Wild bee-plant network of Madeira Island with a comparison to Porto Santo (Madeira Archipelago, Portugal)

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With 7 figures and 5 tables

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ABSTRACT: The aim of this study was to analyse wild bee-plant interactions in Madeira Island and construct a network structure covering the largest parts of the island and most altitudes and habitat types. The interaction data were sampled at 179 localities from 1989 to 2012 mainly by the authors; additionally, data from the collections of the Laboratório Agrícola da Madeira, Camacha (ICLAM) and the Museu de História Natural do Funchal, Madeira, Portugal, were used. Twelve wild-bee species (the complete species pool of permanently established Madeiran wild-bee species) were collected or observed on 81 plant taxa (belonging to 30 plant families). The total dataset from Madeira Island includes 637 data points of bee-plant interactions. We assigned the data set to the main thermotypes – infra- / thermo-Mediterranean zone as well as meso-Mediterranean / temperate zone – and constructed two networks. In contrast to most of the mainland networks of temperate and Mediterranean ecosystems with more wild-bee than plant species, the bee-plant networks demonstrate high asymmetry, with many more plant than bee species. This phenomenon has also been documented, *e.g.*, in Porto Santo (Madeira Archipelago). Wild-bee species and plant species were highly interconnected within the network, showing that even under difficult and strong climatic conditions with unequal resource availabilities, there were enough alternatives for obtaining food resources. Ten of the wild-bee species are euryanthic, with only two species (the introduced *Hylaeus pictipes* and the endemic *Andrena maderensis*) showing stenanthy. The high individual numbers and euryanthic behaviour of most wild-bee species met the precondition for network stability. The plant families with the highest importance as food resources are in the orders Asteraceae (51%), Brassicaceae (14%), Fabaceae (8%) and Boraginaceae (8%). These offer different flower types (actinomorphic, zygomorphic, Asteroideae and Cichorioideae types) and a variability of flower types for wild-bee species of different body sizes and foraging behaviour. Similar to the results of the bee-plant network of Porto

Santo, most of the foraged plant species were endemic or native species. Introduced and cultivated plant species mainly showed minor importance. We found no disturbances of the network by the introduced masked bee *Hylaeus s. signatus* and the probably introduced bumblebee *Bombus r. ruderatus*. Differences and similarities between the bee-plant networks of Madeira Island (infra- / thermo-Mediterranean zone) and the corresponding areas of the much older island Porto Santo (xeric- / infra-Mediterranean zone) are discussed in this paper.

Keywords: bipartite graph, endemism, flower types, flower-visiting behaviour, introduced species, island biogeography, Hymenoptera Apoidea, Madeira Archipelago, native species.

RESUMO: O objetivo deste estudo foi analisar as interações entre abelhas silvestres e plantas na Ilha da Madeira e construir uma estrutura de rede que abrangesse a maior parte da ilha, a maioria das altitudes e tipos de habitat. Os dados de interação foram amostrados em 179 localidades de 1989 a 2012, principalmente pelos autores; adicionalmente, foram utilizados dados das coleções do Laboratório Agrícola da Madeira, Camacha (ICLAM) e do Museu de História Natural do Funchal, Madeira, Portugal. Doze espécies de abelhas silvestres (todas as espécies de abelhas silvestres estabelecidas permanentemente na Madeira) foram recolhidas ou observadas em 81 taxa de plantas (pertencentes a 30 famílias). O conjunto total de dados da Ilha da Madeira inclui 637 pontos de dados de interações abelha-planta. Atribuímos o conjunto de dados aos principais termótipos – zona infra- / termo-mediterrânea, bem como zona meso-mediterrânea / temperada – e construímos duas redes. Em contraste com a maioria das redes continentais de ecossistemas temperados e mediterrâneos com mais espécies de abelhas silvestres do que de plantas, as redes estudadas demonstram alta assimetria, com muito mais plantas do que espécies de abelhas. Este fenómeno foi também documentado, por exemplo, no Porto Santo (Arquipélago da Madeira). As espécies de abelhas silvestres e espécies de plantas estavam altamente interligadas dentro da rede, mostrando que, mesmo sob condições climáticas difíceis e fortes, com disponibilidade de recursos desiguais, havia alternativas suficientes para a obtenção de recursos alimentares. Dez das espécies de abelhas silvestres são generalistas (visitam uma grande variedade de plantas), com apenas duas espécies (a introduzida *Hylaeus pictipes* e a endémica *Andrena maderensis*) mostrando uma especialização numa família de plantas. Os altos números individuais e o comportamento generalista da maioria das espécies de abelhas selvagens cumpriram a pré-condição para a estabilidade da rede. As famílias de plantas com maior importância como recursos alimentares estão nas ordens Asteraceae (51%), Brassicaceae (14%), Fabaceae (8%) e Boraginaceae (8%). Estes oferecem diferentes tipos de flores (tipos actinomórficos, zigomórficos, Asteroideae e Cichorioideae) e uma variabilidade de tipos de flores para espécies de abelhas selvagens de diferentes tamanhos corporais e comportamento de alimentação. À semelhança dos resultados da rede de abelhas do Porto Santo, a maioria das espécies de plantas alimentares eram espécies endémicas ou nativas. As espécies de plantas introduzidas e cultivadas mostraram principalmente menor importância. Não encontramos distúrbios na rede provocados pela abelha introduzida *Hylaeus s. signatus* e pelo abelhão, provavelmente introduzido *Bombus r. ruderatus*. As diferenças e semelhanças entre as redes apícola da ilha da Madeira (zona infra- termo-mediterrânica) e as áreas correspondentes da muito mais antiga ilha do Porto Santo (zona xérica- / infra-mediterrânica) são discutidas neste trabalho.

Palavras-chave: gráfico bipartido, endemismo, tipos de flores, comportamento de visitar flores, espécies introduzidas, biogeografia de ilhas, Hymenoptera Apoidea, Arquipélago da Madeira, espécies nativas.

INTRODUCTION

An analysis of the wild-bee fauna of the Macaronesian Archipelagos showed that the Azores, the Madeira Archipelago and the Canary and Cape Verde Islands differ considerably in wild-bee species composition, number of species and proportion of endemic, native and introduced wild-bee species (Kratochwil & Schwabe, 2018a). The reasons for these differences are, among others, the geology and history of the islands and archipelagos, the climatic conditions, the diversity of orography and habitats, the age of the islands and the distances to the colonisation sources of neighbouring islands and the mainland.

The lowest wild-bee species numbers were detected in the Azores (17 species, most of them introduced) and Cape Verde (14 species), as well as in the Madeira Archipelago with 19 species. The highest species numbers were found in the Canary Islands, with a total number of 124 species (highest wild-bee diversity: Fuerteventura with 67 species) (Kratochwil & Schwabe, 2018a).

Many habitat types on oceanic islands are considered highly endangered due to invasive plant and animal species, directly or indirectly introduced by humans. Thus, compared to the mainland, oceanic islands often have introduced wild-bee species (Russo, 2016). Examples can be found in: the Galápagos (Rasmussen *et al.*, 2012); Fiji, Samoa and Vanuatu (Groom *et al.*, 2014a, 2014b); French Polynesia (Groom *et al.*, 2016); Hawaii (Snelling, 2003; Magnacca & King, 2013).

The number of introduced wild-bee species in the Macaronesian archipelagos displays a gradient from north to south (Kratochwil & Schwabe, 2018a): the Azores are mostly affected by wild-bee introductions. Of the 17 species that occur there, only one (*Hylaeus azorae*, of whom only a single specimen was found) is considered indigenous or, in this case, endemic. All others were introduced after human colonisation (95%). In the Canary Islands, there are only four introduced species out of 124 total (3%) and in the Cape Verde Islands, one of 14 species (7%) (Kratochwil & Schwabe, 2018a).

For the flora of the Macaronesian archipelagos, the percentages are partly comparable: the Azores are characterised by appr. 80% introduced plant species (Schaefer *et al.*, 2011) and the Madeira Archipelago by appr. 33% (Borges *et al.*, 2008). In the Canary Islands, the percentages of introduced plant species are by appr. 37% (Arechavaleta *et al.*, 2010) and Cabo Verde by appr. 60% (National Directorate of Biodiversity in Cabo Verde, 2015).

Wild bees can be considered essential pollinators for the native and endemic plant species of the Macaronesian islands (García, 2000; Kratochwil & Scheuchl, 2013; Kratochwil *et al.*, 2014; Kratochwil & Schwabe, 2018b), although other insect groups (in particular, *e.g.*, Diptera, Coleoptera and other Hymenoptera) and sometimes lizard (Olesen & Valido, 2003a; Olesen *et al.*, 2012) and bird species (Olesen & Valido, 2003b; Ollerton *et al.*, 2009) are also pollinators.

