al. 2016). CWM characterizes the most frequent trait values of a community and is based on the mass ratio hypothesis, which predicts that

the most frequent traits determine ecosystem processes (Garnier et al. 2016). MFD is the mean pairwise functional distance between all species in a community, weighted by species abundances. MFD is a functional diversity index, unrelated to species richness (de Bello et al. 2016). MFD was calculated with the function 'melodic' (de Bello et al. 2016).

In order to reduce the number of environmental variables and their collinearity and to characterize the environmental gradient of the coast-inland transects with a single composite variable, a PCA was performed with the variables soil nitrogen (N), soil phosphorus (P), soil organic matter (OM) and the climatic variables mean annual precipitation (MAR) and temperature annual range (TAR). These environmental variables were largely correlated and all of them had high absolute loadings in the first axis (PC1, 67.2% of the total variation explained; Figure S2). PC1 indicated a clear gradient from inland to coastal sites, with an increasing soil nutrient concentration and MAR and decreasing TAR. Because soil fertility, MAR, and TAR are stress factors which limit photosynthesis and the plant growing season in Mediterranean regions (Fernández-Alés et al. 1993), we used the scores of PC1 as a proxy for a productivity gradient in further analyses.

To construct the functional structure of the studied grassland communities, we first performed a principal component analysis (PCA) with the CWM of the eight traits for the 60 plots from Spain and the 60 plots from California. For each region, we ran linear models with the first two principal components as response variables and the productivity gradient as the predictor variable. In addition, we used a null model to determine whether trait diversity of communities is the result of a non-random selection of species from the regional pool of species based on their traits, reflecting environmental filtering (Cornwell and Ackerly 2009). For each plot, we recalculated MFD 499 times after shuffling species labels in the original plot × species abundance matrix, and retained the mean across randomizations (de Bello et al. 2012). We included the entire regional pool of species in the randomizations because all species are known to occur across each region, and maintained the observed species richness within

plots to account for differences in local diversity within sites. If there are environmental constraints filtering plant traits from the regional pool, we might expect communities to be less functionally diverse than expected by chance, i.e. the observed MFD would be less than MFD obtained from the randomizations (i.e. functional convergence). In contrast, an observed MFD equal to or greater than the randomization suggests random assembly of species or limiting similarity (i.e. functional divergence), respectively. To determine whether trait convergence or divergence is explained by productivity, we ran a linear model with the difference between the *observedMFD* and the *nullMFD* as the dependent variable.

To assess the differences in the functional structure between coloniser and non-coloniser species in the donor communities, and coloniser and native species within the recipient communities, we investigate, for each region independently, changes in the CWM and MFD across to the productivity gradient for each species pool. For each region, we first fitted a linear model with the syntax *MFD ~ origin × productivity* to assess whether MFD depends on species origins and the productivity of the site. Then, we followed the method proposed by Gross et al. (2013) to assess the effects of niche partitioning and habitat filtering in the assembly of native, coloniser and non-coloniser species along the productivity gradient. We first assessed whether CWMs differ between coloniser and native (or non-coloniser) species, and whether they change along the productivity gradient, by fitting a linear model with the syntax *CWM ~ origin × productivity* for each trait and region. We then explored whether the observed trait differences reflect patterns of trait convergence or divergence. For each trait and plot, we calculated the functional difference (FD) between colonisers and other species as the CWM difference between the two species pools divided by the mean difference across plots within the region (eqn 2 in Gross et al. 2013). In addition, for each region, we compared the observed FD against null models to determine whether it differs from the random expectation. For this, we randomized species abundances within columns 99 times in the plot × species abundance matrix and, for each randomization, calculated FD between colonisers and

others per trait and plot. This maintains species abundances within regions but allows changes in species richness within plots. Finally, for each plot, we compared the observed FD against the 95% confidence intervals of the null model to determine whether it reflects niche differentiation (coloniser and other species are more different than expected by chance) or functional convergence (coloniser and other species are more similar than expected by chance). We ran a linear model with the syntax *FD ~ productivity* to explore whether productivity determines niche partitioning and habitat fitlering. FD was log-transformed to meet assumptions of normality and homoscedasticity of residuals.

All statistical analyses were performed with the software R v4.0.3 (R Core Team 2020).

Results

Functional structure of grassland communities in Spain and California

The PCA of the community weighted trait means reflected that trait differences among plots are related to site differences. The first two principal components explained 65.32% of the total variance (Figure 1). Our results indicated a clear orthogonal segregation between regions. Spanish plots segregated significantly along PC1 ($F_{3,56} = 85.0$, $p < 0.001$), which accounted for the covariation of SRL_{CWM}, $\delta^{13}C_{CWM}$ and Seed weight$_{CWM}$; while California plots segregated significantly along PC2 ($F_{3,56} = 109.5$, $p < 0.001$), which represented a positive covariation of Height$_{CWM}$, $LDMC_{CWM}$ and $RDMC_{CWM}$.

In Spain, the productivity gradient explained 75.83% of the community functional variance of PC1 ($F_{1,58} = 181.98$, $p < 0.001$; Figure 2a), and 24.20% of the variance of PC2 ($F_{1,58} = 18.52$, $p < 0.001$; Figure 2b). Communities in less productive sites showed higher SRL_{CWM} and SLA_{CWM}, whereas plots of wetter fertile sites had greater $\delta^{13}C_{CWM}$ and Seed weight$_{CWM}$. In California, whereas the productivity gradient did not have a significant effect on PC1 ($F_{1,58} = 1.67$, $p = 0.20$; Figure 2c), we found a quadratic relationship between the productivity gradient and PC2,

explaining 84.40% of the variance, such that the least productive site supported communities with the least conservative strategy, and the most conservative strategy was in an intermediate site ($F_{1,58} = 154.29$, $p < 0.001$; Figure 2d).
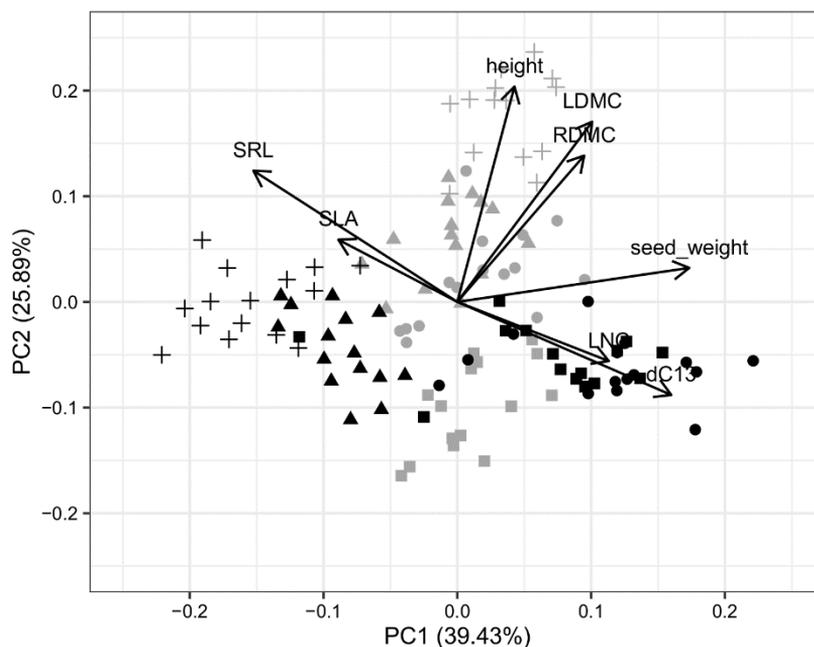

Figure 1. Principal Component Analysis of the CWM of Spanish and California grassland communities. Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda. Sites in Spain are mostly differentiated along PC1, while sites in California are differentiated along PC2.

In addition, MFD values mostly fell below the null expectation (Figure 3), which supports evidence from the PCA that strong habitat filtering is taking place at the regional scale. That is, in both regions, species that co-occurred in the same plot tend to be more functionally similar than expected by chance (49 out of 60 plots in California; 58 out of 60 in Spain). In Spain, species within a community were functionally more similar than expected by chance regardless the productivity of the site ($F_{1,58} = 2.09$, p = 0.154; Figure 3a). While in California, there was a positive linear

relationship between productivity of the site and trait convergence ($F_{1,58} = 151.44$, $p < 0.001$; Figure 3b).
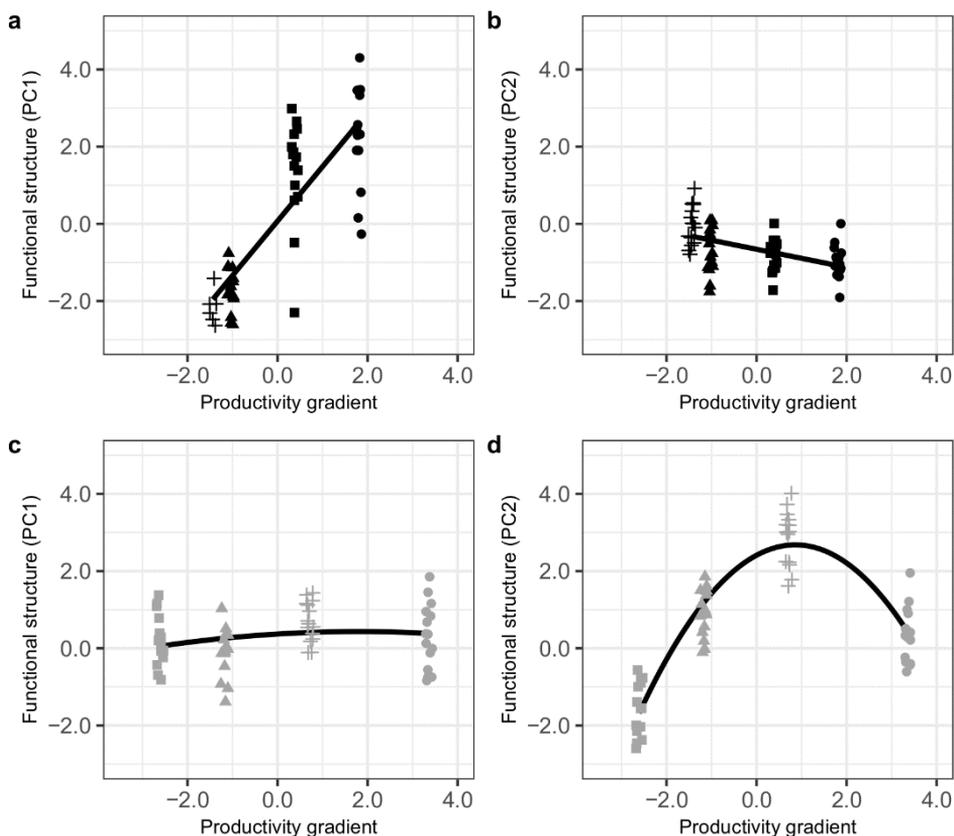

Figure 2. Changes in the functional structure of Spanish and California grassland communities (Figure 1) along the productivity gradient indicated by PC1 (a) and PC2 (b) in Spain and PC1 (c) and PC2 (d) in California. Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda.

Functional structure of coloniser, non-coloniser, and recipient native assemblages along the productivity gradient

In both regions, the assemblage of coloniser species was functionally more diverse than that of the other coexisting species (Spain: colonisers$_{MFD}$ = 3.07±0.07, non-colonisers$_{MFD}$ = 2.49±0.09; California: colonisers$_{MFD}$ = 2.91±0.09, natives$_{MFD}$ = 2.19±0.09).
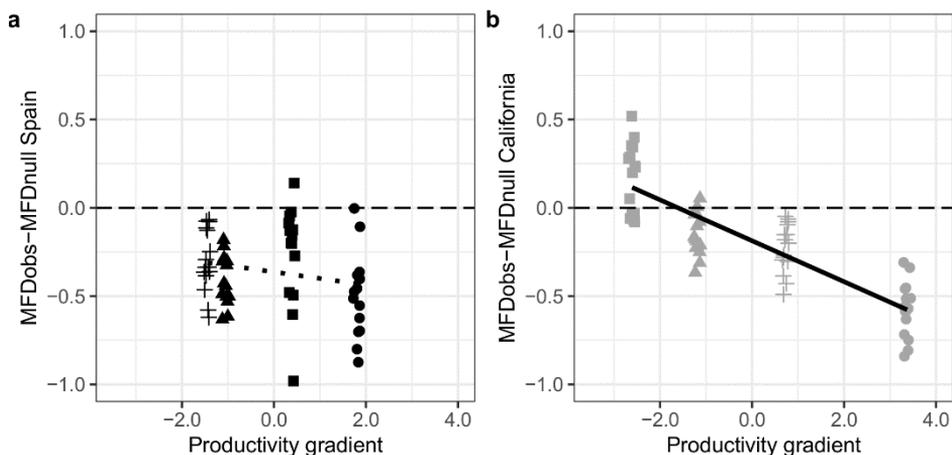
Figure 3. Functional assembly of donor and recipient grassland communities in (a) Spain and (b) California compared to the random expectation. An observed MFD less than the null MFD reflects functional convergence and suggests the environment is filtering traits from the regional pool; an observed MFD near the null MFD suggests random assembly; and an observed MFD greater than the null MFD suggests limiting similarity (i.e. functional divergence). Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda.

In addition, there were significant differences in the response of the CWM of colonisers and other species to productivity (native species in California, non-coloniser species in Spain) between regions. In Spain, coloniser assemblages had greater SLA_{CWM}, $\delta^{13}C_{CWM}$ and $Height_{CWM}$ than other species (Table 2). Also, all CWM showed a significant relationship with the productivity gradient. Particularly, SLA_{CWM} and $\delta^{13}C_{CWM}$ of native and coloniser species decreased significantly with productivity. This indicates that no significant changes in niche segregation patterns occur between both groups of species (Figure 4 and Figure S3).

Table 2. Changes in the functional structure of Spanish and California grassland communities (CWM and MFD) in response to species origin and productivity. For each trait and region, we ran a linear model with the following syntax: CWM ~ origin × productivity. Asterisks denote significant terms are significant: * $p < 0.5$, ** $p < 0.01$, *** $p < 0.001$. See Table 1 for trait identity.

