REVIEW ARTICLE

Plant reproductive ecology and evolution in the Mediterranean islands: state of the art

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ABSTRACT

The *ca.* 12,000 islands and islets that encompass the Mediterranean Basin represent a biodiversity hotspot. They have been disconnected from each other and from the continent for hundreds of thousands to millions of years and encompass a high incidence of endemic plant species, with values that can exceed 20% of the local flora. Despite this, relatively few studies have been carried out to unravel ecological and evolutionary aspects of plant reproduction. We synthesise here the available information on the breeding systems, pollination and seed dispersal mode of the Mediterranean island flora. The main objective is to identify general patterns as well as to detect the main gaps in information on reproductive ecology in these particular and vulnerable systems in the face of global change. We also briefly review the information on impacts of invasive species on plant reproduction and dispersal, as these are some of the main threats to island biodiversity in general and Mediterranean island plant diversity in particular. The review has revealed that most available information is very geographically biased towards the western Mediterranean islands, especially the Balearic Islands, although a good fraction of studies have also been carried out on the eastern islands in the Aegean archipelago. Moreover, the majority of data come from species-focused studies, mainly endemic species of restricted range, whereas only a small fraction of studies have been performed at a community level. Relatively little work has involved genetic analyses, mainly focused on assessing the genetic differentiation and variability on narrow endemics. Contrary to our expectations, most island species do not rely on autonomous selfing, which might be related to the relatively high diversity of pollinators. The small, uninhabited, islands might be the last refuges of peculiar interactions that evolved in them in ancient times; they thus should be considered as sanctuaries of extraordinary biodiversity. Finally, we point out the main gaps of information and formulate a set of hypotheses that we believe are worth testing in future studies if we are to advance knowledge on the reproductive biology of Mediterranean island plants.

INTRODUCTION

Islands represent small and less complex ecosystems than their mainland neighbours, which make them ideal in many ecological and evolutionary studies. Islands have disharmonic biota compared to nearby mainland areas (*i.e.* they have a composition and proportion of the different orders and families that differ from the biota of the source region, usually the closest continent), contain a variable fraction of endemic species, and often show peculiar interactions rarely observed in the continental mainland. For these reasons – simplicity and disharmonic biota –, in addition to being excellent biological laboratories in which to study ecological and evolutionary processes, these insular ecosystems are vulnerable and easily disturbed, especially if they are small and isolated (Whittaker & Fernández-Palacios 2007).

The degree of biota disharmony is determined to a large extent by island origin. Oceanic islands, which originate from submarine volcanic activity, show the highest degree, largely because species composition within them depends mainly on the ability of organisms to colonise new emerged lands

(although habitat filtering can also play an important role; see Carvajal-Endara *et al.* 2017). In contrast, continental fragments (*i.e.* ancient fragments of continental rock stranded out in the ocean by plate tectonic processes, and separated from the continent by wide and deep water) and continental shelf islands (*sensu* Whittaker & Fernández-Palacios 2007; located on the continental shelf and separated from the continent by narrow, shallow water) show a lower disharmony, as most were created by rising sea levels – many of them during the Holocene – and their flora and fauna are more contingent upon the history of isolation, island size, founder effect and genetic drift (see Shimizu 1984; Itow 1988; Thompson 1999; Whittaker & Fernández-Palacios 2007). This is actually why non-oceanic islands provide a privileged setting for studying the effects of geographic isolation on the remains of a flora and fauna that was, in many cases, initially established.

The Mediterranean Basin comprises one of the most diverse assemblages of islands in the world to study ecological and evolutionary processes (ca. 12,000 islands and islets; following Arnold 2008). While a few islands have a volcanic origin (*e.g.* Columbretes, Aeolian Islands, Santorini), most Mediterranean

islands are continental fragments (*e.g.* the Balearic archipelago, Corsica, Sardinia, Sicily, Malta, Crete, Cyprus) or continental shelf islands (*e.g.* Elba, Rhodes, Djerba) very heterogeneous in size and that are the product of processes of isolation of lands, already colonised by organisms in the recent past (<6 million years; Thompson 2005; Médail 2017). To this complex historical biogeography and profound environmental heterogeneity, a relatively recent human occupation (during the last 8,000–10,000 years), with very different degrees of intensity (Blondel 2008), must be added. For this reason, it is not foreseeable that the traits of the biota are the result of the selection filter to which they have been subjected during their establishment, but rather have been influenced by the history of isolation since island formation and, in some cases, recent human perturbation (Blondel 2008). In fact, one would expect that the characteristics of these island biotas and their relationships have evolved independently under the intrinsic historic, geographic and ecological conditions of each island (Thompson 2005).

Mediterranean islands constitute a hotspot of biodiversity because of the high species richness, high endemicity, long history and tolerance to diverse kinds of perturbations, thus playing a very important role as a natural laboratory for evolutionary studies (Delanöe *et al.* 1996; Bramwell & Caujapé-Castells 2011). Despite this, little is known, for instance, on the reproductive system and dispersal mechanism of most insular plant species, including many that are at risk of extinction. Most available information on Mediterranean insular flora is on systematics, with still relatively few studies on plant ecology. Such information, however, is critical in order to evaluate the survival of species and be able to elaborate the best plans for their conservation.

The main objective of this review is to gather all available information on the breeding systems, pollination and seed dispersal modes of the Mediterranean island flora. We aim to identify the main gaps in information on reproductive ecology in these particular and vulnerable systems in the face of global change, as well as patterns that can be later compared to those found in the Mediterranean mainland flora. We further briefly review the information on impacts of invasive species on plant reproduction and dispersal, as this is one of the main threats to island biodiversity in general and Mediterranean island plant diversity in particular. Such findings might thus enable stakeholders to establish appropriate management policies for plant conservation. Based on the results of our review, we formulate hypotheses that can be tested in the future when more data, that are less geographically biased, are available.

METHODS

A literature search was done in Web of Science and Scopus with the terms: 'plant reprod* or plant breeding or pollin* or seed disper* or ambophily) and (Mediterra* isla*)' to obtain most information published on the subject. Other searches that provided additional studies were geographically oriented through including the name of the main Mediterranean islands and the term 'plant reprod*' or 'plant breeding or pollin*'. After filtering out those papers not directly related to plant reproduction *sensu lato*, we ended up with a total of 167 studies (Table S2). We are convinced that other information must exist in grey literature, including unpublished reports. However, we believe that our compilation

should be sufficient to discern the main patterns emerging from the studies performed so far.

RESULTS

One first pattern that emerges from the review is that the available information is geographically biased. Most studies (79%) encompass the western Mediterranean islands, especially the Balearic Islands (65%), but also Sardinia, Corsica and the Hyères archipelago (14%); a lower fraction (16%) of studies have been carried out in the eastern islands, mostly in Lesbos and Crete. Even less work (10%) has been performed in the central part (Sicily, Tuscan Archipelago, Malta). Only *ca.* 5% of studies involve islands across the Mediterranean, including both eastern and western islands. One major gap that we thus identify is knowledge along the longitudinal gradient. It would certainly be most interesting to be able to compare species that live in such a gradient, with contrasting environmental (both abiotic and biotic) conditions, especially in order to make predictions on the future of their population sizes in the face of global change.