Many native and endemic plant species require cross-pollination; see, *e.g.*, Aldridge (1981) and, for *Echium*, Kraemer & Schmitt (1997). Nevertheless, many plant species are also (often in addition to animal pollination) self-pollinators, *e.g.*, some Brassicaceae as *Cakile maritima* (Davy *et al.*, 2006) occurring on Porto Santo, or are characterised by apomixis, *e.g.*, for *Rubus*, Sochor *et al.* (2015). The Macaronesian woody *Echium* species are self-incompatible outbreeders (Aldridge, 1981), which is, *e.g.*, also the case for the non-endemic herbaceous *E. plantagineum* (Flacher *et al.*, 2017).

We use the term 'flower visitor-plant network' and not 'pollinator-plant network' or 'mutualistic network' because successful pollination cannot be proved for most interactions. As shown in many studies, the specific flower-visiting behaviour is much more important for successful pollination than the quantity of visits (Estfeld *et al.*, 2009).

We studied the flower visitor-plant network in Porto Santo (Madeira Archipelago) for wild-bee species (Hymenoptera, Apoidea, Anthophila) and butterfly species (Papilionoidea) (Kratochwil *et al.*, 2018a, Kratochwil & Schwabe, 2018b). In contrast to other network studies (Olesen *et al.*, 2002), we suggest that it is useful to analyse taxa-related networks. If, *e.g.*, interactions for different insect orders are analysed together, each one's importance for pollination is often not comparable.

The investigations of the bee-plant network of Porto Santo provided the following results (Kratochwil & Schwabe, 2018b):

(1)   The bee-plant network showed high asymmetry (six wild-bee species versus 29 plant species).

(2)   All species in the network are highly interconnected.

(3)   Euryanthic wild-bee species were more frequently found than were stenanthic, but in no case did a single bee species cover the entire spectrum of flowering plant species. The dominant generalist wild-bee species of Porto Santo is *Amegilla quadrifasciata maderae* (an endemic subspecies of *Amegilla quadrifasciata* distributed in the Madeira Archipelago).

(4) There is one stenanthic wild-bee species in the network (*Andrena portosanctana*).

(5) The majority of plant species visited by wild bees can be classified as endemic or native.

(6) Introduced plant species have some significance in the network, especially under extreme environmental conditions in very dry years and low flower densities of native flora. This was shown for *Oxalis pes-caprae* (introduced from the Cape region of South Africa).

Only one introduced wild-bee species (*Hylaeus pictipes*) was present, though without evidence of permanent establishment (Kratochwil & Schwabe, 2018b). According to our data, at present, introduced wild-bee species have had no negative effects at the ecosystem level. Investigations of the butterfly-plant network (Kratochwil *et al.*, 2018a) yielded similar results. The introduction of rabbits and hybridisation of the endemic *Echium portosanctensis* with planted *Echium* species caused severe problems for island-typical biodiversity (Kratochwil & Schwabe, 2018b).

In the study of the wild bee-plant network in Madeira Island we ask the following questions:

(1) Is there a highly asymmetric network similar to that of Porto Santo with a small number of wild-bee species and a higher number of visited plant species?

(2) Are the wild-bee and plant species in the network highly interconnected?

(3) Are there differences between the main thermotypes of Madeira Island in the network structure?

(4) Which plant families and species were visited by wild bees?

(5) Which wild-bee species show euryanthic behaviour and which species are stenanthic?

(6) Are there special patterns of the relationships between endemic and native wild-bee species and endemic and native plant species?

(7) What is the impact of introduced wild-bee species and introduced plant species on the bee-plant network of Madeira Island?

(8) Are there differences between the bee-plant network of Madeira Island (infra-/thermo-Mediterranean zone) and that of Porto Santo (xeric-/infra-Mediterranean zone)?

Physico-geographical factors

Madeira Island, the largest island of the Madeira Archipelago, covers about 730 km² and has an age of about 4.6 Ma. Together with the Desertas Islands (3.6 Ma), it is much younger than Porto Santo (11.1 to 14.3 Ma) (Galopim de Carvalho & Brandão, 1991; Geldmacher *et al.*, 2000). During the last glacial period (18,000 years BP), a land bridge connected Madeira Island with the Desertas Islands (Brehm *et al.*, 2003). During the last glacial optimum the sea level was 120 m lower than today (Garcia-Talavera, 1999). Madeira Island has a strong relief and is rich in ribeiras (steep valleys); the highest elevation is the Pico Ruivo de Santana (1,862 m *a.s.l.*). The coast lines are generally steep.

The climate is oceanic and trade winds blow from northeast most of the year. On the windward side, the annual precipitation reaches more than 1,500 mm/a (de Lima & de Lima, 2009), the lee sides have less precipitation by about 500 to 600 mm/a. The southern coastline and the eastern area (Ponta de S. Lourenço) are relatively dry. Frost and snow fall occur in the winter months only in altitudes above 1,200 m. *a.s.l.* (Tavares, 1965).

In times of the discovery of the Madeiran Archipelago, Madeira was nearly totally arboreous, as documented by the Florentine sea map of 1351. In the report of the discoverer Zarco (1419), arboreous vegetation was mentioned as stretching from the coastal line to the mountain peaks. To a large extent, the original vegetation was destroyed, fragmented or replaced by secondary vegetation. The vegetation has been studied, *e.g.*, by Sjögren (1972), Oberdorfer (1975), Capelo *et al.* (1999, 2005) and Costa *et al.* (2012).

METHODS

Biogeographic differentiation

Rivas-Martínez (1996, 2009), Rivas-Martínez *et al.* (1999) and Mesquita *et al.* (2004) developed biogeographical differentiation of the Island into thermo- and ombrotypes (among other approaches), which we used to separate the summarised infra- and thermo-Mediterranean zones versus the colder and more humid temperate zone *s.l.* (summarised meso-Mediterranean and temperate zones). This approach was also the basis for comparing the bee-plant networks of Madeira Island and Porto Santo; the latter comprises mainly the xeric- / infra-Mediterranean zone.

Database

The bee-plant networks are based on the database of collected or observed specimens of Hymenoptera Anthophila compiled by A. F. Aguiar, A. Kratochwil and

J. Smit. We also included data from the collections of the Laboratório Agrícola da Madeira, Camacha (ICLAM) and the Museu de História Natural do Funchal (Madeira, Portugal). All bee specimens were checked by the authors. The interaction data were sampled at 179 localities from 1989 to 2012 mainly by the authors. The total dataset included 637 data points of bee-plant interactions for Madeira Island: 12 wild-bee species (Table 1) and 81 plant taxa (Table 2). Plant taxa represent 30 plant families.

The data were collected by: A. Kratochwil, A. Schwabe, C. F. Kratochwil (402 collected bees on flowers and 55 observations of interactions), A. F. Aguiar (eight collected bees on flowers and 82 observations of interactions), J. Smit (27 collected bees on flowers from 24 data points published in Smit & Smit, 2003), ICLAM (60 collected bees on flowers) and the Museu de História Natural do Funchal (three collected bees on flowers). In some cases, we only found data for plant taxa on the family level, which we included.

Additionally, there are 10 interaction data points from the Desertas Islands (Doca, Deserta Grande): *Amegilla quadrisfasciata maderae* on *Carlina salicifolia* (2 males, 1 female; ICLAM n = 2, A. F. Aguiar n = 1), five specimens visiting *Mesembryanthemum crystallinum* (A. F. Aguiar) and *Lasioglossum villosulum* visiting yellow Asteraceae (1 female); for Bugio, there is one female of *A. q. maderae* visiting *Mesembryanthemum crystallinum* (Museu de História Natural do Funchal).

We did not include the semi-domesticated honeybee *Apis mellifera* Linnaeus, 1758, although flower visits were available. The local and temporal occurrences of honeybees are strongly influenced by human activity and so results are not generalisable.

We found almost no data about single bee-plant interactions of Madeira Island in the literature (see also Valido & Olesen, 2010). Fellendorf *et al*. (1999) often did not distinguish whether a specific interaction was observed on Porto Santo or Madeira Island or did not differentiate single bee-plant interactions; also, there have been problems with species determinations (Kratochwil *et al*., 2018a).

For the nomenclature of wild-bee species, we used the updated checklist from Kratochwil *et al*. (2018b). The nomenclature of plant species follows Jardim & Menezes de Sequeira (2008); additionally, we checked Press & Short (1994) for further information.

Twelve wild-bee species could be included into the network analysis of Madeira Island (this means the complete species pool with established populations). For four further species, there were only some very rare detections (*Hoplitis acuticornis*, *Megachile versicolor*, *Megachile pusilla*, *Stelis ornatula*), indicating that these species are likely to have been introduced, but have not established populations (Kratochwil *et al*., 2018b). *Megachile pusilla* was collected on flowers of *Euphorbia hypericifolia*, cultivar 'Breathless White' in the Municipal Gardens of Funchal, by M. Andrade. *E. hypericifolia* is native to the southernmost parts of the U. S., Mexico, the West Indies, Central America and South America.

The wild-bee species were classified into the categories 'endemic for Madeira Archipelago' (end.), 'endemic for Macaronesia' (mac.), 'native' (nat.), 'probably native' (nat.?), 'introduced' (intr.) and 'probably introduced' (intr.?). Only one wild-bee species of the network can be considered introduced (*Hylaeus s. signatus*). For *Bombus r. ruderatus*, we suppose an early introduction (Kratochwil *et al*., 2018). The wild-bee species represent the families Colletidae, Andrenidae, Halictidae, Megachilidae, Anthophoridae and Apidae (Table 1).

