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Comments on the butterfly fauna (Papilionoidea) of Porto Santo (Madeira Archipelago): species list, distribution patterns, and butterfly-plant network

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With 2 figures and 3 tables

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ABSTRACT: Porto Santo (Madeira Archipelago) is a relatively old (11.1 to 14.3 Ma) and small volcanic island in the Atlantic Ocean. The main part of the island is characterised by semiarid climate and xeric vegetation, while the higher altitudes show subhumid conditions. So far, 11 butterfly species (Papilionoidea) have been detected on Porto Santo. The occurrence of *Macroglossum stellatarum* (Sphingidae) is published for the first time. The butterfly species of Porto Santo are commented and some comparisons with Madeira Island are discussed.

The distribution of butterfly species on Porto Santo was studied during March 2017 (Papilionoidea; n = 204). Some observations of previous years were added (n = 21) and *Macroglossum stellatarum* (Sphingidae; n = 3) was also included. The butterfly-plant network was sampled during March 2017 (115 flower visits).

Three species (*Colias croceus*, *Pieris rapae* and *Vanessa cardui*) show a wide occurrence on Porto Santo. As an exception, *Vanessa vulcania* prefers the subhumid regions. *Leptotes pirithous*, *Macroglossum stellatarum*, *Pararge aegeria* (which all newly colonised Porto Santo), and the migratory *Danaus plexippus* show a scattered distribution. On the whole, 115 butterfly-plant interactions could be recorded. The network shows more plant than butterfly species and is asymmetric: Seven butterfly species used 15 plant species. The butterfly and plant species were interconnected. The woody *Echium* species, *E. nervosum* (endemic to the Madeira Archipelago) and *E. portosanctensis* (endemic to Porto Santo), including hybrids, are key species as nectar resources for *Vanessa atalanta*, *V. cardui*, and *V. vulcania*. *Vanessa vulcania* could be found only within one grid in the north of the island at an altitude of 235 m *a.s.l.* *Vanessa vulcania* is probably a remnant of an earlier time period, where – due to lack of human impact – larger areas with microforests and in part *Apollonias barbujana* laurisilva existed.

Keywords: Lepidoptera, Papilionoidea, Sphingidae, island biogeography, butterfly diversity, *Vanessa vulcania*, Madeira Archipelago, Porto Santo.

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RESUMO: Porto Santo (Arquipélago da Madeira) é uma pequena ilha vulcânica relativamente antiga (11.1 a 14.3 Ma) situada no Oceano Atlântico. A parte principal da ilha é caracterizada por ter um clima semiárido e vegetação xérica, enquanto as altitudes mais altas mostram condições sub-húmidas. Até agora, 11 espécies de borboletas (Papilionoidea) foram detectadas no Porto Santo. A ocorrência de *Macroglossum stellatarum* (Sphingidae) é publicada pela primeira vez. As espécies de borboletas do Porto Santo são comentadas e algumas comparações com a ilha da Madeira são discutidas. A distribuição das espécies de borboletas no Porto Santo foi estudada durante março de 2017 (Papilionoidea; n = 204). Algumas observações de anos anteriores foram adicionadas (n = 21) e *Macroglossum stellatarum* (Sphingidae; n = 3) também foi incluído. A rede de plantas de borboletas foi amostrada durante março de 2017 (115 visitas de flores). Três espécies (*Colias croceus*, *Pieris rapae* e *Vanessa cardui*) são bastante frequentes no Porto Santo. Como exceção, *Vanessa vulcania* prefere as regiões sub-úmidas. *Leptotes pirithous*, *Macroglossum stellatarum*, *Pararge aegeria* (todas introduções recentes no Porto Santo), e a espécie migratória *Danaus plexippus* migratórias mostram uma distribuição mais dispersa. No total, foram registradas 115 interações borboleta-planta. A rede inclui mais plantas do que espécies de borboletas e é assimétrica: sete espécies de borboletas usaram 15 espécies de plantas. As espécies de borboletas e plantas estavam interligadas. As espécies lenhosas do género *Echium*, *E. nervosum* (endémica do arquipélago da Madeira) e *E. portosanctensis* (endémica do Porto Santo), incluindo os seus híbridos, são espécies-chave como recursos de néctar para *Vanessa atalanta*, *V. cardui*, e *V. vulcania*. *Vanessa vulcania* só foi encontrada dentro de uma grade no norte da ilha a uma altitude de 235 m. *Vanessa vulcania* é provavelmente um remanescente de um período de tempo anterior, em que – devido à falta de impacto humano – existiam áreas maiores com microflorestas, assim como Laurissilva do Barbusano.

Palavras-chave: Lepidoptera, Papilionoidea, Sphingidae, biogeografia de ilhas, diversidade de borboletas, *Vanessa vulcania*, Arquipélago da Madeira, Porto Santo.

INTRODUCTION

The first list of Papilionoidea of Madeira Island (seven species) was published by Felder (1862), based on specimens collected during the Novara Expedition (1857-1859), the first broad-scale scientific mission of the Austrian Imperial Navy (Basch-Ritter, 2008). The collector was the Austrian zoologist Georg von Frauenfeld (1807-1873), though he did not visit Porto Santo.

