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PLANT INVASIONS:
A MULTI-DISCIPLINARY COMPARISON
BETWEEN COEXISTING NATIVE AND
NON-NATIVE PLANT PAIRS

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Doctoral Programme in Plant Biology

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NON-NATIVE PLANT PAIRS**

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Doctor by the Universitat de les Illes Balears

بحب أهدي هاي الأطروحة لعائلتي ولكل عائلة لبنانية جبرتها الظروف أنو تعيش بعيدة عن بعضها

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Thesis report

This doctoral thesis has been prepared from **compendiums of publications or articles**. The structure consists of a summary, general introduction, objectives, three main chapters, general discussion, conclusions, references, and supplementary material. The language used in the structure is English.

Three articles has been derived from this doctoral thesis, one from each main chapter, the PhD candidate is the first and corresponding author of all of them. Two of them has been already published and one is under review.

Derived from Chapter 1 (published):

Abdallah M, Hervías-Parejo S and Traveset A (2021) Low Pollinator Sharing Between Coexisting Native and Non-native Plant Pairs: The Effect of Corolla Length and Flower Abundance. *Frontiers in Ecology and Evolution* 9:709876. <https://doi.org/10.3389/fevo.2021.709876>, JCR Impact Factor (2022): 4.171 [Q1].

Derived from Chapter 2 (under review):

Abdallah M, El-Keblawy A, Flexas J, Mitterand FT, Ramamoorthy K and Traveset A (2021) Contrasting performance of coexisting native and non-native plant pairs under different resource environments. *Neobiota* (Under review). JCR Impact Factor (2020): 3.684 [Q1]

Derived from Chapter 3 (published):

Abdallah M, Douthe C and Flexas J (2022) Leaf morpho-physiological comparison between coexisting native and non-native plant species in a Mediterranean island. *Biological Invasions* <https://doi.org/10.1007/s10530-022-02797-4>. JCR Impact Factor (2020): 3.133 [Q1].

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Summary

Plant invasions are considered one of the most devastating ecological problems of the 21st century. The current world trends, in particular those related to international trades and human movements, are expected to increase dramatically the extent and frequency of the introduction of non-native species. Although a high number of studies have been dedicated to analyzing how invasions by non-native plants occur, it is still not well understood why some non-native plant species become successfully established outside their native ranges while others do not. In this context, the overarching goal of this Ph.D. thesis was to understand the different mechanisms that underlie under such successful establishment, using a multi-disciplinary approach: ecology, phytochemistry, and leaf physiology. We first evaluated differences between native and non-native species as two different groups of plants, and then we used multiple-species pair experiments (each pair formed by a native and a non-native coexisting species) to search if the observed general patterns can be applied to every particular non-native species in comparison with its native coexisting species. We combined field observations and experiments under controlled conditions to highlight the ecological relevance of our results while allowing us to better investigate the cause-effect mechanisms.

Direct observations revealed that the proportion of pollinators shared by native and non-native species fluctuated from 0 to 33%, and the pollinators most commonly shared in each plant pair were not the most generalized species. The non-native plants tended to acquire a largely different set of pollinators than their native counterparts, suggesting that non-native species caused little interference on the pollination success of the native species. Among the assessed floral traits, corolla length at opening and flower abundance showed to be important in determining the differences in flower visitation rate between natives and non-natives. Our results on the comparisons of morphological and chemical traits showed that only a few of them differed significantly between native and non-native species. On the other hand, the significance of such differences was inconsistent between different resource environments. Such findings indicate that the performance

of non-native plants is 'context-dependent', and does not concur with the idea of non-natives species consistently outperforming native species in high-resource environments and that the latter surpasses non-natives in low-resource environments.

Regarding the phytochemical approach, the impacts of allelochemicals and antioxidant defense mechanisms on non-native plants and their native counterparts were not conclusive. The leaf-physiological approach showed that the assessed non-native species on a Mediterranean island tended to have advantageous values in their leaf physiological traits, such as possessing lower leaf construction cost as compared to the co-occurring native ones. Non-native species also possess larger mesophyll conductance (g_m) and lower mesophyll conductance limitation to photosynthesis (l_m), two novel traits to be added to the 'leaf physiological trait invasive syndrome'. When it comes to the leaf economics spectrum, our findings suggest that native and non-native species are placed on the opposite sides of the leaf economics spectrum, with the non-native species positioned on the fast return end.

Most of our findings support the general trend that the successful establishment of non-native species in new geographical zones could be influenced by one or multiple mechanisms. Yet, they also illustrate that this cannot be generalized for every particular non-native plant when comparing it with its native coexisting plant species. This fact highlights the importance of evaluating other mechanisms or approaches (e.g., evolutionary ecology, genetics) at multiple stages of the invasion process, and across a larger number of species, to assess whether there is a general pattern contributing to the invasion success of non-native species.

Resumen

Las plantas invasoras son consideradas uno de los problemas ecológicos más devastadores del siglo XXI. De acuerdo con las proyecciones globales actuales, en particular las relacionadas con el comercio internacional y la movilidad de seres humanos, se proyecta que el alcance y la frecuencia de la introducción de especies no autóctonas aumentará drásticamente. Aunque se han dedicado una gran cantidad de estudios a analizar cómo se producen las invasiones de plantas no nativas, aún existe un gran desconocimiento sobre por qué algunas especies de plantas pueden establecerse con éxito fuera de sus áreas de distribución nativas mientras que otras no. En este contexto, el objetivo general de esta tesis doctoral fue comprender los diferentes mecanismos que subyacen a este establecimiento exitoso, utilizando para ello una aproximación multidisciplinar que combina tres enfoques: ecología, fitoquímica y fisiología foliar. En primer lugar, evaluamos las diferencias entre las especies nativas y no nativas como dos grupos diferenciados, y después realizamos experimentos de pares de especies (cada par formado por una especie nativa y una no nativa coexistente) para buscar si los patrones generales observados se pueden aplicar a cada especie no nativa en particular en comparación con las especies nativas coexistentes. Esta tesis, además, combina observaciones de campo y experimentos en condiciones controladas, lo que permite obtener resultados relevantes a nivel ecológico y, al mismo tiempo, investigar mejor los mecanismos de causa y efecto.

Observaciones directas en campo mostraron que la proporción de polinizadores compartidos por especies nativas y no nativas fue de 0-33%, y que los polinizadores más comúnmente compartidos entre las especies nativas y no nativas coexistentes no fueron los polinizadores más generalistas. Nuestros resultados demuestran que las especies no nativas tienden a adquirir un conjunto de polinizadores muy distinto al de las plantas nativas con las que cohabitan, lo que sugiere que las especies no nativas interfieren poco en el éxito de polinización de las especies nativas. Al estudiar las diferencias entre las plantas nativas y no nativas en la tasa de visitas de polinizadores a las flores, encontramos que la longitud de la corola hasta la apertura y la abundancia de flores son rasgos florales determinantes. En los referidos a los rasgos morfológicos y químicos, nuestros resultados mostraron

que solo unos pocos de los rasgos analizados diferían significativamente entre especies nativas y no nativas. Además, la importancia de tales diferencias fue inconsistente al comparar ambientes que diferían en la disponibilidad de recursos. Tales hallazgos indican que el rendimiento de las plantas no nativas depende del contexto, y no concuerda con la idea de que las especies no nativas superan consistentemente a las especies nativas en ambientes con alta disponibilidad de recursos y que las nativas superan a las no nativas en ambientes con baja disponibilidad de recursos.

Con respecto al enfoque fitoquímico, no se obtuvieron resultados concluyentes al comparar los impactos de los aleloquímicos y los mecanismos de defensa antioxidante de plantas nativas y no nativas coexistentes. El enfoque centrado en la fisiología foliar mostró que las especies no nativas evaluadas en las islas del Mediterráneo tienden a tener rasgos fisiológicos foliares beneficiosos, como un menor coste de construcción de hojas, en comparación con las especies nativas con las que cohabitan. Las especies no nativas también mostraron una mayor conductancia del mesófilo (g_m) y una menor limitación de la conductancia del mesófilo para la fotosíntesis (l_m), dos nuevos rasgos que esta tesis incorpora al "síndrome invasivo del rasgo fisiológico foliar". Con respecto al espectro de economía foliar, nuestros hallazgos sugieren que las especies nativas y no nativas se ubican en los lados opuestos del espectro de la economía foliar, con las especies no nativas ubicadas en el extremo de rápido retorno. Es necesario que estudios futuros evalúen si este es un patrón generalizable a otras especies.

La mayoría de nuestros hallazgos respaldan la tendencia general de que el establecimiento exitoso de especies no nativas en nuevas zonas geográficas podría estar influenciado por uno o múltiples mecanismos. Sin embargo, también ilustran que esto no se puede generalizar para cada planta no nativa en particular cuando se compara con su especie nativa coexistente. Este hecho destaca la importancia de evaluar otros mecanismos o enfoques (p. ej., ecología evolutiva, genética) en múltiples etapas del proceso de invasión y en un mayor número de especies, para evaluar si existe un patrón general que contribuya al éxito de la invasión de especies no nativas.

Resum

Les plantes invasores són considerades un dels problemes ecològics més devastadors del segle XXI. D'acord amb les projeccions globals actuals, en particular les relacionades amb el comerç internacional i la mobilitat d'éssers humans, es preveu que l'abast i la freqüència de la introducció d'espècies no autòctones augmentarà dràsticament. Encara que s'han dedicat una gran quantitat d'estudis a analitzar com es produeixen les invasions de plantes no natives, encara existeix un gran desconeixement sobre per què algunes espècies de plantes poden establir-se amb èxit fora de les seves àrees de distribució natives mentre que d'altres no. En aquest context, l'objectiu general d'aquesta tesi doctoral va ser comprendre els diferents mecanismes que sustenten aquest establiment exitós, utilitzant per a això una aproximació multidisciplinària que combina tres enfocaments: ecologia, fitoquímica i fisiologia foliar. En primer lloc, avaluem les diferències entre les espècies natives i no natives com dos grups diferenciats, i després realitzem experiments de parells d'espècies (cada parell format per una espècie nativa i una no nativa coexistent) per a buscar si els patrons generals observats es poden aplicar a cada espècie no nativa en particular en comparació amb les espècies natives coexistents. Aquesta tesi, a més, combina observacions de camp i experiments en condicions controlades, la qual cosa permet obtenir resultats rellevants en l'àmbit ecològic i, al mateix temps, investigar millor els mecanismes de causa i efecte.

Observacions directes al camp van mostrar que la proporció de pol·linitzadors compartits per espècies natives i no natives va ser de 0-33%, i que els pol·linitzadors més comunament compartits entre les espècies natives i no natives coexistents no van ser els pol·linitzadors més generalistes. Els nostres resultats demostren que les espècies no natives tendeixen a adquirir un conjunt de pol·linitzadors molt diferent del de les plantes natives amb les quals cohabituen, el que suggereix que les espècies no natives interfereixen poc en l'èxit de pol·linització de les espècies natives. En estudiar les diferències entre les plantes natives i no natives en la taxa de visites dels pol·linitzadors a les flors, trobem que la longitud de la corol·la fins a l'obertura i l'abundància de flors són trets florals determinants. En referència als trets morfològics i

químics, els nostres resultats van mostrar que només uns pocs dels trets analitzats diferien significativament entre espècies natives i no natives. A més, la importància de tals diferències va ser inconsistent en comparar ambients que diferien en la disponibilitat de recursos. Tals resultats indiquen que el rendiment de les plantes no natives depèn del context, i no concorda amb la idea que les espècies no natives superen consistentment a les espècies natives en ambients amb alta disponibilitat de recursos i que les espècies natives superen a les no natives en ambients amb baixa disponibilitat de recursos.

Respecte a l'enfocament fitoquímic, no es van obtenir resultats concloents en comparar els impactes de les substàncies al·loquímiques i els mecanismes de defensa antioxidant de plantes natives i no natives coexistents. L'enfocament centrat en la fisiologia foliar va mostrar que les espècies no natives avaluades a les illes del Mediterrani tendeixen a tenir trets fisiològics foliars beneficiosos, com un menor cost de construcció de fulles, en comparació amb les espècies natives amb les quals cohabiten. Les espècies no natives també van mostrar una major conductància del mesòfil (g_m) i una menor limitació de la conductància del mesòfil per a la fotosíntesi (l_m), dos nous trets que aquesta tesi incorpora a la "síndrome invasiva del tret fisiològic foliar". Respecte a l'espectre d'economia foliar, les nostres troballes suggereixen que les espècies natives i no natives se situen en els costats oposats de l'espectre de l'economia foliar, amb les espècies no natives situades en l'extrem de ràpid retorn. És necessari que estudis futurs avaluïn si aquest és un patró generalitzable a altres espècies.

La majoria dels nostres resultats recolzen la tendència general que l'establiment exitós d'espècies no natives en noves zones geogràfiques podria estar influenciat per un o múltiples mecanismes. Tanmateix, també il·lustren que això no es pot generalitzar per a cada planta no nativa en particular quan es comparen amb la seva espècie de planta nativa coexistent. Aquest fet destaca la importància d'avaluar altres mecanismes o enfocaments (p. ex., ecologia evolutiva, genètica) en múltiples etapes del procés d'invasió i en un major nombre d'espècies, per a avaluar si existeix un patró general que contribueixi a l'èxit de la invasió d'espècies no natives.

With nearly 5,000 years of history, **Lebanon** is one of the world's oldest countries. Though much of the late 20th and early 21st century was scarred by violence, underneath is a country filled with stories and brilliant possibilities for rewarding journeys. Along this Ph.D. I will be taking you for a little promenade throughout my magical country.



Legend has it that the Lebanese capital of **Beirut** was rebuilt from the ashes seven times, making it an urban phoenix in mythology.

Photo by Carlos Haidamous

General introduction

Invasive plant species

According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report (IPBES, 2018a), invasive plant species are defined as plants introduced, purposely or accidentally, into places out of their natural range of distribution, where their establishment and spread can generate a series of impacts on the hosting ecosystems. So far, plant invasions are considered to be one of the most potent global ecological threats during the 21st century (Early et al., 2016). On a global level, the total number of plant species introduced in novel ranges worldwide has continuously increased since centuries, but the current world trends, in particular those for international trades and human movements, are increasing dramatically the extent and frequency of non-native species introduction (Humair et al., 2015; van Kleunen et al., 2018).

However, the level of invasion varies differently among regions, biomes, and habitats (Chytrý et al., 2008; Andreu and Vilá, 2011). It has been shown that temperate regions are more susceptible to invasions than the tropics (Lonsdale, 1999; Rejmánek et al., 2005), the new world invaded more often than the old world (Pyšek et al., 2017), and islands and coastal mainland regions more than mainland regions (Dawson et al., 2017). The trend of introducing non-native species has caused an increase in the likelihood of new invasion events with subsequent important impacts on the structure, function, and dynamics of ecosystems, as well as major socio-economic damages. Numerous studies have summarized the impact of these species. According to Pearson et al. (2018), non-native species can interfere in the establishment of native species and consequently affect plant community structure and assembly. The newly arrived species can threaten biodiversity leading to extinctions (Powell et al., 2011; Bellard et al., 2016), and change soil properties (Castro-Díez et al., 2019), nutrient cycling (Vilá et al., 2011), fire regimes (Brooks et al., 2004) and hydrology (Levine et al., 2003). They also present a severe economic impact. Novoa et al. (2021) demonstrated that the

global costs associated with non-native plants are massive, at least US\$ 8.9 billion between 1970 and 2017, and they are increasing rapidly.

Invasion process

To become invasive, a species must pass through a number of transitions (the invasion process) (IPBES, 2018a). This process is divided into three stages (introduction of the species, initial colonization and establishment, and subsequent dispersal and spread).

Introduction of plant species

The majority of long-distance introductions of non-native species to new areas are the direct or indirect result of human activities, and social and economic factors are often as much critical as biological factors are in their introductions. Throughout the history, many non-native plant species were introduced deliberately due to their economic (forage, fiber, and/or timber production), environmental (erosion control and reforestation campaign) or cultural (landscape gardening) benefits (Liu et al., 2012; Pipek et al., 2020; Pyšek et al., 2020). Other species have been introduced accidentally as stowaways or contaminants, impure crop seeds, adhesion to domesticated animals, or human clothes (Saul et al., 2017). It is evident that the vectors (ship, train, aircraft, or other vehicles) through which non-native species are transported and introduced to new regions are changing over time (Hulme et al., 2008; Essl et al., 2015) and it is apparent that some of the most problematic invasive species arrive through multiple vectors (Essl et al., 2015; Saul et al., 2017) and repeated introductions (Wilson et al., 2009).

Initial colonization and establishment

Colonization of new habitats requires that the first arrivals initiate new populations. Species with multiple reproductive strategies (e.g., both vegetative reproduction and seeds) or plants with multi-seeded fruits may be good colonists (Riccardi and Jones, 2011). After initial successful arrival, the next stage of invasion is characterized by establishment of a self-sustaining and viable population. This stage in the invasion process requires that non-native individuals both survive and reproduce in the new environment, and hence that barriers to survival and reproduction are overcome (Rojas-

Sandoval and Acevedo-Rodríguez, 2015; Pyšek et al., 2020). Invasiveness of the newly arrived species and the invasibility of the recipient ecological network are interlinked (Hui et al., 2021). Establishment success is a function of the interaction between traits of the species (e.g., behavior, physiology, life history) and invasibility of the environment (e.g., climate, habitat) (Alpert et al., 2000). But crucially it also depends on human actions and factors related to the introduction event, such as propagule pressure (Duncan et al., 2003; Redding et al., 2019).

Subsequent dispersal and spread

Once initial establishment has occurred, non-native species will disperse and spread across the new environment, increasing the size of their geographic distribution (Williamson, 1996). Wind, water, and animals, particularly birds, are most often the dispersal agents of seeds; these dispersal agents not only move seeds away from parent plants but also may spread the seeds to similar sites with similar conditions, thus increasing the probability of seedling survival (Schiffman, 1997; Traveset et al., 2014).

Predicting invasiveness based on different disciplines

Researchers have intensively investigated the attributes that give the newly arrived species their invasive capacity. These attributes have been shown to be multiple, ranging from biotic to abiotic interactions to many other ecological features (Traveset and Richardson, 2021). Several studies have demonstrated that the presence of these interactions can influence the invasion trajectories by facilitating the performance, abundance, and population growth of non-native plants (Richardson et al., 2012). Other studies, however, have linked invasion to specific traits. Non-native plants have shown to possess higher growth-related traits (Ridenour et al. 2008; Caño et al., 2009; Ni et al., 2020), larger photosynthetic capacity (Zunzunegui et al., 2020; Morais et al., 2021), more flowers/inflorescences (Padrón et al., 2009; Kaiser-Bunbury et al., 2011), and higher allelopathic effect (Thiébaud et al., 2019) than native ones.

Biotic interactions

Biotic interactions are defined as the relations that are established between at least two organisms of one or more species. These interactions are essential for the survival of any species, and this is certainly true for non-native plant species in a novel environment (Hui and Richardson, 2017; Hui et al., 2020). The consideration of biotic interactions in invasion ecology has facilitated a better understanding of the mechanisms that allow non-native species to integrate into receptive communities, and the effects that such interactions have during the invasive process on the functioning of invaded communities (Hui and Richardson, 2017). Besides habitat suitability, the success of non-native species depends on biotic interactions in a profound way. Plant invaders interact not only with other plant species via resource competitors (Wandrag and Catford, 2020), but also depend on species from different guilds such as soil microbial communities, herbivores, and pollinators (Aizen and Morales, 2020).

Nearly 90% of all flowering plants rely to some extent, or benefit from, pollinators (Ollerton et al., 2011). Nevertheless, a recent review shows that pollination does not always act as an effective barrier to invasion, as most introduced plants are able to receive suitable pollination service from resident pollinators, while others can minimize their reliance on pollinators through different mechanisms (Montero-Castaño and Traveset, 2020). It has been argued that non-native plants that attract a wide range of pollinators, i.e. generalists, are expected to easily form novel interactions with pollinators in the introduced range (the *New Associations Hypothesis*), which will enhance establishment and invasion success (Baker and Stebbins, 1965; Baker, 1974). Not only plants with generalist pollination systems infiltrate resident plant – pollinator communities: plants with specialist pollinators can also be integrated in different ways (Rodger et al., 2010). However, the integration of a particular plant invader will completely depend on different pollinator and flower traits (Montero-Castaño and Traveset, 2020).

Pollinators use flower traits, such as abundance, shape, color, symmetry, and corolla size to locate pollen–nectar sources and discriminate between different flower species (Chittka and Raine, 2006). Various studies have demonstrated that such “cues” are considered to be among the most influential in the flowering plant–pollinator interactions (Gibson et al., 2012; Junker et al., 2013). Darwin (1859) was first to suggest that non-native plants should find higher competition for the same resource in the presence of close relatives in the native flora (*Darwin’s naturalization hypothesis*; DNH). Indeed, in their meta-analysis, Morales and Traveset (2009) reported that non-native species phenotypically similar to natives in floral symmetry and color are especially

unfavorable to native species pollination and reproduction, and the more closely related the non-native and native species were, the more negative was the effect of the non-native species on the native species reproduction.

Abiotic interactions

Several studies have been carried out on the importance of resource availability for explaining invasion success. These studies have shown that native species appear to have a competitive advantage over non-native species in low-resource systems (Funk, 2013; Cramer et al., 2014), while high-resource ecosystems tend to accumulate more non-natives (Huenneke et al., 1990; Gross et al., 2005; Stohlgren et al., 2008). It is difficult to identify a suite of general traits explaining invasiveness, since the invasive capacity of any given species depends as well on characteristics of the invaded habitats (Daehler, 2003; Pyšek and Richardson, 2007; Tecco et al., 2010; Funk, 2013).

Allelopathy

Allelopathy is defined as the effect (stimulatory and inhibitory) of a plant on the development of neighboring plants through the release of secondary compounds. By releasing phytotoxic chemicals into soils via root exudation, litter decomposition or leachates, non-native species may reduce competitive fitness and gain an advantage in resource competition against native species (Smith-Ramesh, 2020). This appears to be the case of a number of non-native species examined, such as bush honeysuckle (*Lonicera maackii*), whose root exudates are toxic to commonly co-occurring native plants (Dorning and Cipollini, 2006). Of the many prominent hypotheses that have been proposed in invasion ecology (Jeschke and Heger, 2018), the *Novel Weapons Hypothesis* (NWH) has been extensively studied. The NWH posits that non-native species release allelopathic chemicals that inhibit and repress potential competitors in their new range. Several studies have shown that non-native species suppressed the native neighbors and facilitated their invasion through the release of chemical compounds into the environment (Vivanco et al., 2004; Ma et al., 2020). However, there are few studies indicating resistance to invasion through allelopathy at community level. For instance, Li et al. (2020) compared the allelopathic suppression of a native community on invasive and native species, finding that the dominant native species, *Vaccinium myrtillus* L., exerted significantly stronger suppression on the invasive species *Picea mariana* (Mill.).

Leaf physiological traits

Among the traits conferring a given species its invasive capacity, the physiological ones have been suggested to play a role in promoting it. Several physiological studies have reported that non-native species have advantageous traits that contribute to their greater success (Funk and Vitousek, 2007; Heberling and Fridley, 2013; Oliveira et al., 2014; Zunzunegui et al., 2020). Such success is generally associated with higher leaf rates of CO₂ assimilation (A) (van Kleunen et al., 2010), higher stomatal conductance (g_s) (Caplan and Yeakley, 2010), water content (Funk, 2013; Oliveira et al., 2014; González-Muñoz et al., 2015) and nitrogen use efficiency (Funk and Vitousek, 2007). Other foliar traits also explain the success of non-native plants (Pattison et al., 1998; Baruch and Goldstein, 1999), since they may contribute to faster growth rates for invaders and confer a competitive advantage over native species (Funk and Vitousek, 2007; Peñuelas et al., 2010). These traits include the leaf mass per area (LMA), which is considered as the ratio between leaf dry mass and leaf area (Poorter et al., 2009). Several studies have demonstrated that non-native species usually possess lower LMA, where this LMA is correlated with physiological traits such that, on average, species with lower LMA tend to have higher leaf nitrogen (N) concentration per unit mass (N_{mass}) and higher photosynthetic rate per unit N (photosynthetic N use efficiency (PNUE)). Another important trait is the leaf area (LA), as Petruzzellis et al. (2021) have shown that non-native plants are likely to have higher LA compared to the co-occurring native species.

