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Wild bees (Anthophila) of Porto Santo (Madeira Archipelago) and their habitats: species diversity, distribution patterns and bee–plant network *

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A b s t r a c t : Porto Santo (Madeira Archipelago) is a relatively old (11.1–14.3 Ma) and small volcanic island in the Atlantic Ocean. Due to the low altitudes of the mountains, the main part of the island is characterised by a semiarid climate and xeric vegetation; only a small part shows subhumid conditions. We were able to study the wild-bee fauna and the bee–plant network (with pan traps, hand-netting or observation) mainly during two stays in March 2012 and 2017. Currently, nine wild-bee species have been detected. Two species are endemic to Porto Santo, and two species and one subspecies to the Madeira Archipelago. An actualised and annotated checklist of the wild-bee species of Porto Santo will be presented. The colonisation history of the endemic species *Andrena dourada* and *A. portosanctana* will be discussed. The distribution patterns show a wide distribution of the endemic and native bee species in the xeric zone. Only *Bombus terrestris lusitanicus* is restricted to the subhumid area.

We detected all in all about 300 bee−plant interactions. In contrast to mainland networks, e.g., in the warm-temperate zone, which are as a rule characterised by many more bee than plant species, the bee−plant network of Porto Santo shows many more plant than bee species and is highly asymmetric. Six wild-bee species used 27 different plant species. Bee and plant species were highly interconnected, showing that under difficult environmental conditions and resource limitations, alternative nectar and pollen resources were available. Especially the woody *Echium* species *E. nervosum* (endemic to Madeira Archipelago) and *E. portosanctensis* (endemic to Porto Santo) are, on the one hand, key species as resources for wild bees and, on the other hand, self-incompatible outbreeders that depend on insect pollination. Even in very dry periods (March 2012, with no precipitation in winter), *Echium* showed rich flower production and was intensively visited by wild bees. The same is true for *Cakile maritima*, which is an important resource for the endemic species *Andrena portosanctana* with priority use of Brassicaceae species. In the wet spring of 2017, there was a reduction of sampled or observed bee individuals compared to 2012 (but more detections without flower visits and fewer on flowers).

K e y w o r d s : *Andrena dourada*, *Andrena portosanctana*, bee–plant network, Hymenoptera Apoidea, island biogeography, wild-bee diversity, pollination, endangered wild-bee species, IUCN list, nomenclature, Madeira Archipelago.

Introduction

Porto Santo (area 42 km^2, length 40 km NE–SW, Madeira Archipelago) is a model area for a relatively old, small and isolated volcanic island that has only a few habitat types

and had strong anthropogenic impact for 500 years. The age of the island is 11.1 to 14.3 Ma, with the latest volcanic activities about 8 million years ago (GELDMACHER et al. 2000, COOK 2008). In contrast, Madeira Island has an age of only 4.6 million years (GALOPIM DE CARVALHO & BRANDÃO 1991, GELDMACHER et al. 2000).

There are about 446 phanerogamic plant species on the island (additionally, two are extinct), nine of which are endemic to Porto Santo, 29 to Madeira Archipelago and 19 to Macaronesia (always species-level): altogether 13% are endemic. Two hundred eighty-six plant species are non-endemic, but native or highly probable to be native (64%) and 103 further species are introduced or probably introduced (23%). Therefore, regarding the 343 native plant species, 57 are endemic to Macaronesia or parts of it (data counted from JARDIM & MENEZES DE SEQUEIRA 2008, 2011; JONES et al. 2014).

For many plant species in Macaronesia, insect pollination is essential for their reproductive success. Especially the Macaronesian woody *Echium* species are all self-incompatible outbreeders (ALDRIDGE 1981), which is, e.g., also the case for the non-endemic herbaceous *E. plantagineum* (FLACHER et al. 2017). We supposed that the Madeira-Archipelago-endemic species *Echium nervosum* and the Porto-Santo-endemic species *E. portosanctensis* would be frequently visited and pollinated by wild bees of Porto Santo.

Until now, wild-bee species and bee–plant networks have been only poorly studied on Porto Santo; especially concerning the knowledge of habitats and networks, there was a data deficit. Underestimation of the insect fauna on Porto Santo was stated also by PRADO E CASTRO et al. (2016) for the example of Calliphoridae (Diptera), but this is also true for wild bees (Anthophila).

In actuality, we find nine wild-bee species on Porto Santo; only the occurrence of seven species had been published in the literature until yet (KRATOCHWIL et al. 2008, 2014, KRATOCHWIL & SCHEUCHL 2013, KRATOCHWIL 2014). Two species are endemic to Porto Santo, and two species and one subspecies to the whole Madeira Archipelago.

The following topics will be introduced in this publication:

(1) An actualised check list of wild-bee species of Porto Santo will be presented. The updated check list of the wild bees of the Madeira Archipelago is published in KRATOCHWIL et al. (2018). A comparison concerning wild-bee diversity, number of endemic species and introduced species of the Madeira Archipelago with other islands of the Macaronesian Archipelagos (Azores, Selvagens, Canary Islands, Cape Verde) is published in KRATOCHWIL & SCHWABE (2018).

(2) We will characterise the habitats of Porto Santo that are especially important to provide wild bees with nectar and pollen.

(3) We will analyse the distribution patterns of wild-bee species and ask for differences between endemic and non-endemic species on Porto Santo.

(4) Mainly based on own studies, a first overview of pollen and nectar resources for the wild-bee species of Porto Santo will be presented, including a few data mentioned in the literature.

(5) We ask about the structure of the bee–plant network on Porto Santo and especially that of the endemic bee and plant species. Also of special interest is whether the wild-bee and plant interactions differ between a dry (2012) and a wet spring (2017).

We expected many more plant than bee species in the network and therefore an asym-

metric network. In most terrestrial natural or semi-natural habitats in warm-temperate or subaridic regions, a network with more bee than plant species is characteristic (e.g., BEIL et al. 2014, SCHLEUNING et al. 2016). Exceptions are, e.g., extreme habitats or habitats with effects of insecticides.

(6) Further, we ask if there is a positive prognosis for the survival of especially the two Porto-Santo-endemic bee species in the highly anthropogenically influenced island.