Except for the two *Hylaeus species* (*H. s. signatus*, *H. maderensis*), all other species included in the two presented bee-plant networks are common and widespread on Madeira Island. The most common wild-bee species in our bee-plant network is *Andrena wollastoni*, followed by *Lasioglossum wollastoni*, *Amegilla quadrifasciata maderae*, *Osmia niveata* and *Lasioglossum villosulum* (Fig. 1).

Andrena wollastoni and *Halictus frontalis* reach the highest altitudes (1,750 m *a.s.l.*), whereas other species are limited to lower altitudes (*Andrena maderensis*, from sea level to up to 750 m *a.s.l.*; *Osmia niveata*, up to 610 m *a.s.l.*).

The aim was to detect the most representative bee-plant interactions for the entire area of Madeira Island and at various altitudes.

The studied bee-plant interactions cover different altitudes of Madeira Island and are spread over the whole island (Fig. 2); these were collected in the 98 grid cells (179 localities) of the UTM map (grid cell = 1 km x 1 km). To elucidate the plant-bee network of the infra- / thermo-Mediterranean zone and to compare the results with Porto Santo (which is restricted to the xeric- / infra-Mediterranean zone), we separated the infra- / thermo-Mediterranean network from the network of the more humid, mainly temperate zone (meso-Mediterranean / temperate zone = temperate zone *s.l.*). For the infra- / thermo-Mediterranean zone we were able to construct a network (covering 54 grid cells) with 530 interactions. For the harsh environment (referring to wild-bee species) of the temperate zone *s.l.* (high humidity, windy sites) we constructed a network of 107 interactions in 44 grid cells.

Table 1 – Species list of wild bees in the Madeira Island bee-plant network, including species status. Families: And = Andrenidae, Ant = Anthophoridae, Api = Apidae, Col = Colletidae, Hal = Halictidae, Meg = Megachilidae. Statuses: end. = endemic (Madeira Island or Madeira Archipelago), intr. = introduced, nat. = native, nat.? = probably native, intr.? = may be introduced.

	Family	Abbreviation	Status
Amegilla quadrifasciata maderae (Sichel, 1868)	Ant	Amequa	end.
Andrena maderensis Cockerell, 1922	And	Andmad	end.
Andrena wollastoni Cockerell, 1922	And	Andwol	end.
Bombus r. ruderatus (Fabricius, 1775)	Api	Bomrud	intr.?
Bombus terrestris lusitanicus Krüger, 1956	Api	Bomter	nat.
Halictus frontalis Smith, 1853	Hal	Halfron	end.
Hylaeus maderensis (Cockerell, 1921)	Col	Hylmad	end.
Hylaeus s. signatus (Panzer, 1798)	Col	Hylsig	intr.
Lasioglossum v. villosulum (Kirby, 1802)	Hal	Lasvil	nat.?
Lasioglossum wollastoni Cockerell, 1922	Hal	Laswol	end.
Osmia madeirensis van der Zanden, 1991	Meg	Osmmad	end.
Osmia niveata (Panzer, 1798)	Meg	Osmniv	nat.
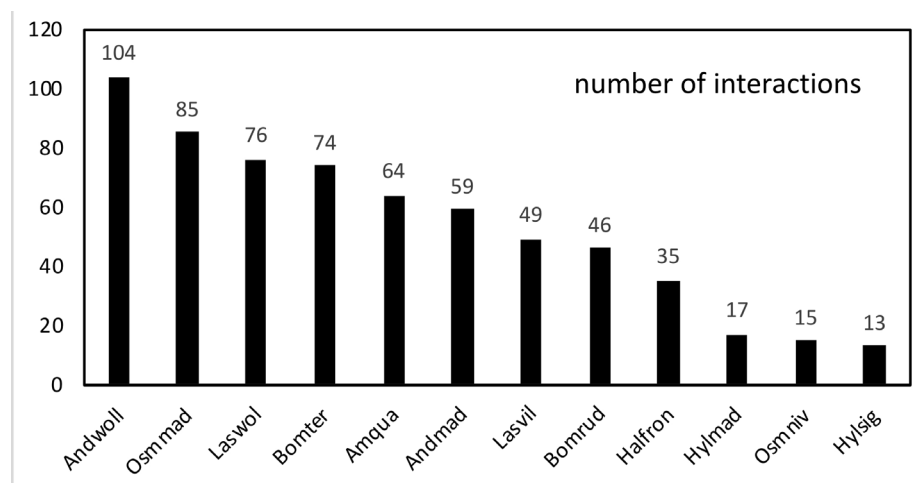
Fig. 1 – Number of wild-bee interactions concerning different bee species (Abbreviations in Table 1).
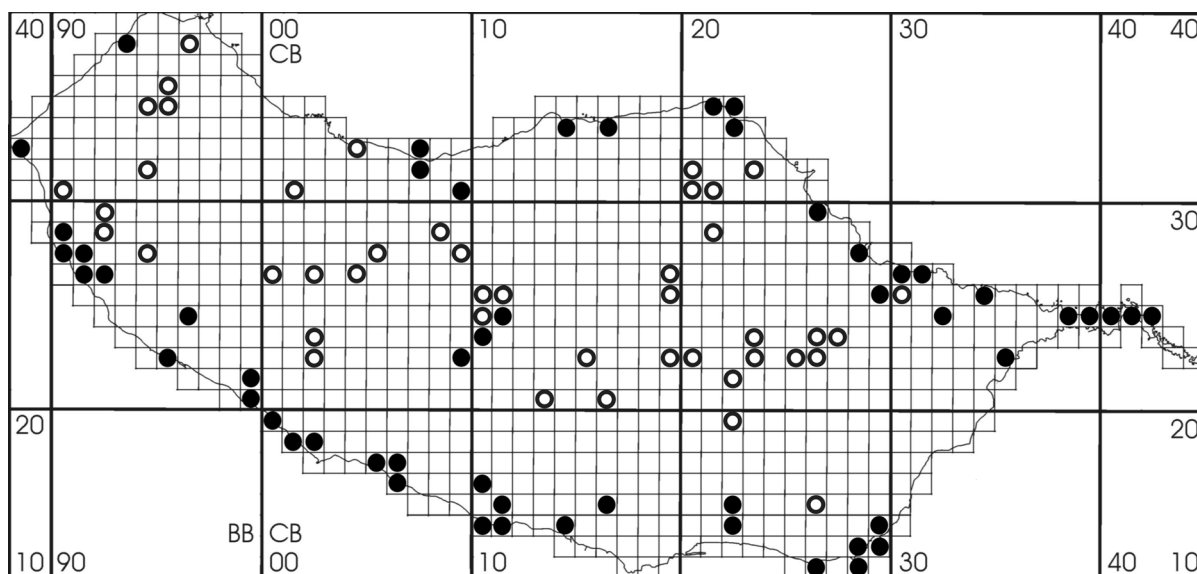
Fig. 2 – Grid elements (1 km x 1 km), based on the 1/25000 scale military map of the Madeira Archipelago (2004). Madeira Island comprises 826 raster elements. Bee-plant interactions were detected in 98 grid elements (179 localities). Black points: 54 grids of the infra- / thermo-Mediterranean zone; White points: 44 grids of the temperate zone *s.l.*, all with sampled interaction data for wild bees and plants. The dominant thermotype of a grid element was assigned according to the map from Capelo *et al.* (2004).

RESULTS AND DISCUSSION

Data analyses

Interaction networks were analysed using the 'bipartite package' (Dormann *et al.*, 2008; R Core Team, 2018). The 'bipartite package' provides functions to visualise webs and calculate a series of indices. For the comparison of the bee-plant networks of Madeira Island and Porto Santo we measured only some suitable network indices. Dormann *et al.* (2009) pointed out, that some indices are sensitive to asymmetry and networks with less than 50 species in both levels are problematic (Blüthgen *et al.*, 2008). These problematic indices are, *e.g.*, interaction evenness, connectance, cluster coefficients, H2', interaction strength asymmetry, togetherness and C-score. Some network indices were tested by Kratochwil *et al.* (2009). We took the following parameters into account: Linkage density (marginal totals-weighted diversity of interactions per species quantitatively; average number of links per species), links per species (mean number of links per species qualitatively; sum of links divided by number of species), mean number of shared plant species, mean number of shared wild-bee species, network size (product of wild-bee species number and plant species number of the network; M = P x B), niche overlap in plant species (mean similarity in interaction patterns), niche overlap in wild-bee species, number of plant species, number of wild-bee species, partner diversity of plant species (weighted mean Shannon diversity of the number of interactions for the plant species), partner diversity of wild-bee species (weighted mean Shannon diversity of the number of interactions for the wild-bee species), Shannon diversity (diversity of interactions; weighted mean Shannon diversity of the number of interactions within the wild-bee species or plant species), species numbers and web asymmetry (definitions: *e.g.*, Blüthgen *et al.*, 2008; Dormann *et al.*, 2008; Dormann *et al.*, 2009; Landi *et al.*, 2018).