Funct. structure	Region	$F_{3,116}$	p	R^2	F_1 origin	F_1 productivity	F_1 origin × productivity
SLA$_{CWM}$	Spain	21.47	0.000	0.36	28.73***	34.74***	0.96
LDMC$_{CWM}$	Spain	10.66	0.000	0.22	12.40***	12.60***	6.99**
SRL$_{CWM}$	Spain	57.65	0.000	0.60	0.26	172.05***	0.62
RDMC$_{CWM}$	Spain	3.05	0.031	0.07	1.61	7.15**	0.39
$\delta^{13}C_{CWM}$	Spain	71.29	0.000	0.65	21.64***	191.72***	0.51
LNC$_{CWM}$	Spain	15.21	0.000	0.28	0.33	38.60***	6.72*
height$_{CWM}$	Spain	7.64	0.000	0.17	8.90**	4.48*	9.44**
seed weight$_{CWM}$	Spain	42.84	0.000	0.53	0.47	125.81***	2.23
MFD	Spain	12.89	0.000	0.23	38.65***	0.02	0.00
SLA$_{CWM}$	California	25.63	0.000	0.40	45.21***	9.49**	22.18***
LDMC$_{CWM}$	California	12.87	0.000	0.25	34.71***	0.94	2.98
SRL$_{CWM}$	California	4.34	0.006	0.10	12.83***	0.18	0.01
RDMC$_{CWM}$	California	24.61	0.000	0.39	47.36***	9.17**	17.29***
$\delta^{13}C_{CWM}$	California	12.66	0.000	0.25	14.85***	10.49**	12.65***
LNC$_{CWM}$	California	8.15	0.000	0.17	0.65	3.12	20.67***
height$_{CWM}$	California	9.97	0.000	0.21	6.40*	6.72*	16.80***
seed weight$_{CWM}$	California	13.16	0.000	0.25	23.12***	3.75	12.62***
MFD	California	20.04	0.000	0.37	5.19***	0.34	4.59*

In contrast, in California, we found significant differences between native and coloniser species for all traits except for LNC (Table 2). Also, there were significant interactions between origin and productivity for SLA$_{CWM}$, RDMC$_{CWM}$, $\delta^{13}C_{CWM}$ and Height$_{CWM}$. Colonisers shifted SLA$_{CWM}$, $\delta^{13}C_{CWM}$ and RDMC$_{CWM}$ along the productivity gradient, whereas natives decreased in SLA$_{CWM}$ (Figure 5 and Figure S4). This results in an increasing niche segregation of their acquisitive (i.e. SLA and $\delta^{13}C$) and resistance (RDMC) strategies with productivity. The opposite pattern is

observed for plant height, with functional convergence occurring in most
productive sites.
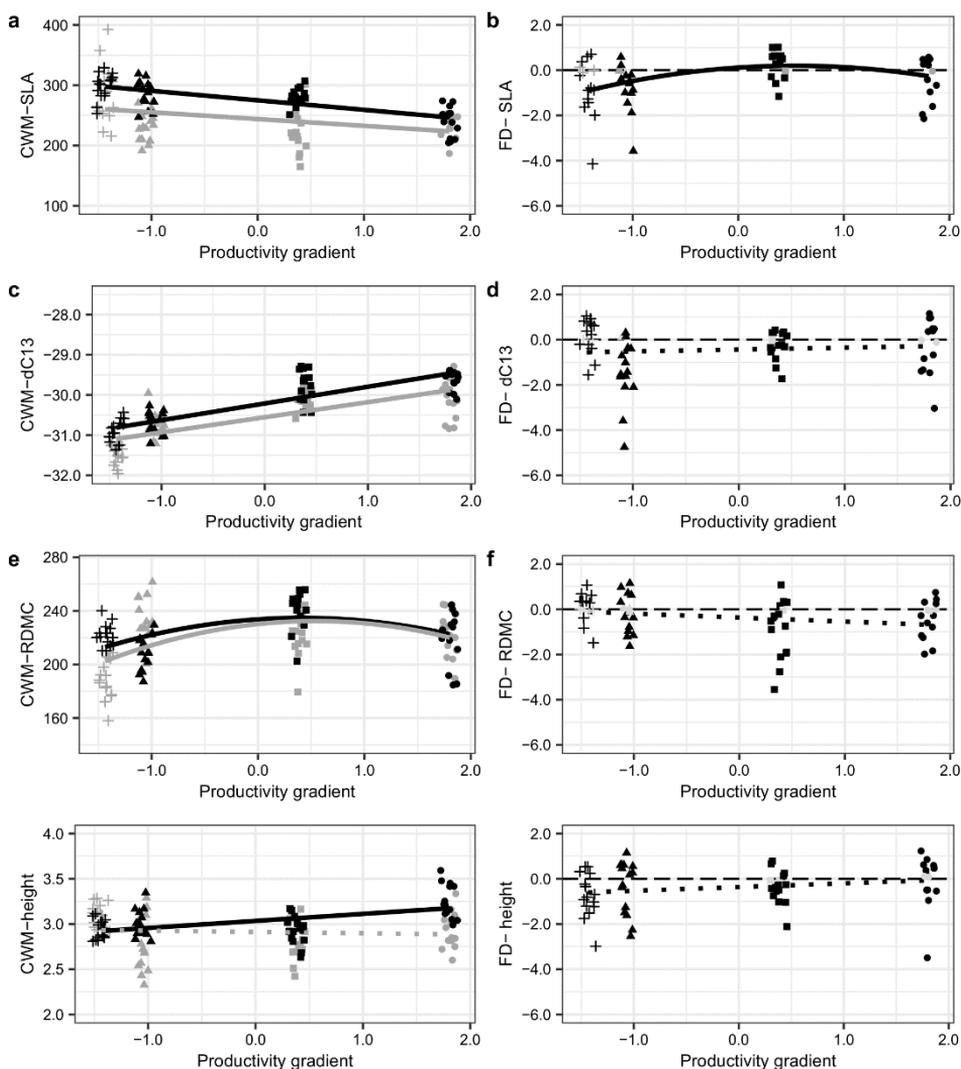
Figure 4. Effects of niche partitioning and habitat filtering in Spain along the
productivity gradient. Left column shows changes in CWM of coloniser (black)
and non-coloniser (grey) species assemblages along the productivity gradient.
Right column shows functional differences between coloniser and other species:
black dots over zero indicate niche differentiation; black dots below zero indicate
functional convergence; grey dots indicate random assembly. Solid lines indicate

significant linear relationships (p < 0.05). Results of other traits can be found in Appendix S4. Sites: + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes.
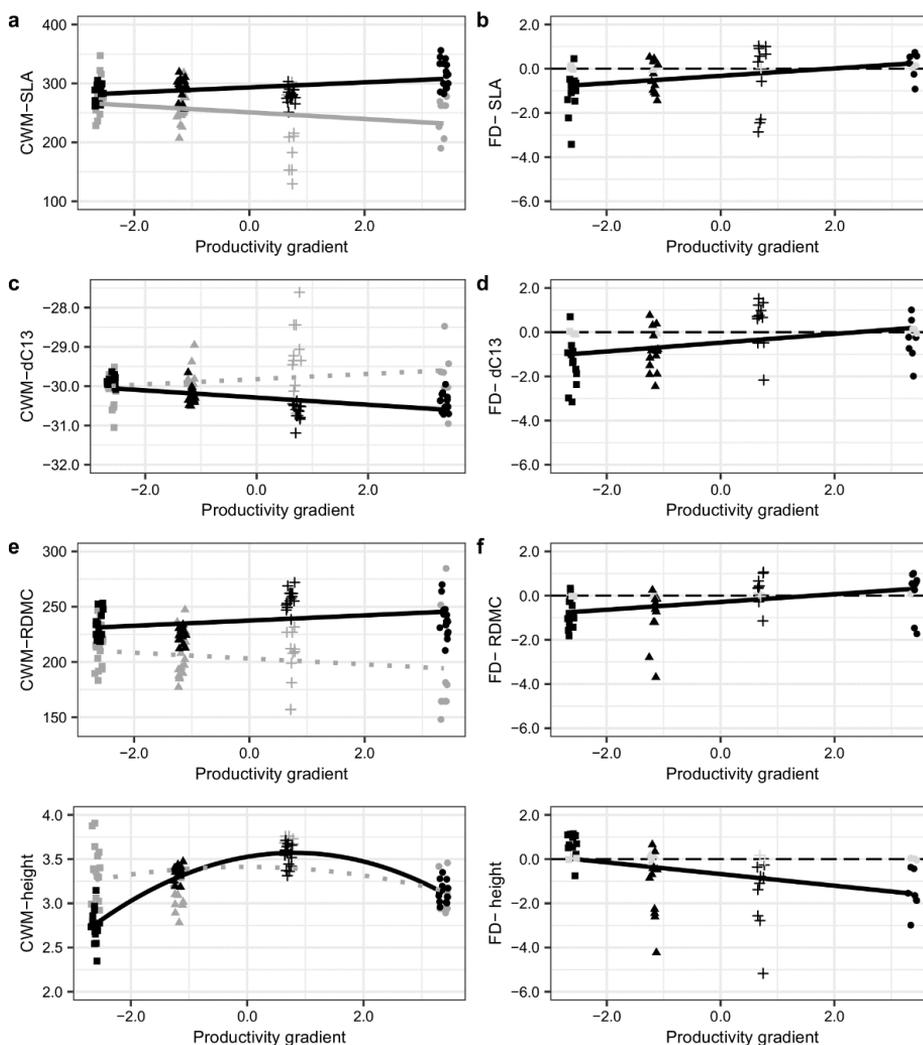

Figure 5. Effects of niche partitioning and habitat filtering in California along the productivity gradient. Left column shows changes in CWM of coloniser (black) and non-coloniser (grey) species assemblages along the productivity gradient. Right column shows functional differences between coloniser and native species: black dots over zero indicate niche differentiation; black dots below zero indicate functional convergence; grey dots indicate random assembly. Solid lines indicate significant linear relationships (p < 0.05). Results of other traits can be found in Appendix S5. Sites: ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda.

Discussion

Functional structure of grassland communities in Spain and California

We have described clear differences in the functional structure of Mediterranean grassland communities, not only between regions, but also among sites. Contrary to our first hypothesis, we found that changes in the trait composition along the productivity gradient differed between the two regions. This suggests that different functional patterns of assembly exist in California and in Spain, despite the high number of species shared by both regions (Galán Díaz et al. 2020). We identified two orthogonal axes of functional variation related to the biogeographical segregation of the study sites: putative donor grasslands in Spain segregated along the first axis mainly by the trade-offs in their resource uptake strategies (i.e. SRL, SLA and δ^{13}C) and reproductive effort (seed mass); while recipient grasslands in California segregated along the second axis as a result of variation in plant height, LDMC and RDMC.

It is frequently assumed that high SLA and SRL facilitate rapid acquisition of resources and consequently faster growth rate, which is a common strategy in productive Mediterranean habitats (de la Riva et al. 2018); while high δ^{13}C and seed mass have been interpreted as a successful conservative strategy to cope with environmental stress such as Mediterranean summer drought (de la Riva et al. 2018, Prieto et al. 2018). However, in contrast with the traditional expectations of the economic spectrum model (ES, Wright et al. 2004; Reich 2014), we observed stress tolerant traits were more common in the most productive environments. This apparent paradox in our dataset can be explained by an underlying pattern in life history of the dominant species. The most productive areas (with higher precipitation and nutrient concentration) were dominated by perennial species, while annual species dominated the communities at the opposite end of the gradient. Perennial species in Mediterranean regions have been shown to be more dehydration tolerant than annuals (Volaire et al. 2009), thanks to their water use efficiency (higher δ^{13}C; Prieto et al. 2018) and higher seed mass, which may enhance seedling competition in

productive environments (Murray et al. 2005). This inversion of the ES has been previously observed in arid and semi-arid regions (Carvajal et al. 2019, de la Riva et al. 2021). Thus, herbaceous plants in Mediterranean regions can survive the most stressful seasons (i.e. summer drought conditions) by having a reduced metabolism (Volaire et al. 2009) or an annual lifespan, persisting in dry and low productive grasslands by maximizing nutrient capture and growth rate and showing an opportunistic behaviour of drought-avoidance. This "opportunistic" resource uptake strategy may enhance the colonisation of dry and nutrient-poor habitats with high seasonal fluctuation (Querejeta et al. 2018), such as Mediterranean grasslands.

In California, the community functional response to productivity involved shifts in plant stature and tissue resistance, the dominant species being taller, with long-lived tissues (high leaf and root dry matter content). This pattern also suggests that species from nutrient poor sites opt for an acquisitive rather than conservative strategy of resource use. Yet, the relationship between this trend in trait variation and the productivity gradient was quadratic. We suspect that this is likely due to the more complex interplay between native species and exotic species in the recipient communities, as we will discuss later.

In both regions, habitat filtering constituted a main factor structuring functional composition along the environmental gradient. This is what we expected to find, because trait convergence is common when comparing communities across large spatial scales (de Bello et al. 2012), which supports that changes in productivity frequently pair with changes in community traits related to carbon storage, nutrient cycling and litter decomposition, as well as anti-herbivore defence (Grime 2006). Yet comparing data from Spain and California also revealed certain differences. Functional convergence in the Spanish communities occurred along the entire gradient, which supports the key role of habitat filtering in the assembly of the donor grasslands. By contrast, communities in the least productive site in California showed greater functional divergence than expected by chance, which resulted in trait convergence increasing with

productivity. This suggests that the degree of habitat filtering increased with productivity, a pattern previously reported in other temperate and Mediterranean grasslands (Pakeman et al. 2011). Although the relationship between productivity and functional diversity is complex and context dependent (Carmona et al. 2012, Bernard-Verdier et al. 2012), Pakeman et al. (2011) argued that a reduction in trait diversity with increased productivity extends Grime's predictions, such that as productivity increases, its filtering effects on community composition also increase.

Functional structure of coloniser, non-coloniser, and recipient native assemblages along the productivity gradient

The functional structure of coloniser and other species differed most markedly in the recipient communities in California, supporting our second hypothesis. In both regions, coloniser species assemblages showed on average higher values than other species for SLA, which suggests that faster resource acquisition may provide a competitive advantage to the coloniser species, allowing these species to dominate Mediterranean grasslands globally (Pyšek et al. 2015, Sandel and Low 2019). Niche differentiation of coloniser species in the donor and recipient communities may reflect preadaptation to disturbance or past environmental, biogeographic, or evolutionary constraints (MacDougall et al. 2018). In California, functional differences between the pools of natives and colonisers was evident for all traits except LNC, indicating that niche differentiation is a key mechanism promoting coexistence among native and exotic species in these grasslands (Molinari and D'Antonio 2014). Assuming that the traits we studied are directly related to different functional strategies and species performance (Violle et al. 2007, Díaz et al. 2016), the observed patterns allow us to elucidate the different community assembly processes that play out among the donor and recipient communities.