In nine expeditions, the British entomologist Thomas Vernon Wollaston (1822-1878) collected much more intensively from the Madeira Archipelago (Machado, 2006), including Madeira Island, the Desertas Islands, and Porto Santo. His main interest was the study of Madeiran Coleoptera (Wollaston, 1854), but also Hymenoptera (*e.g.*, wild bees; Kratochwil, 2018) and Lepidoptera (Karsholt, 2000). For generations, this immense material served as a base for further analyses, which resulted in numerous publications and species descriptions. Baker (1891) analysed the Papilionoidea (11 species) collected by Wollaston and commented the list (*e.g.*, abundancy, morphological features, differences to mainland forms), but without further information (*e.g.*, on which island they had been collected). As a rule, Wollaston had labelled or colour-marked the specimens according to the islands where they were collected, or (in most cases) had numbered and listed them in books (Machado, 2006). However, Baker (1891) obviously did not consider localities as important. Furthermore, most of the details had been documented by Wollaston in lists, but some of them were hard to find or lost. Baker (1891) was the first who mentioned *Macroglossum stellatarum* in relation to Madeira Island.

Rebel (1917) listed 13 Papilionoidea species for the Madeira Archipelago without further comments and without notes of the occurrences on different islands; Rebel (1940) listed 11 species (without *Pieris rapae* and *Vanessa atalanta*, mentioned in Rebel, 1917). A more detailed list by Martin (1941) refers only to Madeira Island.

The first list of the Papilionoidea of Porto Santo was published by Carvalho (1983). In 1980 and 1981, he observed four species in one locality (Achada de Baixo): *Pieris rapae*, *Colias croceus*, *Lampides boeticus*, and *Vanessa cardui*. His list also included *Vanessa indica occidentalis*, cited by Baker (1891), but the Sphingid species *Macroglossum stellatarum* was not mentioned. Owen *et al*. (1987) listed 14 species for Madeira Island.

A comprehensive overview of the butterflies of the Madeira Archipelago was given by Meyer (1993).

He distinguished the different islands of the Madeira Archipelago and found the following species numbers without vagrants: Madeira Island, 14 species; Porto Santo, five species; Deserta Grande, Bugio, Selvagem Grande, and Selvagem Pequena, one species each. Owen & Smith (1993) analysed the butterfly fauna of Macaronesia and stated the same species numbers for Madeira Island and Porto Santo as Meyer (1993).

An updated list of the butterflies of the Madeira Archipelago was presented by Aguiar & Karsholt (2006). The first distribution maps of the endemic butterflies (Papilionoidea) of Madeira Island were produced by Wakeham-Dawson *et al*. (2002a), but distribution maps of all species were not available. Wakeham-Dawson *et al*. (2002b) also provided some further notes of the butterflies of the Madeira Archipelago, and Wakeham-Dawson *et al*. (2004) presented the last published checklist of Madeira Island (13 species) and Porto Santo (10 species).

Although numerous studies have already focused on the butterflies of Porto Santo, their distribution patterns and networks with flowering plants have not been studied until now.

An overview of wild bees (Hymenoptera, Anthophila) on Porto Santo has been recently published by Kratochwil & Schwabe (2018), which proves the existence of a wide distribution of most wild-bee species – except for the bumblebee *Bombus terrestris lusitanicus*, which prefers the subhumid regions – and demonstrates the significant importance of the *Echium* species for flower-visiting bees.

The following topics will be presented in this study:

(1) a commented checklist of butterfly species of Porto Santo;

(2) a first overview of the distribution patterns of 11 butterfly species occurring on Porto Santo and their nectar resources;

(3) the structure of the butterfly-plant network in Porto Santo.

Physico-geographical factors

Porto Santo is a relatively old (11.1 to 14.3 Ma) and small volcanic island (area 42 km^2) within the Madeira Archipelago (Geldmacher *et al*., 2000), with latest volcanic activities occurring about eight million years ago (Cook, 2008). The island is separated from Madeira Island by an ocean bed more than 2000 m deep.

Geologically Porto Santo has a volcanic base, and the summits (*e.g*., Pico do Facho 517 m *a.s.l*., Pico da Gandaia 499 m *a.s.l*., Pico Branco 451 m *a.s.l*.) are characterised mainly by trachyte and basaltic structures. More than a third of the island is covered by quaternary sediments, mainly between the northeastern and southwestern mountain areas. Calcareous sand from the Pleistocene period formed eolianites, which is solidified with more than 50 m vertical thickness in part. The southern coast is dominated by a long sandy beach, while the other parts of the coast are characterised by steep cliffs. Perennial water currents are not present, but some perennial springs exist (Faust-Lichtenberger, 1988).

The bioclimate was classified as Mediterranean xeric oceanic by Rivas-Martínez (2009) with a pronounced summer aridity. Precipitation values are very low from June to August (376 mm/a), while mean temperature varies between 15.7 °C (February) and 22.8 °C (August).

There are only few habitat types, and for the last 500 years there has been a strong anthropogenic impact. There are about 446 phanerogamic plant species (nine endemic species for Porto Santo, 29 endemic species for the Madeira Archipelago, and 19 endemic species for Macaronesia). All in all, 286 plant species are (probably) native, and 103 species are (probably) introduced (Jardim & Menezes de Sequeira, 2008; Jardim & Menezes de Sequeira, 2011; Jones *et al*., 2014; Kratochwil & Schwabe, 2018).