To measure the degree of generalisation, the linkage levels of the plant and bee species were assessed (Olesen *et al.*, 2002; Dupont *et al.*, 2003). Linkage levels characterise the number of interactions per species. The linkage level L_m of a bee species m is the number of plant species visited by m. The linkage level L_n of a plant species n is the number of bee species visiting n. For comparisons, the linkage level was standardised as the relative linkage of bee species $l_m = L_m/P$ (P = total number of bee species). Species with high linkage levels utilise more species than do species with low linkage levels.

Network structure

The bipartite graphs of the bee-plant networks of Madeira Island (Fig. 3, Fig. 4) show the flower-visiting bee species on the top row and the plant taxa and visited plant species on bottom row. Wild-bee species and plant taxa are connected with interaction links.

Both bee-plant networks demonstrate high asymmetry (Fig. 3: infra- / thermo-Mediterranean zone with 12 wild-bee species versus 61 plant taxa; Fig. 4: temperate zone *s.l.* with eight wild-bee species versus 34 plant taxa). This phenomenon of the asymmetry of bee-plant networks seems to be typical for oceanic islands and extreme habitats (see below); it has also been documented for Porto Santo (Kratochwil & Schwabe, 2018b), with six wild-bee species versus 29 plant species (see below).

Central European and Mediterranean bee-plant networks are in most cases characterised by reverse asymmetry, with many wild-bee species visiting fewer plant species (Motten, 1982, in Dormann *et al.*, 2009; Ollerton *et al.*, 2003; Beil *et al.*, 2014; Schleuning *et al.*, 2016).

There are several hypotheses for this asymmetry on oceanic islands. The dispersal of wild-bee species is far more difficult than that of many plant species, where small seeds can be dispersed (*e.g.*, by birds) over long distances. Also, the establishment of wild-bee species is difficult (Kratochwil, 2003). Generally, only a few wild-bee species reach remote oceanic islands. It is generally characteristic that the pollinator fauna is poor in species (*e.g.*, Linsley & Usinger, 1966). Olesen & Jordano (2002) analysed 29 complete plant-pollinator networks that encompassed arctic, alpine, temperate, Mediterranean and subtropical-tropical areas (including five oceanic island networks) and found that oceanic island networks have poor numbers of animal pollinators (lower ratios of animal to plant species compared to mainland networks).

Other asymmetric bee-plant networks with low numbers of wild-bee species and higher numbers of plant species are, *e.g.*, known from subalpine and alpine networks. In the Victorian Alps (Australia), Johanson *et al.* (2018) detected 22 wild-bee species on 67 plant species in the network.

All 12 wild-bee species that occur permanently on Madeira Island are included in our study. We suppose that *Hoplitis acuticornis*, *Megachile versicolor*, *Megachile pusilla*, and *Stelis ornatula* are examples of species that reached Madeira Island through natural processes or human

Table 2 – List of the plant taxa of the bee-plant network of Madeira Island including abbreviations and species status. Plant families: Aiz = Aizoaceae, Ama = Amaryllidaceae, Api = Apiaceae, Ast = Asteraceae, Bor = Boraginaceae, Bra = Brassicaceae, Cac = Cactaceae, Cle = Clethraceae, Con = Convolvulaceae, Cra = Crassulaceae, Cuc = Cucurbitaceae, Eri = Ericaceae, Eup = Euphorbiaceae, Fab = Fabaceae, Ger = Geraniaceae, Hyd = Hydrangeaceae, Hyp = Hypericaceae, Lam = Lamiaceae, Mal = Malvaceae, Oxa = Oxalidaceae, Pap = Papaveraceae, Pla = Plantaginaceae, Poa = Poaceae, Pro = Proteaceae, Res = Resedaceae, Ros = Rosaceae, Scr = Scrophulariaceae, Tro = Tropaeolaceae, Val = Valerianaceae, Ver = Verbenaceae.

Statuses: end. = endemic Madeira Archipelago, mac. = endemic Macaronesia, intr. = introduced, nat. = native, nat.? = probably native, intr.? = probably introduced, cult. = cultural plant taxa. Ten plant species were only used by males (*Aeonium glandulosum*, *Calendula arvensis*, *C. maderensis*, *Centranthus calcitrapae*, *Clethra arborea*, *Hydrangea macrophylla*, *Hypochoeris radicata*, *Lantana camara*, *Petroselinum crispum*, *Tagetes* spec.).

	Abbreviation	Family	Status
Aeonium glandulosum	Aeoglan	Cra	end.
Aeonium glutinosum	Aeoglu	Cra	end.
Agapanthus praecox	Agapra	Ama	cul.
Ageratina adenophora	Ageade	Ast	intr.
Aichryson villosum	Aicvil	Cra	mac.
Andryala glandulosa	Andgla	Ast	nat.
Aptenia cordifolia	Aptcor	Aiz	intr.
Arctium minus	Arcmin	Ast	nat.
Argyranthemum pinnatifidum s.l.	Argpin	Ast	end.
Asteraceae (yellow)	Astyel	Ast	
Bidens pilosa	Bidpil	Ast	intr.
Bituminaria bituminosa	Bitbit	Fab	nat.
Brassica napus subsp. *rapifera*	Branap	Bra	cul.
Brassica oleracea	Braole	Bra	cul.
Calendula arvensis	Calarv	Ast	nat.
Calendula maderensis	Calmad	Ast	end.
Carlina salicifolia	Carsal	Ast	mac.
Centranthus calcitrapae	Cencal	Val	nat.
Chrysanthemum segetum	Chrseg	Ast	intr.
Cirsium vulgare	Cirvul	Ast	intr.
Clethra arborea	Clearb	Cle	end.
Crassula ovata	Craovu	Cra	intr.
Crepis andryaloides	Creand	Ast	end.
Crepis vesicaria subsp. *haenseleri*	Creveh	Ast	nat.
Cucurbita pepo subsp. *pepo*	Cucpep	Cuc	cult.
Cytisus scoparius subsp. *scoparius*	Cytsco	Fab	intr.
Digitalis purpurea	Digpur	Scr	nat.
Echium candicans	Echcan	Bor	end.
Echium nervosum	Echner	Bor	end.
Echium plantagineum	Echpla	Bor	nat.
Erica platycodon subsp. *maderincola*	Eripla	Eri	end.
Erigeron karwinskianus	Erikar	Ast	intr.
Erysimum bicolor	Erybic	Bra	mac.
Eschscholzia californica	Esccal	Pap	intr.
Euphorbia pulcherrima	Euppul	Eup	cult.
Galactites tomentosa	Galtom	Ast	nat.
Gazzania spec. (yellow)	Gazyel	Ast	cult.
Geranium maderense	Germad	Ger	end.
Hakea sericea	Hakser	Pro	intr.
Helichrysum foetidum	Helfoe	Ast	intr.
Helminthotheca echioides	Helech	Ast	nat.?
Hibiscus spec.	Hibspe	Mal	cult.
Hydrangea macrophylla	Hydmac	Hyd	intr.
Hypericum spec.	Hypspe	Hyp	
Hypochoeris radicata	Hyprad	Ast	intr.
Ipomoea purpurea	Ipopur	Con	intr.
Lantana camara	Lancam	Ver	intr.
Lathyrus clymenum	Latcly	Fab	nat.
Leontodon taraxacoides subsp. *longirostris*	Leotar	Ast	nat.
Misopates orontium	Misoro	Scr	nat.
Oenanthe divaricata	Oendiv	Api	end.
Opuntia tuna	Oputun	Cac	intr.

Table 2 (continued).