The large majority of studies are species-focused, *i.e.* are centred on one or a few species in which some aspect of reproductive biology or genetic structure relating it to breeding system has been assessed. Only 11% of the studies have been performed at a community level; most have examined patterns of plant–pollinator interactions using the network theory tools (see below), either in the Balearics (*e.g.* Tur *et al.* 2013, 2014; Castro-Urgal & Traveset 2014, 2016) or in the Aegean archipelago (Petanidou *et al.* 2013; Lázaro *et al.* 2016), whereas at least one assessed the plant–disperser interactions at community level (González-Castro *et al.* 2012). Likewise, only 14% of the compiled studies involve genetic analyses; the genetic differentiation and variability has often been assessed on narrow endemics (*e.g.* Fernández-Mazuecos *et al.* 2014), whereas there are far less studies on gene flow and local adaptation comparing island populations with their relatives on the mainland (but see Juan *et al.* 2012; Garnatje *et al.* 2013). Still another bias, detected in the study of life forms might be associated with the lack of long-term monitoring programmes for tree and shrub species, which are more difficult to monitor in a short period of time. Most (*ca.* 53%) studied species are herbs, whereas shrubs (and much less, trees) appear to have received less attention, in spite of many being endemic. There is actually a number of small trees or shrub species that are single island endemics, some currently threatened, and for which there is little or no information about their reproductive biology; these include, to mention a few examples, *Zelkova abelicea* from Crete, *Ribes multiflorum* and *R. sardoum* from Sardinia, *Genista aetnensis* from Sicily and Sardinia, *Atriplex lanfrancoi* from Malta, *Hedera cypria* from Cyprus, and *Anthyllis hystrix* from Menorca.

Next, we review the main findings on the different topics into which we have divided our survey.

Plant breeding systems and specialised pollination in Mediterranean islands

Knowledge of plant breeding systems is essential to understand the degree of plant adaptation to specific biotic conditions. The various reproductive strategies in angiosperms are often closely

related to different adaptations of flowers, fruits and seeds. Thus, floral designs and displays, for example, have a large influence on the quantity and quality of pollen dispersed during pollination events (Barrett 1998). Given that the islands' floras and faunas are normally depauperated and disharmonic compared to those of the continent, island plants must 'readjust' their pollinator-dependent propagation mechanisms to successfully establish themselves. Therefore, we expect that island plant species that present generalist and self-independent syndromes or reproductive mechanisms have a higher probability of success than those requiring a very specialised interaction. In this sense, Strid (1969) and Comes *et al.* (2008), in their referential works on the adaptation of plant breeding systems in the Mediterranean islands, showed a change in the reproductive system of insular species of the genus *Nigella* from continental outcrossed ancestors to selfed species in some pollinator-depauperated islands. In a recent review on the self-compatibility of plants worldwide, Grossenbacher *et al.* (2017) found this mechanism is over-represented in the islands, although few data come from the Mediterranean Islands.

In some cases, the observed differences in floral traits between insular and continental floras respond to the selection imposed by disharmonic immigration (*e.g.* the absence of heterostylous species in the flora of New Zealand – Webb & Kelly 1993; or species with other complex pollination systems – Barrett 1996), while in others, differences respond to the loss of specialised structures or mechanisms in the insular flora, which in turn reflects its local adaptation to the generalist pollinating island fauna, as Godley (1979) and Lloyd (1985) argued decades ago. An example is a decrease in the size of the corollas observed by Inoue *et al.* (1996), interpreted as an adaptation to a new group of floral visitors, when compared to the floral traits of the genus *Campanula* between the mainland and the Izu islands (Japan). However, in the Mediterranean island flora, there are specialised pollination systems, such as those required by orchids (Fig. 1), or many species with specialised pollination vectors like heterostylous species. In a study across

the Mediterranean Basin examining the incidence of heterostyly in the genera *Lithodora* and *Glandora*, Ferrero *et al.* (2017) found that several species inhabiting Mediterranean islands, such as *Lithodora hispidula* and *Glandora rosmarinifolia*, maintain these complex polymorphic systems with high reciprocity between morphs and isoplethic populations. The presence of these 'healthy' populations of heterostylous species in these islands is of great interest because heterostyly is mainly supported by specialised pollination (Lloyd & Webb 1992; Ferrero *et al.* 2011a).

The orchid genus *Ophrys* is another paradigmatic case of pollination specialisation. The Mediterranean Basin is a centre of diversification of this genus, and many species are present exclusively in a single Mediterranean island. Each *Ophrys* species has its own insect pollinator and depends almost entirely on that species for its survival (Paulus 2006). *Ophrys* orchids never produce nectar and are exclusively pollinated by male hymenopterans (solitary bees, but in some cases scoliid or sphecid wasps). Since each *Ophrys* species usually copies species-specific signals that trigger particular behaviours in the pollinator males (and in related species), the relationship between the plant and the male pollinator is necessarily highly specialised (Paulus 2006). Thus, the *Ophrys* flower is a sexual deception flower and the pollination mechanism has been called 'pseudocopulation'. In his review, Paulus (2006) predicts that the evolution of new *Ophrys* species is always a consequence of a change in pollinator, and there is a general consensus that diversification in these orchids is driven by pollinators (Paulus & Gack 1990). In fact, the Mediterranean islands shelter a large number of orchids of this genus. Only in Cyprus, these authors show that at least 12 species of *Ophrys* have specialised pollination by native bees.

Also interesting is the persistence of the complex pollination system of many endemic Araceae of the Mediterranean islands, which attract flies and beetles through olfactory deceit and thermal claim (Quilichini *et al.* 2010; Urru *et al.* 2010). The thermogenesis of several island *Arum* species has actually been

Fig. 1. Examples of plant–animal interactions in the Balearic flora. a: *Rhodanthidium septemdentatum* and *Megascholia bidens* on flowers of *Orchis coryophora*, photo credit: C. Morales; b: *Podarcis lilfordi* feeding on the fruits of *Cneorum tricoccon*, photo credit: X. Rotllàn; c: *Macroglossum stellatarum* on *Vitex agnus-castus*, photo credit: JP. González-Varo; d: *Oxythyrea funes*ta on flowers of *Echium sabulicola,* photo credit: A. Traveset.

examined in detail in several studies (Seymour *et al.* 2009 and references therein). However, although the presence of these singular interactions that require the joint participation of very specific pairs of species in the Mediterranean islands allows us to think that the flora and its pollinating fauna is not as disharmonic as one might expect on an island, the reality is that there are also reasons for concern derived from the anthropisation of these fragile ecosystems (Blondel 2008). Petanidou *et al.* (2013), studying 88 populations of the orchid *Spiranthes spiralis* across multiple habitats in Lesbos, showed that large populations in olive groves had significantly lower fruit set than small populations of the orchid in natural areas. They suggest that olive groves are less favourable sites for pollinators of this species and that populations with greater failure are the result of severe management changes in recent years, and so are more vulnerable to reductions in reproductive output. Hence, severe alteration of ecosystems in the Mediterranean islands is likely to disrupt such specialised pollination systems.