In the native range in Spain, functional differences between coloniser species and other species were either absent or constant along the productivity gradient. This result is in agreement that habitat filtering acts

as the main driver of the assembly patterns in Spanish grasslands. This filtering is frequently associated with abiotic constraints (Cornwell and Ackerly 2009, de Bello et al. 2012), but it also can be due to biotic filtering when resource competition is high (de Bello et al. 2012, de la Riva et al. 2018). Whatever the case, these patterns point to the importance of functional convergence as a coexistence mechanism that equalizes fitness differences, rather than niche partitioning (Spasojevic and Suding 2012). The functional convergence among species pools in Spain compared to California might reflect that plant species in Spain have been exposed to agricultural habitats for longer than California natives. It has been widely argued that early agricultural activities in Europe might have selected for traits, or favoured species that thrive in agricultural landscapes (La Sorte and Pyšek 2009, MacDougall et al. 2018). Thus, we expect most species in managed grasslands in Spain to be well adapted to disturbed and productive habitats. This might also be responsible for the high number of species in agricultural landscapes in Europe (Eriksson 2013). In contrast, the arrival of European agriculturalists led to rapid biodiversity declines in California (Stromberg and Griffin 1996, Minnich 2008), which may also explain the low species diversity of invaded Californian grassland communities compared to European grassland communities (Leiva et al. 1997, Galán Díaz et al. 2020).

In California, functional traits related to different aspects of plant strategies were filtered in different ways for natives and colonisers at each end of the gradient, pointing out that traits which promote invasion are highly context dependent (Hulme and Bernard-Verdier 2018a, Galán Díaz et al. 2021). Particularly, resource uptake strategies (i.e. SLA and $\delta^{13}C$) tended to diverge with increasing productivity, while plant height showed the opposite pattern. The increasing divergence in SLA and $\delta^{13}C$ with productivity supports previous studies which found that resource-use attributes of native and exotic species diverged as environmental stress decreased, with exotics being more acquisitive (Burns 2006, Gross et al. 2013, Henn et al. 2019, El-Barougy et al. 2020). This highlights that the environment limits the establishment of species to those with functional

profiles that allow to cope with the abiotic constraints present in Mediterranean grasslands (Carmona et al. 2012, de la Riva et al. 2018). On the other hand, the increasing convergence of plant height with productivity probably reflects greater interspecific competition for light under favourable conditions, facilitating competitive exclusion of the smaller species (Grime 2006, Bernard-Verdier et al. 2012). The divergence in acquisitive traits might promote the coexistence of the native species with more conservative traits (Ackerly and Cornwell 2007, de la Riva et al. 2017). Thus, our results suggest that the conservative profile of the native species would potentially buffer them from competition with exotic coloniser species in these resource-rich environments.

Conclusions

Our study shows that functional traits are informative markers to disentangle the role of exotic species in communities and to understand the strategies plant communities adopt to cope with environmental constraints, and how community assembly responds to those constraints. The environment acts as a primary filter that structures trait composition and diversity at the local scale. Thus, to correctly interpret trait differences between coexisting native and exotic species, it is necessary to study the patterns from a regional perspective and consider particular habitats and environmental gradients. While invasion history and mechanisms cannot be directly inferred from current patterns, our results suggest that the naturalization of many colonisers was not random but rather reflects their competitive advantage in their native region. Still, the greater niche differences between native and coloniser groups of species in California grasslands might help explain the strong impacts of coloniser species on the functional structure of their introduced range. We show that studying exotic species in their native range allows for new and sophisticated insights on their impacts away from home, underscoring the importance of factors such as trait diversity and preadaptation to understand patterns of plant invasions.

Acknowledgments and funding

Supplementary Material

Table S1. Characteristics of the grassland sites in Spain (donor communities) and in California (recipient communities). Mean annual rainfall (MAR) and temperature annual range (TAR) were extracted from WorldClim (Fick and Hijmans 2017). Soil characteristics (mean ± 1SE): total percentage nitrogen (N), available phosphorus (P), carbon to nitrogen ratio (C:N), and organic matter (OM). Colonisers are Spanish origin species that have been introduced in California; natives are species which occur naturally in California; non-colonisers refer to species native to Spain which have not established in California.

	Site	Coord.	Altitude (m)	MAR (mm)	TAR (°C)	N (%)	P (mg/kg)	C:N	OM (%)	Total richness	Non-colonisers	Colonisers
Spain	Ventas	37.7610°, -5.7553°	280	617	32	0.13± 0.02	7.26± 0.95	12.31± 0.52	2.78± 0.47	60	23	37
	Navalagrulla	37.6636°, -5.9355°	300	596	31	0.13± 0.01	10.70 ± 1.46	12.41± 0.07	2.88± 0.16	63	18	45
	Puerto	36.6156°, -5.5287°	245	796	24	0.17± 0.02	8.10± 0.79	12.32± 0.87	3.64± 0.49	58	28	30
	Montes	36.6021°, -5.5810°	180	753	23	0.23± 0.03	13.72 ± 3.92	12.18± 0.35	4.80± 0.77	53	23	30
California	San Joaquin	37.0842°, -119.7198°	310	519	35	0.08± 0.01	8.86± 3.30	13.01± 0.94	1.80± 0.21	31	17	14
	Merced	37.3779°, -120.4086°	100	375	34	0.23± 0.05	4.54± 1.00	10.70± 0.49	4.26± 1.05	32	19	13
	Santa Cruz	36.9834°, -122.0701°	115	769	20	0.19± 0.02	4.44± 1.37	12.18± 0.63	3.99± 0.35	31	8	23
	La Honda	37.3312°, -122.2825°	405	794	19	0.28± 0.03	18.66 ± 4.16	12.40± 0.68	5.82± 0.62	31	7	24

Figure S1. Trait measurements and covariation.

Traits were measured using standardised protocols (Pérez-Harguindeguy et al. 2013). Leaf area and leaf fresh mass were measured in water-saturated leaves. Leaf dry mass was measured after drying the leaves at 65ºC for 48 hours. Dried leaves were subsequently ground to measure LNC and δ^{13}C with a Flash HT Plus elemental analyser (Thermo Fisher Scientific, Bremen, Germany). Roots were obtained by excavating the first 5-20 cm of soil around the plant, cleaned and scanned in double-mirror scanner. The length of fine roots (< 2mm) was estimated using the software WinRHIZO 2009 (Regent Instruments Inc., Quebec, Canada). Root dry mass was measured after drying the samples at 65ºC for 48 hours. Height was measured as the distance between the ground and the top of the plant, defined as the position at which flowers are produced and seeds disperse. Average seed weight was retrieved from Fernández-Alés et al. (1993) and SID (2020).

Trait covariation was explored with a Principal Component Analysis using regional means for each species and trait (natives are shown in grey, colonisers in black; × California, ● Spain).


	PC1	PC2	PC3	PC4
SLA	0.49	-0.35	0.16	-0.03
LDMC	-0.11	-0.37	-0.60	-0.24
SRL	0.45	0.24	-0.33	-0.34
RDMC	-0.08	-0.41	-0.53	0.34
dC13	-0.46	0.10	0.03	0.35
LNC	-0.00	-0.54	0.38	-0.35
height	-0.37	0.29	-0.15	-0.62
seed weight	-0.43	-0.31	0.19	-0.24
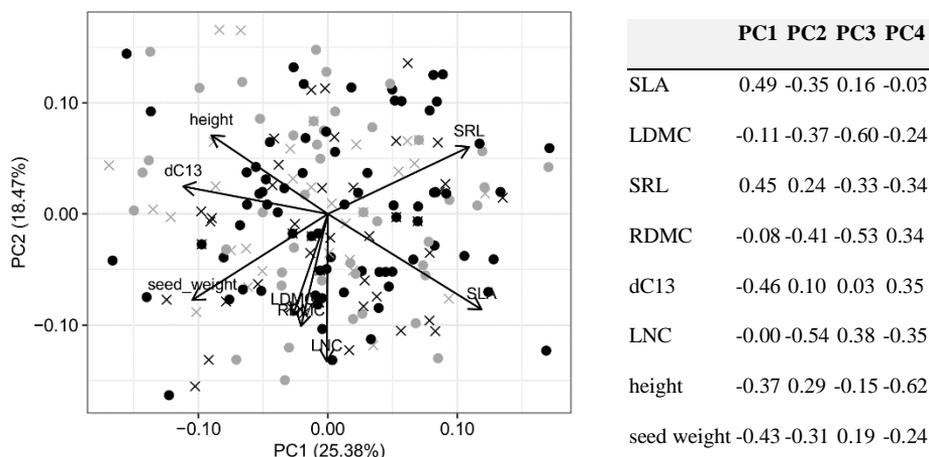
Figure S2. Principal component analysis of environmental variables. The first principal component represents a positive covariation of MAR, soil organic matter, available phosphorus and total nitrogen (i.e. productivity gradient).


	PC1	PC2
OM	0.50	0.41
N	0.46	0.54
P	0.37	-0.13
MAR	0.41	-0.65
TAR	-0.49	0.27
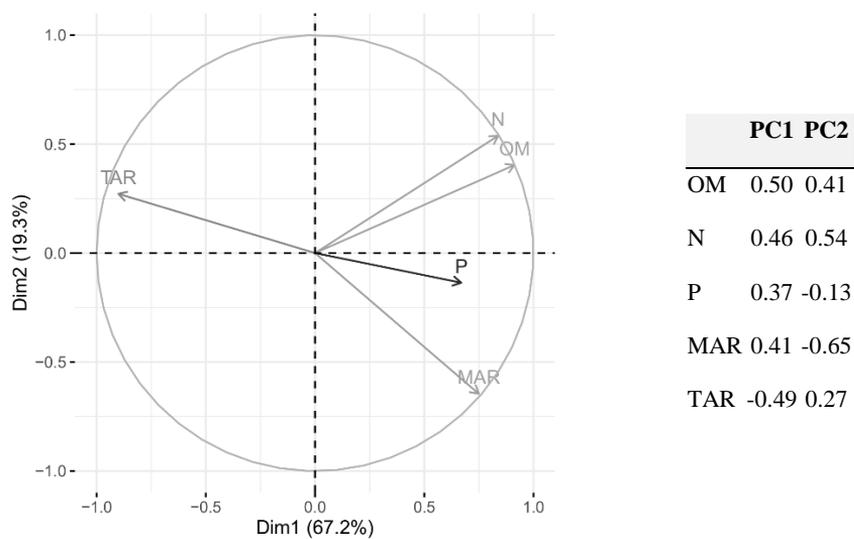
Figure S3. Effects of niche partitioning and habitat filtering in Spain along the productivity gradient. Left column shows changes in CWM of coloniser (black) and non-coloniser (grey) species assemblages along the productivity gradient. Right column shows functional differences between coloniser and other species: black dots over zero indicate niche differentiation; black dots below zero indicate functional convergence; grey dots indicate random assembly. Solid lines indicate significant linear relationships (p < 0.05). Sites: + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes.
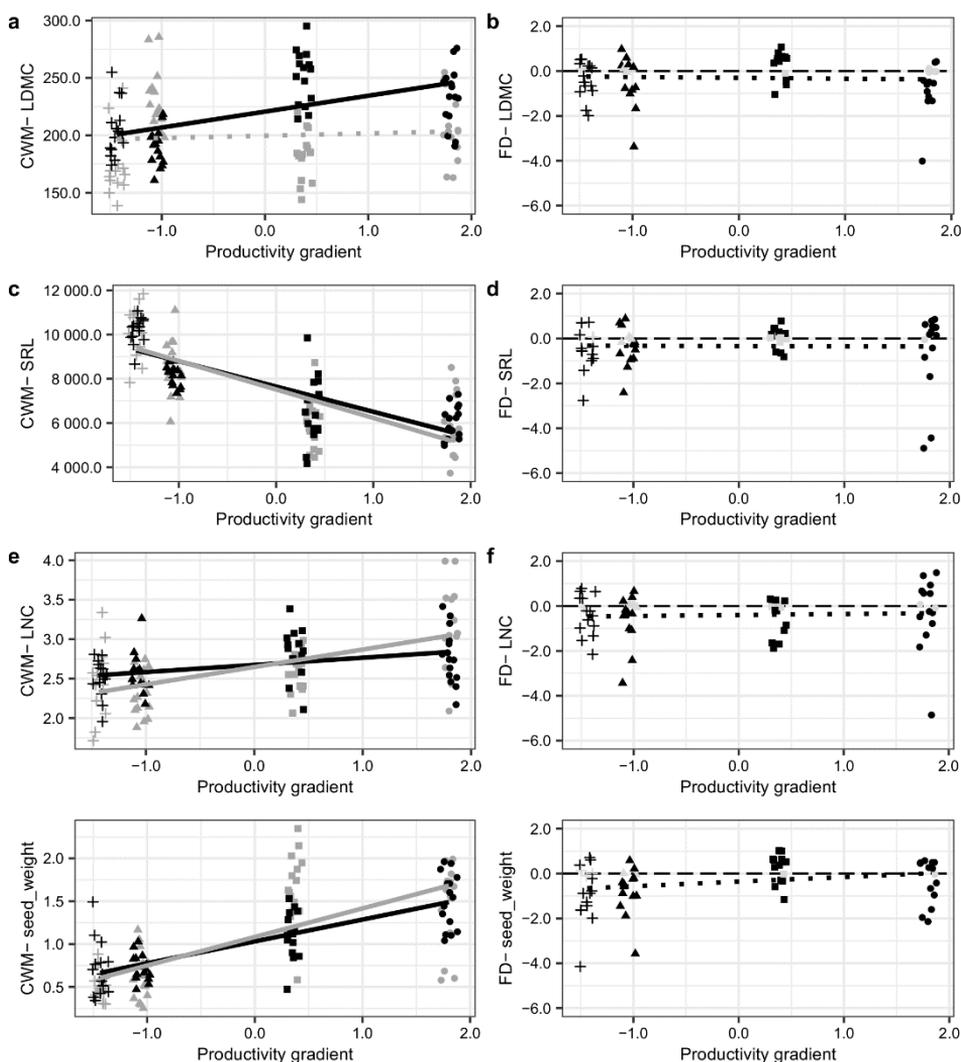
Figure S4. Effects of niche partitioning and habitat filtering in California along the productivity gradient. Left column shows changes in CWM of coloniser (black) and non-coloniser (grey) species assemblages along the productivity gradient. Right column shows functional differences between coloniser and native species: black dots over zero indicate niche differentiation; black dots below zero indicate functional convergence; grey dots indicate random assembly. Solid lines indicate significant linear relationships (p < 0.05). Sites: ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda.
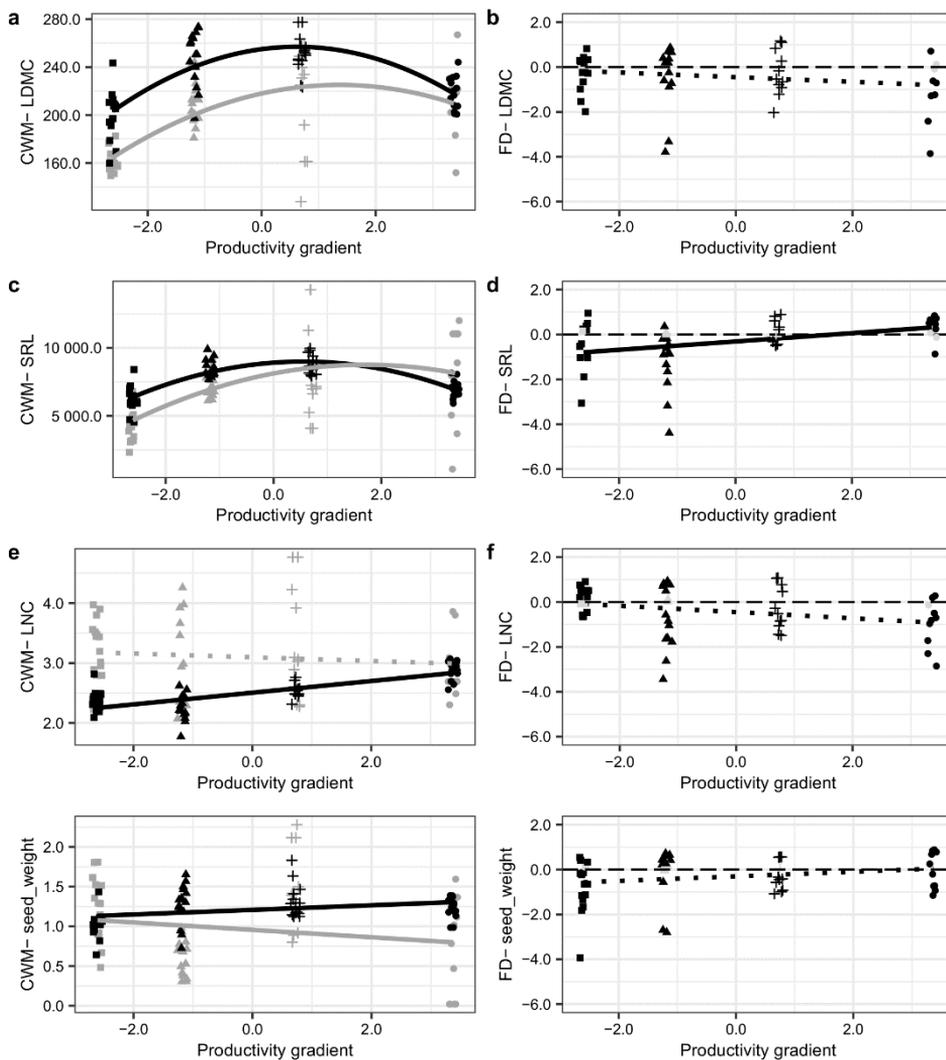
Chapter 3

Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities

Parque Natural de Los Alcornocales, Cádiz, Spain (15th May 2018)

Abstract

Functional segregation among species in a community depends on their mean trait values (i.e. functional distinctiveness), and the range of trait attributes exhibited by each species (i.e. functional diversity). Previous evidence suggests that invasive plants tend to display traits related to a more acquisitive resource-use strategy than natives. However, the contribution of intraspecific trait variation to functional diversity has received little attention in community ecology, and might provide interesting information about community processes. In this study, we used eight plant traits related to carbon and nutrient acquisition of coexisting dominant native and invasive plants in eight communities across the Mediterranean biome to determine sources of functional segregation between native and invasive species. We found three major axes of functional variation, related to leaf economics, resource-use efficiency, and plant height. Invasive species across communities had leaf traits related to an acquisitive resource-use strategy in contrast to native species, whereas differences in the second and third axes were community dependent. Invasive species were more functionally diverse than native species across the dataset and in four out of the eight communities. Intraspecific variance accounted for 11%–27% of total trait variation and was on average greater in invasive species, and especially important in the axis related to resource use efficiency. These results, although dependent on the trait and community considered, offer interesting insights to the sources of functional trait diversity of native and invasive species within communities, indicating that intraspecific variation might not be equally distributed between native and invasive species.

Introduction

Functional segregation among species in a community depends on the mean difference between their trait values, which represents their functional distinctiveness; and the range of trait values exhibited by each species, which contributes to functional diversity (Violle and Jiang 2009, Hulme and Bernard-Verdier 2018b). High functional distinctiveness

allows invasive species to establish in the recipient community by minimizing interspecific competition (MacDougall et al. 2009, Cadotte et al. 2018, Divíšek et al. 2018, de la Riva et al. 2019). Previous evidence suggests that invasive species tend to display traits related to fast return on investments of nutrients, such as higher specific leaf area or lower tissue construction costs, than native congeners (Pyšek and Richardson 2007), or coexisting natives (Daehler 2003, Ordonez et al. 2010, Funk et al. 2016). This is often the case in Mediterranean habitats, where invasive plants frequently display traits of rapid resource acquisition in comparison with coexisting native species (D'Antonio and Vitousek 1992, Arianoutsou et al. 2013).

Mediterranean regions are frequently dry and low-resource environments where strong abiotic constraints structure trait composition (de la Riva et al. 2018, Michelaki et al. 2019). Thus, functional distinctiveness between native and invasive species might be limited within the environmental constraints of Mediterranean communities (environmental filtering; Cadotte et al. 2018). It has been argued that environmental filtering is important at higher scales, with species from the same biome being functionally similar (Echeverría-Londoño et al. 2018), whereas functional distinctiveness operates at a local scale (Loiola et al. 2018). For instance, plant species adapted to dry habitats, such as the Mediterranean, often show contrasting resource uptake strategies due to opportunistic behaviour with respect to water and nutrient use efficiency (Querejeta et al. 2018, Carvajal et al. 2019). Furthermore, studies have observed invaders with very different functional profiles to establish in Mediterranean habitats (Tecco et al. 2010, de la Riva et al. 2019), suggesting that different mechanisms of invasion might operate.

Functional diversity of a community depends on interspecific and intraspecific trait variance (Violle and Jiang 2009). Intraspecific variance depends on the species and traits under consideration (Albert et al. 2011, Siefert et al. 2015), environmental constraints (i.e. climate and resource availability), and ecological processes operating in each community (Grime and Mackey 2002, Messier et al. 2010, Walters and Gerlach 2013).

Because intraspecific trait variance often accounts for a smaller proportion (~ 25%) of total trait diversity than interspecific variance (Albert et al. 2011, Siefert et al. 2015), it is frequently overlooked in the context of biological invasions (Hulme and Bernard-Verdier 2018; but see Helsen et al. 2020). However, the sources and extent of intraspecific trait variance might differ between native and invasive species within the same community. It has been argued that, whereas native species occupy specific suitable patches within their range (Gallien et al. 2010), invasive plants are often generalist species (Okimura and Mori 2018), able to thrive under diverse ecological constraints (Clavel et al. 2011), and may show greater plasticity than phylogenetically related non-invasive species (Sultan 2001, Funk 2008, Davidson et al. 2011, Martín-Forés et al. 2017). Thus, we might expect that, in a given community, the contribution of intraspecific variance to total trait diversity will be greater in invasive than native species.

To correctly assess the role of intraspecific variance in the functional segregation of native and invasive species, it is necessary to consider two things. First, the relative contribution of intraspecific trait variance to total diversity might largely depend on the observed interspecific variance (de Bello et al. 2011). Thus, a greater contribution of intraspecific trait variance to total diversity of invasive species might just reflect that native species are overall more diverse, i.e. are more different among themselves (have greater interspecific variance). Second, native and invasive species across Mediterranean Regions tend to show contrasting life forms, with invasive species being more frequently annual species in contrast to native perennial species (Arianoutsou et al. 2013, Funk et al. 2016). Therefore, intraspecific trait variance in Mediterranean communities could depend on species' life forms, rather than origin per se. It has been argued that long-lived plant species might show higher intraspecific variation in traits related to leaf morphology due to greater ontogenetic (Watson et al. 1995, Sultan 2004), but be more physiologically constrained by costly leaf tissues than ruderal and fast-growing plant species (Maire et al. 2013). It

is crucial to assess these considerations to correctly understand functional segregation in trait-space.

Plant performance is rarely determined by a single trait, thus it is necessary to move towards a whole-plant approach by exploring trait covariation along functional axes (Albert et al. 2011, Díaz et al. 2016, Hulme and Bernard-Verdier 2018a). There are several axes of trait covariation, such as leaf and water economy, light competition or reproductive effort (Laughlin 2014, Díaz et al. 2016, Prieto et al. 2018). In this regard, the best known axis of plant trait covariation is the leaf economics spectrum (Wright et al. 2004), which represents a trade-off between acquisition and conservation of resources, i.e. quick or slow return of investments. Whereas the acquisitive-end of this spectrum encompasses species with short-lived leaves with high maximum photosynthetic rates and leaf nutrient content, the conservative-end includes species with long-lived leaves and high construction costs. As there are several known axes of trait covariation, it is necessary to use tools that allow to estimate functional segregation considering all functional axes simultaneously such as trait hypervolumes based on kernel density estimation methods (Blonder et al. 2018). Hypervolumes define high-dimensional, non-continuous shapes and permit an accurate quantification of the amount of trait-space occupied by a species (i.e. functional diversity) (Blonder et al. 2018). Hence, hypervolumes may be a useful tool to explore functional segregation between native and invasive species (see Guerin et al. 2019; Helsen et al. 2020).

To test this framework, we analysed native and invasive species' traits data from eight communities across the five Mediterranean-climate regions (Funk et al. 2016). Previous analyses with a focus on single traits showed that invasive species had traits related to faster resource acquisition and use than native species, and that this difference was related to life form (Funk et al. 2016). Here, we aim to understand how native and invasive species segregate in trait-space by exploring the two sources of functional segregation, i.e. functional distinctiveness and diversity. First, we identified the major axes of trait covariation, and determined whether

native and invasive species occupy different positions along them (i.e. functional distinctiveness). Second, we compared the functional diversity of native and invasive species, and quantified whether the contribution of intraspecific trait variance to the total functional diversity differs between invasive and native species.

Methods

Field data collection

Table 1. Studied communities and their soil characteristics, mean annual precipitation, management regimes, and number of species grouped by origin and life form. Regions: Australia (AU), Spain (SP), California (CA), South Africa (SA) and Chile (CH).

	Community	Soil N (g N/100 g soil)	Soil P (mg P/kg soil)	Soil pH	Mean annual rainfall	Grazing	Years since last fire	Number of native species	Number of invasive species	Annual	Herbaceous perennial	Woody	Total
AU	banksia woodland	0.05	47.7	5.38	834	Low	>20	10	8	5	9	4	18
	coastal banksia woodland	0.06	150.9	5.74	734	Low	>30	7	6	3	7	3	13
SP	coastal grassland	0.05	117.8	7.96	550	High	>50	20	9	11	10	8	29
CA	serpentine grassland	0.23	30	6.69	760	Low	>50	23	4	17	6	4	27
	coastal sage scrub	0.19	628.3	6.58	330	Low	3	14	9	10	6	7	23
SA	acid sands fynbos	0.03	31	4.81	522	Low	10	11	5	3	6	7	16
	renosterveld	0.29	304	5.75	515	Low	>50	11	5	5	3	8	16
CH	sclerophyll woodland	0.09	1001	7.15	360	Low	>100	13	5	5	5	8	18

We analysed plant traits of dominant native and invasive species of eight representative communities from five Mediterranean regions collected by Funk et al. (2016, 2017) (Table 1). Particularly, we measured eight traits of leaf morphology, physiology (leaf chemical compounds) and plant size related to plant resource-use and acquisition strategies (Table 2). These

traits have been widely studied in the literature because of their importance in community assembly (Tecco et al. 2010, Michelaki et al. 2019, Henn et al. 2019, Helsen et al. 2020). The database included a total of 734 observations: 137 species and four to five replicate plants per species and community (Table S1). Eighteen species were present in more than one community.

Table 2. Traits considered in this study, abbreviation, units and functional role.

trait	abb.	units	significance
Leaf mass per area	LMA	$g \times m^{-2}$	Plant investment in structural leaf tissue. High LMA indicates a conservative resource-use strategy.
Mass-based photosynthetic rate	Amass	$nmol\ CO_2 \times g^{-1} \times s^{-1}$	Photosynthetic rate per leaf mass at saturating light levels.
Instantaneous water-use efficiency	WUE	$\mu mol\ CO_2 \times mmol\ H_2O^{-1}$	Ratio between CO_2 assimilation and transpiration.
Mass-based leaf nitrogen content	Nmass	$mg\ N \times g^{-1}$	Amount of nitrogen per leaf mass. Related to plant growth and economics.
Photosynthetic nitrogen-use efficiency	PNUE	$mmol\ CO_2 \times mol^{-1}\ N \times s^{-1}$	Photosynthetic capacity per unit leaf nitrogen.
Mass-based leaf phosphorus content	Pmass	$mg\ P \times g^{-1}$	Amount of phosphorus per leaf mass. Related to plant growth and economics.
Photosynthetic phosphorus-use efficiency	PPUE	$mmol\ CO_2 \times mol^{-1}\ P \times s^{-1}$	Photosynthetic capacity per unit leaf phosphorus.
Plant height	Height	cm	Indicates the position of the plant in the vertical light gradient of the community.

Species were classified according to their origin as native or invasive; and according to their life form as annual, herbaceous perennial, or woody. Here ''invasive'' follows the definition of Richardson et al. (2000), i.e. non-native species with great reproductive potential which become very abundant locally and are able to quickly spread from the area of introduction. The category annual were therophytes, i.e. species that spend the summer in the seed bank mostly grasses and forbs. Herbaceous

perennials were plants without lignified stems but with dormant organs below or near the ground. Woody species included shrubs and trees.

