

# The importance of generalist pollinator complexes for endangered island endemic plants

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To investigate whether endangered endemic plants of the Azores are threatened by pollinator limitation, we studied the insect pollinator communities of *Azorina vidalii*, *Euphrasia azorica*, *Myosotis azorica* and *Solidago azorica* on Corvo Island. We found no evidence for dependence on a specialised pollinator. Instead, we found five to 21 mostly generalist insect pollinators per plant species, six of them probably introduced species. Diptera, with at least 12 species, and Hymenoptera, with at least nine species, are the most important insect orders and also most important in visitation frequency. The relatively high pollinator diversity for each of the studied plants and the high proportion of generalists indicate that the pollination networks of the four study plant species are rather resilient, i.e. the loss of a species would not constitute an immediate threat. Seed counts and numbers of juvenile plants indicate that reproductive success of all four species is stable. Altogether, our results suggest that there is no pollinator limitation in the four study species. Conservation measures should therefore focus on other threats, on Corvo mainly on grazing pressure.

Key words: generalist pollinators, island endemic plants, pollinator limitation, pollinator networks.

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## INTRODUCTION

Endemic plants on oceanic islands constitute an important proportion of global biodiversity and at the same time are one of the most threatened groups of organisms in the world (Kreft et al. 2008; Caujapé-Castells et al. 2010). The flora of the Azores, an archipelago of nine volcanic islands close to the Middle-Atlantic ridge in the Northern Atlantic Ocean (Fig. 1), comprises c. 70 endemic flowering plant species, about one third of the total indigenous flora (Schaefer 2005b, Silva et al. 2010). Nine of these endemics are listed among the top 100 conservation priority plant and animal species of Macaronesia and a

multitude of threat factors have been identified for them (Cardoso et al. 2008). Because of this, recent studies highlight the importance of holistic approaches (Caujapé-Castells et al. 2010; Silva et al. 2015; Kueffer & Kaiser-Bunbury 2013), studying a broad range of factors relevant for a population's survival, especially mutualistic interactions with insects, vertebrates, and fungi (Kaiser-Bunbury et al. 2010).

Pollination, one of these key mutualisms, is thought to differ fundamentally on islands compared to continental systems, because of often reduced numbers of potential pollinators (Valido & Olesen 2010; Olesen et al. 2012). In some islands, there is evidence for adaptation to

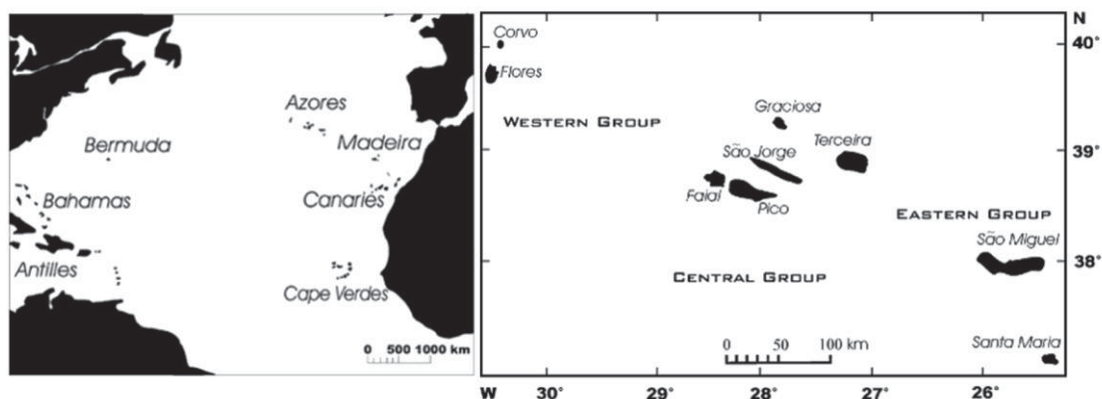


Fig. 1. Map of the Northern Atlantic islands (left), Azores archipelago (right) (modified from Schaefer et al. 2011)

specialist pollinators including birds (Valido et al. 2004), lizards (Olesen & Valido 2003) and locusts (Micheneau et al. 2010). In other islands, generalist pollinator complexes seem to dominate (Olesen et al. 2002). Insular pollination systems in general are thought to be particularly vulnerable to extinction of species, habitat fragmentation, and invasion of introduced species (Kaiser-Bunbury et al. 2010; Valido & Olesen 2010). It has been suggested that the decline of some endemic plant species on islands could be a result of the loss of their specialist pollinators (Robertson et al. 1998; Cox & Elmqvist 2000; Montgomery et al. 2001; Wheelwright et al. 2006).

Knowledge on the pollination biology of Azorean endemics is very limited (but see Pereira 2008). An annotated checklist with some ecological information is only available for the bees (Weissmann et al. 2017), while knowledge on other important clades like Diptera is still very limited for the archipelago (Borges et al. 2010b). Expanding knowledge in this area is crucial, because the many ex-situ and in-situ conservation measures by the Azorean government, universities and NGOs will fail if lack of pollinators limits the reproductive success of the study plants. Here we test the hypothesis that the decline of Azorean endemic plants is partly due to loss of specialist pollinators during the past five centuries of human-mediated environmental changes in the

archipelago. Specifically, we test for pollinator limitation indicated by low number of pollinator visits and reduced seed set.

## MATERIAL AND METHODS

### Study site

Fieldwork was carried out by the first author from June 20 to August 30, 2015, mainly on Corvo island, with a few additional observations on the neighbouring island Flores. Corvo is the smallest inhabited Azorean island with a size of only c. 17 km<sup>2</sup> and 450 inhabitants, all living in a single settlement at the southern tip. The island mainly consists of one big crater, with steep cliffs on the north and west sides, pastures covering most of the land surface and a few small forest spots. Like in most of the Azores archipelago, most natural habitats on Corvo have been replaced by pasture land and cattle farming is the most important economy on the island. We chose Corvo for our study because it is the last refuge for some of the rarest and most endangered endemics of the Azores, including *Myosotis azorica*, *Veronica dabneyi*, *Euphrasia azorica*, *Euphorbia stygiana* and also hosts a large population of the endemic Azores bellflower (*Azorina vidalii*).

