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Impact of habitat disturbance in pollination services of *Jasione maritima* var. *sabularia* (Cout.) Sales & Hedge

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Abbreviations

d.f. – degrees of freedom

e.g. - (L. *exempli gratia*) for example

et al. - (L. *et alia*) and other

i.e. - (L. *id est*) that is

ID - identification

IUCN – International Union for Conservation of Nature

LSmeans – least square means

P – probability

SE – standard error

sp. – (L. *species*) species

spp. - (L. *species*) species in plural

LM – Linear Models

LMM – Linear Mixed Models

GLM – Generalized Linear Models

GLMM – Generalized Linear Mixed Models

RLMM – Robust Linear Mixed Models

Note: all the units used follow the SI (Système International d’Unités)

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Abstract

Jasione maritima var. *sabularia* (Cout.) Sales & Hedge is an endangered endemic species from the north-west coast of the Iberian Peninsula, being confined to coastal sand dunes. This species is threatened by the loss and fragmentation of the dune system, mainly due to urbanization and spreading of invasive alien species. Habitat loss and fragmentation are the paramount threat to biodiversity worldwide, being considered the main threat to pollinators. The extreme dependence of *J. maritima* on pollinators, not only because it is a self-incompatible plant, but also because pollinators are essential to trigger the stigmatic receptivity, suggest that this species might be particularly vulnerable to habitat disturbance. Therefore, the aims of this work were: 1) to evaluate how habitat disturbance affects the populations of *J. maritima* and of its pollinators, 2) to assess if habitat disturbance reduces the fitness of *J. maritima* due to increased pollen limitation levels, and 3) to understand how habitat disturbance affects the structure of its pollination networks. Habitat disturbance was classified as the amount of suitable area for the growth of *J. maritima*: high disturbance (0 to 40% of available area), medium disturbance (41 to 70% of available area) and low disturbance (71 to 100% of available area). Overall, the results revealed that *J. maritima* presents a generalized pollination system, mainly composed by Hymenoptera and Diptera, and that this plant species represents the main resource for pollinators during its flowering period, being important for the maintenance of pollinator populations. The habitat disturbance had a negative effect on the pollination services provided by insects to *J. maritima*. Habitats with low levels of disturbance had a higher density of *J. maritima* and of floral resources (open inflorescences), which makes them more attractive to pollinators, being reflected in a richer pollinator community. Surprisingly, the frequency of interaction was similar at habitats with high and low disturbance, being the lowest at the intermediate level of disturbance. However, at habitats with higher disturbance, the reproductive success was lower and the levels of pollen limitation were higher. This may be the consequence of a differential behaviour by the pollinator community in response to the availability of resources of *J. maritima*, which may result in an excessive deposition of conspecific, poor-quality pollen at disturbed locations. Furthermore, high disturbance level habitats presented more connected and more generalised interaction networks, with a more homogeneous distribution of the interactions, which is associated to a simplification of the system. This

study showed, how disturbance and loss of suitable habitat may impair the pollination services provided by insects to a plant species, thus demanding for effective conservation and restoration measures that can preserve both groups involved in this tightly intertwined relationship.

Key words: endangered species; pollen limitation; habitat disturbance; reproductive success; interaction networks

Resumo

Jasione maritima var. *sabularia* (Cout.) Sales & Hedge é uma espécie ameaçada, endêmica da costa noroeste da Península Ibérica, estando confinada a sistemas dunares costeiros. Esta espécie está ameaçada pela perda e fragmentação do sistema dunar, devido, principalmente, à urbanização e disseminação de espécies exóticas invasoras. A perda e fragmentação do habitat constituem a principal ameaça à biodiversidade global, sendo consideradas uma das principais ameaças das populações de polinizadores. A extrema dependência de *J. maritima* nas populações de polinizadores, não só por ser uma espécie auto-incompatível, mas também por estes serem essenciais para desencadear a sua receptividade estigmática, sugere que esta espécie é particularmente vulnerável à perturbação do habitat. Assim, os objectivos do presente trabalho são: 1) avaliar como a perturbação do habitat afecta as populações de *J. maritima* e dos seus polinizadores, 2) perceber se a perturbação do habitat reduz o fitness de *J. maritima*, devido a um aumento dos níveis de limitação de pólen, e 3) compreender se a perturbação do habitat afecta a estrutura das suas redes de polinização. A perturbação do habitat foi classificada de acordo com percentagem de área disponível para o crescimento de *J. maritima*: 1) perturbação elevada (0 a 40% de área disponível), perturbação média (41 a 70% de área disponível) e perturbação baixa (71 a 100% de área disponível). De maneira geral, os resultados revelaram que *J. maritima* apresenta um sistema de polinização generalizado, maioritariamente composto por himenópteros e dípteros. *J. maritima* é o principal recurso para os polinizadores durante o seu período de floração, sendo importante para a manutenção das populações de polinizadores. A perturbação do habitat teve um efeito negativo nos serviços de polinização fornecidos pelos insectos de *J. maritima*. Habitats com níveis baixos de perturbação apresentaram uma maior densidade de *J. maritima* e de recursos florais (inflorescências abertas), tornando-os mais atractivos para os polinizadores, o que se reflectiu numa maior comunidade de polinizadores. Surpreendentemente, a frequência de interacção foi semelhante em habitats com alto e e baixo nível de perturbação, sendo mais baixa no nível de perturbação médio. Contudo, nos habitats com perturbação elevada, o sucesso reproductivo foi menor e os níveis de limitação de pólen foram mais elevados. Este resultado pode ser a consequência de um comportamento diferencial da comunidade de polinizadores em resposta à disponibilidade de recursos de *J. maritima*, o que pode levar a uma deposição excessiva de pólen conspécífico, de baixa qualidade, nos sítios perturbados. Além disso, habitats

com nível de perturbação elevado apresentaram redes de interação mais conectadas e generalizadas, o que pode estar associado a uma simplificação do sistema. Este estudo permitiu mostrar como é que a perturbação e a perda de habitat podem prejudicar os serviços de polinização fornecidos pelos insectos a uma espécie de planta, exigindo, assim, medidas eficazes de conservação e restauração que possam preservar ambos os grupos envolvidos nesta relação fortemente interligada.

Palavras-chave: espécie ameaçada; limitação de pólen; perturbação do habitat; sucesso reprodutivo; redes ecológicas

*Este resumo não foi escrito segundo o novo acordo ortográfico em vigor.

Introduction

Habitat loss and fragmentation are a paramount threat to biodiversity worldwide, currently being the primary cause of species extinction (Pimm & Raven 2000). The expansion of human population, and the consequent demand for resources have directly modified more than 50% of Earth's ice free land area (Foley et al. 2015; Hooke et al. 2012). Habitat loss, i.e., the loss of the amount of habitat of a particular species (e.g. due to urbanization, or plantations), leads to changes in land cover composition and to a gradual degradation of habitat quality (IPBES 2016; Hadley & Betts 2012; Hanski 2011 Fischer & Lindenmayer 2007). Habitat loss results in the sub-division of continuous habitats into smaller patches, which is surrounded by a matrix of unsuitable and structurally poor landscape, i.e. habitat fragmentation, changing the area and the spatial configuration of the landscape (Hadley & Betts 2012; Dauber et al. 2010; Fisher & Lindenmayer 2007; Fahrig 2003). Thus, fragmentation leads to the reduction of the patch size, increases the isolation of patches, and reduces the connectivity between them. Therefore, habitat loss and habitat fragmentation originate small isolated populations that create a barrier to gene flow, and increase inbreeding depression and the risk of extinction through demographic stochasticity (Vanbergen 2014; Kearns et al. 1998).

Another major cause of biodiversity loss are invasive alien species, i.e., species that have successfully established and proliferated in areas outside their historical range and have become locally dominant (Raizada et al. 2008; Vitousek et al. 1997; Elton 1958). Invasive species lead to the degradation of habitats and pose a significant threat to the function and structure of the invaded ecosystems. Although biological invasions can occur naturally, globalisation has increased the rate of species introduction worldwide, thus promoting biological invasions (Mack et al. 2000). Humans, deliberately or accidentally, act as the main dispersal agents of vascular plants, transporting seeds, plants and propagules from their native ranges to new areas (Mack & Lonsdale 2001; Chapin et al. 2000). In the new environment, alien species need to overcome a series of barriers to become naturalized or invasive, whereby only a small percentage of alien species become invasive (Pyšek & Richardson 2008; Lodge 1993). However, most of the ecosystems present invasive species and the degree to which an ecosystem is invaded depends on its susceptibility (invasibility) and on the propagule pressure to which the ecosystem is exposed (Pyšek & Richardson 2008; Lonsdale 1999). The inherent invasibility of the ecosystem is related with the resources available (Davis et al. 2000), the disturbance level (Pyšek & Richardson 2008), the climatic similarities (Lonsdale 1999), the absence of herbivores, pathogens and predators that control the growth of these species in their native

range (Keane & Crawley 2002; Marchante 2001) and with the availability of mutualistic partners (Simberloff & Holle 1999). Moreover, there are several traits that are related to the invasive character of a species, such as ability to reproduce sexually and asexually (vegetative reproduction), rapid growth, phenotypic plasticity, high tolerance to environmental heterogeneity (Sakai et al. 2001), an efficient long distance dispersal mechanism and a high soil seed bank (Marchante 2001). Invasive plant species present severe consequences for the species diversity and for the community structure by competing with native plant species for resources, such as space, nutrients and light (Levine et al. 2003), changing soil properties, nutrient cycling (Raizada et al. 2008; Ehrenfeld 2003), water resources (Dyer & Rice 1999), fire regimes (D'Antonio 2000), hybridization (Reaser et al. 2007), and disrupting ecological interactions (Traveset & Richardson 2006). Moreover, biological invasions can have severe impacts in the configuration of the habitats, leading to the fragmentation, degradation and complete replacement of the natural vegetation (Reaser et al. 2007). Many invasive plant species form dense stands that result in the biotic homogenization of the landscape, leading to habitat loss for native plant species that can culminate in the local extinction of many of these native species (Mckinney & Lockwood 1999; Richardson et al. 1989).

The extent of such transformations jeopardizes the biodiversity and leads to the disruption of interactions between species and, ultimately, of ecological processes (Haddad et al. 2015), leading to the current unnaturally high extinction rates (Pimm et al. 2014; Chapin et al. 2000).

Interactions among species represent one of the main components of community structure and ecosystem functioning (Olesen et al. 2007). One of the most important plant-animal interactions that plays a critical role in shaping much of Earth's biodiversity and complexity is the mutualism between flowering plants and pollinators (Bascompte 2009; Aizen & Feinsinger 2003), with more than 87.5% of flowering plants requiring, to some degree, animals for their pollination (Ollerton et al. 2011; Fisher et al. 2009). Since plants are immobile, sexual reproduction of angiosperms relies, completely or partially, on vectors (in this case biotic vectors) to transport viable pollen grains from anthers to receptive and compatible stigmas, ensuring the production of offspring and their persistence in nature (Proctor et al. 1996). Despite being a relationship beneficial for both elements, it is not cooperative, since animals visit flowers not with the intent of pollinating them, but with the purpose of collecting essential resources for their nutrition, attraction of mates or nest construction, like pollen, nectar, floral tissues, oils, fragrances

and resins (Waser & Ollerton 2006; Ollerton 1999; Proctor et al. 1996). Thus, pollination constitute a major ecological function, not only crucial for the reproduction of wild plants, but also for insect's populations maintenance. Pollination is also an ecosystem service essential for agricultural production (involved in 35% of the world's crop production) and provides vital micronutrients for human welfare (IPBES 2016; Vanbergen & IPI 2013; Eilers et al. 2011; Klein et al. 2007).

Although being a crucial ecosystem function, pollination was only discovered between the late 17th and the early 18th centuries (Proctor et al. 1996). The flower's sexual organs were recognized in 1694 by Rudolf Camerarius, in a published letter entitled *Epistola de Sexu Plantarum* (Faegri & van der Pijl 1971; Zarsky & Tupy 1995). However, the different types of pollination and the role of insects on the sexual reproduction of plants would only be recognized later on by Joseph Kölreuter and Christian Sprengel (Faegri & van der Pijl 1971; Sprengel 1793; Kolreuter 1763). Sprengel acknowledged that for some plants cross pollination is obligatory, and described many structural adaptations of flowers to insect pollination, referring to them as an intentional design (Faegri & van der Pijl 1971; Proctor et al. 1996). Later, Charles Darwin, inspired by Sprengel's observations, interpreted plant-pollinator interactions from an evolutionary perspective. Besides that, Darwin gave very important contributions to pollination ecology with the publication of three books (Darwin 1862, 1876, 1877) about the floral features that promote cross-pollination, the advantages and disadvantages of cross- and self-fertilization for plant fitness, and about sexual polymorphisms (Barrett 2010). For this reason, Darwin is considered the founder of plant reproductive biology, and his work was key to the subsequent interest in pollination biology, providing the framework for many studies to date (Barrett 2010).

The importance of the plant-pollinator mutualism for Earth's biodiversity is highlighted by the fact that plants that are pollinated by biotic vectors have diversified more than those relying on abiotic ones (Bascompte & Jordano 2008; Eriksson & Bremer 1992). The enormous diversity of flowering plants is attributed to the adaptation to a multitude of pollinator species from several functional groups (Van der Niet et al. 2014). Flowering plants and pollinators impose selective pressures on each other, influencing the evolution of many plant and pollinator features, i.e., coevolution (Bronstein et al. 2006; Fenster et al. 2004; Kiester et al. 1984). For instance, the diversification and dominance of angiosperms from the mid-Cretaceous onward appears to be correlated with the diversification of some groups of pollinators, specifically of some extant clades of

bees (Ollerton 2017; Cardinal & Danforth 2013). Although numerous plant-pollinator relationships are generalized, the evidences for coevolution are abundant in the literature and there are also examples of cospeciation in a few highly specialized insect-plant mutualisms (Bronstein et al. 2006; Machado et al. 2005; Fenster et al. 2004). From the plant point of view, the dependence on the pollination mutualism is conditioned by the breeding system of plant, which can range from facultative outcrossing, in self-compatible species, to obligate outcrossing, in self-incompatible or dioecious species (Richards 1997; Bond 1994). Self-incompatibility, present in approximately 60% of the angiosperms, is a genetically determined pre-zygotic barrier to fertilization by self- or self-related pollen, and such species have a high dependence on pollen vectors because they can only use outcross pollen to produce seeds (Hiscock & McInnis 2003; Aizen et al. 2002).

There are approximately 350,000 known species of pollinators (including insects, birds, bats, rodents, lizards and many others) with their biodiversity changing with both latitude and continent (Ollerton 2017). Although not all species of insects are pollinators, they constitute the major group of pollinators, in particular from the orders Hymenoptera, Diptera, Lepidoptera and Coleoptera, with bees being the dominant pollinators in most ecosystems, closely followed by flies (Ollerton 2017, IPBES 2016, Waser & Ollerton 2006). Although the most known pollinator in Europe is the managed honey bee (*Apis mellifera*), the majority of the wild plants are pollinated by wild pollinators and some of them can provide a more efficient pollination service than the honey bee (IPBES 2016; Vanbergen & IPI 2013). However, the persistence of wild plant populations pollinated by animals may be jeopardized since pollinators are declining at local, regional and global scales (Ollerton 2017; Kearns et al. 1998). For example, of the 68 bumblebee species (genus *Bombus*) present in Europe, 31 species are declining (Potts et al. 2015). This pollinator crisis has been a concern for several years among the scientific community, with many international initiatives being carried out in order to understand and tackle the risks faced by pollinators. The most recent initiative includes a global pollinator assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, which evaluated the value of pollination and the status, trends and threats to pollinators (IPBES, 2016).

Among the many drivers of the pollinator decline are: (1) habitat loss and fragmentation; (2) agricultural intensification; (3) chemicals, including insecticides (especially neonicotinoids), herbicides and fungicides; (4) pests and diseases; (5) alien

invasive species; (6) climate change; and (7) artificial light (Knop et al. 2017; IPBES 2016; Potts et al. 2010; Kearns et al. 1998). These drivers have an impact on different levels of biological organization and rarely act in isolation, thus, having combined effects (Potts et al. 2015; Vanbergen & IPI 2013; Potts et al. 2010). Moreover, the specific ecological requirements of the different groups of pollinators makes them differentially affected by these pressures (Potts et al. 2015). Nevertheless, there is a consensus that the main threat to pollination is the anthropogenic driven habitat disturbance, namely habitat loss, fragmentation and the overall simplification of landscapes structure (Traveset et al. 2017; Nicolson & Wright 2017; Winfree et al. 2009; Aizen & Feinsinger 2003; Kearns et al. 1998). Specifically, habitat loss and fragmentation may disrupt pollination by affecting three important components of the pollination system: (1) plant biodiversity, (2) pollinator biodiversity, and (3) pollinator behaviour, in particular their movement within and between habitat fragments (IPBES 2016; Hadley & Betts 2012). Decline in any of these elements can cause the reduction or failure of pollination services (Hadley & Betts 2012). As it is expected from the positive species-area relationship theory (MacArthur & Wilson 1967), habitat loss and fragmentation impact plant and pollinator populations by reducing the diversity of plants and pollinators in a given area (Blaauw & Isaacs 2014). An impoverishment in plant populations, decreases the diversity of conspecific plants, which leads to a disruption in the pattern of pollen flow, because there is less pollen in the system and more limited options for outcrossing (Xiao et al. 2016; Hadley & Betts 2012). The diversity of pollinators drops with the reduction of the habitat available due to the consequent loss of nesting, oviposition and foraging sites (Winfree et al. 2011; Potts et al. 2010; Aizen & Feinsinger 2003). In addition, since food availability is one of the most important factors influencing pollinators occurrence (Xiao et al. 2016; Aizen & Feinsinger 2003), with the decline in plant diversity, food sources for pollinators become scarcer leading to the decline of pollen vectors. Although responses to habitat disturbance are mostly negative, flower visitor-functional groups do not respond in the same way to habitat disturbance as a result of different ecological traits of the insect pollinators (e.g. sociality, nesting habit, diet breadth, feeding adaptations, mobility and body size) (Traveset et al. 2017; Vanbergen 2014; Winfree et al. 2011; Winfree et al. 2009). Moreover, fragmentation, especially patch size and the distance between patches, influences pollinator's foraging behaviour (Xiao et al. 2016). For example, it is also not advantageous for them to visit small patches with long inter-patch distance because it leads to higher foraging costs and increased exposure to predators (Hadley & Betts 2012;

Wilcock & Neiland 2002). Additionally, this may impose spatial restrictions on their foraging if inter-patch distances are beyond their flying capabilities (Ghazoul 2005).

The declines in pollinator and plant diversity, resulting from habitat disturbance, can thus decrease the pollination services of wild plants populations pollinated by animals, and increase the magnitude of pollen limitation (Potts et al. 2010; Burd 1994), because the pollen delivered to stigmas is inadequate in quantity or quality, resulting in a reduction of the number of ovules fertilized (Xiao et al. 2016; Aizen & Harder 2007). Consequently, there is a decrease in seed quantity and quality, which reduces plant reproductive output (Wilcock & Neiland 2002; Aizen et al. 2002). The reduction of the sexual seed production is considered the first step in the demographic collapse of plant populations (Aizen et al. 2002), because it compromises the possibility of an independent dispersal phase, the opportunity to maintain or increase genetic diversity and the potential to adapt to new environments (Wilcock & Neiland 2002). The continued decrease in plant fitness will impact population dynamics and might cause a feedback loop that results in further loss of pollen vectors and individuals (Blaauw & Isaacs 2014). This has been observed for example in Britain and in the Netherlands with wild bees and hoverflies and the plants pollinated by them (Biesmeijer et al. 2006). Hence, self-incompatible plants pollinated by biotic vectors are most vulnerable to habitat disturbance (Aguilar et al. 2006; Knight et al. 2005; Bond 1994), and further concern occurs in the case of endemic, endangered and/or rare species (Aguilar et al. 2006; Knight et al. 2005; Bond 1994).