The leaf economic spectrum, or LES, is one of the most studied trait dimensions for understanding the limits of plant productivity and their competitive ability in different habitats (Wright et al., 2004; Peñuelas et al., 2010). Wright et al. (2004) have described it as the coordinated changes in the leaf structure/function relationships, running from a slow return end, encompassing species with high LMA, low nutrient content and light saturated photosynthetic rates per unit mass (A_{mass}), to a fast return end with the opposite suite of traits. Recent work has suggested that non-native and native species are aligned on opposite sides of a leaf economics spectrum, placing non-native species cluster on the fast return end of the spectrum with higher values of leaf N and A_{mass} and lower values of LMA relative to native species (Peñuelas et al., 2010; Petruzzellis et al., 2021).

Coexistence between native and non-native species

Despite the large number of studies focused in understanding the different traits underlying the successful establishment of non-native species, the comparison between pairs of native and non-native species that coexist in the same habitat has still received little attention (but see Vilà et al., 2004; Morales and Traveset, 2009; Ha et al., 2020; Gianoli and Molina-Montenegro, 2021). What is clear is that coexistence between native and non-native plant species is common at both local and regional scales in plant communities worldwide (Heard and Sax, 2013) and that this coexistence has often occurred over decades or centuries (Sax and Gaines, 2008; Heard et al., 2012). Closely examining the traits by which each pair of native and non-native coexist may therefore provide an insight on assessing whether the general patterns that explain plants' invasion success are also observed at the scale of coexisting plant pairs.

Objectives

The overarching goal of this Ph.D. thesis was to contribute to the understanding of the different mechanisms that underlie the successful establishment of non-native species in new geographical zone. To reach such goal, we used a multi-disciplinary approach: Ecology (Chapter 1 and 2), Phytochemistry (Chapter 2), and Leaf Physiology (Chapter 3). We combined field observations (Chapter 1) and experiments under controlled conditions (Chapters 2 and 3) to highlight the ecological relevance of our results while allowing us to better investigate the cause-effect mechanisms.

Along this thesis, we first evaluated differences between native and non-native species as two different groups of plants, and then we used a multiple species pair experiments to search if the observed general patterns can be applied to every particular non-native species in comparison with its native coexisting species. For this, we focused on different coexisting plant pairs, each consisting of a native and a non-native species. The selected plant pairs were based on their abundance as coexisting native and non-native species across different locations, varying in their environmental conditions and topographic positions. For the species selection, we chose native and non-native species that were observed to frequently grow side by side in the field.

The thesis is structured in three independent chapters, each addressing specific objectives. However, the chapters are interconnected and contain cross references to other chapters. The specific objectives of each chapter are the following:

In Chapter 1, we evaluated if non-native species attract a new assemblage of pollinators and share only a small proportion of pollinator species with their native counterparts. We measured, under field conditions, to what extent coexisting native and non-native plants share pollinators and tested

whether the most frequently shared pollinator species among the different pairs are the most generalized species. We also wanted to assess if specific floral traits (e.g., flower abundance, corolla shape, symmetry, and size) can explain the difference in diversity and frequency of the pollinators. To accomplish this, we did direct observations in the field of insect flower visitation on four coexisting pairs.

In Chapter 2, we investigated if non-native species are better adapted to both low and high nutrients environments than native species. Specifically, we assessed the differences between coexisting native and non-native plants on their morphological and chemical traits under two different resource environments. Then, we characterized the nature of their interactions and the effect of allelochemicals and antioxidant defense mechanisms on their coexistence. For this, we used five coexisting pairs that were grown in controlled growth chambers under two resource environments (i.e., high and low nutrients availability).

In Chapter 3, we assessed if non-native species on a Mediterranean island possess distinct physiological-related parameters than native species. To do so, we measured and compared the leaf morpho-physiological traits between the coexisting pairs. In association with these traits, we assessed whether any photosynthetic limitation may contribute to a larger photosynthetic capacity of non-native species in comparison to the native ones. Lastly, we checked if the studied non-native plants on a Mediterranean island are also positioned on the high-return end of the leaf economics spectrum. For this, we used eight coexisting pairs that were grown in controlled growth chamber in the absence of stress.



Baalbek, known as The City of the Sun, is an ancient Phoenician city and a home to the Temples of Jupiter, Bacchus, and Venus.

Photo by Carlos Haidamous

Chapter 1

Low pollinator sharing between coexisting native and non-native plant pairs. The effect of corolla length and flower abundance

Understanding the mechanisms by which non-native plants can attract pollinators in their new geographical zones is important because such species infiltrate native communities and can disrupt native ecological interactions. Despite the large number of studies assessing how invasive plants impact plant-pollinator interactions, the specific comparison of pollination interactions between native and non-native plant pairs has received much less attention. Here we focused on four coexisting co-flowering pairs of common native and non-native species, both with abundant flowers but different floral traits, and asked: (1) to what extent native and non-native plants share pollinator species, and whether the non-native plants attract a different set of pollinators, (2) whether the most shared pollinators are the most frequent floral visitors and the most generalized in their interactions, and (3) how much of the variation in the diversity and frequency of pollinator species between native and non-native plant species can be explained by floral trait dissimilarity and flower abundance. Direct pollinator observations revealed that the plant pairs shared a low fraction (0-33%) of insect species, i.e., non-native plants tended to acquire a different set of pollinators than their native counterparts. The most shared pollinators in each plant pair were the most common but not the most generalized species, and non-native species attracted both generalized and specialized pollinators. Corolla length at opening and flower abundance showed to be important in determining the differences in flower visitation rate between natives and non-natives. Our findings support the general pattern that non-native species have no barriers at the pollination stage to integrate into native communities and that they may attract a different assemblage of pollinators relative to those that visit native plants with which they coexist.

Introduction

Among the different interactions that flowering non-native plants establish with other organisms in their new areas, those that involve their pollinators are expected to play an important role in plant reproduction and hence invasion success (Stout and Tiedeken, 2017). This is especially the case of most angiosperms that depend on, or benefit from, animal pollination to set fruits (Klein et al., 2007; Ollerton et al., 2011). Moreover, most of the top invasive plants in the world, at least the woody ones, are biotically pollinated (Traveset and Richardson, 2014). A recent review also shows that the large majority of non-native plants receive suitable pollination service from resident pollinators, whereas other species can minimize their reliance on pollinators by increasing their selfing levels (Montero-Castaño and Traveset, 2020).

An increasing body of literature has emerged in the last two decades assessing how invasive plants infiltrate native plant communities and impact plant-pollinator interactions in them (Aizen and Morales, 2020). Once in a new area, invasive plants attract pollinators that were previously monopolized by the natives (Thijs et al., 2012). Such pollinator “usurpation” can imply lower visitation rates to native flowers which can lead to decreases in seed set (Brown et al., 2002; Moragues and Traveset, 2005; Larson et al., 2006; Lopezaraiza-Mikel et al., 2007; Matsumoto et al., 2010; Thijs et al., 2012) and long-term changes in population size and species richness in the invaded habitats (Emer et al., 2015). By contrast, invasive plants can have a facilitative effect by enhancing pollinator abundance, diversity, and pollination success in native plants (Memmott and Waser, 2002; Feldman et al., 2004; Moragues and Traveset, 2005; Larson et al., 2006; Tepedino et al., 2008). Alternatively, neutral effects of invasive plants on native pollination interactions have been also documented (Aigner, 2004; Moragues and Traveset, 2005; Thijs et al., 2012). Different meta-analyses have indeed shown that the impact of plant invaders on native plant-pollinator interactions is context-dependent, varying among species, local populations, environmental conditions, study designs and other local-scale effects (Morales and Traveset, 2009; Emer et al., 2015; Charlebois and Sargent, 2017). Despite the large number of studies, however, the comparison of pollination interactions between pairs of co-flowering common species that coexist in the same habitat with abundant flowers but with different floral traits has still received little attention (Brown et al., 2002; Morales and Traveset, 2009; Ha et al., 2020).

According to the Darwin’s Naturalization Hypothesis (DNH), non-native plants should find higher competition for the same resource in the presence of close relatives in the native flora (Darwin, 1859). Darwin’s idea was that closely related species are more likely to have similar ecological niches due to

common ancestry, and therefore would be competing for the same resources. By contrast, 'unrelated' species would be relatively free from competition, hence they could more easily enter the new environment. Community-level studies have shown that non-native plants easily integrate into native pollination webs by being visited by resident pollinators (Memmott and Waser, 2002; Traveset et al., 2015; Valdovinos, 2019). This could be expected as non-native species use a wide range of pollinator taxa including generalized species of different functional groups, such as eusocial and solitary bees, flies, other Diptera and Coleoptera (Wilson et al., 2004; Matsuyama et al., 2009; Gómez et al., 2015), but also specialist species (i.e., visit one or very few plant species; Stouffer et al., 2014).

Whether one group of pollinators will be more likely to integrate a particular plant invader than another will depend on different pollinator and plant traits (Parra-Tabla et al., 2019; Montero-Castaño and Traveset, 2020). In the case of plants, flower abundance, shape, color, symmetry and corolla size (width and length) are among the most influential in the flowering plant-pollinator interactions (Gibson et al., 2012; Junker et al., 2013), acting as 'cues' used by flower visitors to discriminate between the different reward sources available (Reverté et al., 2016). In a review study, Morales and Traveset (2009) found that the effect of non-native species on pollination visitation of native plants was more likely to be negative if the native and non-native plants have similar flower symmetry or color, whereas the effect was not significant when species differed in such traits. Co-flowering plant species with dissimilar floral traits have been found to usually attract different pollinator assemblages and thus are not likely to reciprocally facilitate pollination (Reverté et al., 2016; Albor et al., 2020; Ha et al., 2020). Other studies, however, have shown either floral trait similarity to be associated with pollination facilitation (Bergamo et al., 2020) or that pollinator sharing was not related with the floral similarity between native and non-native species (Muñoz and Cavieres, 2019). Therefore, a consensus regarding the role of floral traits on pollinator interactions between native and non-native plant species remains elusive.

In this study, we focused on four different coexisting co-flowering pairs of one native and one non-native species that have morphologically distinct flowers. The two species of each pair are unrelated and very common in the study sites and their flowers are the most abundant in the community. First, we aimed to determine to what extent the coexisting pairs share pollinators, and if specific floral traits (e.g., flower abundance, corolla shape, symmetry, and size) can explain the difference in diversity and frequency of the pollinators. Secondly, we wanted to assess which are the most frequently shared pollinator species and functional groups among the different pairs. Our specific hypotheses were:

(1) Non-native species attract a new assemblage of pollinators, including pollinators of different functional groups, and share only a small proportion of pollinator species with their native counterparts, in accordance with the DNH.

(2) The shared pollinators by each plant pair are the most frequent and/or the most generalized species.

(3) Differences in pollinator species richness, the number of shared pollinator species and visitation rates between native and non-native plant species can be explained by floral trait dissimilarity and flower abundance.

Materials and Methods

Study sites and plant species

The study was carried out at three sites on Mallorca (Balearic Islands, Western Mediterranean Sea), two at the south of the island (Torrent de Sa Riera: 39° 35' 12.6" N, 2° 38' 17.6" E; Platja de Ca'n Pere Antoni: 39° 33' 45.7" N, 2° 39' 43.5" E), and the other at the western part (Torrent d'Esporles: 39° 39' 56.5" N, 2° 34' 46.8" E). Torrent de Sa Riera is an intermittent stream predominately occupied by the native *Withania somnifera* (L.) Dunal and non-native species such as *Nicotiana glauca* Graham and *Physalis peruviana* L. Ca'n Pere Antoni is a sandy beach mostly dominated by species dispersed along its shore such as the native *Glaucium flavum* Crantz and the non-native *Mesembryanthemum crystallinum* L. Lastly, Torrent d'Esporles is also a temporary stream with abundant species such as the annual native *Convolvulus arvensis* L. and *Cyperus involucratus* Rottb and the non-natives *Tropaeolum majus* L. and *Arundo donax* L.

At each study site, the selected co-flowering plant pair, of one native and one non-native species, was based on the species spatial co-occurrence and high flower abundance (Fig. 1; Table 1). Because pollinator activity and flowering characteristics (e.g., flower opening and receptivity) usually fluctuate during daytime and nighttime, we ensured that the chosen flowers of both species within a pair were open and receptive simultaneously, particularly during the direct observations.

Pair 1: *Convolvulus arvensis* L. and *Tropaeolum majus* L

Convolvulus arvensis (Convolvulaceae), native to the Mediterranean Basin, is a climbing perennial plant with solitary flowers on long peduncles. It grows in a wide range of conditions from full sun to full shade, on all soils, particularly on warm, dry soils, and is drought tolerant (Culhavi and Manea, 2011). Its flowering stalk occasionally branches and can produce 1-3 flowers. *Tropaeolum majus* (Tropaeolaceae), native to the Andes Mountains in South America, is a fast growing climbing annual plant. It has single flowers and can form extensive carpet-like growths in sunny torrent banks and beds (Garzón and Wrolstad, 2009).

Pair 2: *Glaucium flavum* Crantz and *Mesembryanthemum crystallinum* L.

Glaucium flavum (Papaveraceae) is a perennial herb, native to the Mediterranean Basin that occurs along its shores and the coasts of Western Europe. Its large flowers have a central tuft of orange stamens and four silky long petals that drop as the long-curved seedpods develop (Thanos et al., 1989). Native to South Africa, *M. crystallinum* (Aizoaceae) is an annual or biennial succulent herb with trailing and branched stem. Its flowers are in cymes, with petals longer than the calyx.

Pair 3: *Hyoscyamus albus* L. and *Nicotiana glauca* Graham

Hyoscyamus albus (Solanaceae) is an herb, primary found in coastal areas in southern Europe and in the Near East, that grows to a height of about 40 or 50 cm. When blooming, it develops a long inflorescence with all flowers attached to the stem. *Nicotiana glauca* (Solanaceae), native to northwestern Argentina and Bolivia, is an evergreen perennial soft-wooded shrub or small tree up to 6 m in height with many branches. It produces flowers that are found in branched clusters (Ollerton et al., 2012).

Pair 4: *Withania somnifera* L. and *Physalis peruviana* L.

Withania somnifera (Solanaceae) is a perennial shrub native to a wide range, spreading from the Mediterranean region through tropical regions of Africa to South Africa and also from the Macaronesian region to the Arabia and Middle East region (Gaurav et al., 2015). Flowers emerge in compact groups from the leaf axils in the shape of a greenish bell. *Physalis peruviana* (Solanaceae) is an herbaceous, semi-shrub, upright, and perennial plant from the subtropical zones of the Andes (South America). It is usually 0.6 to 0.9 m tall, although in some cases it can grow up to 1.8 m. Its hermaphrodite flowers are formed singly in the axils of the leaves on pedicels 1-2 cm long (Cedeño and Montenegro, 2004).

Table 1. Qualitative and quantitative (Mean and SD) values of floral traits and number of open flowers of each studied plant species. Number of measured flowers for bell and corolla width and length =15.

Pair	Species	Status	Shape	Flower symmetry	Corolla length at opening	Corolla total length	Corolla width	Bell width	N open flowers
1	<i>Convolvulus arvensis</i>	native	Funnel	Radial	5.03 ± 0.61	25.13 ± 3.1	31.11 ± 2.19	3.58 ± 0.32	5.7 ± 1.56
	<i>Tropaeolum majus</i>	non-native	Funnel	Bilateral	27.4 ± 2.59	41.11 ± 4.61	60.59 ± 6.43	15.82 ± 1.13	7.9 ± 1.12
2	<i>Glaucium flavum</i>	native	Bell	Radial	21.95 ± 1.92	35.36 ± 3.15	45.67 ± 5.96	30.86 ± 2.03	6.15 ± 1.97
	<i>Mesembryanthemum crystallinum</i>	non-native	Tubular	Bilateral	5.06 ± 0.48	14.22 ± 0.58	23.89 ± 1.59	12.44 ± 1.04	7.85 ± 1.82
3	<i>Hyoscyamus albus</i>	native	Funnel	Bilateral	18.74 ± 0.86	33.83 ± 2.16	22.76 ± 1.94	6.57 ± 0.46	17.9 ± 2.96
	<i>Nicotiana glauca</i>	non-native	Tubular	Bilateral	14.91 ± 0.87	41.56 ± 1.39	9.91 ± 0.83	4.73 ± 0.38	121.9 ± 22.87
4	<i>Withania somnifera</i>	native	Bell	Bilateral	4.42 ± 0.55	8.47 ± 0.71	5.76 ± 0.81	2.88 ± 0.24	37.35 ± 8.36
	<i>Physalis peruviana</i>	non-native	Tubular	Radial	4.88 ± 0.36	14.1 ± 0.83	17.18 ± 1.14	5.1 ± 0.37	4.88 ± 1.67

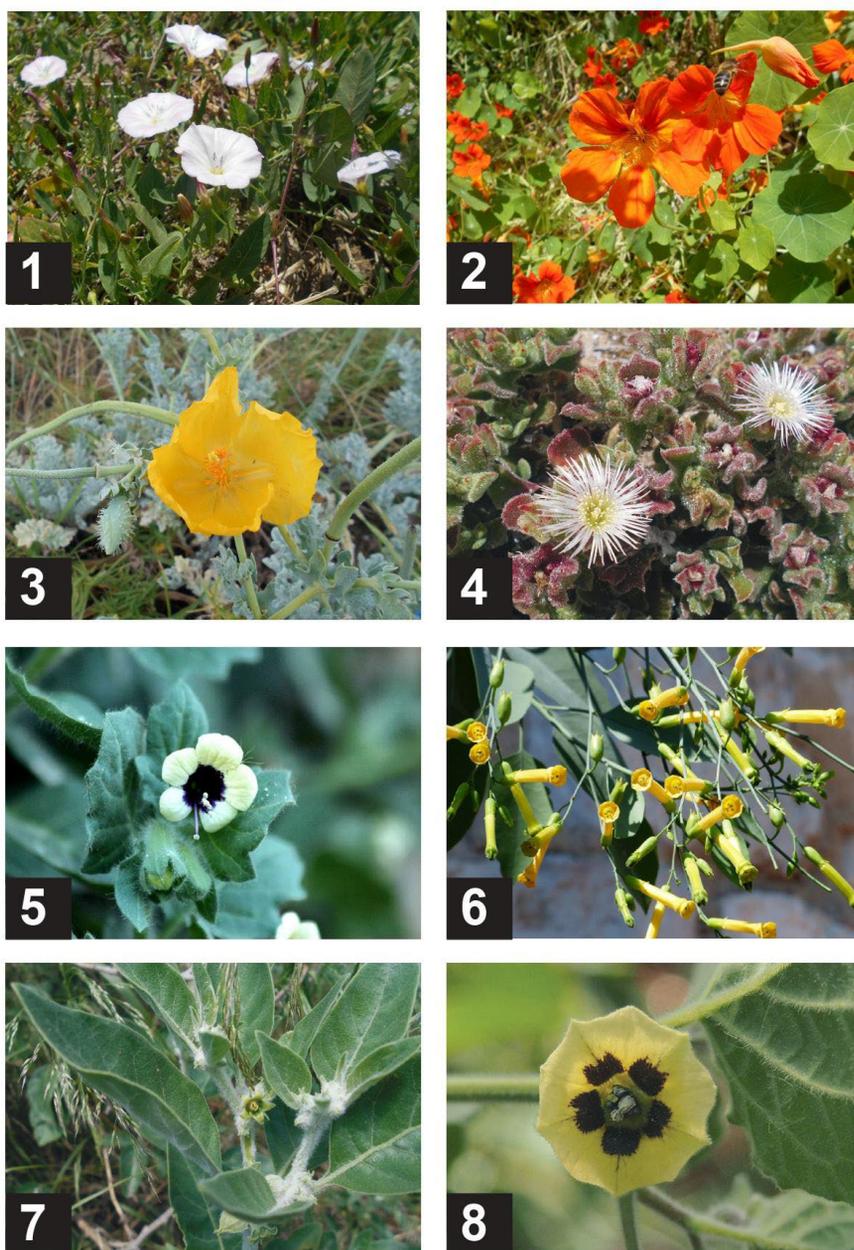


Figure 1. Images of the flowers of all species pairs studied on Mallorca (pictures on the left represent native species whereas their corresponding partners are shown at right). (1) *Convolvulus arvensis* L. (Convolvulaceae) and (2) *Tropaeolum majus* L. (Tropaeolaceae) in Torrent d'Esporles are pair 1; (3) *Glaucium flavum* Crantz (Papaveraceae) and (4) *Mesembryanthemum crystallinum* L. (Aizoaceae) in Ca'n Pere Antoni are pair 2; (5) *Hyoscyamus albus* L. and (6) *Nicotiana glauca* Graham; and (7) *Withania somnifera* L. and (8) *Physalis peruviana* L. (Solanaceae) in Torrent de Sa Riera are pair 3 and 4, respectively

All eight species flower between April and September and are insect-pollinated, although *C. arvensis* (pair 1) (Prokop and Neupauerova, 2014), *H. albus* (Fettig and Hufbauer, 2017) and *N. glauca* (pair 3), (Issaly et al., 2020) and *W. somnifera* (pair 4) (Kaul et al., 2005) can also be self-pollinated. For the eight plant species, seven floral morphology traits were measured on three fresh flowers from five individuals by the same observer (M. Abdallah). Four morphological traits were measured with a digital caliper: corolla length and diameter at opening, corolla total length and corolla bell diameter at nectary level. Following codes by Castroviejo (1986), floral shape was classified as: (1) tubular, (2) funnel, and (3) bell, whereas floral symmetry was either (1) radial or (2) bilateral (Table 1).

Pollinator censuses

Direct observations of insect flower visitation were done in 2018, from April 6th to June 25th. Each plant species was censused on an average of 10 h in total, during an average of four days, between 10:00 am to 8:00 pm. Between 10 and 30 individuals per species were observed during 25 min periods from a 1 m distance. In each census, we recorded the insect species (or morphospecies) visiting the flowers, the number of legitimate visits (i.e., times that the visitor entered the corolla and contacted the reproductive organs), the number of flowers contacted by each visitor, the number of flowers observed during the census, and the total number of open flowers in the individual plant as a proxy of flower abundance. All insects performing legitimate visits were considered as pollinators regardless of their effectiveness. After finishing each census, flowers were closely inspected to confirm the insect species or to collect them for further identification. Identifications were performed at the Mediterranean Institute for Advanced Studies (IMEDEA), using the pollinator reference collection available at this institution. All pollinators were grouped into the following functional groups: Coleoptera, Diptera, Formicidae, Hemiptera, Hymenoptera and Lepidoptera.

For each plant species and census day, we estimated pollinator species richness (SR) as the total number of species visiting the flowers, insect visitation rate (IVR) as the number of legitimate visits to the plant by any insect, regardless the number of flowers contacted, and flower visitation rate (FVR) as the number of flowers contacted by each insect species, standardized by the number of flowers observed in each census and by total flower abundance of the plant species.

The observed pollinator species were categorized as either specialized or generalized based on the number of flowering plant species they visited

according to published information and on our own data from Mallorcan pollinators. To do this, we searched for records on flower visitation from previous pollination studies in Mallorca island and by using the search engine Google Scholar with the following keywords: ("pollinator species" OR "pollinator genus") AND ("pollinat *" OR "flower visit*" OR "nectarivor*"). Arbitrarily, we considered a pollinator as specialized if it visited less than five plant species (even if these did not belong to the same family) and as a generalized if it visited at least five different plant species from different families.

Data analysis

For each pair, we obtained the number of shared and non-shared pollinator species with its native counterpart. Contingency tables were used to compare the number of functional groups between natives and non-native plants with the function 'chisq.test' from the R package 'car'. To test whether the pollinators shared between native and non-natives within each pair are the most frequent and/or the most generalized species, a generalized linear model (GzLMs) with binomial distribution was performed using shared/non-shared species as response variable, and insect visitation frequency (IVR), and generalized/specialized species as independent variables. Finally, a set of generalized linear mixed models (GLMMs) were built for each of the response variable (SR, IVR and FVR) to test if variation in SR (Poisson distribution) and visitation rate (either IVR or FVR; Gamma distribution) can be explained by differences in floral traits, flower abundance and origin status of the species (native *vs* non-native). For this, we included shape, symmetry, corolla size, flower abundance and status, and their interactions, as independent variables, and "pair" as a random variable, using the 'glmer' function from the package 'lme4' in R version 3.6.3. Because the study species differ greatly in color regardless of their status (Fig. 1), and because floral spectral readings by insects were not available, we decided not to include this variable in the statistical analyses.