### Study species

Out of the c. 40 endemic angiosperms existing on Corvo (Silva et al. 2010), we shortlisted ten

threatened insect-pollinated plants as potential study species: *Azorina vidalii* (Wats.) Feer, *Centaurium scilloides* (L. f.) Samp., *Cerastium azoricum* Hochst., *Euphorbia stygiana* Wats., *Euphrasia azorica* Wats., *Myosotis azorica* Wats., *Platanthera pollostantha* R.M. Bateman & M. Moura, *Ranunculus cortusifolius* Willd., *Solidago azorica* Hochst. ex Seub. and *Veronica dabneyi* Hochst. ex Seub. After arrival on the island, we chose the four species *Azorina vidalii*, *Euphrasia*

*azorica*, *Myosotis azorica* and *Solidago azorica*, because they were found to be in flower and grew in accessible areas. Two of the study species, *E. azorica* and *M. azorica*, are restricted to higher elevation habitats, while the other two are mainly coastal species. For three of the species, the study period overlapped with peak flowering, for *S. azorica*, only parts of the population were in flower during our stay and peak flowering was later in September.



Fig. 2. *Myosotis azorica* in steep coastal cliff with the invasive *Hydrangea macrophylla* on the upper left; insert shows single flower with blue petals and orange-white scales limiting access to the corolla tube. Photos: J. Weissmann, Corvo 2015.

*Myosotis azorica*, Boraginaceae, is endemic to Corvo and the neighbouring island Flores and grows at 400-600 m altitude in steep and humid cliffs (Fig. 2). Its radially symmetric flowers are up to 7 mm in diameter and arranged in groups of 30-50 in dense umbel-like cymes (Schaefer 2005a). Five tiny scales narrow the entrance to the corolla tube, thereby reducing access for larger insects (Weryszko-Chmielewska 2003). Like in many other species of the genus, self-pollination probably plays a certain role in this species despite its very showy attractive inflorescences (Robertson & Lloyd 1991). The second species,

*Euphrasia azorica* (Fig. 3), Orobanchaceae, is also endemic to the western group (Yeo 1973). It is an annual species (Vitek 2015) found in steep slopes, cliffs and waterfalls at 500 to 800 m altitude. Its bilaterally symmetric white flowers with yellow spots are nototribic, i.e. place pollen on the back of the insect. Like in most large-flowered species of *Euphrasia*, flower morphology does not support self-pollination (Liebst & Schneller 2005; French et al. 2005). The third species, *Solidago azorica* (Fig. 4), Asteraceae, occurs on all islands of the archipelago, mostly in coastal cliffs and lava fields, but also in disturbed

habitats like roadside slopes and landfills. Restricted to coastal habitats in most islands, it can be found at altitudes up to 900 m on Corvo and Flores. Its inflorescences are composed of up to 400 capitulae, with about ten yellow ray and disk florets each. *Solidago azorica* is most likely self-incompatible, like its close relative *S.*

*sempervirens* (Innes & Hermanutz 1988; Schaefer 2015). Among the predominantly European flora of the Azores, it is one of the few examples of American origin (Schaefer 2015). Finally, *Azorina vidalii* (or better: *Campanula vidalii* H.C. Wats.) (Fig. 5), Campanulaceae, is another endangered endemic with a particularly enigmatic



Fig. 3. *Euphrasia azorica* in natural high altitude grassland at the rim of the volcanic crater; insert shows the white two-lipped flower with yellow marking on the lower lip and anthers close to the upper lip. Photos: J. Weissmann, Corvo 2015.

pollination biology: while its large and robust, pink campanulate flowers would fit best to bird pollination (Olesen et al. 2012; Mühlbauer et al. 2000), birds have never been observed visiting its flowers. Flower morphology and dichogamy in *A. vidalii* prevent self-pollination within one flower but it seems possible within a single inflorescence. A certain contribution of wind-pollination has been suggested earlier for the

species (Olesen et al. 2012) and self-compatibility is known from other *Campanula* species on islands (Inoue 1990; Inoue & Amano 1986). Although most common in the western group of the Azores, *Azorina vidalii* occurs on all islands of the archipelago, usually in coastal rocks and cliffs, often in habitats with elevated nitrogen levels (Schaefer 2003).



Fig. 4. *Solidago azorica* in coastal lowland along a small stone wall in agricultural area; the insert shows the yellow capitulate with 5-12 ray florets and 7-10 disk florets. Photos J. Weissmann, Corvo 2015.

#### Distribution mapping

Distribution data for our study plants was available at low resolution from the Azores bioportal (Borges et al. 2010a; <http://azoresbioportal.uac.pt>). During the first days on the island, the first author performed a quick survey on foot, to obtain more detailed range maps for each of the study plants. Distribution maps were then gradually improved during the whole study period by GPS-mapping of each newly detected individual.

For each of the subpopulations, we surveyed for evidence of major threat factors following Caujapé-Castells et al. (2010) and Kueffer & Kaiser-Bunbury (2013).

#### Pollinator observation

Pollinator observations were carried out on different times of day and night to take into account potential species-specific variations in pollinator activity. We chose a standard observation period of 30 minutes plus occasional shorter periods of c. 5 min. To be categorised as

pollinator, a species had to be observed at least once touching the stamens or stigma of the plant. A series of pictures were taken for identification and as evidence for the activity of the animal in the flower. For identification, we used keys for Europe (Haupt & Haupt 1998; and Kormann 2002 [for Diptera]; Amiet et al. 2001; Amiet & Krebs 2014; Falk & Lewington 2015; and Scheuchl & Willner 2016 [for Hymenoptera]; Kueppers 2008; and Sterling & Parsons 2012 [for Lepidoptera]). We were also supported by taxonomic experts for particular groups (see Acknowledgements). With only few exceptions, identification was possible to species or at least genus level. Each species was counted only once per observation period to avoid double-counting of the same returning individual. Finally, we calculated visitation frequencies for the different pollinator groups as their percentage of the counted observations summed over all observation periods. The native or introduced status of all species was classified following Borges et al. (2010b) and Weissmann et al. (2017).

### Reproductive success

Towards the end of the field season, total seed set was assessed based on 10-30 control plants per species by estimating the percentage of well-developed versus dead seeds. To assess

reproductive success of previous years, the number of juvenile plants per population was counted, except for *Euphrasia azorica* which is an annual plant.