Coastal sand dunes are dynamic and heterogeneous habitats, representing the first effective physical barrier against the advance of the sea inland (Marchante 2011; Martínez et al. 2008a). Dune systems are characterized by an environmental gradient that determines a characteristic coast-to-inland plant community zonation (Ciccareli & Bacaro 2016; Acosta et al. 2007), and harbours a high diversity of native plant species, structurally and floristically distinct. These plant communities are essential to hold the sand, minimizing the effects of erosion, and controlling the dune morphology (Ciccareli & Bacaro 2016; Acosta et al. 2007; Marchante 2001). Psammophilous plants are adapted to the harsh and challenging environmental conditions of dune systems, withstanding the constant wind and salt spray, the scarcity of nutrients and water in the soil and the high salinity (Calvão et al. 2013; Martins et al. 2013). Therefore, this environmental isolation led to speciation processes, resulting in a high proportion of endemic plant species in this system (Neto et al. 2007). The ecological importance of the Portuguese dune system, and its high number of endemism, is highlighted by the fact that 35% of the Portuguese

“Nature 2000” habitats correspond to coastal types (Martins et al. 2013, Neto et al. 2007). Unfortunately, coastal sand dunes are considered one of the most vulnerable and disturbed landscapes in Europe and the Portuguese coastal dunes are also strongly threatened by natural and anthropogenic pressures (Martínez et al. 2008a; Martínez et al. 2008b; Marchante 2007). In Portugal, coastal areas are the most densely populated areas in the country, with more than 75% of the population living on the coast (Calvão et al. 2013; DGA 2000). This, along with the increasing touristic activity in these areas, leads to intense pressures on the dune system, due to (1) the construction of infrastructures, (2) dune trampling, (3) removal of native plant species, (4) plantation and expansion of alien species, and (5) agricultural tillage (Martins et al. 2013; Marchante 2007). These contribute to a decrease in the heterogeneity of the landscape and, consequently, to habitat loss, the reduction of the dune patch size and to an increase in habitat fragmentation and isolation of the remaining patches (Calvão et al. 2013; Curr et al. 2000), which may endanger the persistence of endemic plant species and its pollinators (Traveset et al. 2017).

Due to the fact that species belong to complex communities, in the last decade there has been an increase in the number of studies that analysed interactions between species using a network approach, where species are viewed as nodes connected by links (e.g. Correia et al. 2017 Heleno et al. 2011; Bascompte & Jordano 2007). This approach allows to explore the patterns of interactions between species, at the level of the whole community, and its consequences for the functioning and stability of ecological processes (Mello et al. 2011; Thebault & Fontaine 2010), and simultaneously study the role of the different species within the network structure (Olesen et al. 2007; Bascompte et al. 2006). Understanding the topology of ecological networks, such as plant-pollinator networks, is essential not only to understand the evolution of mutualisms in communities (Jordano et al. 1997, Fontaine et al. 2011), but also to assess the effects of habitat disturbance and species loss at the community level (Ferreira et al. 2013; Albrecht et al. 2014). Nestedness is one of the most common form of network structure, and that has been extensively studied (Bascompte et al. 2003). Moreover, most plant-pollinator networks present a nested (i.e. specialist species are well defined subset of the links of generalists) and consequently asymmetric structure, which confers stability to the loss of species, due to the cohesion and high redundancy of the system (Bascompte & Jordano 2007; Bascompte et al. 2003). Nevertheless, this stability can be compromised if the most connected species are eliminated, which may trigger a cascade of secondary extinctions,

leading to a collapse of the system (Lever et al. 2014; Vanbergen 2014; Kaiser et al. 2010; Memmott et al. 2004). Therefore, ecological networks are useful to plan effective conservation strategies (Memmott et al. 1999, Correia et al. 2017), by providing quantitative information on the structure and function of communities (Kaiser-Bunbury et al. 2017; Schleuning et al. 2015).

Nevertheless, in the last years a few studies have been published highlighting the importance of understanding the processes at the population level, since populations present intra-population variability such as different individual phenotypes, and for that reason it becomes important to downscale the study of pollination networks to the individual level, which allows, for example, to understand the patterns of mating between phenotypically different individuals of a population (Valverde et al. 2016; Dupont et al. 2014; Tur et al. 2015; Gómez & Perfectii 2012; Gómez et al. 2011).

Jasione maritima presents a complex breeding system. Firstly, like the sister species, *J. montana* (Parnell 1982, 1987), it is a self-incompatible species (M Castro & C. Siopa, unpublished results). Secondly, like other species in the Campanulaceae family, *J. maritima* exhibits secondary pollen presentation, in which pollen is presented in the female structures, namely on the stylar brush (pollen presenter), rather than on the anthers (Howel et al. 1993; Faegri & van der Pijl 1979; Yeo 1993). As the flowers open, the stylar brush grows through the anthers, collects the pollen and exceeds the petal, presenting the pollen grains to the pollinators (Yeo 1993). Flower visitors are fundamental in this phase, because as they remove pollen from the pollen presenter, they touch the hairs of the stylar brush and this physical contact promotes the invagination of its hairs. When the pollen has been removed, the hairs are fully retracted, and the two stigmatic lobes start to diverge so that the stigma becomes receptive. By presenting this temporal separation of the male and female function within the flowers (i.e. dichogamy, in particular protandry) and a self-incompatibility system, *J. maritima* minimizes the risk of self-interference and promotes outcrossing (Barrett 2002; Howel 1993; Lloy & Webb 1986), strictly relying on pollen vectors to produce offspring.

Objectives

The extreme dependence of *Jasione maritima* on flower visitors, not only because it is self-incompatible, but also because they are essential to trigger the receptivity of stigmas, suggest that this endangered species could be particularly vulnerable to habitat loss and fragmentation of the dune system, and to the reduction of flower visitors and pollinator populations. Therefore, in order to understand the vulnerability of *J. maritima* to habitat disturbance and to plan conservation strategies it is essential to understand the dynamics of the interaction between this species and the community of its pollinators across its habitat and in environments with different disturbance levels. In this context, the aims of this work were: (1) to study the pollination ecology of the endangered endemic species *J. maritima* var. *sabularia*; (2) to evaluate how habitat disturbance affects the populations of *J. maritima* and of its pollinators; (3) to assess if habitat disturbance reduces the fitness of *J. maritima* due to limited pollination services; and (4) to understand how habitat disturbance affects the structure of the individually based pollination networks.

Material and methods

Study site and experimental design

The present study was carried in the northern Portuguese coastal sand dunes, between Silvalde (40°59'9.93"N, 8°38'43.99"W) and Torreira Sul (40°44'27.55"N, 8°43'6.02"W), stretching 29 km in the north-west coast of Portugal and covering part of the municipalities of Espinho, Ovar and Aveiro. The study area is located in the transition between the Eurosiberian (in the North) and the Mediterranean biogeographic regions (in the South) (Honrado et al. 2010; Rivas-Martínez 2002; Costa et al. 1998), which influences the type of vegetation present in the dune system (Martins et al. 2013). The native vegetation of the interdunar space and the grey dunes, the main habitat of *J. maritima*, is characterized by low plant cover with herbaceous species (e.g. *Malcomia littorea* (L.) R.Br., *Helichrysum italicum* subsp. *picardi* (Boiss. & Reut.) Franco, *Sedum sediforme* (Jacq.) Pau, *Seseli tortuosum* L., *Euphorbia portlandica* L., *Pancreatium maritimum* L., *Silene* sp. L., *Linaria* sp. Mill., *Anagallis monelli* L.) and a few shrubs (e.g. *Corema album* (L.) D. Don and *Artemisia campestris* subsp. *maritima* Arcang.).

Acacia longifolia (Andrews) Willd. (Fabaceae), a shrub or small tree native to Australia, is the most problematic of the invasive species, being especially common in the north and central coast of Portugal, but referenced to all coastal areas of the country (Marchante 2007b). *Acacia longifolia* was introduced in the 20th century to stabilize coastal sand dunes and with ornamental purposes, but it has escaped, replacing, since then, the native vegetation and creating monospecific stands (Marchante et al. 2007a). This species has the ability to fix nitrogen and produce a great amount of litter with a slow rate of decomposition, which accumulates in thick layers (Marchante et al. 2011). The other main invasive species is *Carpobrotus edulis* (L.) N. E. Br. (Aizoaceae), a South African prostrate succulent species that was also introduced during the 20th century for the same purposes of *A. longifolia*. The species has spread widely, displacing the native flora (Novoa et al. 2013; D'Antonio et al. 1991). *Carpobrotus edulis* grows from multiple axes rooting where nodes contact the soil (Conser & Connor 2009), creating a thick mat of living and dead plant material, spreading more than 1 m per year (D'Antonio 1990).

Characterization of habitat quality and population density

Prior to field work a 29 km long transect, with the northernmost point located in Silvade (40°59'9.93"N, 8°38'43.99"W), was systematically defined along the interdunal space and the grey dunes. Along this distance, twenty-nine 1 ha plots parallel to the sea, and 1 km apart, were prospected for *J. maritima* (Table 1) (Fig. 1a). Each of these plots was characterized according to: (1) geographical coordinates; (2) presence/absence of *Jasione maritima* and (3) type of habitat disturbance (invasive species; urbanization; altered vegetation) (Table 1) (Fig. 2). *Jasione maritima* was only present in 15 of the 29 sites, and those 15 sites were then selected for further analysis. After this preliminary survey, we quantified the percentage of area available for the growth of *J. maritima*, with the aid of satellite images from Google Earth, using the Earth Point tool for Google Earth (<http://www.earthpoint.us/>) (Table 1).

The level of habitat disturbance was categorized considering the percentage of available area for the growth of *J. maritima*: (1) habitats with up to 40% of available area were categorized as high disturbance level habitats; (2) habitats with 41% to 70% of available area were categorized as medium disturbance level habitats; and (3) habitats with 71% to 100% of available area were classified as low disturbance level habitats (Table 2).

Population size of *J. maritima* was estimated in April of 2018. At each study area of 1 ha, we conducted four transects perpendicular to the sea and 25 m apart. Along each transect, a 1×1m quadrat was placed at each 15 m and the number of reproductive individuals of *J. maritima* was counted.

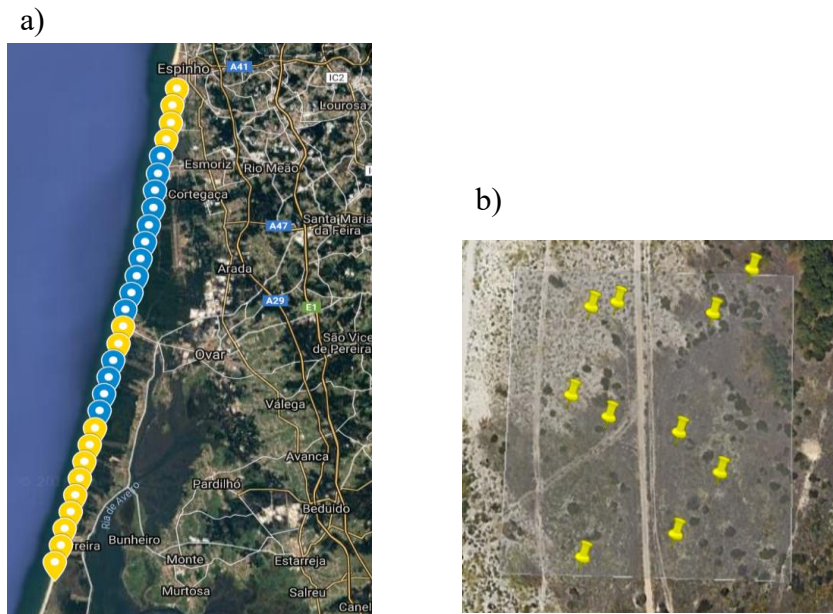


Figure 1. Characterization of the studied area. a) Geographical location of the 29 prospected plots. Yellow pins represent the geographical location of the populations of *Jasionie maritima*. b) Representation of 1 ha plot (in this case, km 14) and of the geographical location of ten patches for pollinator monitoring.



Figure 2. General view of some of the studied areas. a) dune system highly degraded due to urbanization; b) dune system invaded by *Acacia longifolia*; c) dune system invaded by *Acacia longifolia* and *Carpobrotus edulis*; d) dune system with no disturbance

Table 1. Characterization and coordinates of each 1 ha plot. Plots were characterized according to disturbance type, percentage of available area and number of individuals of *Jasione maritima*.

Localities	Coordinates	Disturbance type	Available area (%)	Density of <i>J. maritima</i> ind*m ⁻² (mean ± SE)
Km 0	40°59'09.93"N, 8°38'43.99"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	79.51	4.25 ± 1.22
Km 1	40°58'48.15"N, 8°38'50.82"W	<i>Carpobrotus edulis</i> , Urbanization; Dune degradation; Altered dune vegetation (grasses);	20.95	1.29 ± 0.92
Km 2	40°58'14.41"N, 8°38'56.11"W	<i>Carpobrotus edulis</i> ; altered dune vegetation (grasses)	78.40	1.36 ± 0.66
Km 3	40°57'35.27"N, 8°39'8.17"W	Urbanization; <i>Carpobrotus edulis</i> ; altered dune vegetation (grasses)	38.65	0.07 ± 0.07
Km 4	40°57'07.36"N, 8°39'20.53"W	Urbanization	0	0
Km 5	40°56'34.35"N, 8°39'27.68"W	Urbanization; land degradation	0	0
Km 6	40°56'02.16"N, 8°39'29.01"W	<i>Acacia longifolia</i>	0	0
Km 7	40°55'31.03"N, 8°39'32.42"W	<i>Acacia longifolia</i>	0	0
Km 8	40°54'58.66"N, 8°39'42.69"W	<i>Acacia longifolia</i>	0	0
Km 9	40°54'27.34"N, 8°39'51.41"W	<i>Acacia longifolia</i>	0	0
Km 10	40°53'55.35"N, 8°39'59.18"W	<i>Acacia longifolia</i>	0	0
Km 11	40°53'23.81"N, 8°40'10.10"W	<i>Acacia longifolia</i>	0	0
Km 12	40°52'52.53"N, 8°40'21.10"W	<i>Acacia longifolia</i>	0	0
Km 13	40°52'22.23"N, 8°40'35.77"W	Urbanization	0	0
Km 14	40°51'52.90"N, 8°40'36.22"W	None	100	3.07 ± 0.84
Km 15	40°51'20.16"N, 8°40'47.77"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i> ; altered vegetation	23.18	0.43 ± 0.43
Km 16	40°50'46.19"N, 8°40'59.40"W	<i>Acacia longifolia</i>	0	0
Km 17	40°50'16.30"N, 8°41'9.44"W	<i>Acacia longifolia</i>	0	0
Km 18	40°49'41.17"N, 8°41'21.39"W	<i>Acacia longifolia</i>	0	0
Km 19	40°49'12.68"N, 8°41'30.33"W	<i>Acacia longifolia</i>	0	0

cont.

Localities	Coordinates	Disturbance type	Available área (%)	Density of <i>J. maritima</i> ind*m ⁻² (mean ± SE)
Km 20	40°48'40.41"N, 8°41'41.73"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	51.33	0.54 ± 0.24
Km 21	40°48'8.43"N, 8°41'51.70"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	38.87	0.04 ± 0.04
Km 22	40°47'35.37"N, 8°42'4.52"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	61.24	0.07 ± 0.07
Km 23	40°47'3.79"N, 8°42'15.78"W	<i>Acacia longifolia</i>	48.05	0.25 ± 0.13
Km 24	40°46'36.90"N, 8°42'21.98"W	<i>Acacia longifolia</i>	50.90	0.61 ± 0.37
Km 25	40°46'5.98"N, 8°42'32.25"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	74.91	0.25 ± 0.19
Km 26	40°45'25.61"N, 8°42'46.45"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	76.90	2.36 ± 0.91
Km 27	40°44'57.06"N, 8°42'55.99"W	<i>Acacia longifolia</i> ; <i>Carpobrotus edulis</i>	18.87	2.89 ± 2.00
Km 28	40°44'27.55"N, 8°43'6.02"W	<i>Carpobrotus edulis</i> ; <i>Acacia longifolia</i> ; Cement road	61.58	8.60 ± 2.76

Table 2. Characterization of each study area according to the percentage of available area for the growth of *Jasione maritima* and to the respective disturbance level.

Localities	Available area (%)	Disturbance level
km 27	18.87	High
km 1	20.95	High
km 15	23.18	High
km 3	38.65	High
km 21	38.86	High
km 23	48.05	Medium
km 24	50.9	Medium
km 20	51.33	Medium
km 22	61.24	Medium
km 28	61.58	Medium
km 25	74.91	Low
km 26	76.9	Low
km 2	78.4	Low
km 0	79.51	Low
km 14	100	Low

Floral visitor's assemblages

The assemblage of floral visitors of *Jasione maritima* was assessed by direct observations made in ten patches of 2.25 m² (1.5m × 1.5m) (Fig.1b), in each of the 15 sites where populations of *J. maritima* were detected. The observations were performed during the flowering peak of 2017 (from June to July), on sunny and low to moderate windy days. The observer was positioned at approximately 1 m from the patch, with small range binoculars, being able to monitor all floral visitors without interfering with their foraging activity. Visits were recorded during 15 min census at different times of the day (from 0900 to 1800 h GMT). A total of 386 censuses were performed, corresponding to a total 96.5 h of observations. In each patch the following parameters were registered: (1) number of open inflorescences per individual plant within the patch; (2) identity and number of each flower visitor that interacted with the reproductive organs of *J. maritima*; (3) number and sequence of flowers visited per patch by each flower visitor. One specimen of each insect type was collected for further identification to the

lowest taxonomic level possible. The frequency of interaction was calculated for 15 min by multiplying insect abundance (number of insects per 15 min) by flower visitation rate (number of flowers visited per 15 min) (Castro et al. 2013; Herrera 1989).

Reproductive success and pollen limitation

To determine the effect of habitat disturbance on the reproductive success of *J. maritima* and to evaluate if the reproductive success of *J. maritima* was limited by pollination services, the following treatments were applied in each site, during the flowering period of 2017: (1) open pollination (control), i.e. flowers without treatment, left open for natural levels of pollination; (2) supplementary pollination, i.e. flowers pollinated with fresh pollen from five different genotypes of *J. maritima* and left open to natural levels of pollination. For this, in each site, thirty individuals were arbitrarily selected to receive both treatments, with one inflorescence being marked to receive natural levels of pollination, while another was labelled to receive pollen supplementation. Since *J. maritima* exhibits secondary pollen presentation (Fig. 3a), we had to assure that the supplemented flowers were fully receptive. Thus, inflorescences with the exterior row of receptive flowers (visible by the lack of pollen and bilobed stigmatic surface) (Fig. 3b) were selected for pollen supplementation. Only this row was considered in the treatment due to time constraints to perform pollinations in all the study sites. Pollen supplementation was made by gently rubbing the inflorescence with inflorescences from distinct inflorescences collected in five different genotypes.

When mature but prior to dehiscence, infructescences were collected for estimation of the number of fruits and seeds. In the laboratory, fruit set (percentage of flowers that developed into fruits) and seed set (number of viable seeds per fruit) were quantified for each individual.

In order to quantify the reproductive success of each individual of *J. maritima* in each population, overall sexual fitness was quantified by multiplying seed set by fruit set.

To estimate pollen limitation, only the exterior row of fruits of the infructescences from both control and supplement treatments was used. Moreover, for each individual of *J. maritima*, proportion of pollen limitation (PPL), a measure of the extent of reproductive success limitation by insufficient pollen delivery, was calculated using the formula:

$$\text{PPL} = C/S$$

where C is the overall sexual fitness of the control plants and S is the overall sexual fitness of the supplemented plants. When PPL values are closer to 1, this means the plants are less pollen limited.



Figure 3. *Jasione maritima* inflorescences. a) secondary pollen presentation (male phase); b) inflorescence with the first flower opened; c) fully receptive stigmas (bilobed stigmatic surfaces).

Network parameters

Fifteen quantitative individual-based plant-floral visitor interaction matrices (one for each population) were built (Appendix 5) using the number of visits per unit time as link weight (Traveset et al. 2017; Castro Urgal et al. 2012). *Jasione maritima* individuals were classified according to the number of open inflorescences and each phenotype was considered a node. The network represents the potential mating events between each phenotype of the plant population and each pollinator species.