|			
Oxalis pes-caprae	Oxacap	Oxa	intr.
Papaver rhoeas	Paprho	Pap	nat.
Petroselinum crispum	Petcri	Api	int.
Plantago spec.	Plaspe	Pla	
Poaceae	Poacea	Poa	
Raphanus raphanistrum subsp. *raphanistrum*	Raprap	Bra	nat.
Rapistrum rugosum s.l.	Raprug	Bra	nat.
Reseda luteola	Reslut	Res	nat.?
Rubus ulmifolius	Rubulm	Ros	nat.
Salvia leucantha	Salleu	Lam	intr.
Sechium edule	Secedu	Cuc	intr.
Sinapidendron angustifolium	Sinang	Bra	end.
Sinapis arvensis	Sinarv	Bra	nat.
Sisymbrium officinale	Sisoff	Bra	nat.
Sonchus asper	Sonasp	Ast	nat.?
Sonchus oleraceus	Sonole	Ast	nat.?
Sonchus spec.	Sonspe	Ast	
Stachys ocymastrum	Staocy	Lam	nat.
Tagetes spec.	Tagspe	Ast	cul.
Taraxacum officinale agg.	Taroff	Ast	nat.?
Torilis arvensis subsp. *neglecta*	Torarv	Api	nat.
Trifolium spec.	Trispe	Fab	
Tropaeolum majus	Tromaj	Tro	intr.
Ulex europaeus subsp. *latebracteatus*	Uleeur	Fab	intr.
Urospermum picroides	Uropic	Ast	nat.?
Vaccinium padifolium	Vacpad	Eri	end.
Verbena bonariensis	Verbon	Ver	intr.
Vicia benghalensis	Vicben	Fab	nat.
Vicia lutea subsp. *lutea*	Viclut	Fab	nat.
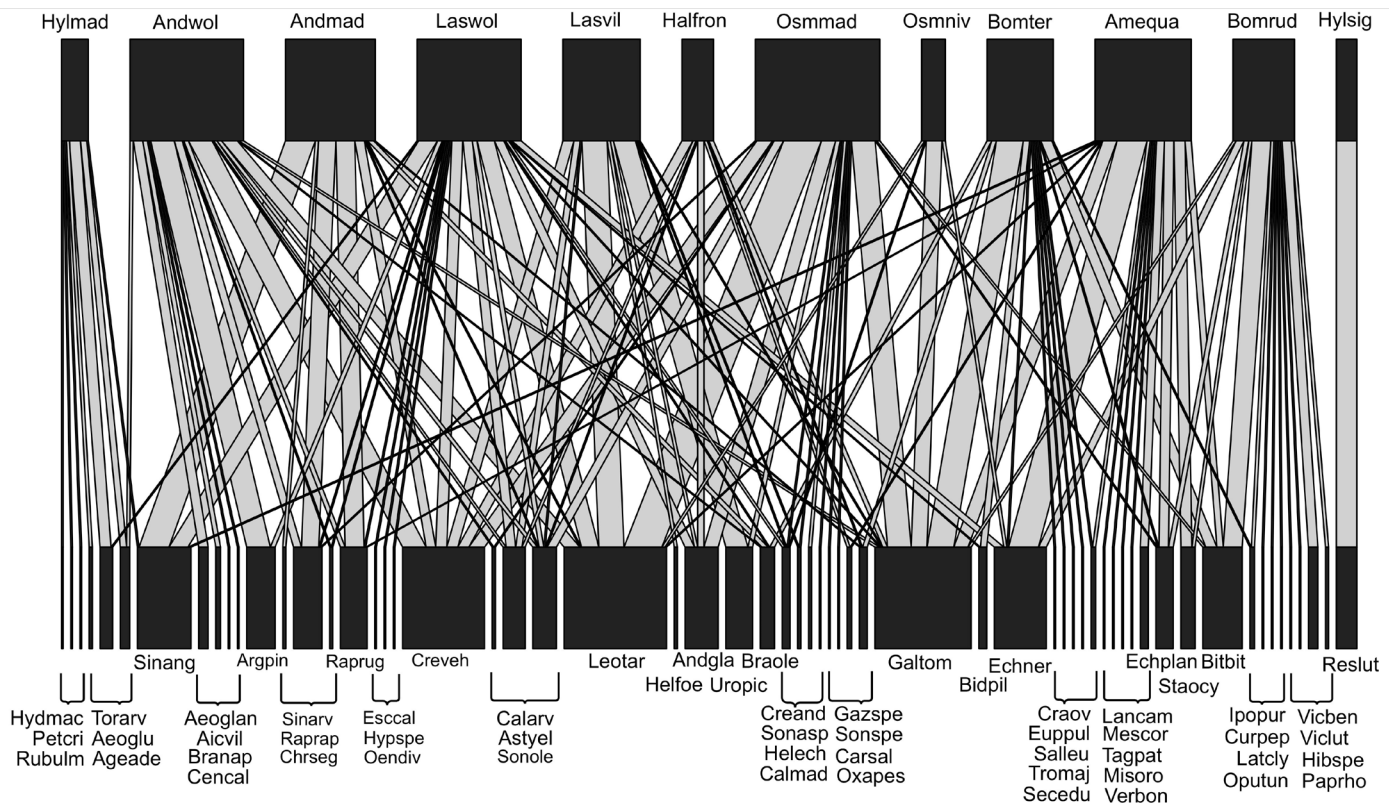
Fig. 3 – Bipartite graph of the bee-plant network of the infra- / thermo-Mediterranean zone of Madeira Island: the top row shows bee species and the bottom row shows plant taxa. For abbreviations see Tables 1 and 2.

impact but did not establish. Kratochwil & Schwabe (2018a) discussed the general aspects of wild-bee colonisation of the Macaronesian archipelagos, such as the distances to mainland sources and the ages and sizes of islands and archipelagos.

Comparing the bee-plant networks of the infra- / thermo-Mediterranean zone and the temperate zone *s.l.* revealed the following characteristics: The numbers of wild bee and plant species involved in the bee-plant network of the infra- / thermo-Mediterranean zone are higher, as are the values of the network size (Table 3). According to our data, *Hylaeus maderensis*, *Lasioglossum v. villosulum*, *Osmia niveata* and *Hylaeus s. signatus* are concentrated in this zone. For *L. v. villosulum*, there also are single observations in the temperate zone *s.l.* in our database, but without flower visits. *Andrena maderensis*, *Amegilla quadrifasciata maderae* and, partly, *Osmia madeirensis* show a preference for this zone and occur with smaller numbers in the upper zone. *A. q. maderae* was found up to 1330 m *a.s.l.* in our database, but without flower-visit data. The temperate zone *s.l.* (Fig. 4) is mainly characterised by *Bombus terrestris lusitanicus* and, especially, *Halictus frontalis*. The web asymmetry is higher in the infra- /thermo-Mediterranean zone.

Shannon diversity, links by species and linkage density are much higher in the infra- / thermo-Mediterranean zone resulting in a higher degree of connectivity and the ratio of wild-bee species to plant species being one to five (temperate zone *s.l.*: one to four).

This is also reflected in the differences in niche overlaps within wild-bee species, but not in plant species. The higher number of plant species visited by wild bees reduces niche overlap (higher values in the temperate zone *s.l.*).

One feature is that the wild-bee species of Madeira Island are euryanthic; many flowering plant species offer pollen and nectar for different bee species. Accordingly, oceanic islands are in general poor in stenanthic wild-bee species. One exception in the native bee fauna is *Andrena maderensis*, known as specialist of Brassicaceae (typical for the subgenus *Suandrena*). *A. maderensis* has the highest flower-visiting rates on Brassicaceae in our study. However, this species also uses Asteraceae in smaller numbers. Remarkably, this flexibility has also been shown for the *Suandrena* species *A. portosanctana*, which is endemic to Porto Santo. *A. portosanctana* is the ancestor of *A. maderensis*. Females of *A. portosanctana* were occasionally detected on Asteraceae and Oxalidaceae (Kratochwil *et al.*, 2014).

A further exception is the introduced *Hylaeus s. signatus* (oligolectic on Resedaceae), which has low population sizes (Smit & Smit, 2003).

**Plant family preferences, important pollen and nectar plants**

Highest frequencies of flower-visiting by wild bees was found for Asteraceae, Brassicaceae, Fabaceae,
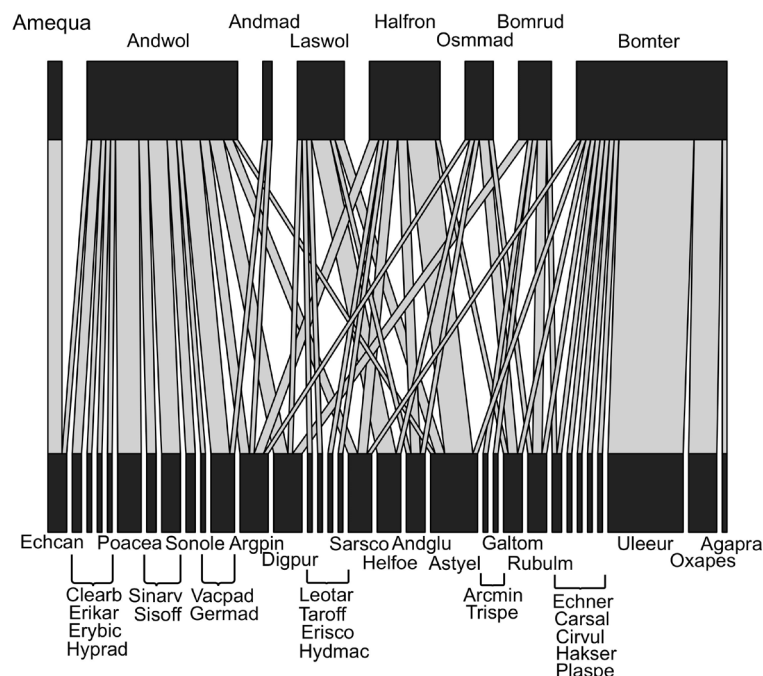
Fig. 4 – Bipartite graph of the bee-plant network of the temperate zone *s.l.* of Madeira Island: the top row shows bee species and the bottom row shows plant taxa. For abbreviations see Tables 1 and 2.