Fig. 5. *Azorina vidalii* in coastal lowland close to the sea; the insert shows the pink campanulate flower with nectar glands at base and large white stigmatic column (upper flower in female phase, lower flower in male phase). Photos J. Weissmann, Corvo 2015

## RESULTS

### Distribution ranges and number of individuals

*Myosotis azorica* was confined to very few and isolated stands on the top of the cliffs in the north and north-western part of the island, where a total of 26 plants in flower and 13 non-flowering individuals were counted in nine sites. *Euphrasia azorica* was mostly found along the ridge and inner slope in the northern part of the crater, and in the highest parts of the cliffs in the western part of the island. In total, c. 560 flowering individuals were counted (Fig. 6). *Solidago azorica* was found in two different habitats: 85 individuals in

the highest parts of the island on the northern ridge of the crater and on its outside slopes, in ravines and cliffs on the north-eastern part of the island. In addition, it also grows in low altitude habitats in and around the village, where we found at least 1000 individuals on coastal cliffs, on slopes along the road and the agricultural areas, in the waste dump and other fallow land (Fig. 6). Here it often grows together with *Azorina vidalii*, of which we found c. 3200 flowering individuals in and around the village (Fig. 6). An additional c. 1000 individuals occurred in the landfill area and the fenced areas of the airport and the petrel breeding site.

### Pollinator observation

We realized a total of nearly 50 hours of observation, partitioned into 91 observation periods of 30 minutes and 17 short observation periods. Nocturnal observations (9 PM - 5 AM) were made only for the two coastal plant species *Solidago azorica* (95 min in total) and *Azorina vidalii* (275 min in total). Total observation time was not equally distributed between the four species: 38% of total observation time was spent on *Azorina vidalii* (total observation time: 17 hrs 50 min), 28% on *Solidago azorica* (13 hrs 20 min), 20% on *Myosotis azorica* (9 hrs 10 min), and 14% on *Euphrasia azorica* (6 hrs 35 min).

The four plant species are visited by a variety of insect species (Table 1) and a few other animal groups (snails, house centipedes, millipedes and mites). None of the latter is likely to transfer pollen between plants and they were therefore excluded. Vertebrates like birds or lizards were not observed on any of the flowers. The most species-rich pollinating insect groups were Diptera (12 species), followed by Hymenoptera (9 species), then Lepidoptera (7 species), and Hemiptera (3 species) (Tables 1 and 2). Regarding visitation frequency, the most important group was again Diptera (52% of total observations), followed by Hymenoptera (29%), Lepidoptera (16%), and Hemiptera (3%). Each of the four study plant species had a different pollinator community (Figs 7-10) but at least eight insect species overlapped and were observed on two or more of the study plant species. For example, both *Sphaerophoria* cf. *scripta* and *Stomorhina* cf. *lunata* pollinated three of the plant species (*E. azorica*, *S. azorica* and *A. vidalii*; and *M. azorica*, *S. azorica* and *A. vidalii* respectively). Formicidae (observed on *Solidago*, *Azorina*) and Thysanoptera (*Azorina*) were not counted even though they touched stamens and/or stigmata but are unlikely to transfer pollen between different plant individuals because they do not or not regularly fly.

Eleven species of pollinating insects were recorded on *M. azorica*. Most frequent were Diptera, which made up 75% of the observations with seven species: three different Calliphoridae (including *Stomorhina* cf. *lunata* and *Pollenia* spec.), one Scathophagidae (*Scathophaga* cf. *stercoraria*), one Sepsidae, one Ephydriidae, and the endemic Syrphid fly *Sphaerophoria nigra*. Lepidoptera made up 22% of the observations and at least three different species (*Micrurapteryx bistrigella*, *Stenoptilia* cf. *zophodactylus*, plus one or two species of *Argyresthia*). In addition, a single species of *Polymerus* (Hemiptera), was observed pollinating *Myosotis*. Nine of the species are native or probably native, at least two of them endemic (*Sphaerophoria nigra*, *Micrurapteryx bistrigella* and possibly *Argyresthia* spec.); two species are probably introduced (Table 2).

Five species of pollinating insects were recorded on *E. azorica*, almost exclusively Diptera, which made up 95% of the observations and were represented by at least four different species: a Scathophagidae (*Scathophaga* cf. *stercoraria*), one species of Sepsidae, one species of Ephydrid and one Syrphid fly (*Sphaerophoria* cf. *scripta*). The only non-dipteran pollinator observed was a Microlepidoptera belonging to the genus *Eudonia* or *Scoparia*. All observed insects are native or probably native, at least one of them (*Eudonia/Scoparia* spec.) possibly endemic (Table 2).

Twenty-one species of pollinating insects were recorded on *S. azorica*, nearly half of them Diptera: two Syrphid flies (*Eristalinus aeneus* and *Sphaerophoria scripta*), one Nematocera (probably a species of Limoniidae), three different Calliphoridae (including *Stomorhina* cf. *lunata* and *Pollenia* spec.), one Tephritinae, one Sepsidae and one Ephydriidae (*Hecamede* cf. *albicans*). Hymenoptera represented 28% of the observed pollinators: at least two different *Halictus* species, *Hylaeus pictipes*, one Vespidae