In order to compare the structure of pollination networks in the three disturbance levels, the following network-level descriptors were calculated (Dormann et al. 2009): (1) weighted connectance, the fraction of possible links divided by the number of species

in the network (Tylianakis et al. 2007); (2) weighted nestedness (WINE), a measure of the extent to which the interactions are hierarchically arranged around a core of generalist interactions (Galeano et al. 2009); (3) interaction evenness, based on Shannon diversity, reflects the uniformity of the interactions between species at network level and uses the total number of realised interactions as the denominator (Tylianakis et al. 2007; Bersier et al. 2002); (4) network specialization (H_2'), a measure of the selectivity of interaction partners of the network, derived from Shannon entropy; this metric is very reliable because it is not affected by network size and sampling effect (Blüthgen et al. 2006); (5) pollinator niche overlap, a measure of the overlap of plant phenotypes pollinated by the various pollinators; (6) plant niche overlap, a measure of the overlap of pollinator species visiting plant phenotypes; (7) plant robustness, a metric quantifying how much pollinator community can withstand the random loss of plant phenotypes; robustness assumes that primary extinctions (loss of species from one level of the network) will trigger the extinction of species on other levels that depend on them (secondary extinctions); this can be represented by an attack tolerance curve (ATC), characterized by its slope (extinction slope), as proposed by Memmott et al. (2014) or by the area under the curve (AUC) of extinction, as proposed by Burgos et al. 2007; (8) pollinator robustness, a reflection the resilience of the plant population to the random loss of pollinators (Memmott et al. 2004); has the same assumptions of plant robustness (9) generality, the mean number of preys per predator (Tylianakis et al. 2007; Bersier et al. 2002); in the present work adapted to the mean number of plant phenotypes per pollinator ; and (10) vulnerability, the number of predators per prey (Tylianakis et al. 2007; Bersier et al. 2002); in the present work adapted to mean number of pollinators per plant phenotype. Moreover, three species level descriptors for plants and for pollinators were calculated: (1) normalised degree for plants and for pollinators, the number of pollinator species visiting each plant phenotype and the number of plant phenotypes visited by each pollinator, respectively, divided by the number of possible interaction partners; characterizes the species network position and gives an estimation of how generalist or not a species is (Emer et al. 2016; Martín González et al. 2010); (2) species strength for plants and for pollinators is the sum of dependencies, i.e. is a measure of plant phenotype's importance for the pollinator community and a measure of pollinator species' importance for plant population, respectively (Bascompte et al. 2006); and (3) specialization (d') for plants and for pollinators, a measure of the level of specialization of each plant phenotype and of each pollinator species, respectively, having in account the available resources provided by

interaction partners; increases with the departure from a random visitation frequency based exclusively on species abundances; this metric is very reliable once it is not affected by sampling intensity and network size (Blüthgen et al. 2006).

Regarding network analyses, to overcome sampling effort differences that could bias network structure, network level descriptors were tested against networks generated by null models (Costa et al. 2015; Vásquez & Aizen 2003), namely Patefield's null model (Patefield 1981), using standardized z-scores ($z = [\text{observed} - \text{null mean}] / \text{null } \sigma$). Moreover, due to presence of decimal values in the matrix, each network was standardized dividing its link weight by the lowest non zero link weight value of the matrix, rounded to the nearest integer. Thus, for each study site, observed network level metrics were corrected using the means from 1000 networks generated by Patefield's null model (Ballantyne et al. 2017).

Statistical analysis

All statistical analyses were performed in R version 3.5.0 (R Core Team 2018).

Species accumulation curves, for each study site, were calculated in order to evaluate sampling completeness of pollinator species (*vegan* package). The minimum estimated asymptotic richness of pollinators was calculated using the non-parametric estimator Chao 2 (Chao 1987). This non-parametric estimator was selected for being robust to reduced sample size, being more reliable than other estimators (Colwell et al. 1994; Walther & Moore 2005). Percentage of sampling completeness was calculated as the observed number of species divided by the estimated number of species (table).

The effect of habitat disturbance on overall sexual fitness, frequency of interaction, proportion of pollen limitation (PPL) and number of individuals of *J. maritima*, was analysed using linear mixed models (LMM; package *lme4* and *lmerTest*), with disturbance level as fixed factor and latitude as random factor. The effect of habitat disturbance on the number of open inflorescences of *J. maritima* per patch was analysed by means of a generalized linear mixed model (GLMM; package *lme4* and *lmerTest*), adjusted to a Gamma distribution, and using latitude as random factor. Regarding frequency of interaction analyses, two extreme values, related to the frequency of

interaction of ant species during two observation periods, were tested as outliers and were removed in order to meet the assumptions of normality and homoscedasticity.

Differences among disturbance levels on pollinator species richness were analysed using a generalized linear model (GLM). Latitude was included as covariate and pollinator species richness was adjusted to a Poisson distribution.

The overall effect of pollen supplementation on overall sexual fitness was analysed using linear mixed models (LMM, package *lme4* and *lmerTest*), including treatment as fixed factor and latitude as random factor. Furthermore, differences between pollination treatments were also assessed for each study site using linear models (LM).

To evaluate the effect of disturbance level on weighted nestedness (WINE), plant robustness and pollinator niche overlap a general linear models (LM) with latitude as covariate was used. The effect of disturbance level on weighted connectance, network specialization (H_2'), pollinator robustness, plant niche overlap, interaction evenness, generality and vulnerability were tested using a generalized linear models (GLM) with latitude as covariate; weighted connectance, pollinator robustness, plant niche overlap and generality were adjusted to an inverse link function; network specialization was adjusted to a log link function.

Differences in plant degree, plant species strength and plant normalised degree between disturbance levels were tested using independent generalised linear mixed models (GLMM), including as random factors latitude, to control for the potential variability associated with the geographic location, and species, to account for differences in species composition between location and avoid pseudo; plant degree was adjusted to a Poisson distribution with a log function; plant species strength and plant normalised degree were adjusted to a log link function. The effect of disturbance level on pollinator species strength was analysed by means of a linear mixed model (LMM), with latitude as random factor. When assessing the effects of habitat disturbance on plant and pollinator specialization, pollinator degree and pollinator normalised degree, the assumptions of normality of the residuals and homoscedasticity for standard regressions were not achieved, due to the presence of extreme values. To overcome the presence of these outliers, these metrics were analysed using a robust linear mixed model (RLMM, *robustlmm* package), which down-weights these influential points on the general trend of

the data and provides better estimates of the regression parameters and their standard errors (Koller 2016; Koller 2013; Cantoni et al. 2006).

Both network and species level metrics were calculated using the *bipartite* package for R (Dormann et al. 2009; Dormann et al. 2008).

Regarding standard regressions, residuals were plotted and analysed for departures from normality and homoscedasticity and response variables were transformed to ensure the best fit to the assumptions of standard regression. The Akaike information criterion (AIC) was also used to select the model with the best fit. Transformations of the response variables that were performed in order to fulfil the assumptions of normality and homoscedasticity are depicted in Appendix 2.1; 2.3; 2.4; 2.5 and 2.6. When data transformation was performed or when data was unbalanced, differences were tested using least square means (package *ls means*), and results were then back-transformed.

When significant differences were found, pairwise differences between disturbance levels were analysed using Tukey tests (R package *multcomp*).

The significance of all models performed is represented in Appendix 2.1, 2.2, 2.3, 2.4, 2.5 and 2.6, depending on the response variable that was being analysed.

Pearson correlation analysis was performed in order to evaluate the correlation between the following variables: frequency of interaction, number of individuals of *J. maritima* per monitoring patch, pollinator richness, overall sexual fitness and proportion of pollen limitation.

Results

Effect of habitat disturbance on floral visitors of *Jasione maritima*

A total of 1336 insects, belonging to 115 morphospecies, were observed visiting the flowers of *J. maritima*. Floral visitors included ants, wasps and bees [Hymenoptera (36.5%), 42 morphospecies]; flies [Diptera (37.4%), 43 morphospecies]; beetles [Coleoptera (10.4%), 12 morphospecies]; and butterflies [Lepidoptera (15.7%), 18 morphospecies] (Fig.5).

Pollinators were identified to the lowest taxonomic level possible: species (40.9%), genus (43.5%), family (6.1%), superfamily (1.7%) and order (7.8%). Hereafter, all these will be referred to as “species” for simplicity (see Appendix 1 for a detailed species list).

Overall, 3124 interactions between *J. maritima* and its visitors were recorded across the 15 sites. The vast majority of the interactions were by Hymenoptera, which accounted for 56.3% of the interactions (1760 interactions). Diptera constituted 29.4% of the interactions (918 interactions), Coleoptera accounted for 11.5% of the interactions (360 interactions), followed by Lepidoptera with 2.8% of the interactions (86 interactions).

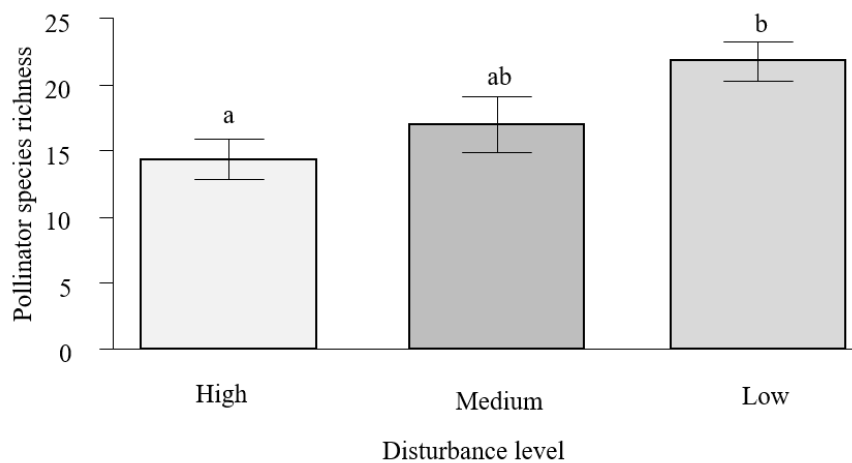
At the population level, *J. maritima* pollination system is very generalized. The observed pollinator species richness ranged from 11 to 25 species, whereas the abundance of pollinator ranged between 32 and 176 individuals (Table 3).

Sampling completeness ranged between 31.4% and 89.6% (Table 3). Nevertheless, sampling effort reached good values, with nine out of the 15 studied sites presenting values of sampling completeness higher than 60.0%. Moreover, the species accumulation curves of the vast majority of the sites sampled reached the asymptotic plateau.

Pollinator richness was significantly affected by habitat disturbance ($\chi^2 = 7.843$, 2 df, $P = 0.02$), but a significant difference was only present between high and low disturbance levels (14.4 ± 1.54 vs 21.8 ± 1.46 , respectively; Tukey test, $P=0.02$; Fig. 4). Medium disturbance level habitats showed intermediate values (mean \pm SE; 17 ± 2.07).

Table 3. Characterization of each studied area, according to disturbance level, pollinator richness, pollinator abundance and percentage of sampling completeness

Localities	Disturbance level	Pollinator richness	Pollinator abundance	Sampling completeness (%)
km 0	Low	18	158	31.35
km 1	High	13	64	83.60
km 2	Low	25	176	89.60
km 3	High	13	84	35.56
km 14	Low	22	69	78.91
km 15	High	20	124	65.98
km 20	Medium	15	47	75.99
km 21	High	11	134	57.59
km 22	Medium	25	88	72.19
km 23	Medium	16	51	44.82
km 24	Medium	16	85	73.46
km 25	Low	25	96	62.02
km 26	Low	19	72	86.68
km 27	High	15	56	39.26
km 28	Medium	13	32	59.72

**Figure 4.** Pollinator species richness (mean \pm SE) in the three disturbance levels studied (high disturbance level; medium disturbance level and low disturbance level). Significant differences among means of disturbance levels are indicated by different letters ($P < 0.05$).

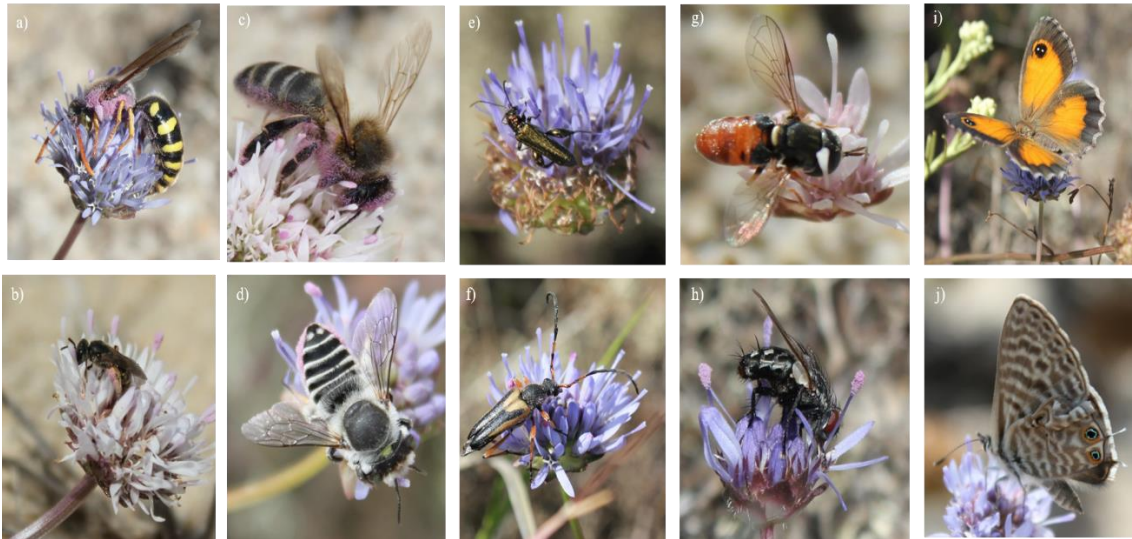


Figure 5. Examples of pollinators of *Jasione maritima* a) *Stizus ruficornis*; b) *Lasioglossum* morphospecies 1; c) *Apis mellifera*; d) *Megachile leachella*; e) *Oedemera flavipes*; f) *Paracorymbia stragulata*; g) *Paragus* morphospecies 1; h) *Sarcophaga* morphospecies; i) *Pyronia cecilia* ; j) *Leptotes pirithous*

Effect of habitat disturbance on population density of *Jasione maritima*

Regarding the effect of habitat disturbance on the population size of *J. maritima*, significant differences were observed ($\chi^2 = 10.405$, 2 df, $P = 0.006$). Low disturbance level habitats presented a significantly higher number of individuals of *J. maritima* per square meter than medium and high disturbance levels (Tukey test: $P = 0.02$ and $P = 0.02$, respectively) (Fig. 6), namely low disturbance level habitats presented 75.4% and 72.9% more individuals, than medium and low disturbance level habitats, respectively.

Effect of habitat disturbance on floral resources

Habitat disturbance significantly affected the number of open inflorescences of *J. maritima* per patch of pollinator monitoring ($\chi^2 = 13.109$, 2 df, $P = 0.001$). A significantly higher number of open inflorescences was obtained in low disturbance habitats when compared to the medium and high disturbance level habitats (Tukey test: $P = 0.002$ and $P = 0.01$) (Fig. 7).

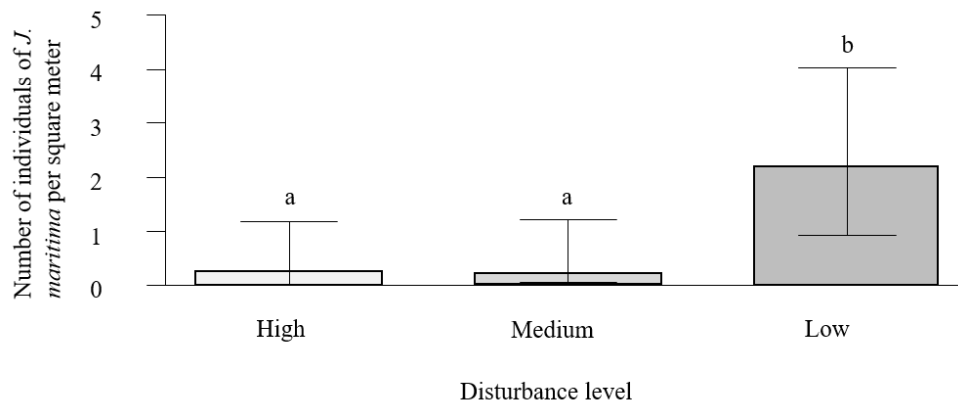


Figure 6. Number of individuals of *Jasione maritima* per square meter across the three different disturbance levels studied. Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Significant differences among least-square means of disturbance levels are indicated by different letters ($P < 0.05$).

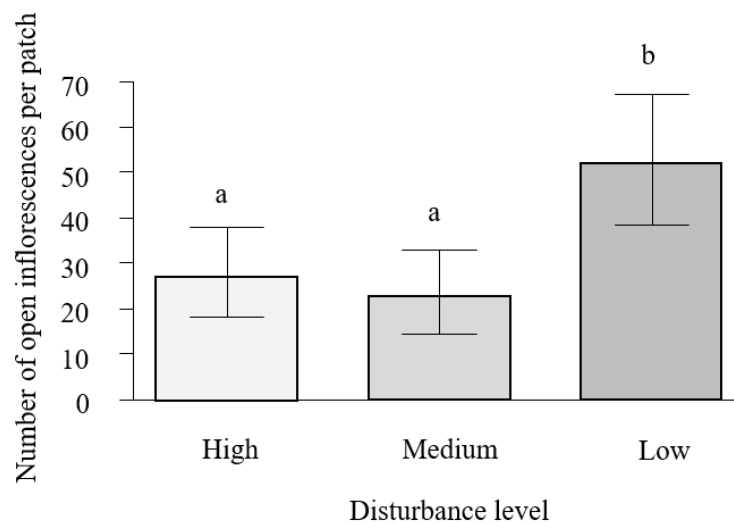


Figure 7. Number of open inflorescences of *Jasione maritima* per patch across the three different disturbance levels studied. Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Significant differences among least-square means of disturbance levels are indicated by different letters ($P < 0.05$).

Effect of habitat disturbance on the frequency of interaction

Habitat disturbance significantly affected the frequency of interaction between *J. maritima* and its floral visitors ($\chi^2 = 16.831$, 2 df, $P < 0.001$), but significant differences were only obtained between habitats with medium and low disturbance levels (Tukey test: $P < 0.001$). Sites with low disturbance level presented the highest frequency of interaction, followed by sites of high disturbance, and medium disturbance levels (Fig. 8).

In populations with high and low disturbance levels, bees were the most frequent visitors, followed by flies. In low disturbance habitats, bees accounted for more than 50.0% of the frequency of interaction, while in high disturbance habitats they only represented 28.2% of this frequency (Table 4). In populations with medium disturbance, flies and wasps were the most frequent floral visitors, representing 47.6% and 21.7% of the frequency of interaction, respectively (Table 4).

The frequency of interaction of all *Jasione maritima* floral visitors is presented in Appendix 4.

Effect of habitat disturbance on the reproductive success of *Jasione maritima*

The fitness of *J. maritima* measured as number of seeds per flower (overall sexual fitness) was significantly affected by habitat disturbance ($\chi^2 = 8.784$, 2 df, $P = 0.012$). Reproductive fitness decreased with increased disturbance, although, only populations characterized by low and high disturbance levels presented significant differences in the overall sexual fitness (Tukey test: $P = 0.011$). The highest values of sexual fitness were observed in populations with low disturbance levels and the lowest in populations with high disturbance levels. Low disturbance level habitats produced on average 41.67% more seeds per flower than high disturbance level habitats (Fig. 9). Populations with medium disturbance levels presented once again intermediate values.

Table 4. Mean frequency of interaction (\pm standard error) for each pollinator functional group observed (ants, wasps, bees, flies, beetles, butterflies), according to the different disturbance levels.