Table 3 – Parameters of the bee-plant networks of Madeira Island.

	infra-/thermo-Mediterranean Zone	Temperate Zone *s.l.*
Number of wild-bee species	12	8
Number of plant taxa	61	33
Taxa numbers	73	41
Network size	732	264
Web asymmetry	-0.6712	-0.6098
Shannon diversity	4.3645	3.6095
Links per species	1.7808	1.2927
Linkage density	5.8084	4.6285
Mean number of shared plant taxa	0.4377	0.4318
Mean number of shared wild-bee species	2.5152	1.1071
Niche overlap in wild-bee species	0.1927	0.1044
Niche overlap in plant taxa	0.1421	0.2479
Partner diversity wild-bee species	2.0227	1.8760
Partner diversity plant taxa	1.0913	0.4797
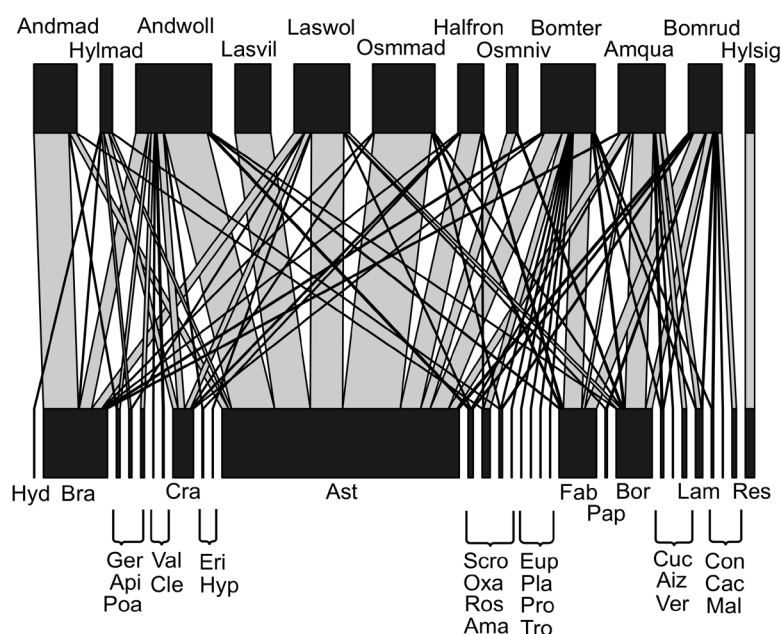
Fig. 5 – Bipartite graph of the whole bee-plant network of Madeira Island: the top row shows wild-bee species and the bottom row shows plant families. For abbreviations, see Table 1 and 2.

Boraginaceae and Crassulaceae (85% of all flower visits; n = 541); Fig. 5:

-    Asteraceae: *Lasioglossum v. villosulum* exclusively visited this family. High visiting rates could also be observed for *Andrena wollastoni*, *Lasioglossum wollastoni*, *Halictus frontalis*, *Osmia madeirensis*, and *Osmia niveata*. Except for *Hylaeus s. signatus* (oligolectic on Resedaceae) all other bee species visited Asteraceae (325 flower visits = 51%).

-    Brassicaceae: Eight wild-bee species and 88 flower visits (14%) were observed on Brassicaceae. *Andrena maderensis* prefers Brassicaceae and is categorised as oligolectic. We found that the species mainly visited Brassicaceae, but also, to a minor extent, Asteraceae

(females and males). *Andrena wollastoni* and *Lasioglossum wollastoni* were also often observed.

-    Fabaceae: With 51 interactions by six bee species, Fabaceae is a frequently visited plant family. *Bombus terrestris lusitanicus* was the top species visiting Fabaceae, but this species could also be found on Asteraceae. *Bombus r. ruderatus*, perhaps introduced (Kratochwil & Schwabe, 2018b), was also highly connected with Fabaceae.

-    Boraginaceae: 49 visits by seven wild-bee species were observed. Most of the flower visits of *Amegilla quadrifasciata maderae* were to Boraginaceae species, but visits to Asteraceae, Lamiaceae, and other families were also observed for this euryanthic bee species.

- Crassulaceae: Wild-bee species of small body sizes preferred species of Crassulaceae (*Andrena wollastoni*, *Hylaeus maderensis*, *Lasioglossum wollastoni*) with few flower visits of *Bombus terrestris lusitanicus*, *Halictus frontalis* and *Osmia madeirensis*.

The most important pollen and nectar plants for wild bees are the following species: *Leontodon taraxacoides* subsp. *longirostris* (n = 66; seven wild-bee species), *Galactites tomentosa* (n = 65; nine wild-bee species), *Crepis vesicaria* subsp. *haenseleri* (n = 52; six wild-bee species), *Echium nervosum* (N = 35, five wild-bee species), *Sinapidendron angustifolium* (N = 34, four wild-bee species), *Bituminaria bituminosa* (n = 35; four wild-bee species) and *Argyranthemum pinnatifidum* s.l. (n = 22; four wild-bee species).

As mentioned in section 'network structure', a wide range of different flower types (actinomorphic, zygomorphic, Asteroideae type, Cichorioideae type) are present to attract different wild-bee species with different body sizes (*e.g.*, small: *Andrena* p.p., *Lasioglossum*; medium size: *Andrena* p.p., *Osmia*; large size: *Amegilla*, *Bombus*) and collecting behaviour (hind leg hairs on coxa and femur: *Andrena*, *Lasioglossum*; hind legs with corbiculae: *Bombus*; hairs brushes on abdominal tergites: *Osmia*) (Kratochwil *et al.*, 2009; Kratochwil & Krausch, 2016).

The studied network shows high diversity of body sizes and collecting behaviour within the wild-bee species. The observation that large wild-bee species are under-represented on oceanic islands (Inoue, 1993; Barret, 1998) cannot be confirmed.

The great importance of Asteraceae, as well as Fabaceae, Boraginaceae and Brassicaceae, for wild-bee species has been shown in other studies (for central European dry grassland ecosystems: Kratochwil, 2003; Kratochwil *et al.*, 2009; Beil *et al.*, 2014; Kratochwil & Krausch, 2016; for alpine ecosystems: Johanson *et al.*, 2018).

Euryanthic and stenanthic wild-bee species

The most abundant wild-bee species on flowers was *Andrena wollastoni*, which visited 11 plant families and 28 plant species, followed by *Osmia madeirensis* (preference for Asteraceae but also visited species from the Brassicaceae, Boraginaceae, Crassulaceae, Fabaceae and Rosaceae families; in total 20 plant taxa), *Lasioglossum wollastoni* (euryanthic; visited species from eight plant families and 22 plant taxa), *Amegilla quadrifasciata maderae* (euryanthic; visited species from nine plant families and 16 plant taxa), *Andrena maderensis* (preference

for Brassicaceae but also visited Asteraceae, Geraniaceae, and Oxalidaceae; 11 plant taxa); see Fig. 5. Both *Bombus* species (*Bombus r. ruderatus* and *B. terrestris lusitanicus*) demonstrated euryanthic behaviour (11 resp. 15 plant families, 17 resp. 21 different plant taxa). There are only few stenanthic bee species: the introduced *Hylaeus s. signatus* (oligolectic on Resedaceae) and *Lasioglossum v. villosulum*, which specialise on Asteraceae. All other wild-bee species on Madeira Island are characterised by high flexibility in flower-visiting. It is remarkable that *Andrena maderensis*, which has a preference for Brassicaceae, shows food niche extension.

In our study, most native and endemic wild-bee species are generalist flower visitors. Due to the rarity of colonisation events and the difficulties of establishment, there are few wild-bee species on Madeira Island. Generally, wild bees favour dry or semi-dry climates; nesting sites in the soil are especially affected by fungi under moist conditions. Only one wild-bee species on Madeira Island shows a certain preference for the cloudy zone of trading winds: *Halictus frontalis*. *Bombus terrestris lusitanicus*, *Andrena wollastoni*, and *Lasioglossum wollastoni* cope with these conditions.

Olesen *et al*. (2002), comparing the islands of Flores (Azores) and îles aux Aigrettes (near Mauritius), pointed out that these islands' endemic pollinators are super-generalists and that the plant species there are characterised by a wide pollination niche. Olesen *et al*. (2002) also showed that super-generalists in pollinator-plant networks represent a widespread island phenomenon. Following our example of Madeira Island, we can conclude that euryanthic species of wild bees are the majority, but the network also contains stenanthic wild-bee species. The conditions are different on Porto Santo, where a super-generalist, *Amegilla quadrifasciata maderae*, characterises the bee-plant network (see section 'Differences between the Madeira Island and Porto Santo bee-plant networks').