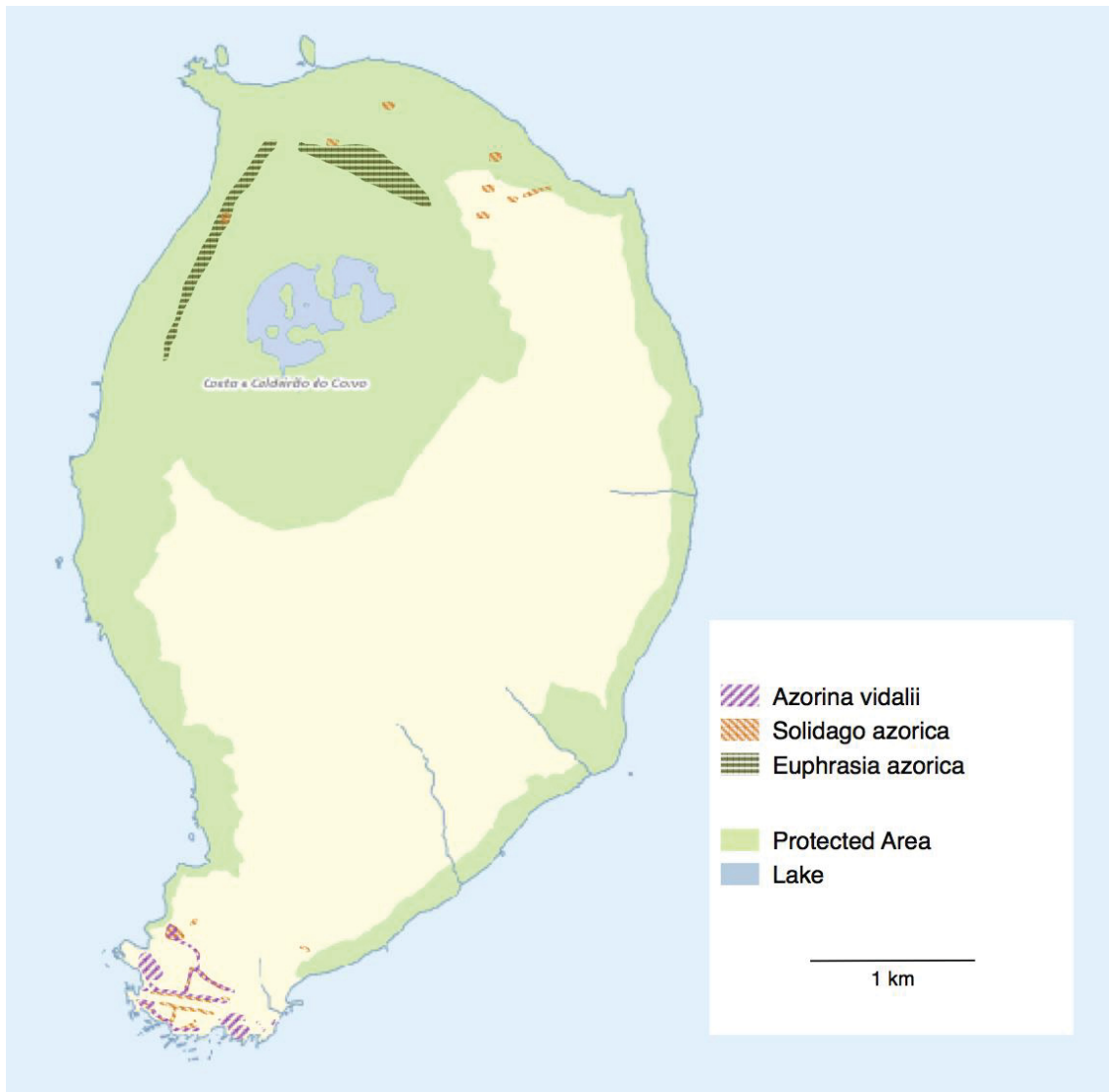


Fig. 6. Occurrence of *Azorina vidalii*, *Euphrasia azorica* and *Solidago azorica* on Corvo island as assessed during fieldwork in 2015. The exact location and GPS coordinates of the *Myosotis azorica* individuals were communicated to the local authorities but are not shown in the map to protect this highly endangered species. The green area indicates the Natura 2000 reserve "Costa e Caldeirão do Corvo". Base map by Ruben Furtado, Wikipedia, creative commons license.



