PhD Thesis 2021 Javier Galán Díaz

Community assembly of exotic plant species across Mediterranean regions

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Cover illustration: La Honda Creek Open Space Preserve, California, United States (Photo by Javier Galán, 5th May 2019).

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Sevilla, 2021

Galán Díaz, J. 2021. Community assembly of exotic plant species across Mediterranean regions. PhD Thesis, Universidad de Sevilla.

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

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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Javier Galán Díaz received financial support from “la Caixa” Banking Foundation INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centres of Excellence (LCF/BQ/IN17/11620012) and the European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 713673.

This PhD thesis was also supported by the project InvasiBES (PCI2018-092939), through the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, and with the funding organisations Spanish Ministry of Science and Innovation (MCI), the State Research Agency (AEI) and the European Fund for Regional Development (FEDER, UE). It also received support from the project EXARBIN (RTI2018-093504-B-I00) funded by MCI, AEI and FEDER, EU.

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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 rol 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).

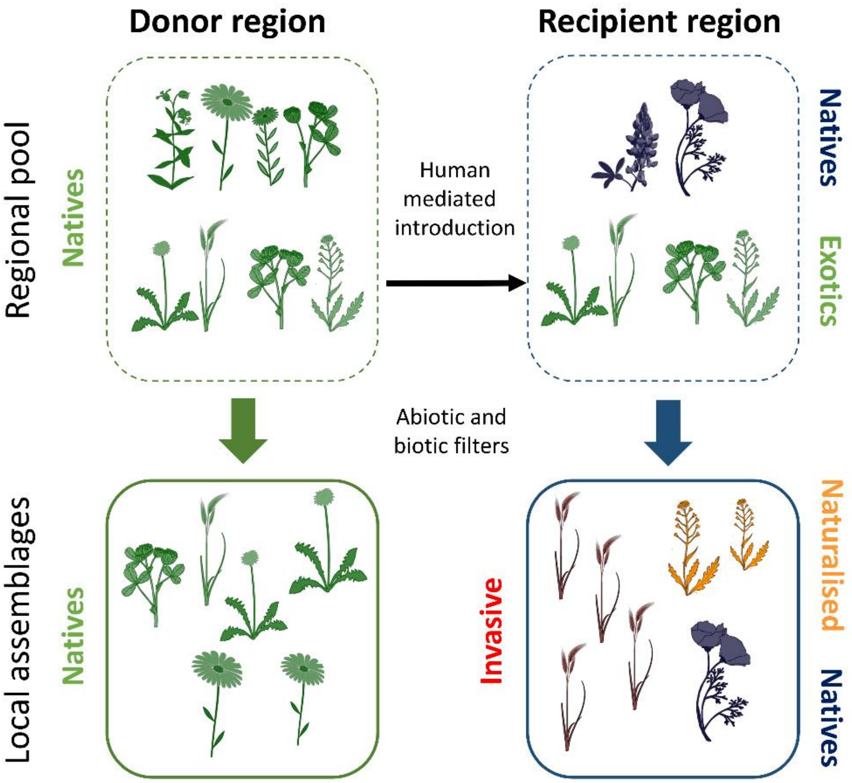


Figure 1. General framework of plant invasions. (a) Species pass geographical barriers assisted by humans. (b) Environmental abiotic and biotic filters, which operate from the regional to the local scale, facilitate or limit the establishment of species with certain characteristics. Some exotic species 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 1992). 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).