Evolution of autogamy and self-fertilisation

In the classical ecological island conceptions, the colonisation and settlement phases are often critical to understanding the structure, and functioning of ecosystems. All biological processes are, in fact, closely linked to the composition and abundance of species (Carlquist 1974; Barrett 1996). In oceanic islands, wind, oceanic drift or birds are often considered the main vectors for the transfer of diaspores to the islands, determining to a great extent the composition of plant communities that are established in them (see Vargas *et al.* 2012 and references therein). On arrival on an island, a species has to be able to establish itself, sometimes from one or a few individuals; this is especially difficult considering that in the early stages of colonisation few pollination vectors are capable of transferring pollen from long distances (Barrett 1996). In this sense, 'Baker's Law' (Baker 1955) states that species with the capacity to reproduce independently (by self-fertilisation or vegetatively) start with an advantage over those that need more individuals of different gender and/or vectors to transfer their gametes. Moreover, it is also known that the capacity of some plant species, once established, to acquire traits that make them less dependent (or totally independent) of animals for their regeneration can also facilitate their survival in depauperate environments (Ramsey & Vaughton 1996). There is much support for this hypothesis (*e.g.* Inoue 1993; see additional references in Barrett 1996), although most data come from oceanic islands. In the Mediterranean islands, there is some empirical evidence of species presenting a breakdown of the self-incompatibility system and/or a shortening of herkogamy (*i.e.* an approximation between male and female reproductive structures) that does not exist in mainland populations of the same species (Grossenbacher *et al.* 2017), although further studies encompassing more species are needed to confirm such a pattern for these islands. An illustrative example comes from the study of Thompson *et al.* (2001), who suggest that variation in floral traits and levels of inbreeding within and among species of insular populations of several *Cyclamen* species point towards the evolution of selfing variants in the derivative species. They find that whilst mainland (presumably outcrossing ancestor) *C. repandum* has large flowers in which pistils are longer than the corolla and anthers are within the corolla, the selfing derivate *C. balearicum* has much smaller flowers with stigmas positioned almost at the level of anthers; *C. balearicum* also has a much lower pollen–ovule ratio than the mainland *Cyclamen* species and reaches a value of 0.72 in the index of autonomous selfing, as against a value of 0.04 of *C. repandum* (Affre & Thompson 1998, 1999). In contrast, *C. creticum,* endemic to Crete and Karpathos, is self-compatible but is unable to set seed in the absence of pollinators, which authors attribute to the stigma–anther separation (Affre & Thompson 1997). Another example is found in *Helianthemum caput-felis*: flowers in its mainland populations are visited by a high diversity of insects and behave as outcrossers (Agulló *et al.* 2015), whereas flowers in the Mallorcan populations, which have a lower pollinator diversity, have lost the incompatibility system and are capable of self-fertilising to adapt their reproductive system to changing and unstable conditions of pollinators (Tébar *et al.* 1997; Rodríguez-Pérez 2005). An alternative efficient mating strategy that ensures plant reproduction when pollinators are scarce is the 'delayed selfing'. This has been reported, for example, in *Fumana juniperina* (Cistaceae) from Sardinia (Carrió *et al.* 2008); this species is self-compatible and capable of autonomous self-pollination through changes in the position of the stigma and anthers at the end of floral anthesis. Still, a species can adapt and become less dependent on pollinators by switching from generative to almost exclusively vegetative reproduction; this has been reported in *Sedum album* subsp. *rupi-melitense* from Malta (Mifsud *et al.* 2015).

In view of the few studies that analyse the selfing of plants on islands, we have put together the available information, with the idea that it will serve as a starting point for future comparisons (Table S1). Two indices related to selfing have been calculated following Lloyd & Schoen (1992): (i) the index of autonomous selfing (IAS), calculated from the fecundity under autonomous self-pollination compared with cross-pollination; this index estimates the ability to set fruit and seed in the absence of pollinators, and values above 0.25 suggest autonomous self-fertilisation; and (ii) the index of self-compatibility (ISC), calculated from the fecundity under induced self-pollination compared with cross-pollination; values of ISC above 0.25 suggest self-compatibility (Lloyd & Schoen 1992; see also Navarro & Guitián 2002). Although the dataset is incomplete and there may be a bias toward the analysis of species that live in healthier pollination environments, or that are more attractive to botanists to study complex flowers and breeding systems, our review shows that most studied species on the Mediterranean islands do not rely on autonomous selfing and their reproduction is at the expense of some vector of pollen transfer. Sixteen species do not show self-fertilisation capacity, compared to eight that do show it. Regarding self-compatibility, there is a strong balance: ten species out of the 20 for which results were obtained are self-compatible, whereas ten are self-incompatible. The self-compatible species, in spite of their dependence on a pollen transfer vector, have the ability to colonise new spaces from a single individual or can reproduce without the need of long-range pollinators. Generalist floral visitors, which induce self-pollination or geitonogamous crosses (transport of pollen within the same individual plant), ensure their reproduction (Gómez & Zamora 1999). In any case, these results are not concordant with those of Grossenbacher *et al.* (2017) in a review of the self-compatibility on islands at a global scale. These authors find that self-compatibility is overrepresented in islands. However, it should be

noted that they find that the proportion of self-compatible species is significantly higher in oceanic islands than in continental ones, as are most Mediterranean islands.

A transition from herkogamous populations to plants with homostylous flowers can greatly help to overcome the problem of lack or scarcity of pollinators (Carlson *et al.* 2008). However, we identified only one case – besides that reported for *C. balearicum* (Thompson *et al.* 2001) – in which there is a shortening in the distance between androecium and gynoecium: *Glandora rosmarinifolia* on the island of Capri (Ferrero *et al.* 2011b). The low proportion of species with self-fertilisation capacity that we found (Table S1) may actually be related to the lack of changes in herkogamy of insular populations. This may respond to the low number of studies addressing this adaptive aspect of insular flora in the Mediterranean, but could also be explained by the diversity and abundance of pollinators in these environments (see below). A more exhaustive study in the shift of these reproductive traits between mainland and island taxa will surely shed light on this interesting aspect of plant adaptations to survive the putative lack or shortage of suitable pollinators in some of these Mediterranean islands (see below).

It is unfortunate that we do not have enough data yet for a robust statistical analysis to test whether plants in the Mediterranean islands are more pollen-limited than their relatives on the mainland. The androdioecious *Phillyrea angustifolia* was studied in the Balearics and in southeast Spain and found to be pollen-limited in both; interestingly, while pollen from both males and hermaphrodite individuals produced similar fruit set on the mainland, pollen from males in the island was more than three times as fertile as pollen from hermaphrodites, supporting the idea that androdioecy must have an adaptive advantage in islands, probably reducing inbreeding depression (Traveset 1994). Another interesting pollen-limited species that has been compared between mainland (southern France) and island (Mallorca) is *Leopoldia comosa* (Morales *et al.* 2012). This species produces sterile flowers that function as a pollinator attraction and enhance pollen deposition on stigmas of young

flowers. However, such sterile flowers promote a higher fruit set only in the island population; presumably, it is the higher inbreeding depression found in insular populations what strongly influences the production of sterile flowers as a mechanism promoting cross-pollination (Fig. 1). The existence of pollen limitation has been observed in other species like *Rhamnus ludovici-salvatoris* (although not consistently across years; Traveset *et al.* 2003), *R. alaternus* (although not consistently in all populations; Gulías *et al.* 2004), *R. lycioides* (although only in a mountain population, not in the coastal one; Gulías & Traveset 2012), *Medicago citrina* (Pérez-Bañón *et al.* 2003), *Thymelaea velutina* (De la Bandera & Traveset 2006), *Buxus balearica* (Lázaro & Traveset 2006), *Myrtus communis* (González-Varo & Traveset 2010), *Thymus capitatus* (Tscheulin & Petanidou 2011), *Arum pictum* (Quilichini *et al.* 2010), *Daphne gnidium* and *D. rodriguezii* (Rodríguez-Pérez & Traveset 2011), *Spiranthes spiralis* (Petanidou *et al.* 2013) and *Glaucium flavum* (Tscheulin & Petanidou 2013). Although not experimentally tested, pollen limitation has been suggested in other species, *e.g. Fumana juniperina* (Carrió *et al.* 2008). In contrast, no pollen limitation has been evidenced in other species, *e.g. Cneorum tricoccon* (Traveset 1995a) or *Limonium barceloi* (Khan *et al.* 2012).

Incidence of anemophily

Many studies have shown that wind pollination can be a reproductive insurance in environments that are impoverished in biotic pollinators (see review in Friedman & Barrett 2009). The transition from animal to wind pollination in *Schiedea* (Caryophyllaceae) in the Hawaiian Islands appears to be one of the best contemporary case studies on the evolution of wind pollination (Golonka *et al.* 2005; Weller *et al.* 2006). But transitions in either direction between animal and wind pollination might involve the use of both animal and wind pollinators, either sequentially or simultaneously (Stelleman 1984). This mixed pollination system, known as ambophily, has been defined as a mechanism that helps to achieve reproduction in stressful environments, with low availability of biotic pollination means, such as those expected for the islands. In this review we have detected a bias towards the study of this phenomenon for the islands of the western Mediterranean.