Physico-geographical factors

Porto Santo was always separated from Madeira Island by an ocean bed more than 2000 m deep. Studies of land snails have shown that Madeira Island (62 species) and Porto Santo (47 species) reflect this separation: only three species are shared (COOK 2008).

Due to the relatively low mountain areas, the summits catch little cloud precipitation (main summits: Pico da Facho 517 m, Pico da Gandaia 499 m, Pico de Juliana 440 m, Pico Branco 451 m and Pico do Castelo 437 m, all in the north-eastern part of the island; in the southwestern part, Pico de Ana Ferreira 283 m).

Geologically, Porto Santo has a volcanic base, and the above-mentioned summits are characterised mainly by trachytic and basaltic structures, but quaternary sediments cover huge parts of the Tertiary formation (15 km^2 of the island are covered by quaternary material, mainly between the north-eastern and southwestern mountain areas). The sand was blown out in glacial times from the shelf. There are Eolianites (calcareous sand from the Pleistocene period, solidified, partly more than 50 m vertical thickness) with fossil land snails (LIETZ & SCHWARZBACH 1971). This quaternary material favours the occurrence of bee colonies, e.g., from *Amegilla quadrifasciata maderae* and *Lasioglossum wollastoni* (see below).

Colluvial sediments fill erosive channels and mantle slopes and give partially an impression of 'badlands' (LIETZ & SCHWARZBACH l.c.). The southern coast is characterised by a huge sand beach (10 km); this is reflected in the name 'Ilha Dourada' ('Golden Island').

The other parts of the coast are characterised by steep cliffs. Perennial water currents are not present, but some perennial springs occur (FAUST-LICHTENBERGER 1988).

The bioclimate was classified as Mediterranean xeric oceanic by RIVAS-MARTÍNEZ (2009). There is a pronounced summer aridity on Porto Santo; precipitation values are very low from June to August (376 mm/a). The mean temperature varies between 15.7 °C (February) and 22.8 °C (August) and precipitation between 62 mm (December) and 4 mm (July), both for the period 1973–2012, 82 m a.s.l. (CROPPER 2013). In the course of climate change, there is a temperature anomaly, with higher temperatures mainly since 1990 on Porto Santo and Madeira Island (CROPPER & HANNA 2014). Annual precipitation values show strong oscillations (CROPPER & HANNA 2014). This unpredictability can also be shown for our main sampling periods. In March 2012, there had been an extremely dry winter with no precipitation from November to March. In the year before, there was an exceptionally extreme drought in the whole Madeira Archipelago from December 2011 to May 2012 (LIBERATO et al. 2017). In the second period (March 2017), there had been a wet winter with 301 mm precipitation from October to March, nearly the precipitation of a whole year (data from Airport Porto Santo, www.wunderground.com; see Fig. 1a-f).

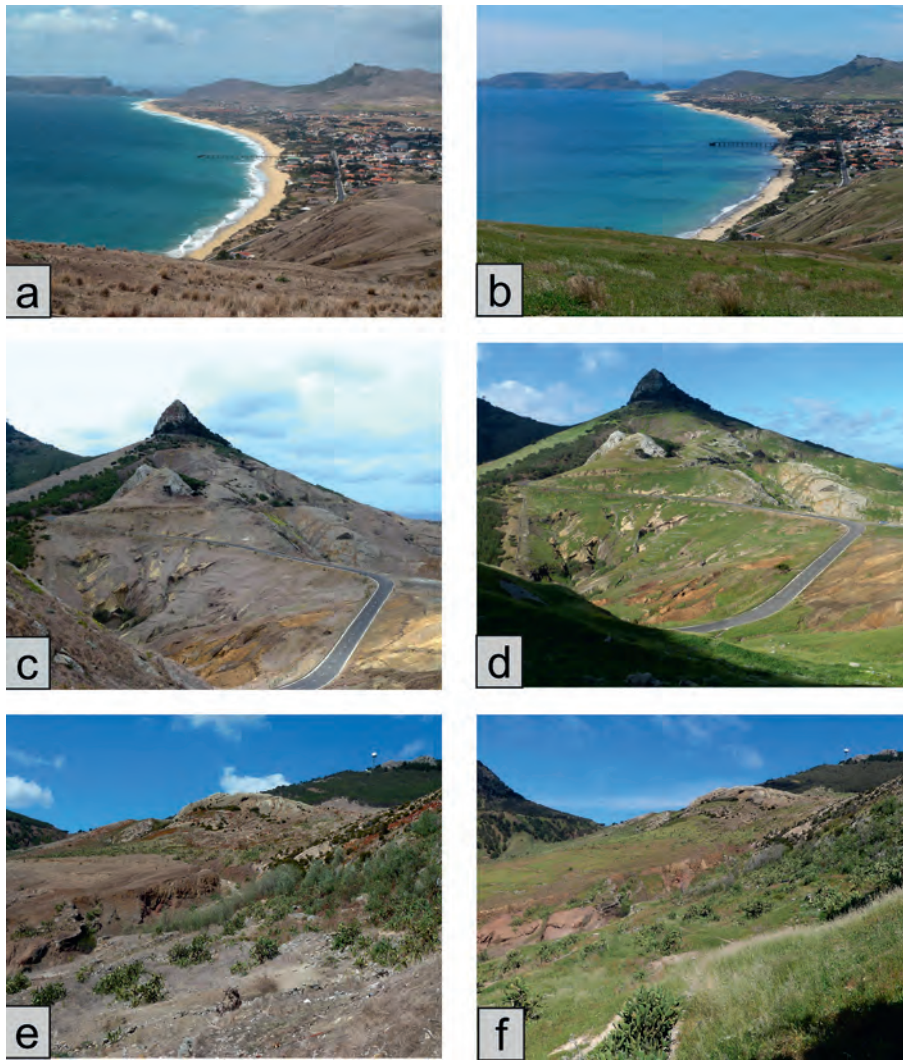

Fig. 1: Aspects from some of our sampling sites and their surroundings in March after an extreme dry winter and a wet winter: Left: March 2012 (November 2011–March 2012, no precipitation); right: March 2017 (October 2016–March 2017, 301 mm precipitation); **a, b**: sand beach with Vila Baleira in the centre; **c, d**: Pico Juliana and mainly fallow land; **e, f**: southern-exposed extensively grazed dry grassland; view from Capela da Graça (in the background right: Pico do Facho with *Pinus* plantations). Photos: A. Schwabe.