The island was cleared to a great extent from woody vegetation (original vegetation: mainly dry microforests of Mayteno umbellatae-Oleo maderensis sigmetum). From the end of the 18th century, afforestations were made with *Pinus pinaster* and *Pinus halepensis*. Most habitats belong to the *Olea maderensis* series (Mayteno umbellatae-Oleo maderensis sigmetum); Capelo *et al*. (2004, 2005). The *Echium* species are the main nectar sources for many butterflies. The natural distribution of *E. nervosum* is concentrated in the southern part, while *E. portosanctensis* occurs naturally in the subhumid zone (Carvalho *et al*., 2010). *Echium nervosum* can also be found in plantings near the roads, while *E. portosanctensis* was planted in the northern part (hybrids exist). Small elements of the subhumidic series are still present around the main summits and on the north-facing slopes (Capelo *et al*., 2004).

Extended sand habitats occur especially in the southeastern part of the island and are relatively rich in *Lotus glaucus*. There are also drift walls with *Cakile maritima*, as well as halonitrophytic rocky and sandy sites with *Matthiola maderensis*, *Mesembryanthemum crystallinum*, and *Senecio incrassatus*. The island has a very rich ruderal flora and vegetation, now mainly characterising fallow land. Ruderal plant species such as *Asphodelus fistulosus*, *Convolvulus althaeoides*, *Rapistrum rugosum*, and *Sonchus oleraceus* play a role as nectar resources for butterflies.

METHODS

Butterfly database

We observed the butterflies of Porto Santo mainly during one visit from 19 to 31 March 2017 (A. Kratochwil and A. Schwabe). We recorded the distribution pattern of the butterflies and their interactions with plants. Qualitative observations from the dry spring of 2012 (16-20 March) preceded the 2017 study. Due to the presence of masses of flowers after the relatively wet winter in 2016/2017 (see Kratochwil & Schwabe, 2018), the time period in March 2017 was very good for butterfly monitoring.

Our approach covered the main habitat types. All in all, we monitored 45 sites in the northern and southern parts of the island – most localities with a full xeric, some localities with a subhumid mesic-xeric bioclimate. The number of observation sites reflected the proportion of the climatic types on the island. Most of these sites were identical with the wild-bee sampling sites (Kratochwil & Schwabe, 2018). We were not able to observe butterflies in the flat central part of the island (airport, golf course) because access to the area was not permitted. The GPS data of all the collected or observed butterfly species were recorded with a Garmin Oregon 700.

We recorded ten butterfly species and 204 butterfly individuals (Table 1), including 115 flower visits. Fourteen further observations by A. F. Aguiar were included in the database (six species from nine localities, and five flower visits on three plant species). Additionally, seven specimens collected on Porto Santo were found in the collections of the Museu de História Natural do Funchal (Madeira, Portugal).

Data analysis

The localities were plotted on 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

Commented checklist of the butterfly species of Porto Santo

We were able to analyse the distribution pattern of 11 species (Table 2, Fig. 1), which are commented below. The Sphingid *Macroglossum stellatarum* (three observations, two flower visits observed) was included in the analysis.

We observed the following species (in alphabetical order):

Colias croceus (Geoffroy in Fourcroy, 1785)

This Palaearctic migrating species – widespread in Europe except the North (occurring in southern Scandinavia, Baltic states; see Tolman & Lewington, 1997), but common in Central and Southern Europe, and with further distribution in North Africa and Southwest Asia (Tshikolovets, 2011) – is native to the Madeira Archipelago and the Canary Islands (Tolman & Lewington, 1997).

On Madeira Island, *C. croceus* was very common on open sites (Salmon & Wakeham-Dawson, 1999), and in July and August 1998, was the most abundant butterfly on the island (Salmon & Wakeham-Dawson, 1999). The main distribution is concentrated in dry coastal areas and near human settlements (Meyer, 1993). *Colias croceus* occurs at all altitudes from sea level up to 1,800 m *a.s.l.* (Meyer & Hellers, 1990; Kudrna, 1997; Salmon & Wakeham-Dawson, 1999). Swash & Askew (1982) reported that *C. croceus* is the most abundant Madeiran butterfly at altitudes above 1,600 m *a.s.l.* *Colias croceus* was also recorded on Porto Santo (Meyer & Hellers, 1990; Aguiar & Karsholt, 2006).

It is suggested that this species (probably) breeds on Madeira Island (Vieira, 1999; Wakeham-Dawson & Aguiar, 2003; Wakeham-Dawson *et al*., 2004). The ratio between breeding and migrant individuals is unknown, but it seems that vagrants are in minority.

Salmon & Wakeham-Dawson (1999) present different varieties (forms) of *C. croceus* from the Madeira Archipelago: var. *cremonae* Verity, 1911; var. *dawsoni* Bollow, 1930; var. *geisleri* Bryk, 1923; var. *radiata* Nitsche, 1932; and var. *faillae* Stefanelli, 1900. Fuchs (1993) also described the high variability of colour forms of *C. croceus* from Faial (Azores). Such wing colour patterns, based on phenotypic plasticity, may be produced physiologically in response to environmental stress (*e.g*., temperature, general stress response) and may be genetically fixed in a population (Otaki *et al*., 2010). This is shown particularly in the genus *Vanessa* (summarised in Hijama *et al*., 2002).

Aguiar & Karsholt (2006) reported that var. *helice* (Hübner, 1879) is rather frequently seen on Porto Santo (5-10% of all populations; Tolman & Lewington, 1997).