We have identified 11 plants species (Table 1), all of them located in western Mediterranean islands, which present this mixed system of pollination by wind and insects (offering some reward in the form of nectar or pollen at least for floral visitors). Perennial shrubs are overrepresented among the species in which the mixed system has been identified. Possibly, ambophily represents an optimum opportunity to overcome the reproductive problems derived from years of poor biotic or abiotic pollination for these perennial species. Even though all the studies belong to the geographic range of the Balearic Islands, it is very likely that this is a more widespread phenomenon occurring in many other Mediterranean islands. In this sense, an increase in the number of studies on natural history and description of the reproduction systems in all the islands of the Mediterranean will be of great help to make comparisons in the future.

Table 1. Species, life form and Mediterranean island in which the mixed system of pollination (ambophily) mediated by wind and insects was described. Superscripts indicate the bibliographic reference where more information can be found.

species	family	life form	island
Apium bermejoi[a]	Apiaceae	Perennial shrub	Menorca
Buxus balearica[b]	Buxaceae	Perennial shrub	Mallorca
Cistus monspeliensis[c]	Cistaceae	Perennial shrub	Mallorca
Cistus salviifolius[c]	Cistaceae	Perennial shrub	Mallorca
Lotus cytisoides[c]	Fabaceae	Perennial shrub	Mallorca
Ranunculus weyleri[d]	Ranunculaceae	Perennial herb	Mallorca
Rhamnus alaternus[e]	Rhamnaceae	Perennial shrub	Mallorca
Rhamnus lycioides[f]	Rhamnaceae	Perennial shrub	Mallorca
Rhamnus ludovici-salvatoris[g]	Rhamnaceae	Perennial shrub	Mallorca
Thymelaea velutina[h]	Thymelaeaceae	Perennial shrub	Mallorca
Ephedra fragilis[i]	Ephedraceae	Perennial shrub	Dragonera

[a]Cursach & Rita (2012a), [b]Lázaro & Traveset (2005), [c]Moragues & Traveset (2005), [d]Cursach & Rita (2012b), [e]Gulías *et al.* (2004), [f]Gulías & Traveset (2012), [g]Traveset *et al.* (2003), [h]De la Bandera & Traveset (2006), [i]Celedón-Neghme *et al.* (2016).

Diversity of pollinators in Mediterranean islands

Despite the fact that the Mediterranean Basin constitutes one of the world's hotspots for diversity of pollinators including

wild bees, flies, beetles and butterflies, our knowledge on them, in general, is quite poor (Michener 2000). The presence in many Mediterranean islands of plant species depending on specialised pollinators (see above) is a sufficiently important reason to consider focused and systematic research on both taxonomic and ecological aspects of native pollinators. Without this basic information, it is difficult to carry out good evaluations of the ecosystem dependence of pollination interactions, or on the consequences that the potential loss of pollinators can have on these fragile ecosystems. In order to solve this historical shortcoming, species lists have recently been published for some islands, such as the Aegean islands (Nielsen *et al.* 2011; Petanidou *et al.* 2013), Maltese islands (Balzán *et al.* 2016) or the Balearics (Baldock 2014). New species to science are still appearing in specific studies (*e.g.* the bee *Dufourea balearica* from Mallorca Island; Baldock 2014). Although the results of these studies suggest that the diversity of pollinators in these islands is high, many detailed studies are still missing in the plethora of islands that occupy the Mediterranean Sea. More information is needed not only on the diversity but also on the abundance of pollination interactions, which will allow identification of general trends, if any.

In work performed at Lesvos, Potts *et al.* (2006) found that the three habitats of greatest overall value for plant–pollinator communities and provision of the healthiest pollination services are oak woodland, managed olive groves and freshly burned pine forests, and that oak woodlands have the highest levels of pollination from generalist species. More recently, in the same island, Tscheulin *et al.* (2011) examined the influence of the Mediterranean landscape context on the diversity and abundance of wild bees, finding that different landscape parameters affected the abundance within bee groups in different ways, although species richness was unaffected. The abundance of small bees seems to be much influenced by landscape parameters at small scales, whereas that of large bees is impacted by landscape parameters at larger scales. These authors also detected that olive groves had a positive influence on bee abundance, while phrygana, conifer forest, broadleaved forest, cultivated land, rock, urban areas and sea had mostly a negative or no impact. They thus stressed the need for a holistic approach, including all land cover types, when assessing the effects of landscape context on bee diversity and abundance in the Mediterranean. In the Balearics, specifically in Mallorca, dune habitats were shown to be highly diverse in insect flower visitors (*ca.* 32 species·ha^{-1}), especially when compared to similar habitats in the Canary Islands; the former have on average more than twice the number of insect flower visitors than the latter (Castro-Urgal & Traveset 2014). Such dune habitats (known to be the areas with the richest bee fauna in Mallorca; Baldock, personal communication) contain nearly twice the diversity of flower visitors found in mountain shrublands in this island (Castro-Urgal *et al.* 2012; Tur *et al.* 2013). A recent study has shown that habitat loss in these dune systems can dramatically alter the abundance of different pollinator functional groups, also modifying the structure of the pollination network (Traveset *et al.* 2017).

One idea that emerges from the few works that exist on diversity of pollinators in individual species of plant in these islands is that Mediterranean insular plants have very diverse assemblages of pollinators both taxonomically and functionally (*e.g.* Affre *et al.* 1995; Pérez-Bañón *et al.* 2003; Lázaro &

Traveset 2005; De la Bandera & Traveset 2006; Vivarelli 2007; Jakobsson *et al.* 2008; Barthell *et al.* 2009; Pisciotta *et al.* 2011; Tscheulin & Petanidou 2011; Cursach & Rita 2012a,b; Khan *et al.* 2012; Alarcón *et al.* 2013; Lamprecht *et al.* 2013). Species like *Euphorbia paralias* is visited by more than 40 insect species, while *Daucus carota, Santolina chamaeciparisus, Teucrium dunense* and the critically endangered *Limonium barceloi* are visited by at least 20 insect species. For most species, however, we do not know to what extent these plants depend on such interactions with flower visitors to set seeds and, thus, the potential impact of a disturbance that leads to pollinator losses on plant reproductive success is not easy to predict. In this sense, a study performed in two Mallorcan communities, one in a mountain shrubland and the other one in a coastal dune system, aimed at evaluating the plant functional dependence on pollinators and at testing whether such dependence (assessed by means of pollinator exclusions) was related to plant specialisation (Tur *et al.* 2013). A phylogenetically controlled regression analysis revealed that plants highly dependent on pollinators were the most generalists, *i.e.* interacted with a higher number of species of pollinator, but this was significant only in the dune community, possibly due to their higher flower -resource heterogeneity and diversity of interactions. Such study showed that plants with a wide assemblage of pollinator species tend to be those that are more strongly dependent upon them for seed production and so might be those more vulnerable to pollinator losses, although this might be context-dependent. From the 27 plant species studied in the coastal dune and the 11 studied in the mountain shrubland, only six showed no dependence on pollinators to set seeds (*i.e.* their seed set was the same regardless of whether their flowers were visited or not by insects). The large majority showed high dependences (values >50%) and at least two species (*Lotus cytisoides* and *L. corniculatus*) showed a total dependence on insects to set seeds (Table S1 in Tur *et al.* 2013).

There are small islands, like the Columbretes Archipelago, in which an entire pollinator functional group (the bees) is missing; in this case, specialised flowers like those of *Medicago citrina* (Fabaceae), which require large floral visitors for tripping (activate the necessary movement of androecium and gynoecium) and pollination, are visited only by flies (Pérez-Bañón *et al.* 2003). In such small islands, pollinators are unpredictable and thus species like the migrant hoverfly *Eristalis tenax* play an important ecological and likely evolutionary role for native plants such as *Daucus carota*, which in this island is represented by a different subspecies (*D. carota* subsp. *commutatu*s) with particular traits (*e.g.* extended stigma receptivity) that may have evolved under such a pollinator-depauperated environment (Pérez-Bañón *et al.* 2007). Indeed, there is additional although scarce evidence that flower traits differ between mainland and island populations in the Mediterranean, which might result from different selective pressures from pollinators. For instance, corolla size in *Helianthemum caput-felis* seems to be somewhat larger in Mallorca (Rodríguez-Pérez 2005) compared to the mainland (Agulló *et al.* 2015), whereas the opposite is found for *Glandora rosmarinifolia* (Ferrero *et al.* 2011b). We must consider, however, that flower size is also determined by nutrient availability and, thus, controlled studies should be conducted to confirm that particular flower traits are indeed selected by pollinators.