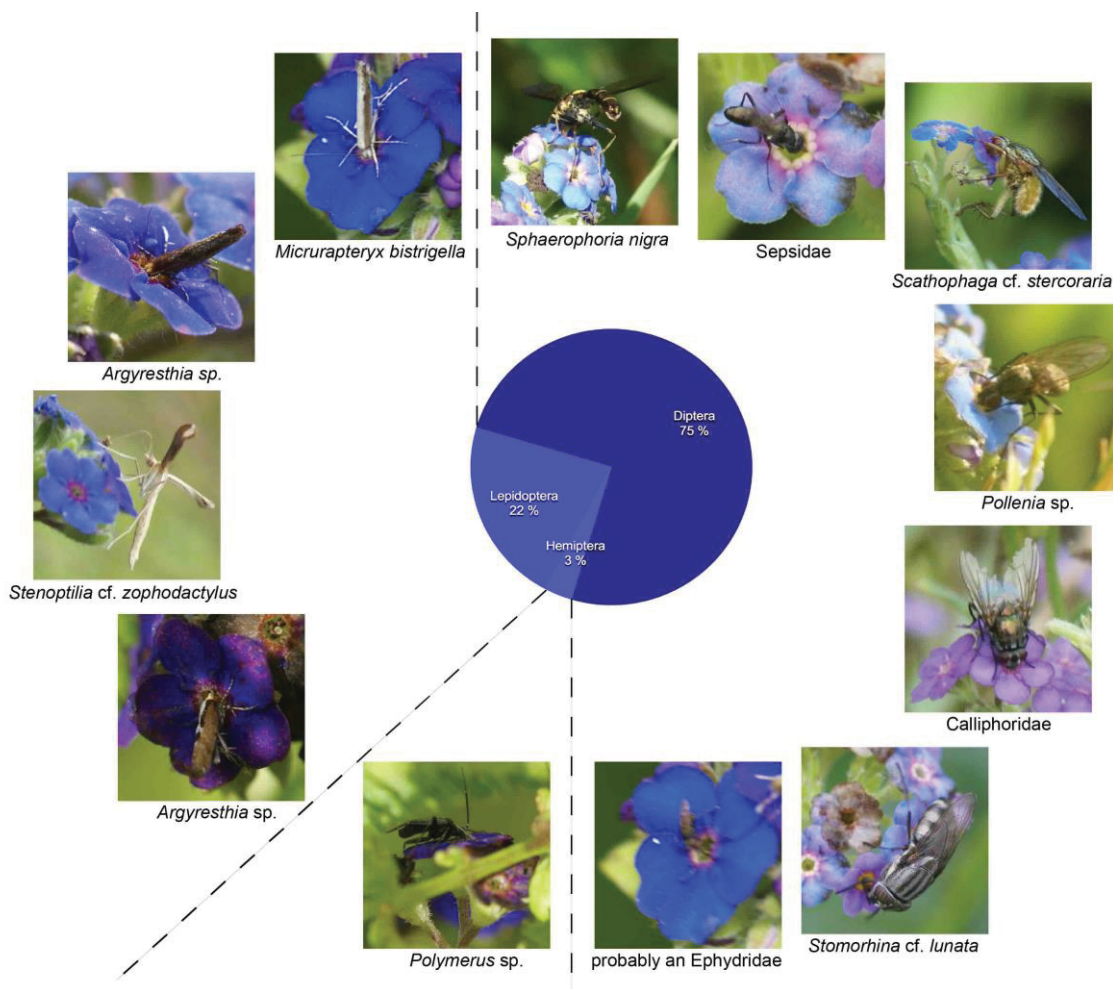


Fig. 7. Pollinator community of *Myosotis azorica* (11 species, 32 counted observations, total observation time: 9 hrs 10 min) with pie chart showing percentage of observations per insect group. Photos J. Weissmann, Corvo 2015.

(*Ancistrocerus* spec.), one Cynipidae and one Ichneumonidae. Lepidoptera made up 17% of the observations: *Helicoverpa armigera*, *Opogona sacchari*, *Argyresthia* spec. and one unidentified Microlepidoptera (possibly *Ephestia elutella*). Finally, four Hemiptera species, the tamarix leafhopper (*Opsius stactogalus*) plus three Heteroptera (*Nysius ericae* and two unidentified species), together represent 7% of the pollinator observations on *Solidago*. Thirteen species are native or probably native, at least one of them

(*Argyresthia* spec.) possibly endemic; five species are introduced or probably introduced, the status of three species is unknown (Table 2).

Nine species of pollinating insects were recorded on *A. vidalii*. Hymenoptera were the most abundant group (72% of the observations), and had the highest species numbers: *Bombus terrestris* and at least two different *Halictus/Lasioglossum* species on Corvo, plus the honeybee *Apis mellifera* and the wasp *Vespula germanica* on Flores island. Diptera constitute

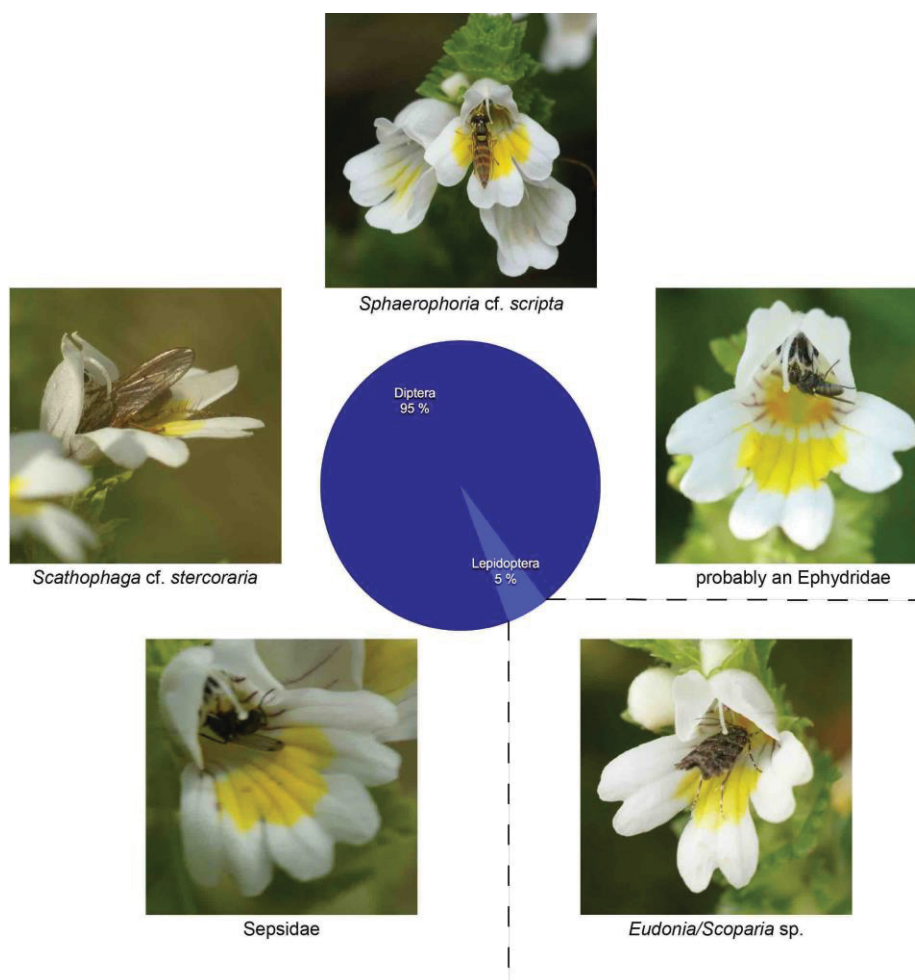


Fig. 8. Pollinator community of *Euphrasia azorica* (five species, 21 counted observations, total observation time: 6 hrs 35 min) with pie chart showing percentage of observations per insect group. Photos J. Weissmann, Corvo and Flores 2015.

14% of the observations, with one Syrphid fly (*Sphaerophoria cf. scripta*) and one Calliphoridae (*Stomorphina cf. lunata*) observed on Corvo, and one *Nematocera* (most probably a *Limoniidae*) observed at night on Flores island. Lepidoptera were represented by up to three macromoth species, the cotton bollworm (*Helicoverpa*

*armigera*) and two unidentified noctuids which may or may not be conspecific with the former. Together they made up 14% of the pollinator observations on *Azorina*. Five species are native or probably native, four species are introduced or probably introduced, including *Apis mellifera* (Table 2).