Data analyses

First, we ran a principal component analysis (PCA) to identify major axes of trait covariation, and reduce the dataset into fewer functional dimensions (Laughlin, 2014). We used the first three principal components for posterior analyses, those with eigenvalues greater than one. Then, we explored the functional distinctiveness between native and invasive species, i.e. if native and invasive species differ in their mean trait values along each principal component. For each principal component, we fitted a linear mixed model for the total dataset with community and species, nested within community, as random effect, and a linear mixed model for each community with species as random effects. We used the Satterthwaite method to approximate degrees of freedom. The residual versus fitted plots revealed that errors were normally distributed and homoscedastic.

Second, to characterize the functional diversity of native and invasive species, we built hypervolumes using a Box kernel density estimation method and Silverman bandwidth estimator (hypervolume package, Blonder et al. 2018). For the trait-space defined by the three principal components, we built several hypervolumes: one for all native species in the dataset, one for all invasive species in the dataset, and one for each group of native and invasive species within each community. We also built hypervolumes to estimate the diversity of the total pool of native and invasive species in each principal component. The units of the hypervolumes are reported as the standard deviations of PCA scores in the first three axes, raised to the power of the number of trait dimensions (SD3). As hypervolumes depend on species richness, and all communities have more native than invasive species, we created 99 randomized communities where the number of native species was adjusted to the number of invasive species in the community (see invasive species column in Table 2). To compare the functional diversity of native and invasive species across randomized communities, we calculated the mean effect

size (Hedges'd) and bias-corrected 95%-bootstrap confidence intervals (effsize package, Torchiano 2018). A mean effect size was considered significantly different from zero when its confidence interval did not bracket zero.

Third, we assessed if the relative contribution of intraspecific variance to total trait diversity (i.e. total variance of a pool of native or invasive species in a given principal component) is greater in invasive than native species. We partitioned the total community variance into interspecific and intraspecific variance as formulated in Eq. 1 of de Bello et al. (2011), i.e. the extent of trait variation in a community which results from variation between coexisting species and variation among individuals of a species. In this formulation, the contribution of each species to the variance partitioning is identical (de Bello et al. 2011). Then, we divided the absolute intraspecific variance by the total community variance to obtain the relative contribution of intraspecific trait variance to total trait diversity (Siefert et al. 2015). We did this for the total pool of native and invasive species, and native and invasive species within each community.

Finally, we explored whether the functional diversity and the contribution of intraspecific trait variance to total diversity of native and invasive species is related to their life forms. For all three dimensions, and each principal component, we estimated the functional diversity of the total pool of annual, herbaceous perennial and woody species with hypervolumes (Blonder et al. 2018), and compared them by computing Hedges'd and bias-corrected 95%-bootstrap confidence intervals between all groups (effsize package, Torchiano 2018). Then, we partitioned the total trait diversity of each group into interspecific and intraspecific variance (de Bello et al. 2011), and calculated their contributions to total diversity (Siefert et al. 2015). If the relative contribution of intraspecific trait variance of native and invasive species is related to their life forms, then we might expect to observe a similar or greater effect size between annual and perennial species compared to between native and invasive.

All statistical analyses were performed, and all figures produced, with the software R v3.6.1 (R Core Team 2019).

Results

Functional strategies of native and invasive species

trait	PC1	PC2	PC3
LMA	-0.44	0.13	-0.02
height	-0.18	0.03	0.77
Amass	0.52	0.14	0.08
WUE	0.09	-0.41	0.52
Nmass	0.31	-0.40	0.13
Pmass	0.32	-0.48	-0.20
PNUE	0.46	0.33	-0.02
PPUE	0.27	0.55	0.26
eigenvalue	3.03	1.77	1.05
variance	0.38	0.22	0.13
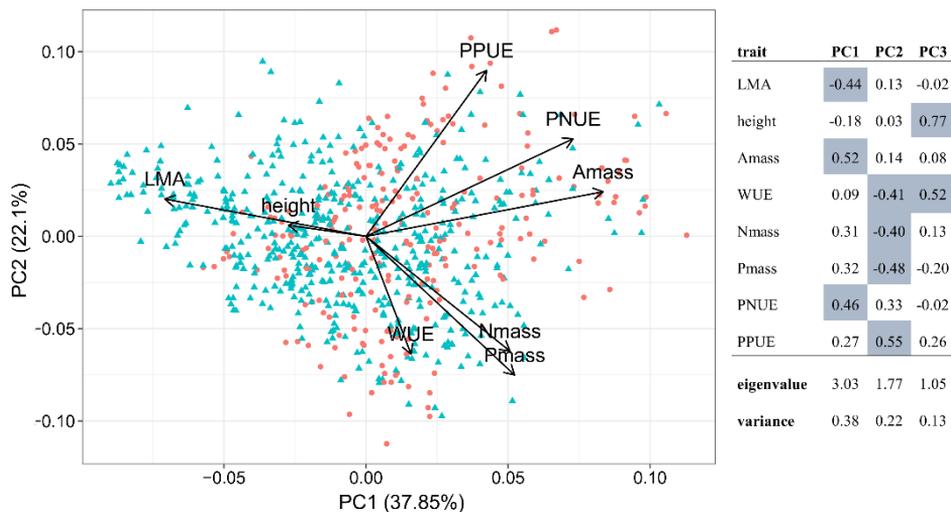
Figure 1. Principal Component Analysis (PCA) of eight plant traits from 137 natives (blue triangles) and invasive (red dots) plant species in Mediterranean communities (4–5 replicates per species). The table shows the loadings and variance associated with each principal component with eigenvalues over 1. The most relevant traits of each principal component have been shaded. Traits: LMA: leaf mass per area, Amass: mass-based photosynthetic rate, WUE: instantaneous water use efficiency, Nmass: mass-based leaf nitrogen concentration, Pmass: mass-based leaf phosphorus concentration, PNUE: photosynthetic nitrogen-use efficiency, PPUE: photosynthetic phosphorus-use efficiency, and Height: vegetative plant height.

The first three components of the PCA accumulated 73.11% of the total variance (Figure 1). The first principal component explained 37.85% of the variance and reflected a coordination between Amass (mass-based photosynthetic rate), LMA (leaf mass per area), and PNUE (photosynthetic nitrogen-use efficiency) (Figure 1), which is representative of the leaf economics spectrum (Wright et al. 2004). The second principal component explained 22.10% of the variance and reflected a covariation between leaf

nutrient concentration, WUE (instantaneous water-use efficiency) and PPUE (photosynthetic phosphorus-use efficiency) and represents the trade-off between water and phosphorous-use efficiency. The third principal component explained 13.15% of the variance and was linked to plant height and, to a lesser extent, WUE.
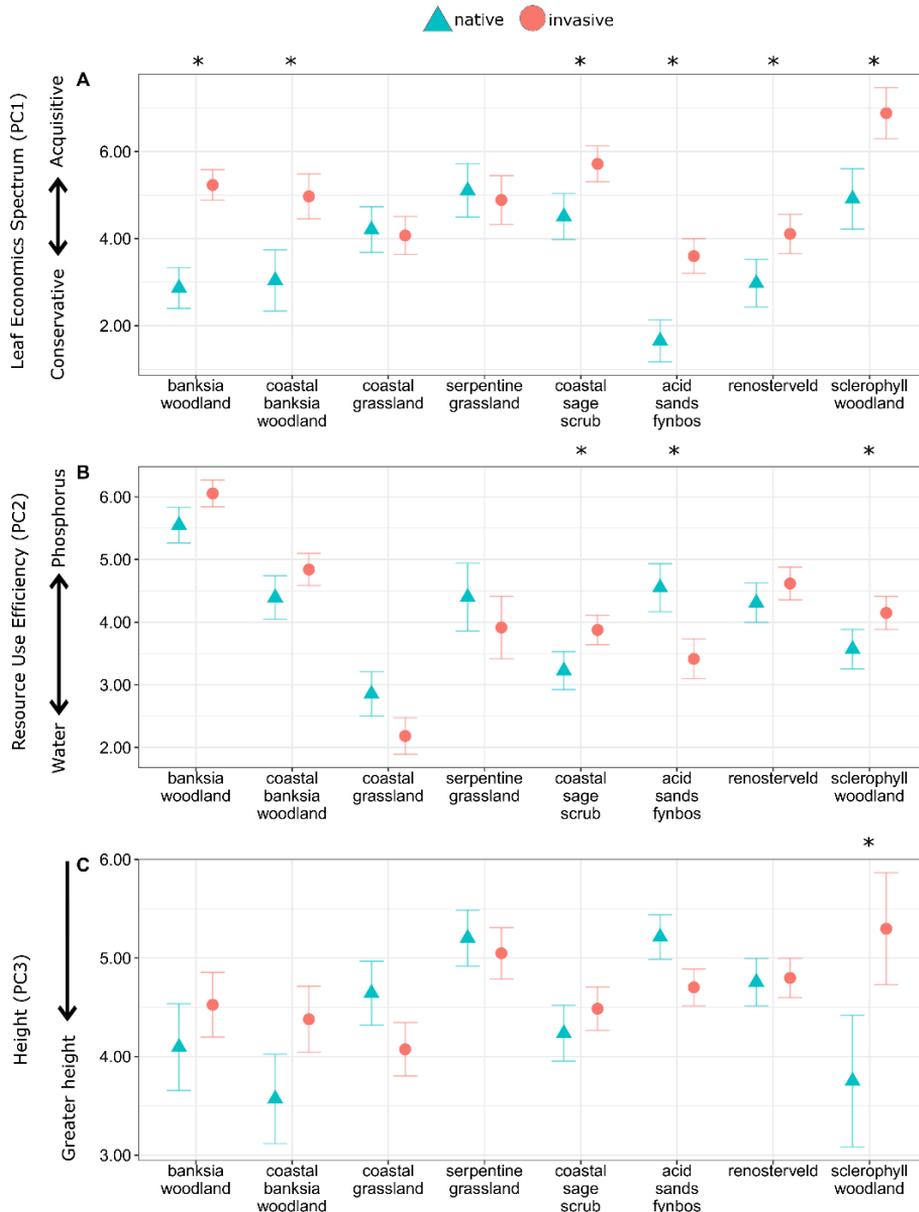
Figure 2. (a) Distribution of native (blue triangles) and invasive (red dots) species along PC1 (leaf economics spectrum) within communities. Greater values of PC1 correspond to the high Amass (mass-based photosynthetic rate) and PNUE (photosynthetic nitrogen-use efficiency) end. (b) Distribution of native and invasive species along PC2 (resource use efficiency). Greater values of PC2 correspond to high PPUE (photosynthetic phosphorus-use efficiency). (c) Distribution of native and invasive species along PC3 (plant height). Greater values of PC3 correspond to the high height end. Values indicate estimates ± standard error of linear mixed models with species as random effect. Asterisks denote significant differences between native and invasive species for a given community and principal component ($p < 0.05$).

Overall, native species occupied the high LMA end of PC1, whereas invasive species occupied the high Amass and PNUE end ($F_{1,157} = 27.04$, $p < 0.001$). Native and invasive species occupied similar positions in PC2 ($F_{1,157} = 0.03$, $p = 0.87$) and PC3 ($F_{1,158} = 0.94$, $p = 0.33$). Within communities, invasive species were significantly displaced towards the high Amass and PNUE end of PC1 in six communities (Figure 2a). Invasive species in sclerophyll woodland and coastal sage scrub occupied a position of greater PPUE end in PC2 than native species, whereas in acid sands fynbos invasive species occupied a position of greater Nmass (mass-based leaf nitrogen content), Pmass (mass-based leaf phosphorus content) and WUE ($p < 0.05$ in all cases) (Figure 2b). Native species in sclerophyll woodland were on average taller than invasive species ($F_{1,18} = 5.34$, $p = 0.03$).

Functional diversity of native and invasive species

Invasive species showed 9.65% greater functional diversity in trait-space respect to natives (natives: 231.28 SD^3 ± 5.8, invasives: 253.6 SD^3 ± 2.3, mean ± standard error). Particularly, invasive species were 26.02% more diverse than native species in PC2 (water and phosphorous use efficiency; nat: 7.84 SD ± 0.09, inv: 9.98 SD ± 0.10), whereas native species showed 4.80% greater functional diversity than invasive species in PC1 (leaf economics spectrum; nat: 10.49 SD ± 0.14, inv: 9.99 SD ± 0.04) and 8.51% in PC3 (height; nat: 7.27 SD ± 0.09, inv: 6.70 SD ± 0.03) (Figure 3). At

the community level, invasive species showed greater functional diversity than natives in serpentine grassland (nat: 50.41 SD^3 ± 5.46, inv: 90.19 SD^3 ± 0.99), coastal sage scrub (nat: 83.16 SD^3 ± 2.33, inv: 108.02 SD^3 ± 0.98), acid sand fynbos (nat: 35.58 SD^3 ± 1.58, inv: 78.16 SD^3 ± 1.34) and renosterveld (nat: 22.41 SD^3 ± 1.23, inv: 28.69 SD^3 ± 0.48) (Figure 3). Native species showed greater functional diversity than invasive species in banksia woodland (nat: 103.44 SD^3 ± 2.55, inv: 50.58 SD^3 ± 0.66), coastal banksia woodland (nat: 104.94 SD^3 ± 2.75, inv: 78.17 SD^3 ± 1.56) and sclerophyll woodland (nat: 170.20 SD^3 ± 9.25, inv: 79.42 SD^3 ± 1.33). Native and invasive species within coastal grassland were equally diverse (nat: 115.53 SD^3 ± 3.57, inv: 109.14 SD^3 ± 0.45).
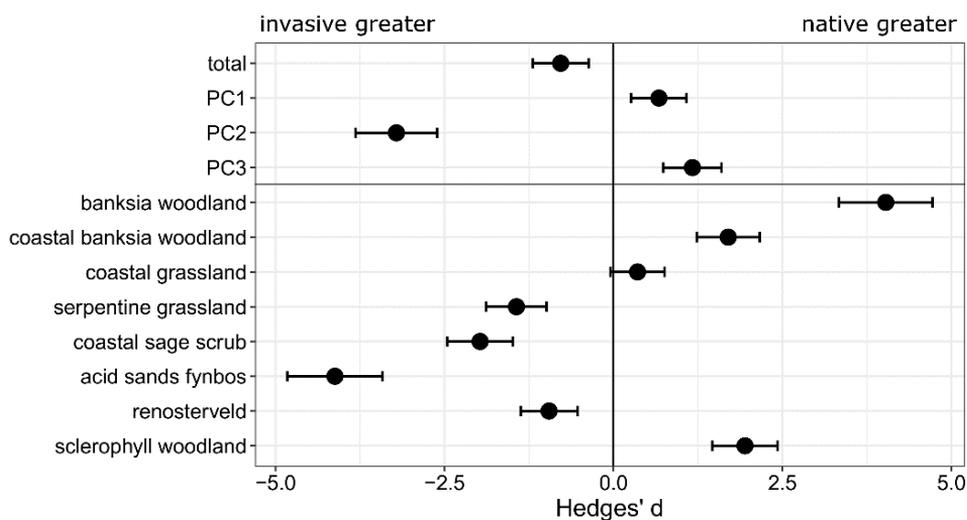

Figure 3. Mean effect size (Hedges' d) and bias-corrected 95%- bootstrap confidence intervals for differences in the native and invasive species hypervolumes for the total pool of native and invasive species in trait-space, the total pool of native and invasive species in each dimension, and native and invasive species in trait-space within each community. Hypervolume sizes are included in Table S3. Negative mean effect sizes indicate that invasive species had on average greater hypervolume size than natives. A mean effect size is significantly different from zero when its confidence interval does not bracket zero.