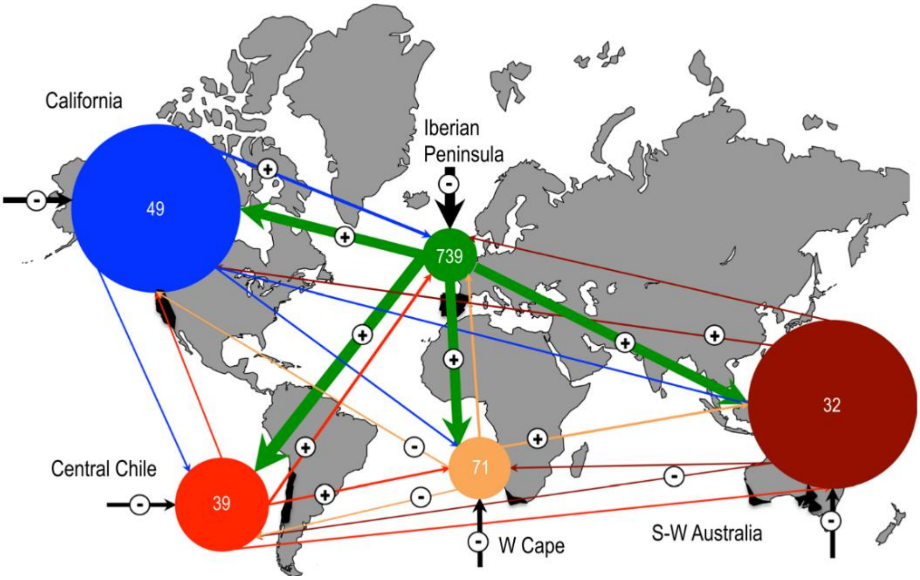


Figure 3. Regions of origin and establishment of unintentionally translocated exotic herbaceous species within the Mediterranean Biome (Casado et al. 2018).

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).

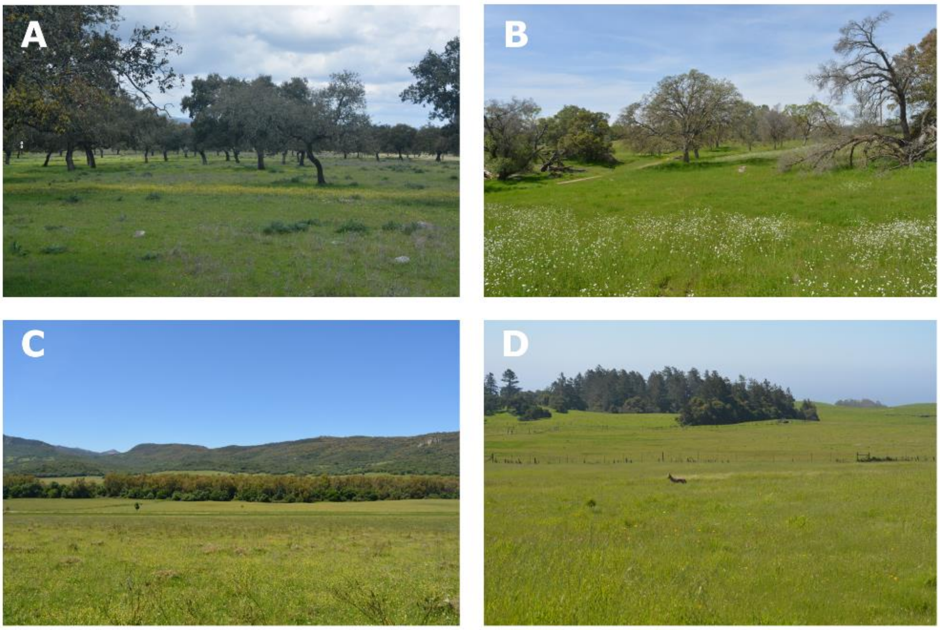


Figure 4. Photographs of grasslands in Spain (a, c) and California (b, d). These habitats are subjected to similar climatic constraints and, after the introduction of herbaceous plant species from the Mediterranean basin to California, share hundreds of species.

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.

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)

Galán Díaz, J., E. G. de la Riva, I. M. Parker, M. J. Leiva, R. Bernardo-Madrid, and M. Vilà. 2020. Plant Community Assembly in Invaded Recipient Californian Grasslands and Putative Donor Grasslands in Spain. Diversity 12:193.

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.