In the Museu de História Natural do Funchal three females of the form '*helice*' are deposited, collected in May 1942 (unknown collector, determined by J. T. Smit in 1998), and also two females of the same form, collected on 30 March 1988 by F. Zino (determined by J. T. Smit in 1998).

Table 1 – List of butterfly species of Porto Santo (MA = Madeira Archipelago, CI = Canary Islands), number of observations and number of flower visits in this study.

Family	Species	Status	Number individuals	Number flower visits
	Data from the authors and Museu de História Natural do Funchal			
Pieridae	*Pieris rapae* (Linnaeus, 1758)	native/introduced?	16	2
Pieridae	*Colias croceus* (Geoffroy in Fourcroy, 1785)	native	82	23
Lycaenidae	*Leptotes pirithous* (Linnaeus, 1758)	introduced?	12	2
Lycaenidae	*Lampides boeticus* (Linnaeus, 1767)	native	4	2
Nymphalidae	*Danaus plexippus* (Linnaeus, 1758)	native/introduced?	6	1
Nymphalidae	*Vanessa atalanta* (Linnaeus, 1758)	native	19	18
Nymphalidae	*Vanessa cardui* (Linnaeus, 1758)	native	68	58
Nymphalidae	*Vanessa vulcania* (Godart, 1819)	endemic (MA, CI)	10	10
Nymphalidae	*Pararge aegeria aegeria* (Linnaeus, 1758)	introduced	5	2
Sphingidae	*Macroglossum stellatarum* (Linnaeus, 1758)	native	3	2
	Data from other observers			
Nymphalidae	*Hypolimnas misippus* (Linnaeus, 1764)	migrant	-	-
Lycaenidae	*Lycaena phlaeas phlaeoides* (Staudinger, 1901)	endemic (MA)	-	-

Table 2 – Numbers of observed individuals, localities, and grids of 11 species. * = including data from Carvalho (1983).

	Number of grids	Localities	Individuals
Colias croceus	19	38	77
Danaus plexippus	4	4	4
Hypolimnas misippus	2	2	3
Lampides boeticus	3*	4*	4
Leptotes pirithous	5	6	12
Macroglossum stellatarum	3	3	3
Pararge aegeria	4	4	5
Pieris rapae	11	13	14
Vanessa atalanta	3	3	19
Vanessa cardui	9	14	68
Vanessa vulcania	1	2	10

Table 3 – Visited plant species and number of observations in March 2017.

	Number flower visits
Echium nervosum (including hybrids)	86
Lotus glaucus	6
Asphodelus fistulosus	5
Leontodon taraxacoides	3
Cakile maritima	2
Convolvulus althaeoides	2
Matthiola maderensis	2
Brassica nigra	1
Echium portosanctensis	1
Galactites tomentosa	1
Mesembryanthemum crystallinum	1
Oxalis pes-caprae	1
Rapistrum rugosum	1
Senecio incrassatus	1
Sonchus oleraceus	1