Aspects of history are summarised in FAUST-LICHTENBERGER (1988) and PEREIRA SILVA (2003). Porto Santo was discovered in the early 15th century. The first settlers from Portugal and a donatory settled in 1450. Dryland farming of wheat, barley and

root crops as well as livestock husbandry and at times viticulture were practised. For centuries, the island had great importance in supplying sailing ships with crops and other food resources.

The island had been cleared to a great extent of woody vegetation. The original vegetation was mainly a dry microforest (Mayteno umbellatae-Oleo maderensis sigmetum; see Section 'Characterisation of the habitats'), probably with many gaps in the dry environment, which facilitated the coexistence with endogeic wild-bee species. Beginning at the end of the 18th century, afforestations were made with *Pinus pinaster* and *Pinus halepensis*, e.g., in the area of the Pico do Castelo.

Especially in the last 50 years, crop farming and livestock husbandry were strongly reduced, and therefore fallow land characterises many parts of the island, including very steep slopes. Since the beginning of the settlement, the impact of introduced Iberian rabbits (*Oryctolagus cuniculus huxleyi*) has been a threat, especially to some endemic plant species (e.g., *Pericallis menezesii*, see JONES et al. 2014). Infections have reduced the rabbit population periodically (JONES et al. 2014); in recent years, myxomatosis had a strong impact (A. Aguiar, pers. comm.).

Characterisation of the habitats

Nearly the whole island belongs to the 'series of *Olea maderensis*' (Mayteno umbellatae-Oleo maderensis sigmetum), indicating a dry, infra-Mediterranean climate (CAPELO et al. 2004, 2005). Sclerophyllous plant species, which are representatives of Palaeo-Mediterranean or Palaeo-African and Palaeo-Arabian taxa, are characteristic of this formation. Formerly, there were occurrences of *Dracaena draco* subsp. *draco*, which is now extinct on Porto Santo but was planted again in the last few years from seedlings that originated on Madeira Island. Historical sources indicate the following: BOWDICH (1825: 92) saw a single *Dracaena* near Pico Facho and reported that there were fewer than 20 left. The author cited a report from Cadamosto's voyage in 1445 'that the dragon trees of Porto Santo were so large, that fishing boats … were made out of the trunks, and that the inhabitants fattened their pigs on the fruit'.

Substitution stages of the '*Olea maderensis* series' are stands with *Euphorbia piscatoria* and *Echium nervosum*, which are still present, mainly on south-exposed slopes. The main natural occurrences of *Echium nervosum* are in the southern part of the island (CARVALHO et al. 2010); the species was probably also an element of the *Olea maderensis* microforest. *Echium nervosum* is still relatively frequent, also due to plantings near the roads. Especially in the northern part, *Echium portosanctensis* (see below) was also planted. Hybrids occur, which is a huge problem for the protection of pure genotypes. *Echium nervosum* (including hybrid types) is the most important pollen and nectar resource for wild bees on Porto Santo.

Also important as a pollen and nectar resource is the Madeira-Archipelago-endemic species *Crambe fruticosa* (Section Dendrocrambe), which we have found as a food resource for *Andrena dourada* on basaltic substrate in low altitude in the Ana Ferreira area (this locality for *Crambe* is also mentioned by PRESS & SHORT 1994). COSTA et al. (2012) listed *Crambe* for the Loto macranthi-Phagnaletum lowei on basaltic leptosols and for the Gennario diphyllae-Euphorbietum piscatoriae (altitudes 120–390 m a.s.l.).

Grazed areas in the 'series of *Olea maderensis*' are, e.g., characterised by the perennial

Cenchro ciliaris-Hyparrhenietum sinaicae and the annual Galactito tomentosae-Brachypodietum distachyae. *Phagnalon saxatile* and *Leontodon taraxacoides* offer important pollen and nectar resources for wild bees; they occur mainly in the perennial communities (COSTA et al. 2004).

Only small elements of the subhumidic series are still present around the main summits and on north-facing slopes (e.g., with *Helichrysum melaleucum*, *Erica platycodon* subsp. *maderincola*, *Juniperus turbinata* subsp. *canariensis* and others; CAPELO et al. 2004). *Apollonias barbujana* occurred but is now extinct (PRESS & SHORT 1994). Two recently described Porto-Santo-endemic species (*Echium portosanctensis* and *Pericallis menezesii*) with low population sizes occur especially in this zone, mainly in the Pico-Branco area (CARVALHO et al. 2010, JONES et al. 2014). *Echium portosanctensis* is an important pollen and nectar resource for wild bees.

Remarkable is the occurrence of six endemic *Ramalina* species (Lichenes), which are excellent indicators for moisture and reflect the subhumidic habitats. The long thallus structures of *Ramalina nematodes* characterise the cloud-influenced rocks near the summits, as was already described by FOLLMANN (1990): 'licht- und nebeloffene Lavafelsen…, 550 m ü. M., Pico do Facho' (original herbarium specimen: 'consort. North American Lichen Herbaria'). The recent distribution of all endemic lichen species was studied by SPARRIUS et al. (2017).

Locally there are active dunes, e.g., with *Lotus glaucus*, *Calystegia soldanella* and *Euphorbia paralias* (Polygono maritimae-Euphorbietum paraliae and Euphorbio paraliae-Lotetum glaucae; see COSTA et al. 2004). Drift lines in the whole 8 km–long area of the sand beach are characterised by scattered occurrences of *Cakile maritima*. It is well known that the annual *Cakile maritima* is a 'migratory' plant, and therefore the occurrences are unpredictable. The seeds can survive in floating seawater for up to 1 year (GANDOUR et al. 2008) and – depending on sea currents – do not establish successfully every year on the same sites. In the two years of our study (2012 and 2017), there were some sites with quite similar population sizes. *Cakile maritima* is mainly outbreeding and therefore dependant on insect pollination (DAVY et al. 2006). *Lotus* and especially *Cakile* are important resources for flower-visiting wild bees. Also, the halonitrophytic community Senecio incrassati-Mesembryanthemum crystallini, which is characteristic, e.g., of rocky or sandy sites near the sea, often with trampling impact (JARDIM et al. 2003, COSTA et al. 2004), is rich in pollen and nectar resources (*Senecio incrassatus*, *Mesembryanthemum crystallinum*, *Aptenia cordifolia*, *Frankenia laevis*).