The mean relative contribution of intraspecific diversity across the dataset was on average greater in invasive than native species for all principal

components (PC1: 25.4% and 10.7%, PC2: 23.9% and 18.5%, PC3: 26.6% and 18.9%). At the community level, the relative contribution of intraspecific variation to PC1 trait diversity was greater for invasive than native species in five communities, and only greater for native species in renosterveld (Figure 4). The relative contribution of intraspecific variation to PC2 trait diversity was greater for invasive than native species in three communities, and greater for native species in three communities. The relative contribution of intraspecific variation to PC3 trait diversity was greater for invasive than native species in four communities, and greater for native species in two communities.
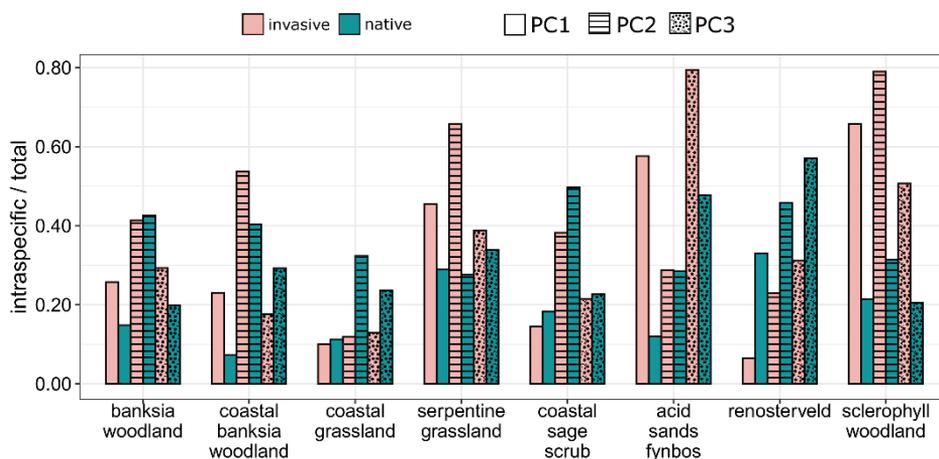

Figure 4. Relative contribution of intraspecific variance of native and invasive species to total trait diversity for principal components with eigenvalues over one.

Overall, woody species (228.3 $SD^3 \pm 2.9$, mean ± standard error) showed 18.05% greater diversity than herbaceous perennial species (193.4 $SD^3 \pm 3.2$) in trait-space, and herbaceous perennial species were 14.85% more diverse than annual species (168.4 $SD^3 \pm 1.8$) (effect sizes in Table S2).

Herbaceous perennial species (10.8 SD ± 0.1) were significantly more diverse than the other life forms in PC1, whereas annual (8.9 SD ± 0.1) and woody species (8.8 SD ± 0.1) were equally diverse. In PC2, annual species (8.9 SD ± 0.1) were significantly more diverse than the other life forms, whereas woody (8.3 SD ± 0.1) and herbaceous perennial species

(8.5 SD ± 0.1) were equally diverse. In PC3, woody species (7.5 SD ± 0.1) were significantly more diverse than herbaceous perennials (5.8 SD ± 0.1), and herbaceous perennials were significantly more diverse than annual species (5.5 SD ± 0.1). In PC1, intraspecific variation accounted for 31.3% of total diversity of annual species, 11.2% for herbaceous perennial species, and 10.5% for woody species. In PC2, intraspecific variation accounted for 27.7% of annual species trait diversity, 29.9% for herbaceous perennial species, and 15.6% for woody species. In PC3, intraspecific variation accounted for 37.0% for annual species trait diversity, 23.2% for herbaceous perennial species, and 19.7% for woody species.

Discussion

Functional strategies of native and invasive species

We found that trait-space was mainly dominated by three axes of trait covariation: leaf economics, water- and phosphorus-use efficiency, and plant height. This supports the idea that certain suites of traits tend to vary together (Laughlin 2014), and plant functioning is constrained to a determined range of viable combinations (Díaz et al. 2016, Lloret et al. 2016). In line with other studies, we found great functional distinctiveness in resource use strategies between invasive species and native species of the recipient community (Pyšek and Richardson 2007, Ordonez et al. 2010, Tecco et al. 2010). These results suggest that contrasting resource use strategies are important in driving the establishment of invasive plants (e.g. Funk et al. 2016; Helsen et al. 2020). In fact, our results confirm previous evidence that the leaf economics spectrum is a main axis of functional differentiation between native and invasive species across Mediterranean communities (Tordoni et al. 2019). That is, the range of trait values displayed by the invasive species is consistent with the 'fast return on investments' end of the leaf economics spectrum not only as a general trend, but also in most of the communities studied separately (significantly different in six of them). These results indicate that higher capacity for the extraction of resources could be an advantageous strategy for invasive

species (Daehler 2003, Ordonez et al. 2010, Funk et al. 2016, Henn et al. 2019); especially in habitats with strong abiotic constraints such as those in Mediterranean regions, where native species display conservative resource uptake adaptations (e.g. Lloret et al. 2016; de la Riva et al. 2017).

It is worth noting that we detected water and phosphorous availability as another trait dimension related to resource constraints. Thus, the particular segregation of native and invasive species across these communities might depend also on specific resource limitations within each community. We found functional differences between native and invasive species with respect to this dimension in sclerophyll woodland (Chile), coastal sage scrub (California), and acid sands fynbos (South Africa). Sclerophyll woodland and coastal sage scrub have the lowest mean annual precipitation and the highest soil phosphorus concentration compared to the other Mediterranean communities. In these communities, native species showed higher water-use efficiency and leaf nutrient concentration than invasive species. It is likely that native species, more frequently perennial species, benefit from having a higher stomatal control, and root systems to enhance nutrient uptake than annuals (Pérez-Ramos et al. 2013, Prieto et al. 2018, Tordoni et al. 2019). By contrast, acid sands fynbos is the community with the lowest phosphorus and nitrogen concentration in the soil, and invasive species occupy the high leaf nutrient concentration and WUE end of the spectrum. These results concur with those from studies of Mediterranean grassland species that found higher WUE in invasive species compared to natives (Vaughn et al. 2011). Higher leaf nutrient concentrations in invasive species in our dataset might reflect their fast resource uptake strategy, particularly during periods of high water availability (Pérez-Ramos et al. 2013). Collectively, these results support the idea that trait variation depends on the specific combination of environmental factors and highlights the utility of such studies for predicting plant and community responses in a changing world (Funk et al. 2016).

Disentangling the functional trait diversity of native and invasive species

Our results show that dominant invasive species are functionally more diverse than native species across communities and in four out of the eight communities, which indicates that many resource-use profiles might allow species to invade communities (Tecco et al. 2010, de la Riva et al. 2019). That is, contrasting with previous findings (Okimura and Mori 2018), we show that invasive species constitute a functionally diverse pool which contributes to a great proportion of the community trait diversity. As discussed by Loiola et al. (2018), this may reflect that invasive species are creating new functional spaces outside the extant native pool, i.e. excluding functionally similar natives or occupying empty space, or filling empty gaps within the existing space. Yet, our approach does not allow us to identify these underlying mechanisms. Interestingly, although the total pool of perennial species was more diverse in trait-space than annuals, the pool of invasive species (most frequently annuals) was more diverse than natives. The sources of functional diversity for native and invasive species differ: greater diversity in water- and phosphorus-use efficiency for invasives and greater diversity in leaf economics and plant height for natives. In this regard, the higher hypervolumes of invasive species in trait-space support the importance of trait distinctiveness between invasive species and the native community (Helsen et al. 2020).

Overall, in agreement with previous findings (Albert et al. 2011, Siefert et al. 2015), our results indicate intraspecific variance contributed 10.7 to 26.6% of the total functional diversity. On average, the contribution of intraspecific variance was greater in invasive compared to native species. Regarding the dimensions related to leaf economics and plant height, where native species were more diverse than invasive species, the greater contribution of intraspecific variance in invasive species might reflect smaller interspecific differences. Interestingly, we show that annual and woody species were equally diverse in leaf economics traits, but the relative contribution of intraspecific variation was three times greater in annual species, which might reflect that annual species have leaves less structurally and physiologically constrained than woody species (Maire et al. 2013).

With regard to the dimension related to water- and phosphorous-use efficiency, invasive species were overall more diverse than native species and the contribution of intraspecific trait variance was 5.4% greater. This supports the theory that invasive species might be physiologically less constrained in trait-space than their native counterparts (Funk 2008, Valliere 2019). In contrast to native species, invasive species might tend to be generalists that perform well along ecological gradients (Gallien et al. 2010, Clavel et al. 2011). While this might reflect to some extent the dependency between origin and life form, studies of co-occurring annual species have found that invasives do not adhere to the same trade-off between growth and water conservation displayed in natives (Valliere 2019). The contribution of intraspecific trait variation to total diversity was twice as much in annual and herbaceous perennial species than woody species. It is likely due to the fact that herbaceous species are more responsive to microhabitat heterogeneity in water and soil nutrient availability (Chapin et al. 1990, Fernández-Alés et al. 1993). Thus, contrasting structures of inter- and intraspecific trait variance might provide interesting insights about functional responses of native and invasive species operating in different communities (Hulme and Bernard-Verdier 2018b), supporting the notion that overlooking intraspecific variation might compromise the ability to correctly infer trait-driven ecological processes (Helsen et al. 2020).

One aspect of our study that warrants further comment is that the above-mentioned patterns were strongly context dependent. In fact, across most communities, intraspecific trait variance was especially important in the second principal component, related to nutrient availability, which is in line with previous evidence highlights how microhabitat heterogeneity might shape leaf attributes (Albert et al. 2010, Jung et al. 2010, Siefert et al. 2015). Invasive species were functionally more diverse than native species in acid sands fynbos and serpentine grassland, in some extent due to greater intraspecific variation. The great diversity of invasive species within these communities, and the substantial contribution of intraspecific variance to this diversity, points to invasive species being generalists with

great phenotypic variation (Sultan 2001, Funk 2008, Clavel et al. 2011, Davidson et al. 2011, Martín-Forés et al. 2017), and more phenotypic variation associated with annual and herbaceous perennial species (Maire et al. 2013). In renosterveld and coastal sage scrub, the contribution of intraspecific variance to total diversity was comparable between invasive and native species, and reflected to some extent that invasive species were overall more diverse. By contrast, native species in banksia and sclerophyll woodlands were more functionally diverse than invasive species. Native species in these communities are more frequently woody perennials, much more diverse in plant height than invasive species (more often herbaceous). Hence, functional trait diversity, and the contribution of intra- and interspecific variation to this diversity, varies among communities. The regional species pools are generally the result of the environmental and historical filtering, while some specific adaptations of invasive species allow them to establish successfully at a broad spatial scale with a completely different morpho-physiological profile to the native pool (Loiola et al. 2018).

Conclusions

We applied a multidimensional analysis of plant traits and trait variation to understand the segregation between native and invasive species in trait-space across Mediterranean communities. We found great functional distinctiveness in leaf economic traits and that invasive species can be more functionally diverse than native species. Therefore, our results suggest that invasive species can employ different functional profiles to thrive in recipient communities. In some communities, intraspecific trait variation can contribute a great proportion of functional trait diversity in invasive species, which might reflect evolutionary and life form differences. These results highlight that intraspecific variation might not be equally distributed between native and invasive species, offering interesting insights to species functional trait diversity within communities.

Acknowledgments and funding

Supplementary Material

Table S1. Communities included in this study and their species grouped by origin.