Results

A total of 50 insect species were observed visiting the flowers of the eight flowering study plants. Nearly one third of them (32%; $n = 16$ spp.) were shared between native and non-native plants, whereas 40% visited only native species and 28% visited only the non-native ones. No differences were

found in the number of functional groups ($X^2 = 6.34$, $df = 8$, $p = 0.609$) visiting native versus non-native species.

Pair 1: *Convolvulus arvensis* vs. *Tropaeolum majus*

Only five (16%) of all insect species were shared by the two species of this plant pair. The non-native *T. majus* showed the highest values in SR, IVR and FVR (Fig. 2). Hymenoptera was the most important pollinator functional group for both species; namely *Lasioglossum malachurum* and *Apis mellifera* for *C. arvensis* and *Polistes dominula* and *Apis mellifera* for *T. majus*.

Pair 2: *Glaucium flavum* vs. *Mesembryanthemum crystallinum*

This pair shared only 12% of the insect species. The native *G. flavum* showed the highest SR, IVR and FVR (Fig. 2). *Sarcophaga carnaria* (Diptera) was the most important visitor of the native plant (in both IVR and FVR), followed by one Coleoptera (*Oedemera simplex*) and one dipteran species (*Ensina sonchi*). The non-native *M. crystallinum* was mostly visited by two hymenopterans *Lasioglossum punctatissimum* and *Nomioides squamigera* and one coleopteran *Tentyria schaumii*.

Pair 3: *Hyoscyamus albus* vs. *Nicotiana glauca*

The flowers of *H. albus* and *N. glauca* were visited by a different set of insect species, i.e., they did not share any visitors. The non-native *N. glauca* recorded the greatest values in SR, IVR and FVR (Fig. 2). The most frequent visitor of *H. albus* was *Sphaerophoria* sp. (Diptera), followed by a wasp (*Braconidae* sp.), whereas *N. glauca* was mainly visited by an alien ant (*Crematogaster scutellaris*) and the fly *Ensina sonchi*.

Pair 4: *Withania somnifera* vs. *Physalis peruviana*

This pair shared six (33%) of the insect species visiting their flowers. The native plant *W. somnifera* recorded the maximum values of SR, IVR and FVR (Fig. 2). *Spilostethus pandurus* (Hemiptera) was the most important visitor for both plant species, followed by *Polistes dominula* (Hymenoptera) and *Oxycarenus lavaterae* (Hemiptera) for *W. somnifera* and *P. peruviana*, respectively.

Results of the GzLM showed that the shared pollinator species between natives and non-natives species were also the most frequent floral visitors ($\beta = 25.78$, $z = 2.20$, $p = 0.028$), but not the most generalized species ($\beta = 0.50$, $z = 0.66$, $p = 0.505$).

Variation in FVR can be explained by corolla length dissimilarity, flower abundance as well as status (native and non-native). Overall, non-native species, usually with larger corolla length at opening and more flowers, showed higher FVR than natives ($\beta = 0.20$, $z = 0.03$, $p < 0.001$; $\beta = 0.02$, $z = 5.46$, $p < 0.001$, respectively). SR and IVR significantly increased with corolla length at opening ($\beta = 0.05$, $z = 2.76$, $p < 0.006$; $\beta = 0.06$, $z = 2.23$, $p = 0.026$, respectively) but it was independent of plant species status (see model selection summary in Table S.1.; Supplementary material).

Discussion

Although previous studies have shown small-scale effects of plant invaders on neighbouring natives (Gibson et al., 2012; Goodell and Parker, 2017; Ramsey et al., 2019), we found that, overall, the shared proportion of pollinators between non-native species and their co-existing native counterparts fluctuated from 0 to 33%, suggesting little ‘interference’ with the pollination success of the latter. This result is in accordance with the Darwin Naturalization Hypothesis, suggesting that “unrelated” flowering non-native plants are more likely to coexist with native ones if they do not compete for resources (i.e., if they share few pollinators). It is important to note that even when comparing pairs of species belonging to the same family (in our case, *Hyoscyamus albus* vs. *Nicotiana glauca* and *Withania somnifera* vs. *Physalis peruviana*, all in the Solanaceae), the number of shared pollinator species is very low (0% in the first pair vs. 33% in the latter). This is probably because of the wide variation found in flower traits and display in this family (Knapp, 2004, 2010; Sarkinen et al., 2013). Species in the two pairs indeed differ much in flower traits, as seen in Table 1.

Our findings are also congruent with those of previous studies that showed that non-native plants can acquire a completely different set of pollinators, encompassing even different orders, than their native counterparts (Ollerton et al., 2012; Ackerman et al., 2014; Maruyama et al., 2016). One possible explanation of the different ways non-native species integrate into resident-pollinators networks is that the non-native species might find their specific pollinators or pollinators functional groups, due to the pollinator’s wide distribution ranges, or because these might have been introduced in the same area as the non-native plant species (Rodger et al., 2010). Indeed, a study conducted by Rodger et al. (2010) showed that the main pollinator of *Lilium formosanum* is the moth *Agrius convolvuli*, whose wide distribution area covers both the native (Taiwan) and the invaded (South Africa) distribution

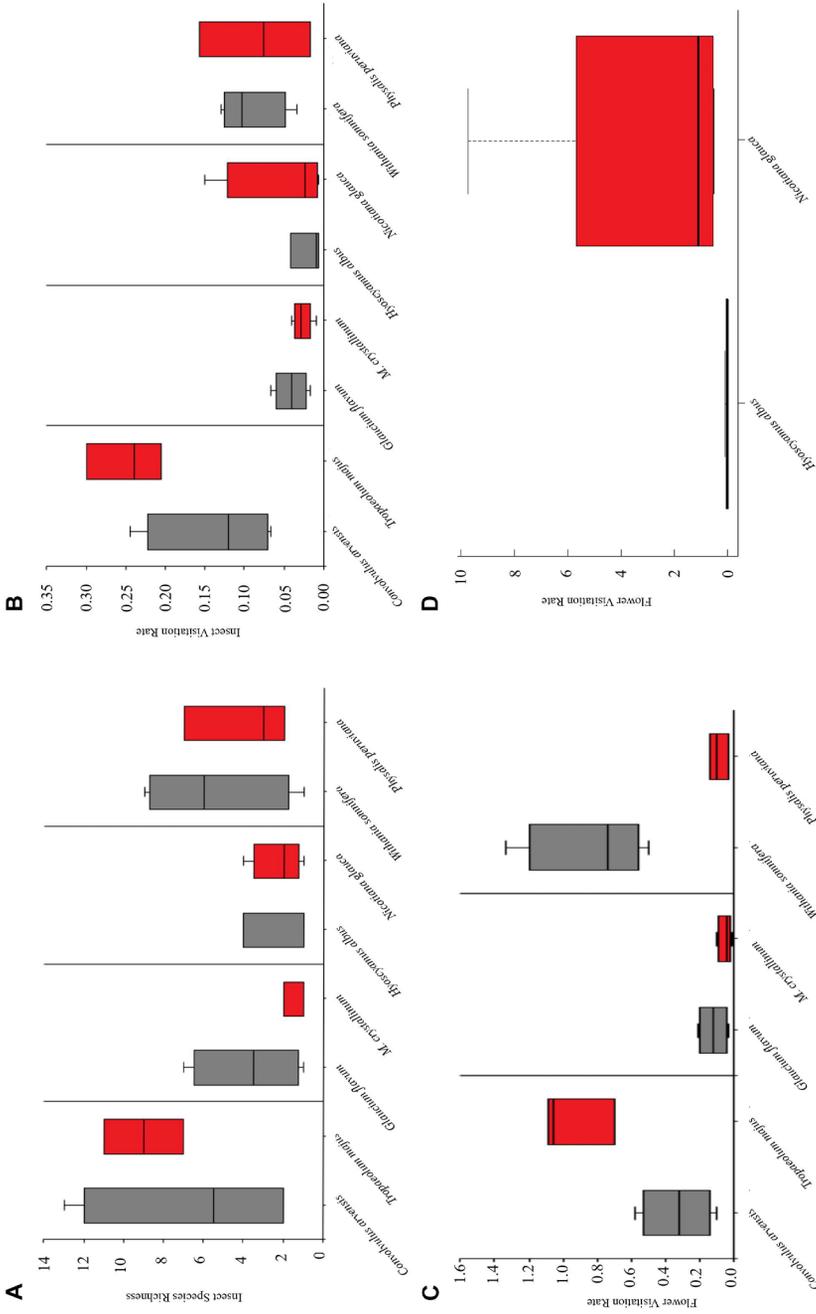


Figure 2. Mean and standard deviation of insect species richness SR (A), insect visitation rate IVR (B) and flower visitation rate FVR (C-D) to native (in grey) and non-native (in red) plant species studied. SR is the number of insect species visiting the flowers, IVR is the number of legitimate visits regardless the number of flowers contacted, and FVR is the number of flowers contacted by each insect species, standardized by the number of flowers observed in each census and by total flower abundance of the plant species.

areas of this lily. In our study, it might also be possible that the “new assemblage” of pollinators do prefer the non-natives. To test this, however, data on the pollinator interactions of native species in sites without the non-native species would be needed.

Overall, we found that the most shared pollinators in each plant pair are the most common but not necessarily the most generalized species. However, the non-native plants did not only interact with generalized but also with specialized species, which might result from the asymmetrical nature of plant-pollinator webs (Aizen and Morales, 2020). The fact that generalized pollinators often introduce non-native plants into pollination networks might simply be a result of their abundance and wide diets and not a preferential linking (Montero-Castaño and Traveset, 2020). However, by analyzing 25 invaded pollination networks, Stouffer et al. (2014) found that specialized pollinators are far more likely to integrate with non-native plants than would be expected by chance. Further studies on the role of specialized resident pollinators integrating non-native species are necessary, both from an ecological and evolutionary viewpoint.

Among the assessed floral traits, we discovered that corolla length at opening was important in explaining variation in the diversity and frequency of pollinators. Our findings revealed that non-native species with longer corollas at opening had higher flower visitation rate than native species. It is well established that the primary function of corollas is to attract pollinators and corolla size can influence such attraction (Ida and Totland, 2014; Gao et al., 2019). However, compared to the considerable attention that has been paid to specific floral traits such as floral color and corolla shape in explaining the differences in pollination attraction between native and non-native species, research on the effect of corolla size is strikingly scarce (Gómez et al., 2016; Gao et al., 2019). Further studies are thus needed to assess whether there is a general pattern in the effect of corolla size on pollinator attraction when comparing native and non-native species. It is also important to note that evaluating other traits (e.g., scent, nectar rewards, volatiles from different parts of the plant) at multiple stages of the pollination process, and across a larger number of species, is necessary to unveil the different mechanisms by which non-native plants can attract pollinators in their new geographical zones (Parra-Tabla and Arceo-Gómez, 2021).

Our non-native plants also produced more flowers and this resulted in higher insect visitation rates. Such finding is consistent with previous studies showing that non-native plants with more flowers/inflorescences tend to attract a wider array of pollinators and receive higher flower visitation rates (Lopezaraiza-Mikel et al., 2007; Padrón et al., 2009; Kaiser-Bunbury et al.,

2011). However, non-native plants might be more attractive to pollinators than natives not only for their flower display but also for their rewards. Indeed, some non-native plants can allocate more resources to both floral display and rewards (Bjerknes et al., 2007) as they are superior competitors for abiotic resources or are released from enemies in the invaded regions (Agrawal and Kotanen, 2003). Besides attracting legitimate pollinators, however, flower abundance also enhances the visits by animals that interact negatively with the pollination process, such as nectar robbers (Irwin et al., 2010). This is actually what we found with *T. majus*. Nectar robbers are important members of the community of floral visitors and have both neutral and negative effects on the visitation rates of pollinators (Irwin et al., 2010; Lobo et al., 2016).

The impact of plant invaders on native interactions varies among species and is influenced by different ecological attributes of plant species. In our study system, the non-native species attract an assemblage of pollinators which are by and large not shared with their native counterparts. This, however, does not preclude that those that are shared interfere with the pollination success of the natives, for instance by usurping floral rewards to natives and reducing fruit/seed set (not measured in this study) or by lowering the quality of pollination (through e.g., allelopathy, stigma clogging or hybridization) (Morales and Traveset, 2009). This highlights the importance of performing long-term studies mainly at the community level to understand under what circumstances non-native species are more likely to be successful and even outcompete native species, using both observational and experimental studies that evaluate pollination success.



Jezzine, Southeast Lebanon, is famous for its 70m high waterfalls and its breathtaking view of one of the largest pine forests in the Mediterranean basin.

Photo by Rami Rizk

Chapter 2

Contrasting performance of coexisting native and non-native plant pairs under different resource environments

Despite the high number of studies on plant invasiveness and habitat invasibility, we still lack a comprehensive understanding of whether non-native plant species become invasive outside their native ranges due to their traits, their interaction with the native species in the recipient habitat, or because of other mechanisms. Moreover, although trait-based approaches have been extensively used, the effect of allelochemicals and the antioxidant defense mechanisms have been suggested to play an important role on their coexistence. Here, we focused here on five coexisting plant pairs, each consisting of a native and a non-native species grown in controlled conditions varying in resource availability. Our aim was (1) to assess trait differences between coexisting native and non-native plants along with different resource environments, (2) to characterize the nature of their interactions, i.e., to unveil whether they facilitate the growth of each other, and (3) to understand the effects of allelochemicals and antioxidant defense mechanisms on their coexistence. Our results show that the performance of non-native plants is 'context-dependent', not concurring with the idea of non-natives species consistently outperforming native species in high-resource environments, and that the latter surpasses non-natives in low-resource environments. We found an overall facilitative interaction between native and non-native plants, i.e., both types of plants grew more when coexisting than when growing alone. However, such interaction fluctuated from facilitative to asymmetric to competitive when we considered a simple pairwise interaction. Finally, the impacts of allelochemicals and antioxidant defense mechanisms on non-native plants and their native counterparts were not conclusive. Our results confirm that the success of non-natives is context-dependent and results from the interaction of a number of ecological attributes.

Introduction

Over the last decades, ecologists have become increasingly interested in how invasions by non-native plants occur and how they affect ecosystems (Elton, 1958; Mack et al., 2000; Charles and Dukes, 2008; Hulme and Bernard-Verdier, 2017). Yet, it is still not well understood why some non-native plant species become invasive outside their native ranges while others do not (Matzek, 2011). Some researchers have looked for answers in the interactions between the newly arrived species and the natives in the recipient habitat (Bernard-Verdier and Hulme, 2019; Lucero et al., 2019) whereas others have identified intrinsic plant traits that make them invasive (Tecco et al., 2013; Funk et al., 2016; Divíšek et al., 2018).

Plant–plant interactions are important determinants of species' diversity, distribution, and abundance within natural communities (Subrahmaniam et al., 2021). So far, there seems to be contrasting evidence on the conclusions drawn from the potential nature of native and non-native plant interactions. For instance, in the Californian Carrizo Plain National Monument, Lucero et al. (2019) found that the native shrubs enhanced the abundance of the annual plant community by facilitating the growth of non-native species 2.75 times more intensely than the native ones. In contrast, other studies showed competitive interactions between the non-native and their native counterparts (Bernard-Verdier and Hulme, 2019; Pearse et al., 2019). These available conclusions comes from both field observations and experiments under controlled conditions (Ni et al., 2010; Dawson et al., 2012; Xio et al., 2013; Liu et al., 2018). Under such conditions, the nature of interactions between native and non-native plants has always been associated to a specific set of traits related to plant size (height and/or biomass), demonstrating that larger individuals possess a competitive advantage due to their ability to pre-empt resources from their co-occurring neighbors.

Different characteristics can grant a given non-native species its invasive capacity (Traveset and Richardson, 2021). Among these, the allelopathic interactions between native and non-native plant species have received an increased attention (Becerra et al., 2018; Thiébaud et al., 2019; Ma et al., 2020). Allelopathy is a process by which a plant releases secondary metabolites (allelochemicals) from litter leachates or root exudates to the surrounding environment (Bachheti et al., 2020). Such compounds have been shown to affect seed germination, growth, survival, and reproduction processes of other adjoining or neighboring plants (Parepa and Bossdorf, 2016; Uddin et al., 2017). The phenolic compounds and flavonoids are considered among the most important allelochemicals due to their phytotoxic activity (Reigosa and Pazos-Malvido, 2007; Xu et al., 2010). These compounds possess biological

toxicity, leading to an increase in the invasiveness ability of non-native species (Marinaş et al., 2018). However, many species have evolved antioxidant defense mechanisms to survive environmental stresses, including allelochemicals (Li et al., 2020).

The differences in traits between native and non-native species have thus frequently been suggested as a mechanism that explains the successful invasion of the newly arrived species (Funk et al., 2008; Leffler et al., 2014). Such differences, however, might change along biotic (e.g., presence of herbivores) and abiotic (e.g., resource availability) environmental gradients (Dainese and Bragazza, 2012). Most studies assessed their trait differences in high-resource environments have shown a successful establishment of non-native species compared to their native counterparts (Tecco et al., 2010; Cleland et al., 2011) whereas in low-resource environments, where plant productivity is severely limited by light, water, or soil nutrient availability, native plants outperformed non-natives. This indicates that natives tolerate stress and extract limited resources more efficiently than non-natives (Cramer et al., 2014).

Based on these gaps in current knowledge, the overarching goals of this study are (1) to assess trait differences between coexisting native and non-native plant species under different resource environments, (2) to characterize the nature of their interactions under controlled conditions, and (3) to understand the effects of allelochemicals and antioxidant defense mechanisms on their coexistence. For this, we used ten plant species, five coexisting pairs, each consisting of a native and a non-native species, that were grown in controlled conditions that varied in resource availability.

Materials and Methods

Study sites and species

The study was carried out in the laboratory of the Research Institute of Sciences and Engineering (RISE), at the University of Sharjah, United Arab Emirates (UAE), from April to July 2019. Five plant pairs of species were chosen, half being native and the other half non-native; the two plants in each pair had been found coexisting in the same habitat. Three pairs were originally chosen from a Mediterranean environment (Mallorca, Spain, Western Mediterranean Sea) (pairs 1, 2 and 3, see details below), and two pairs

(pairs 4 and 5) from a desert environment (Sharjah). Those pairs were selected based on their abundant presence as coexisting native and non-native species across different locations, differing in their environmental conditions and topographic positions, in both environments. For the species selection, we discarded native and non-native species growing at a same zone but in separate patches or micro-environments, selecting instead those pairs that were observed to frequently grow side by side in the field. Seeds of all species were collected during summer - autumn 2018 and preserved in paper bags in a dry, cool place to be later grown under controlled conditions.

Pair 1: *Mesembryanthemum nodiflorum* L. and *Mesembryanthemum crystallinum* L.

Mesembryanthemum nodiflorum (Aizoaceae) is an annual herb native to the Mediterranean, always living along the coast. Occasionally it forms a kind of carpet or lawn on soils that used to be bare ground, is very common on islets, often near the gull colonies. At the end of spring, it acquires a distinguished reddish color. Native to South Africa, *Mesembryanthemum crystallinum* (Aizoaceae) is an annual to biennial succulent herb. It is a salt accumulator that leaches salts upon death, increasing soil salinity in the vicinity. The increase in soil salinity reduces the competitive ability of associated native plant species, increasing the germination and seedling establishment of *M. crystallinum*, helping it dominate the salt marsh habitat (Abd El-Gawad and Shehata, 2014).

Pair 2: *Hyoscyamus albus* L. and *Nicotiana glauca* Graham

Hyoscyamus albus (Solanaceae) is native to the coastal areas in southern Europe and the Near East. It is a perennial herb with lobed margin leaves and a slightly fleshy touch that grows to a height of about 40 or 50 cm. The plant is an inhabitant of cities, grows next to walls, and in very remote places. *Nicotiana glauca* (Solanaceae) is an evergreen shrub or small tree native to central northwest Argentina and Bolivia. It has successfully invaded disturbed areas of semi-arid habitats worldwide. Its functional traits, such as high fruit and seed set, high seed viability, and successful seedling recruitment, enable *N. glauca* to form dense monodominant stands (Ollerton et al., 2012).

Pair 3: *Withania somnifera* L. and *Physalis peruviana* L.

Withania somnifera (Solanaceae) is a small perennial shrub that inhabits disturbed sunny and dry areas. It is native to a wide range, spread from the

Mediterranean region to Africa's tropical region and South Africa and from the Cape Verde Islands and Canary region to the Arabia and Middle East region like India, southern China, and Sri Lanka (Gaurav et al. 2015). *Physalis peruviana* (Solanaceae) is an herbaceous, perennial small shrub common in the subtropical zones of the Andes (South America). It has been introduced as a cultivated plant in different geographical regions but escaped into natural habitats, forming thickets and crowding out native plants (Cedeño and Montenegro, 2004).

Pair 4: *Prosopis cineraria* (L.) Druce and *Chenopodium album* L.

Prosopis cineraria (Fabaceae) is native to the arid part of Western Asia and the Indian Subcontinent. It is a small thorny evergreen tree with irregular branches that make a thin, open crown. It can reach about 6.5 meters high. This species forms a symbiotic relationship with some soil bacteria to fix atmospheric nitrogen (Kaur et al., 2012). *Chenopodium album* (Chenopodiaceae) is a cosmopolitan weed with an unclear geographical origin. *C. album* grows most vigorously in temperate and sub-temperate regions. Still, it is also a potentially serious weed in almost all winter-sown crops of the tropical and sub-tropical regions. It is a problematic weed of most summer- and winter-sown crops in temperate climates (Mandák et al., 2012). *Chenopodium album* is usually present under the canopies of *P. cineraria* in its native range of Arabia (Slate et al., 2020)

Pair 5: *Emex spinosa* (L.) Campd. and *Prosopis juliflora* (Sw.) DC.

Emex spinosa (Polygonaceae) is an annual herb native to a wide geographical range extended from islands and countries bordering the Mediterranean to most of the Arab Gulf region. This species is a relatively weak competitor but has several strong colonizing characteristics, including drought tolerance, rapid growth, abundant seed production, seed dormancy, seed heteromorphy, and high dispersal abilities (Shaltout et al., 2009). *Prosopis juliflora* (Fabaceae) is a big shrub native to Central and South America. It has been introduced to many hot subtropical arid deserts of the Arab Gulf regions for greening and fixing sand dunes and combating desertification. The IUCN has considered *P. juliflora* as one of the worst 100 alien plants in the world. It produces allelochemicals that enable it to outcompete and displace native species (El-Keblawy and Al-Rawai, 2007; Palacios et al., 2011; Slate et al., 2020). *E. spinosa* was seriously affected under the crown of *P. juliflora* but grew well at the canopy's edge, indicating a negative allelopathic effect of the latter on the former species (El-Keblawy and Al-Rawai, 2007).

Growth conditions

The collected seeds were sown in plastic pots (11 cm diameter top; 8.8 cm depth; capacity: 0.52 Liters) containing peat (Silver Torf, Agrochimica, Bolzano, Italy) and Agriperlite® (70:30 v: v). The experiment lasted a total of 90 days. It was conducted in two Conviron-E15 plant growth chambers with controlled growth conditions (60% air humidity, 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation (white light), 12/12 h light/dark regime and temperature fixed at 27/22°C day/night), located at the University of Sharjah.

Experimental design

Three treatments were implemented on each plant pair, with four replicates (pots) per treatment. Four individual plants were planted in each replicate. The treatments were the following:

- Control: Four individuals of the same species' status, where each pot was irrigated with 0.2 L of 100% Hoagland three times a week.
- High-Resource Environment (HRE): Two native and their corresponding non-native partner individuals, where each pot was irrigated with 0.2 L of 100% Hoagland solution three times a week.
- Low-Resource Environment (LRE): Two native and their corresponding non-native partner individuals, where each pot was irrigated with 0.2 L of 100% Hoagland once a week.

In both treatments, control and HRE, the amount of the added Hoagland solution was around 30-35% of the soil field capacity, enabling optimum water absorption and aeration conditions. Soil moisture content was measured and monitored using a probe meter (MPM-160-B; 12-bit resolution; International Pty Ltd). By contrast, in the LRE treatment, the soil moisture content reached low levels (10-15%) by the end of the week; a small amount of water was eventually added for plants to recover temporary wilting.