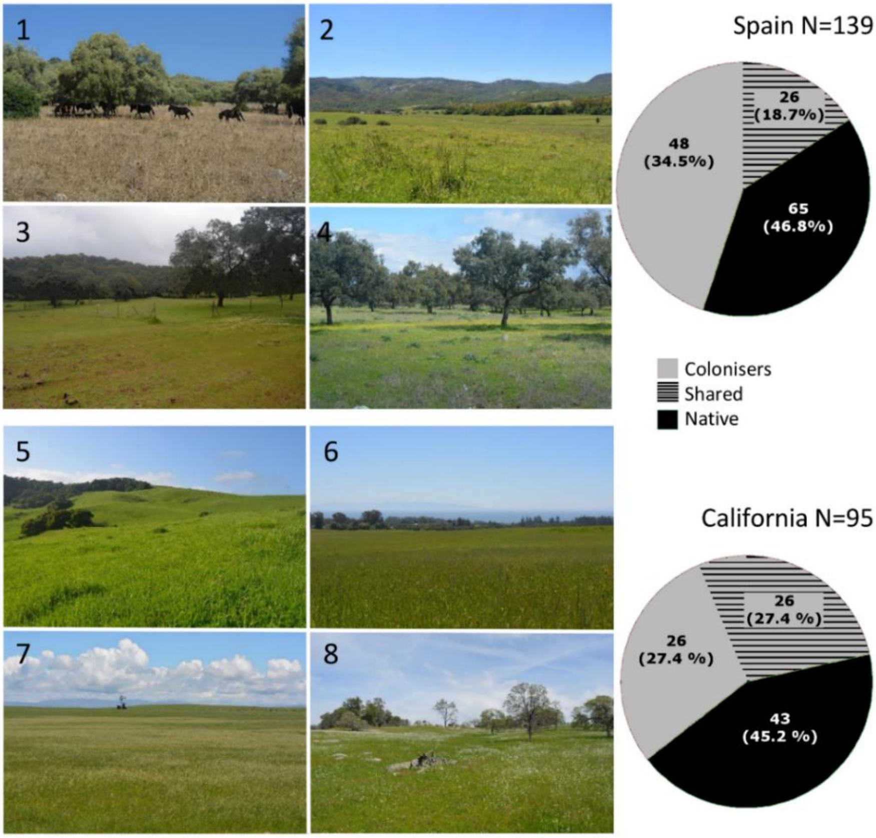


Figure 1. Study grassland sites in the native and the introduced range. Spain (native region): 1. Puerto de la Pared, 2. Montes de Propios, 3. Ventas Quemadas, 4. Navalagrulla. California (introduced region): 5. La Honda Creek, 6. University of California Santa Cruz, 7. Merced Vernal Pools and Grassland 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 (ºC)**	**MCM (ºC)**	**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:

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

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).