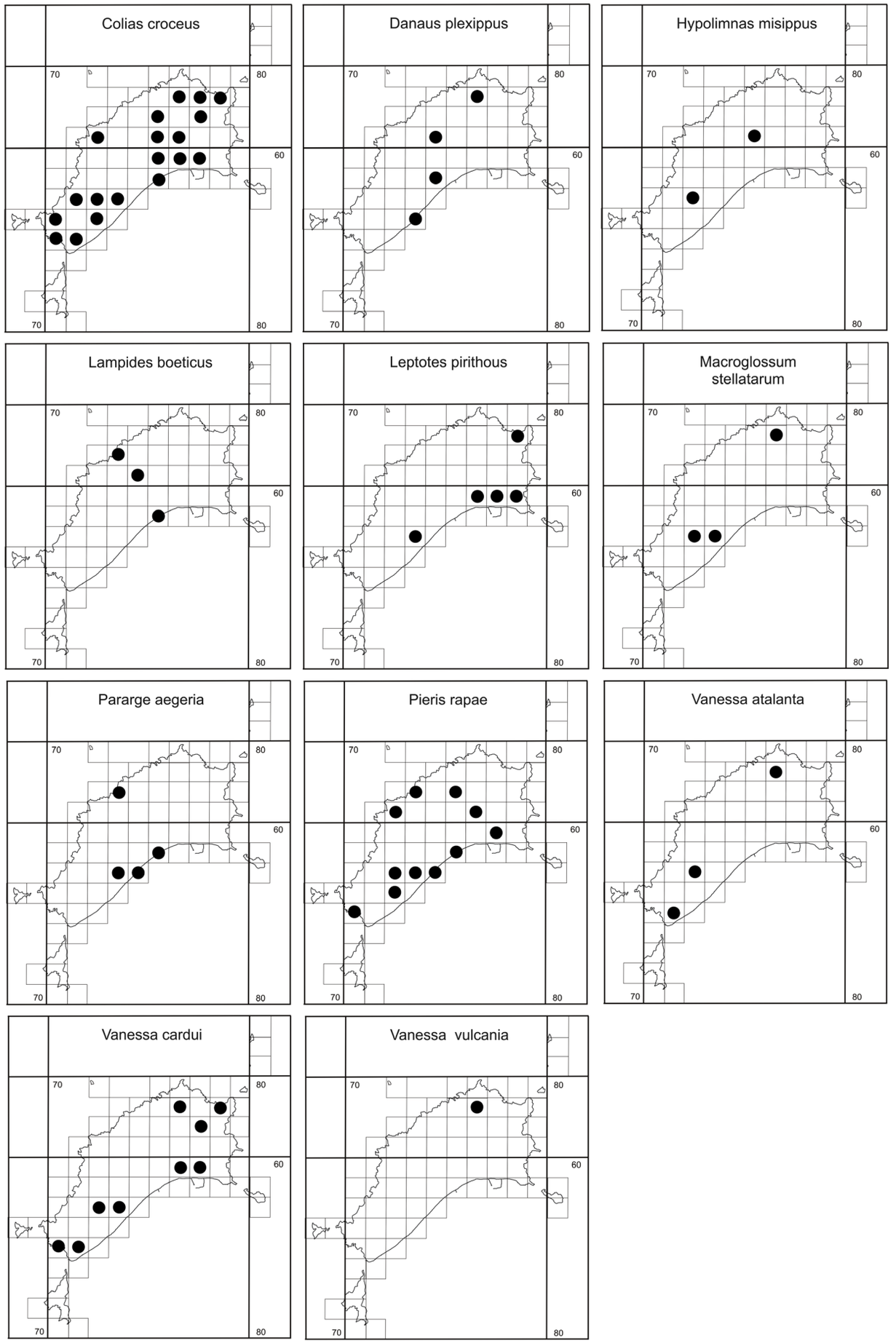

Fig. 1 – Distribution patterns of 11 butterfly species from Porto Santo.

If we use the form '*helice*' in the broader sense for all bright forms (white to yellowish wing colour; '*alba*' polymorphism), four of the specimens we observed have to be assigned to this form. So far, the literature has reported the form 'helice' only for female butterflies (Lorkovic & Herman, 1961; Limeri & Morehouse, 2016; Limeri, 2017).

Our observations demonstrate that *C. croceus* is also quite common throughout Porto Santo from sea level up to the highest mountains (19 grids, 38 localities; Fig. 1). *Colias croceus* could be detected on the flowers of ten plant species: *Asphodelus fistulosus* (Xanthorrhoeaceae) n = 5; *Brassica nigra* (Brassicaceae) n = 1; *Convolvulus althaeoides* (Convolvulaceae) n = 2; *Echium nervosum* (Boraginaceae) n = 1; *Galactites tomentosa* (Asteraceae) n = 1; *Leontodon taraxacoides* (Asteraceae) n = 3; *Lotus glaucus* (Fabaceae) n = 6; *Matthiola maderensis* (Brassicaceae) n = 2; *Mesembryanthemum crystallinum* (Aizoaceae) n = 1; and *Oxalis pes-caprae* (Oxalidaceae) n = 1.

Danaus plexippus (Linnaeus, 1758)

This species, originally native to North and Central America, nowadays has – by migration events or man-made introductions – a presence in the warmer zones (southern Portugal, southern Spain, India, Papua New Guinea, other East Indian islands, Australia, New Zealand, Hawaii, and southern Peru to Canada; Tolman & Lewington, 2008). There are migratory and non-migratory populations (Freedman *et al*., 2018). *Danaus plexippus* is classified as a migratory species in Madeira, Porto Santo, and Canary Islands (Owen & Smith, 1993). According to Aguiar & Karsholt (2006), this species has occurred periodically on Madeira Island since 1889, and was seen for the first time in Porto Santo in 1955 (Pereira, 1989). The exact date of arrival is unknown, and not recorded by Baker (1891) nor Cockerell (1923). A successful colonisation was possible because the species is able to use introduced plant species as larval food (Owen & Smith, 1989). Local populations established in the Canary Islands in 1880 or 1887 (Higgins & Riley, 1970; Leestmans, 1975; Báez, 1998), and the species was also spotted on Madeira Island (Sousa, 1986, 1991) and Porto Santo (Gardner & Classey, 1960; Vieira, 1999). The establishment on Madeira and Porto Santo is believed to have happened in August 1980 (Aguiar & Karsholt, 2006). Salmon & Wakeham-Dawson (1999) and Showler (2001) hypothesised an intended introduction. During the last two decades, *D. plexippus* has also become a resident species in the Azores (Neves *et al*., 2001).

In the Museu de História Natural do Funchal one female, collected on 14 June 1970 (unknown collector) and one male, collected in September 1957 (unknown collector), are deposited; both were determined by J. T. Smit in 1998.

One flower visit of this species was observed on *Bougainvillea* by A. F. Aguiar. On Porto Santo, *D. plexippus* was detected on four grids and in four localities (Fig. 1) flying at high speed with directed movement.

Lampides boeticus (Linnaeus, 1767)

This seasonal migratory species is widely distributed all over the world in southern regions with higher temperatures, and in subtropic and tropic zones: Southern Europe (reaching occasionally to Germany and the British Isles), North Africa, subtropical and dryer regions in South and Southeast Asia, Australia, New Zealand, and Hawaii. In Macaronesia *L. boeticus* is distributed on the Canary Islands, the Azores (Felder, 1862; Leestmans, 1974), and Madeira Island (Rebel, 1940; Meyer & Hellers, 1990; Meyer, 1993; Tolman & Lewington, 1997; Tshikolovets, 2011). On Madeira Island the species was recorded by Baker (1881), Swash & Askew (1982), and Salmon & Wakeham-Dawson (1999), and classified both as common by Owen *et al*. (1987) and as not common by Wakeham-Dawson *et al*. (2004).