Morphological Traits

The measured morphological traits were: total number of leaves (TNL) (including green, yellow, and dead leaves), plant height (PH, cm) (both *H. albus* and *E. spinosa* were excluded from PH assessment due to their rosette

form), and dry biomass (DB, g). To assess DB, we placed each individual plant in a paper envelope inside a ventilation oven (70-80°C) until it reached a constant weight. The obtained dry weight values were used to calculate the relative interaction index (RII) (Armas et al., 2004). This index is based on the dry biomass data to determine the existence of negative and/or positive interactions between the interacting plant species. It is calculated based on the equation $RII = (B_w - B_o) / (B_w + B_o)$, where B_w represents the dry biomass of the species that grows along with neighboring plants (we used HRE) and B_o represents the dry biomass of the species that grows in the absence of such neighbors (control). RII varies from -1 (negative interaction) to 1 (positive interaction).

Chemical Traits

Photosynthetic Pigments

Chlorophyll-a (Ch-a), Chlorophyll-b (Ch-b), and carotenoids (Car) were extracted from 50 mg fresh leaf fragments obtained from each individual in all treatments. After an overnight extraction in 5 ml of methanol at 4°C in the dark, pigments were spectrophotometrically determined at 665.2, 652.4, and 470 nm using Epoch 2, microplate spectrophotometer, BioTek Instruments, Inc, USA.

Phenols and Flavonoids

The total amount of phenols (P) was determined using colorimetry with Folin-Ciocalteu's reagents. An amount of 20 µl of the methanolic extracts was mixed with 100 µl of 10x diluted FC reagent and 80 µl of 7.5% sodium carbonate solution. The absorbance was measured at 700 nm. Gallic acid extinction coefficient values were used to calculate the total phenolic content, following Singleton and Rossi (1965).

The total amount of flavonoids (F) was determined in microplates according to a procedure proposed by Chang et al. (2002). Aliquots of 25 µl of respective samples were mixed with 75 µl of 95% ethanol (v/v). Subsequently, 5 µl of 10% $AlCl_3 \cdot 6H_2O$ and 5 µl of 1 mol/L potassium acetate were added manually with a multi-channel pipette followed by the addition of 140 µl of deionized water. The samples were vortexed and left for 30 min at ambient temperature. Subsequently, the absorbance of clear supernatants was recorded at $\lambda = 415$ nm against deionized water. Quercetin, within different concentrations (0, 10, 25, 50, 100 and 200 µg /ml) dissolved in methanol/water (4/1, v/v), was used as a reference compound to calculate the actual concentration of total

flavonoid content of the samples. Every measurement was performed in triplicate, and the results obtained were expressed in $\mu\text{g}/\text{ml}$.

Antioxidant Activity

Following Luqman et al. (2012), the antioxidant activity (A) was determined using the ferric reducing antioxidant power (FRAP) method. The Ferric reducing power of all the sample extracts was determined using the FRAP assay. This method is based on the reduction of colorless ferric complex (Fe^{3+} tripyridyltriazine) to blue-colored ferrous complex (Fe^{2+} tripyridyltriazine) by the action of electron-donating antioxidants at low pH. The reduction was monitored by measuring the change of absorbance at 593 nm. The working FRAP reagent was prepared by mixing 10 volumes of 300 mM acetate buffer, pH 3.6, with 1 volume of 10mM TPTZ (2,4,6-tri(2-pyridyl)-s-triazine) in 40 mM HCl and with 1 volume of 20 mM ferric chloride. All the required solutions were freshly prepared before their use. An amount of 50 μl of the samples were added with 300 μl of FRAP reagent and incubated at ambient temperature for 5 min and the absorbance of the samples was measured at 593 nm. The difference between the absorbance of the sample and the blank absorbance was used to calculate the FRAP value equivalent to ascorbic acid (μM). All measurements were calculated from the value obtained from triplicate assays.

Data analysis

To test for differences in the morphological and chemical traits between native and non-native plant species in each treatment, a linear mixed-effects model (LMM) was performed using each trait as response variable, including 'pair nested within status (native and non-native)' as fixed effect, and 'species' and 'pot' as random effects to account for differences in the growth among species and to control for any potential pot effect. For that, we used the 'lmer' function, and afterwards an "emmeans" posthoc test was performed for pairwise comparisons. The residuals of the linear models were acceptable, and the principles of homoscedasticity and normal distribution were verified before data analysis. All data were analyzed using R v.3.4.3 (R Core Team, 2017).

Results

Across the different treatments, native plants consistently differed from the non-natives in some of the assessed traits. In the control treatment, the plant status (native vs. non-native) had a significant effect on most traits, except on the amount of both chlorophyll-a (Ch-a) and carotenoids (Car) (Table 2). Under the HRE treatment, by contrast, plant status was only significant on the total number of leaves (TNL), DB, total phenols (P), and antioxidant activity (A) (Table 3). Finally, under the LRE treatment, plant height (PH), DB, and amount of Ch-a were significantly affected by plant status (Table 4). The significant effect of plant status varied between the different treatments on both DB and the total flavonoids (F), sometimes being higher for non-native plants and others for the native ones. Specifically, DB showed the highest values for non-native species in both control and HRE treatments (Fig. 3 and 4), whereas it was highest for natives in the LRE treatment (Fig. 5). Similarly, F was highest for native species under control treatment (Fig. 3), but the opposite occurred under the LRE treatment (Fig. 5). Despite being affected by the same plant's status, some traits showed contrasting performance between treatments. TNL was greater for non-natives in HRE (Fig. 4) than control (Fig. 5). By contrast, native plants showed higher values of PH, totals of P and A when grown alone in the control treatment (Fig. 3) than when coexisting with their native counterparts in different treatments (Fig. 4 and 5). Lastly, plant status affected the amount of Ch-a and Ch-b under one treatment only. Ch-b was highest for native plants in the control treatment (Fig. 3), whereas Ch-a was highest for non-natives in the LRE treatment (Fig. 4).

Table 2. Chisq and P values of the morphological and chemical traits grown in control treatment, considering status and pairs nested in status. Morphological traits (total number of leaves (TNL), plant height (PH), dry biomass (DB)). Chemical traits (the amount of chlorophyll-a (Ch-a), chlorophyll-b (Ch-b), carotenoids (Car), the total of phenols (P), flavonoids (F), and antioxidant activity (A)).

	Status		Status/Pairs	
	Chisq	P-value	Chisq	P-value
TNL	29.07	< 0.001	178.88	< 0.001
PH	9.56	< 0.05	223.67	< 0.001
DB	14.89	< 0.001	142.87	< 0.001
Ch-a	2.52	0.122	94.25	< 0.001
Ch-b	4.34	< 0.05	172.57	< 0.001
Car	2.58	0.107	72.03	< 0.001
P	29.17	< 0.001	312.89	< 0.001
F	7.02	< 0.05	127.32	< 0.001
A	152.53	< 0.001	149.40	< 0.001

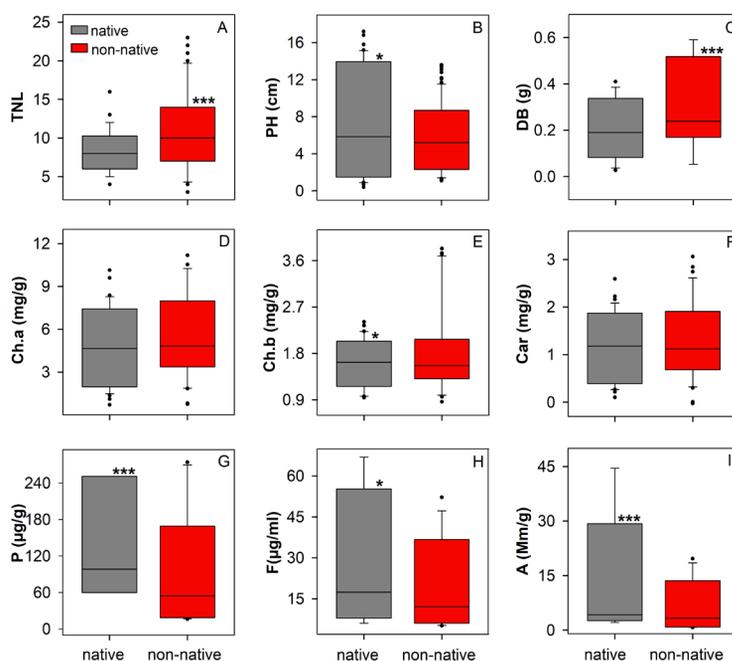


Figure 3. Box plots of the morphological and chemical traits of native (grey) and non-native (red) plant species grown in control treatment. (A) total number of leaves (TNL), (B) plant height (PH), (C) dry biomass (DB), (D) the amount of chlorophyll-a (Ch-a), (E) chlorophyll-b (Ch-b), (F) carotenoids (Car), (G) the total of phenols (P), (H) flavonoids (F) and (I) antioxidant activity (A). * Denotes statistically significant difference at $p < 0.05$ and *** $p < 0.001$.

Table 3. Chisq and P values of the morphological and chemical traits grown in HRE treatment, considering status and pairs nested in status. Morphological traits (total number of leaves (TNL), plant height (PH), dry biomass (DB)). Chemical traits (the amount of chlorophyll-a (Ch-a), chlorophyll-b (Ch-b), carotenoids (Car), the total of phenols (P), flavonoids (F), and antioxidant activity (A)).

	Status		Status/Pairs	
	Chisq	P-value	Chisq	P-value
TNL	9.51	< 0.001	48.29	< 0.001
PH	0.13	0.715	49.73	< 0.001
DB	160.25	< 0.001	599.16	< 0.001
Ch-a	0.16	0.686	138.12	< 0.001
Ch-b	3.01	0.082	55.74	< 0.001
Car	0.18	0.667	107.65	< 0.001
P	5.49	< 0.05	13.67	< 0.001
F	0.92	0.338	530.97	< 0.001
A	16.77	< 0.001	268.19	< 0.001

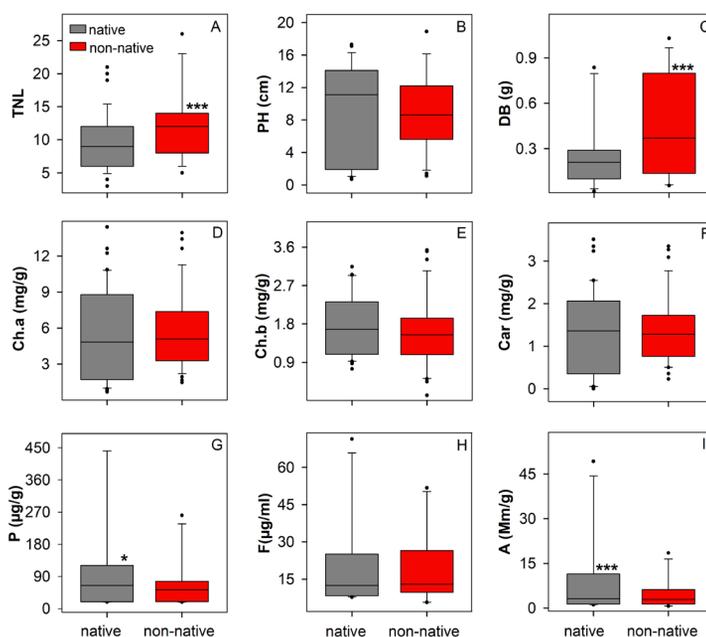


Figure 4. Box plots of the morphological and chemical traits of native (grey) and non-native (red) plant species grown in HRE treatment. (A) total number of leaves (TNL), (B) plant height (PH), (C) dry biomass (DB), (D) the amount of chlorophyll-a (Ch-a), (E) chlorophyll-b (Ch-b), (F) carotenoids (Car), (G) the total of phenols (P), (H) flavonoids (F) and (I) antioxidant activity (A). *Denotes statistically significant difference at $p < 0.05$ and *** $p < 0.001$.

Table 4. Chisq and P values of the morphological and chemical traits grown in LRE treatment, considering status and pairs nested in status. Morphological traits (total number of leaves (TNL), plant height (PH), dry biomass (DB)). Chemical traits (the amount of chlorophyll-a (Ch-a), chlorophyll-b (Ch-b), carotenoids (Car), the total of phenols (P), flavonoids (F), and antioxidant activity (A)).

	Status		Status/Pairs	
	Chisq	P-value	Chisq	P-value
TNL	1.37	0.245	63.05	< 0.001
PH	7.30	< 0.001	45.58	< 0.001
DB	8.62	< 0.001	81.69	< 0.001
Ch-a	3.94	< 0.05	134.34	< 0.001
Ch-b	4.31	0.285	139.97	< 0.001
Car	0.75	0.385	107.27	< 0.001
P	0.01	0.920	466.01	< 0.001
F	12.45	< 0.001	360.94	< 0.001
A	0.39	0.529	509.36	< 0.001

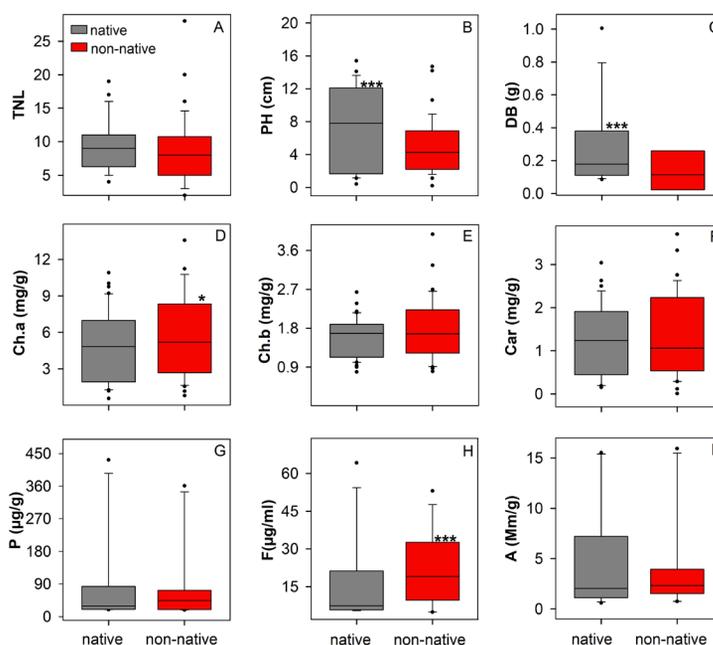


Figure 5. Box plots of the morphological and chemical traits of native (grey) and non-native (red) plant species grown in LRE treatment. (A) total number of leaves (TNL), (B) plant height (PH), (C) dry biomass (DB), (D) the amount of chlorophyll-a (Ch-a), (E) chlorophyll-b (Ch-b), (F) carotenoids (Car), (G) the total of phenols (P), (H) flavonoids (F) and (I) antioxidant activity (A). *Denotes statistically significant difference at $p < 0.05$ and *** $p < 0.001$.

When considering each plant pair, the “status” effect was not consistently found on the assessed traits across all treatments:

Pair 1: *Mesembryanthemum nodiflorum* vs. *Mesembryanthemum crystallinum*

In the control treatment, TNL, PH, P, F and A were significantly higher in *M. nodiflorum*, whereas DB was higher in *M. crystallinum* (Table 5). PH was higher in *M. nodiflorum*, DB and Car were higher in *M. crystallinum* under HRE (Table 6). Under LRE, all traits affected by the species’ status were higher for *M. nodiflorum* (Table 7).

Pair 2: *Hyoscyamus albus* vs. *Nicotiana glauca*

H. albus had significantly higher values of DB, amount of Car, and total of P in the control treatment, whereas TNL, the amount of Ch-a and Ch-b were higher in *N. glauca* (Table 5). In both HRE and LRE treatments, *H. albus* had higher values than its native counterpart. However, some of these traits were sometimes favored under high resource conditions whilst other traits were favored under low resources. The non-native *H. albus* grew more (higher FB and TNL values) in low resource conditions than in high ones, whereas it produced more allelochemicals (P and F) in high resource conditions (Table 6 and 7).

Pair 3: *Withania somnifera* vs. *Physalis peruviana*

The PH, DB, and Ch-a and Ch-b contents were significantly higher in the non-native (*P. peruviana*) under the three treatments. When grown alone, *P. peruviana* attained the highest PH, whereas had bigger biomass and higher Ch-a level when coexisting with *W. somnifera* in HRE (Table 5).

Pair 4: *Prosopis cineraria* vs. *Chenopodium album*

P. cineraria had significantly higher values of PH and P in the control treatment, whereas DB, the total of F and A were higher for *Ch. album* (Table 5). The amounts of Ch-a, Ch-b, and Car were higher in *P. cineraria* in the HRE treatment (Table 6). Still, the total of both allelochemicals (P and F) and the antioxidant activity (A) were higher for *C. album* in both the HRE and LRE treatments, with more production under high than low resource conditions (Tables 6 and 7).

Table 5. Average (\pm SD) values of the morphological and chemical traits of the studied species grown in control treatment. For each trait, values labeled with the same letter are not significantly different from other means for the same trait according to “emmeans” pairwise comparisons procedure at the < 0.05 level of significance. * Both *Hyoscyamus albus* and *Emex spinosa* were excluded from PH assessment due to their rosette form across the 3 treatments.

Species	Status	TNL	PH (cm)	DB (g)	Ch-a (mg/g)	Ch-b (mg/g)	Car (mg/g)	P (μ g/g)	F (μ g/ml)	A (mM/g)
<i>M. nodiflorum</i>	native	10 \pm 3 ^a	7.61 \pm 3.77 ^a	0.04 \pm 0.01 ^a	1.66 \pm 0.56 ^a	1.03 \pm 0.09 ^a	0.26 \pm 0.15 ^a	123.70 \pm 6.56 ^a	17.42 \pm 5.97 ^a	5.04 \pm 0.87 ^a
<i>M. crystallinum</i>	non-native	5 \pm 1 ^b	4.02 \pm 1.27 ^b	0.22 \pm 0.02 ^b	1.94 \pm 0.80 ^a	1.06 \pm 0.14 ^a	0.33 \pm 0.24 ^a	18.40 \pm 2.17 ^b	5.83 \pm 0.41 ^b	0.81 \pm 0.01 ^b
<i>H. albus</i>	native	8 \pm 1 ^a	*	0.24 \pm 0.18 ^a	5.74 \pm 1.96 ^a	1.86 \pm 0.36 ^a	1.42 \pm 0.49 ^a	57.90 \pm 17.95 ^a	10.08 \pm 2.69 ^a	2.49 \pm 1.00 ^a
<i>N. glauca</i>	non-native	10 \pm 1 ^b	1.48 \pm 0.20	0.05 \pm 0.01 ^b	5.46 \pm 3.55 ^b	1.87 \pm 0.76 ^b	1.23 \pm 0.86 ^b	33.24 \pm 21.04 ^b	8.85 \pm 3.59 ^a	1.53 \pm 1.18 ^a
<i>W. somnifera</i>	native	8 \pm 2 ^a	1.22 \pm 0.46 ^a	0.20 \pm 0.09 ^a	6.02 \pm 2.26 ^a	1.81 \pm 0.33 ^a	1.42 \pm 0.70 ^a	57.12 \pm 21.38 ^a	9.83 \pm 5.31 ^a	2.99 \pm 0.88 ^a
<i>P. peruviana</i>	non-native	7 \pm 1 ^a	5.99 \pm 1.75 ^b	0.42 \pm 0.11 ^b	9.16 \pm 2.15 ^a	3.11 \pm 0.74 ^b	1.80 \pm 0.62 ^a	60.71 \pm 20.13 ^a	13.88 \pm 4.34 ^a	3.35 \pm 1.24 ^a
<i>P. cineraria</i>	native	15 \pm 6 ^a	13.99 \pm 2.22 ^a	0.18 \pm 0.09 ^a	6.77 \pm 2.39 ^a	1.84 \pm 0.44 ^a	1.49 \pm 0.65 ^a	340.01 \pm 115.50 ^a	66.81 \pm 0.14 ^a	41.75 \pm 3.85 ^a
<i>C. alburnum</i>	non-native	11 \pm 1 ^b	7.42 \pm 2.17 ^b	0.21 \pm 0.03 ^a	6.56 \pm 2.37 ^a	1.70 \pm 0.31 ^a	1.59 \pm 0.61 ^a	97.81 \pm 14.83 ^b	42.30 \pm 3.42 ^b	4.63 \pm 0.66 ^b
<i>E. spinosa</i>	native	16 \pm 3 ^a	*	0.33 \pm 0.07 ^a	3.24 \pm 1.83 ^a	1.40 \pm 0.28 ^a	1.04 \pm 0.77 ^a	228.82 \pm 48.24 ^a	43.77 \pm 12.62 ^a	19.47 \pm 5.17 ^a
<i>P. juliflora</i>	non-native	5 \pm 1 ^b	10.46 \pm 2.66	0.61 \pm 0.13 ^b	6.70 \pm 2.00 ^b	1.72 \pm 0.45 ^a	1.73 \pm 0.61 ^a	259.51 \pm 16.92 ^b	33.56 \pm 20.26 ^a	16.58 \pm 2.96 ^a

Table 6. Average (\pm SD) values of the morphological and chemical traits of the studied species grown in HRE treatment. For each trait, values labeled with the same letter are not significantly different from other means for the same trait according to “emmeans” pairwise comparisons procedure at the < 0.05 level of significance.

Species	Status	TNL	PH (cm)	DB (g)	Ch-a (mg/g)	Ch-b (mg/g)	Car (mg/g)	P (μ g/g)	F (μ g/ml)	A (mM/g)
<i>M. nodiflorum</i>	native	15 \pm 4 ^a	13.90 \pm 1.87 ^a	0.22 \pm 0.01 ^a	1.19 \pm 3.89 ^a	1.02 \pm 0.70 ^a	0.10 \pm 0.99 ^a	19.20 \pm 0.41 ^a	8.35 \pm 0.73 ^a	1.25 \pm 0.11 ^a
<i>M. crystallinum</i>	non-native	14 \pm 5 ^a	8.74 \pm 2.96 ^b	0.27 \pm 0.08 ^a	2.25 \pm 3.24 ^a	0.89 \pm 0.84 ^a	0.50 \pm 0.81 ^b	19.00 \pm 0.61 ^a	7.40 \pm 2.76 ^a	1.71 \pm 1.81 ^a
<i>H. albus</i>	native	11 \pm 2 ^a		0.06 \pm 0.01 ^a	7.42 \pm 4.12 ^a	2.22 \pm 0.72 ^a	1.87 \pm 1.09 ^a	52.15 \pm 34.75 ^a	10.11 \pm 2.86 ^a	2.11 \pm 0.88 ^a
<i>N. glauca</i>	non-native	7 \pm 1 ^b	1.20 \pm 0.17	0.24 \pm 0.18 ^b	5.36 \pm 0.92 ^a	1.81 \pm 0.27 ^a	1.05 \pm 0.18 ^a	62.32 \pm 11.40 ^b	12.83 \pm 2.95 ^b	4.27 \pm 0.81 ^a
<i>W. somnifera</i>	native	6 \pm 2 ^a	1.52 \pm 0.57 ^a	0.03 \pm 0.02 ^a	7.54 \pm 1.10 ^a	2.20 \pm 0.35 ^a	1.72 \pm 0.34 ^a	57.59 \pm 18.96 ^a	11.73 \pm 2.88 ^a	1.38 \pm 3.07 ^a
<i>P. peruviana</i>	non-native	8 \pm 3 ^a	9.49 \pm 4.83 ^b	0.78 \pm 0.28 ^b	9.96 \pm 3.16 ^b	2.74 \pm 0.70 ^a	2.30 \pm 0.94 ^a	23.42 \pm 15.36 ^a	6.48 \pm 2.80 ^a	3.46 \pm 1.33 ^a
<i>P. cineraria</i>	native	10 \pm 1 ^a	11.41 \pm 2.96 ^a	0.12 \pm 0.02 ^a	8.98 \pm 3.45 ^a	2.11 \pm 0.56 ^a	2.11 \pm 0.86 ^a	441.37 \pm 138.97 ^a	65.83 \pm 7.91 ^a	44.33 \pm 6.94 ^a
<i>C. albus</i>	non-native	20 \pm 14 ^a	9.45 \pm 8.50 ^a	0.07 \pm 0.02 ^a	4.94 \pm 1.48 ^b	1.29 \pm 0.44 ^b	1.26 \pm 0.37 ^b	46.60 \pm 8.18 ^b	22.51 \pm 5.64 ^b	2.87 \pm 0.02 ^b
<i>E. spinosa</i>	native	5 \pm 1 ^a		0.78 \pm 0.07 ^a	2.83 \pm 1.22 ^a	1.27 \pm 0.44 ^a	0.82 \pm 0.51 ^a	130.03 \pm 107.73 ^a	24.28 \pm 9.03 ^a	12.31 \pm 7.84 ^a
<i>P. juliflora</i>	non-native	13 \pm 2 ^b	10.89 \pm 2.77	0.59 \pm 0.24 ^a	6.12 \pm 1.40 ^a	1.48 \pm 0.51 ^a	1.56 \pm 0.38 ^b	201.97 \pm 83.32 ^b	48.01 \pm 5.27 ^b	12.32 \pm 8.73 ^a

Table 7. Average (\pm SD) values of the morphological and chemical traits of the studied species grown in LRE treatment. For each trait, values labeled with the same letter are not significantly different from other means for the same trait according to “emmeans” pairwise comparisons procedure at the < 0.05 level of significance.