Region	Community	Species	Origin
California	coastal sage scrub	*Avena fatua*	Invasive
California	coastal sage scrub	*Brassica nigra*	Invasive
California	coastal sage scrub	*Bromus diandrus*	Invasive
California	coastal sage scrub	*Bromus madritensis*	Invasive
California	coastal sage scrub	*Cynara cardunculus*	Invasive
California	coastal sage scrub	*Erodium cicutarium*	Invasive
California	coastal sage scrub	*Festuca perennis*	Invasive
California	coastal sage scrub	*Malva parviflora*	Invasive
California	coastal sage scrub	*Medicago polymorpha*	Invasive
California	coastal sage scrub	*Amsinckia menziesii*	Native
California	coastal sage scrub	*Artemisia californica*	Native
California	coastal sage scrub	*Dichelostemma capitatum*	Native
California	coastal sage scrub	*Encelia californica*	Native
California	coastal sage scrub	*Isocoma menziesii*	Native
California	coastal sage scrub	*Lotus scoparius*	Native
California	coastal sage scrub	*Lupinus bicolor*	Native
California	coastal sage scrub	*Lupinus truncatus*	Native
California	coastal sage scrub	*Malacothamnus fasciculatus*	Native
California	coastal sage scrub	*Malosma laurina*	Native
California	coastal sage scrub	*Marah macrocarpus*	Native
California	coastal sage scrub	*Nassella lepida*	Native
California	coastal sage scrub	*Rhamnus ilicifolia*	Native
California	coastal sage scrub	*Salvia mellifera*	Native
California	serpentine grassland	*Anagalis arvensis*	Invasive
California	serpentine grassland	*Avena fatua*	Invasive
California	serpentine grassland	*Bromus hordaceous*	Invasive
California	serpentine grassland	*Hordeum marinum*	Invasive
California	serpentine grassland	*Festuca perennis*	Invasive
California	serpentine grassland	*Vicia sativa*	Invasive
California	serpentine grassland	*Agoseris heterophylla*	Native
California	serpentine grassland	*Allium falcifolium*	Native
California	serpentine grassland	*Allium serra*	Native
California	serpentine grassland	*Astragalus gambelianus*	Native
California	serpentine grassland	*Calandrinia ciliata*	Native
California	serpentine grassland	*Calycadenia multiglandulosa*	Native
California	serpentine grassland	*Calystegia subacaulis*	Native
California	serpentine grassland	*Castilleja densiflora*	Native
California	serpentine grassland	*Castilleja rubicundula*	Native
California	serpentine grassland	*Chlorogalum pomeridianum*	Native
California	serpentine grassland	*Crassula connata*	Native
California	serpentine grassland	*Cryptantha flaccida*	Native
California	serpentine grassland	*Dichelostemma capitatum*	Native
California	serpentine grassland	*Dodecatheon hendersonii*	Native
California	serpentine grassland	*Elymus multisedus*	Native
California	serpentine grassland	*Epilobium brachycarpum*	Native

California	serpentine grassland	*Eschscholzia californica*	Native
California	serpentine grassland	*Gilia clivorum*	Native
California	serpentine grassland	*Hemizonia congesta*	Native
California	serpentine grassland	*Hesperevax sparsiflora*	Native
California	serpentine grassland	*Hordeum brachyantherum*	Native
California	serpentine grassland	*Lasthenia californica*	Native
California	serpentine grassland	*Layia gaillardioides*	Native
California	serpentine grassland	*Layia platyglossa*	Native
California	serpentine grassland	*Lepidium nitidum*	Native
California	serpentine grassland	*Lessingia nemaclada*	Native
California	serpentine grassland	*Linanthus parviflorus*	Native
California	serpentine grassland	*Lomatium utriculatum*	Native
California	serpentine grassland	*Lotus wrangelianus*	Native
California	serpentine grassland	*Melica californica*	Native
California	serpentine grassland	*Micropus californicus*	Native
California	serpentine grassland	*Microseris douglasii*	Native
California	serpentine grassland	*Minuartia douglasii*	Native
California	serpentine grassland	*Muilla martima*	Native
California	serpentine grassland	*Stipa pulchra*	Native
California	serpentine grassland	*Plagiobothrys nothofulvus*	Native
California	serpentine grassland	*Plantago erecta*	Native
California	serpentine grassland	*Poa secunda*	Native
California	serpentine grassland	*Ranunculus californicus*	Native
California	serpentine grassland	*Sanicula bipinnatifida*	Native
California	serpentine grassland	*Sisyrinchium bellum*	Native
California	serpentine grassland	*Trifolium albopurpureum*	Native
California	serpentine grassland	*Trifolium depauperatum*	Native
California	serpentine grassland	*Trifolium variagatum*	Native
California	serpentine grassland	*Triteleia laxa*	Native
California	serpentine grassland	*Vulpia bromoides*	Native
California	serpentine grassland	*Vulpia microstachys*	Native
Chile	Sclerophyll woodland	*Anthriscus caucalis*	Invasive
Chile	Sclerophyll woodland	*Conium maculatum*	Invasive
Chile	Sclerophyll woodland	*Avena fatua*	Invasive
Chile	Sclerophyll woodland	*Bromus berterianus*	Native
Chile	Sclerophyll woodland	*Eschscholzia californica*	Invasive
Chile	Sclerophyll woodland	*Leontodon sp.*	Invasive
Chile	Sclerophyll woodland	*Papaver somniferum*	Invasive
Chile	Sclerophyll woodland	*Ageratina glechonophylla*	Native
Chile	Sclerophyll woodland	*Alstroemeria pulchra*	Native
Chile	Sclerophyll woodland	*Baccharis linearis*	Native
Chile	Sclerophyll woodland	*Calceolaria corymbosa*	Native
Chile	Sclerophyll woodland	*Cestrum parqui*	Native
Chile	Sclerophyll woodland	*Cryptocarya alba*	Native
Chile	Sclerophyll woodland	*Geranium berteroanum*	Native
Chile	Sclerophyll woodland	*Loasa triloba*	Native
Chile	Sclerophyll woodland	*Lobelia excelsa*	Native
Chile	Sclerophyll woodland	*Peumus boldus*	Native
Chile	Sclerophyll woodland	*Solanum ligustrinum*	Native
Chile	Sclerophyll woodland	*Trevoa trinervis*	Native
South Africa	acid sands fynbos	*Acacia saligna*	Invasive
South Africa	acid sands fynbos	*Avena barbata*	Invasive
South Africa	acid sands fynbos	*Briza maxima*	Invasive
South Africa	acid sands fynbos	*Erodium botrys*	Invasive

South Africa	acid sands fynbos	*Festuca perennis*	Invasive
South Africa	acid sands fynbos	*Antholyza ringens*	Native
South Africa	acid sands fynbos	*Anthospermum spathulatum*	Native
South Africa	acid sands fynbos	*Ehrharta calycina*	Native
South Africa	acid sands fynbos	*Leucodendron salignum*	Native
South Africa	acid sands fynbos	*Leucospermum hypophyllocarpodendron*	Native
South Africa	acid sands fynbos	*Metalasia muricata*	Native
South Africa	acid sands fynbos	*Montinia caryophyllacea*	Native
South Africa	acid sands fynbos	*Phylica cephalantha*	Native
South Africa	acid sands fynbos	*Protea scolymocephala*	Native
South Africa	acid sands fynbos	*Tribolium uniolae*	Native
South Africa	acid sands fynbos	*Wildenowia sulcata*	Native
South Africa	Renosterveld	*Anagallis arvensis*	Invasive
South Africa	Renosterveld	*Avena fatua*	Invasive
South Africa	Renosterveld	*Brassica nigra*	Invasive
South Africa	Renosterveld	*Briza maxima*	Invasive
South Africa	Renosterveld	*Festuca perennis*	Invasive
South Africa	Renosterveld	*Anthospermum spathulatum*	Native
South Africa	Renosterveld	*Chrysocoma coma-aurea*	Native
South Africa	Renosterveld	*Cyanella hyacinthoides*	Native
South Africa	Renosterveld	*Eriocephalus africana*	Native
South Africa	Renosterveld	*Helichrysum patulum*	Native
South Africa	Renosterveld	*Indigofera complanata*	Native
South Africa	Renosterveld	*Olea europaea*	Native
South Africa	Renosterveld	*Oxalis strigosa*	Native
South Africa	Renosterveld	*Podalyria sericea*	Native
South Africa	Renosterveld	*Rhus laevigata*	Native
South Africa	Renosterveld	*Salvia africana-lutea*	Native
Spain	coastal grassland	*Acacia longifolia*	Invasive
Spain	coastal grassland	*Arctotheca calendula*	Invasive
Spain	coastal grassland	*Arundo donax*	Invasive
Spain	coastal grassland	*Asclepias curassavica*	Invasive
Spain	coastal grassland	*Oxalis pes-caprae*	Invasive
Spain	coastal grassland	*Ricinus communis*	Invasive
Spain	coastal grassland	*Solanum sodomeum*	Invasive
Spain	coastal grassland	*Tropaeolum majus*	Invasive
Spain	coastal grassland	*Vinca difformis*	Invasive
Spain	coastal grassland	*Anagallis arvensis*	Native
Spain	coastal grassland	*Avena barbata*	Native
Spain	coastal grassland	*Chamaerops humilis*	Native
Spain	coastal grassland	*Chrysanthemum coronarium*	Native
Spain	coastal grassland	*Echium lycopsis*	Native
Spain	coastal grassland	*Erodium cicutarium*	Native
Spain	coastal grassland	*Hedysarum glomeratum*	Native
Spain	coastal grassland	*Hordeum murinum*	Native
Spain	coastal grassland	*Dittrichia viscosa*	Native
Spain	coastal grassland	*Lagurus ovatus*	Native
Spain	coastal grassland	*Leontodon taraxacoides*	Native
Spain	coastal grassland	*Limonium sinuatum*	Native
Spain	coastal grassland	*Malva sylvestris*	Native
Spain	coastal grassland	*Medicago polymorpha*	Native
Spain	coastal grassland	*Pancratium maritium*	Native
Spain	coastal grassland	*Pistacia lentiscus*	Native

Spain	coastal grassland	*Plantago major*	Native
Spain	coastal grassland	*Rapistrum rugosum*	Native
Spain	coastal grassland	*Retama monosperma*	Native
Spain	coastal grassland	*Scirpus holoschoenus*	Native
Spain	coastal grassland	*Silybum marianum*	Native
W Australia	Banksia woodland	*Arctotheca calendula*	Invasive
W Australia	Banksia woodland	*Avena barbata*	Invasive
W Australia	Banksia woodland	*Briza maxima*	Invasive
W Australia	Banksia woodland	*Ehrharta calycina*	Invasive
W Australia	Banksia woodland	*Gladiolus caryophyllaceus*	Invasive
W Australia	Banksia woodland	*Lupinus cosentinii*	Invasive
W Australia	Banksia woodland	*Pelargonium capitatum*	Invasive
W Australia	Banksia woodland	*Sonchus oleraceus*	Invasive
W Australia	Banksia woodland	*Acacia saligna*	Native
W Australia	Banksia woodland	*Angiozanthos manglesii*	Native
W Australia	Banksia woodland	*Banksia menziesii*	Native
W Australia	Banksia woodland	*Corymbia callophylla*	Native
W Australia	Banksia woodland	*Hakea prostrata*	Native
W Australia	Banksia woodland	*Kennedia prostrata*	Native
W Australia	Banksia woodland	*Mesomelaena pseudostygia*	Native
W Australia	Banksia woodland	*Patersonia occidentalis*	Native
W Australia	Banksia woodland	*Ptilotus polystachyus*	Native
W Australia	Banksia woodland	*Stirlingia latifolia*	Native
W Australia	Coastal banksia woodland	*Anagallis arvensis*	Invasive
W Australia	Coastal banksia woodland	*Avena barbata*	Invasive
W Australia	Coastal banksia woodland	*Ehrharta calycina*	Invasive
W Australia	Coastal banksia woodland	*Euphorbia terracina*	Invasive
W Australia	Coastal banksia woodland	*Gladiolus caryophyllaceus*	Invasive
W Australia	Coastal banksia woodland	*Pelargonium capitatum*	Invasive
W Australia	Coastal banksia woodland	*Sonchus oleraceus*	Invasive
W Australia	Coastal banksia woodland	*Acacia saligna*	Native
W Australia	Coastal banksia woodland	*Austrostipa flavescens*	Native
W Australia	Coastal banksia woodland	*Banksia attenuta*	Native
W Australia	Coastal banksia woodland	*Banksia menziesii*	Native
W Australia	Coastal banksia woodland	*Clematis linearifolia*	Native
W Australia	Coastal banksia woodland	*Ptilotus polystachyus*	Native
W Australia	Coastal banksia woodland	*Xanthorrhoea preissi*	Native

Table S2. Comparison of hypervolumes of annual, herbaceous perennial and woody species. We report the effect size (Hedges' d) and bias-corrected 95%-bootstrap confidence intervals. Positive mean effect sizes indicate that the first term in each pairwise comparison had on average greater hypervolume. A mean effect size is significantly different from zero when its confidence interval does not bracket zero.

	EfSize	**lowCI**	**UpCI**
PC1	0.67	0.26	1.08
PC2	-3.21	-3.81	-2.61
PC3	1.17	0.74	1.60
total	-0.78	-1.19	-0.37
coastal grassland	0.36	-0.04	0.76
acid sands fynbos	-4.12	-4.82	-3.42
banksia woodland	4.03	3.34	4.72
coastal banksia woodland	1.70	1.23	2.16
sclerophyll woodland	1.95	1.46	2.43
serpentine grassland	-1.44	-1.88	-0.99
coastal sage scrub	-1.97	-2.46	-1.49
renosterveld	-0.95	-1.37	-0.53

Table S3. Effect size (Hedges' d) and bias-corrected 95%-bootstrap confidence intervals of Figure 3. We compare the hypervolumes of the total pool of native and invasive species in trait-space, the total pool of native and invasive species in each dimension, and native and invasive species in trait-space within each community. A mean effect size is significantly different from zero when its confidence interval does not bracket zero. Negative mean effect sizes indicate that invasive species had on average greater hypervolume size than natives.

	PC	Hedges'd	lowCI	UpCI
annual-herbaceous perennial	all	-0.70	-1.11	-0.29
annual-woody	all	-2.66	-3.21	-2.11
herbaceous perennial-woody	all	-1.84	-2.31	-1.37
annual - herbaceous perennial	PC1	-4.46	-5.20	-3.72
annual - woody	PC1	0.13	-0.27	0.52
herbaceous perennial - woody	PC1	4.26	3.54	4.98
annual - herbaceous perennial	PC2	0.97	0.55	1.40
annual - woody	PC2	1.24	0.81	1.68
herbaceous perennial - woody	PC2	0.38	-0.02	0.78
annual - herbaceous perennial	PC3	-0.91	-1.33	-0.49
annual - woody	PC3	-4.73	-5.50	-3.95
herbaceous perennial - woody	PC3	-2.32	-2.83	-1.81

General discussion

Biological invasions are a major driver of global change, affecting both biodiversity and ecosystem functioning. Therefore, we urgently need to understand how exotic species establish and affect the invaded communities. Using a biogeographical functional trait approach, this thesis compares exotic plant species in their native and introduced regions and investigates how they assemble in introduced communities. The study of exotic plant species in their regions of origin has emerged as an informative framework to address questions such as the importance of abiotic and biotic factors, species traits and preadaptation in plant invasions.

We have explored four aspects of plant invasions: (i) the role of exotic species in the structure of donor and recipient communities based on their abundances, (ii) the differences between native and exotic species traits, (iii) the relationship between the functional structure of native and exotic species and the environment, and (iv) the extent of intraspecific trait variance in assemblages of native and exotic species.

The role of exotic species in the taxonomic structure of donor and recipient Mediterranean communities

Through comparing grassland flora in California and Spain, along a similar environmental gradient, we found that the abundance of exotic species in their putative communities of origin is a good proxy for their abundance abroad. Only a small subset of exotic species, those categorised as pest, achieved greater abundance in the recipient than in the putative donor communities (**Chapter 1**). This supports recent studies of other temperate and Mediterranean ecosystems (Firn et al. 2011, Pearson et al. 2018), and challenges the assumption that exotic species are more abundant in introduced regions (Hierro et al. 2005). Our findings also indicate that biogeographical factors that promote spread are less determinant in plant invasions than species attributes and environmental constraints (Colautti et al. 2014), and offer a parsimonious perspective on biological invasions, where exotic plant species are ecological generalists equipped with a set of

attributes that allow them to thrive across regions with comparable climate and disturbance regimes (Clavel et al. 2011). In fact, the ecological tolerances of the exotic species in their native range, or number of habitats they occupy, is a main determinant of their naturalisation success abroad (Pyšek et al. 2015, Casado et al. 2018).