	High Disturbance		Medium Disturbance		Low disturbance	
	Mean (\pm SE)	%	Mean (\pm SE)	%	Mean (\pm SE)	%
Ants	1.57 (\pm 0.79)	10.5	0.90 (\pm 0.70)	12.5	4.26 (\pm 1.60)	12.5
Wasps	2.23 (\pm 0.93)	14.9	1.57 (\pm 0.50)	21.7	0.35 (\pm 0.12)	1.03
Bees	4.22 (\pm 0.88)	28.20	0.51 (\pm 0.15)	7.05	19.48 (\pm 3.71)	57.13
Flies	3.88 (\pm 0.80)	25.91	3.45 (\pm 0.61)	47.61	5.97 (\pm 1.22)	17.50
Beetles	2.97 (\pm 0.83)	19.85	0.63 (\pm 0.11)	8.67	3.63 (\pm 1.41)	10.65
Butterflies	0.09 (\pm 0.04)	0.62	0.18 (\pm 0.06)	2.48	0.42 (\pm 0.10)	1.22

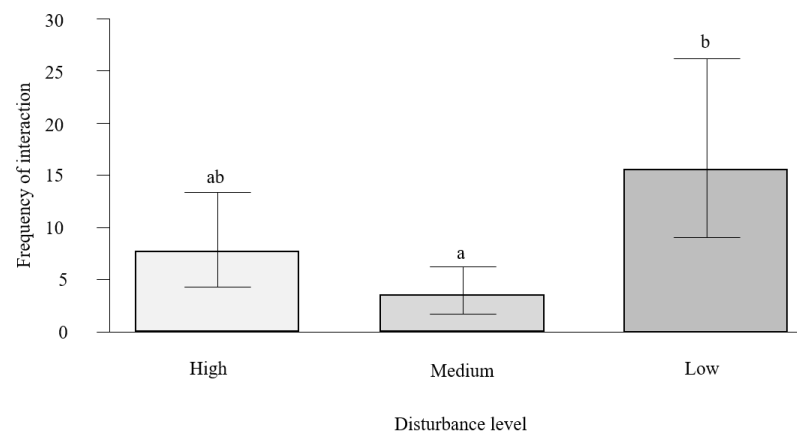


Figure 8. Frequency of interaction (insect abundance \times flower visitation rate) of *J. maritima* for the three disturbance levels studied (high disturbance; medium disturbance; low disturbance). Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Significant differences among least-square means are indicated by different letters ($P < 0.05$) between disturbance levels.

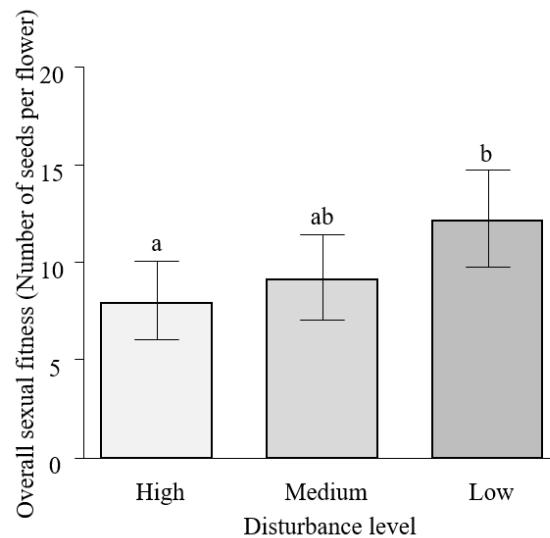


Figure 9. Reproductive success (overall sexual fitness) of *Jasiona maritima* for the three disturbance levels studied (high disturbance; medium disturbance; low disturbance). Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Significant differences among least-square means of disturbance levels are indicated by different letters ($P < 0.05$).

Effect of habitat disturbance on pollen limitation

Strong significant differences between open pollinated and pollen supplemented flowers were observed in *Jasiona maritima* ($\chi^2 = 123.8$, 1df, $P < 0.001$). At the population level, in 13 of the sites studied, the flowers that were pollen supplemented had a significantly higher sexual fitness, i.e., there was an increase in the number of seeds per flower, than open pollinated flowers (Fig 10.; Appendix 2.3). In two populations (km 14 and km 25), although supplemented flowers had a greater sexual fitness than open pollinated ones, no significant differences were observed between the two pollination treatments (Fig 10.; Appendix 2.3).

Habitat disturbance had a significant effect on the proportion of pollen limitation ($\chi^2 = 7.4081$, 2 df, $P = 0.025$). Overall, the decrease in the disturbance level resulted in an increase in the proportion of pollen limitation. However, significant differences were only observed between populations in habitats with low and high disturbance level (Tukey test, $P = 0.02$) (Fig. 11), with habitats with low disturbance exhibiting lower pollen limitation values than habitats with high disturbance levels. Habitats with medium disturbance level, showed intermediate values.

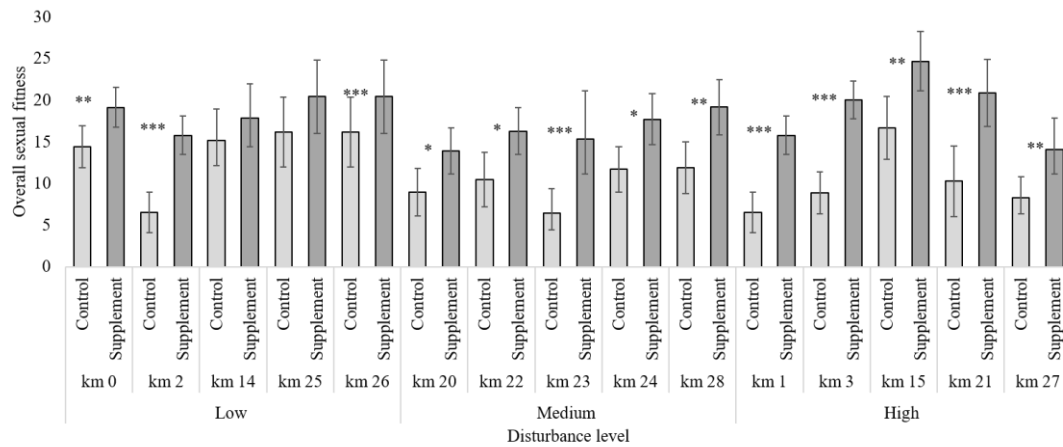


Figure 10. Pollen limitation in the populations of *Jasione maritima* studied. Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Pollination treatments: control – open pollinated flowers; supplement – open pollinated flowers supplemented with outcrossing pollen. Populations: km 0, km 1, km 2, km 3, km 14, km 15, km 20, km 21, km 22, km 23, km 24, km 25, km 26, km 27, km 28; Disturbance level – low disturbance, medium disturbance, high disturbance; asterisks indicate significant differences between treatments within populations after LM analyses: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

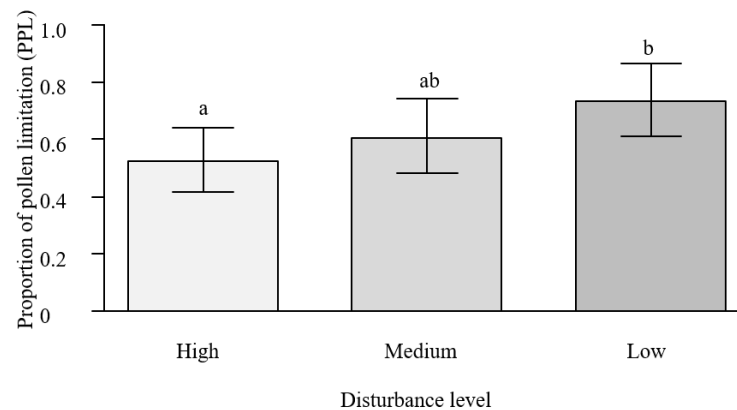


Figure 11. Proportion of pollen limitation of *Jasione maritima* for the three disturbance levels studied (high disturbance; medium disturbance; low disturbance). Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals. Significant differences among least-square means of disturbance levels are indicated by different letters ($P < 0.05$).

Correlation between plant and pollinator variables

There was a significant positive relationship between pollinator richness and the number of individuals of *J. maritima* per patch of pollinator monitoring ($r = 0.588$, $P = 0.021$). Moreover, the proportion of pollen limitation was also significantly correlated with the number of individuals of *J. maritima* per patch ($r = 0.641$, $P = 0.010$), i.e. an increase in the number of individuals of *J. maritima*, lead to a lower pollen limitation. None of the other correlations between the variables studied were significant (table).

Table 5. Pearson correlation coefficient for comparisons between the variables studied. Significant correlations are highlighted in bold ($P < 0.05$).

Variables	Number of individuals of <i>Jasione maritima</i> per patch	Frequency of interaction	Pollinator richness
Frequency of interaction	$r = 0.200$, $P=0.473$		
Pollinator richness	$r = 0.588$, $P = 0.021$	$r = 0.296$, $P = 0.282$	
Overall sexual fitness	$r=0.495$, $P= 0.060$	$r=0.334$, $P = 0.224$	$r=0.424$, $P=0.115$
Proportion of pollen limitation (PPL)	$r= 0.641$, $P= 0.010$	$r=0.311$, $P=0.259$	$r=0.478$, $P=0.072$

Effect of habitat disturbance on network structure and species metrics

Habitat disturbance had a significant effect on weighted connectance ($\chi^2=9.049$, 2 df, $P=0.01$), interaction evenness ($\chi^2=6.508$, 2 df, $P =0.039$), network specialization (H_2') ($\chi^2=6.993$, 2 df, $P =0.030$) and generality ($\chi^2=9.346$, 2 df, $P =0.009$) (Table 6, Fig. 12). Regarding weighted connectance, interaction evenness and generality, significant differences between disturbance levels were only found between high and low disturbance levels (Tukey test, $P=0.04$ for all the metrics), with habitats with high disturbance level presenting higher values for each one of the metrics (fig 6.). Habitats with medium disturbance level presented intermediate values. Furthermore, habitats with high disturbance level presented a significantly lower specialization of the network, when compared to low disturbance level habitats (Tukey test, $P.< 0.05$).

Habitat disturbance had a marginal effect on vulnerability and plant niche overlap. No significant differences were found between the three habitat disturbance levels regarding weighted nestedness (Appendix 2.4).

Regarding plant and pollinator species strength, normalised degree and specialization (d'), no significant differences were found between the three disturbance levels studied (Appendix 2.5; Appendix 2.6). (table 7; table 8).

Species metrics for each plant and pollinator species are depicted in Appendix 3.1 and 3.2.

Table 6. Z-score (\pm SE) of network level descriptors the three disturbance levels studied. *P* significance values are presented.

Metric	Disturbance level			<i>P</i>
	High	Medium	Low	
Weighted connectance	-11.13 \pm 1.64	-7.91 \pm 2.40	-17.51 \pm 3.21	0.01
Weighted nestedness	-1.46 \pm 0.35	-1.60 \pm 0.87	-3.06 \pm 0.68	0.280
Interaction evenness	-17.07 \pm 3.61	-11.80 \pm 3.36	-26.01 \pm 4.42	0.039
H ₂ ' (Specialization)	17.07 \pm 26.01	11.80 \pm 3.35	26.01 \pm 4.42	0.030
Pollinators Niche overlap	-5.25 \pm 1.50	-4.07 \pm 1.32	-6.85 \pm 0.66	0.559
Plants Niche overlap	-7.14 \pm 0.92	-5.54 \pm 1.44	-9.67 \pm 2.65	0.077
Plants Robustness	-11.44 \pm 3.78	-10.35 \pm 4.08	-9.90 \pm 0.93	0.440
Pollinators Robustness	-11.44 \pm 3.41	-6.25 \pm 1.79	-11.95 \pm 0.99	0.666
Generality	-11.09 \pm 1.38	-8.30 \pm 2.61	-17.53 \pm 3.38	0.009
Vulnerability	-10.51 \pm 2.18	-7.45 \pm 2.26	-15.99 \pm 2.64	0.05

Table 7. Mean (\pm SE) of species level descriptors for the three disturbance levels studied.

Metric	Disturbance level		
	High	Medium	Low
d' - Plants	0.10 \pm 0.02	0.14 \pm 0.03	0.06 \pm 0.01
Normalised degree - Pollinators	0.28 \pm 0.03	0.31 \pm 0.02	0.24 \pm 0.02
d' - Pollinators	0.11 \pm 0.02	0.10 \pm 0.02	0.12 \pm 0.02

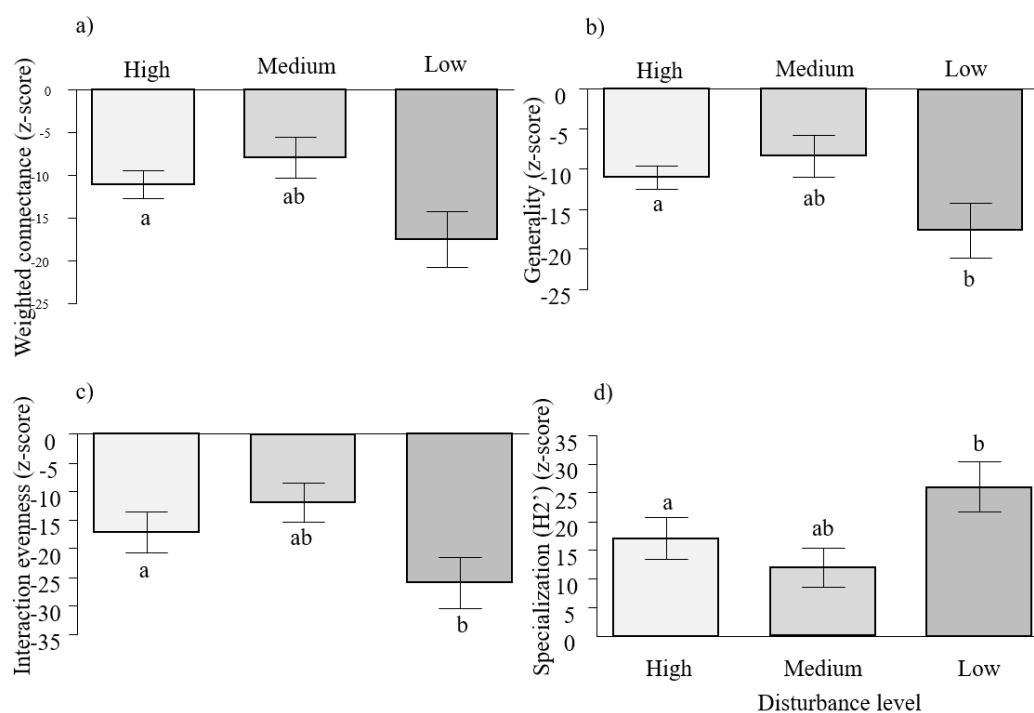


Figure 12. Network level descriptors (z-score) for the three disturbance levels studied: (a) weighted connectance; (b) generality; (c) interaction evenness; and (d) network specialization (H_2'). Significant differences among means are indicated by different letters ($P < 0.05$) between disturbance levels.

Table 8. Species level descriptors for the three disturbance levels studied. Values are given as model-adjusted back-transformed least-square means and 95% confidence intervals

Metric	Disturbance level					
	High		Medium		Low	
	Mean	95% C.I.	Mean	95% C.I.	Mean	95% C.I.
Species strength - Plants	0.67	0.40-0.99	1.05	0.60-1.64	0.99	0.58-1.53
Normalised degree - Plants	0.18	0.14-0.22	0.19	0.15-0.24	0.18	0.14-0.22
Species strength - Pollinators	0.27	0.17-0.44	0.20	0.13-0.32	0.22	0.14-0.34

Discussion

Jasione maritima presents a generalized pollination system, with its flowers being visited by 115 species from distinct functional groups. Although there was a large variation in the composition of the floral visitor's community, its structure was similar across all the populations, with a few abundant species and a high number of rare species. Moreover, this diverse array of flower visitors was mainly composed by Hymenoptera and Diptera. Despite the fact that plant species vary widely in their degree of specialization, generalization is a prevalent characteristic of pollination systems, as the vast majority of plant species are pollinated by several animal species of different taxa (Gómez et al. 2007; Waser et al. 1996; Herrera 1996), with a diverse morphology, behaviour and size. This generalization is expected to confer resilience to the plant community from changes in the pollinator's assemblages, buffering against the loss of pollinators (Morris 2003). It is worth noticing that this endangered endemic species is self-incompatible and, thus, it completely relies on pollinators for its successful reproduction, being particularly vulnerable to the loss of pollinators due to habitat disturbance. Consequently, the increasing urbanization and spreading of invasive plant species in the Portuguese dune system can lead to the decline of the pollinator fauna of *J. maritima*, and compromise the persistence of *J. maritima* populations.

Although the effects of habitat loss and fragmentation depend on a combination of species specific traits (Henle et al. 2004), fragmented area is considered a key factor in determining the persistence of plant and pollinator populations, since smaller patches commonly contain fewer individuals and species than larger ones (Hagen et al. 2012; Fahrig 2003; Bender et al. 1998; McArthur & Wilson 1967). Indeed, decreases in pollinator species richness due to smaller patches created by habitat loss and fragmentation have been demonstrated by several authors (e.g. Blaauw & Isaacs 2014; Öckinger et al. 2010; Aizen & Feinsinger 1994). Thus, as expected, habitat disturbance affected the richness of *J. maritima* floral visitors, with habitats with low disturbance level presenting a significantly higher number of pollinator species than habitats with high disturbance level. Larger habitat patches are structurally more heterogeneous and usually can support larger communities of pollinators, by presenting higher availability and quality of nesting sites, nesting resources (Hopfenmüller et al. 2014; Potts et al. 2005) and food resources (pollen and nectar) due to a higher floral abundance and diversity in these areas (Hopfenmüller et al. 2014; Blaauw & Isaacs 2014). For example, floral resource availability is considered to be the major driver of population abundance and

community diversity of bees (Roulston & Goodell 2011). Regarding the abundance of individuals of *J. maritima*, low disturbance level habitats presented significantly higher densities than the other two disturbance levels. Nevertheless, in the 15 populations studied, during the flowering peak of *J. maritima* this plant was the main floral resource for the pollinator community, given that, with just a few exceptions, there were no other co-flowering plants. This extreme dependence on *J. maritima* for nutrition during this period also highlights the importance of *J. maritima* for the maintenance of the pollinators community.

The abundance of *J. maritima* in each level of habitat disturbance is also reflected in its attractiveness to pollinators, with habitats with low disturbance level presenting a significantly higher number of open inflorescences per patch than the other disturbance levels. Moreover, pollinator richness is correlated with the number of individuals of *J. maritima* per patch and with the number of open inflorescences. These findings support the consensus that smaller populations are less attractive or less apparent to pollinators than larger populations, which is fundamental in determining not only the diversity of pollinators in a particular area, but also the patterns of pollen flow (Sih & Baltus 1987). Thus, increased floral density attracts more pollinators and may increase flower visitation rates (e.g. Buide 2006). However, when analysing the effect of habitat disturbance in the frequency of interaction, the results were not so straightforward. The frequency of interaction in habitats with high disturbance level was similar to that in habitats with low and medium disturbance levels, but significant differences were detected between medium and low disturbance levels. Furthermore, no correlation between frequency of interaction and pollinator richness was found. This result could be explained by the fact that in low disturbance habitats there are few pollinators, but floral resources are also scarce, so to assure their energy demands, pollinators would have to visit more flowers, increasing the frequency of interaction in these areas. Similar results were observed in a study conducted by Campbell & Husband (2007) where rates of insect visitation increased with decreasing population size of the self-incompatible plant *Hymenoxys herbacea*.

The present study shows that habitat disturbance influences the sexual fitness of *J. maritima*, as populations from low disturbance level habitats presented a higher number of seeds per flower than populations from high disturbance level habitats. The reduction in the sexual fitness of *J. maritima* is consistent with other studies that document decreases in the reproductive fitness of self-incompatible plants due to habitat loss and

fragmentation (e.g. Steffan-Dewenter & Tschardtke 1999, Moody-Weis & Heywood 2001, Jacquemyn et al. 2002). In a review by Ghazoul (2005), the author showed that, in 12 out of 16 studies, small populations of self-incompatible plants had lower fitness than large ones. Although seed and fruit set can be influenced by many ecological and genetic factors (Campbell 2007; Caruso et al. 2005), pollen limitation is one of the most important factors influencing sexual fitness in plants (Knight et al. 2005; Ashman et al. 2004), and is considered one of the main causes for the reduction of plant fitness in fragmented habitats (Aguilar et al. 2006). Knight et al. (2005) reviewing 482 studies on fruit set concluded that, in 63% of them, species presented pollen limitation at some sites or years. Indeed, the pollen supplementation experiment showed that *J. maritima* plants were strongly pollen limited at the regional level, with plants supplemented with outcross pollen presenting a significantly higher fitness when compared with control plants. However, pollen limitation can vary temporally (e.g. Santranderu & Lloret 1999) and spatially (e.g. Knight 2003) within the same species, and *J. maritima* was not an exception, given that two populations from the habitats with low disturbance level did not present pollen limitation. Furthermore, habitats with low disturbance level presented lower pollen limitation when compared to habitats with higher level of disturbance. Our study shows that one of the major factors leading to pollen limitation in *J. maritima* is the loss and fragmentation of the habitat that affects plant-pollinator interactions and consequently affects the sexual fitness of its individuals. The decline in the sexual fitness of *J. maritima* appeared to be correlated with an increase in pollen limitation, due to habitat disturbance.