Due to the former importance of agriculture, the island still has very rich ruderal flora, now mainly characterising fallow land. COSTA et al. (2004) listed a lot of different ruderal communities for Porto Santo. All in all, especially in years with sufficient precipitation in winter, there is a big offer of pollen and nectar resources to wild bees by ruderal plant species. *Rapistrum rugosum*, *Brassica nigra* and *Sinapis arvensis* (all Brassicaceae) are visited by wild bees, as are *Asphodelus fistulosus*, *Echium plantagineum*, *Convolvulus althaeoides*, *Calendula arvensis* and others. The invasive plant species *Oxalis pes-caprae*, which especially occurs on microclimatically moister fallows, also plays a role as a pollen and nectar resource.

Methods

1. Database of wild-bee species

An updated list compared to KRATOCHWIL et al. (2008) was compiled. We studied the distribution pattern of wild bees and their interactions with plants during three visits on Porto Santo on 31 March 2005, 16–20 March 2012 and 19–31 March 2017.

We applied (1) direct sampling on defined flower resources or (2) on the ground (hand nets), (3) direct determination concerning easy detectable species and (4) in 2012 and 2017, pitfall trapping (white and yellow pitfalls, diameter 20 cm, filled with water and a drop of a biodegradable detergent, checked daily).

Our approaches covered the main habitat types (see section 'Characterisation of the habitats'). All in all, we sampled 15 sites in the northern and 14 sites in the southern part of the island, four of them with a subhumid mesic-xeric and the others with a full xeric bioclimate; the quantity of the sites reflected the proportion of the climatic types on the island.

We were not able to sample or observe wild bees in some areas of the flat central part of the island (airport, golf course) because it was not allowed. We did not survey the flat, stormy uninhabited islands that belong to Porto Santo. One specimen from one of the small islands (Ilhéu do Farol) was collected by F. Zino, 11.06.1949, and deposited in the Museu de História Natural do Funchal (*Amegilla quadrifasciata maderae*, det. I.H.H. Yarrow, 1958).

The semi-domesticated honeybee occurs, but we did not include interactions. The GPS data of all collected or observed wild bees were recorded with a Garmin Oregon 700.

By using these methods, we were able to catch or detect nine bee individuals in 2005, 157 individuals in 2012, and 289 individuals as well as 170 bees in colonies in 2017 (Table 1). We got nine flower–bee interactions in 2005, 130 in 2012 and 178 in 2017 (Table 1).

Table 1: Numbers of observed or collected wild-bee species by the authors with and without flower visits in 2005, after the dry winter 2011/2012, and after the wet winter 2016/2017 (for precipitation data, see text). *: additionally: two colonies detected (ca. 150 and 20 nests, 170 individuals).

without and with flower visit	with	without	with	without	with
	2005	2012	2012	2017	2017
Andrena dourada	0	11	6	14	8
Andrena portosanctana	0	1	24	1	0
Lasioglossum wollastoni	0	1	5	85	21
Osmia latreillei iberoafricana	0	8	24	7	7
Amegilla quadrifasciata maderae	9	3	51	4*	130
Bombus terrestris lusitanicus	0	3	20	0	12
sum	9	27	130	111	178

There are nearly no data about flower–bee interactions from other authors. Two interactions were given by COCKERELL (1922), one by A. Aguiar (pers. comm.); the interactions given by FELLENDORF et al. (1999) often do not separate if a specific interaction was observed on Porto Santo or Madeira Island, or there are problems with the species determinations (e.g., *Andrena cyanomicans* and *Echium candicans* do not occur on Porto Santo). We did not use data of FELLENDORF et al. (1999) with unspecific numbers of males of *Lasioglossum wollastoni* that visited *Euphorbia paralias*.

The total dataset (with and without flower visits) included 691 data for Porto Santo (625 own data).

2. Data analyses

The localities were attributed to a grid (1 km x 1 km) based on the military map of the Madeira Archipelago (2004). Interaction networks were analysed using the bipartite package (DORMANN et al. 2008, R CORE TEAM 2018).

Results and discussion

1. Synoptic list of the wild bees of Porto Santo

According to the new updated checklist of the wild-bee species of the Madeira Archipelago (KRATOCHWIL et al. 2018), nine wild-bee species have been detected on Porto Santo (Table 2), 15 species on Madeira Island and four on Desertas (KRATOCHWIL et al. 2018).

There are taxonomically related species pairs on Madeira Island and Porto Santo. The phylogenetically older species are those of Porto Santo. Obviously, founder individuals reached Madeira Island from Porto Santo (45 km) and developed new endemic species. The species pairs are as follows (Porto Santo/Madeira Island): *Andrena dourada* – *A. wollastoni*; *Andrena portosanctana* – *A. maderensis*; *Osmia latreillei iberoafricana* (not endemic, also found inter alia in Spain) – *O. madeirensis*.

The native species *L. villosulum*, *O. latreillei iberoafricana* and *B. terrestris lusitanicus* and the introduced *H. pictipes* show west Palaearctic-Mediterranean distributions.

The nine wild-bee species will be characterised with some comments. The semi-domesticated honeybee *Apis mellifera* LINNAEUS, 1758, is not included in the list.

Hylaeus maderensis: Until now, there was only one detection of this rare species on Porto Santo; additionally, there are data from Deserta Grande (1 ind.) and Madeira Island (15 ind.). The type specimen (COCKERELL 1921), collected by T.V. Wollaston on Deserta Grande, is deposited in the Hope Entomological Collections (Oxford University). High-resolution photos of the type specimen were analysed by A. Kratochwil.

Given its small population sizes in small distribution areas, this species should get the rank ‘vulnerable’ (IUCN categories; http://www.iucnredlist.org).

Table 2: Current list of the wild-bee species of Porto Santo. M = endemic to Madeira Archipelago; P = endemic to Porto Santo.