The diversity of pollinators visiting a plant species has rarely been compared between insular and mainland plant

populations in the Mediterranean islands. Nonetheless, the expected higher diversity of pollinators in mainland areas has been confirmed for several species like *Cyclamen balearicum* (Affre *et al.* 1995), *Medicago citrina* (Pérez-Bañón *et al.* 2003) and *Buxus balearica* (Lázaro & Traveset 2005). In *M. citrina*, up to 46 species of insect were detected on its flower on the mainland compared to the only 15 species observed in Mallorca (Rodríguez-Pérez 2005). In *B. balearica*, a larger insect diversity was found in two mainland sites (19 and 15 taxa) than in three island areas in Mallorca (where zero, four and 11 taxa were recorded); insects on the mainland visited a proportionally higher number of flowers, and remained longer on the plants than insects on the island, although the overall frequency of flower visitation did not differ between mainland and island populations (Lázaro & Traveset 2005). Scarcity of pollinators in the island seems to have an effect on the pollination mode of *B. balearica*, an ambophilous (*i.e.* pollinated by wind and insects) and selfing species, although the largest variation in breeding system was found at a more local scale.

Given the lower flower resource availability in islands, we might expect island pollinators to be more generalists than their mainland counterparts, as has been found for some archipelagos (Traveset *et al.* 2015). A study on the global patterns of mainland and insular pollination networks, however, showed that the richness of pollination interactions is rather similar between mainland and continental islands, with only oceanic islands having a lower interaction diversity (Traveset *et al.* 2016). From the data obtained in the pollination networks in Mallorca, several insect species were identified as highly generalists, visiting the flowers of more than 15 species. These include beetles like *Spermophagus* sp., *Meligethes* sp., *Oedemera flavipes*, *O. caud*ata, several species of *Psilothrix*, hoverflies like *Paragus tibialis* or *Sphaerophoria* sp., small flies *Dilophus antipedalis*, bees like *Rhodanthidium septemdentatum* and *Apis mellifera*, wasps such as *Polistes dominulus*, and lepidopterans like *Macroglossum stellatarum*, *Vanessa cardui* and *Polyommatus icarus*. Also a highly generalist ant species found in more than ten plant species is *Plagiolepis pygmaea*.

Although much work remains to be done, our review shows that most studies on pollination ecology in this geographic area have been done on specific systems such as narrow endemic species. There is still a need for a good overall assessment of plant–pollinator interactions at community level. Recent studies using a network approach have been carried out, mainly in the Balearics (*e.g.* Padrón *et al.* 2009; Tur *et al.* 2013, 2014; Castro-Urgal & Traveset 2014). Overall, such networks show a nested pattern (the interactions of the specialised species are proper subsets of the interactions of the most generalised species) as well as modular structure (with groups of species that interact among themselves more strongly than with other species), patterns that do not differ from most mainland pollination networks (Traveset *et al.* 2016). There is also a strong network asymmetry, with many more flower visitors than visited plants, as well as a strong interaction asymmetry, thus plants that depend strongly on pollinators (are visited by a high number of species) are visited by species that do not depend strongly on plants (*i.e.* have few links with them). All such traits provide stability to the community, making it less vulnerable to perturbations (species losses). More recent data from Lesbos (Lázaro *et al.* 2016) have shown that moderate levels of livestock grazing by sheep and goats may help in preserving the

complexity and diversity of the rich Mediterranean pollinator communities, which have a long history of grazing with these domestic animals.

Peculiar and threatened mutualistic interactions on Mediterranean islands

As a response to mutualist and food shortage and to reduced predation risk, there is usually a niche expansion process in island ecosystems, whereby species direct novel mutualists and prey (Carlquist 1974; Cox & Ricklefs 1977). That is, island species often experience a release in their interaction structure, which has been termed 'interaction release' (Traveset *et al.* 2016; within the wider concept 'ecological release'; MacArthur *et al.* 1972), promoting the exploitation of new interaction possibilities. Indeed, islands have a high proportion of generalist species showing novel and opportunistic interactions (Olesen & Valido 2003). Some of these interactions have proved to be very important not only for reproduction and plant dispersal but also for plant community structure and biodiversity in general (Traveset 1999; Traveset *et al.* 2009b). The importance of mutualistic interactions, in particular, is especially evident in islands where the loss of native pollinators or dispersers has had demographic and evolutionary consequences for the plants that depend on them (Anderson *et al.* 2011; Wotton & Kelly 2012; Traveset *et al.* 2012). Ancient species interactions may also prevail in islands as they have served as refuge for many species, either as climate refuge or as refuge from the introduction of predators (especially true for small uninhabited islands/islets). This is why we usually find more unusual, odd interactions in islands than in the mainland (*e.g.* pollination by lizards).

In the Mediterranean islands there is still relatively little information on plant–vertebrate mutualistic interactions, although this topic has received increasing attention during the last two decades. Again, most available data come from the Balearics, where the interaction between endemic or distribution-limited plants and lacertid lizards has been studied in different islands. By examining this interaction in the shrub *Euphorbia dendroides* in Cabrera Island, Traveset & Sáez (1997) were the first to empirically demonstrate that lizards can effectively act as pollinators, being even more important (at least quantitatively) than insects. Lizards visit a large number of flowering plants in the Balearics (Sáez & Traveset 1995) and such a role in pollination was further documented in other species (Pérez-Mellado & Traveset 1999) as well as on other archipelagos, like the Canary Islands (Rodríguez-Rodríguez *et al.* 2013). More recently, the pollination system has been assessed for the dioecious gymnosperm, *Ephedra fragilis*, which produces a sugar-rich nectar drop in its female reproductive structures that is rapidly consumed by both lizards and insects. Celedón-Neghme *et al.* (2016) found that this plant in Dragonera (Balearic Islands) is primarily wind-pollinated although lizards and insects contribute also with *ca.* 30% to its fitness. Birds have also been documented as effective pollinators of several species, such as *Brassica oleracea* in Ventotene Island (Italy); their flower visits outnumbering those of insects (Cecere *et al.* 2011a). A study carried out on this island and in Antikythira Island (Greece) actually showed that nectar could be an important food resource for migrants, warblers in particular (mainly *Sylvia* spp., but also *Phylloscopus* spp.), which land

at stopover sites (Cecere *et al.* 2010). These authors suggest that nectar consumption in the Mediterranean region, as well as in the African stopover sites, is mostly associated with the early successional stages of vegetation, rich in flowering plants and potentially utilised by passeriform birds. Ventotene Island, in particular, is reached by many migrants after having crossed *ca.* 500 km of open sea and, thus, birds arrive in poor physical condition and with reduced size of digestive organs; therefore, nectar represents a good source of water and energy easily found and quick to digest (Cecere *et al.* 2011b). By feeding upon nectar, pollen grains are attached to the birds' bill and plumage and are transported between different stopover sites. A mixed-mating system of birds and insects acting as pollinators has also been described in a species of *Scrophularia* in Sardinia (Ortega-Olivencia *et al.* 2012). We are convinced that future studies will document many more plant–bird pollination interactions in Mediterranean islands, as found in other sites in Europe (da Silva *et al.* 2014). In fact, preliminary data from the Balearics suggest that this is actually a rather common phenomenon (F. Fuster & A. Traveset, unpublished data).