Despite the influence of habitat disturbance in the pollination system of *J. maritima*, it is puzzling that there was no correlation between frequency of interaction and pollinator species richness or plant fitness related parameters (sexual fitness and proportion of pollen limitation). Pollen limitation is a consequence of the reduction, not only in quantity but also in quality, of the pollen deposited on stigmas (Wilcock & Neiland 2002; Aizen & Harder 2007). Moreover, successful pollination depends on many factors, such as number of flowers, distance between plants, plants breeding system, genetic diversity, pollinator diversity and efficiency, pollinator movement and pollinator diet breadth (Hadley & Betts 2012; Kremen et al. 2007; Ghazoul 2005). Thus, in order to understand the differences in frequency of interaction and reproductive success of *J. maritima* in the three disturbance levels studied, the spatial distribution of individuals of

J. maritima and the distance between conspecific plants should have also be taken in account. *Jasione maritima* individuals in most populations are not evenly distributed in the dune system, but rather occur in clusters. This spatial distribution is even more pronounced in high disturbance level habitats, where the available area is scarce and the individuals are extremely clustered. Although plants spaced more closely together usually set more seeds than more dispersed plants (Kunin 1997), in high disturbance habitats, most of the individuals may be siblings or genetically closely related, and even a moderate frequency of interaction may lead to excessive deposition of conspecific, poor-quality pollen (incompatible pollen, i.e. geitonogamous or genetically related pollen in self-incompatible species), causing stigmatic clogging and consequently a decrease in the reproductive success of the population. In medium disturbance habitats, clusters of *J. maritima* individuals are more spaced in the dune system, and despite the lower frequency of interaction, pollinators may disperse better quality pollen, increasing the reproductive success in these habitats. The low disturbance habitats hold larger populations of *J. maritima* and the high frequency of interaction allows, for more diverse and evenly frequent mating types, and therefore the vast majority of the pollen received will be compatible, increasing the reproductive fitness in these habitats.

The fact that pollinator richness was not correlated with overall sexual fitness may be related with the efficiency of different species in removing and transporting pollen to conspecific stigmas. In generalized pollination systems, the pollination effectiveness often varies among different flower visitors, which has consequences for the plant reproductive fitness (Castro et al. 2013; Larsson et al. 2005). Pollinators differ not only in the quantity of high-quality pollen they deposit (success through the female component), but also on the quantity of pollen they remove from flowers (success through the male component), whereby the effectiveness of a flower visitor depends on both deposition and removal ratios of the pollen (ability to touch anthers, carry pollen and contact stigmas), in the distance it travels and on foraging behaviour (e.g. whether or not the visitor moves between conspecific flowers) (Kremen et al. 2017; Ollerton 2017; Herrera 1987). Moreover, some visitors are larcenists, behaving as robbers, i.e. pierce flowers to extract nectar rather than legitimately entering them, or behaving as “thieves”, i.e. entering flowers but transferring little or no pollen (Irwin et al. 2001). In low disturbance level habitats, bees accounted for 57.13% of the frequency of interaction, which may also explain the higher reproductive success of these populations. Bees are

hairy and are the only group of insects that rely totally on nectar and pollen for both adult and larval nutrition (Willmer 2011), being considered very efficient pollinators in most of the pollination systems, even though efficiency can vary between species (Larsson et al. 2015). For example, Klein et al. (2003) showed that fruit set of *Coffea arabica* is highly dependent of bee diversity. In medium disturbance level habitats, the main pollinator group was completely different. Bees had a much lower frequency of interaction (7.05%) and flies accounted for 47.61% of the frequency of interaction. Although flies have been acknowledged as efficient pollinators of several wild and crop plants (Ollerton 2017, Jauker & Wolters 2008, Kearns 2001), they might not be the most efficient pollinators of *J. maritima*. Therefore, future studies should have in account the abundance and efficiency of different species and functional groups, to evaluate which pollinators are more relevant for the reproductive outcome of *J. maritima*.

Interactions between pollinators and the different phenotypes of *J. maritima* were more uniformly distributed in habitats with high disturbance level than in habitats with low disturbance level. High disturbance level habitats, presented a higher interaction evenness, thus a more homogeneous distribution of interactions within the networks. This pattern is consistent with a previous study that demonstrated that along a gradient of urbanisation, landscape context influences interaction evenness, with interactions in plant-pollinator networks showing a more homogeneous distribution in urban areas when compared to suburban and agricultural areas (Geslin et al. 2013). Nevertheless, this result is a little bit counter intuitive since it has been shown that interaction evenness is negatively related with habitat disturbance, promoting an uneven community with the dominance of some interactions (Tylianakis et al. 2007). This unexpected pattern in high disturbance level habitats can be associated to a response to the scarcity of the floral resources, leading to a overexploitation of them and consequently to a evenly distribution of the interactions. A higher evenness of interactions is related to a higher generality and lower network specialization, contributing to increase the overlap of visited species (even though plant niche overlap was only marginally significant). Although vulnerability was only marginally significant, high and medium disturbance levels exhibited a higher number of pollinators per plant phenotype when compared to low disturbance level habitats. Weighted connectance was also significantly higher in high disturbance level habitats when compared to low disturbance level habitats. The increase of this metric in high disturbance habitats could be related with a decrease in species richness (Soares et

al. 2017; Bosch et al. 2009). However, connectance does not exhibit a general pattern of response to the reduction of environmental quality and caution should be taken when analysing this metric (Soares et al. 2017; Heleno et al. 2012).

There is a consensus that more connected and generalised networks [lower network (H_2') and species specialization(d')] are associated with greater functional redundancy and lower mutual dependencies, increasing the resilience of the communities and increasing the robustness to local loss of a certain species (Kaiser-Bunbury et al. 2017;2008). Nevertheless, no significant differences in plant and pollinator robustness were found in the three disturbance levels. Moreover, the greater functional redundancy on high disturbance levels was certainly not expected. However, this can be linked to a network simplification due to increasing proportion of generalist interactions (Soares et al. 2017), with plant and pollinator communities becoming more generalized with the increase in habitat fragmentation, since in these habitats there is an impoverishment in floral resources, and, in order to survive, pollinators will need to spread their pollination activity across more individuals (Xiao et al. 2016; Ashworth et al. 2004). Nevertheless, despite this apparent functional redundancy advantage, there are higher costs for the plant population, associated with the high transference of low-quality pollen by these generalist pollinators, as mentioned before. Moreover, notwithstanding the redundancy of the pollination network, given that the composition of the pollination community is more homogeneous in high disturbance habitats, *J. maritima* could still be at risk of a higher reproductive failure if it relies more on a guild of pollinators that respond similarly to a future anthropogenic effect (Kremen et al. 2017). As acknowledged by Kaiser-Bunbury et al. (2010), anthropogenic actions and ecological processes can result in a selective decline of some of the most important species of the system leading to irreversible negative effects on the plant population, and ultimately to the overall collapse of the plant-pollinator network.

Furthermore, pollinators presented no preferences towards any plant phenotype in the three disturbance levels, which is explained by the fact that there were no differences in the pollinator species importance for the plant population. Moreover, the number of phenotypes visited by each pollinator was not significantly affected by habitat disturbance. This might be related to the heavily clustered distribution of the individuals of *J. maritima*, and in order to maximize their foraging bouts pollinators did not differentiate between phenotypes. Indeed, as acknowledged by Robertson & Macnair

(1995), the size of the floral display, i.e. flower number, may not be related to pollinator attraction, since pollinators appear to use all floral resources in an even manner. Moreover, although larger floral displays are usually related with higher visitation rates and higher deposition of outcross pollen (e.g. Galloway et al. 2002), there are some studies that highlight that the sequence of flower visitation in larger flower displays may lead to an increase in the genetic heterogeneity of the offspring, since it can result in higher self-pollination rates of some flowers and also reduce pollen export per flower (Karron & Mitchell 2012; Karron et al. 2009).

Additionally, future studies should include the interplay of pollination and herbivory (or seed predation) in the reproductive success of *J. maritima*. During seed processing it was possible to observe that many fruits and seeds were completely damaged due to predation by weevils (Coleoptera: Curculionidae) and their larvae. Although they may transfer pollen between inflorescences (possibly with low efficiency rates), the pollination benefit must be very low when compared to the high costs of seed loss by predation, severely decreasing the offspring number (Dalglish et al. 2012).

Besides anthropogenic activities and invasive plant species, another threat that the dune system faces is the invasion by the argentine ant, *Linepithema humile*. This ant species was the only formicidae observed visiting *J. maritima* flowers. *Linepithema humile* is native to South America and has invaded all Mediterranean ecosystems of the world, competitively displacing native ant species where it was introduced (Suarez et al. 2001). Despite only being abundant in some of the populations studied, future studies should evaluate the consequences of this new interaction for *J. maritima*, given that it has been shown in other systems that it can decrease the number of visitors to the flowers, and modify the behaviour of some pollinators (Blancafórt & Gómez 2005).

One of the limitations of the present work, regarding the assemblage of plant-pollinator interactions, is that it was done during only a flowering season. Pollination networks are not static entities, presenting strong temporal dynamics, with evidence showing that the composition of interactions in a community can vary within and among days, months and years, due to species turnover or interaction rewiring (CaraDonna et al. 2017; Devoto et al. 2012). Sampling completeness was not equal for all the populations, but it was very similar in the three studied levels, indicating that although not all interactions have been sampled, the results are directly comparable.

As acknowledge before, another caveat of the study is that it was assumed that all flower visitors were equally effective. Future studies should be directed into understanding which species contribute more to the community functioning and which functional groups were more affected by habitat disturbance. Moreover, understanding the rewiring capacity of the different flower groups due to habitat disturbance and the consequences for the plant population should also be taken into account. Besides that, studies of the effect of stigmatic clogging and pollen quality on sexual fitness of *J. maritima* would be valuable to confirm our results.

Regarding sampling design, it is worth noticing that the configuration within the sampling plot was not considered. Exploring the spatial configuration, such as number of fragment patches and distances between them, could be useful to explain some of the patterns observed.

Conclusion

This is the first study that looked at the effects of habitat disturbance on the reproductive fitness of *J. maritima*, and how the pattern of interactions with its pollinator community is affected. Here, it is shown that the loss and fragmentation of suitable habitat within the dune system is one of the main factors leading to pollen limitation, and consequently to a decrease in the sexual fitness of *J. maritima*. This self-incompatible species is highly reliant on the pollinator community, and the structural changes to its network of interaction with pollinators may have detrimental effects on the maintenance of the pollinator community, ultimately, compromising the persistence of viable populations of *J. maritima*. This study provides information on the pollination ecology of this endemic plant, being a first step to devise a strategy for the implementation of conservation measures. The control of invasive species will be one of the key tasks for the maintenance of the populations, enabling the creation of more suitable habitats for the species. It is also essential to maintain an effective pollinator community, critical for the long-term persistence of this endemic species.

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Appendices

Appendix 1. Pollinator species list

Order	Family	Pollinator taxa			
Hymenoptera	Formicidae	<i>Linepithema humile</i>			
	Braconidae	<i>Braconidae</i>			
	Ichneumonidae	<i>Ichneumonidae</i>			
	Crabronidae		<i>Bembix oculata</i>		
			<i>Bembix flavescens</i>		
			<i>Stizus ruficornis</i>		
			<i>Tachytes freygessneri</i>		
			Tachysphex sp.		
			Sphecidae		<i>Podalonia hirsuta</i>
					<i>Prionyx kirbii</i>
	<i>Prionyx subfuscatus</i>				
	<i>Ammophila</i> sp.				
	<i>Ammophila heydeni</i>				
	Halictidae		<i>Lasioglossum</i> morphospecies 1		
			<i>Lasioglossum</i> morphospecies 2		
			<i>Lasioglossum</i> morphospecies 3		
			<i>Lasioglossum</i> morphospecies 4		
			<i>Lasioglossum</i> morphospecies 5		
			<i>Lasioglossum</i> morphospecies 6		
			<i>Lasioglossum</i> morphospecies 7		
			<i>Lasioglossum</i> morphospecies 8		
			<i>Lasioglossum</i> morphospecies 9		
			<i>Lasioglossum</i> morphospecies 10		
			<i>Lasioglossum</i> morphospecies 11		
			<i>Lasioglossum</i> morphospecies 12		
			<i>Halictus subauratus</i>		
			<i>Halictus</i> sp.		
<i>Nomioides</i> sp.					
Apidae		<i>Apis mellifera</i>			
		<i>Bombus terrestris</i>			
		<i>Bombus pascuorum</i>			
		<i>Bombus</i> sp.			
		<i>Anthophora bimaculata</i>			
		<i>Ceratina</i> sp.			
Colletidae		<i>Colletes</i> sp.			
Megachilidae		<i>Megachile leachella</i>			
		<i>Megachile maritima</i>			
		<i>Megachile</i> morphospecies 1			
		<i>Megachile</i> morphospecies 2			
		<i>Dasypoda hirtipes</i>			

cont.

Order	Family	Pollinator taxa
	Andrenidae	Andrenidae non i.d.
	Non id	Non id 1
Diptera	Sarcophagidae	<i>Sarcophaga</i> morphospecies <i>Sarcophaga longestylata</i> <i>Sarcotachina</i> sp. <i>Sarcotachina umbrinervis</i> <i>Sarcophagidae</i>
	Bombyliidae	<i>Exhyalanthrax melanchlaenus</i> <i>Exhyalanthrax afer</i> <i>Thyridanthrax elegans</i> <i>Thyridanthrax nebulosus</i> <i>Thyridanthrax</i> sp. <i>Hemipenthes velutina</i> <i>Bombylius</i> morphospecies 1 <i>Bombylius</i> morphospecies 2 <i>Bombylius</i> morphospecies 3 <i>Bombylius</i> morphospecies 4 <i>Bombylius</i> morphospecies 5 <i>Systoechus</i> sp.
	Syrphidae	<i>Paragus</i> morphospecies 1 <i>Paragus</i> morphospecies 2 <i>Paragus</i> morphospecies 3 <i>Paragus</i> morphospecies 4 <i>Paragus</i> morphospecies 5 <i>Paragus</i> morphospecies 6 <i>Paragus</i> morphospecies 7 <i>Paragus</i> morphospecies 8 <i>Eristalinus</i> sp. <i>Eristalinus aeneus</i> <i>Eristalis tenax</i> <i>Eristalis arbustorum</i> <i>Syritta pipiens</i> <i>Sphaerophoria</i> sp. <i>Sphaerophoria scripta</i>
	Mythicomyiidae	<i>Empidideicus</i> sp.
	Tachinidae	<i>Besseria</i> sp. <i>Besseria zonaria</i> <i>Besseria lateritia</i>
	Conopidae	<i>Thecophora</i> sp.
	Calliphoridae	<i>Stomorphina lunata</i>

cont.

Order	Family	Pollinator taxa
		<i>Melinda</i> sp.
	Oestroidea	Oestroidea
	Non id	Non id 2
		Non id 3
		Non id 4
Lepidoptera	Pieridae	<i>Pontia daplidice</i>
		<i>Colias croceus</i>
	Nymphalidae	<i>Pyronia cecilia</i>
		<i>Maniola jurtina</i>
		<i>Hipparchia statilinus</i>
	Lycaenidae	<i>Leptotes pirithous</i>
		<i>Lampides boeticus</i>
		<i>Polyommatus icarus</i>
	Papilionidae	<i>Papilio machaon</i>
	Hesperiidae	<i>Carcharodus alceae</i>
	Sesiidae	<i>Pyropteron hispanica</i>
		<i>Pyropteron</i>
	Scythrididae	<i>Scythris</i> sp
	Choreutidae	<i>Tebenna micalis</i>
	Sphingidae	Sphingidae
	Non id	Microlepidoptera non id 1
		Microlepidoptera non id 2
		Non id 5
Coleoptera	Melyridae	<i>Psilothrix</i> sp.
	Oedemeridae	<i>Oedemera flavipes</i>
		<i>Chrysanthia</i> sp.
		<i>Chrysanthia viridissima</i>
	Cerambycidae	<i>Paracorymbia stragulata</i>
	Mordellidae	Mordellidae
	Curculionidae	Curculionidae
	Malachiidae	Malachiidae
	Nitidulidae	<i>Carpophilus</i> sp.
	Coccinellidae	<i>Scymnus</i> sp.
	Non id	Non id 6
		Non id 7

Appendix 2.1. Results for the Linear Mixed Models (LMM), Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs), comparing different response variables between the three disturbance levels. Chi-square test was performed on deviance of the final model against that of a null model ^a. An Anova of each model was performed to check the significance of our predictor. ^b.

Response variable and model structure	Parameter	Estimate \pm SE	t- test/Z value	P
Overall sexual fitness: LMM; sqrt transformation; identity link; normal errors Random factor: latitude	Intercept	2.815 \pm 0.164	17.185	< 0.001
	Low disturbance	0.667 \pm 0.231	2.886	0.014
	Medium disturbance	0.200 \pm 0.232	0.865	0.405
	$\chi^2 = 8.1799$, 2 df, $P = 0.017$ ^a			
Disturbance: $\chi^2 = 8.784$, 2 df, $P = 0.0123$ ^b				
Frequency of interaction: LMM; log _{1p} transformation; identity link; normal errors Random factor: latitude	Intercept	2.14 \pm 0.236	9.078	< 0.001
	Low disturbance	0.662 \pm 0.329	2.010	0.068
	Medium disturbance	-0.659 \pm 0.327	-2.016	0.068
	$\chi^2 = 12.761$, 2 df, $P = 0.002$ ^a			
Disturbance: $\chi^2 = 16.831$, 2 df, $P < 0.001$ ^b				
Proportion of pollen limitation (PPL): LMM; log _{1p} transformation; identity link; normal errors Random factor: latitude	Intercept	0.421 \pm 0.033	12.630	< 0.001
	Low disturbance	0.128 \pm 0.047	2.712	0.019
	Medium disturbance	0.054 \pm 0.049	1.088	0.296
	$\chi^2 = 7.173$, 2 df, $P = 0.028$ ^a			
Disturbance: $\chi^2 = 7.408$, 2 df, $P = 0.025$ ^b				

cont.

Response variable and model structure	Parameter	Estimate \pm SE	t- test/Z value	<i>P</i>
Pollinator species richness: GLM; identity link; Poisson error family	Intercept	85.880 \pm 575.147	0.149	0.881
	Low disturbance	7.403 \pm 2.690	2.751	0.006
	Medium disturbance	2.453 \pm 2.801	0.876	0.381
	Latitude	-1.749 \pm 14.072	-0.124	0.901
	$\chi^2=7.8609, P = 0.048^a$			
Disturbance: $\chi^2=7.843, 2 \text{ df}, P = 0.02^b$				
Latitude: $X^2 = 0.015, 2 \text{ df}, P = 0.903^b$				
Number of individuals of <i>J. maritima</i> per square meter: LMM; sqrt transformation; identity link; normal errors	Intercept	0.510 \pm 0.264	1.936	0.077
	Low disturbance	0.971 \pm 0.357	2.719	0.019
	Medium disturbance	-0.068 \pm 0.396	-0.171	0.867
	$\chi^2 = 9.366, 2 \text{ df}, P = 0.009^a$			
	Disturbance: $\chi^2 = 10.405, 2 \text{ df}, P = 0.006^b$			
Random factor: latitude				
Number of open inflorescences of <i>J. maritima</i> (plots): GLMM; identity link; Gamma error family	Intercept	5.227 \pm 0.488	10.712	< 0.001
	Low disturbance	1.968 \pm 0.703	2.803	0.005
	Medium disturbance	-0.445 \pm 0.688	-0.648	0.517
	$\chi^2 = 7.9478, 2 \text{ df}, P = 0.018^a$			
	Disturbance: $\chi^2 = 13.109, 2 \text{ df}, P = 0.001^b$			
Random factor: latitude				

Appendix 2.2. Result for the Linear Mixed Models (LMM), assessing the effect of pollen supplement treatment on overall sexual fitness.

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Overall sexual fitness: LMM; Identity link; model errors Random factor: latitude	Intercept	12.101±0.756	16.00	< 0.001
	Supplement treatment	6.775±0.581	11.66	< 0.001
	$\chi^2=123.8$, 1df, $P < 0.001$			

Appendix 2.3. Result for the Linear Models (LM), assessing the effect of pollen supplement treatment on overall sexual fitness in each population studied.