Colletidae	*Hylaeus* (*Paraprosopis*) *maderensis* (COCKERELL, 1921)	endemic M
Colletidae	*Hylaeus* (*Paraprosopis*) *pictipes* NYLANDER, 1852	introduced
Andrenidae	*Andrena* (*Micrandrena*) *dourada* KRATOCHWIL & SCHEUCHL 2013	endemic P
Andrenidae	*Andrena* (*Suandrena*) *portosanctana* COCKERELL, 1922	endemic P
Halictidae	*Lasioglossum* (*Evylaeus*) *villosulum* (KIRBY, 1802)	native
Halictidae	*Lasioglossum* (*Evylaeus*) *wollastoni* COCKERELL, 1922	endemic M
Megachilidae	*Osmia* (*Helicosmia*) *latreillei iberoafricana* (PETERS, 1975)	native
Anthophoridae	*Amegilla* (*Amegilla*) *quadrifasciata maderae* (SICHEL, 1868)	endemic M
Apidae	*Bombus* (*Bombus*) *terrestris lusitanicus* KRÜGER, 1956	native

Hylaeus pictipes: There is only one detection within the Madeira Archipelago on Porto Santo. A male was collected by W. Barkemeyer (Oldenburg), Pedras Pretas, dune wall, 10.06.1987, deposited in the collection of the Übersee-Museum (Bremen, Germany); pers. comm. H. Dathe (Senckenberg German Entomological Institute, Müncheberg, Germany). There is no doubt that the detection of this west Palaearctic species on Porto Santo is based on an unintential introduction by man.

Andrena dourada (Fig. 2a): KRATOCHWIL & SCHEUCHL (2013) detected *A. dourada* from Porto Santo as a species of its own, which differs in numerous morphological and morphometric characteristics from *A. wollastoni* from Madeira Island. According to several morphological features, *A. dourada* shows a close relation to *A. tiaretta* WARNCKE, 1974 (KRATOCHWIL 2015). Our hypothesis is that *A. tiaretta* first colonised Porto Santo (or former stepping-stone islands) from the North African mainland and evolved into the endemic *A. dourada*, which colonised Madeira Island from Porto Santo and developed into the endemic *A. wollastoni*.

Given its small population sizes in small distribution areas, this endemic species should get the rank 'vulnerable' (IUCN categories; http://www.iucnredlist.org).

Andrena portosanctana (Fig. 2b): COCKERELL (1922) described *Andrena maderensis* Cockerell, 1922 and *A. portosanctana* COCKERELL, 1922. KRATOCHWIL et al. (2014) gave a differential diagnosis: We hypothesised that *A. portosanctana* (Porto Santo) is the ancestor of *A. maderensis* (Madeira) and that *A. portosanctana* (Porto Santo) descended from the mainland species *A. fratella* WARNCKE, 1968 (Morocco) or an ancestor of this species (KRATOCHWIL et al. 2014).

Given its small population sizes in small distribution areas, this endemic species got the rank 'vulnerable' (IUCN categories; http://www.iucnredlist.org).