One striking interaction between plants and lizards has been documented in Aire Island, at the southeast of Menorca, specifically between *Podarcis lilfordi* and the fly-pollinated dead horse arum, *Dracunculus muscivorus* (Pérez-Mellado *et al.* 2000), which reaches an extremely high density in this area (30,000 individuals·ha^{-1}). The density of lizards is also very high in this island (*ca.* 2,200 individuals·ha^{-1} in 2003), and during the blooming period of this plant, lizards exhibit intense foraging behaviour on open inflorescences, capturing flies trapped on the spathes within the tubules. The lizards transport only a few pollen grains on their bodies, apparently not acting as effective pollinators for this plant; however, they feed upon the fruits, thus acting as legitimate dispersers (Pérez-Mellado *et al.* 2006). It would thus be interesting to know whether the benefit of seed dispersal compensates for the potentially detrimental effect that lizards have on pollination success by preying on the flies that would otherwise transport pollen to other individuals; the high plant densities reached in the last years do support such hypothesis (Pérez-Mellado *et al.* 2006).

Seed dispersal in Mediterranean islands

Seed dispersal is a key process in the reproductive cycle of a plant and, like pollination, is crucial for maintaining gene flow and plant population dynamics. The study of this important process, however, has not received much attention throughout the Mediterranean islands except for the western ones, mainly the Balearics. Thus, the information we have on this topic is geographically biased, unfortunately.

The plant species that have received most attention are the fleshy-fruited ones, *i.e.* those that depend upon animals for their dispersal (*e.g.* Rodríguez-Pérez *et al.* 2005). Most frugivorous species are birds, although lizards also play an important role as dispersers of a good number of plant species in many islands of the world. In fact, lizards that in the mainland tend to be exclusively insectivorous, expand the trophic niche in islands, including also fruits in their diets (Olesen & Valido 2003). This has actually been reported in different studies carried out in the Balearics (Sáez & Traveset 1995; Pérez-Mellado & Traveset 1999; Rodríguez-Pérez *et al.* 2005). In some periods

of the year, fruits can even represent the most important item in lizards' diet according to the high number of seeds found in their droppings. Such seeds, of species like *Rubia peregrina, Rubus ulmifolius, Solanum luteum, S. nigrum*, etc., are able to germinate and, thus, lizards have proved to act as effective dispersers for a large variety of island plants (Rodríguez-Pérez *et al.* 2005). In some cases, the plant–lizard interaction is 'unique', as no other native dispersers exist for the plant (see below). Dispersal limitation in lizard-dispersed species, therefore, may be encountered in areas or islands where lizards have decreased dramatically or even gone extinct. In contrast, the ornithochorous (bird-dispersed) species studied so far have not been shown to be limited by seed dispersal, and bottlenecks in their reproductive cycle usually occur in other phases (*e.g.* Traveset *et al.* 2001, 2003; Gulías *et al.* 2004). Habitat disturbance, in general, may considerably alter the patterns of plant recruitment by increasing seed predation or seedling recruitment. This is especially detrimental for endemic species with restricted and rather small populations, for instance *Rhamnus ludovici-salvatoris,* endemic to Mallorca and Menorca, where only a few populations persist (Traveset *et al.* 2003), but also for the more widespread *R. alaternus* (Gulías *et al.* 2004). Both species are mainly bird-dispersed although ants may act as secondary seed dispersers when feeding upon the seed elaiosome. Avian frugivory has also been studied in the Mediterranean widespread shrub *Myrtus communis* (Traveset *et al.* 2001), which produces two fruit morphs (white and blue); removal of both fruit morphs is very high (*ca.* 90%) suggesting that there is no dispersal limitation in this species and that a colour preference by frugivores is not involved in the maintenance of the polymorphism. Birds were found to increase germinability of myrtle seeds, in contrast to alien pine martens (*Martes martes*), which also consume the fruits of this species but showed no effect on germination, what might be related to the different seed retention time in their guts and/or the chemical composition of the food ingested along with the seeds. The existence of different selective pressures exerted by lizards and birds on seed traits was evaluated in the Mediterranean *Rubia peregrina* by Nogales *et al.* (2013), comparing it with the Macaronesian endemic *R. fruticosa*. In the Balearic Islands, *R. peregrina* has evolved mostly with birds, although lizards are also known to eventually consume its fruits. In contrast, *R. fruticosa* has evolved mostly interacting with lizards and only recently with birds. No differences were detected, however, in either seed coat thickness or germination patterns after being ingested by either frugivore type in either of the two *Rubia* species. The Rubiaceae is an ancestral family in the Mediterranean (both on the continent and islands) and probably interacted with both birds and lizards in the past.

Highly specific plant–lizard interactions have only been found in a few systems so far, although they are likely to be more widespread and in different Mediterranean islands. One case is that of *Daphne rodriguezii*, a paleoendemic relict shrub, endemic to Menorca Island and to a small islet (Illa d'en Colom) offshore Menorca. The endemic lizard *Podarcis lilfordi*, present in this islet, maintains a strong interaction with the plant, which is quite abundant in the coastal shrubland that it inhabits. In contrast, the plant is declining from the few remaining populations in Menorca where the lizard has gone extinct after the introduction of predators since human arrival (Traveset & Riera 2005). This case actually illustrates well how

biological invasions can cause a disruption of a specialised plant–vertebrate mutualism that sets the plant partner on the road to extinction. On the other hand, it represents one example that shows how an islet can act as refuge of an interaction that survives in it only because of the lack of pressure exerted by predators. Finally, it further represents an example showing that the interactions usually disappear before the species become extinct and, thus, this loss of interactions among species can only be recorded when considering them in biodiversity surveys. Another interesting example of a unique plant–lizard interaction is that between another Tertiary relict species in the Cneoraceae family (*Cneorum tricoccon*), native to the western Mediterranean area, and the two endemic lizards of the Balearics, *Podarcis lilfordi* and *P. pityusensis*. This plant–lizard interaction also survives today only on the islands and islets with lizards, whilst it has become extinct from the larger islands, Mallorca and Menorca, where alien mammals (mostly pine martens) are now the main dispersers of the plant. The most ancient fossil records of lizards from the Balearics are from the late Miocene (Alcover *et al.* 1981), although it is possible that they were present much earlier. In Eivissa and Menorca, fossil seeds of *C. tricoccon* from the Plio-Pleistocene have been found, with a structure very similar to that of current seeds (Traveset *et al.* 2005), suggesting that the selective pressures on seed traits have not varied much in time in this species (Traveset 1995b). The disruptions of such plant–seed disperser interactions have been shown to have both demographic and evolutionary consequences for the maintenance of plant populations (see section on seed dispersal disruptions).

Ants may also be important dispersers for a number of plants in Mediterranean habitats. Besides those already known from other mainland studies to be ant-dispersed, a few island species have been reported as mirmecochorous. These include, for instance, the Menorcan narrow endemic *Apium bermejoi*, dispersed mainly by *Messor bouvieri* (Cursach & Rita 2012a), and the Balearic endemic *Thymelaea velutina,* a heterocarpic shrub that produces both fleshy fruits and dry fruits (De la Bandera & Traveset 2006). Seeds in fleshy fruits are consistently larger, heavier and more likely to be dispersed than seeds in dry fruits, but germinability, germination rate and seedling survival is similar among fruit types. Heterocarpy in this species is currently maintained as there is no apparent factor that exerts any strong selective pressure on either fruit type. These authors suggest that the two fruit types might even have different 'functions': fleshy fruits serving especially for dispersal and population expansion and dry fruits for producing a seed bank that ensures eventual germination. Still another ant-dispersed plant is *Anchusa crispa*, endemic to Corsica and Sardinia (Quilichini & Debussche 2000); this dispersal system seems to be disrupted by the invasion of the alien Argentine ant, *Linepithema humile*, with detrimental consequences for the plant population dynamics of *A. crispa*.