Patterns of relationships between endemic, native and introduced wild-bee species and endemic, native and introduced plant species

Similar to the results of the bee-plant network of Porto Santo (Kratochwil & Schwabe, 2018b), most of the visited plant species are endemic or native species (Fig. 6). They were already present about 500 years ago, before the beginning of strong human impact. Therefore, the use of the flower resources of these plant species by
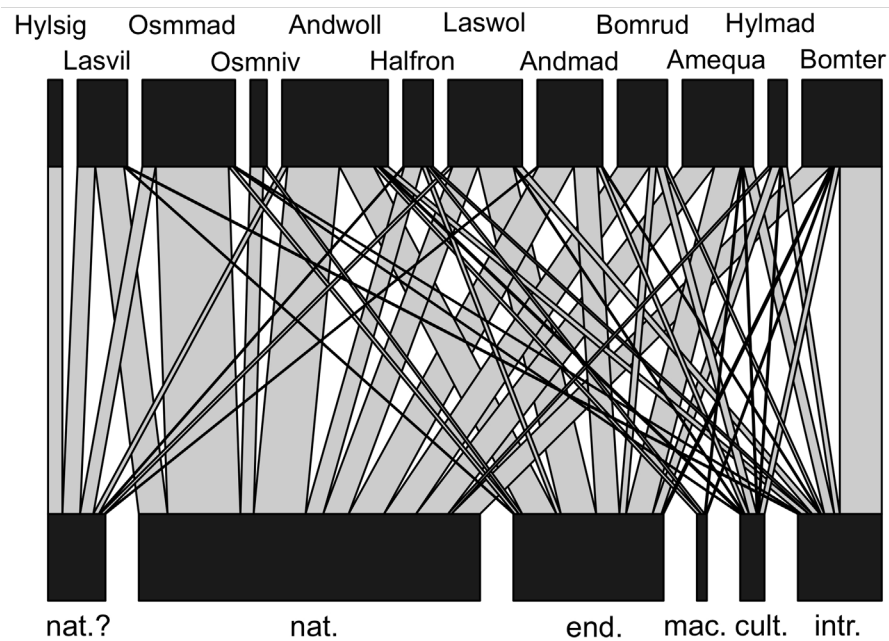
Fig. 6 – Bipartite graph of the bee-plant network of Madeira Island: top row shows wild-bee species and the bottom row shows the statuses of the visited plant taxa. For abbreviations, see Tables 1 and 2.
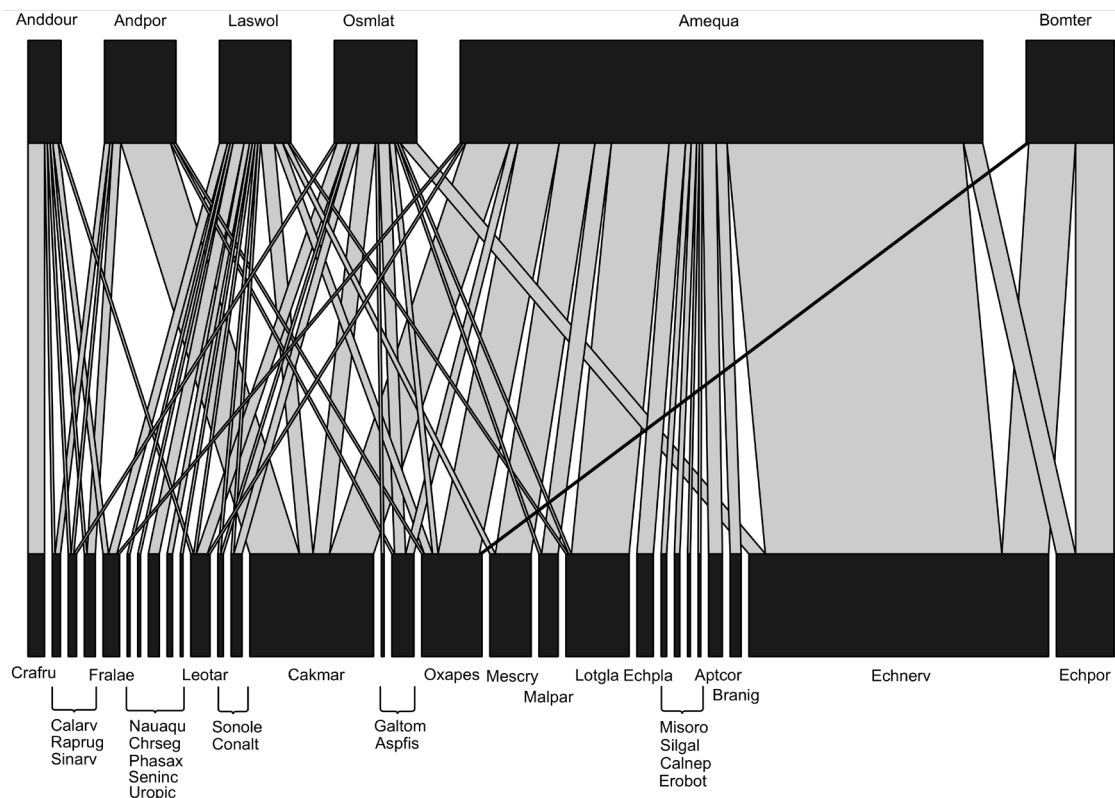
Fig. 7 – Bipartite graph of the bee-plant network of Porto Santo: the top row shows wild-bee species and the bottom rows shows the visited plant species. Abbreviations of wild-bee species: Amequa = *Amegilla quadrifasciata maderae*, Anddou = *Andrena dourada*, Andpor = *Andrena portosanctana*, Bomter = *Bombus terrestris lusitanicus*, Laswol = *Lasioglossum wollastoni*, Osmlat = *Osmia latreillei iberoafricana*. Abbreviations of plant species: Aptcor = *Aptenia cordifolia*, Aspfis = *Asphodelus fistulosus*, Branig = *Brassica nigra*, Cakmar = *Cakile maritima*, Calarv = *Calendula arvensis*, Calnep = *Calamintha nepeta*, Chrseg = *Chrysanthemum segetum*, Conalt = *Convolvulus althaeoides*, Crafru = *Crambe fruticosa*, Echnerv = *Echium nervosum*, Echpla = *Echium plantagineum*, Echpor = *Echium portosanctensis*, Erobot = *Erodium botrys*, Fralae = *Frankenia laevis*, Galtom = *Galactites tomentosa*, Leotar = *Leontodon taraxacoides* subsp. *longirostris*, Lotgla = *Lotus glaucus*, Malpar = *Malva parviflora*, Mescry = *Mesembryanthemum crystallinum*, Misoro = *Misopates orontium*, Nauaqu = *Nauplius aquaticus*, Oxapes = *Oxalis pes-caprae*, Phasax = *Phagnalon saxatilis*, Raprug = *Rapistrum rugosum*, Seninc = *Senecius incrassatus*, Sinarv = *Sinapis arvensis*, Silgal = *Silene gallica*, Sonole = *Sonchus oleraceus*, Uropic = *Urospermum picroides*.

wild-bee species is probably an old feature. According to our material, introduced plant species play a minor role; some cultivated plants, *e.g.*, *Brassica* taxa, were regularly visited by wild bees (Fellendorf *et al.*, 1999). *Bombus terrestris lusitanicus* visited introduced plant species to a greater extent, but all other native and endemic wild-bee species could also extend their food resources using introduced plant species. It was not possible to investigate if introduced plant species benefit from the pollination capability of *Bombus terrestris lusitanicus* or of other wild-bee species of Madeira Island.

Hylaeus s. signatus, which is certainly introduced, does not disturb the bee-plant network because of its specialisation in Resedaceae and its probably small population sizes.

Our bee-plant network shows that *Bombus r. ruderatus*, which is probably introduced, seems to be well adapted and does not behave like a strong invader. *B. r. ruderatus* was introduced to the Azores (Weissmann *et al.*, 2017) and was first recorded in 1865 (Godman, 1870). On Tenerife, *B. ruderatus* is an invader (Pérez & Macías-Hernández, 2012). *B. ruderatus* (subspecies not known) was introduced to South America (Chile) for pollination purposes. This species established and massively extended its range (Schmid-Hempel *et al.*, 2014).

Differences between the Madeira Island and Porto Santo bee-plant networks

Comparing the bee-plant networks of Madeira Island (Fig. 3) and Porto Santo (Fig. 7) reveals some similarities, *e.g.*, network asymmetry with a lower number of wild-bee species and a higher number of visited plant species. However, there are also differences in network structure related to differences in geological history, island size and physico-geographical conditions.

Madeira Island has an age of about 4.8 Ma, while Porto Santo is much older (11.1 to 14.3 Ma) (Galopim de Carvalho & Brandão, 1991; Geldmacher *et al.*, 2000). Madeira covers 728 km², while Porto Santo is only 42 km². The reliefs are also very different. Madeira Island is extremely mountainous and rich in ribeiras, with the highest elevation of the Pico Ruivo de Santana reaching 1862 m *a.s.l.* The highest peak in Porto Santo reaches 517 m *a.s.l.* (Pico do Facho).