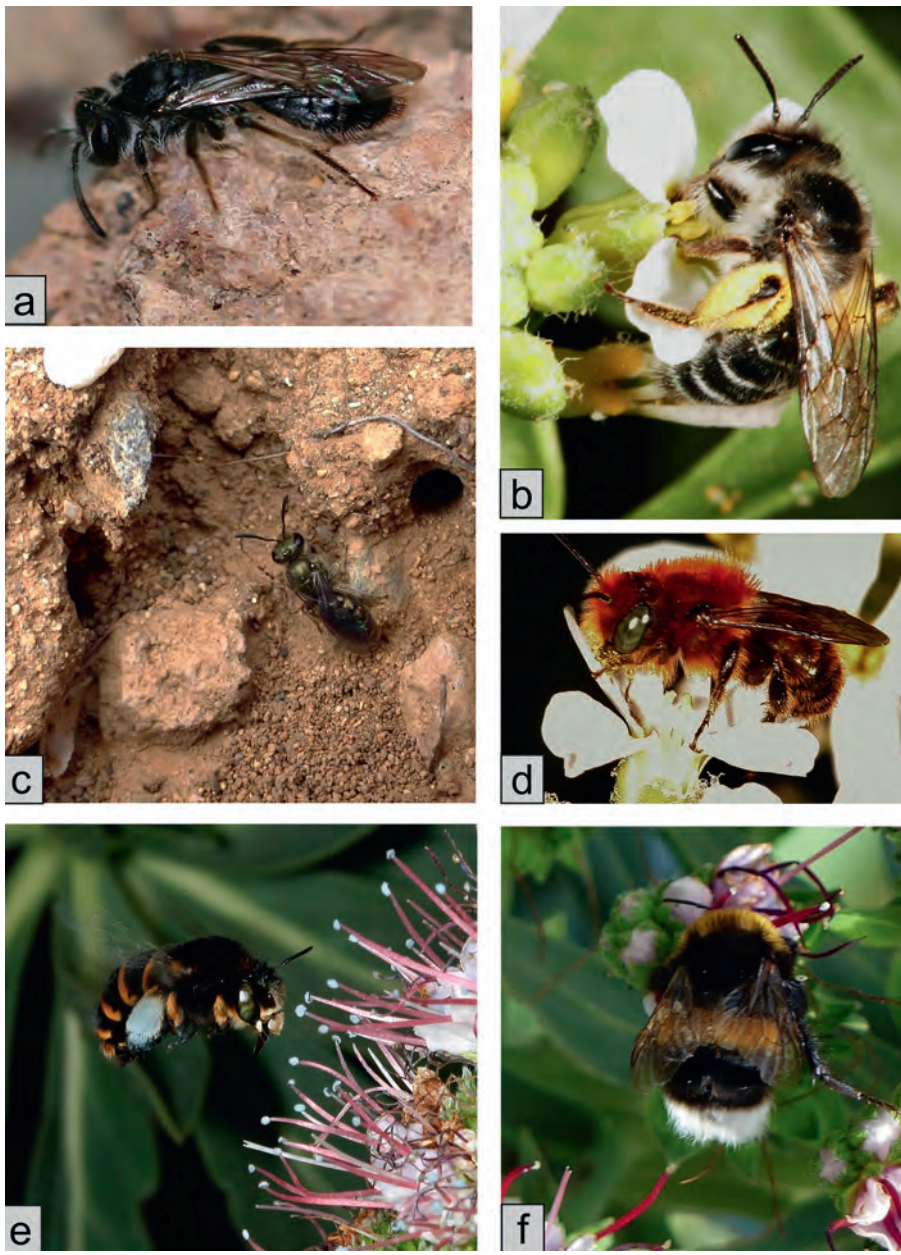

Fig. 2a-f: **a)** *Andrena dourada*, female; **b)** *Andrena portosanctana*, female collecting pollen on *Cakile maritima*; **c)** *Lasioglossum wollastoni*, female in front of nesting site; **d)** *Osmia latreillei iberoafricana*, male visiting *Cakile maritima*; **e)** *Amegilla quadrifasciata maderae*, female collecting pollen on *Echium portosanctensis*, **f)** *Bombus terrestris lusitanicus*, worker, collecting pollen on *Echium portosanctensis*. Photos: A. Kratochwil (a, b, e), A. Schwabe (c, d, f).

Lasioglossum villosulum: We suppose that this trans-Palaearctic species is native to the Madeira Archipelago. One hundred seventy-five individuals were found on Madeira Island, but detections on Porto Santo are rare (one female, collected by P. Wirtz, 20.05.1993, det. M. Fellendorf, collection of the Museu Municipal do Funchal, Madeira, photo checked by A. Kratochwil; one female, collected by P. Wirtz, 20.05.1993, det. M. Fellendorf, deposited in the Stuttgart State Museum of Natural History and checked by H.-R. Schwenninger). There are no data about flower visits for Porto Santo.

Lasioglossum wollastoni (Fig. 2c): *L. wollastoni* is endemic to the Madeira Archipelago. On Madeira Island and Porto Santo, this species is widely distributed and occurs locally in high individual numbers. This Madeira-Archipelago-endemic species is not an endangered species.

Osmia* (*Helicosmia*) *latreillei iberoafricana (Fig. 2d): According to our investigations this species is within the Madeira Archipelago only distributed on Porto Santo and not on Madeira Island. VAN DER ZANDEN (1983) and FELLENDORF et al. (1999) pointed out that the species occurs in Madeira Island. We hypothesise that *O. l. iberoafricana* of Porto Santo colonised Madeira Island and developed into the endemic *O. madeirensis*.

Amegilla quadrifasciata maderae (Fig. 2e): The *Amegilla* taxon '*maderae*' was described by SICHEL (1868) as species of its own. There are some morphological features differentiating it from other *A. quadrifasciata* specimens, e.g., from the Canary Islands or the European mainland. An assignment as a subspecies is certainly justified. Further morphological, morphometric and molecular-genetic analyses are necessary to prove the taxonomical status of populations of the Madeira Archipelago, the Canary Islands and the mainland.

Bombus terrestris lusitanicus (Fig. 2f): The *Bombus* taxon '*maderensis*' was sometimes regarded as species of its own (ERLANDSSON 1979; RASMONT 1984). This is not accepted by WIDMER et al. (1998), RASMONT et al. (2008) and WILLIAMS et al. (2012). We will follow RASMONT et al. (2008), who assigned the specimens of the Madeira Archipelago to *B. terrestris lusitanicus*; see also COPPÉE (2010).

2. Distribution patterns

The distribution patterns of six wild-bee species of Porto Santo are summarised in Table 3 and Fig. 3.

Table 3: Numbers of individuals, localities and grids of six bee species.

numbers of	individuals	localities	grids
Amegilla quadrifasciata maderae	204	47	20
Lasioglossum wollastoni	111	23	23
Osmia latreillei iberoafricana	91	22	13
Andrena dourada	45	19	12
Andrena portosanctana	28	10	9
Bombus terrestris lusitanicus	39	11	4