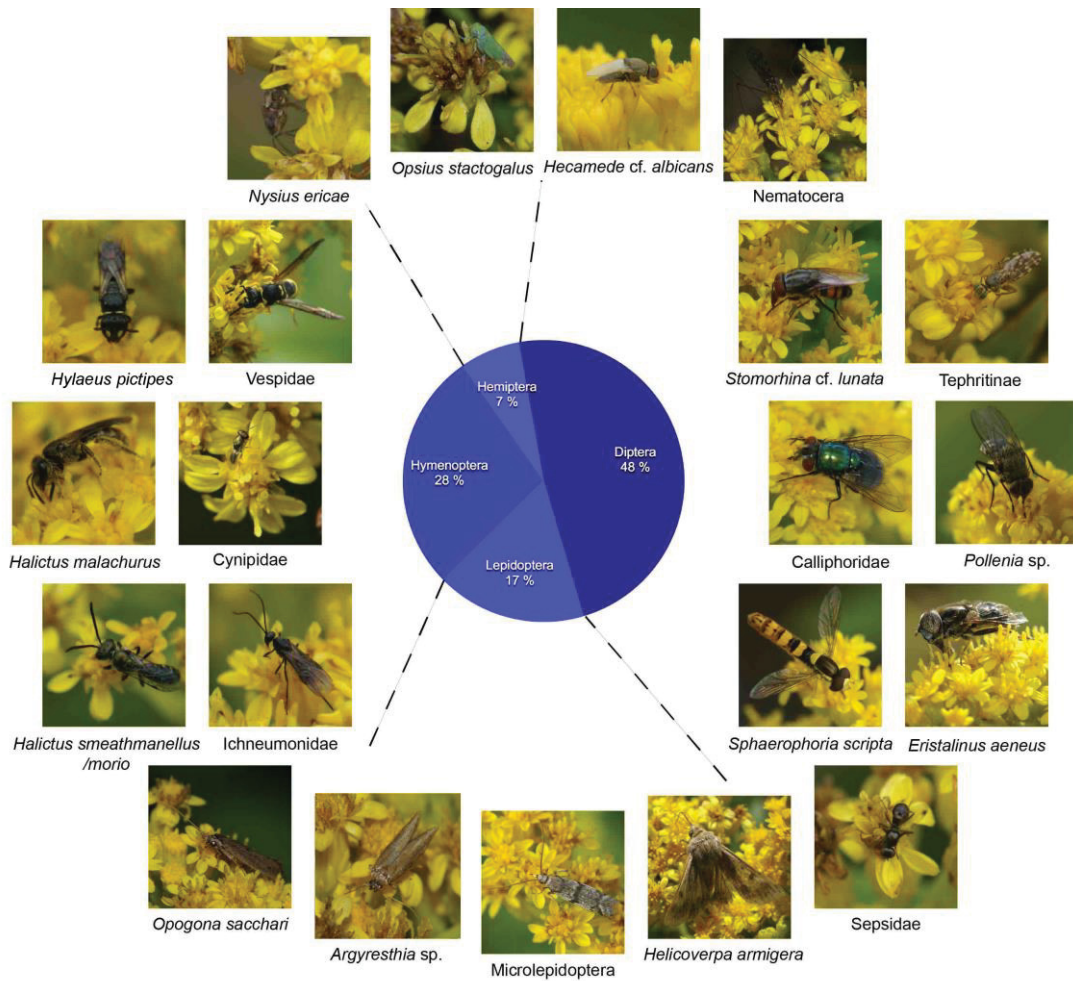


Fig. 9. Pollinator community of *Solidago azorica* (22 species, 58 counted observations, total observation time: 13 hrs 20 min) with pie chart showing percentage of observations per insect group. Photos J. Weissmann, Corvo 2015.

### Reproductive success

The seeds of all control individuals of *M. azorica*, *A. vidalii* and *E. azorica* were mostly well developed. In contrast, more than half of the controlled *S. azorica* seeds seemed dead or

damaged by caterpillars and beetle larvae. The populations of both *M. azorica* and *A. vidalii* consisted of about one third of young plants, whereas the population of *S. azorica* contained only c. 6% of young individuals.