Species	Status	TNL	PH (cm)	DB (g)	Ch-a (mg/g)	Ch-b (mg/g)	Car (mg/g)	P (μ g/g)	F (μ g/ml)	A (mM/g)
<i>M. nodiflorum</i>	native	15 \pm 4 ^a	13.90 \pm 1.87 ^a	0.22 \pm 0.01 ^a	1.19 \pm 3.89 ^a	1.02 \pm 0.70 ^a	0.10 \pm 0.99 ^a	19.20 \pm 0.41 ^a	8.35 \pm 0.73 ^a	1.25 \pm 0.11 ^a
<i>M. crystallinum</i>	non-native	14 \pm 5 ^a	8.74 \pm 2.96 ^b	0.27 \pm 0.08 ^a	2.25 \pm 3.24 ^a	0.89 \pm 0.84 ^a	0.50 \pm 0.81 ^b	19.00 \pm 0.61 ^a	7.40 \pm 2.76 ^a	1.71 \pm 1.81 ^a
<i>H. albus</i>	native	11 \pm 2 ^a		0.06 \pm 0.01 ^a	7.42 \pm 4.12 ^a	2.22 \pm 0.72 ^a	1.87 \pm 1.09 ^a	52.15 \pm 34.75 ^a	10.11 \pm 2.86 ^a	2.11 \pm 0.88 ^a
<i>N. glauca</i>	non-native	7 \pm 1 ^b	1.20 \pm 0.17	0.24 \pm 0.18 ^b	5.36 \pm 0.92 ^a	1.81 \pm 0.27 ^a	1.05 \pm 0.18 ^a	62.32 \pm 11.40 ^b	12.83 \pm 2.95 ^b	4.27 \pm 0.81 ^a
<i>W. samnifera</i>	native	6 \pm 2 ^a	1.52 \pm 0.57 ^a	0.03 \pm 0.02 ^a	7.54 \pm 1.10 ^a	2.20 \pm 0.35 ^a	1.72 \pm 0.34 ^a	57.59 \pm 18.96 ^a	11.73 \pm 2.88 ^a	1.38 \pm 3.07 ^a
<i>P. peruviana</i>	non-native	8 \pm 3 ^a	9.49 \pm 4.83 ^b	0.78 \pm 0.28 ^b	9.96 \pm 3.16 ^b	2.74 \pm 0.70 ^a	2.30 \pm 0.94 ^a	23.42 \pm 15.36 ^a	6.48 \pm 2.80 ^a	3.46 \pm 1.33 ^a
<i>P. cineraria</i>	native	10 \pm 1 ^a	11.41 \pm 2.96 ^a	0.12 \pm 0.02 ^a	8.98 \pm 3.45 ^a	2.11 \pm 0.56 ^a	2.11 \pm 0.86 ^a	441.37 \pm 138.97 ^a	65.83 \pm 7.91 ^a	44.33 \pm 6.94 ^a
<i>C. albus</i>	non-native	20 \pm 14 ^a	9.45 \pm 8.50 ^a	0.07 \pm 0.02 ^a	4.94 \pm 1.48 ^b	1.29 \pm 0.44 ^b	1.26 \pm 0.37 ^b	46.60 \pm 8.18 ^b	22.51 \pm 5.64 ^b	2.87 \pm 0.02 ^b
<i>E. spinosa</i>	native	5 \pm 1 ^a	10.89 \pm 2.77	0.78 \pm 0.07 ^a	2.83 \pm 1.22 ^a	1.27 \pm 0.44 ^a	0.82 \pm 0.51 ^a	130.03 \pm 107.73 ^a	24.28 \pm 9.03 ^a	12.31 \pm 7.84 ^a
<i>P. juliflora</i>	non-native	13 \pm 2 ^b		0.59 \pm 0.24 ^a	6.12 \pm 1.40 ^a	1.48 \pm 0.51 ^a	1.56 \pm 0.38 ^b	201.97 \pm 83.32 ^b	48.01 \pm 5.27 ^b	12.32 \pm 8.73 ^a

Pair 5: *Emex spinosa* vs. *Prosopis juliflora*

In the control treatment, TNL was significantly higher in *E. spinosa*, whereas DB, the amount of Ch-a, and the total of P were higher in *P. juliflora* (Table 5). DB was higher in *E. spinosa*, in contrast to TNL. The amount of Car, the total of P and F were higher in *P. juliflora* under both HRE and LRE (Table 6 and 7). FB showed the highest values for *E. spinosa* when coexisting with *P. juliflora*, and the latter produced more phenols, both under high resource conditions.

When it comes to the interaction between our assessed species, the positive values of the relative interaction index (RII) of both the native species (0.11) and the non-natives (0.18) revealed a facilitative interaction. However, not all the non-native plants across our assessed pairs interacted the same way with their native counterparts. Our simple pairwise interactions varied from being facilitative in pairs 1 and 2 (*M. nodiliflorum* (0.70) - *M. crystallinum* (0.11); *H. albus* (0.08) - *N. glauca* (0.02)) to asymmetric (-/+) in pairs 3 and 5 (*W. somnifera* (-0.67) - *P. peruviana* (0.30); *E. spinosa* (0.40) - *P. juliflora* (-0.01)), and to competitive (-/-) in pair 4 (*P. cineraria* (-0.19) - *C. album* (-0.48)).

Discussion

Two important mechanisms are often used to explain the successful establishment of non-native species. These are (1) the ability to capture resources and (2) trait differences between natives and non-natives (Matzek, 2011). Our study has revealed that only a few traits differ significantly between native and non-native species. The significance of such differences is inconsistent among the different resource environments. Our results are thus aligned with those of previous studies (e.g., Daehler et al., 2004; Matzek, 2011; Leffler et al., 2014), showing that the performance of non-native plants is “context-dependent”. Such findings lead us to discard the idea that non-natives consistently outperform native species in high-resource environments and that the latter surpass non-natives in low-resource environments. Our species-pairs comparisons showed that not all non-native species are “super plants” under high-resource environments and that not all natives can maintain their “superiority” over the co-occurring non-native species in low-resource environments. Such expectations might be influenced by the species selection and the fact that the greatest trait differences between native and non-native species were found in studies performed in the field rather than in manipulated plots or pot experiments (Leffler et al., 2014), as we did in the present study. The context-dependent performance of our non-native species supports the claim that trait-based differences between native and non-native

species alone cannot predict future invasion (Thompson and Davis, 2011). Processes other than trait differences can drive plant invasions, such as the order of species arrival (Daleo et al., 2009), presence of natural enemies (Keane and Crawley, 2002; Zuppinger-Dingley et al., 2011), or propagule pressure (Von Holle and Simberloff, 2005).

The degree of trait differences between native and non-native plants may be more important in determining the influence of the latter on the former rather than in predicting invasion (Vitousek, 1990; Strayer, 2012). The positive RII values of both the native and the non-native species revealed a facilitative interaction, an uncommon finding in interaction experiments under controlled conditions (Belote and Weltzin, 2006; Jordan et al., 2008; Ni et al., 2010; Xio et al., 2013; Liu et al., 2018). The yield of such interaction is usually known as having a mutually beneficial relationship for both plant partners. In our case, both the native and the non-native species grew more when coexisting together than when growing alone; specifically, the dry biomass values were higher for both native and non-native species when they coexist (Fig. 3 and 4). However, such interaction was not repeated the same along all our assessed pairs. A facilitative interaction was shown in two pairs, (*M. nodiliforum* - *M. crystallinum*) and (*H. albus* - *N. glauca*), with an increase in the dry biomass value in the native and non-native plants in both pairs (Table 5 and 6). In two other pairs (*W. somnifera* - *P. peruviana*) and (*E. spinosa* - *P. juliflora*), an asymmetric interaction was revealed; sometimes, benefiting non-native plants and others for the native ones. *P. peruviana* grew more with their native counterparts (*W. somnifera*) than when growing alone, whereas *E. spinosa* grew more with their non-native (*P. juliflora*) counterparts than when growing alone (Table 5 and 6). Lastly, a competitive interaction was demonstrated in one pair (*P. cineraria* - *C. album*), decreasing the dry biomass value in the native and non-native plants in both pairs (Table 5 and 6). Ni et al. (2010) demonstrated that simple pairwise interactions could be highly conditional, and therefore the outcomes we obtained here are likely to be different under different conditions. Biomass-based assessment is important in defining the outcome of plant-plant interactions (Armas et al., 2004), but our results suggest that it might not be the only factor. The different outcomes we found impede us from stating whether our study species were more constrained by intraspecific than the interspecific competition, or the opposite, in the presence of their counterparts. Indeed, the relative balance of intra- vs. interspecific competition is thought to influence the ability of plant species to coexist (Wandrag and Catford, 2020). However, understanding the factors that influence the strength of the competition within species is important, as plants, regardless of their status (native vs. non-native), can often display marked intraspecific trait variations that reflect ontogeny (e.g.,

seedling vs. adult), heritable genetic variation, as well as phenotypic plasticity (Violle et al., 2012).

Interactions between plants usually involve interference, which can be due to competition for resources (e.g., water, nutrients, etc.) or mediated by chemicals, such as the production of specialized metabolites (allelochemicals) in a process known as allelopathy (San Emeterio et al., 2007). This study confirms the presence of both phenolic and flavonoid compounds, as well as an antioxidant activity in all our assessed species across the different resource environments. However, the presence of such compounds was not repeatedly significant among the different treatments. Given that we used small plants in potting soils, the allelochemicals were expected to be released as root exudates to the soils rather than after litter decomposition. Soil exudates can directly interfere with the associated plants or indirectly affect soil microbes that facilitate or inhibit the associated plants (Hierro and Callaway, 2003; Elsheikh et al., 2021). While it has been demonstrated that non-native plants usually possess both higher growth-related traits and stronger chemical defenses (Ridenour et al., 2008; Caño et al., 2009; Ni et al., 2020), our results were not consistent with these previous studies. Meanwhile, it is difficult to generalize as only one pair (*W. somnifera* - *P. peruviana*) followed this trend. Along the three treatments (Table 5, 6 and 7), the non-native *P. peruviana* registered higher morphological and chemical traits values than its native counterpart (*W. somnifera*). Plants co-evolved with species with an allelopathic ability may be less susceptible to allelochemicals, while newly exposed species to such allelopathic effect may exhibit less resistance (the “novel weapon hypothesis”, Callaway and Aschehoug, 2000; Callaway and Ridenour, 2004). Consequently, allelochemicals released by native plants could also affect the growth of invasive species and would, thus, constitute a biotic resistance against plant invasion (Christina et al., 2015). All these inconsistent or contrasting results suggest that the impact of allelochemicals and antioxidant defense mechanisms on native and non-native plants is either highly conditional or/and the cost is growth stage-related and, therefore, it is hard to detect in our study.

In short, further studies are needed to fully understand how non-native plant species become invasive outside their native ranges and how this may vary according to both the traits of such species and the traits of the recipient community. We found that the success of non-native species was “context-dependent”, which might be due to processes other than trait differences for predicting future invasion. Our contrasting results when assessing the type of interaction between native and non-native pairs showed that a biomass-based approach is a challenging tool for distinguishing the nature of such interaction. Overall, the effect of allelochemicals and antioxidant defense

mechanisms on the interaction of our assessed species is either highly conditional or/and ontogeny dependent. In any case, our results add to the growing body of evidence that the chance of successful invasion might be influenced by different ecological attributes. For a better understanding of these attributes, long-term studies at local and regional scales are needed.



Balou' Balaa, Northeast Lebanon, is very famous for its 250 meters deep natural sink hole that has been carved by water 160 million years ago!

Photo by Rami Rizk

Chapter 3

Leaf morpho-physiological comparison between coexisting native and non-native plant pairs in a Mediterranean island

Islands tend to be more prone to plant invasions than mainland regions, and this pattern has also been found on the Mediterranean ones. To date, a large number of studies on comparing the leaf morphological and physiological traits between native and non-native plants in Mediterranean environments, but none of these studies has been performed on Mediterranean islands. To fill this gap, we focused here on eight coexisting pairs, each pair formed by a native and a non-native plant species, grown in a controlled growth chamber in the absence of stress. We aimed (1) to characterize the leaf morpho-physiological traits between native and non-native plants on Mediterranean islands and (2) to deepen in the underlying causes of the differential photosynthetic traits displayed by non-native species. We evaluated these traits between native and non-native species as two different groups of plants at first, then we run pairwise analysis on the coexisting species pairs, to assess if the observed general patterns can be applied to every particular non-native species in comparison with its native coexisting species. Results show that in Mediterranean islands, non-native plant species show on average larger values of net CO₂ assimilation, stomatal conductance, photosynthetic nitrogen-use-efficiency, among others, and lower leaf mass area and leaf thickness, compared to the native ones. This study reports two novel traits for non-native species, to be added to the 'leaf physiological trait invasive syndrome' being on average larger mesophyll conductance and lower mesophyll conductance limitations than native species. We also found that on Mediterranean islands, native and non-native species are placed on the opposite sides of the leaf economics spectrum, with the non-native species being placed on its "fast-return" end. Finally, we observed that these general patterns cannot be always applied to every particular coexisting plant pair. In conclusion, our findings demonstrate that non-native species inhabiting Mediterranean islands possess distinct leaf morphological and physiological traits compared to co-occurring native species, at least during the favorable growth season, which might explain their successful invasion.

Introduction

Plant invasions are considered to be one of the most potent global ecological threats during the 21st century, having a wide range of impacts on ecosystems and their functioning (Vilà and Hulme, 2017; Castro-Díez et al., 2019). It has been shown that the level of invasions varies differently among regions, biomes, and habitats (Chytrý et al., 2008). Notably, islands tend to be more prone to invasions than mainland region (Dawson et al., 2017), and this pattern has also been found for the Mediterranean islands (Gimeno et al., 2006; Celesti-Grapow et al., 2016; Guarino et al., 2021).

The characteristics conferring a given non-native species its invasive capacity are multiple, ranging from biotic interactions to many other ecological features (Traveset and Richardson, 2021). Among these, the physiological traits have been suggested to play an important role in plant invasiveness. Non-native plants have shown to possess higher leaf rates of net CO₂ assimilation (A) (van Kleunen et al., 2010; Oliveira et al., 2014; Le et al., 2019), stomatal conductance (g_s) (Durand and Goldstein, 2001; Caplan and Yeakley, 2010), photosynthetic nitrogen use efficiency (PNUE) (Durand and Goldstein, 2001; Heberling and Fridley, 2013; Petruzzellis et al., 2021), among others. The leaf morphological traits have also been suggested to be responsible for the success of non-native plants. Several studies have demonstrated that non-native species generally possess lower leaf mass per area (LMA). These studies have also found correlations between the lower LMA and some of the physiological traits, indicating that non-native species with lower LMA tend to have higher leaf nitrogen (N), nitrogen concentration per unit mass (N_{mass}), and higher PNUE (Peñuelas et al., 2010; Morais et al., 2021). Another important morphological trait is the leaf area (LA), where it have shown that non-native plants are likely to have higher LA compared to the co-occurring native species (Daehler et al., 2004; Petruzzellis et al., 2021). To date, there have been studies on comparing the leaf morphological and physiological traits variations between native and non-native plants in Mediterranean environments (Zunzunegui et al., 2020; Morais et al., 2021; Petruzzellis et al., 2021), but none of these studies has been performed in Mediterranean islands.

Bringing together the leaf morphological and physiological traits, Wright et al (2004) have described a universal spectrum of leaf economics reflecting the coordinated changes in the leaf structure and function relationships. This leaf economics spectrum (LES) has been described as running from a “slow-return” end, encompassing species characterized by high LMA, low nutrient contents (N_{mass} and P_{mass} , respectively), low respiration rates, and light-saturated photosynthetic rates per unit mass (A_{mass}) to a “fast-return” end with the opposite suite of traits. Surprisingly, its use in the field of invasion

ecology is rare. The very few studies that applied the LES have suggested that non-native and native species are aligned on its opposite sides, placing non-native species cluster on the “fast-return” end, with higher values of N_{mass} and A_{mass} , and lower values of LMA relative to native species (Peñuelas et al., 2010; Ordonez and Olff, 2013; Petruzzellis et al., 2021).

Based on the above evidences, it appears that photosynthesis and photosynthesis-related parameters may have a crucial role in favoring the invasive character of non-native species. Mechanistically, photosynthesis can be limited by either diffusional (i.e., stomatal and/or mesophyll conductance) or photo-biochemical limitations. Grassi and Magnani (2005) proposed a method to quantify photosynthetic limitations by separating the relative controls on the net CO_2 assimilation rate (A) resulting from stomatal (l_s), mesophyll conductance (l_m) and biochemical limitations (l_b) - the latter pooling together potential photochemical and biochemical factors. To the best of our knowledge, no study so far has quantified the photosynthetic limitations of non-native species as compared to native ones. Quantifying these limitations is important, as perhaps a different sharing of photosynthetic limitations between native and non-native species could confer some advantages to the latter. In particular, it has been shown that increased photosynthetic capacity along the land plant's phylogeny is associated to a progressive diminution from a predominant l_m in bryophytes to an almost matched co-limitation by l_s , l_m , and l_b in angiosperms (Gago et al., 2019). Decreased l_m over l_s is associated with increasing both water-use-efficiency (WUE) and PNUE along plant's phylogeny (Flexas and Carriqui, 2020), but also with increased WUE within angiosperms themselves (Flexas et al., 2013). Large WUE and PNUE might be important traits conferring competitive advantage in source-poor environments, such as those encountered in Mediterranean islands, especially if achieved by means of reducing stomatal conductance and transpiration on one hand and nitrogen content on the other, rather than by increasing photosynthesis itself. Since a high mesophyll conductance is often associated with a low LMA, it could happen that non-native species have large photosynthesis due to low l_m .

In spite of the commonness of studies on plant invasions worldwide, the comparison between coexisting pairs of native and non-native plants has still received little attention (but see Vilà et al., 2004; Morales and Traveset, 2009; Heard and Sax, 2013). However, what is clear that coexistence between native and non-native plants is common at both local and regional scales in plant communities worldwide, and it has often occurred over decades or centuries (Sax and Gaines, 2008; Heard et al., 2012; Heard and Sax, 2013). Closely examining the traits by which each pair of native and non-native coexist may therefore provide an insight on assessing whether the general patterns that

explain plants' invasion success are also observed at the scale of coexisting plant pairs.

Based on the described gaps in the current knowledge, the aims of this study were (1) to characterize the leaf morpho-physiological traits between native and non-native plants on Mediterranean islands and (2) to deepen in the underlying causes of the differential photosynthetic traits displayed by non-native species. To do so, eight coexisting pairs, each pair formed by a native and a non-native plant species, were grown in a controlled growth chamber in the absence of stress. This experimental approach based on field observations allowed us to investigate cause-effect mechanisms while keeping the results relevant ecologically. Then, we evaluated the leaf morpho-physiological traits differences between native and non-native species as two different groups of plants. And last, we run pairwise analysis on the coexisting species pairs, to assess if the observed general patterns can be applied to every particular non-native species in comparison with its native coexisting species. Our specific hypotheses were:

- (1) On Mediterranean islands, the non-native plant species show advantageous values in their leaf physiological traits as compared to the co-occurring native ones.
- (2) In association with the leaf morphological traits, the decreased l_m may contribute to the larger A, WUE and PNUE of non-native species.
- (3) The non-native and native plant species are aligned on the opposite sides of the leaf economics spectrum, placing non-native species cluster on the "fast-return" end of the spectrum (in accordance with previous studies on non-island species).
- (4) The general patterns found when comparing native and non-native species as two different groups of plants are also found for each coexisting species plant pair.

Table 8. Family, status, and description of the eight studied plant pairs.

Pair	Species (Family)	Status	Description
1	<i>Physalis peruviana</i> (Solanaceae)	non-native	Herbaceous, perennial small shrub common in the subtropical zones of the Andes (South America). It has been introduced as a cultivated plant in different geographical regions (Cedeño and Montenegro, 2004).
1	<i>Withania somnifera</i> (Solanaceae)	native	Perennial small shrub that inhabits disturbed sunny and dry areas. Native to a wide range of areas, spreading from the Mediterranean region to regions like India and Sri Lanka (Gaurav et al., 2015).
2	<i>Nicotiana glauca</i> (Solanaceae)	non-native	Evergreen shrub native to central northwest Argentina and Bolivia. It has successfully invaded disturbed areas of semi-arid habitats worldwide by forming dense monodominant stands (Ollerton et al., 2012).
2	<i>Hyoscyamus albus</i> (Solanaceae)	native	Annual to biennial herb, native to the coastal areas in southern Europe and the Near East. This plant is an inhabitant of cities, which grows next to walls, and in very remote places.
3	<i>Tropaeolum majus</i> (Tropaeolaceae)	non-native	Fast growing climbing annual plant, native to the Andes Mountains. It can form extensive carpet-like growths in sunny torrent banks and beds (Garzón and Wrolstad, 2009).
3	<i>Convolvulus arvensis</i> (Convolvulaceae)	native	Climbing perennial plant, native to the Mediterranean Basin. It grows in a wide range of conditions from full sun to full shade, on all soils (Culhavi and Manea, 2011).
4	<i>Solanum linnaeanum</i> (Solanaceae)	non-native	Perennial shrub, native to southern Africa, is found occasionally in many Mediterranean countries and considered a serious invasive alien in parts of Australia and New Zealand (Vorontsova and Knapp, 2012).
4	<i>Solanum nigrum</i> (Solanaceae)	native	A predominantly Eurasian species, ranging from being annual to biennial herb sometimes. It appears to be distributed throughout the world, from Finland in the northern hemisphere to New Zealand in the southern hemisphere (Jagatheeswari et al., 2013).

Table 8 (Continuation). * Pairs 5 - 6 and 7 shared the same non-native. Those pairs were initially selected according to their abundant presence as coexisting native and non-native species across different coasts in Mallorca.

Pair	Species (Family)	Status	Description
5, 6, 7*	<i>Mesembryanthemum crystallinum</i> (Aizoaceae)	non-native	Annual to biennial succulent herb, native to South Africa, mostly found on coasts. It is a salt accumulator that leaches salts upon death, increasing soil salinity in the vicinity. Such increase reduces the competitive ability of associated native plant species, increasing its germination and establishment (Abd El-Gawad and Shehata, 2014).
5	<i>Glaucium flavum</i> (Papaveraceae)	native	Perennial herb, native to the Mediterranean Basin that occurs along its shores and the coasts of Western Europe (Thanos et al., 1989).
6	<i>Mesembryanthemum nodiflorum</i> (Aizoaceae)	native	Annual succulent herb, native to the Mediterranean, always living along the coast. Occasionally it forms a kind of carpet or lawn on soils that used to be bare ground (Soliman et al., 2014).
7	<i>Crithmum maritimum</i> (Apiaceae)	native	Facultative halophyte growing on maritime cliffs and sometimes in sand. It is widely distributed along coastal areas of the Mediterranean Sea and of the Atlantic Ocean (Meot-Duros et Magné, 2009).
8	<i>Arundo donax</i> (Poaceae)	non-native	Perennial, herbaceous grass, occurring over a wide range of climatic habitats. It is originally from East Asia but was introduced and diffused widely across the Mediterranean area and around the world through human activity (Corno et al., 2014).
8	<i>Phragmites australis</i> (Poaceae)	native	Perennial grass from Eurasian origin, present in a wide range of habitats, from cold temperate regions to the wetlands of hot and moist tropics in almost all continents, especially Asia and Europe (Vymazal, 2013).