Porto Santo has an extraordinarily large sandy beach, which is characterised by plants such as *Cakile maritima* (the main pollen resource for the endemic *Andrena portosanctana*) and *Lotus glaucus*. This situation is also

reflected in the characteristics of climate and vegetation. Porto Santo is an old, already heavily eroded island, with consequent losses in area/size, elevation relief and habitat diversity (Kratochwil & Schwabe, 2018a, 2018b). While there are seven bioclimatic types in Madeira (Rivas-Martínez, 1996; Rivas-Martínez *et al.*, 1999; Mesquita *et al.*, 2004), Porto Santo Island has mainly the xeric-/infra-Mediterranean type (Rivas-Martínez, 2009; Kratochwil & Schwabe, 2018b) with very low precipitation (De Lima & De Lima, 2009). Subhumid conditions exist on Porto Santo only near the mountain peaks and on the north side of the island. To a large extent, the woody vegetation, consisting of a dry microforest (see detailed in Kratochwil & Schwabe, 2018b), has been cleared. There are 1136 Spermatophyta species on Madeira Island, and only 463 on Porto Santo (Borges *et al.*, 2008). To achieve better comparability, we only used the network of the infra- / thermo-Mediterranean zone of Madeira Island. Fig. 7 shows the bipartite graph of Porto Santo (modified from Kratochwil & Schwabe, 2018b).

The numbers of wild-bee and plant species involved in the bee-plant network of the infra- / thermo-Mediterranean zone of Madeira Island are higher, as are the values of the network size of Porto Santo, but web asymmetry and the ratio of wild-bee species to plant species are similar (one to five); Shannon diversity and linkage density are higher for Madeira Island (Table 4). The number of links per species is approximately the same for both networks (Table 4). The plant taxa on Porto Santo share more wild-bee species than those of Madeira Island (Table 4). This is also reflected in the differences in niche overlaps within wild-bee species and plant taxa (higher values on Porto Santo). Due to the higher network diversity on Madeira Island, the values of partner diversity are higher.

We investigated whether the wild-bee species which are present on both islands show similar foraging behaviour. These species are *Amegilla quadrifasciata maderae*, *Bombus terrestris lusitanicus* and *Lasioglossum wollastoni* (Table 5, group A). However, the dataset of *Hylaeus maderensis* and *Lasioglossum v. villosulum* from Porto Santo was insufficient for analysis.

Amegilla quadrifasciata maderae often visits species of the Boraginaceae family. On Madeira Island this bee species is not dominant in the network, but locally there may be dominance (*e.g.*, in gardens of Funchal; Fellendorf *et al.*, 1999). The situation is different on Porto Santo, where *A. q. maderae* acts as a super-generalist (high lm value). Especially in years of great drought on Porto Santo, the woody *Echium* species flower in large numbers during

Table 4 – Parameters of the bee-plant networks of Madeira Island (infra- / thermo-Mediterranean zone) and Porto Santo (xeric- / infra-Mediterranean zone).

	infra-/thermo-Mediterranean Zone Madeira Island	xeric-/infra-Mediterranean Zone Porto Santo
Number of wild-bee species	12	6
Number of plant taxa	61	29
Species numbers	73	35
Network size	732	174
Web asymmetry	-0.6712	-0.6571
Shannon diversity	4.3645	3.1270
Links per species	1.7808	1.6285
Linkage density	5.8084	4.4528
Mean number of shared plant taxa	0.4377	3.0666
Mean number of shared wild-bee species	2.5152	0.7857
Niche overlap in wild-bee species	0.1927	0.2474
Niche overlap in plant taxa	0.1421	0.3488
Partner diversity wild-bee species	2.0227	1.8329
Partner diversity plant taxa	1.0913	0.6732

Table 5 – Linkage level (lm), number of visited plant families (n plf), number of visited plant species (n pls) and preferred plant family or families (plf pref).

	Wild-bee species	Island	lm	n plf	n pls	plf pref
A	*Amegilla quadrifasciata maderae*	Madeira	1,33	9	16	Bor, Ast
	Amegilla quadrifasciata maderae	Porto Santo	3,17	5	19	Bor, Bra
	Bombus terrestris lusitanicus	Madeira	1,75	17	22	Ast, Fab
	Bombus terrestris lusitanicus	Porto Santo	0,50	5	3	Bor
	Lasioglossum wollastoni	Madeira	1,83	8	22	Ast, Bra
	Lasioglossum wollastoni	Porto Santo	2,17	5	13	Ast
B	*Andrena wollastoni*	Madeira	2,42	12	29	Ast, Bra
	Andrena dourada	Porto Santo	1,00	6	6	Bra
	Andrena maderensis	Madeira	0,92	4	11	Bra
	Andrena portosanctana	Porto Santo	1,00	5	6	Bra
	Osmia maderensis	Madeira	1,58	5	19	Ast
	Osmia latreillei iberoafricana	Porto Santo	2,00	4	12	Ast, Bra, Bor
C	*Bombus r. ruderatus*	Madeira	1,42	11	17	Fab, Bor
	Halictus frontalis	Madeira	0,92	5	11	Ast
	Hylaeus maderensis	Madeira	0,58	6	7	Cra
	Hylaeus s. signatus	Madeira	0,08	1	1	Res
	Lasioglossum v. villosulum	Madeira	0,83	1	10	Ast
	Osmia niveata	Madeira	0,33	2	4	Ast, Bor

much of the year and offer this wild-bee species a large food supply (Kratochwil & Schwabe, 2018b). *A. q. maderae* is well adapted to dry climatic conditions.

Comparing the two islands reveals that *Bombus terrestris lusitanicus* differs in flower-visiting behaviour. On the climatically less extreme Madeira Island the species is much more euryanthic than on Porto Santo. *B. t. lusitanicus* needs more subhumid conditions and is therefore concentrated at a few higher areas of Porto Santo, visiting the flowers, *e.g.*, of *Echium portosanctensis*. This is the reason for a low lm value. Similar to *A. q. maderae*, *Echium* species are of great importance.

Lasioglossum wollastoni behaves relatively similarly on both islands and prefers Asteraceae. The greater diversity of visited plant species on Madeira Island causes a lower lm value.

There are phylogenetically related endemic species pairs (one exception) on Porto Santo and Madeira Island: *Andrena dourada – A. wollastoni*; *Andrena portosanctana – A. maderensis*; *Osmia latreillei iberoafricana* (this taxon is not endemic and thus is found inter alia in Spain) – *O. madeirensis*. The phylogenetically older species are those of Porto Santo. Clearly, founder individuals reached Madeira Island from Porto Santo and developed into new endemic species (Kratochwil & Scheuchl, 2013; Kratochwil *et al*., 2014; Kratochwil, 2018; Kratochwil & Schwabe, 2018b). The question arises if there are similarities or differences in the flower-visiting behaviour of the related species pairs.

Andrena portosanctana and *A. maderensis* belong to the subgenus *Suandrena*, whose representatives are characterised by stenanthy in Brassicaceae. This also applies to these two species, which also have similar lm values (1.00; 0.92) on both islands in the network. The number of plant taxa used by *A. maderensis* is higher. On the one hand, the plant supply for *A. maderensis* is larger on Madeira Island; on the other hand, *A. maderensis* has larger population sizes and is not as rare as *A. portosanctana*. *A. portosanctana* shows some flexibility in flower visiting and was also found visiting plant species of other families (Kratochwil *et al*., 2014). This is probably a reaction to the lack of sufficient flowering of Brassicaceae species in dry years (Kratochwil & Schwabe, 2018b).

Larger differences were found in the other two species pairs (Table 5, group B). According to our data, *Andrena dourada* from Porto Santo uses a much smaller plant-species spectrum than does *A. wollastoni* from Madeira Island. This may be due to the different resource situation on the islands. Another reason could be a niche widening of the Madeira younger coloniser, as it uses far more plant families and plant species than *A. dourada*. The preferred plant family of *A. wollastoni* is Asteraceae, followed by Brassicaceae, while *A. dourada* prefers only Brassicaceae.

Comparing *Osmia madeirensis* and *O. latreillei iberoafricana* shows that the endemism of the first species probably led to higher specialisation. *O. latreillei iberoafricana* is not endemic for Porto Santo and occurs in the Iberian Peninsula as well (Kratochwil *et al*., 2018).

Furthermore, in group C, the remaining wild-bee species are characterised in Table 5 regarding linkage level, number of visited plant families, number of visited plant species and preferred plant family or families. The highest level of euryanthy is reached by *Bombus r. ruderatus* and the least by the Resedaceae-specialist *Hylaeus s. signatus*. In the same way *Lasioglossum v. villosulum* visited only one plant family (Asteraceae), but 10 different plant species of this family.

CONCLUSIONS

Native wild-bee species of Madeira Island and Porto Santo have established themselves in the long term by colonisation and, in some cases, by evolving into endemic subspecies or species. It can be concluded that the bee-plant network on Madeira Island is the result of evolutionary adaptation processes, where certain generalist life-forms guarantee functional stability. The asymmetric network is stabilised by the endemic and native bee and plant species and shows high connectivity. This corresponds to the results in the network study of Porto Santo (Kratochwil & Schwabe, 2018b). According to our network data introduced bee and plant species do not play quantitative roles on both islands. There is no invader complex (d'Antonio & Dudley, 1993; Olesen *et al*., 2002) or disruption of bee-plant interactions (Traveset & Richardson, 2006), but changes in the network structure by invasions are possible and often problematic, as has been shown for the Galápagos Islands (Traveset *et al*., 2013). All invasion processes must be monitored carefully and continuously, because the consequences for the bee-plant network may be dramatic.

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