Carvalho (1983) reported this species in two localities on Porto Santo (Achada de Baixo, 18 September 1980, and Farrobo, near the airport, 17 September 1980). The species was observed in two further localities (Vila Baleira, 16 July 2001; road to Fonte da Areia, 6 July 2017). *Lampides boeticus* was detected in three grids (Fig. 1) and one flower visit on *Lotus glaucus* was observed. Wakeham-Dawson & Aguiar (2003) documented egg laying on *Lotus glaucus* on Porto Santo (in July 2002).

Leptotes pirithous (Linnaeus, 1767)

The range of *L. pirithous* spans from North Africa, Southern and Central Europe, Turkey, the Middle East, Saudi Arabia, and Central Asia to India (Tolman & Lewington, 1997). The species is also present in the Canary Islands (Tshikolovets, 2011), where the first detection occurred in 1998 (Aguiar & Karsholt, 2006). Probably originating from the Canary Islands, *L. pirithous* was introduced to the Madeira Archipelago. Records of *L. pirithous* on Madeira Island and Porto Santo were reported in 2001 by Hall & Russell (2001), Wakeham-Dawson *et al*. (2002b), and Aguiar *et al*. (2002). One flower visit of this species was observed on *Rosmarinus officinalis* by A. F. Aguiar. Wakeham-Dawson *et al*. (2002b) reported observations of this species flying around *Lotus glaucus* in the sand dunes of Calheta (Porto Santo). On Porto Santo, *L. pirithous* was detected on five grids and in six localities (Fig. 1).

Macroglossum stellatarum (Linnaeus, 1758)

This migratory species has a permanent distribution in the southern Palaearctic region including North Africa, the Near East, and Pakistan, reaching eastwards to China and Japan. The northern areas are populated only in warmer months.

The first record of *M. stellatarum* was reported by Baker (1891), who characterised this species as common for Madeira Island. Further detections were reported by Rebel (1940, 1940b) and Martin (1941). *Macroglossum stellatarum* was also detected on Selvagem Grande (Aguiar & Karsholt, 2006). On Porto Santo, *M. stellatarum* was found on three grids and three localities (Fig. 1), only on flowers of *Echium nervosum* (Boraginaceae) n = 2.

Pararge aegeria aegeria (Linnaeus, 1758)

The nominal species is distributed in Maghreb, the Iberian Peninsula, the Balearic Islands, southern and southwestern France, southwestern Switzerland, Peloponnesus, Corsica, Sardinia, Sicily, southern Italy, Crete, Lesbos, Samos, Kos, Karpathos, Cyprus, southern Turkey, and the Near East (Tshikolovets, 2011). Madeira was recently colonised – the first specimen was observed by the lepidopterist Hoegh-Guldberg in 1967 on Madeira Island (Oehmig, 1983). Numerous detections of this introduced species were documented in the mid-seventies (Higgins, 1977; Oehmig, 1977, 1982; Owen *et al*., 1987; Aguiar & Karsholt, 2006). In 1981, *P. a. aegeria* was at least as common as *P. xiphia* on Madeira Island (Swash & Askew, 1981). Nowadays, *P. a. aegeria* is one of the more common butterflies on Madeira Island living in lower elevations mainly in residential areas, disturbed habitats, cultivation sites, and gardens (Lace & Jones, 1984; Owen *et al*., 1987; Shreeve & Smith, 1992; Fernández-Rubio & Garcia-Barros, 1995; Owen *et al*., 2008). It was not seen on Porto Santo in 1981 (Swash & Askew, 1982), but a single specimen was detected in 1998 (Vieira, 1999).

On Porto Santo, *P. a. aegeria* was detected on four grids and in four localities (Fig. 1) and could be observed on two plant species: *Cakile maritima* (Brassicaceae) n = 1 and *Senecio incrassatus* (Asteraceae) n = 1. Territorial and mating behaviours were noted.

Pieris rapae (Linnaeus, 1758)

This species has a trans-Palaearctic, North-African distribution including the Arabian Peninsula and subtropical Asia. It was introduced and is now resident in North America and Australia (Tshikolovets, 2011), and it is less frequent in northern Fennoscandia (Tolman & Lewington, 1997). The first indications for an occurrence on Madeira Island came from Rebel (1917), but in his checklist the taxon *P. rapae* is characterised by a question mark. In a footnote he referred to Otto Sterz, who observed *P. rapae* on Madeira Island in March 1909. A voucher specimen does not exist.

P. rapae is a recent introduction on Madeira Island and has become one of the most abundant butterfly species (Aguiar & Karsholt, 2006). According to Wolff (1975), a specimen of *P. rapae* from Madeira Island is deposited in the Museu de História Natural do Funchal, Madeira, collected on 15 December 1971. Wolff (1975) documented a single observation in 1973, but occurrence in substantial numbers started in 1974. Three years later, *P. rapae* was widespread on the island and extremely common. The altitudinal distribution of this butterfly species spans from sea level up to more than 1,500 m *a.s.l*., and it is found mainly on coastal sites and at lower altitudes (human settlements and agricultural areas).