Materials and Methods

Species selection

General monitoring of the presented plant species has been done across different sites in Mallorca (Balearic Islands, Western Mediterranean Sea), which differs in their environmental conditions and topographic positions, including mountain areas, riparian sites of intermittent streams, and coastal areas. Across these sites, we noticed the presence of a unified pattern which is the coexistence of native and non-native plants grown side by side as a pair in the same spot. Such a pattern was abundantly found across all the assessed sites. Hence from these sites and for the species selection, we collected seeds from pairs that were observed to frequently grow side by side in the field.

For this, seeds of eight pairs (three pairs shared the same non-native species) (see details Table 8), were collected during summer-autumn 2018. The collected seeds were preserved in paper bags in a dry, cool place to be later grown under controlled conditions.

Experimental site and growth conditions

The study was carried out in the laboratory of the Plant Physiology Department of the University of the Balearic Islands (UIB). For this study, six individuals per species (84 plant individuals in total, 14 species x 6 replicates), were grown individually, each in a plastic pot (11 cm diameter top; 8.8 cm depth; capacity: 0.52 Liters) containing peat (Silver Torf, Agrochimica, Bolzano, Italy) and Agriperlite® (70:30 v: v). Each pot was irrigated with 0.2 L of 100% Hoagland solution, three times a week. The plants were grown for 90 days in a plant growth chamber under controlled growing conditions (60% air humidity, 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetic active radiation (white light), 12/12 h light/dark regime and temperature fixed at 27/22°C day/night) before starting the measurements.

Leaf morphological traits and Carbon/Nitrogen contents and isotopes

Choosing one young fully expanded leaf per individual ($n = 6$ leaves per species), the leaf morphological traits and Carbon/Nitrogen contents and isotopes were fully characterized by implementing the following steps. Leaf area (cm^2) was scanned using Canon CanoScan LiDE 220 where its projected leaf area was determined using IMAGEJ software (Schneider et al., 2012). Using a caliper as a measurement tool, leaf thickness (cm) was assessed. After obtaining leaf thickness, the same leaf was placed in a paper envelope inside a ventilation oven ($70\text{-}80^\circ\text{C}$) until constant dry weight (g) was reached to calculate the dry leaf mass per unit leaf area (LMA, g m^{-2}). After estimating LMA, the maximum net assimilation rate per unit dry mass (A_{mass} , $\text{nmol g}^{-1} \text{s}^{-1}$) was calculated as the ratio of net CO_2 assimilation (A) (see details below) to LMA.

On the other hand, the obtained dry leaves were grinded into fine and uniform powder using a mixer mill (MM-200; Retsch, Haan, Germany). From the obtained powder, 2 mg from each individual were used for Carbon and Nitrogen isotopes ratios. The carbon isotopic ratio ($\delta^{13}\text{C}$) has been used as a proxy for long-term WUE (Farquhar et al., 1989), and the nitrogen isotopic ratio ($\delta^{15}\text{N}$) is an integrated measure of nitrogen fluxes, assimilation, and allocation in plants, allowing to distinguish N_2 -fixing from non-fixing species (Kalcsits et al., 2014). Isotopic ratios were determined with a Continuous-Flow Isotope Ratio Mass Spectrometry (CF-IRMS) combined with gas chromatography (Thermo Delta XPlus, Bremen, Germany) to analyze gas of mass 44/45/46 (for CO_2) and 28/29 (for N_2) after separation on a GC column (Flash EA 1112 Thermo Finnigan elemental analyzer). Each estimation of the isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, %) of a given sample with the CF-IRMS was corrected following the known value of the standard used during the measurements (here Peach-leaf control samples), given by the National Institute of Standards and Technology (NIST 1547). For determination of mass-based leaf carbon and nitrogen content (C_{mass} and N_{mass} , %), a linear relationship was established between the area of the peak of Carbon 44 or Nitrogen 28 and the weight of C or N present in the standards (Peach-Leaf) used during the measurements. From these obtained weights, the ratio of Carbon to Nitrogen (C: N) was then estimated. Finally, to assess the photosynthetic nitrogen-use-efficiency (PNUE) (see details below), the area-based nitrogen content (N_{area} , g m^{-2}) was calculated as: $N_{\text{mass}} \times \text{LMA}$.

Leaf Physiological Traits

Leaf physiological traits were conducted using a portable photosynthesis system (Li-6400; Li-Cor, Inc., Lincoln, NE, USA) with an infrared gas analyzer (IRGA) coupled with a 2 cm² leaf fluorescence chamber (Li -6400-40 leaf chamber fluorometer; Li-Cor, Inc.) Choosing one young fully expanded leaf per individual (n= 6 leaves per species), instantaneous measurements were carried out between 09:00 to 13:00 h (Central European summer time), at 400 μmol CO₂ mol⁻¹ air and saturating photosynthetic photon flux density (PPFD) at 1200 μmol m⁻² s⁻¹, and 90:10 red:blue light. This light intensity was used to ensure saturation and was chosen after performing light response curves for all the species (Supplementary Fig. S.1.). Net CO₂ assimilation (A, μmol m⁻²s⁻¹) and stomatal conductance (g_s, mol m⁻²s⁻¹) were taken from the instantaneous measurements. From these obtained data with the data recorded for (N_{area}), both the intrinsic water-(WUE) and nitrogen-use-efficiency (PNUE) were assessed. Intrinsic WUE (μmol mol⁻¹) was calculated as the ratio of A to g_s and PNUE (μmol mol⁻¹ s⁻¹) as the ratio of A to N_{area}. Despite very different leaf morphologies, no significant differences were observed for either leaf temperature or leaf-to-air vapor pressure deficit among species (Table S.2.; Supplementary material), for which all measurements are comparable.

The electron transport rate (ETR) was estimated as $ETR = PPFD \times \Phi_{PSII} \times \alpha\beta$ (Genty et al., 1989), Φ_{PSII} being the quantum efficiency of photosystem II, α the leaf absorbance, and β the partitioning of absorbed photons between photosystems I and II. Φ_{PSII} was estimated as $\Phi_{PSII} = (F_m' - F_s) / F_m'$ (Genty et al., 1989), with F_m' as maximum fluorescence under illumination, and F_s as steady-state fluorescence. The $\alpha\beta$ parameter was estimated from A/C_i curves performed under low oxygen (1% O₂), following (Valentini et al., 1995). Once we got the corrected ETR, the ratio of ETR to A then was calculated (μmol mol⁻¹). Finally, the mesophyll conductance (g_m) was estimated following Harley et al. (1992), as:

$$g_m = \frac{A}{C_i - \frac{\Gamma^* \times [ETR + 8 \times (A + R_d)]}{ETR - 4 \times (A + R_d)}}$$

where Γ^* is CO₂ compensation point in absence of R_d (here we assumed a value of 37.4 μmol mol⁻¹ (following Sharkey et al., 2007), and R_d (μmol m⁻²s⁻¹) is the non-photorespiratory respiration during the day, which was estimated by dividing by 2 the respiration rate measured after 2 h of darkness (Niinemets et al., 2005, Martins et al., 2013, Veromann-Jürgenson et al., 2017). The ratio between net CO₂ assimilation rate and respiration was also calculated (A/R_d, Pattison et al., 1998; Galmés et al., 2007). After calculation,

g_m data were filtered following the reliability criterion established by Harley et al. (1992):

$$\partial C_c / \partial A = 12 \times \Gamma^* \times \frac{ETR}{(ETR - 4 \times (A + R_d))^2}$$

Data in the range of $10 < \partial C_c / \partial A < 50$ were considered as reliable. Aberrant values of g_m following this criterion were discarded, together with all the other photosynthetic parameters of that replicate. Photosynthetic limitations - i.e., stomatal limitation (l_s), mesophyll conductance limitation (l_m) and biochemical limitation (l_b) - were estimated following Grassi and Magnani (2005), as follows:

$$l_s = \frac{g_{tot}/g_s + \partial A / \partial C_c}{g_{tot} + \partial A / \partial C_c}$$

$$l_m = \frac{g_{tot}/g_m + \partial A / \partial C_c}{g_{tot} + \partial A / \partial C_c}$$

$$l_b = \frac{g_{tot}}{g_{tot} + \partial A / \partial C_c}$$

Where g_{tot} is the total CO₂ diffusion conductance, calculated as $g_{tot} = 1/(1/g_s + 1/g_m)$ and $\partial C_c / \partial A$ is considered as the initial slope of the A - C_c response curve.

Data Analysis

To test for differences in the leaf morphological, Carbon/Nitrogen isotopes, and leaf physiological traits between native and non-native plant species as a whole and as a pair, a linear mixed-effects model (LMM) was performed using each trait as response variable, including 'pair nested within status (native and non-native)' as fixed effect, and 'species' as a random effect, the latter to account for differences for each species. For that, we used the 'lmer' function, and afterwards an "emmeans" posthoc test was performed for pairwise comparisons. models were validated by visually checking their residuals for normality and homoscedasticity (Zuur et al., 2009). To identify general trends in the variables that have been significantly affected by the plant 'status, and to understand how these traits were related in a multivariate context, a Principal Component Analysis (PCA) was performed. Lastly, correlations among parameters were performed using Spearman correlation. All data have been analyzed using R v.3.4.3 (R Core Team, 2017).

Results

We found statistically significant differences between native and non-native species for all the morphological traits ($p < 0.05$; Table S.3.). Our results show that on Mediterranean islands, non-native plants showed on average larger values of leaf area (LA), where the native ones registered the highest values for both Leaf thickness (LT) and Leaf mass per Area (LMA) (Fig. 6). Whereas for the Carbon/Nitrogen contents and isotopes, the plant' status has significant effect on most the traits of this category except the mass-based nitrogen content (N_{mass}) and the Carbon: Nitrogen ratio (C: N) ($p > 0.05$; Table 2). Both the mass-based carbon content (C_{mass}) and the Nitrogen isotope ratio ($\delta^{15}\text{N}$) showed the highest values for non-native species, whereas the carbon isotope ratio ($\delta^{13}\text{C}$) was highest for the native ones, although all the species showed values typical of non- N_2 -fixing species (Fig. 6). Similarly, the plant' status has significant effect on most of the leaf physiological traits except on the intrinsic water-use efficiency (WUE), respiration (R_d) and both stomatal (l_s) and biochemical limitations (l_b) ($p > 0.05$; Table S.3.). All the traits differing significantly, except the mesophyll conductance limitation (l_m), attained larger values in non-native plants (Fig. 7).

When considering each plant pair, the "status" effect was not consistently found on the assessed traits across all pairs:

Pair 1: *Physalis peruviana* and *Withania somnifera*

In the morphological traits, the status effect was significant on both LA and LMA. *P. peruviana* registered the biggest LA, whereas *W. somnifera* had the largest LMA. Similarly, in the Carbon/Nitrogen contents and isotopes, the traits that were significantly affected by the plant' status (C: N; $\delta^{15}\text{N}$) were larger for *W. somnifera* (Table S.4.). The net CO_2 assimilation (A), the maximum net assimilation rate per unit dry mass (A_{mass}), the electron transport rate (ETR), the mesophyll conductance (g_m), the intrinsic water-use efficiency (WUE), the photosynthetic nitrogen-use efficiency (PNUE), and the stomatal limitation (l_s) were larger for *P. peruviana*, contrary to respiration (R_d) and the biochemical limitation (l_b) which were larger for *W. somnifera* (Table S.5.).

Pair 2: *Nicotiana glauca* vs. *Hyoscyamus albus*

Both LA and LT were significantly affected by the plant' status, attaining the largest values for the non-native (*N. glauca*). For the Carbon/Nitrogen contents and isotopes, only the C: N was significantly larger for *H. albus* showing the largest ratio (Table S.4.). For the leaf physiological traits, A, A_{mass} ,

ETR, g_m , WUE, PNUE, and l_m were significantly larger for *N. glauca*, and l_s was significantly lower for the native *H. albus* (Table S.5.).

Pair 3: *Tropaeolum majus* vs. *Convolvulus arvensis*

Similarly to pair number 1, both LA and LMA were significantly affected by the plant' status, with higher LA biggest for the non-native *T. majus*, and larger LMA for the native *C. arvensis*. Only $\delta^{13}\text{C}$ was largest for *C. arvensis* (Table S.4.). A , A_{mass} , g_s , PNUE and l_b were significantly larger for *T. majus*, contrarily to WUE and l_s which were larger for *C. arvensis* (Table S.5.).

Pair 4: *Solanum linnaeanum* vs. *Solanum nigrum*

Opposite results were found in some of the traits within this pair, in comparison to the previous ones. Both LA and LMA were significantly larger for the non-native *S. linnaeanum*. C: N was significantly larger for the native *S. nigrum* (Table S.4.). A , A_{mass} , ETR, g_s , g_m , PNUE and l_b were significantly larger for *S. nigrum*, in contrary to R_d being larger for *S. linnaeanum* (Table S.5.).

Pair 5: *Mesembryanthemum crystallinum* vs. *Glaucium flavum*

Only LT differed significantly between the two species among the morphological traits, with larger values for the non-native *M. crystallinum* (0.9 ± 0.01 mm). Similarly, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were also larger for *M. crystallinum* (Table S.4.). In contrast, g_m , WUE, PNUE and l_s were significantly larger for the native *G. flavum* (Table S.5.).

Pair 6: *Mesembryanthemum crystallinum* vs. *M. nodiflorum*

Both LA and LT were significantly affected by the plant' status, with larger LA values for the non-native *M. crystallinum*, and larger LT for *M. nodiflorum*. In the Carbon/Nitrogen contents and isotopes, C_{mass} and C: N were significantly larger for *M. crystallinum*, while N_{mass} and $\delta^{13}\text{C}$ were larger for the native *M. nodiflorum* (Table S.4.). g_s , l_m and l_b were significantly larger for *M. crystallinum*, whereas g_m , WUE and l_s were higher for the native one (Table S.5.).

Pair 7: *Mesembryanthemum crystallinum* vs. *Crithmum maritimum*

LT and LMA were significantly larger for the native (*C. maritimum*). In the Carbon/Nitrogen isotopes, N_{mass} , and $\delta^{15}\text{N}$ were significantly larger for *M. crystallinum*, whereas the opposite occurred for C: N (Table S.4.). A , A_{mass} ,

ETR, g_s , PNUE, and l_m were significantly larger for *M. crystallinum*, whereas A/g_s , R_d , WUE, and l_s were larger for *C. maritimum* (Table S.5.).

Pair 8: *Arundo donax* vs. *Phragmites australis*

Only LA differed significantly among all the morphological traits, with larger values for the non-native *A. donax*. Similarly, $\delta^{15}\text{N}$ was also larger for *A. donax* (Table S.4.). A , A_{mass} , ETR, g_s , g_m , WUE, PNUE, A/R_d , and l_s were also the highest for *A. donax*, whereas only the l_b were higher for the native one (Table S.5.).

Principal Component Analysis and correlations among traits

Native and non-native species showed different patterns in the bidimensional space generated by the horizontal and vertical axes. These axes stood for the first and second Principal Components of the PCA, which account for 57.72 percent of the variance of the assessed parameters (Fig. 8). The first axis of PCA (PC1) represented by the leaf physiological traits, morphological traits, and Carbon/Nitrogen isotopes, characterized by high A/R_d , PNUE, g_m and A on the upper right and higher LMA and LT on the upper left. The second (PC2) represented as well by all these characterized by high ETR, A_{mass} , g_s on the lower right and high l_m on the lower left. Non-native species had a greater value for the physiological and morphological traits than the native species, which occupied the higher range of variation, presented high PNUE, A , and g_m , while native species were related to higher LMA and LT on the upper left.

While the PCA suggests some positive and negative relations between some of the leaf physiological traits and morphological traits, Spearman correlation only showed a significantly negative correlation between A_{mass} and LMA ($r = -0.75$; $p < 0.001$), placing the non-native and the natives at a different end, with the non-native possessing larger values in A_{mass} and lower values in LMA, in contrast to the natives (Fig. 9, A). However, we found no significant correlation between both A_{mass} and N_{mass} ($r = 0.08$; $p = 0.55$) (Fig. 9, B) or A and R_d ($r = -0.21$; $p = 0.11$) (Fig. 9, C) and, in fact, no other significant correlation was found between any of the studied parameters, except the obvious ones (e.g., A vs g_s and g_m , A vs PNUE, etc. - data not shown).

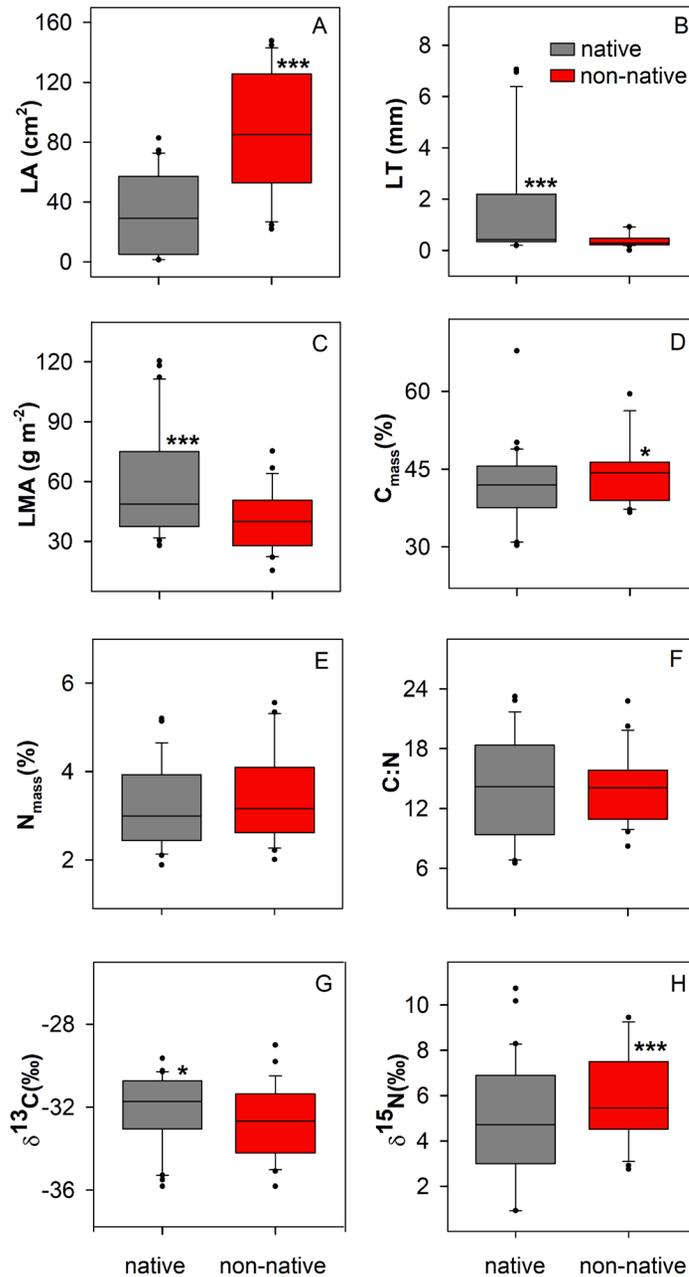


Figure 6. Box plots of the leaf morphological traits and Carbon/Nitrogen contents and stable isotopes. (A) leaf area (LA), (B) leaf thickness (LT), (C) leaf mass per area (LMA), (D) mass-based carbon content (C_{mass}), (E) mass-based nitrogen content (N_{mass}), (F) carbon:nitrogen ratio (C:N), (G) carbon isotope ratios ($\delta^{13}\text{C}$), and (H) nitrogen isotope ratios ($\delta^{15}\text{N}$) for native (in grey) and non-native (in red) plant species studied. *Denotes statistically significant difference at $p < 0.05$ and *** $p < 0.001$.

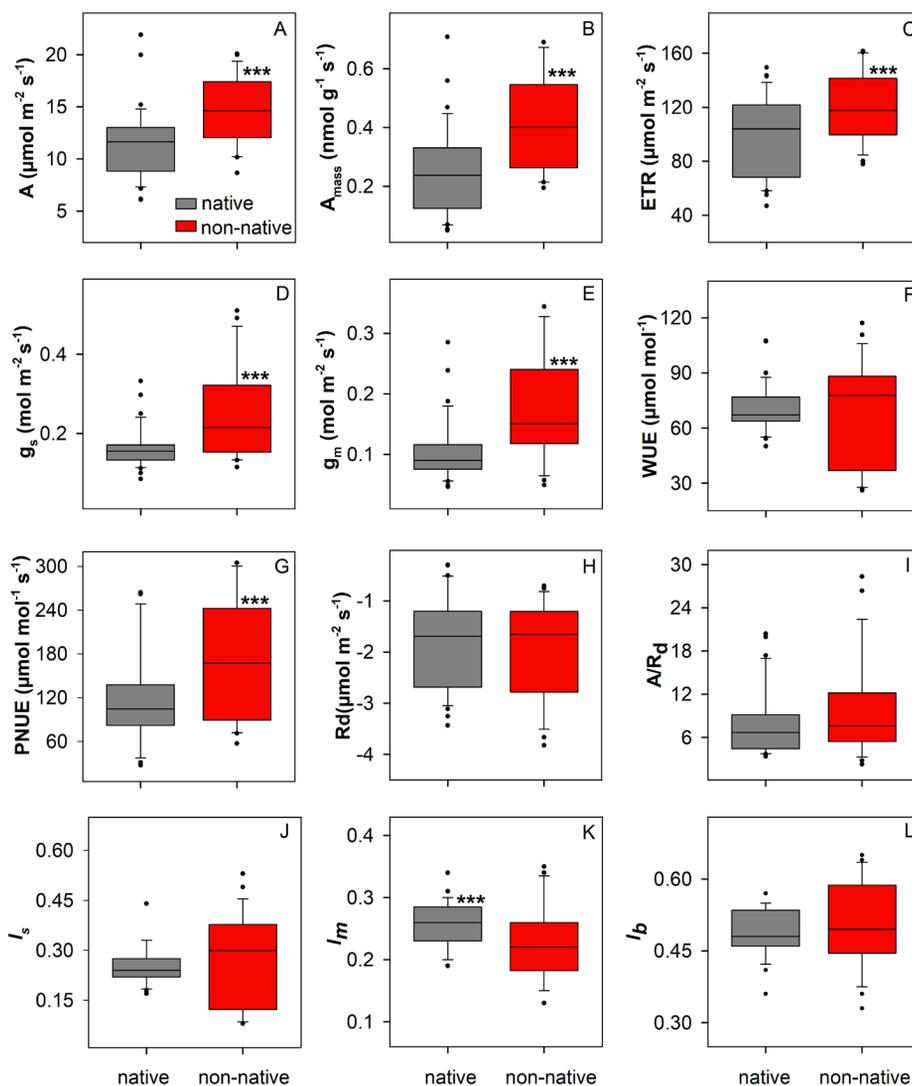


Figure 7. Box plots of the leaf physiological traits. (A) net CO₂ assimilation (A), (B) maximum net assimilation rate per unit dry mass (A_{mass}), (C) electron transport rate (ETR), (D) stomatal conductance (g_s), (E) mesophyll conductance (g_m), (F) intrinsic water-use efficiency (WUE), (G) photosynthetic nitrogen-use efficiency (PNUE), (H) respiration (R_d), and (I) photosynthetic CO₂ assimilation over respiration (A/R_d), (J) stomatal limitation (l_s), (K) mesophyll conductance limitation (l_m) and (L) biochemical limitation (l_b) for native (in grey) and non-native (in red) plant species studied. *Denotes statistically significant difference at $p < 0.05$ and *** $p < 0.001$.