At the community level, there is only one study – to our knowledge – that examines the plant–seed disperser interactions in a Mediterranean island. González-Castro *et al.* (2012) compared two Mallorcan seed dispersal networks with two Canarian ones and with one mainland network, finding that island networks were smaller and less complex (a lower number of observed links than expected for their size) than the mainland network. As expected, connectivity (number of links out of all those possible in the network) was higher within

islands than on the mainland, whereas relative nestedness (which accounts for network size) was lower within islands, whether continental or oceanic. The lower species number and greater specialisation in insular seed dispersal systems appears to lead to the prevalence of more symmetric interactions than those found on the mainland, which seems to indicate that insular mutualistic interactions and interacting species are more vulnerable than mainland ones to disturbances, as previous work has suggested that asymmetrical interactions facilitate the maintenance of biodiversity and act as a resilience mechanism against species extinction (González-Castro *et al.* 2012 and references therein). More community-level studies are needed from other Mediterranean islands to ascertain the patterns of interactions and their vulnerability to the different drivers of global change in order to be able to elaborate better management plants to mitigate such effects (Kaiser-Bunbury *et al.* 2010).

Consequences of seed dispersal disruptions

Seed dispersal by animals has been identified as one of the biological interactions related to vegetation dynamics that is most vulnerable to human disturbance (Neuschulz *et al.* 2016). In fact, disruptions of seed dispersal systems are increasingly being reported from different ecosystems, especially from islands (Traveset & Richardson 2014). The drivers of such disruptions include alien invasions, habitat loss and fragmentation, logging, hunting, and also climate change. Nevertheless, we still have poor empirical evidence of the long-term consequences of such disruptions. Specifically, seed dispersal disruptions may lead to the loss of genetic variability due to genetic drift, decreased fitness and reduced potential to adapt to changing environments (evolutionary costs), and may also have important demographic effects on the plants, the animal disperser/s, or both, leading to decreases in their populations and even to their extinction (ecological costs). In the Mediterranean islands, we have at least two examples that evidence such ecological and evolutionary consequences of seed dispersal disruptions. Both examples involve the abovementioned plant species (*Daphne rodriguezii* and *Cneorum tricoccon*) with a specific strong interaction with lizards.

Daphne rodriguezii – Traveset & Riera (2005) hypothesised that the loss of lizards from the Menorcan populations was the factor causing the regression of this plant. Through observation and experimentation in the field and laboratory, they found strong evidence that a lack of seed dispersal was the main cause of the low seedling recruitment. Seedlings in Menorca were recruited almost exclusively under the parent plants, whereas in Colom islet, lizards consumed large amounts of fruits and moved seeds to sites suitable for plant establishment. During a period of 10 years, Rodríguez-Pérez & Traveset (2012) analysed the plant demographic consequences of the lizard extinction, by collecting demographic data from five populations, four from Menorca and one from Colom islet. They found that the population dynamics of *D. rodriguezii* is stable under the current conditions, but where dispersal is most limiting, important environmental changes (*e.g.* in habitat suitability and/or rainfall regime) may lead to local extinctions. Another study showed that in the absence of lizards' dispersal, plants establish in favourable locations, but a decline in density is evidenced near adults attributed to higher competition (Rodríguez-Pérez *et al.* 2012). The negative impacts of disperser loss on genetic

diversity and relatedness in the smaller and more isolated populations of *D. rodriguezii* have been demonstrated by Calviño-Cancela *et al.* (2012). Their results also suggested an old isolation of the species due to seed dispersal, probably occurring well before the extinction of the lizard (*ca.* 2,000 years ago). Gene flow might have been maintained *via* pollination in the past; however, the seed disperser loss might ultimately have hindered pollinator-mediated gene flow, as a result of reduced probabilities of effective pollination among increasingly distant and scarce individuals.

Cneorum tricoccon – Traveset *et al.* (2012) investigated the demographic parameters among 26 insular and mainland populations of this shrub along its entire distribution range, comparing populations with lizards with those in which lizards are extinct (due to the introduction of alien predators), but in which alien mammals currently act as seed dispersers. They found plant recruitment to be higher on island populations with lizards than on those with mammals, and the long-term effects of the native disperser's loss were detected in all vital phases of plant regeneration. Previously, Riera *et al.* (2002) and Traveset (2002) had reported that pine martens remove high proportions of fruits and that they have considerably modified the distribution of the plant on Mallorca. The fossil records tell us that lizards lived at low altitudes (<500 m a.s.l.; Alcover *et al.* 1981) while the plant is currently found up to 1,000 m a.s.l. Furthermore, data suggest that lizards may be exerting a selective pressure on seed size, different from that exerted by pine martens (A. Traveset, G. Escribano-Ávila, J.M. Gómez-Reyes, A. Valido, unpublished data), which implies another evolutionary consequence of the seed dispersal disruption. In order to explore to what extent the alien disperser could replace the role played by the native disperser, Celedón-Neghme *et al.* (2013) compared the quality of seed deposition provided by lizards and pine martens to *C. tricoccon* by studying the pattern of seed distribution among sites generated by both dispersers as well as the suitability of those sites for seedling emergence and establishment in coastal shrublands and in pine forests. Lizards and mammals showed contrasting patterns of seed deposition and, where lizards were absent, mammals took on their role as seed dispersers in pine forests but not in coastal shrublands. The lack of seed dispersal in the coastal shrubland seriously limits recruitment by concentrating seeds under conspecifics and hindering colonisation opportunities, marking a long-term trend towards decline. More recently, a genetic study using microsatellite markers has shown that the genetic structure and diversity of *C. tricoccon* do not differ between lizard-dispersed and mammal-dispersed populations, which is partly attributed to the habitat preferences (mostly forest areas) of the alien mammals as well as to the different population sizes (Lázaro-Nogal *et al.* 2016).

Seed dispersal disruptions are not only occurring nowadays but have certainly taken place for millions of years. It is well known that Mediterranean islands acted as reservoirs of the Tertiary flora, refuging plants from the climatic fluctuations of the Pleistocene and of the changes produced in vegetation belts (Médail & Diadema 2009; Woolbright *et al.* 2014). Likewise, they acted as refuges for many animal species, especially mammals such as dwarf elephants, hippos, dwarf deer, pikas, carnivores like the Sardinian dwingle, etc., most of which disappeared due to a combined effect of climate change and hunting by humans (van der Geer *et al.* 2010). Their loss most

likely had an important effect on vegetation dynamics, especially considering that they dispersed a large number of plants as their relatives currently do in other parts of the world. Although such plant–mammal interactions are no longer prevalent, we cannot ignore that at least some of the plant traits – particularly fruit traits – still prevalent in the Mediterranean Basin, including the islands, must have been selected by those animals. Hence, when trying to understand the current reproductive traits of some of the plants we see today in Mediterranean islands we must take into account the fauna that co-evolved with them over millions of years.

The impact of invasive species on plant reproductive success in Mediterranean Islands

Current threats imposed on mutualistic systems on many islands, and the Mediterranean ones are no exception, are primarily driven by alien species and their direct and indirect competition for pollinators and seed dispersers (plants) and for floral resources and fruits (animals) (Kaiser-Bunbury *et al.* 2010; Traveset & Richardson 2014).

Invasive plants, for example, can compete for mutualistic services with native plants. This has been found in the Balearics with the highly invasives *Carpobrotus* spp. (Moragues & Traveset 2005) and *Oxalis pes-caprae* (Albrecht *et al.* 2016). Nonetheless, depending on the native species and also on the scale of the study, the effect may be facilitative (Jakobsson *et al.* 2009; Albrecht *et al.* 2016). On the other hand, the integration of aliens into resident communities can be facilitated through generalist pollinators and dispersers that include nectar and pollen or fleshy fruits in their diets. This was found in Menorca when studying how the invader *Opuntia maxima* is integrated in the pollination (Padrón *et al.* 2009) as well as the seed dispersal communities (Padrón *et al.* 2011). On Lesbos Island, Tscheulin *et al.* 2009 and Tscheulin & Petanidou (2013) examined the impact of the alien invasive *Solanum elaeagnifolium* on seed set of the native *Glaucium flavum*, finding that it significantly enhanced pollen limitation due to disturbed honeybee visitation to the native plant in the presence of the invader.