A colonisation with established populations on Madeira Island was confirmed by, *e.g*., Oehmig (1977), Swash & Askew (1982), Lace & Jones (1984), Sousa (1986), and Meyer & Hellers (1990).

While Meyer (1993) hypothesised an introduction with vegetables from the mainland, Wolff (1975) is convinced that numerous specimens were transported from Portugal to Madeira Island during special weather periods. He pointed out a particularly favourable meteorological condition for air transport in 1974. Furthermore, Wolff (1975) stated that the specimens of Madeira must be classified as form '*metra*' (Stephens, 1824), which also occurs in Portugal.

The first record on Porto Santo was reported by Carvalho (1983) at Achada de Baixo on 17 September 1981; see also Owen & Smith (1993) and Aguiar & Karsholt (2006). Meyer & Hellers (1990) observed the species on Porto Santo, too, and it was also found on Deserta Grande (Swash & Askew, 1982).

P. rapae is quite common throughout Porto Santo (11 grids, 13 localities; Fig. 1) and could be detected on the flowers of two plant species: *Cakile maritima* (Brassicaceae) n = 1; and *Sonchus oleraceus* (Asteraceae) n = 1.

Vanessa atalanta (Linnaeus, 1758)

This migratory butterfly species is widespread throughout North America, down south to Guatemala, Cuba, Hispaniola, the Atlantic islands, North Africa, Europe, Ireland, Britain, southern Fennoscandia, the Mediterranean islands, Pakistan, Kashmir, and north of the

Himalayas to the Amur river (Field, 1971; Tolman & Lewington, 1997; Tshikolovets, 2011). The American and Old World populations were characterised as separate subspecies (Vane-Wright & Hughes, 2007).

Wollaston collected three specimens (Madeira Island, The Mount, without date), which is recorded by Baker (1891) and Rebel (1917). Swash & Askew (1982) stated that *V. atalanta* is never numerous on Madeira Island, in contrast to the observations of Wakeham-Dawson *et al*. (2004) which classified the occurrence as relatively common. The preferred habitats are human settlements with gardens (Lace & Jones, 1984; Owen *et al*., 1987; Wakeham-Dawson *et al*., 2004). *Vanessa atalanta* was also recorded on Porto Santo and Deserta Grande (Aguiar & Karsholt, 2006; see also Meyer & Hellers, 1990).

On Porto Santo, *V. atalanta* is restricted to sites with high abundancies of *Echium* flowers (3 grids, 3 localities; Fig. 1) and could be detected only on the flowers of *Echium nervosum* (Boraginaceae) n = 18.

Vanessa cardui (Linnaeus, 1758)

This cosmopolitan migratory species (except for Australia and New Zealand) is widely distributed and a permanent resident of North Africa and the Mediterranean zone (Tolman & Lewington, 2008). *Vanessa cardui* was also recorded in Venezuela (Tshikolovets, 2011). The species is resident on the Madeira Archipelago (Madeira Island, Porto Santo, Deserta Grande, Selvagem Grande and Selvagem Pequena) (Aguiar & Karsholt, 2006). On Madeira Island, the species is common from 50 to 400 m *a.s.l.* in cultivated terraces and coastal sites (Wakeham-Dawson *et al*., 2004), and, similar to *Colias croceus*, also concentrated on drier sites (abundant in Ponta de São Lourenço; Owen *et al*., 1987), and near human settlements (Meyer, 1993). *Vanessa cardui* is also quite common throughout Porto Santo from sea level up to the highest mountains (9 grids, 14 localities; Fig. 1), but not so common as *Colias croceus*.

There is evidence that this species breeds on Madeira Island but appears to be also a migrant (Owen, 1989; Salmon & Wakeham-Dawson, 1999). Breeding in winter was observed by Owen (1987).

On 18 January 1921, Cockerell (1923) collected an aberration of *V. cardui* on Porto Santo, deposited in the Oxford University Museum of Natural History (OUMNH). Such similar stress-induced colour-pattern modifications were considered as phenotypic plasticity in *V. cardui* (Otaki, 2007).

V. cardui could be detected on the flowers of three plant species, with high preference of *Echium* (Boraginaceae): *E. nervosum* n = 55; *E. portosanctensis* n = 1; and *Rapistrum rugosum* (Brassicaceae) n = 2.

Vanessa vulcania (Godart, 1819)

In the literature this species was classified as a subspecies of *V. indica* Herbst, 1797 (*e.g*., Field, 1971; Tolman & Lewington, 2008) or a species of its own (*e.g*., Bernardi, 1961; Leestmans, 1975b, 1978; Tshikolovets, 2011). Synonyms are *Pyrameis* (?) *vulcania* Godart, 1819, and *Pyrameis callirhoe* var. *occidentalis* Felder, 1862. Leestmans (1978) demonstrated the clear separation between *V. vulcania* and *V. indica*.

V. vulcania is a Macaronesian endemic species, occurring in the Madeira Archipelago and the Canary Islands (Baker, 1891; Meyer & Hellers, 1990; Tolman & Lewington, 1997; Wakeham-Dawson & Aguiar, 2003; Vane-Wright & Hughes, 2007; Tshikolovets, 2011). Within the Madeira Archipelago, *V. vulcania* was detected on Madeira Island, Porto Santo, and Deserta Grande (Meyer & Hellers, 1990; Aguiar & Karsholt, 2006).