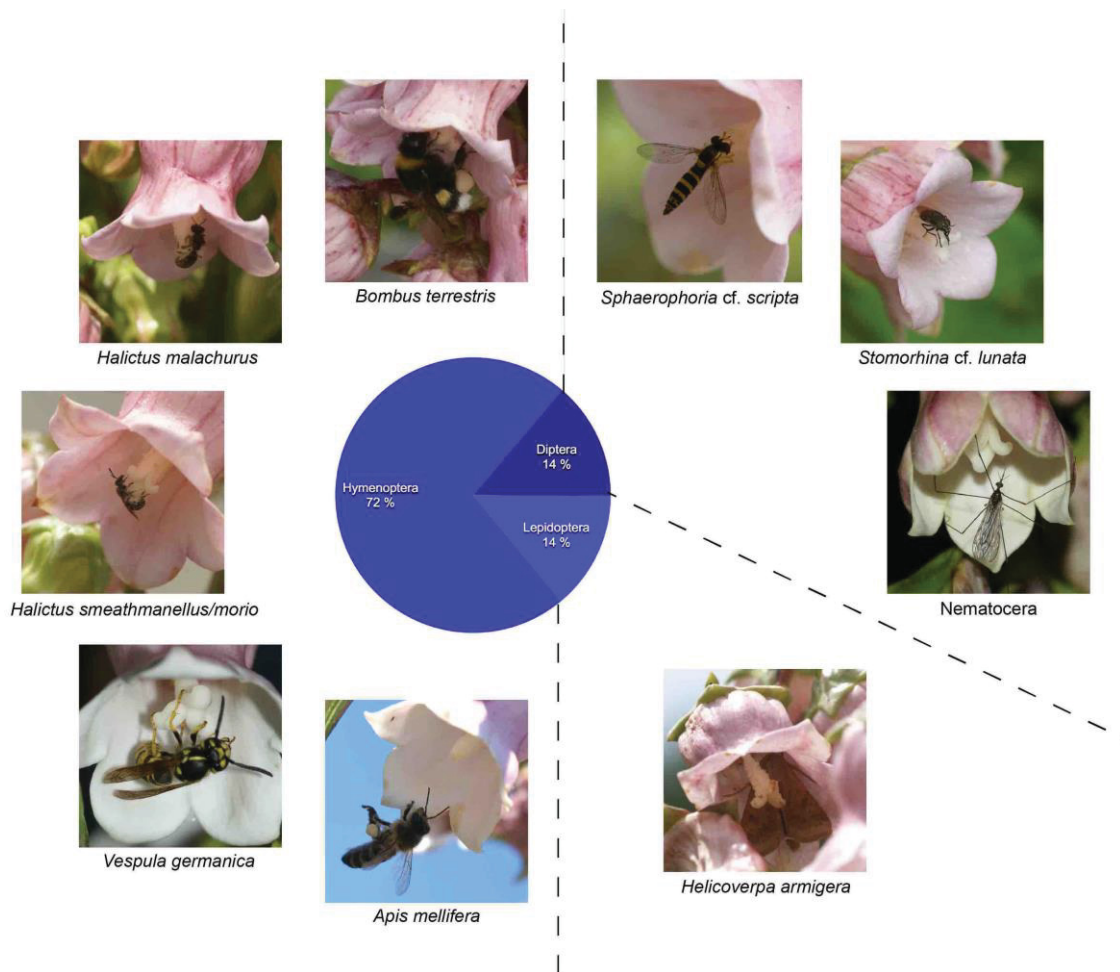


Fig. 10. Pollinator community of *Azorina vidalii* (nine species, 36 counted observations, total observation time: 17 hrs 50 min) with pie chart showing percentage of observations per insect group. Photos J. Weissmann, Corvo and Flores 2015.

Table 1. Pollinator species per insect order for the four study plants.

	<i>Myosotis azorica</i>	<i>Euphrasia azorica</i>	<i>Solidago azorica</i>	<i>Azorina vidalii</i>	total species number
<b>Diptera</b>	7	4	9	3	12
<b>Hymenoptera</b>	0	0	6	5	9
<b>Lepidoptera</b>	3	1	4	1	7
<b>Hemiptera</b>	1	0	2	0	3
<b>Total</b>	11	5	21	9	31

Table 2. Insect pollinators of the study plant species. Status information is based on Borges et al. (2010b) and Weissmann et al. (2017); END = endemic; END<sub>g</sub> = all Azorean species of this genus

endemic; n = native; n<sub>g</sub> = all Azorean species of this genus are native; n<sub>f</sub> = all Azorean species of this family are native or endemic to the Azores/Macaronesia; i = introduced; i<sub>g</sub> = all Azorean species of this genus are introduced; ? = status unknown).

Species	Family	Status
<b>Diptera</b>		
<i>Calliphora</i> spec.?	Calliphoridae	i <sub>g</sub>
<i>Pollenia</i> spec.	Calliphoridae	i <sub>g</sub>
<i>Stomorphina</i> cf. <i>lunata</i> (Fabricius, 1805)	Calliphoridae	n
<i>Hecamede</i> cf. <i>albicans</i> (Meigen, 1830)	Ephydriidae	n
?	Ephydriidae?	n <sub>f</sub>
?	Nematocera, (Limoniidae?)	n <sub>f</sub>
<i>Scathophaga</i> cf. <i>stercoraria</i> (Linnaeus, 1758)	Scathophagidae	n
<i>Sepsis</i> spec.	Sepsidae	n <sub>f</sub>
<i>Eristalinus aeneus</i> (Scopoli, 1763)	Syrphidae	n
<i>Sphaerophoria scripta</i> (Linnaeus, 1758)	Syrphidae	n
<i>Sphaerophoria nigra</i> (Frey, 1945)	Syrphidae	END
?	Tephritidae	?
<b>Hymenoptera</b>		
<i>Apis mellifera</i> (Linnaeus, 1758)	Apidae	i
<i>Bombus terrestris</i> (Linnaeus, 1758)	Apidae	probably i
<i>Halictus malachurus</i> (Kirby, 1802) syn. <i>Lasioglossum malachurum</i>	Apidae	probably i
<i>Halictus smeathmanellus</i> (Kirby, 1802) or <i>H. morio</i> (Fabricius, 1793) syn.: <i>Lasioglossum smeathmanellum</i> / <i>L. morio</i>	Apidae	probably i
<i>Hylaeus pictipes</i> (Nylander, 1852)	Apidae	possibly n
?	Cynipidae	?
?	Ichneumonidae	n <sub>f</sub>
<i>Ancistrocerus</i> spec.	Vespidae	n <sub>g</sub>
<i>Vespula germanica</i> (Fabricius, 1793)	Vespidae	n
<b>Lepidoptera</b>		
<i>Eudonia/Scoparia</i> spec.	Crambidae	END <sub>g</sub>
<i>Micrurapteryx bistrigella</i> (Rebel, 1940)	Gracillariidae	END
<i>Helicoverpa armigera</i> (Hübner, 1808)	Noctuidae	n
<i>Stenoptilia</i> cf. <i>zophodactylus</i> (Duponchel, 1840)	Pterophoridae	n
<i>Opogona sacchari</i> (Boyer, 1856)	Tineidae	i
<i>Argyresthia</i> spec.	Yponomeutidae	END <sub>g</sub>
?	Microlepidoptera	?
<b>Hemiptera</b>		
<i>Opsius stactogalus</i> (Fieber, 1866)	Cicadellidae	n
<i>Nysius ericae ericae</i> (Schilling, 1829)	Lygaeidae	n
<i>Polymerus</i> spec.	Miridae	n <sub>g</sub>

## DISCUSSION

### Pollination and reproductive success

Even though our study was limited to just a single season, all four plant species were found to be pollinated by a mix of introduced and native insects from up to four different orders (Diptera, Hymenoptera, Lepidoptera, and Hemiptera). The overall high species diversity in flower visitors for each of the studied plants (5-21 species) indicates that none of the target species depends on a single pollinator and they are therefore not at high risk of pollinator loss. *Euphrasia azorica*, the species with the lowest number of pollinators, received the smallest amount of total observation time (c. 7 hours), so the observed five species probably underestimate its pollinator community.

Of the 31 pollinator species found during the study (Table 2), 21 are probably native but only two of them are endemic to the Azores: the micromoth *Micrurapteryx bistrigella* and the syrphid fly *Sphaerophoria nigra*. On Corvo, both were only seen in the flowers of *M. azorica*. Nevertheless, they do not seem to be specialised: *Sphaerophoria nigra* was seen visiting a range of Asteraceae and Lamiaceae on São Jorge (JAW & HS, pers. obs.) and *Micrurapteryx bistrigella* has been reported from parts of the archipelago where *M. azorica* does not exist (Borges et al. 2010b). There might be additional endemics among the unidentified species on our list, especially among the Microlepidoptera, but the majority of the observed insects clearly are generalists and at least six of them are introduced species (Table 2).