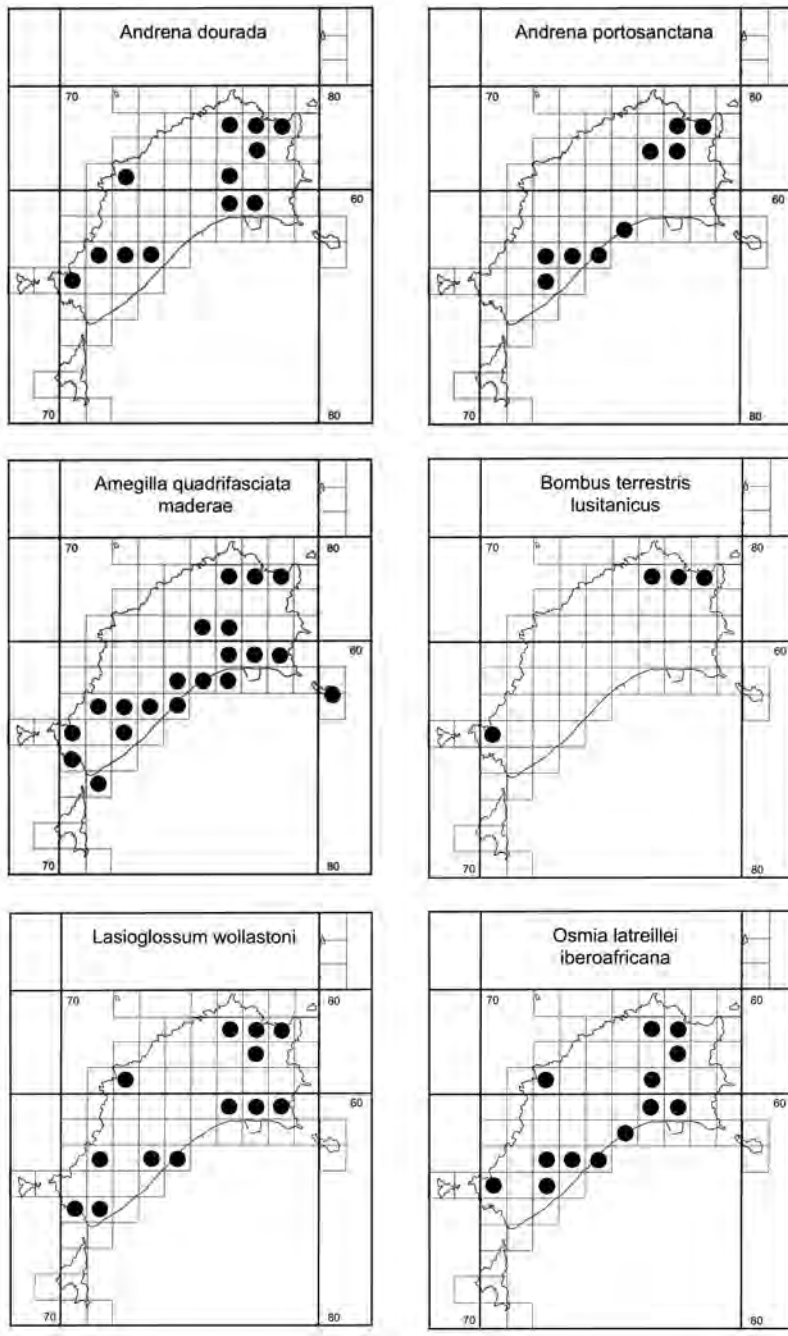

Fig. 3: Distribution patterns of six wild-bee species (grid size 1km x 1 km).

The two Madeira-Archipelago-endemic species, *Amegilla quadrifasciata maderae* and *Lasioglossum wollastoni*, show the widest distribution on the island (20 and 23 grids). A colony of *L. wollastoni* was detected near Cabeço da Ponta. Colonies of *A. q. maderae* were found nesting in solidified sand (fossil dunes) near Ponta da Calheta (approximately 150 nests) and in volcanic material below the summit of Pico Castelo (appr. 20 nests).

The native *Osmia latreilli iberoafricana* is also widely distributed on Porto Santo (13 grids, covering the whole island).

The two Porto-Santo-endemic species, *Andrena dourada* and *A. portosanctana*, occur in many parts of the island. *A. dourada* was detected in 12 grids and *A. portosanctana* in nine grids.

Bombus terrestris lusitanicus was only detected in subhumid areas of the northern coast/near the coast and in a locally more humid zone in the southwest (all in all, four grids).

3. Wild-bee abundances and flower visits in the dry year 2012 and the wet year 2017

The numbers of our observed or collected wild-bee individuals with and without flower visits after the dry winter (March 2012) and the wet winter (March 2017) are summarised in Table 1. In the dry year 2012, we detected all in all 31.4 individuals per day, whereas in the wet year 2017, there were only 26.3 individuals per day (without flower visit or in pan traps 2012: 5.4, 2017: 10.1 per day; with flower visits 2012: 26.0, 2017: 16.2 per day). We hypothesise that the concentration of bees under low flower density led to a proportionally higher flower-visiting rate.

All our data concerning *A. portosanctana* with flower visits are from the dry year 2012 (mainly *Cakile maritima*); in 2017, we detected only one individual in a pan trap. In 2017 *Cakile maritima* was intensively foraged, mainly by *Amegilla quadrifasciata maderae*.

4. Bee–plant network

The bipartite graph of the bee–plant network of Porto Santo (Fig. 4) shows the visited plant species on the left side and the flower-visiting bee species on the right side, both connected with interaction links. The bee–plant network demonstrates high asymmetry: six wild-bee species versus 29 plant species. In Central European networks, the proportion is mostly reversed. Two plant species were only used by males (*Galactites tomentosa* and *Chrysanthemum segetum*). The species are highly interconnected, showing that even under difficult environmental conditions with unequal resources, there are alternatives.

The bee–plant network shows that the most abundant bee species on flowers is *Amegilla quadrifasciata maderae*, with a polylectic use of pollen and nectar sources. The endemic *Andrena dourada* shows high rates of visits on the archipelago-endemic *Crambe fruticosa*. *Bombus terrestris lusitanicus* mainly visited the Porto-Santo-endemic species *Echium portosanctensis* and the Madeira-Archipelago-endemic species *E. nervosum* (including hybrid types). Beside *Amegilla quadrifasciata maderae*, two other bee species are polylectic: *Lasioglossum wollastoni* and *Osmia latreiilei iberoafricana*.