Locality	Response variable and model structure	Parameter	Estimate±SE	t- test	P
Km 0	Overall sexual fitness: LM; identity link; normal errors	Intercept	14.445±1.250	11.560	< 0.001
		Supplement treatment	4.700±1.719	2.734	0.009
		Adjusted R²=0.111, F_{1,51}=7.474, P = 0.009			
Km 1	Overall sexual fitness: LM; identity link; normal errors	Intercept	6.507±1.203	5.409	< 0.001
		Supplement treatment	9.264±1.658	5.587	< 0.001
		Adjusted R²=0.4495, F_{1,36}= 31.22, P < 0.001			

cont.

Locality	Response variable and model structure	Parameter	Estimate±SE	t- test	P
Km 2	Overall sexual fitness: LM; identity link; normal errors	Intercept	11.578± 1.588	7.29	< 0.001
		Supplement treatment	8.758± 2.095	4.18	< 0.001
		Adjusted R²=0.2636, F_{1,45}=17.47, P < 0.001			
Km 3	Overall sexual fitness: LM; identity link; normal errors	Intercept	8.879±1.248	7.113	< 0.001
		Supplement treatment	11.161±1.682	6.637	< 0.001
		Adjusted R²=0.473, F_{1,47}=44.05, P < 0.001			
Km 14	Overall sexual fitness: LM; log transformation; identity link; normal errors	Intercept	2.721±0.110	24.550	< 0.001
		Supplement treatment	0.169±0.153	1.048	0.3
		Adjusted R²=0.002, F_{1,51}=1.098, P = 0.299			
Km 15	Overall sexual fitness: LM; identity link; normal errors	Intercept	16.673±1.862	8.954	< 0.001
		Supplement treatment	8.008±2.575	3.109	0.003
		Adjusted R²=0.168, F_{1,42}=9.668, P = 0.003			
Km 20	Overall sexual fitness: LM; identity link; normal errors	Intercept	8.974±1.407	6.376	< 0.001
		Supplement treatment	4.942±1.968	2.511	0.016
		Adjusted R²=0.112, F_{1,41}=6.307, P = 0.016			
Km 21	Overall sexual fitness: LM; identity link; normal errors	Intercept	10.272±2.094	4.905	< 0.001
		Supplement treatment	10.566±2.887	3.660	< 0.001
		Adjusted R²=0.251, F_{1,36}=13.4, P < 0.001			

cont.

Localit y	Response variable and model structure	Parameter	Estimate±SE	t- test	P
Km 22	Overall sexual fitness: LM; identity link; normal errors	Intercept	10.487±1.624	6.457	< 0.001
		Supplement treatment	5.792±2.142	2.704	0.010
		Adjusted R²=0.1393, F_{1,38}=7.313, P = 0.01			
Km 23	Overall sexual fitness: LM; log transformation; identity link; normal errors	Intercept	1.8670±0.1842	10.137	< 0.001
		Supplement treatment	0.8646±0.2423	3.568	< 0.001
		Adjusted R²=0.210, F_{1,43}=12.73, P < 0.001			
Km 24	Overall sexual fitness: LM; identity link; normal errors	Intercept	11.702±1.339	8.742	< 0.001
		Supplement treatment	5.997±2.020	2.968	0.005
		Adjusted R²=0.139, F_{1,39}=7.313, P = 0.01			
Km 25	Overall sexual fitness: LM; identity link; normal errors	Intercept	16.168±2.070	7.812	< 0.001
		Supplement treatment	4.255±3.003	1.417	0.165
		Adjusted R²=0.025, F_{1,38}=2.008, P = 0.165			
Km 26	Overall sexual fitness: LM; identity link; normal errors	Intercept	14.600±1.074	13.598	< 0.001
		Supplement treatment	5.989±1.469	4.078	< 0.001
		Adjusted R²=0.215, F_{1,56}=16.63, P < 0.001			

cont.

Locality	Response variable and model structure	Parameter	Estimate±SE	t- test	P
Km 27	Overall sexual fitness: LM; log transformation; identity link; normal errors	Intercept	2.113±0.132	15.98	< 0.001
		Supplement treatment	0.534±0.176	3.03	0.004
		Adjusted R²=0.148, F_{1,46}=9.182, P = 0.004			
Km 28	Overall sexual fitness: LM; identity link; normal errors	Intercept	11.886±1.532	7.756	< 0.001
		Supplement treatment	7.275±2.264	3.214	0.002
		Adjusted R²=0.166, F_{1,46}=10.33, P = 0.002			

Appendix 2.4. Results for the Linear Models (LMs) and Generalized Linear Models (GLMs), comparing different network metrics between the three disturbance levels studied. Chi-square test was performed on deviance of the final model against that of a null model ^a. An Anova of each model was performed to check the significance of our predictor. ^b

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Weighted connectance: GLM; inverse link; normal errors	Intercept	1180.992± 514.911	2.294	0.042
	Low disturbance	-2.838±2.376	-1.194	0.257
	Medium disturbance	0.166±2.622	0.063	0.951
	Latitude	-29.168±2.599	-2.315	0.041
	$\chi^2=420.28, P < 0.001$ ^a			
Disturbance: $\chi^2=9.049, 2$ df, $P = 0.01$ ^b				
Latitude: $\chi^2=15.271, 1$ df, $P < 0.001$ ^b				

cont.

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Weighted nestedness: LM; identity link; normal errors	Intercept	-9.689±3.183	-3.044	0.011
	Low disturbance	0.030± 0.013	2.297	0.042
	Medium disturbance	-0.006±0.030	-0.188	0.854
	Latitude	0.234±0.078	3.019	0.012
	Adjusted R ² =0.02607, F _{3,11} =1.125, P = 0.3811 ^a			
Disturbance: F=1.432, 2 df, P = 0.280 ^b				
Latitude: F=0.158, 1df, P = 0.699 ^b				
H2: GLM; log link; normal errors	Intercept	83.499±213.901	0.390	0.704
	Low disturbance	-1.599± 0.987	-1.620	0.134
	Medium disturbance	-0.324±1.090	-0.297	0.772
	Latitude	-2.079± 5.234	-0.397	0.699
	$\chi^2=1033.8, P < 0.001$ ^a			
Disturbance: X²=6.993, 2 df, P = 0.030 ^b				
Latitude: X²=15.849, 1df, P < 0.001 ^b				
Robustness higher level: GLM; inverse link; normal errors	Intercept	-146.007±40.356	-3.618	0.004
	Low disturbance	0.419±0.172	2.435	0.033
	Medium disturbance	0.041±0.288	0.143	0.889
	Latitude	3.640±0.986	3.691	0.004
	$\chi^2=138.93, P = 0.388$ ^a			
Disturbance: $\chi^2=1.640, 2 df, P = 0.440$ ^b				
Latitude: $\chi^2=2.889, 1 df, P = 0.090$ ^b				

cont.

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Robustness lower level: LM; identity link; normal errors	Intercept	-26.989±18.555	-1.455	0.174
	Low disturbance	-0.029±0.033	-0.881	0.397
	Medium disturbance	0.091±0.084	1.074	0.306
	Latitude	0.658±0.453	1.452	0.175
	Adjusted R ² =0.338, F _{3,11} =3.384, P = 0.058 ^a			
Disturbance: F=0.421, 2 df, P = 0.666 ^b				
Latitude: F=5.104, 1 df, P = 0.045 ^b				
Niche overlap higher level: LM; identity link; normal errors	Intercept	1361.832±607.872	2.240	0.047
	Low disturbance	-0.511±2.806	-0.182	0.859
	Medium disturbance	2.228±3.096	0.720	0.487
	Latitude	-33.602±14.874	-2.259	0.045
	Adjusted R ² =0.130, F _{3,11} =1.697, P = 0.225 ^a			
Disturbance: F=0.613, 2 df, P = 0.559 ^b				
Latitude: F=2.199, 1 df, P = 0.166 ^b				
Niche overlap lower level: GLM; inverse link; normal errors	Intercept	522.503±355.925	1.468	0.170
	Low disturbance	-1.605±1.643	-0.977	0.350
	Medium disturbance	0.040±1.813	0.022	0.983
	Latitude	-12.913±8.709	-1.483	0.166
	$\chi^2=144.75$, P = 0.001 ^a			
Disturbance: $\chi^2=5.117$, 2 df, P = 0.077 ^b				
Latitude: $\chi^2=11.250$, 1 df, P < 0.001 ^b				

cont.

Response variable and model structure	Parameter	Estimate±SE	t- test	P	
Interaction evenness: GLM; identity link; normal errors	Intercept	-19.475±8.247	-2.361	0.038	
	Low disturbance	0.051±0.030	1.694	0.118	
	Medium disturbance	0.038±0.058	0.660	0.523	
	Latitude	0.472±0.201	2.345	0.039	
	$\chi^2=1011.6, P < 0.001^a$				
	Disturbance: $\chi^2=6.508, 2$ df, $P = 0.039^b$				
Latitude: $\chi^2=14.302, 1$ df, $P < 0.001^b$					
Generality: GLM; inverse link; normal errors	Intercept	3034.493±806.927	3.761	0.003	
	Low disturbance	-8.943±3.724	-2.401	0.035	
	Medium disturbance	-1.313±4.110	-0.319	0.755	
	Latitude	-74.666±19.744	-3.782	0.003	
	$\chi^2=446.14, P < 0.001^a$				
	Disturbance: $\chi^2=9.346, 2$ df, $P = 0.009^b$				
Latitude: $\chi^2=13.350, 1$ df, $P < 0.001^b$					
Vulnerability: GLM; identity link; normal errors	Intercept	-9.496± 3.372	-2.817	0.017	
	Low disturbance	0.034±0.0151	2.237	0.047	
	Medium disturbance	0.003±0.031	0.087	0.932	
	Latitude	0.230±0.082	2.792	0.018	
	$\chi^2=368.15, P < 0.001^a$				
	Disturbance: $\chi^2=5.892, 2$ df, $P = 0.05^b$				
Latitude: $\chi^2=12.741, 1$ df, $P < 0.001^b$					

Appendix 2.5. Results for Generalized Linear Mixed Models (GLMMs) and Robust linear mixed models (RLMMs) comparing plant species metrics between the three disturbance levels. Chi-square test was performed on deviance of the final model against that of a null model ^a. An Anova of each model was performed to check the significance of our predictor. ^b.

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Species strength: GLMM; log1p transformation; log link; normal errors	Intercept	-0.672±0.175	-3.833	< 0.001
	Low disturbance	0.304±0.171	1.776	0.076
	Medium disturbance	0.343±0.171	2.008	0.045
	Random factors: latitude and species	$\chi^2=4.054$, 2df, $P = 0.131$ ^a		
	Disturbance: $\chi^2=4.806$, 2df, $P = 0.090$ ^b			
Normalised degree: GLMM; log1p transformation; log link; normal errors	Intercept	5.956±0.599	9.943	< 0.001
	Low disturbance	0.009±0.432	0.022	0.982
	Medium disturbance	-0.254±0.419	-0.607	0.544
	Random factors: latitude and species	$\chi^2=0.4875$, 2df, $P = 0.7837$ ^a		
	Disturbance: $\chi^2=0.502$, 2df, $P = 0.778$ ^b			
d: RLMM; identity link; normal errors	Intercept	0.076±0.017	4.605	< 0.001
	Low disturbance	-0.022±0.018	-1.248	1.907
	Medium disturbance	0.028±0.021	1.373	1.527
Random factors: latitude and species				

Appendix 2.6. Results for Linear Mixed Models (LMMs) and Robust linear mixed models (RLMM) comparing pollinator species metrics between the three disturbance levels. Chi-square test was performed on deviance of the final model against that of a null model ^a. An Anova of each model was performed to check the significance of our predictor. ^b.

Response variable and model structure	Parameter	Estimate±SE	t- test	P
Species strength: LMM; log; transformation; identity link; normal errors Random factors: latitude and species	Intercept	-1.290±0.226	-5.703	< 0.001
	Low disturbance	-0.230±0.289	-0.793	0.443
	Medium disturbance	-0.304±0.296	-1.026	0.323
	$X^2=1.314, 2df, P = 0.518$ ^a			
Disturbance: $\chi^2=1.133, 2df, P = 0.567$ ^b				
Normalised degree: RLMM; identity link; normal errors Random factors: latitude and species	Intercept	0.230±0.024	9.633	0.0000
	Low disturbance	-0.024±0.030	-0.819	3.716
	Medium disturbance	0.051±0.030	1.668	0.858
d: RLMM; identity link; normal errors Random factors: latitude and species	Intercept	0.066±0.014	4.610	< 0.001
	Low disturbance	0.019±0.019	1.043	2.675
	Medium disturbance	-0.010±0.020	-0.502	5.541

Appendix 3.1. Species level metrics of each pollinator species

Localities	Species	Normalised degree	Species strength	Specialization (d')
Km 0	<i>Lasioglossum</i> morphospecies 1	0.46	1.34	0.00
	<i>Lasioglossum</i> morphospecies 10	0.75	6.75	0.00
	<i>Lasioglossum</i> morphospecies 2	0.13	0.49	0.19
	<i>Lasioglossum</i> morphospecies 9	0.04	0.03	0.09
	<i>Apis mellifera</i>	0.88	11.91	0.00
	<i>Bombus terrestris</i>	0.38	2.14	0.00
	<i>Bombus pascuorum</i>	0.21	0.16	0.00
	<i>Anthophora bimaculata</i>	0.08	0.11	0.00
	Braconidae	0.04	0.01	0.00
	<i>Exhyalanthrax melanchlaenus</i>	0.04	0.02	0.02
	<i>Bombylius</i> morphospecies 4	0.08	0.02	0.00
	<i>Eristalinus aeneus</i>	0.04	0.05	0.41
	<i>Empidideicus</i> sp	0.04	0.10	0.43
	<i>Leptotes pirithous</i>	0.04	0.05	0.40
	<i>Colias croceus</i>	0.04	0.33	0.75
	Curculionidae	0.17	0.24	0.00
	<i>Psilothrix</i> sp	0.04	0.01	0.15
Mordellidae	0.17	0.22	0.00	
Km 1	<i>Halictus subauratus</i>	0.16	0.56	0.00
	<i>Lasioglossum</i> morphospecies 5	0.05	0.19	0.29
	<i>Lasioglossum</i> morphospecies 11	0.21	1.01	0.00
	<i>Lasioglossum</i> morphospecies 12	0.16	0.67	0.00
	<i>Lasioglossum</i> morphospecies 3	0.05	0.40	0.66
	<i>Lasioglossum</i> morphospecies 4	0.63	6.89	0.00
	<i>Nomioides</i> sp	0.58	4.76	0.00
	<i>Sarcophaga</i> morphospecies	0.32	1.26	0.00
	<i>Paragus</i> morphospecies 1	0.11	0.33	0.00
	<i>Syritta pipiens</i>	0.05	0.67	0.80
	<i>Thecophora</i> sp.	0.21	1.59	0.32
	Mordellidae	0.16	0.61	0.00
	Curculionidae	0.05	0.06	0.19
km2	<i>Linepithema humile</i>	0.78	2.60	0.00
	<i>Podalonia hirsuta</i>	0.11	0.15	0.19
	<i>Stizus ruficornis</i>	0.06	0.06	0.30
	<i>Bombus terrestris</i>	0.06	0.06	0.23
	<i>Apis mellifera</i>	0.72	4.40	0.00
	<i>Megachile leachella</i>	0.17	0.14	0.06
	<i>Megachile</i> morphospecies 2	0.28	0.92	0.09
	<i>Lasioglossum</i> morphospecies 5	0.50	1.45	0.00

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	<i>Lasioglossum</i> morphospecies 6	0.56	2.12	0.00
	<i>Lasioglossum</i> morphospecies 7	0.22	0.41	0.15
	<i>Dasygaster hirtipes</i>	0.06	0.08	0.26
	<i>Sarcophaga</i> morphospecies	0.33	0.63	0.00
	<i>Sarcotachina</i> sp.	0.11	0.09	0.15
	<i>Paragus</i> morphospecies 2	0.17	0.22	0.11
	<i>Paragus</i> morphospecies 3	0.06	0.16	0.45
	<i>Paragus</i> morphospecies 4	0.22	0.38	0.15
	<i>Paragus</i> morphospecies 5	0.28	0.43	0.03
	<i>Syrphoctonus pipiens</i>	0.17	0.28	0.00
	<i>Sarcophaga longestylata</i>	0.17	0.28	0.18
	<i>Pyronia cecilia</i>	0.06	0.06	0.30
	<i>Pontia daplidice</i>	0.22	0.20	0.01
	<i>Leptotes pirithous</i>	0.17	0.43	0.28
	Mordellidae	0.67	1.49	0.00
	Curculionidae	0.44	0.88	0.00
	Malachiidae	0.11	0.08	0.12
km3	<i>Bombus terrestris</i>	0.08	0.20	0.55
	<i>Nomioides</i> sp.	0.77	5.37	0.00
	<i>Lasioglossum</i> morphospecies 7	0.08	0.11	0.23
	<i>Lasioglossum</i> morphospecies 6	0.08	0.41	0.47
	<i>Lasioglossum</i> morphospecies 12	0.31	0.90	0.00
	<i>Sarcophaga</i> morphospecies	0.46	0.97	0.00
	<i>Paragus</i> morphospecies 5	0.31	0.71	0.00
	<i>Eristalis tenax</i>	0.23	0.84	0.00
	<i>Exhyalanthrax afer</i>	0.08	0.08	0.00
	<i>Empidideicus</i> sp.	0.54	3.01	0.00
	<i>Carcharodus alceae</i>	0.08	0.03	0.00
	Curculionidae	0.15	0.26	0.11
	<i>Oedemera flavipes</i>	0.08	0.12	0.27
km14	Braconidae	0.07	0.14	0.49
	<i>Podalonia hirsuta</i>	0.36	0.93	0.00
	<i>Stizus ruficornis</i>	0.14	0.21	0.12
	<i>Bombus pascuorum</i>	0.50	0.73	0.00
	<i>Bombus terrestris</i>	0.29	0.41	0.00
	<i>Megachile maritima</i>	0.36	0.83	0.02
	<i>Eristalis tenax</i>	0.07	0.09	0.13
	<i>Paragus</i> morphospecies 2	0.07	0.06	0.12

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	<i>Paragus</i> morphospecies 5	0.14	0.32	0.27
	<i>Sphaerophoria</i> sp.	0.36	1.93	0.00
	<i>Bombylius</i> morphospecies 2	0.14	0.14	0.00
	<i>Stomorhina lunata</i>	0.14	0.37	0.00
	<i>Pyronia cecilia</i>	0.07	0.04	0.13
	<i>Maniola jurtina</i>	0.14	1.11	0.65
	<i>Lampides boeticus</i>	0.14	0.09	0.00
	<i>Papilio machaon</i>	0.57	1.17	0.00
	<i>Pyropteron hispanica</i>	0.21	0.56	0.00
	<i>Oedemera flavipes</i>	0.71	4.58	0.00
	<i>Paracorymbia stragulata</i>	0.07	0.06	0.12
	<i>Chrysanthia</i> sp.	0.07	0.13	0.34
	Mordellidae	0.07	0.07	0.16
	Curculionidae	0.07	0.02	0.00
km15	Ichneumonidae	0.08	0.05	0.18
	<i>Prionyx kirbii</i>	0.62	2.95	0.00
	<i>Tachytes freygessneri</i>	0.08	0.15	0.00
	<i>Tachysphex</i> sp.	0.15	0.32	0.25
	<i>Ceratina</i> sp.	0.08	0.05	0.00
	<i>Megachile</i> morphospecies 1	0.23	0.39	0.00
	<i>Sarcophaga</i> morphospecies	0.15	0.14	0.00
	Sarcophagidae	0.08	0.12	0.00
	<i>Paragus</i> morphospecies 5	0.54	1.01	0.00
	<i>Paragus</i> morphospecies 1	0.08	0.11	0.27
	<i>Stomorhina lunata</i>	0.31	0.69	0.00
	<i>Thyridanthrax elegans</i>	0.23	0.33	0.00
	<i>Empidideicus</i> sp.	0.15	0.50	0.00
	<i>Pyronia cecilia</i>	0.15	0.48	0.37
	<i>Pyropteron hispanica</i>	0.23	0.36	0.08
	<i>Pyropteron</i> sp.	0.08	0.02	0.00
	<i>Oedemera flavipes</i>	0.85	3.33	0.00
	<i>Paracorymbia stragulata</i>	0.08	0.18	0.44
	Mordellidae	0.62	0.71	0.00
	Curculionidae	0.62	1.12	0.00
km20	<i>Linepithema humile</i>	0.25	0.90	0.46
	<i>Ammophila heydeni</i>	0.25	0.10	0.00
	<i>Tachysphex</i> sp.	0.75	1.99	0.00