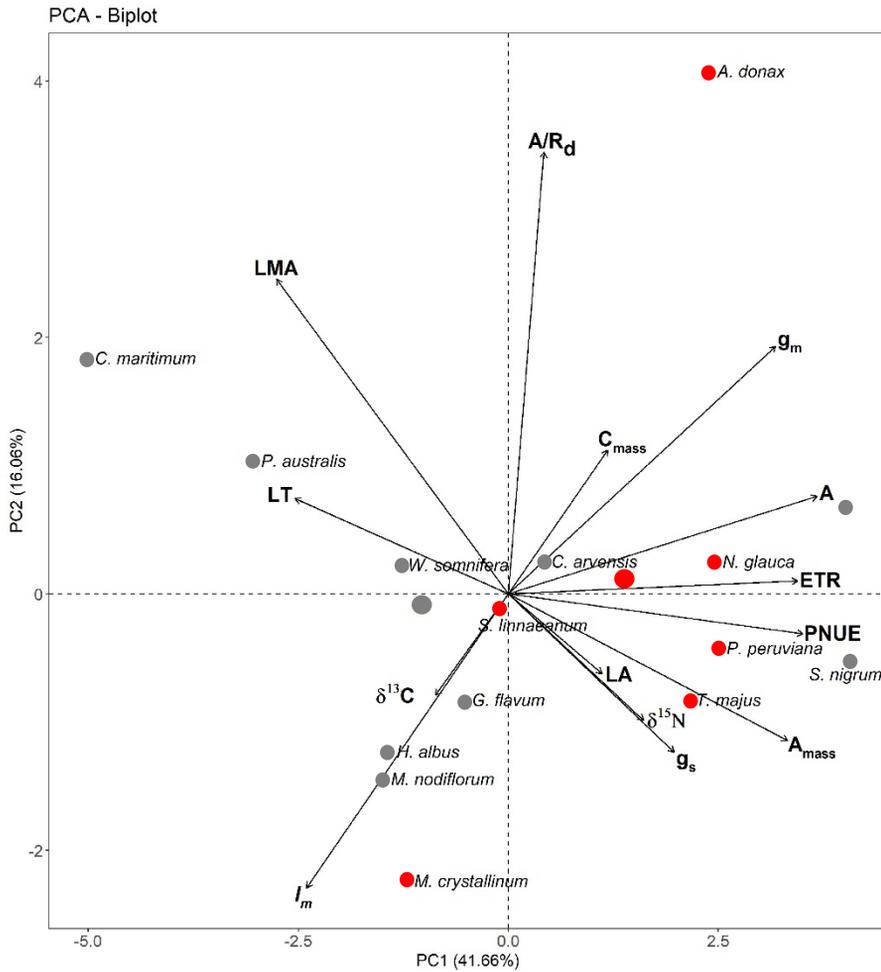


Figure 8. Principal Component Analysis (PCA) of the significant variables for the leaf morphological traits, Carbon/Nitrogen contents and stable isotopes, and leaf physiological traits between for native (in grey) and non-native (in red) plant species studied. The 2 big points represent the centroids of both native and non-native plant species.

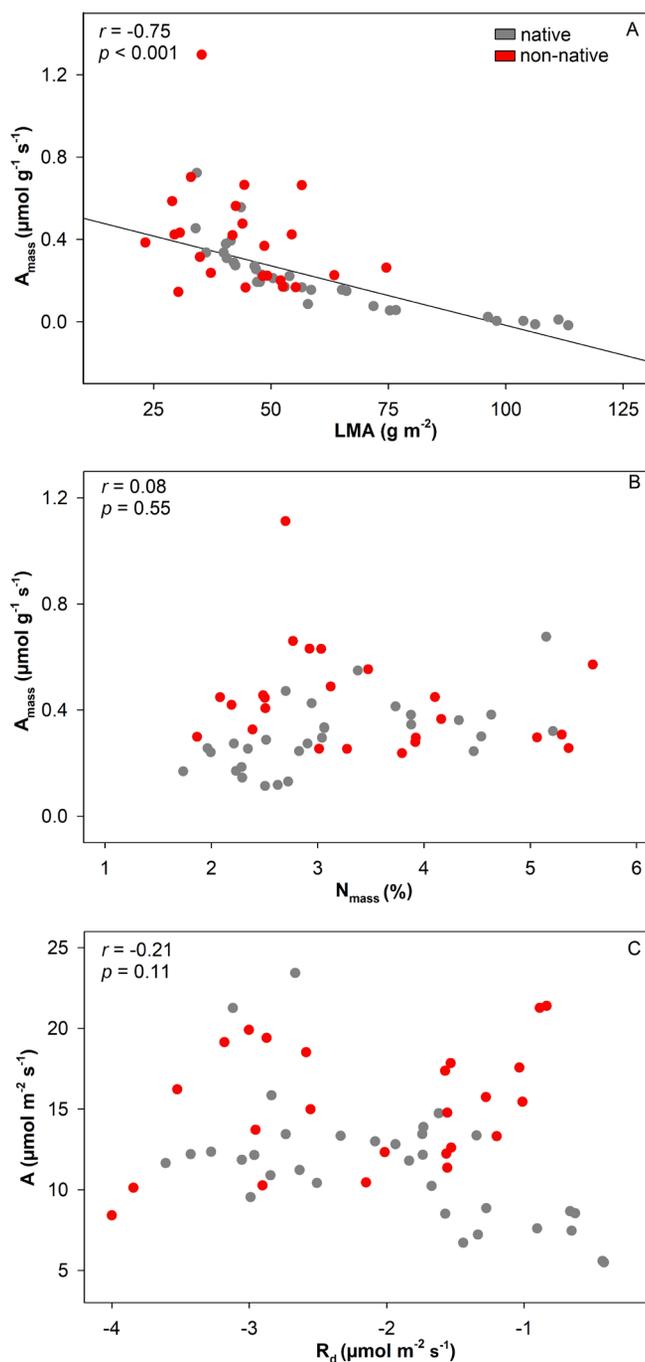


Figure 9. Relationship between the maximum net assimilation rate per unit dry mass (A_{mass}) vs. leaf mass per area (LMA) (A), mass-based nitrogen content (N_{mass}) (B), and net CO_2 assimilation (A) vs. respiration (R_d) (C) for native (in grey) and non-native (in red) plant species studied.

Discussion

Our results showed that non-native plant species present in Mediterranean islands tend to have advantageous values in their leaf physiological traits, such as large A , A_{mass} , g_s , PNUE, among others (Fig. 7), while possessing lower leaf construction cost in terms of LT and LMA, when comparing them to the co-occurring native ones (Fig. 8). Many of these traits partly explain the success of non-native plant species (Baruch and Goldstein, 1999; Funk and Vitousek, 2007) since they may contribute to a faster growth rates and confer a competitive advantage over native species (Peñuelas et al., 2010; Matzek, 2011; Funk, 2013; Kunstler et al., 2015), at least under favorable weather conditions which, in the Mediterranean, usually coincide with the plant's growing season. Of course, traits conferring tolerance to environmental stresses occurring especially in summer may also contribute to different species fitness, yet this is out of the scope of the present study. The results presented here are in accordance with previous views for native and non-native plants comparisons from other environments. Peñuelas et al. (2010) have reported that alien species throughout Oahu Island (Hawai'i) had enhanced capacities in terms of productivity (photosynthetic capacity) and lower LMA, causing such species to have higher photosynthetic returns from their foliar biomass investment. More recent studies also showed that the high photosynthetic rates of non-native species reflect their potential to accumulate more biomass, which convey higher competitive ability leading to invasion success (Tordoni et al., 2019; Zunzunegui et al., 2020; Morais et al., 2021).

Along with the long list of distinguished physiological traits between native and non-native plants, the present study reveals a novel trait which is the mesophyll conductance (g_m), being on average higher in non-native species. Here we show that g_m plays a major role in setting the difference of the photosynthetic capacity between native Mediterranean plants and non-native species. Such difference is usually correlated with leaf anatomy (Flexas et al., 2008; Terashima et al., 2011). Lower g_m appears to be related to the significantly higher LMA observed in native species (Fig. 6, C). Large LMA is associated to high leaf thickness, which appears to be an adaption to stressful environments like those in the Mediterranean climate (Niinemets, 1999). Besides LMA, sub-cellular anatomical traits, not studied here, had been shown to determine low g_m , such as thick cell walls and low chloroplast coverage of intercellular air spaces (Tomás et al., 2013; Tosens et al., 2016; Carriquí et al., 2019; Gago et al., 2019). When performing the photosynthetic limitations analysis, only the mesophyll conductance limitation (l_m) differed significantly, being on average higher in native species (Fig. 7, K). Such finding is in accordance with the fact that l_m tends to be large in native

Mediterranean species (Flexas et al., 2014). Regardless of the mechanisms, which remain unknown, this study report, for the first time, that a lower l_m may be a significant physiological trait for contributing to the 'invasive syndrome' of non-native species. Despite of it, our results were not in full accordance with the 2nd hypothesis, as the WUE did not significantly differ between the native and non-native species. This result is in contrary to the findings of Zunzunegui et al. (2020) and Morais et al. (2021). Such result with the significantly lower $\delta^{13}\text{C}$ for non-native plants (Fig. 6, G), suggest lower WUE in the long term. Considering this, it could be speculated that under water stress the non-native may not perform as well as the native, making them less adaptive to the substantial warmings and prolonged periods of water shortage predicted to occur in Mediterranean ecosystems (Cramer et al., 2018). To test this, however, further studies should be performed under stress conditions.

When it comes to the leaf structure and function relationships described in the leaf economics spectrum, our results were in accordance with the few other studies that used it in the field of invasion ecology (Ordonez and Olff 2013; Petruzzellis et al., 2021). We report that non-native species of Mediterranean islands, as a group, differ from natives in both individual traits and their positioning along the LES, locating them predominantly at the "fast-return" end of it, with faster investment strategies than co-occurring native species, associated with higher values of A, PNUE and lower values of LMA. This high PNUE in 'fast' strategy plants may be due to a greater proportional allocation of C and N to structural than metabolic components of the leaf in low LMA leaves (Poorter et al., 2009). Such finding highlights the importance of the particular ecological-abiotic background a species faces once introduced. Consequently, introduction success is not only dependent of area of origin, but also on introduced species having a suite of traits that enable them to use the new habitat (Thompson and Davis, 2011). However, and surprisingly, only the A_{mass} vs LMA relationship was significant, while the A_{mass} vs N_{mass} and the A vs R_d relationships were not, contrary to what is described for LES for plants in general (Wright et al., 2004) and native/non-native comparisons in particular (Petruzzellis et al., 2021). McDowell (2002) attributed the higher PNUE of non-native species to their lower N content and this is confirmed in our study since, however, although the leaf N value in our assessed non-native plants was not significantly different to that in native species when expressed on a mass basis ($p = 0.08$) it was significantly lower ($p < 0.001$) when expressed on an area basis.

Although our findings show that non-native species, as a group, have distinct leaf morpho-physiological traits, at the same time, they also illustrate that this cannot be generalized for every particular non-native plant when comparing

it with its native coexisting plant species. Indeed, for example in pairs 4, 5 and 6, the values of most of the assessed traits were in the opposite direction than the general patterns, which means that the native species (*S. nigrum*, *G. flavum* and, *M. nodiflorum*) presented the distinct leaf morpho-physiological traits compared to their co-occurring non-native species (Table S.4. and S.5.). This indicates that the found general patterns cannot be applied to every coexisting plant pair. Other studies also showed contradictions in the performance of non-native and native species (Palacio-López and Gianoli, 2011; Flores-Moreno and Mole, 2013), which might be influenced by the selection of species and the fact that the invasive behavior of a given species can be achieved by multiple combinations of traits (Manea and Leishman, 2011). When comparing coexisting species pairs of non-native and native species, if the physiological approach is 'worst' in the non-native species, its success might be due to other traits associated to their reproduction, and/or strategies related to better coping with the biotic-abiotic disturbances with which it might be confronted. Consequently, further studies considering the nature of pair-wise experimental designs are thus needed to assess whether there is a general pattern contributing to the invasion success of non-native species.

Conclusions

We described a leaf physiological trait syndrome for non-native species invading Mediterranean islands that is similar to that previously described for non-native species in other environments, consisting of larger A , A_{mass} , g_s , PNUE and lower LMA and LT, among others. While the vast majority of our assessed traits followed the same trend in non-native possessing advantageous values, the WUE was not significant in here. This lack of advantage on a key parameter under semi-arid conditions may perhaps reduce the success of non-native species when they are subject to water stress. Hence, this should be confirmed in further experiments. Among the assessed traits, we report for the first-time larger g_m , and lower l_m in non-native species, which seems to be linked to their lower LMA. These novel traits to be added to the 'leaf physiological trait invasive syndrome', though, as discussed, it may not be always encountered when analyzing just a given coexisting pair of native and non-native species. Finally, our results confirm that the non-native plants on Mediterranean islands are also positioned on the "fast-return" end of the LES. However, that only one significant LES relationship (A_{mass} vs LMA) was found here might be explained by the fact that our plants were not grown in the field but in a growth chamber with addition of nutrient solution containing large amounts of N. This is interesting although it deserves confirmation. If so, it would mean that the A_{mass} vs LMA relationship is the most robust among studied LES traits, for which it possibly is a central or primary one, while others being secondary or consequences of it.



Hey, it's **Jezzine** again!

Photo by Rami Rizk

General discussion

The scale and consequences of plant invasions around the world have constantly increased the curiosity of scientists to understand the mechanisms underlying the successful invasion of introduced plants in their new ranges. It is well documented that the characteristics conferring a given species its invasive capacity are multiple, ranging from biotic interactions to many other ecological features (Traveset and Richardson, 2021). The main goal of this PhD thesis was to contribute to unveil such mechanisms. When comparing the pollinators between non-native species and their co-existing native counterparts, the shared proportion fluctuated from 0 to 33%, suggesting little “interference” with the pollination success of the latter. Such result is in accordance with the Darwin’s Naturalization Hypothesis, suggesting that “unrelated” flowering non-native plants are more likely to coexist with native ones if they do not compete for resources (i.e., if they share few pollinators). The non-native plants showed to have acquired a largely different set of pollinators than their native counterparts, while the most commonly shared in each plant pair were not the most generalized species. This finding indicates that the non-natives interacted not only with generalized pollinators but also with the specialized ones. Our results are aligned with those of previous studies (e.g., Rodger et al., 2010; Ollerton et al., 2011; Ackerman et al., 2014; Maruyama et al., 2016), showing that a new diverse assemblage of pollinators is far more likely to integrate with non-native plants than would be expected by chance.

Among the assessed floral traits, corolla length at opening was shown to be important in determining the differences in flower visitation rate between native and non-native species. Such findings revealed that non-native species with longer corollas at opening had higher flower visitation rate than native species. However, research on the effect of the corolla size in explaining the differences in pollination attraction between native and non-native species is still rare (but see Gómez et al., 2016; Gao et al., 2019). Adding to the longer corollas at opening for non-native species, their higher flower abundance was also shown to be a significant trait in explaining their higher insect visitation rates. Our findings are also congruent with those of previous studies showing

that non-native plants with more flowers/inflorescences tend to attract a wider array of pollinators and receive higher flower visitation rates (Lopezaraiza-Mikel et al., 2007; Padrón et al., 2009; Kaiser-Bunbury et al., 2011). Along with the wider array of pollinators, flower abundance also enhances visitors that interact negatively with the pollination process, such as nectar robbers (Irwin et al., 2010). This is actually what we found with one of the assessed species.

While the biotic interactions between the native and non-native plants supported the general pattern that non-native species have no barriers at the pollination stage to integrate into native communities, the abiotic ones showed that the performance of the latter was limited. The abiotic environmental gradients (e.g., resource availability) were shown to impact the difference in traits between native and non-native species, whereby non-natives consistently outperform native species in high-resource environments whilst the latter surpass non-natives in low-resource environments (Tecco et al., 2010; Cleland et al., 2011; Cramer et al., 2014). This study has revealed that, among the morphological and chemical traits that we assessed, only a few traits differ significantly between native and non-native species. The significance of such differences is inconsistent among the different resource environments. Such results are aligned with those of previous studies (Daehler et al., 2004; Matzek, 2011; Leffler et al., 2014), showing that the performance of non-native plants is 'context-dependent' discarding the idea that all non-native species are considered as super plants under high-resource environments and that all natives surpass non-natives in low-resource environments. The 'context-dependent' performance of the non-native species, presented here, supports the claim that trait-based differences between native and non-native species alone cannot predict future invasion (Thompson and Davis, 2011). Processes other than trait differences can drive plant invasions, such as the order of species arrival (Daleo et al., 2009), presence of natural enemies (Keane and Crawley, 2002 ; Zuppinge-Dingley et al., 2011), or propagule pressure (Von Holle and Simberloff, 2005). We found an overall facilitative interaction between native and non-native plants, both the native and the non-native species grew more when coexisting together than when growing alone; specifically, the dry biomass values were higher for both native and non-native species when they coexist. When it comes to the impacts of allelochemicals and antioxidant defense mechanisms, our results were not consistent with the previous studies demonstrating that all non-native plants usually possess both higher growth-related traits and stronger chemical defenses (Ridenour et al., 2008; Caño et al., 2009; Ni et al., 2020). The *Novel Weapons Hypothesis* (NWH) explained that the plants co-evolved with species with an allelopathic ability may be less susceptible to allelochemicals, while newly exposed species to such allelopathic effect may

exhibit less resistance. Consequently, the impacts of allelochemicals and antioxidant defense mechanisms on non-native plants and their native counterparts are highly dependent on their surrounding conditions or/and on the plants' ontogeny.

Lastly, the leaf physiological approach showed that the assessed non-native species on a Mediterranean island tended to have advantageous values in their leaf physiological traits, such as large leaf rates of net CO₂ assimilation (A) and higher photosynthetic nitrogen-use efficiency (PNUE), among others, while possessing lower leaf construction cost in terms of leaf thickness (LT) and leaf mass per area (LMA) as compared to the co-occurring native ones. Along with the list of known differential morpho-physiological traits between native and non-native species, this study unravels two novel traits to be added to the 'leaf physiological trait invasive syndrome': non-native species present larger mesophyll conductance (g_m) and lower mesophyll conductance limitations (l_m). Such finding is in accordance with the fact that l_m tends to be large in native Mediterranean species (Flexas et al., 2014). Here we show that mesophyll conductance plays a major role in setting the difference of the photosynthetic capacity between native Mediterranean plants and non-Mediterranean species. Such difference is usually correlated with leaf anatomy (Flexas et al., 2008; Terashima et al., 2011). Lower g_m appears to be related to the significantly higher leaf mass area (LMA) observed in native species. We found that the intrinsic water-use efficiency (WUE) did not differ on average between the native and non-native species in our study, and the $\delta^{13}C$ was significantly lower in non-natives, suggesting lower WUE in the long term. Considering this, it could be speculated that under water stress the non-native may not perform as well as the native, making them less adaptive to extreme environmental conditions predicted to occur in a future climate change scenario. To test this, however, further studies should be performed under stress conditions.

When it comes to the leaf economics spectrum (LES), the present results concur with other studies (Ordonez and Olff, 2013; Peñuelas et al., 2010; Petruzzellis et al., 2021). These findings report that on a Mediterranean island, native and non-native species, at least the studied ones, are placed on the opposite sides of the leaf economics spectrum, with the non-native species positioned on the fast return end. However, and surprisingly, only the A_{mass} vs LMA relationship was significant, while the A_{mass} vs N_{mass} and the A vs R_d relationships were not, contrary to what is described for LES for plants in general (Wright et al., 2004) and for native and non-native comparisons in particular (Petruzzellis et al., 2021).

However, although most of our findings support the general trends that non-native have distinct traits, at the same time, they also illustrate that this cannot be generalized for every particular non-native plant when comparing it with its native coexisting plant species. Indeed, the flower visitation rate and the flower abundance were not consistently high for non-native species along all the assessed pairs. The facilitative interaction between native and non-native species was not repeatedly the same across all the pairs. It fluctuated from being facilitative to asymmetric to competitive when we considered a simple pairwise interaction, suggesting that the biomass-based assessment might not be the only factor in defining the outcome of plant-plant interactions (Armas et al., 2004). Only one pair among the five we assessed followed the trend of non-native species possessing both higher growth-related traits and stronger chemical defenses. Lastly, five non-native species of the eight assessed pairs showed distinct leaf morpho-physiological traits compared to their co-occurring native species. This indicates that the found general patterns cannot be applied to every coexisting plant pair. Other studies also showed contradictions in the performance of non-native and native species (Palacio-López and Gianoli, 2011; Flores-Moreno and Mole, 2013), which might be influenced by the selection of species and the fact that the invasive behavior of a given species can be achieved by multiple combinations of traits (Manea and Leishman, 2011). When comparing coexisting species pairs of non-native and native species, if the physiological approach is 'worst' in the non-native species, its success might be due to other traits associated to their reproduction, and/or strategies related to better coping with the biotic-abiotic disturbances with which it might be confronted. Consequently, further studies considering the nature of pair-wise experimental designs are thus needed to assess whether there is a general pattern contributing to the invasion success of non-native species.

Conclusions

This doctoral thesis has studied the different mechanisms that underlie the successful establishment of non-native species in new geographical zone. Concretely, we used a multi-disciplinary approach: Ecology, Phytochemistry, and Leaf Physiology.

Hence, the conclusions of this Ph.D. are:

1. The successful establishment of non-native species in new geographical zones could be influenced by one or multiple mechanisms.
2. Non-native plants can acquire a completely different set of pollinators, encompassing even different orders, than their native counterparts.
3. Non-native plants can attract both generalized and specialized pollinators.
4. Along with flower abundance, corolla length at opening is also an important trait in determining the differences in flower visitation rate between natives and non-natives.
5. Not all non-native species are 'super plants', their success is context-dependent.
6. Biomass-based assessment might not be the only factor in defining the outcome of plant-plant interactions.
7. The impacts of allelochemicals and antioxidant defence mechanisms on non-native plants and their native counterparts are highly dependent on their surrounding conditions or/and on the plants' ontogeny.
8. The leaf physiological trait syndrome for non-native species invading a Mediterranean island is similar to that previously described for non-native species in other environments.

9. Non-native species possess larger mesophyll conductance (g_m), and lower mesophyll conductance limitations (l_m), two novel traits to be added to the 'leaf physiological trait invasive syndrome'.
10. The studied non-native plants on a Mediterranean island are also positioned on the high-return end of the leaf economics spectrum.
11. All these findings cannot be generalized on every coexisting plant pair.



Byblos, North Lebanon, is considered as one of the oldest continuously inhabited towns in the world. Modern archaeological excavations have revealed that Byblos was occupied at least by the Neolithic Period (New Stone Age; c. 8000–c. 4000 BC).

Photo by Elie Korkomaz

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Supplementary material

This section comprises supplementary material for Chapter 1 and Chapter 3.

Appendix A provides the supplementary tables and figures of Chapter 1 and Chapter 3. It comprises 5 tables and 1 figure.

Appendix B provides the original publications derived from Chapter 1 and Chapter 3.

Appendix A

This Appendix provides the supplementary tables and figures of Chapter 1 and Chapter 3. It comprises 5 tables and 1 figure.

Table S.1. Model selection summary of the three best models constructed to explain variation in SP, IVR and FVR.