Introduced vertebrates are well known to have detrimental effects on the native island flora and fauna and thereby affect native mutualisms indirectly (Traveset & Richardson 2014). The introduction of carnivores, specifically, has had devastating effects on the native endemic lizards in the two main Balearic Islands, cascading down the plants that depended on such lizards (see above). Likewise, the introduction of snakes has been very harmful to other native island vertebrates (including lizards but also rodents, dormice, etc.). In the Pityusic Islands (Ibiza and Formentera), for instance, the introduction of snakes such as the horseshoe whip snake (*Hemorrhois hippocrepis*, introduced in Eivissa in 2003), the Montpellier snake (*Malpolon monspessulanus*) and the ladder snake (*Rhinechis scalaris*) is causing the decline of the endemic *Podarcis pithyusensis* populations, which will certainly have consequences on the reproductive and dispersal success of a number of plants that might disappear even before their biology has been studied.

The negative impact of introduced goats, rabbits, rats, mice or parrots – all commonly introduced in islands – on plant fitness and dispersal can be many-fold. It includes the direct consumption of vegetative or reproductive parts of native plants and, more indirectly, the reduction of populations of legitimate

seed dispersers. There is evidence that rodents, cats, invasive ants – like *Linepithema humilis* – have had devastating effects on the native biota in many islands. A review on the effects of alien rodents in the Balearic Islands (and the Canary Islands) can be found in Traveset *et al.* (2009a). A specific study on the endangered plant endemic *Medicago citrina* in Cabrera Island (Latorre *et al.* 2013) showed that herbivore pressure by European rabbits, black rats and house mice has an important effect on plant performance. On the other hand, Bourgeois *et al.* (2005) found that rats and rabbits are the primary seed dispersers of the invasive *Carpobrotus* spp. on the Hyères archipelago, not detecting such dispersal activity on the adjacent mainland. Seed ingestion by rats and rabbits also enhanced seed germination rates, in spite of an associated reduction in seed size. In return, *Carpobrotus* provides a water/energy-rich food source during the dry summer season, thus demonstrating a clear case of an invasion complex, *i.e.* mutualism between invaders. Herbivory pressure by goats has also been shown to be high in some populations of narrow endemics like *Ranunculus weyleri* (Cursach & Rita 2012b), and reducing such pressure should be a high priority for environmental managers in many Mediterranean islands. It is interesting to note, however, that the effect that grazing can have on a particular species cannot be easily extrapolated at the community level. In this sense, Lázaro *et al.* (2016) studying the effect of grazing by goats on the pollination networks of Lesbos found that intermediate grazing resulted in larger, more generalised, more modular and more diverse, and even interactions, which might confer more stability to the networks. Future studies are necessary to assess whether this is a general pattern.

Conclusions and future research avenues

The Mediterranean islands system is composed of a highly fragmented complex of mostly continental islands that have been disconnected from each other and from the continent in relatively recent geological times (*ca.* <5.2 Ma). At the time they became insular, they already carried a flora and fauna that were probably fully adapted and diversified and with established interactions between organisms. In this context, with few ecological empty spaces – in contrast to what occurs in oceanic islands –, it is not expected that organisms will be subject to strong evolutionary challenges (Gillespie & Roderick 2002), although at least for some organisms with large home ranges, isolation *per se* might have posed serious selective pressure. The changes that occurred likely responded to small adjustments to adapt to the current environmental conditions or, above all, to anthropic processes. In any case, Mediterranean islands provide a premier setting for studying the effects of past range fragmentation *via* geologically dated sea barriers, and thus for testing genetic drift models of allopatric speciation and non-adaptive radiation (Schluter 2000 and references therein). We must take into account in these studies, however, that ancient genetic shuffling due to commercial routes across the Mediterranean might have blurred some (or many) of those ecological and evolutionary patterns.

Most studies on plant reproductive biology that we have identified in this review correspond to endemic species of restricted range. This result is not surprising. Indeed, Mediterranean islands are among the areas of higher incidence of endemism, with values that sometimes can exceed 20% of a local flora (Médail & Quezel 1997). On islands like Sicily, Crete, Cyprus, Corsica and Sardinia, and the Balearic Islands, the rates of narrow endemism are at their highest (reviewed in Thompson 2005). The study of plant reproductive systems in these narrow endemics, their dependence on pollinators to complete their life cycle or the analysis of adaptations for the particular needs of island environments, is much necessary for environmental managers to be able to elaborate adequate plans that ensure species maintenance in the ecosystem. Our review has also evidenced that most available information is very geographically biased towards the western Mediterranean islands, especially the Balearic Islands. More studies throughout the longitudinal gradient would allow testing for differences between contrasting biotic and abiotic conditions. Moreover, the large majority of data come from species-focused studies, and only a small fraction have been performed at a community level. Such community studies are very necessary now, especially given the high rate of habitat loss and modification; they provide information on how species interact and how the entire community functions, and thus allow detecting more easily its vulnerability in the face of environmental changes. We also found that less than 15% of the studies involve genetic analyses, mainly focused on assessing the genetic differentiation and variability of narrow endemics. More work is thus needed for studying gene flow and local adaptation, comparing island populations with their relatives on the mainland.

Contrary to what might have been expected, our review shows that most island species studied so far do not rely on autonomous selfing, and their reproduction is dependent on some pollen vector. In fact, a good number of specialised pollination systems have been identified in the Mediterranean island flora (*e.g.* those required by orchids or those of heterostylous species). Such specialised systems are, on the other hand, more vulnerable to pollination disruptions due to the severe ecosystem alteration, either through the arrival of alien invasive species or habitat modification, as has already been found in the islands. The almost lack of changes in floral traits that promote plant reproduction independently of biotic pollination vectors, together with the putative high frequency of specialised interactions found, might be explained by the diversity and abundance of insect pollinators in these environments. The Aegean archipelago, in particular, is a hotspot for bees, whereas the Balearic archipelago is also rich in hymenopterans in general (nearly 400 species). More systematic research on both taxonomic and ecological aspects of these native pollinators is necessary throughout all Mediterranean islands. We urgently need more data on the ecosystem dependence of pollination interactions, as well as on the consequences that the potential loss of pollinators can have on these fragile ecosystems. Future studies should also aim to document plant–vertebrate mutualistic interactions in the islands; systems such as those found on the Balearics – often quite specialised like some plant–lizard interactions – are much more likely to be present in many other Mediterranean islands. Given the current scenario of habitat destruction or modification, the small, uninhabited islands are often the only ones preserving old interactions that evolved millions of years ago. Hence, these islands should be considered as sanctuaries of relict biodiversity.

We hope that this synthesis will catalyse a new set of studies that will be able to build upon the existing knowledge compiled here and take our understanding of the function of pollination

and seed dispersal systems in Mediterranean islands to a whole new level. both in terms of scope (*i.e.* the community level) and detail. Besides filling the gaps of information pointed out above, it would be interesting in future studies to test a set of specific hypotheses in order to advance such understanding. For instance, (i) Mediterranean island plants that present generalised and self-independent syndromes or reproductive mechanisms (including ambophily) are more likely to succeed than those requiring specialised interactions; (ii) self-fertilisation and self-compatibility are higher in Mediterranean island plants than in the nearby mainland; (iii) Mediterranean island plants are more pollen- and seed dispersal-limited than their relatives on the mainland, which translates into an overall lower plant genetic diversity and higher genetic differentiation; (iv) the diversity of mutualists visiting a particular plant species is lower in the islands than in the mainland; (v) island mutualists are more generalists than their mainland counterparts; and (vi) the effect of landscape changes on mutualist diversity and abundance, and subsequently on plant reproductive success, are higher in the islands than on the mainland due to the lower functional redundancy in the former.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. List of species, and the island in which they were studied, for which published information has been found that allow the calculation of self-fertilisation (IAS) and self-incompatibility (ISI) indices.

Table S2. Literature review references for the 167 papers found on Mediterranean plants and pollination systems.

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