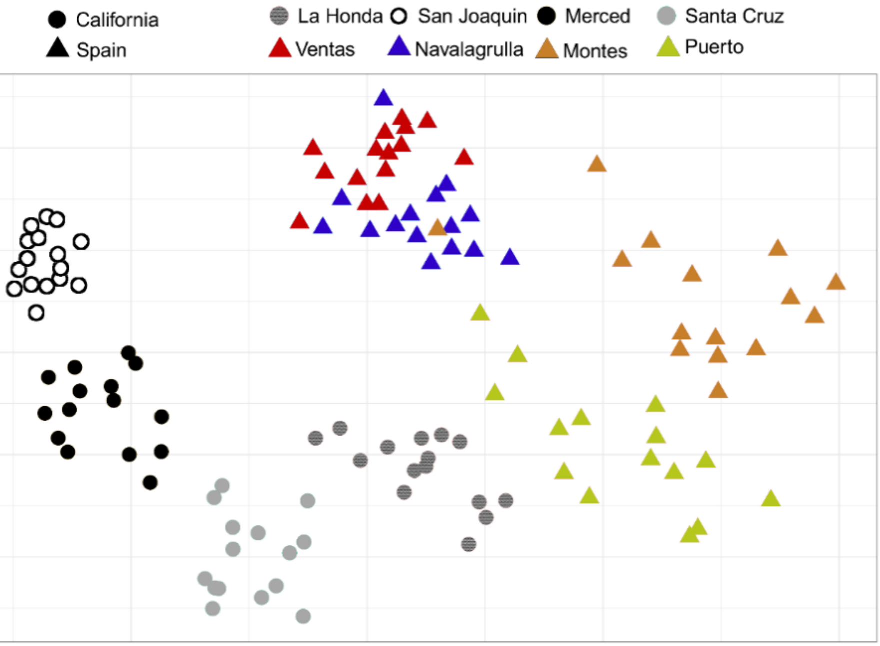


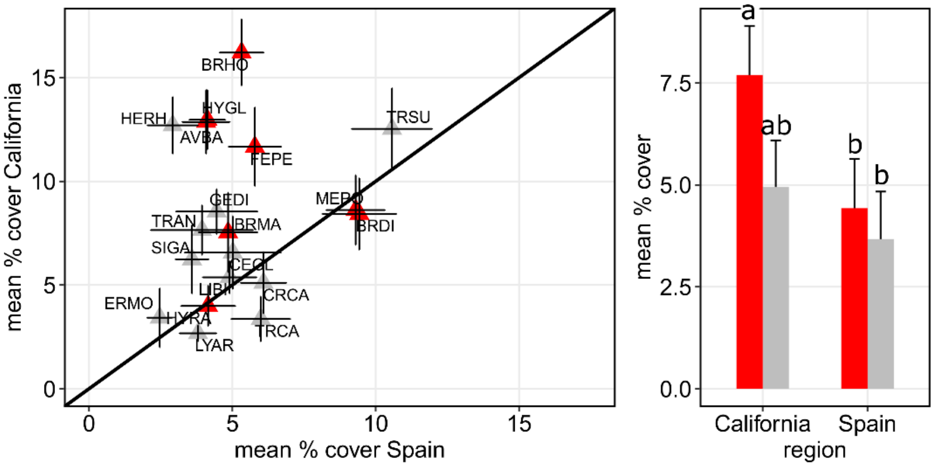
Figure 2. Non-metric multidimensional scaling (nMDS) analysis with species composition and abundance in grassland plots in California (circles) and Spain

(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).



(a) **(b)**

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*.

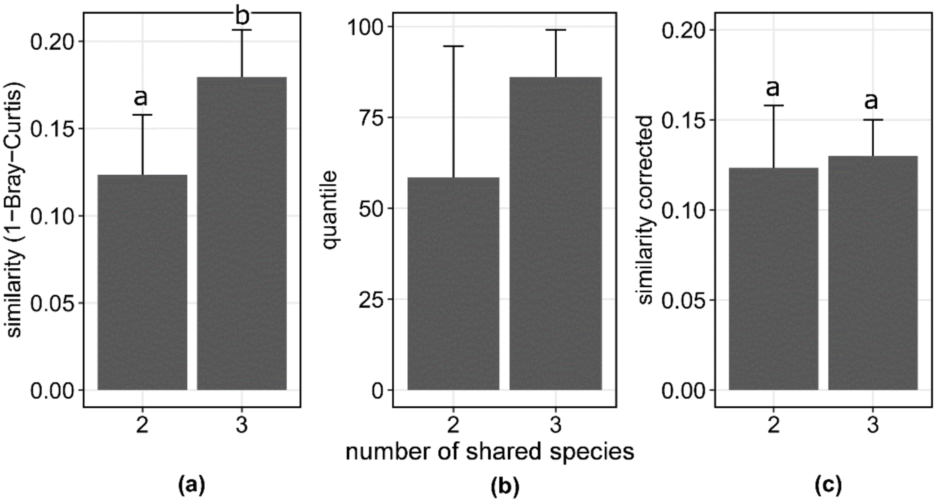


Figure 4. (a) averaged observed similarities between pairs of Californian and Spanish plots grouped by the number of shared species. (b) proportion of null communities with similarities (1–Bray–Curtis) smaller than the observed similarity. (c) comparison of the averaged observed similarities of pairs 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

We thank Caroline Dykstra, David Ragel and Rosa Sutcliffe for fieldwork assistance. This study has received financial support from “la Caixa” INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centres of Excellence (LCF/BQ/DI17/11620012), the European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 713673, and the Belmont project InvasiBES (PCI2018-092939) funded by the Forum-BiodivERsA and the Spanish Ministry of Science and Innovation (MCI).