Model	Explanatory variable	Random	Error distribution	Link Function	df	AICc	delta	weight
Pollinator species richness (SR)								
1	Corolla length at opening	pair	Poisson	log	3	151.86	0.00	0.33
null		pair	Poisson	log	2	152.34	0.48	0.26
6	Corolla length at opening x Status	pair	Poisson	log	5	152.84	0.98	0.20
Insect visitation rate (IVR)								
1	Corolla length at opening	pair	Gamma	log	4	-92.55	0.00	0.50
null		pair	Gamma	log	3	-91.09	1.45	0.24
5	Corolla length at opening + Flower abundance	pair	Gamma	log	5	-90.18	2.36	0.15
Insect visitation rate (IVR)								
5	Corolla length at opening x Status + Flower abundance	pair	Gamma	log	6	0.03	0.00	0.70
3	Corolla length at opening x Status + Shape	pair	Gamma	log	8	1.73	1.70	0.30

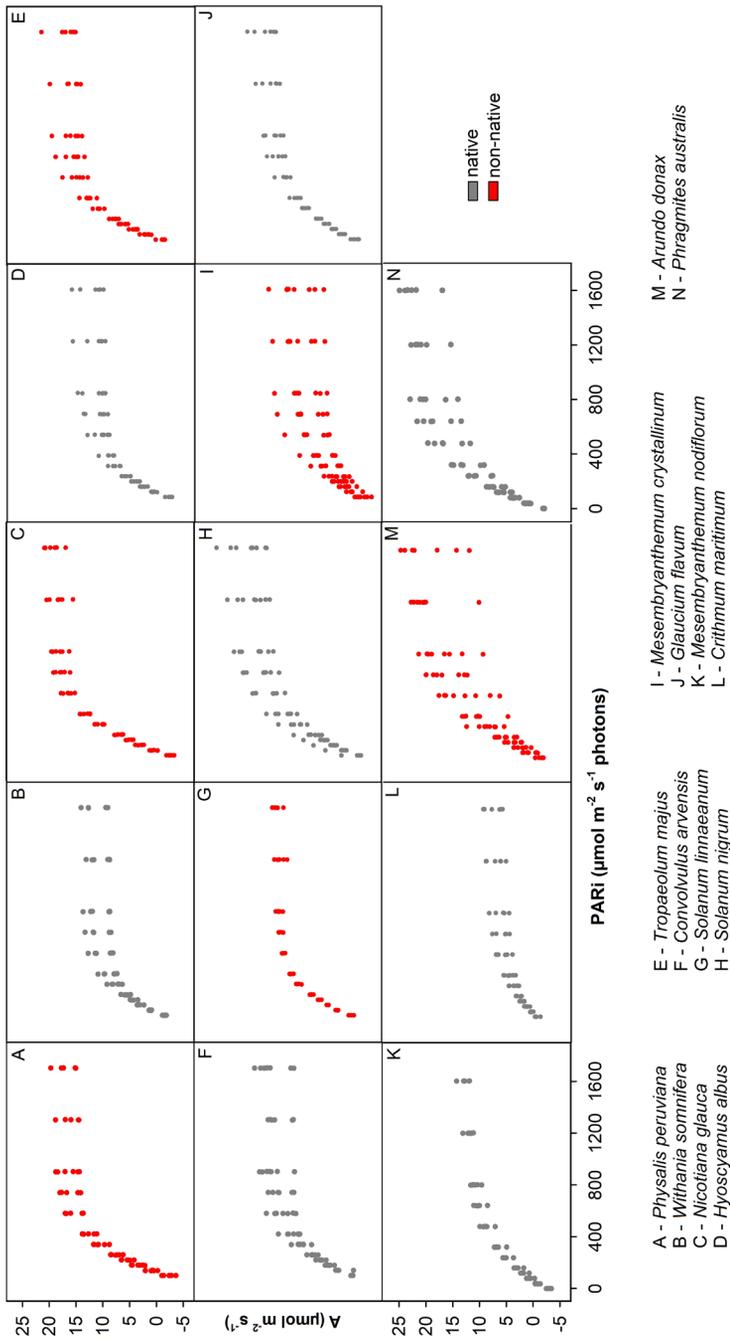


Figure S.1. Supplemental figure with the light saturation curves which represents the net CO₂ assimilation (A) to the In-Chamber quantum sensor (PARI) for native (in grey) and non-native (in red) plant species studied.

Table S.2. Averaged values of leaf-to-air vapor pressure deficit (VPD) and leaf temperature (CTleaf) (n = 6 per species)

Species	Status	VPD	CTleaf
<i>Physalis peruviana</i>	non-native	2.08	28.46
<i>Withania somnifera</i>	native	1.94	28.34
<i>Nicotiana glauca</i>	non-native	1.94	28.28
<i>Hyoscyamus albus</i>	native	1.8	28.94
<i>Tropaeolum majus</i>	non-native	1.66	27.54
<i>Convolvulus arvensis</i>	native	1.98	28.95
<i>Solanum linnaeanum</i>	non-native	2	28.81
<i>Solanum nigrum</i>	native	1.58	28
<i>Mesembryanthemum crystallinum</i>	non-native	1.65	28.28
<i>Glaucium flavum</i>	native	2.09	28.18
<i>Mesembryanthemum nodiflorum</i>	native	2.1	28.09
<i>Crithmum maritimum</i>	native	1.72	28.12
<i>Arundo donax</i>	non-native	1.74	27.7
<i>Phragmites australis</i>	native	1.54	27.86

Table S.3. Chisq and P values of the leaf morphological traits, Carbon/Nitrogen contents and isotopes, and leaf physiological traits taking into consideration status and pairs nested in status.

Leaf Morphological traits (leaf area (LA), Leaf thickness (LT), Leaf mass per area (LMA), **Carbon/Nitrogen contents and isotopes** (mass-based carbon content (C_{mass}), mass-based nitrogen content (N_{mass}), Carbon: Nitrogen ratio (C: N), carbon isotope ratios ($\delta^{13}\text{C}$), nitrogen isotope ratios ($\delta^{15}\text{N}$), Leaf physiological traits (net CO_2 assimilation (A), maximum net assimilation rate per unit dry mass (A_{mass}), electron transport rate (ETR), stomatal conductance (g_s), mesophyll conductance (g_m), intrinsic water-use efficiency (WUE), photosynthetic nitrogen-use efficiency (PNUE), respiration (R_d), photosynthetic CO_2 assimilation over respiration (A/R_d), stomatal limitation (l_s), mesophyll limitation (l_m) and biochemical limitation (l_b)).

	Status		Status/Pairs	
	Chisq	P-value	Chisq	P-value
Leaf morphological traits				
LA	401.07	< 0.001	603.90	< 0.001
LT	425.05	< 0.001	2938.61	< 0.001
LMA	50.17	< 0.001	246.32	< 0.001
C/N contents and isotopes				
C_{mass}	5.78	< 0.05	59.71	< 0.001
N_{mass}	2.99	0.08	139.51	< 0.001
C: N	0.27	0.60	290.55	< 0.001
$\delta^{13}\text{C}$	8.80	< 0.05	319.86	< 0.001
$\delta^{15}\text{N}$	13.60	< 0.001	227.36	< 0.001
Leaf physiological traits				
A	79.91	< 0.001	283.45	< 0.001
A_{mass}	40.99	< 0.001	123.36	< 0.001
ETR	33.31	< 0.001	229.09	< 0.001
g_s	58.01	< 0.001	173.33	< 0.001
g_m	76.61	< 0.001	247.93	< 0.001
WUE	0.28	0.59	235.47	< 0.001
PNUE	20.69	< 0.001	72.09	< 0.001
R_d	1.40	1.40	237.19	< 0.001
A/R_d	8.32	< 0.05	247.84	< 0.001
l_s	3.10	0.07	247.68	< 0.001
l_m	36.78	< 0.001	235.98	< 0.001
l_b	2.09	0.14	144.41	< 0.001

Table S.4. Leaf morphological traits and Carbon/Nitrogen contents and isotopes. Leaf area (LA), leaf thickness (LT), leaf mass per area (LMA), mass-based carbon content (C_{mass}), mass-based nitrogen content (N_{mass}), carbon: nitrogen ratio (C:N), carbon isotope ratios ($\delta^{13}\text{C}$), nitrogen isotope ratios ($\delta^{15}\text{N}$). Values are average \pm SD ($n = 6$ per species). For each trait, values labeled with the same letter are not significantly different from other means for the same trait according to “emmeans” pairwise comparisons procedure at the < 0.05 level of significance.

Species	Status	LA (cm ²)	LT (mm)	LMA (g m ⁻²)	C_{mass} (%)	N_{mass} (%)	C:N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. peruviana</i>	non-native	106.5 \pm 20.74 ^a	0.3 \pm 0.16 ^a	23.9 \pm 6.61 ^a	57.8 \pm 17.09 ^a	3.9 \pm 1.25 ^a	14.8 \pm 0.61 ^a	-30.4 \pm 1.18 ^a	5.0 \pm 0.74 ^a
<i>W. somnifera</i>	native	26.2 \pm 2.65 ^b	0.4 \pm 0.04 ^a	63.9 \pm 13.35 ^b	50.1 \pm 12.06 ^a	2.5 \pm 0.44 ^a	20.2 \pm 2.62 ^b	-31.5 \pm 0.77 ^a	7.1 \pm 0.75 ^b
<i>N. glauca</i>	non-native	98.5 \pm 21.29 ^a	0.5 \pm 0.04 ^a	40.4 \pm 3.32 ^a	39.3 \pm 4.51 ^a	2.7 \pm 0.37 ^a	14.7 \pm 0.97 ^a	-31.6 \pm 0.70 ^a	4.7 \pm 2.64 ^a
<i>H. albus</i>	native	39.7 \pm 8.01 ^b	0.4 \pm 0.05 ^b	54.9 \pm 13.12 ^a	40.4 \pm 2.17 ^a	2.3 \pm 0.14 ^a	17.9 \pm 1.04 ^b	-32.2 \pm 0.61 ^a	7.1 \pm 1.09 ^a
<i>T. majus</i>	non-native	38.3 \pm 14.77 ^a	0.2 \pm 0.05 ^a	28.6 \pm 6.23 ^a	42.9 \pm 2.73 ^a	2.8 \pm 0.49 ^a	15.5 \pm 3.44 ^a	-34.9 \pm 0.57 ^a	5.5 \pm 0.98 ^a
<i>C. arvensis</i>	native	4.9 \pm 0.44 ^b	0.2 \pm 0.01 ^a	43.1 \pm 7.92 ^b	45.4 \pm 2.77 ^a	2.7 \pm 0.54 ^a	17.1 \pm 4.93 ^a	-32.5 \pm 1.58 ^b	6.1 \pm 1.27 ^a
<i>S. linnaeanum</i>	non-native	138.1 \pm 9.35 ^a	0.2 \pm 0.01 ^a	48.1 \pm 2.94 ^a	46.2 \pm 6.72 ^a	4.7 \pm 0.70 ^a	9.8 \pm 1.00 ^a	-32.9 \pm 0.55 ^a	9.6 \pm 2.40 ^a
<i>S. nigrum</i>	native	72.9 \pm 2.28 ^b	0.2 \pm 0.01 ^a	33.7 \pm 7.75 ^b	44.7 \pm 3.33 ^a	3.5 \pm 0.45 ^a	12.9 \pm 0.72 ^b	-33.1 \pm 0.76 ^a	10.4 \pm 0.40 ^a
<i>M. crystallinum</i>	non-native	74.3 \pm 6.37 ^a	0.9 \pm 0.01 ^a	44.8 \pm 16.74 ^a	41.2 \pm 4.13 ^a	3.6 \pm 0.47 ^a	11.5 \pm 0.69 ^a	-32.1 \pm 0.99 ^a	5.3 \pm 0.95 ^a
<i>G. flavum</i>	native	65.2 \pm 14.94 ^a	0.7 \pm 0.06 ^b	39.7 \pm 4.66 ^a	42.3 \pm 3.98 ^a	3.9 \pm 0.91 ^a	11.2 \pm 2.16 ^a	-35.4 \pm 0.28 ^b	0.2 \pm 2.04 ^b
<i>M. nodiflorum</i>	native	1.5 \pm 0.15 ^b	2.2 \pm 0.02 ^b	37.6 \pm 10.09 ^a	31.6 \pm 1.79 ^b	4.5 \pm 0.41 ^b	7.00 \pm 0.49 ^b	-30.2 \pm 0.27 ^b	4.0 \pm 0.93 ^a
<i>C. maritimum</i>	native	63.1 \pm 9.70 ^a	6.5 \pm 0.76 ^b	110.8 \pm 8.95 ^b	40.6 \pm 3.75 ^a	2.9 \pm 0.19 ^b	14.1 \pm 0.99 ^b	-31.5 \pm 0.64 ^a	3.3 \pm 0.56 ^b
<i>A. donax</i>	non-native	27.7 \pm 3.14 ^a	0.2 \pm 0.01 ^a	72.1 \pm 4.64 ^a	45.8 \pm 2.93 ^a	2.3 \pm 0.26 ^a	20.1 \pm 2.37 ^a	-32.2 \pm 0.36 ^a	3.5 \pm 0.24 ^a
<i>P. australis</i>	native	10.5 \pm 1.16 ^b	0.3 \pm 0.04 ^a	73.1 \pm 31.34 ^a	47.3 \pm 2.35 ^a	2.5 \pm 0.14 ^a	18.8 \pm 0.15 ^a	-33.1 \pm 0.75 ^a	1.1 \pm 0.22 ^b

Table S.5. Leaf physiological traits. Net CO₂ assimilation (A), net assimilation rate per unit dry mass (A_{mass}), electron transport rate (ETR), stomatal conductance (g_s), mesophyll conductance (g_m), intrinsic water-use efficiency (A/g_s), Photosynthetic nitrogen-use efficiency (PNUE), respiration (R_d), photosynthetic CO₂ assimilation over respiration (A/R_d), stomatal limitation (l_s), mesophyll conductance limitation (l_m) and biochemical limitation (l_b). Values are average ± SD (n = 6 per species). For each trait, values labeled with the same letter are not significantly different from other means for the same trait according to “emmeans” pairwise comparisons procedure at the < 0.05 level of significance.

Species	Status	A ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	A _{mass} ($\text{nmol g}^{-1}\text{s}^{-1}$)	ETR ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	g _s ($\text{mol m}^{-2}\text{s}^{-1}$)	g _m ($\text{mol m}^{-2}\text{s}^{-1}$)	A/g _s ($\mu\text{mol mol}^{-1}$)	PNUE ($\mu\text{mol mol}^{-1}\text{s}^{-1}$)	R _d ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	A/R _d
<i>P. peruviana</i>	non-native	15.1 ± 3.74 ^a	0.7 ± 0.37 ^b	133.0 ± 22.65 ^a	0.2 ± 0.05 ^a	0.21 ± 0.08 ^a	91.7 ± 9.03 ^a	291.5 ± 225.65 ^a	-2.6 ± 0.94 ^a	6.9 ± 3.89 ^a
<i>W. somnifera</i>	native	10.9 ± 1.91 ^b	0.2 ± 0.06 ^b	89.6 ± 21.31 ^b	0.1 ± 0.01 ^a	0.11 ± 0.02 ^b	73.1 ± 11.82 ^b	109.9 ± 22.62 ^b	-1.5 ± 0.21 ^b	7.3 ± 0.85 ^a
<i>N. glauca</i>	non-native	17.4 ± 1.28 ^a	0.4 ± 0.04 ^b	147.0 ± 11.38 ^a	0.2 ± 0.04 ^a	0.29 ± 0.05 ^a	98.5 ± 18.07 ^a	226.3 ± 17.5 ^a	-2.9 ± 0.39 ^a	6.1 ± 1.13 ^a
<i>H. albus</i>	native	10.8 ± 1.29 ^b	0.2 ± 0.04 ^b	106.6 ± 13.02 ^b	0.2 ± 0.01 ^a	0.08 ± 0.02 ^b	67.9 ± 8.42 ^b	122.9 ± 28.78 ^b	-2.3 ± 0.50 ^a	4.9 ± 1.37 ^a
<i>T. majus</i>	non-native	15.5 ± 1.08 ^a	0.6 ± 0.11 ^a	111.4 ± 11.97 ^a	0.4 ± 0.09 ^a	0.13 ± 0.01 ^a	40.9 ± 11.37 ^a	277.3 ± 45.87 ^a	-1.1 ± 0.26 ^b	14.0 ± 3.56 ^b
<i>C. arvensis</i>	native	13.6 ± 0.61 ^b	0.3 ± 0.07 ^b	125.7 ± 5.37 ^a	0.1 ± 0.02 ^b	0.16 ± 0.04 ^a	98.2 ± 15.85 ^b	174.6 ± 77.8 ^b	-1.4 ± 0.19 ^a	9.6 ± 1.14 ^a
<i>S. linnaeanum</i>	non-native	12.1 ± 0.62 ^a	0.2 ± 0.02 ^a	96.3 ± 4.56 ^a	0.1 ± 0.02 ^a	0.15 ± 0.02 ^b	80.2 ± 8.91 ^a	76.5 ± 13.80 ^a	-1.4 ± 0.28 ^a	8.8 ± 2.10 ^a
<i>S. nigrum</i>	native	20.9 ± 1.35 ^b	0.6 ± 0.11 ^b	146.2 ± 4.56 ^b	0.3 ± 0.02 ^b	0.26 ± 0.03 ^a	66.5 ± 0.91 ^a	255.3 ± 9.43 ^b	-2.7 ± 0.31 ^b	7.7 ± 1.39 ^a
<i>M. crystallinum</i>	non-native	10.7 ± 1.94 ^a	0.3 ± 0.12 ^b	99.2 ± 23.52 ^a	0.3 ± 0.13 ^a	0.06 ± 0.01 ^a	33.3 ± 12.33 ^a	101.6 ± 33.74 ^a	-2.8 ± 0.74 ^a	4.0 ± 1.31 ^a
<i>G. flavum</i>	native	13.1 ± 1.45 ^b	0.3 ± 0.07 ^a	121.8 ± 16.23 ^b	0.2 ± 0.03 ^b	0.09 ± 0.01 ^b	61.2 ± 7.72 ^b	124.0 ± 31.54 ^b	-2.3 ± 0.51 ^a	5.9 ± 1.20 ^a
<i>M. nodiflorum</i>	native	11.9 ± 0.67 ^a	0.3 ± 0.09 ^b	115.8 ± 9.06 ^a	0.2 ± 0.01 ^b	0.10 ± 0.01 ^b	76.4 ± 8.05 ^b	106.1 ± 36.33 ^a	-2.9 ± 0.38 ^a	4.1 ± 0.62 ^a
<i>C. maritimum</i>	native	7.4 ± 1.36 ^b	0.1 ± 0.02 ^b	59.6 ± 8.78 ^b	0.1 ± 0.03 ^b	0.06 ± 0.01 ^a	62.2 ± 8.92 ^b	35.1 ± 7.17 ^b	-0.6 ± 0.41 ^b	15.9 ± 6.08 ^b
<i>A. donax</i>	non-native	20.9 ± 1.55 ^a	0.3 ± 0.02 ^a	155.1 ± 9.96 ^a	0.2 ± 0.01 ^a	0.34 ± 0.14 ^a	89.1 ± 4.36 ^a	176.8 ± 13.41 ^a	-0.8 ± 0.07 ^a	27.0 ± 1.15 ^a
<i>P. australis</i>	native	7.8 ± 0.17 ^b	0.1 ± 0.04 ^b	59.5 ± 2.10 ^b	0.1 ± 0.01 ^b	0.08 ± 0.01 ^b	65.1 ± 1.91 ^b	60.3 ± 32.75 ^b	-0.8 ± 0.33 ^a	10.4 ± 4.21 ^b

Table S.5. Continuation

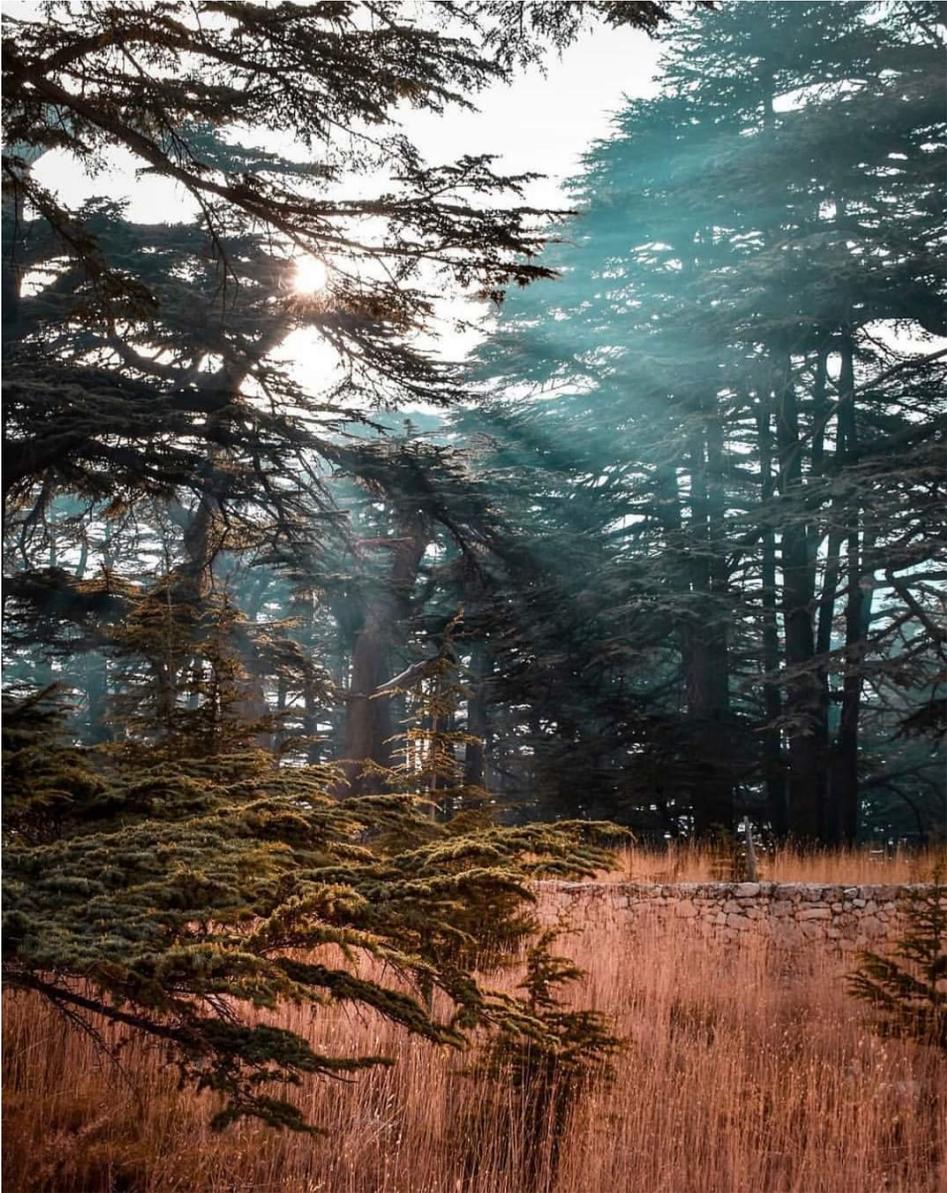
Species	Status	I_s	I_m	I_b
<i>P. peruviana</i>	non-native	0.38 ± 0.05^a	0.20 ± 0.04^a	0.42 ± 0.03^a
<i>W. somnifera</i>	native	0.27 ± 0.05^b	0.23 ± 0.02^a	0.50 ± 0.05^b
<i>N. glauca</i>	non-native	0.42 ± 0.10^a	0.16 ± 0.02^a	0.41 ± 0.08^a
<i>H. albus</i>	native	0.23 ± 0.04^b	0.29 ± 0.02^b	0.48 ± 0.02^a
<i>T. majus</i>	non-native	0.14 ± 0.04^a	0.26 ± 0.01^a	0.60 ± 0.04^a
<i>C. arvensis</i>	native	0.39 ± 0.09^b	0.22 ± 0.03^a	0.39 ± 0.05^b
<i>S. linnaeanum</i>	non-native	0.31 ± 0.04^a	0.21 ± 0.02^a	0.48 ± 0.03^a
<i>S. nigrum</i>	native	0.26 ± 0^a	0.20 ± 0.01^a	0.55 ± 0.01^b
<i>M. crystallinum</i>	non-native	0.10 ± 0.04^a	0.32 ± 0.03^a	0.58 ± 0.06^a
<i>G. flavum</i>	native	0.21 ± 0.03^b	0.30 ± 0.01^a	0.50 ± 0.04^a
<i>M. nodiflorum</i>	native	0.27 ± 0.04^b	0.27 ± 0.02^b	0.46 ± 0.03^b
<i>C. maritimum</i>	native	0.21 ± 0.03^b	0.27 ± 0.01^b	0.52 ± 0.04^a
<i>A. donax</i>	non-native	0.37 ± 0.04^a	0.17 ± 0.05^a	0.48 ± 0.02^a
<i>P. australis</i>	native	0.24 ± 0.01^b	0.23 ± 0.02^a	0.53 ± 0.01^b

Appendix B.

This Appendix provides the original publications derived from Chapter 1 and Chapter 3.

Abdallah M, Hervías-Parejo S and Traveset A (2021) Low Pollinator Sharing Between Coexisting Native and Non-native Plant Pairs: The Effect of Corolla Length and Flower Abundance. *Frontiers in Ecology and Evolution* 9:709876. doi: <https://doi.org/10.3389/fevo.2021.709876>

Abdallah M, Douthe C and Flexas J (2022) Leaf morpho-physiological comparison between coexisting native and non-native plant species in a Mediterranean island. *Biological Invasions*. doi: <https://doi.org/10.1007/s10530-022-02797-4>



And of course, you cannot visit **Lebanon** without being its divine **cedar tree** forests.

Photo by Kameel Rayes