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	<i>Megachile leachella</i>	0.38	0.52	0.00
	<i>Sarcophaga</i> morphospecies	0.25	0.13	0.00
	<i>Paragus</i> morphospecies 5	0.50	0.89	0.00
	<i>Paragus</i> morphospecies 6	0.13	0.13	0.27
	<i>Paragus</i> morphospecies 1	0.25	0.18	0.02
	<i>Eristalinus aeneus</i>	0.50	1.00	0.00
	<i>Bombylius</i> morphospecies 5	0.13	0.06	0.00
	<i>Besseria zonaria</i>	0.50	1.60	0.00
	<i>Pontia daplidice</i>	0.13	0.13	0.27
	<i>Lampides boeticus</i>	0.13	0.12	0.00
	<i>Scythris</i> sp.	0.13	0.12	0.00
	<i>Microlepidoptera non id 1</i>	0.13	0.14	0.31
km21	<i>Linepithema humile</i>	0.82	5.17	0.00
	<i>Sarcophaga</i> morphospecies	0.36	0.91	0.00
	<i>Sarcotachina umbrinervis</i>	0.18	0.20	0.00
	<i>Paragus</i> morphospecies 5	0.73	2.76	0.00
	<i>Eristalinus aeneus</i>	0.18	0.40	0.29
	<i>Thyridanthrax elegans</i>	0.09	0.11	0.35
	<i>Systoechus</i> sp.	0.18	0.23	0.04
	<i>Oedemera flavipes</i>	0.27	0.36	0.00
	Mordellidae	0.09	0.50	0.74
	Curculionidae	0.18	0.30	0.16
	Non id 6	0.09	0.07	0.20
km22	<i>Linepithema humile</i>	0.13	0.02	0.00
	<i>Tachytes freygessneri</i>	0.38	0.07	0.00
	<i>Tachysphex</i> sp.	0.38	0.18	0.00
	<i>Stizus ruficornis</i>	0.25	0.04	0.00
	<i>Prionyx kirbii</i>	0.25	0.81	0.28
	<i>Podalonia hirsuta</i>	0.38	0.18	0.00
	<i>Megachile leachella</i>	0.63	0.36	0.00
	<i>Bombus</i> sp.	0.38	0.15	0.00
	<i>Bombus pascuorum</i>	0.50	0.28	0.00
	<i>Sarcophaga</i> morphospecies	0.63	0.45	0.00
	<i>Bombylius</i> morphospecies 1	0.75	0.93	0.00
	<i>Bombylius</i> morphospecies 2	0.25	0.05	0.00
	<i>Hemipenthes velutina</i>	0.25	0.07	0.00
	<i>Paragus</i> morphospecies 5	0.63	0.58	0.00
	<i>Paragus</i> morphospecies 7	0.63	1.09	0.00
	<i>Eristalinus aeneus</i>	0.50	0.43	0.00

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	<i>Sphaerophoria</i> sp.	0.50	0.15	0.00
	non id 2	0.13	0.03	0.11
	<i>Scythris</i> sp.	0.25	0.04	0.00
	<i>Leptotes pirithous</i>	0.25	0.03	0.00
	<i>Maniola jurina</i>	0.13	0.03	0.11
	<i>Oedemera flavipes</i>	0.88	1.74	0.00
	<i>Paracorymbia stragulata</i>	0.25	0.06	0.00
	Mordellidae	0.38	0.14	0.00
	Curculionidae	0.25	0.09	0.17
km23	<i>Bembix oculata</i>	0.36	2.59	0.00
	<i>Podalonia hirsuta</i>	0.09	0.12	0.28
	<i>Paragus</i> morphospecies 1	0.09	0.05	0.19
	<i>Paragus</i> morphospecies 4	0.18	0.36	0.06
	<i>Paragus</i> morphospecies 5	0.55	1.91	0.00
	<i>Paragus</i> morphospecies 8	0.18	0.53	0.24
	<i>Sphaerophoria scripta</i>	0.09	0.10	0.00
	<i>Eristalinus aeneus</i>	0.45	0.97	0.00
	<i>Besseria lateritia</i>	0.18	0.34	0.30
	<i>Thyridanthrax nebulosus</i>	0.09	0.08	0.16
	<i>Empidideicus</i> sp.	0.18	0.14	0.04
	<i>Polyommatus icarus</i>	0.09	0.24	0.37
	<i>Scythris</i> sp.	0.09	0.50	0.69
	Microlepidoptera non id 2	0.18	0.25	0.00
	Curculionidae	0.64	2.75	0.00
	<i>Carpophilus</i> sp.	0.09	0.06	0.21
km24	<i>Linepithema humile</i>	0.54	2.10	0.00
	<i>Tachysphex</i> sp.	0.23	0.51	0.00
	<i>Tachytes freygessneri</i>	0.08	1.00	1.00
	<i>Sarcophaga</i> morphospecies	0.85	4.99	0.00
	<i>Bombylius</i> morphospecies 3	0.15	0.15	0.00
	<i>Besseria lateritia</i>	0.08	0.06	0.18
	<i>Melinda</i> sp.	0.23	0.31	0.00
	non id 3	0.15	0.49	0.00
	non id 4	0.08	0.56	0.69
	Oestroidea	0.15	0.14	0.00
	<i>Lampides boeticus</i>	0.15	0.21	0.00
	<i>Tebenna micalis</i>	0.08	0.33	0.69
	<i>Scythris</i> sp.	0.08	0.11	0.38
	<i>Oedemera flavipes</i>	0.54	0.79	0.00

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	Curculionidae	0.23	0.47	0.07
	Mordellidae	0.54	0.78	0.00
km25	Braconidae	0.10	0.07	0.23
	<i>Linepithema humile</i>	0.20	0.07	0.00
	<i>Tachytes freygessneri</i>	0.30	0.10	0.00
	<i>Ammophila</i> sp.	0.20	0.04	0.00
	<i>Apis mellifera</i>	0.50	0.51	0.00
	<i>Bombus terrestris</i>	0.20	0.17	0.05
	<i>Bombus pascuorum</i>	0.10	0.27	0.51
	<i>Sarcophaga</i> morphospecies	1.00	4.09	0.00
	<i>Sphaerophoria</i> sp.	0.50	0.76	0.00
	<i>Paragus</i> morphospecies 5	0.20	0.43	0.22
	<i>Paragus</i> morphospecies 2	0.10	0.04	0.19
	<i>Eristalinus aeneus</i>	0.60	1.00	0.00
	<i>Eristalis arbustorum</i>	0.10	0.04	0.22
	<i>Exhyalanthrax afer</i>	0.20	0.17	0.18
	<i>Thyridanthrax</i> sp.	0.30	0.79	0.11
	<i>Bombylius</i> morphospecies 1	0.20	0.19	0.00
	<i>Bombylius</i> morphospecies 2	0.20	0.12	0.07
	<i>Besseria</i> sp.	0.10	0.02	0.00
	Diptera non id 3	0.20	0.16	0.11
	<i>Sarcophaga longestylata</i>	0.10	0.07	0.10
	Lepidoptera	0.10	0.14	0.52
	Sphingidae	0.20	0.14	0.10
	<i>Oedemera flavipes</i>	0.20	0.58	0.34
	<i>Scymnus</i> sp.	0.10	0.02	0.00
	non id 1	0.10	0.02	0.07
km26	<i>Linepithema humile</i>	0.38	1.05	0.00
	<i>Bembix oculata</i>	0.15	0.12	0.00
	<i>Stizus ruficornis</i>	0.15	0.27	0.01
	<i>Bombus pascuorum</i>	0.23	0.21	0.00
	<i>Megachile leachella</i>	0.77	2.81	0.00
	<i>Lasioglossum</i> morphospecies 7	0.38	0.81	0.00
	<i>Sarcophaga</i> morphospecies	0.69	2.15	0.00
	<i>Paragus</i> morphospecies 7	0.15	0.26	0.23
	<i>Paragus</i> morphospecies 6	0.08	0.22	0.22
	<i>Eristalinus aeneus</i>	0.54	2.64	0.00
	<i>Syritta pipiens</i>	0.08	0.09	0.00
	<i>Sphaerophoria</i> sp.	0.23	0.34	0.00

cont.

Localities	Species	Normalised degree	Species strength	Specialization (d')
	<i>Bombylius</i> morphospecies 1	0.38	0.55	0.00
	<i>Exhyalanthrax afer</i>	0.46	0.70	0.00
	<i>Besseria</i> sp.	0.08	0.06	0.00
	<i>Papilio machaon</i>	0.15	0.26	0.32
	<i>Chrysanthia viridissima</i>	0.08	0.04	0.10
	<i>Oedemera flavipes</i>	0.15	0.11	0.00
	Curculionidae	0.08	0.33	0.69
km27	<i>Bembix flavescens</i>	0.57	1.12	0.00
	<i>Bembix oculata</i>	0.71	2.11	0.00
	<i>Ammophila</i> sp.	0.29	0.10	0.00
	<i>Prionyx subfuscatus</i>	0.14	0.01	0.00
	<i>Prionyx kirbii</i>	0.71	0.61	0.00
	<i>Megachile leachella</i>	0.71	1.08	0.00
	<i>Lasioglossum</i> morphospecies 8	0.43	0.11	0.00
	Andrenidae non id	0.43	0.19	0.00
	<i>Colletes</i> sp.	0.14	0.04	0.20
	<i>Sarcophaga</i> morphospecies	0.14	0.50	0.70
	<i>Thyridanthrax elegans</i>	0.57	0.35	0.00
	<i>Paragus</i> morphospecies 5	0.43	0.61	0.00
	<i>Paragus</i> morphospecies 7	0.29	0.13	0.00
	<i>Paragus</i> morphospecies 2	0.14	0.02	0.00
	Non id 7	0.14	0.02	0.00
km28	Braconidae	0.17	0.02	0.00
	<i>Bembix flavescens</i>	0.83	2.12	0.00
	<i>Apis mellifera</i>	0.17	0.02	0.00
	<i>Ammophila</i> sp.	0.50	0.25	0.00
	<i>Lasioglossum</i> morphospecies 8	0.33	0.21	0.00
	<i>Halictus</i> sp.	0.33	0.23	0.00
	<i>Megachile leachella</i>	0.67	1.36	0.00
	<i>Megachile maritima</i>	0.33	0.25	0.00
	<i>Paragus</i> morphospecies 5	0.50	1.26	0.36
	<i>Bombylius</i> morphospecies 1	0.33	0.17	0.00
	<i>Bombylius</i> morphospecies 2	0.17	0.02	0.00
	<i>Hipparchia statilinus</i>	0.17	0.06	0.25
	Malachiidae	0.17	0.04	0.00

Appendix 3.2. Species level metrics for each plant phenotype (characterized according to the number of open inflorescences)

Localities	Number of open inflorescences per individual	Normalised degree	Species strength	Specialization (d')
km 0	1	0,44	2,54	0,00
	2	0,28	0,61	0,00
	3	0,28	1,46	0,00
	4	0,44	2,80	0,00
	5	0,28	0,52	0,00
	6	0,22	0,46	0,00
	7	0,17	0,12	0,00
	8	0,28	0,89	0,01
	9	0,22	1,08	0,00
	10	0,33	1,97	0,00
	11	0,17	0,11	0,00
	12	0,06	0,00	0,11
	13	0,17	0,10	0,00
	15	0,22	0,53	0,03
	17	0,06	0,10	0,50
	18	0,11	0,06	0,00
	22	0,33	1,60	0,25
	23	0,06	0,07	0,00
	24	0,06	0,05	0,00
	25	0,11	0,37	0,01
26	0,17	1,03	0,35	
28	0,06	0,05	0,00	
29	0,17	1,04	0,01	
33	0,17	0,45	0,13	
km1	1	0,54	1,66	0,00
	2	0,15	0,14	0,00
	3	0,46	3,01	0,00
	4	0,08	0,33	0,66
	5	0,08	0,10	0,00
	6	0,08	0,06	0,00
	7	0,15	0,07	0,00
	8	0,31	0,40	0,00
	9	0,46	1,21	0,00
	12	0,23	0,58	0,00
	13	0,08	0,11	0,21
	14	0,15	0,12	0,00
	15	0,08	0,14	0,24
	17	0,08	0,06	0,00
	21	0,15	1,07	0,59
	33	0,08	0,21	0,28
34	0,23	0,38	0,06	

cont.

Localities	Number of open inflorescences per individual	Normalised degree	Species strength	Specialization (d')
	37	0,23	1,41	0,59
	72	0,38	1,93	0,00
km2	1	0,44	3,66	0,00
	2	0,20	0,84	0,00
	3	0,32	1,40	0,00
	4	0,36	0,94	0,00
	5	0,44	1,40	0,00
	6	0,32	2,06	0,00
	7	0,20	0,94	0,00
	8	0,36	1,66	0,00
	9	0,36	1,66	0,00
	10	0,36	1,23	0,00
	11	0,20	0,56	0,03
	12	0,08	0,12	0,00
	14	0,16	0,87	0,00
	17	0,16	0,34	0,00
	25	0,12	0,67	0,28
	27	0,32	3,47	0,00
	34	0,16	0,96	0,16
44	0,24	2,22	0,00	
km3	1	0,23	0,33	0,01
	2	0,15	0,31	0,36
	3	0,38	1,30	0,00
	4	0,08	0,04	0,24
	9	0,23	0,46	0,00
	10	0,31	1,57	0,00
	11	0,08	0,05	0,00
	15	0,38	1,38	0,00
	17	0,08	0,11	0,00
	25	0,23	0,63	0,27
	27	0,23	1,12	0,10
	36	0,38	2,37	0,25
58	0,46	3,34	0+A45:E75	
km14	1	0,36	3,40	0,00
	2	0,45	4,44	0,00
	3	0,50	4,47	0,00
	4	0,32	1,77	0,00
	5	0,27	2,09	0,36
	6	0,05	0,04	0,00
	7	0,09	0,17	0,00
	8	0,18	0,42	0,00

cont.

Localities	Number of open inflorescences per individual	Normalised degree	Species strength	Specialization (d')
	9	0,18	1,17	0,29
	10	0,14	0,61	0,00
	13	0,18	0,75	0,24
	14	0,05	0,50	0,84
	21	0,18	1,41	0,00
	40	0,09	0,77	0,00
km15	1	0,40	1,76	0,00
	2	0,20	0,91	0,18
	3	0,25	0,45	0,00
	4	0,30	1,69	0,00
	5	0,25	0,99	0,00
	6	0,05	0,08	0,18
	7	0,20	1,37	0,09
	8	0,35	1,99	0,00
	9	0,20	0,41	0,00
	11	0,30	1,13	0,00
	14	0,25	2,03	0,10
	29	0,25	1,23	0,00
	36	0,50	5,95	0,00
km20	1	0,60	5,30	0,00
	2	0,40	3,00	0,11
	3	0,33	2,55	0,00
	4	0,13	0,94	0,24
	5	0,33	1,47	0,00
	6	0,20	0,80	0,00
	7	0,27	0,59	0,00
	22	0,07	0,35	0,44
km21	1	0,18	0,11	0,01
	2	0,64	2,45	0,05
	3	0,55	2,31	0,01
	4	0,27	0,92	0,12
	5	0,18	0,24	0,00
	6	0,18	0,36	0,00
	7	0,27	1,58	0,75
	8	0,27	0,84	0,07
	13	0,27	1,31	0,40
	15	0,18	0,59	0,47
	33	0,18	0,29	0,00
km22	1	0,72	6,18	0,00
	2	0,76	7,12	0,00
	3	0,60	3,17	0,00

cont.

Localities	Number of open inflorescences per individual	Normalised degree	Species.strength	Specialization (d')
	4	0,20	0,41	0,00
	5	0,28	1,63	0,00
	6	0,08	0,57	0,38
	7	0,48	5,76	0,00
	8	0,04	0,16	0,05
km23	1	0,31	3,06	0,25
	2	0,50	3,32	0,03
	3	0,19	0,74	0,25
	4	0,38	2,63	0,00
	5	0,13	1,16	0,52
	6	0,06	0,26	0,48
	7	0,13	0,55	0,40
	8	0,19	0,83	0,00
	9	0,06	0,09	0,34
	14	0,25	1,59	0,00
	19	0,25	1,77	0,00
km24	1	0,44	2,37	0,00
	2	0,31	1,90	0,00
	3	0,50	3,09	0,00
	4	0,38	1,03	0,00
	5	0,31	0,89	0,13
	6	0,13	0,25	0,00
	7	0,06	1,00	1,00
	8	0,44	2,08	0,00
	9	0,19	1,22	0,37
	10	0,06	0,03	0,00
	11	0,25	0,60	0,00
	14	0,13	0,27	0,31
	33	0,19	1,28	0,46
km25	1	0,44	5,81	0,00
	2	0,48	5,71	0,00
	3	0,44	4,55	0,00
	4	0,12	0,45	0,10
	5	0,20	1,69	0,08
	6	0,16	0,50	0,00
	7	0,08	0,35	0,33
	8	0,28	3,41	0,00
	9	0,08	0,30	0,05
	49	0,16	2,23	0,31
km26	1	0,37	2,52	0,00
	2	0,53	2,40	0,00

cont.

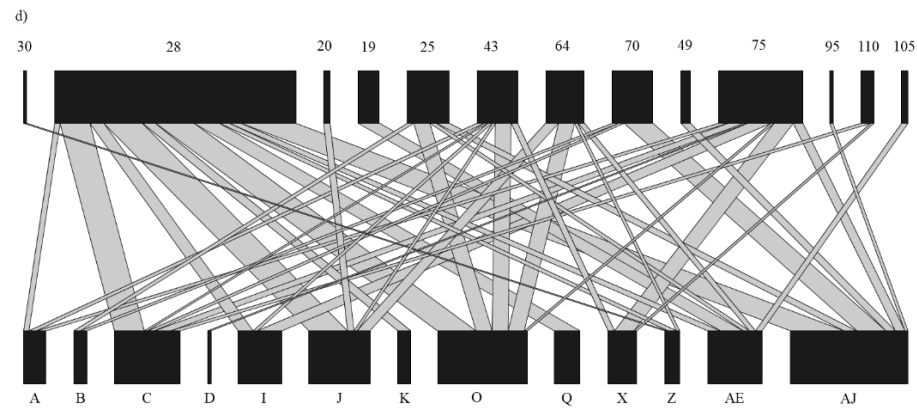
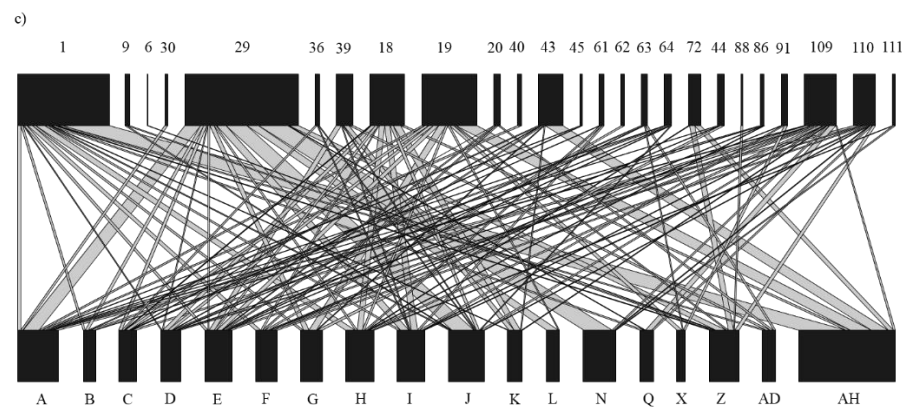
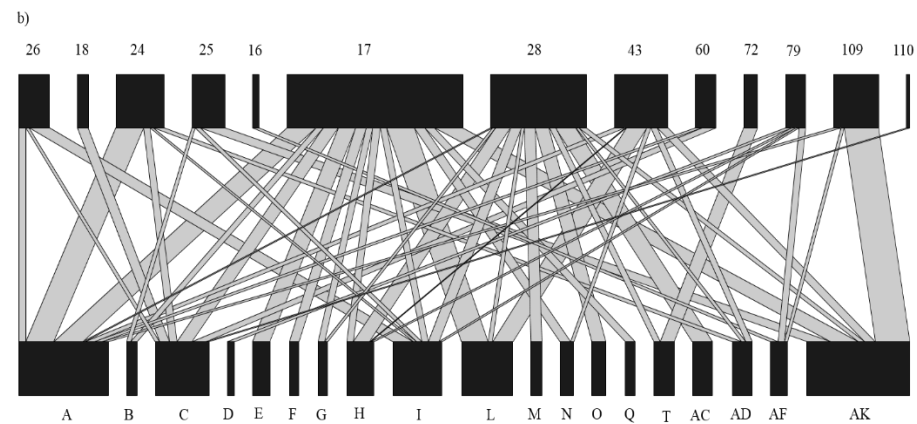
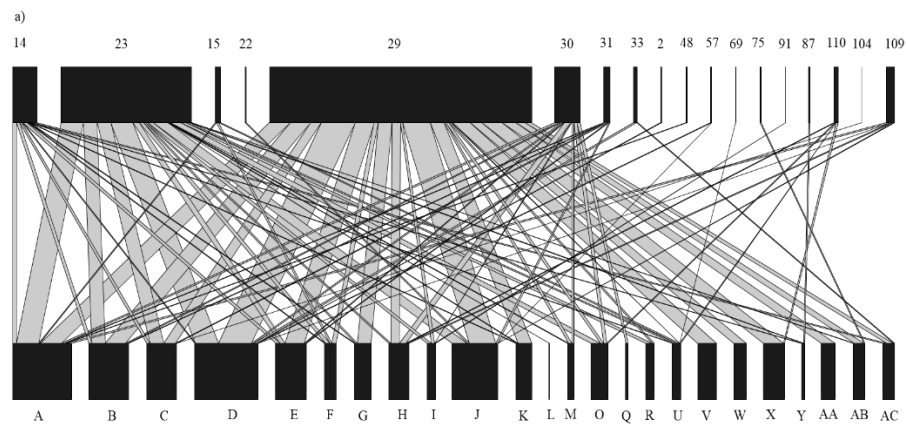
Localities	Number of open inflorescences per individual	Normalised degree	Species strength	Specialization (d')
	3	0,37	1,35	0,00
	4	0,58	4,08	0,00
	5	0,37	1,68	0,00
	6	0,21	0,29	0,00
	7	0,26	1,59	0,00
	8	0,21	1,27	0,00
	10	0,21	0,85	0,00
	11	0,16	0,93	0,11
	12	0,05	0,03	0,08
	21	0,11	1,08	0,37
	24	0,16	0,94	0,16
km27	1	0,87	7,47	0,00
	2	0,60	1,98	0,00
	3	0,47	2,25	0,00
	4	0,40	1,18	0,00
	6	0,20	0,81	0,00
	7	0,07	0,10	0,00
	13	0,13	1,21	0,31
km28	1	0,85	8,47	0,00
	2	0,54	2,67	0,00
	3	0,31	0,74	0,00
	4	0,08	0,22	0,21
	5	0,31	0,65	0,00
	7	0,08	0,25	0,58

cont.