The high proportion of generalists indicates that the pollination networks of the four plant species are relatively resilient, i.e. the loss of individual species would not constitute an immediate threat (Kaiser-Bunbury et al. 2017). The effectiveness of generalist pollinators has been investigated in many studies (e.g. Larsson 2005; Maldonado et al. 2013), with particular attention directed towards the impact of human-induced shifts in pollinator composition (e.g. Traveset & Richardson 2006; Picanço et al. 2017). In our case, the proportion of Diptera in pollinators of the four studied plant species is particularly high for *E. azorica* and *M. azorica*,

the two plant species growing in higher elevations in the crater of the island which is in large parts used as cattle pasture. Two of the most frequent Dipteran flower-visitors, *Scathophaga stercoraria* and *Sepsis* species are tied to animal excrements in their lifecycle, while *Calliphora* lay their eggs on corpses or other protein-rich substrates and *Pollenia* parasitizes on earthworms, which are all introduced to the islands. This indicates a shift in pollinators related to transformation of the once almost completely forest-covered islands into pasture land. Introduced Diptera probably replaced more specialised native pollinators, which could have negatively impacted the reproductive success of native plants. Diptera in general do not collect pollen or nectar for their larvae but only use it for direct consumption. They also use the flowers as protection from wind, as sites for predatory activity, for mating or to lay eggs. As they do not specifically visit the reproductive structures of the flowers, they are most likely less efficient pollinators than specialised Hymenoptera or Lepidoptera. Nevertheless, because of their high abundance, the probability of pollen transport by flies is relatively high (Ssymank et al. 2008; Inouye et al. 2015; Orford et al. 2015) and even though they are less efficient, due to their high numbers, they might be an important substitute for extinct specialist pollinators.

Honeybees were observed only on *A. vidalii*, not on the other study plants and only in the population on Flores Island. No honeybees were observed on the study plants on Corvo, probably because only eight beehives existed there in 2015, all in the eastern part of the island (Pedro M. Domingos, pers. comm., 28.08.2015), where invasive plants (e.g., *Pittosporum undulatum*, *Acacia melanoxylon*) provide plenty of nectar. Honeybees can negatively impact the reproductive biology of endemic plants (Valido & Olesen 2010) or sometimes save endemic plants whose native mutualistic networks collapsed (Kueffer & Kaiser-Bunbury 2013). Their role on Corvo so far can be neglected, but in case of an expansion of beekeeping on the island, their impact on pollination networks of the endemic flora would have to be carefully assessed.

Specialist pollinators like birds or lizards were not at all observed on the study plant species. The Eurasian blackcap, *Sylvia atricapilla*, is the only Azorean bird known to pollinate flowering plants. On Flores and Terceira, it regularly visits the flowers of the introduced *Aloe arborescens* (HS, pers. obs.), but never any of the study species. Lizard pollination of *Azorina vidalii* has been reported from Santa Maria and Terceira (Olesen et al. 2012) but was not witnessed on Corvo. The only lizard species in the Azores, *Lacerta dugesii*, is a recent introduction from Madeira (Brehm et al. 2003; Medeiros et al. 2010), and therefore unlikely to be a legitimate pollinator of the Azores bellflower.

The large proportion of well-developed seeds in *A. vidalii*, *M. azorica* and *E. azorica*, and a relatively high proportion of young individuals in the former two species suggests that they successfully reproduce. The generalised pollinator network we found with possibly additional contribution of wind pollination in *A. vidalii* and some selfing in *M. azorica* therefore seems largely effective. For the annual *E. azorica*, monitoring of the population size over a period of several years would be required to examine whether the relatively high number of individuals in 2015 is representative or a consequence of favourable conditions in this year.

The reduced seed set and relatively low proportion of young individuals in the *S. azorica* populations are probably linked to higher levels of pre-dispersal seed predation, a widespread phenomenon in species of this family (Bode & Gilbert 2016; Pickering 2009). Due to its high vegetative reproduction and in general high population size, *S. azorica* so far seems to be stable, at least in the coastal areas (Schaefer 2015) but more studies on the efficiency of sexual reproduction in this species are required.

The very small and fragmented population of *M. azorica* so far is still reproducing but self-pollination might be largely responsible for the relatively high seed set in spite of its fragmented distribution on Corvo. A detailed genetic monitoring and in-situ management are therefore required to save it from extinction.

### Implications for conservation

The results of this study suggest that there is no

pollinator limitation in the four study species, and reproductive success seems stable in *A. vidalii*, *E. azorica* and *M. azorica*. Therefore, conservation measures should focus on other threats. The two mainly coastal species *A. vidalii* and *S. azorica* seem to have stable populations in and around the village at the moment but since most of their habitat is not legally protected, they are particularly susceptible to land use changes. For the species growing at higher altitudes in protected areas of the crater (*M. azorica*, *E. azorica*, high altitude population of *S. azorica*), the often high grazing pressure and trampling by cows and goats is the main threat. In inaccessible areas, landslides and invasive plants are the biggest problem. Fencing off parts of the crater area and hereby reducing the grazing pressure seems to be the most promising conservation measure. Rabbits are so far absent from Corvo, so the fences could be relatively simple and cheap. Similar approaches on the Canaries, Madeira, and other parts of the Azores allowed for quick regeneration of threatened endemic populations (Garzón-Machado et al. 2010).

### CONCLUSIONS

All plants were found to be pollinated by a mix of introduced and native insect species (Diptera, Hymenoptera, Lepidoptera and Hemiptera) with possibly some additional selfing and wind-pollination in *M. azorica* and *A. vidalii*. None of them seem to be threatened by pollinator loss. It is likely, however, that the pollinator networks as we observe them today, are very different from the situation found by the first human settlers in the Azores some 500 years ago. We can speculate that endemic specialist pollinators might have played a significant role in the pristine Azores ecosystems but this is almost impossible to test.

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