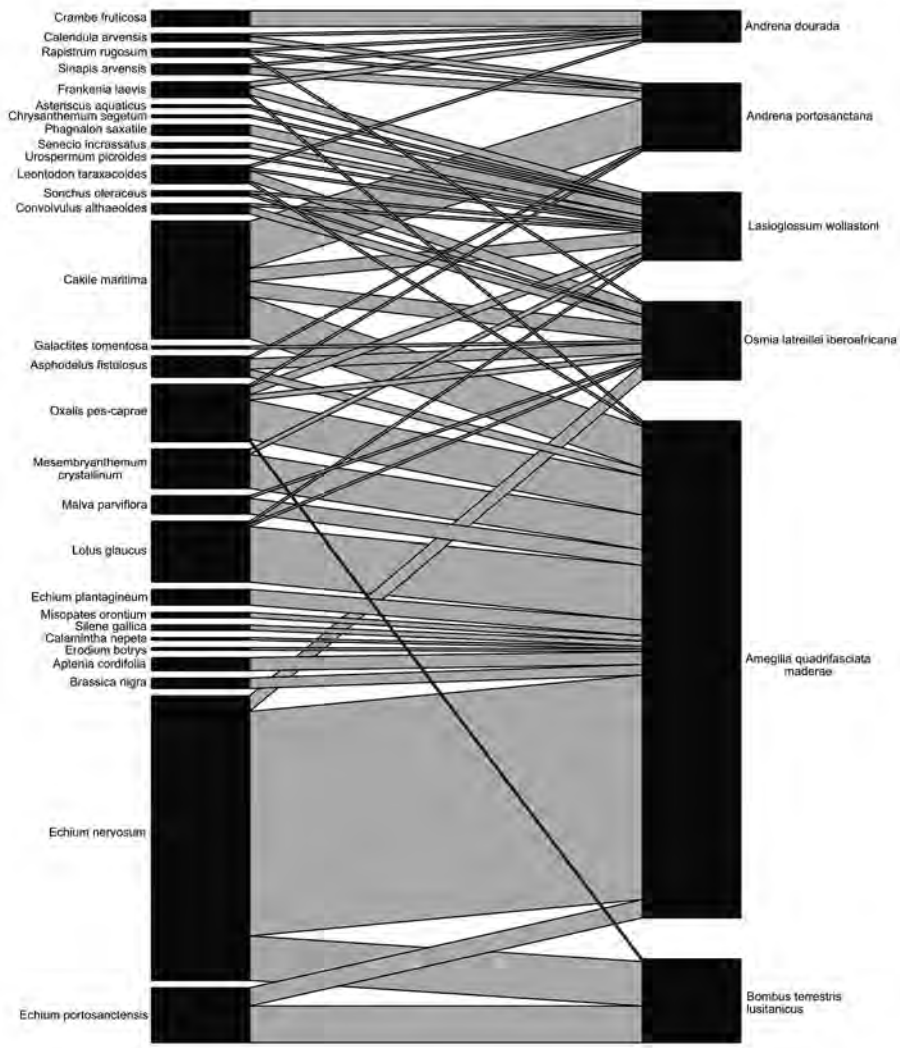

Fig. 4: Bipartite graph of the bee-plant network of Porto Santo.

Most of the used plant species are endemic species or native; therefore, they were already present about 500 years ago, before the beginning of the strong human impact. Examples are in the dry microforest and in open rocky, dry habitats: *Echium nervosum*, *Crambe fruticosa*; in sandy habitats (partly with salt influence): *Lotus glaucus*, *Cakile maritima*, *Senecio incrassatus*, *Frankenia laevis*; in open rocky habitats of the subhumid zone: *Echium portosanctensis*. With high probability, the use of the flower resources of these plant species by the wild bees of Porto Santo is therefore an old feature.

Conclusions

Porto Santo, a relatively old and small volcanic island in the Atlantic Ocean, is a model area for the colonisation of islands by wild-bee species of different area-geographical origin. Some wild bees of Porto Santo have developed into endemic species. Porto Santo served as an important colonisation source for Madeira Island, where new endemic species developed.

Still today, Madeira Island and Porto Santo have remarkable differences in bee-species composition despite their small distance of 45 km. This can only be understood from the biogeographical point of view.

Because wild bees are important pollinators, they are drivers of the bee–plant network. The bee–plant network of Porto Santo shows a clear asymmetry: few bees are connected with many plant species. This seems to be a rule for oceanic islands.

The wild-bee species have developed a high number of adaptations to the prevailing environmental conditions. Partly, these developments have led to endemism. The populations show high adaptations to the harsh and unpredictable environment. Five wild-bee species are widely distributed on Porto Santo; this also applies to the endemic wild-bee species (see maps, Fig. 3). Nevertheless, the two endemic mining bees *Andrena dourada* and *A. portosanctana* are endangered species because they have only small numbers of individuals. In the case of *A. portosanctana*, the existence of large *Cakile maritima* populations is of great importance.

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Zusammenfassung

Porto Santo (Madeira Archipel) ist eine relativ alte (11.1–14.3 Mio. Jahre) und kleine vulkanische Insel im Atlantischen Ozean. Aufgrund der geringen Höhe der Berge ist der Hauptteil der Insel durch ein semiarides Klima und Trockenvegetation gekennzeichnet; nur ein kleiner Teil zeigt subhumide Bedingungen. Wir konnten die Wildbienenfauna und das Bienen-Pflanzen-Netzwerk (mit Farbschalen, Handnetz oder Beobachtung) hauptsächlich während zweier Aufenthalte im März 2012 und 2017 untersuchen. Bis heute sind neun Wildbienenarten nachgewiesen worden. Zwei Arten sind für Porto Santo endemisch und zwei Arten und eine Unterart für den Madeira Archipel. Eine aktualisierte und kommentierte Checkliste der Wildbienenarten von Porto Santo wird vorgestellt. Die Evolution der endemischen Arten *Andrena dourada* und *A. portosanctana* wird disku-

tiert. Sowohl die endemischen als auch die einheimischen Bienenarten zeigen auf Porto Santo eine weite Verbreitung in der Trockenzone. Nur *Bombus terrestris lusitanicus* ist auf den subhumiden Bereich beschränkt. Wir haben insgesamt etwa 300 Bienen-Pflanzen-Interaktionen beobachtet und analysiert. Im Gegensatz zu Festland-Netzwerken, z.B. in der warm-gemäßigten Zone, die in der Regel durch wesentlich mehr Bienen- als Pflanzenarten gekennzeichnet sind, zeigt das Bienen-Pflanzen-Netzwerk von Porto Santo viel mehr Pflanzen- als Bienenarten und ist damit stark asymmetrisch. Sechs Wildbienenarten nutzten 27 verschiedene Pflanzenarten. Bienen- und Pflanzenarten sind deutlich miteinander vernetzt, was bedeutet, dass für die Bienenarten auch unter schwierigen Umweltbedingungen und Ressourcenbeschränkungen alternative Nektar- und Pollenressourcen zur Verfügung bestehen. Insbesondere die verholzten *Echium*-Arten *E. nervosum* (endemisch für den Madeira-Archipel) und *E. portosanctensis* (endemisch für Porto Santo) sind einerseits Schlüsselarten als Ressourcen für Wildbienen. Als selbstinkompatible Pflanzenarten sind sie andererseits von Insektenbestäubung abhängig. Selbst in sehr trockenen Perioden (März 2012, im Winter keine Niederschläge) zeigte *Echium* eine reiche Blütenproduktion und wurde intensiv von Wildbienen besucht. Dasselbe gilt für *Cakile maritima*, die eine wichtige Ressource für die endemische Art *Andrena portosanctana* (spezialisiert auf Brassicaceae) darstellt. Im feuchteren Frühjahr 2017 gab es einen Rückgang in der Anzahl insgesamt nachgewiesener Wildbienen-Individuen im Vergleich zu 2012. Im trockeneren Frühjahr 2017 wurden proportional mehr Individuen an Blüten beobachtet und weniger Vorkommen ohne Blütenbesuch festgestellt.

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Nomenclature

The nomenclature for plant species names follows JARDIM & MENEZES DE SEQUEIRA (2008). One plant species was newly described in the year 2010: *Echium portosanctensis* Carvalho, Pontes, Batista-Marques & Jardim, 2010; see CARVALHO et al. (2010).

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