Exotic species aggregate in disturbed habitats (Arianoutsou et al. 2013), and often facilitate the establishment of other exotic species (Simberloff and Holle 1999, Stotz et al. 2020). Thus, exploring different aspects of community assembly is of utmost importance in the emergence of these novel ecosystems and the homogenisation of species pools across landscapes (Hobbs et al. 2009). We have proposed a new approach to explore synergic effects in community assembly by testing whether communities assemble more similarly as the number of shared species increases (**Chapter 1**). We could not reach consistent conclusions due to the limited number of pairs of Spain-California plots with over three shared species. We encourage future research to consider this analysis in order to determine whether synergic effects of species interactions play an important role in the assembly of exotic species in communities outside their native region.

Trait differences between native and exotic species in Mediterranean communities

The strong environmental constraints in Mediterranean regions might limit the attributes of coexisting species. Yet, we found that native and exotic species had different functional strategies not only in Mediterranean grassland communities (**Chapter 2**), but also across other Mediterranean community types (**Chapter 3**). The higher specific leaf area and photosynthetic rates of exotic species compared to native species was the main pattern that emerged from this thesis, and results in communities dominated by fast-growing and resource acquisitive exotic species. In comparison, native species showed conservative resource uptake adaptations. Thus, being functionally different may be an advantage in Mediterranean communities, as it has been demonstrated in ecosystems

from other biomes, such as Temperate (Helsen et al. 2020), Antarctic (Mathakutha et al. 2019) or Tropical (Henn et al. 2019).

As we studied current invasion patterns, we cannot directly infer whether exotic species displaced functionally similar species or occupied a previously empty niche. However, it is worth mentioning two considerations in this regard. First, we showed that exotic species already display traits related to a more acquisitive strategy of resources than other species in their native grassland communities (**Chapter 2**). Many of these species have been preadapted to agricultural landscapes for millennia (MacDougall et al. 2018). Preadaptation had conferred these species suites of traits to thrive in managed landscapes, facilitating their naturalisation in the Mediterranean Basin. Preadaptation could also explain the impoverishment of California flora (**Chapter 1**). Therefore, while introduced European species had thousands of years to adapt to the new ecological niches created by pastoralism and cultivation (Eriksson 2013), California flora was naïve to intensive agricultural practices and probably failed to compete with species that arrived from Europe (HilleRisLambers et al. 2010). Second, many exotic species across Mediterranean communities were herbaceous species from a few plant families, whereas native species were mostly woody (**Chapter 3**). Woody plants have high stomatal control and nutrient conservation, a widespread strategy in highly seasonal environments such as Mediterranean ecosystems (Pérez-Ramos et al. 2013, Tordoni et al. 2019). Evolutionary constraints might have limited the potential of some native lineages to develop certain life history strategies (Mack 2003). In this regard, we might hypothesise that exotic species might be occupying an empty niche. Overall, the findings of this thesis elucidate that, under similar propagule pressures, species that establish successfully seem to be those that allocate more resources to growth and have an annual life cycle (Kowarik 1995), and that the establishment of European species abroad might have not been random, but rather a reflection of their competitive advantage at home (**Chapters 1 and 2**).

Unfortunately, we could not assess the functional trait differences between naturalised and invasive species. We separated exotic species into these two categories in **Chapter 1**, but we merged them in **Chapter 2** in order to have enough representation of all groups per plot to undertake analyses. Also, all exotic species included in **Chapter 3** were invasive in the introduced areas. Many studies have highlighted that certain traits are related to different levels of invasiveness (Divíšek et al. 2018, Mathakutha et al. 2019). We argue that, in order to answer this question, a large screening of plant traits controlling by habitat types is necessary. This might be of particular interest in regions known to be "donors" of exotic species (Van Kleunen et al. 2015, Casado et al. 2018). Thus, we could prioritise management actions by targeting exotic species according to the information we have about their native regions and elaborate lists of potential invaders to complement lists of current exotic species.

Environmental gradients and the context-dependency of plant functional traits

We consistently found that abiotic factors shape the functional structure of communities, making traits very context-dependent. Mediterranean regions are subjected to strong environmental stress, which is expected to constrain the attributes displayed by coexisting species. For instance, we found that resource availability was a main source of segregation among communities in the trait-space, and that water and phosphorus use strategies of both native and exotic species were highly constrained within communities (**Chapter 3**). The context-dependence of trait comparisons can be summarised under the "join-the-locals" or "try-harder" hypotheses (Tecco et al. 2010). These hypotheses respectively suggest that the environment acts as a filter on native and exotic species traits causing functional convergence of the entire community, or that exotic species outcompete natives by being functionally different. We have described that productivity modulated trait segregation between native and exotic species in the invaded region in California **(Chapter 2)**. While leaf and root traits of native and exotic species converged in less productive sites, we found evidence of trait divergence with exotic species being more acquisitive in

more productive sites. This supports that exotic species "join-the-locals" in resource poor environments, and "try-harder" as productivity increases (Henn et al. 2019, El-Barougy et al. 2020). The opposite pattern was found for plant height, which supports that nutrient availability increases competition for light (Grime 2006).

In the native range in Spain, we did not find changes in the level of niche segregation along the productivity gradient (**Chapter 2**). We argue that the effect of exotic species may be buffered at home due to the high diversity and turnover of native species observed across plots and sites (Levine et al. 2004), as well as the long exposure of the species pool to intense agricultural regimes (MacDougall et al. 2018). In addition, we found synchronous responses of the entire community to productivity. Communities in less productive sites had higher specific leaf area and root length, reflecting a higher ratio of annual species (**Chapter 2**). It is frequently expected that plants in resource limited conditions show traits that assure continue leaf function (Wright et al. 2004). Yet, our results indicate that fast resource uptake might also be advantageous for species in highly seasonal environments by maximising growth rates and completing their life cycles during spring. We also found that herbaceous exotic species in phosphorus and nitrogen impoverished sites can have higher leaf nutrient concentration than natives (**Chapter 3**). Thus, having short life cycles can also be beneficial for exotic species in unproductive environments.

Another noteworthy aspect are root traits, one of the less explored functional traits in plant communities (de la Riva 2016). Our analyses indicate that root traits associated to the acquisition of resources (i.e. specific root length) and resistance to disturbance (i.e. root dry matter content) are important in community assembly processes (**Chapter 2**). Whereas specific root length was very sensitive to environmental variation in Spain, root dry matter content constituted a main axis of differentiation between native and exotic species along the environmental gradient in California. Exotic species had greater root dry matter content than natives, indicating that higher longevity and resistance to disturbance of below-

ground organs might be beneficial in highly disturbed habitats. In addition, our study supported that leaf and root traits together explain how herbaceous species in Mediterranean grasslands respond to productivity. These results urge future investigations to consider belowground traits to fully comprehend how native and exotic species coexist and respond to the environment.

Trait intraspecific variability in highly invaded communities

Another aspect of plant function explored in this thesis is the importance and extent of intraspecific trait variation across communities. The consideration of intraspecific variation within regions substantially increased our ability to understand changes in the functional structure of communities with productivity (**Chapter 2**). Intraspecific variation accounted for 23 to 29% of the total variance in root traits and the isotopic carbon fraction. This indicates that below ground organs and species' water use efficiencies are flexible and very responsive to water and nutrient availability. Thus, failing to consider the response of a given taxon to the ecological limitations of a site might result in overstating other components of functional variation, such as species abundance or occurrence. This is especially concerning in studies of plant invasions, as exotic species are frequently generalists that thrive along ecological gradients (Gallien et al. 2010, Clavel et al. 2011).

A few patterns emerged when comparing the extent of intraspecific variation in native and exotic assemblages of highly invaded communities (**Chapter 3**). First, our results are in line with several studies which highlighted that intraspecific variance accounts for around a 25% of the total trait variance and, therefore, constitutes a non-negligible source of functional variation within communities (Albert et al. 2010, Siefert et al. 2015). Hence, neglecting intraspecific variance might result in over or understating community diversity and related ecosystem processes. Second, the contribution of intraspecific variance was on average higher in the functional axis related to resource use efficiency and leaf nutrient concentration. This supports that morphological traits, such as leaf mass

per area, might be moderately conserved within populations, whereas physiological traits are more flexible and responsive to the environment (Kazakou et al. 2014, Siefert et al. 2015). Third, the contribution of intraspecific variance to trait diversity was slightly greater in exotic species. We show that, although the pool of native species was double that of exotic species in four out of eight communities, exotic species were more diverse than natives (**Chapter 3**). Whereas the main source of functional diversity of native species seemed to be interspecific differences in plant height. Intraspecific variance was a main source of total trait variance in some exotic communities such as serpentine grassland and acid sand fynbos. This is an interesting finding because taxonomic richness increases the probability of finding functionally distinct species, and shows that exotic species might display great phenotypic variation (Sultan 2001, Funk 2008). On the other hand, differences in the extent of intraspecific variability between native and exotic species might be largely driven by differences in life forms. Exotic species were mostly therophytes, whose tissues are probably less structurally constrained (Maire et al. 2013) and more responsive to environmental heterogeneity (Chapin et al. 1990) than long-lived species. We encourage future research to address the extent of different sources of variation in native and exotic species, and consider intraspecific variation in order to reach accurate inferences of trait-driven ecological processes.

Conclusions

We explored how exotic species assemble in communities of their native and introduced Mediterranean regions from a taxonomic and functional approach. This thesis contributes to our understanding of invaded Mediterranean communities, and provides interesting insights to predict which species might have intrinsic potential to invade.

I. The pool of exotic species from the Mediterranean Basin is rich and abundant in their donor communities in Spain and recipient communities in California. This results in a great floristic similarity between the native and invaded grassland communities.

II. In Mediterranean grassland communities, the abundance of herbaceous species in their native range (Spain) is a good proxy of their potential abundance in the introduced range (California). Only a small subset of exotic species is significantly more abundant in the introduced range.

III. Exotic plants in Mediterranean communities have higher specific leaf area and maximum photosynthetic rates than native species from the invaded communities and other species from their native range, which indicate that an acquisitive profile is advantageous across their distribution range.

IV. Differences in height, leaf and root attributes between native and exotic species are constrained by resource availability. In the invaded communities, niche segregation between native and exotic species increased with productivity, with exotics being frequently more acquisitive.

V. Intraspecific variation makes up about a third of trait variation in plant communities. The contribution of intraspecific variation to total community trait variance may be greater in exotic assemblages, probably reflecting invasive herbs are generalist

species less structurally and physiologically constrained than perennial natives.

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Agradecimientos

He tenido la suerte de conocer a un montón de personas que de una forma u otra me han acompañado y apoyado estos últimos años, haciendo el camino más fácil, y a las que tengo que agradecer que esté hoy aquí escribiendo esto. Para no olvidar ninguna quiero empezar (a dar las gracias) por el principio.

Primero quiero dar las gracias a mi familia. A mis padres y a mi hermana, por estar ahí siempre apoyándome en las buenas y las malas y conseguir que llegar hasta aquí no haya sido tan complicado. Gracias por darme espacio para ir a Virtus a hacer mi pequeño trabajo de investigación, pagarme un máster en Londres y aguantarme durante el camino. Además, no puedo dejar de pensar que mi mayor influencia para haber elegido este camino ha sido mi abuelo José, quien me enseñó a disfrutar el campo y sus madrugones, a hacer mi primer herbario, a pescar y hacer fuego para asar chorizos mientras esperábamos que los galgos pasasen corriendo detrás de la liebre. Me has dejado el mejor legado posible. Por supuesto gracias a mi abuela Aurelia; y a mis abuelos Kiko y Tili, ojalá pudiese compartir esto con vosotros. Gracias a mis primos y mis tíos. Me siento muy privilegiado por tener una familia así.

Gracias a mis amigos de Santa Eugenia: Andrés, Cañas, Clara, Jesús, Laura, Rafa y los que se van sumando a la aventura. Porque a pesar de la distancia estamos cerca y seguimos compartiendo el camino juntos.

Gracias Ale, Alex, David y Paula, mis amigos de la Universidad Autónoma de Madrid. Y Alba, Fami y Mario, mi familia de Londres.

Gracias Mercedes, por enseñar flora ibérica tan bien, y aceptar la propuesta de trabajo de fin de grado de un estudiante lleno de ilusión cuando ya no tenías necesidad de hacer esas cosas. Has sido (con mucha diferencia) la profesora más influyente que he tenido, y ojalá cualquier estudiante pueda encontrar alguien así en el colegio o la universidad.

Gracias David por tu apoyo en el campo, con la identificación de especies y procesando muestras, y a la gente del IRNAS por facilitar el procesado de las muestras de raíz y suelo. También, gracias a la gente de NEON, Open Space, UC Merced Vernal Pools & Grassland Reserve y UC Santa Cruz Natural Reserves, por luchar por la conservación de los paisajes naturales de California, y hacer que la logística y organización del trabajo de campo de un estudiante extranjero fuese más fácil en Estados Unidos que en su propio país.

Gracias Ingrid y a todo el Parker lab por arroparme desde mi primer día en Santa Cruz. Gracias Remy, por dejarme tu coche para conocer California sin apenas conocerme, y Ricky, por las tardes que echamos veleando en la Bahía de Monterrey. Gracias Carla y Tom por abrirme las puertas de vuestra casa en Santa Barbara, y Jennifer por esa breve estancia en Los Ángeles y apoyarme en sacar el primer artículo de esta tesis.

Gracias Diana, Gael, Ivy y Gio por dejarme acompañaros durante cuatro meses, alimentarme y invitarme a vuestras fiestas. Gracias a vosotros mi estancia en Cottbus no fue sólo productiva, sino muy divertida. Gracias también Claudia, Coliette y Klaus, por facilitar mi estancia en la Universidad Tecnológica de Brandemburgo de todas las maneras posibles.

Gracias a todos los amigos que me llevo de Sevilla, ya para siempre. Gracias a mis hermanos en la aventura INPhINIT: Juan, Lina y Nicola. Gracias Rubén por hacerme sentir en casa desde el minuto uno. Gracias Ale, Berni, Dani, Elena, Eneko, Enrico, Grego, Hyeun-Ji, Irene, Javi, Jorge, Manu, Pedro, Rosa, Sarai y Víctor por el aprendizaje juntos, los viajes, las fiestas…

Gracias Josephine por estos tres años.

17 de marzo 2021