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	-

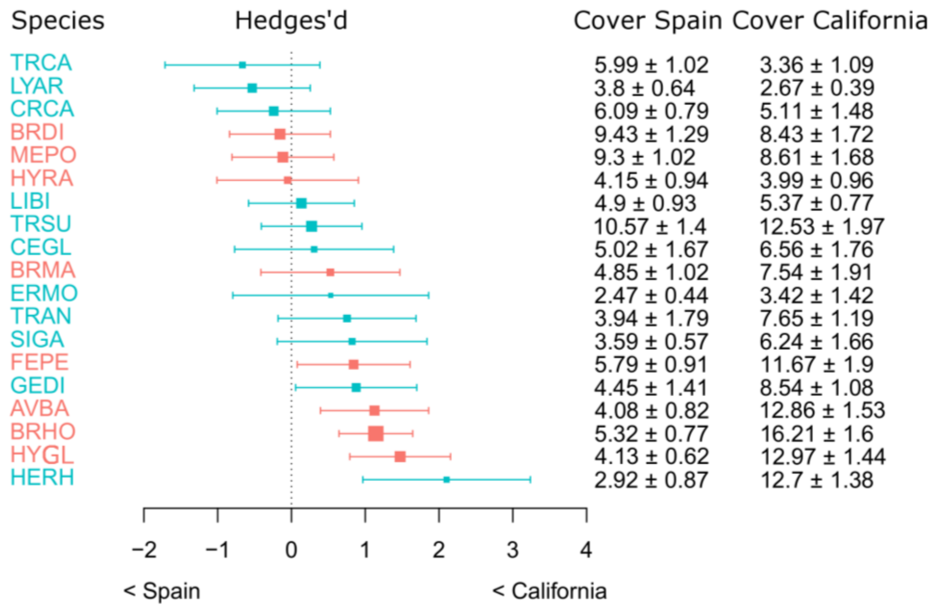
Table S2. Soil properties of studied sites.

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	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

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.

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)

Galán Díaz, J., E. G. de la Riva, J. L. Funk, and M. Vilà. 2021. Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities. Biological Invasions 23:253–266.

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.

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. 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 belowground 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 Alexis, Bea, Carolina, Gareth, Peter y Tom por hacerme disfrutar tanto el master en Kew.

Gracias Isabel por ayudarme a sacar el máximo de mi experiencia investigadora en Londres, darme la oportunidad de trabajar en el laboratorio y herbario del Jardín Botánico de Kew, ayudarme a publicar y hacerme partícipe de tus proyectos.

Gracias a mis directores Montse y Quique, a pesar de mis ansias siempre he tenido la sensación de estar en buenas manos. Montse, gracias por dejarme hacer de mi tesis una experiencia personal, darme la oportunidad de conocer California y respetar mis derechos como doctorando. El tiempo ha demostrado que en cada momento me has ayudado a tomar las decisiones correctas. Quique, gracias por estar ahí en absolutamente todo incluso antes de ser mi director. Siento que he tenido una suerte inmensa de llegar a la EBD poco antes de que te fueses. Tus decisiones, pragmatismo y seguridad a la hora de trabajar han hecho que esta tesis sea posible en algo más de tres años.

Gracias Ana, Diana, Gisela, Paola y todo el equipo de la Fundación la Caixa, por diseñar un programa de becas que busca no solo el crecimiento profesional de los doctorandos, sino también el personal.

Gracias a mis compañeros del cincopuntoseis Ale, Berni, Carlos, Curro, Miguel Ángel, Nacho, Vary, Rocío y Tano. No se puede pedir mejor ambiente de trabajo.

Gracias María José por compartir tu experiencia en California conmigo y ayudarme a arrancar la tesis.

Gracias Caroline y Rosa, por empatizar con un estudiante de doctorado en su pico de estrés, sacar trabajo adelante tan eficientemente siempre con una sonrisa. Hemos aprendido juntos.

Gracias Iñigo y Mariano del Zoobotánico de Jerez, por vuestra labor en la conservación de la naturaleza, y dejarme pasar un día con vosotros aprendiendo sobre la flora y fauna del Parque Natural de Alcornocales.

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