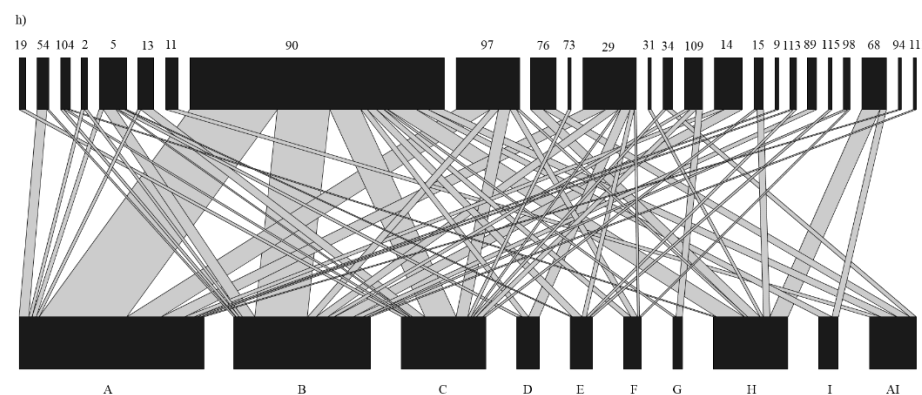
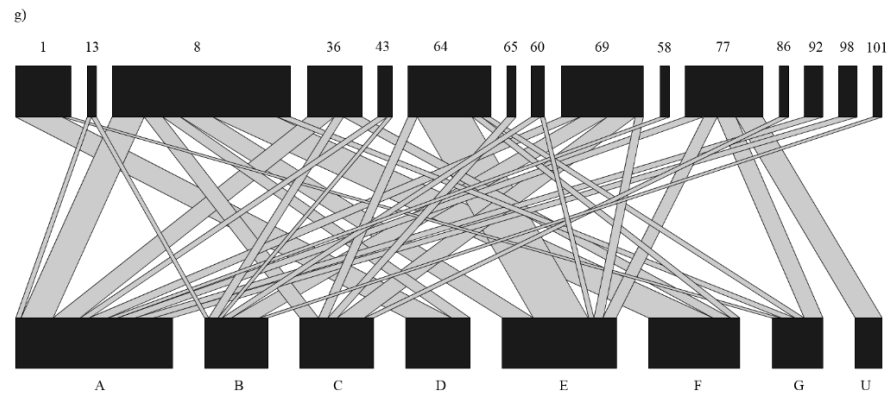
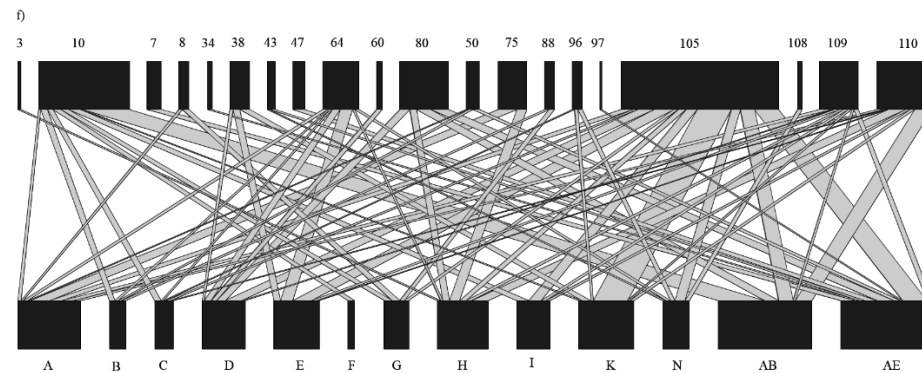
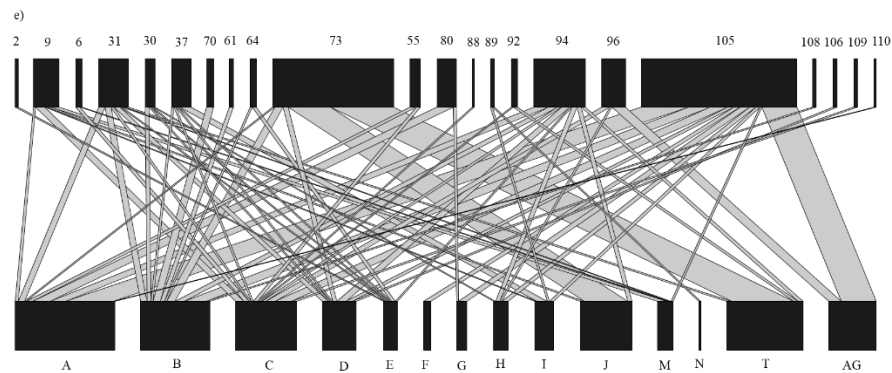
Order	Family	Species	Km 0	Km 1	Km 2	km 3	Km 14	Km 15	km 20	Km 21	Km 22	Km 23	Km 24	Km 25	Km 26	Km 27	km 28	Total	%		
Lepidoptera	Pieridae					0.13			0.03									0.17	0.06		
		<i>Pontia daplidice</i>																			
		<i>Colias croceus</i>	0.06																0.06	0.02	
	Nymphalidae		<i>Pyronia cecilia</i>			0.03		0.06	0.14											0.23	0.08
			<i>Mantola jurtina</i>					0.12				0.04								0.15	0.06
			<i>Hipparchia statilinus</i>															0.03	0.03	0.01	
	Lycenidae		<i>Leptotes pirithous</i>	0.03		0.20						0.15								0.38	0.13
			<i>Lampides boeticus</i>					0.18		0.06				0.28						0.52	0.19
			<i>Polymnatus icarus</i>									0.03							0.03	0.01	
	Papilionidae		<i>Papilio machaon</i>					1.06							0.10				1.15	0.41	
	Hesperiidae		<i>Carcharodus alceae</i>				0.04												0.04	0.01	
	Sesiidae								0.47	0.14									0.61	0.22	
			<i>Pyropteron hispanica</i>							0.03									0.03	0.01	
	Scythrididae		<i>Scythris sp</i>							0.06		0.07	0.03	0.06					0.22	0.08	
	Choreutidae		<i>Tebenna micalis</i>											0.06					0.06	0.02	
	Sphingidae		Sphingidae												0.14				0.14	0.05	
	Non id		Microlepidoptera non id 1							0.03									0.03	0.01	
			Microlepidoptera non id 2										0.09						0.09	0.03	
			Non id 5												0.05				0.05	0.02	
			Total	0.08	0.00	0.37	0.04	1.88	0.31	0.19	0.00	0.26	0.14	0.39	0.19	0.10	0.00	0.03	3.98	1.42	
	Coleoptera	Melyridae			0.03														0.03	0.01	
		Oedemeridae		<i>Psalothrix sp.</i>	0.03															0.03	0.01
				<i>Oedemera flavipes</i>				0.07	18.47	5.10		0.90	1.19		0.67	0.38	0.19			26.97	9.64
			<i>Chrysanthia sp.</i>					0.06											0.06	0.02	
		<i>Chrysanthia viridissima</i>													0.05			0.05	0.02		
Cerambycidae			<i>Paracorymbia stragulata</i>					0.12	0.07		0.11							0.30	0.11		
Mordellidae			Mordellidae	0.33	2.41	2.30		0.12	1.03		0.40	0.19		1.00				7.78	2.78		
Curculionidae			Curculionidae	0.14	0.05	1.00	0.21	0.06	2.14		0.20	0.07	0.29	0.33	0.00	0.05			4.54	1.62	
Malachiidae			Malachiidae				0.07											0.06	0.13	0.04	
Nitidulidae			<i>Carpophilus sp.</i>									0.03							0.03	0.01	
Coccinellidae			<i>Scymnus sp.</i>												0.05				0.05	0.02	
Non id			Non id 6								0.10								0.10	0.04	
			Non id 7															0.05	0.05	0.02	
			Total	0.50	2.45	3.37	0.29	18.82	8.34	0.00	1.60	1.56	0.31	2.00	0.43	0.29	0.05	0.06	40.07	14.33	
Total				53.00	13.14	34.90	11.43	28.00	17.97	4.71	27.80	11.04	4.86	19.94	23.33	16.33	11.00	2.26	279.71		

Appendix 5. Quantitative pollination networks for each study site; a) Km 0; b) Km 1; c) Km 2; d) Km 3; e) Km 14; f) Km 15; g) Km 20; h) Km 21; i) km 22; j) km 23; k) km 24; l) km 25; m) km 26; n) km 27; and o) km28

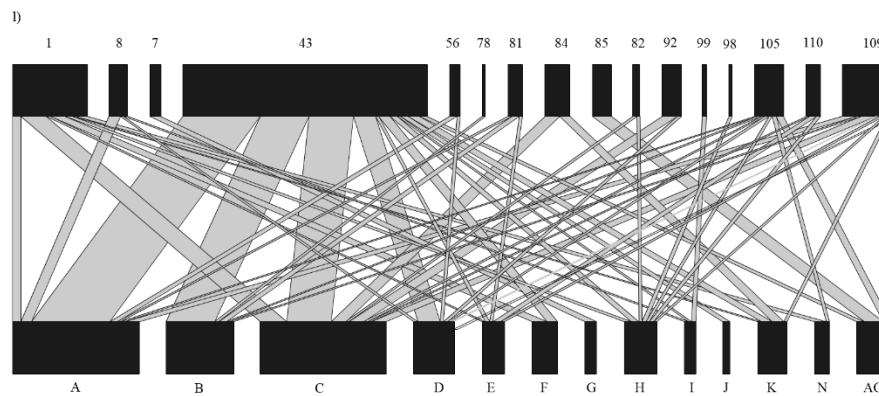
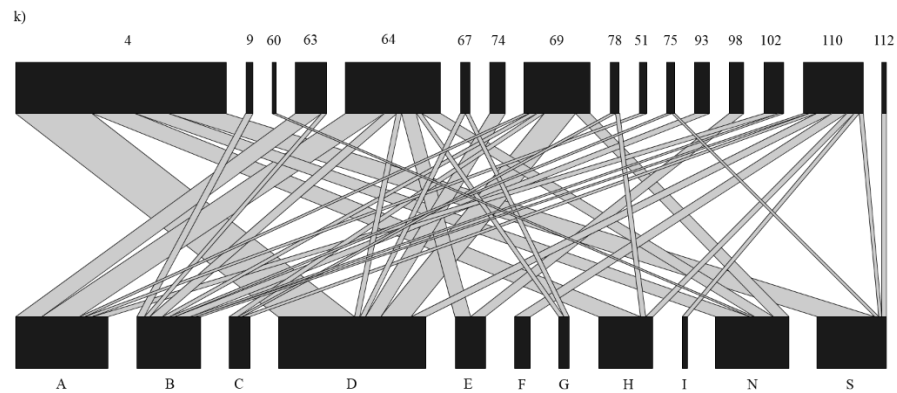
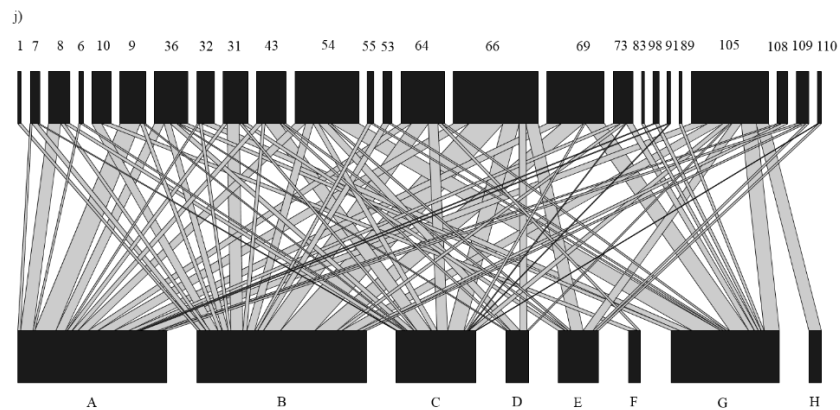
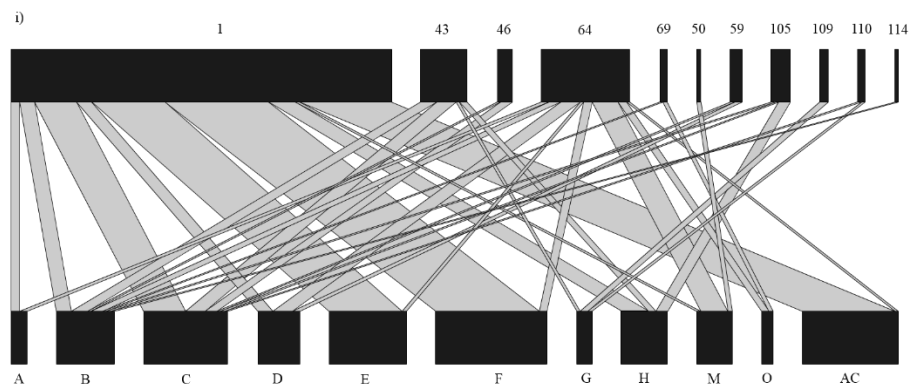
Pollinators: 1-*Linepithema humile*; 2-Braconidae; 3-Ichneumonidae; 4-*Bembix oculata*; 5-*Bembix flavescens*; 6-*Stizus ruficornis*; 7-*Tachytes freygessneri*; 8-*Tachysphex* sp.; 9-*Podalonia hirsuta*; 10-*Prionyx kirbii*; 11-*Prionyx subfuscatus*; 12-*Ammophila* sp.; 13-*Ammophila heydeni*; 14-*Lasioglossum* morphospecies 1; 15-*Lasioglossum* morphospecies 2; 16-*Lasioglossum* morphospecies 3; 17-*Lasioglossum* morphospecies 4; 18-*Lasioglossum* morphospecies 5; 19-*Lasioglossum* morphospecies 6; 20-*Lasioglossum* morphospecies 7; 21-*Lasioglossum* morphospecies 8; 22-*Lasioglossum* morphospecies 9; 23-*Lasioglossum* morphospecies 10; 24-*Lasioglossum* morphospecies 11; 25-*Lasioglossum* morphospecies 12; 26-*Halictus subauratus*; 27-*Halictus* sp.; 28-*Nomioides* sp.; 29-*Apis mellifera*; 30-*Bombus terrestris*; 31-*Bombus pascuorum*; 32-*Bombus* sp.; 33-*Anthophora bimaculata*; 34-*Ceratina* sp.; 35-*Colletes* sp.; 36-*Megachile leachella*; 37-*Megachile maritima*; 38-*Megachile* morphospecies 1; 39-*Megachile* morphospecies 2; 40-*Dasypoda hirtipes*; 41-Andrenidae non i.d.; 42-Non id 1; 43-*Sarcophaga* morphospecies; 44-*Sarcophaga longestylata*; 45-*Sarcotachina* sp.; 46-*Sarcotachina umbrinervis*; 47-Sarcophagidae; 48-*Exhyalanthrax melanchlaenus*; 49-*Exhyalanthrax afer*; 50-*Thyridanthrax elegans*; 51-*Thyridanthrax nebulosus*; 52-*Thyridanthrax* sp.; 53-*Hemipenthes velutina*; 54-*Bombylius* sp. 1; 55-*Bombylius* sp. 2; 56-*Bombylius* sp. 3; 57-*Bombylius* sp. 4; 58-*Bombylius* sp. 5; 59-*Systoechus* sp.; 60-*Paragus* morphospecies 1; 61-*Paragus* morphospecies 2; 62-*Paragus* morphospecies 3; 63-*Paragus* morphospecies 4; 64-*Paragus* morphospecies 5; 65-*Paragus* morphospecies 6; 66-*Paragus* morphospecies 7; 67-*Paragus* morphospecies 8; 68-*Eristalinus* sp.; 69-*Eristalinus aeneus*; 70-*Eristalis tenax*; 71-*Eristalis arbustorum*; 72-*Syritta pipiens*; 73-*Sphaerophoria* sp.; 74-*Sphaerophoria scripta*; 75-*Empidideicus* sp.; 76-*Besseria* sp.; 77-*Besseria zonaria*; 78-*Besseria lateritia*; 79-*Thecophora* sp.; 80-*Stomorhina lunata*; 81-*Melinda* sp.; 82-*Oestroidea*; 83-Non id 2; 84-Non id 3; 85-Non id 4; 86-*Pontia daplidice*; 87-*Colias croceus*; 88-*Pyronia cecilia*; 89-*Maniola jurtina*; 90-*Hipparchia statilinus*; 91-*Leptotes pirithous*; 92-*Lampides boeticus*; 93-*Polyommatus icarus*; 94-*Papilio machaon*; 95-*Carcharodus alceae*; 96-*Pyropteron hispanica*; 97-*Pyropteron* sp.; 98-*Scythris* sp.; 99-*Tebenna micalis*; 100-Sphingidae; 101-Microlepidoptera non id 1; 102-Microlepidoptera non id 2; 103-Non id 5; 104-*Psilothrix* sp.; 105-*Oedemera flavipes*; 106-*Chrysanthia* sp.; 107-*Chrysanthia viridissima*; 108-*Paracorymbia stragulata*; 109-Mordellidae; 110-Curculionidae; 111-Malachiidae; 112-*Carpophilus* sp.; 113-*Scymnus* sp.; 114-Non id 6; 115-Non id 7; and *J. maritima* phenotypes (number of open inflorescences): A-1; B-2; C-3; D-4; E-5; F-6; G-7; H-8; I-9; J-10; K-11; L-12; M-13; N-14; O-15; P-16; Q-17; R-18; S-19; T-21; U-22; V-23; W -24; X-25; Y-26; Z-27; AA-28; AB-29; AC-33; AD-34; AE-36; AF-37; AG-40; AH-44; AI-49; AJ-58; and AK-72



cont.



cont.



cont.