There were also occasional detections (natural or introductions) of *V. vulcania* in Germany (Gerisch, 1975, 1978; Reinhardt & Gerisch, 1982), Western and Northern Europe (Opheim, 1960), and the Iberian Peninsula (Fernández-Vidal, 1989; Fernández-Rubio, 1991) with no establishment.

One of the first records came from Felder (1862): A male was collected during the Novara Expedition (1857-1859) by Georg von Frauenfeld on Madeira Island and described as *Pyrameis Callirhoë* Hübner, var. *occidentalis* Felder, 1862. Alfred Russel Wallace (1889) cited Wollaston (Wollaston, 1856) and noted that specimens from Porto Santo are much smaller and darker than those of Madeira (cited also in Salmon & Wakeham-Dawson, 1999). Rebel (1940) mentioned that the specimens from Madeira Island are not different from those of the Canary Islands.

V. vulcania is widely distributed on Madeira Island from sea level to altitudes up to 1,000 m *a.s.l.*, but it is not common (Wakeham-Dawson & Aguiar, 2002; Wakeham-Dawson *et al*., 2004). In contrast, Owen & Smith (1993) noted that *V. vulcania* is well established and common, more abundant than *V. atalanta*. Swash & Askew (1982) reported frequent observations, mostly at low and medium altitudes in cultivated areas (see also Owen *et al*., 1987).

Shapiro (1992a) suggests a possible introduction by Portuguese traders; however, this is not the opinion of Salmon & Wakeham-Dawson (1999). Shapiro (1992a, b) noted a habitat preference for laurisilva forests and hypothesised that *V. vulcania* could be also considered as a relict species of former broadleaved forests.

There are two different hypotheses of the origin of *V. vulcania*:

(1) Leestmans (1978) suggested that during glacial maxima, the taxon of the *V. indica* complex could have been distributed in the eremic zone of North Africa, towards the east to Somalia and the Arabian Peninsula, and from there to the Iranian Plateau, the Thar Desert and the Tien Shan, and *V. vulcania* or its ancestor reached the Canary Islands and Madeira Archipelago via southern Morocco. In this scenario *V. vulcania* and *V. indica* indica should be sister taxa (Leestmans, 1978). Wahlberg & Rubinoff (2011) note that the position of *V. vulcania* is not clear within the *V. indica* complex, but it does appear to be a separate lineage. This hypothesis is compatible with the results on mitochondrial genetic variability within the *Hyles euphorbiae* sensu lato lineage (Lepidoptera, Sphingidae, Macroglossinae) in the western Palaearctic (Hundsdoerfer *et al*., 2010). Most haplotypes of *H. tithymali* in Macaronesia, North Africa, and Yemen build a cluster of similar haplotypes.

(2) Alternatively, Vane-Wright (2007) discussed the hypothesis of a North-American taxon reaching the Atlantic islands from eastern North America, rather than North Africa, while the Asian *indica*-group species reached Asia from western North America via Beringia, a theory supported by molecular findings.

On Porto Santo, *V. vulcania* is restricted to subhumid sites with high abundancies of *Echium* flowers (1 grid, 2 localities; Fig. 1) and could be detected only on the flowers of *Echium nervosum* (Boraginaceae) n = 10.

There are additional data of other observers:

Hypolimnas misippus (Linnaeus, 1764)

The occurrence of this migrant nymphalid species was recorded in Tennent *et al*. (2013). *Hypolimnas misippus* is widespread (Africa, Asia, Australia, West Indies, and parts of Central and North America); Tolman & Lewington (2008). This species is resident on the Cape Verde Islands, occasionally reported in the Azores, the Canary Islands, and the Madeira Archipelago (Tennent *et al*., 2013). There had been three detections in Porto Santo: both sexes, Pico do Castelo, 16 November 2012; and one female at the golf club, 18 November 2012, on flowers of *Lantana camara* (2 grids, 2 localities; Fig. 1).

Lycaena phlaeas phlaeoides (Staudinger, 1901)

Lycaena phlaeas (Linnaeus, 1761) is a widespread species with 22 subspecies in the Palaearctic, oriental, and Ethiopian regions, and six subspecies in the North American region (Kohler, 2007). *Lycaena phlaeas phlaeoides* represents an endemic subspecies on the Madeira Archipelago (Rebel, 1940; Bernardi, 1961; Leestmans, 1975; Meyer & Hellers, 1990; Meyer, 1993; Tolman & Lewington, 1997; Wakeham-Dawson & Aguiar, 2003; Aguiar & Karsholt, 2006; Tshikolovets, 2011). Kohler (2007) described the subspecies as follows: 'The rich brown, somewhat mottled colour and jagged whitish postmedian band of the ventral hind wing on this subspecies are distinctive'. This subspecies is represented in the Madeira Archipelago also in different forms: form '*elea*' (Fabricus, 1798), form '*coeruleapunctata*' (Rühl, 1895), form '*obsoleta*' (Tutt, 1896), and form '*radiata*' (Tutt, 1896); see also Salmon & Wakeham-Dawson (1999). Cockerell (1923) detected a specimen without any dark colours (ordinary form '*phlaeas*'). The subspecies rank was not accepted, *e.g*., by Swash & Askew (1982). According to Meyer (1993), the Madeiran populations are native.

L. phlaeas was mentioned by Felder (1862): A male was collected during the Novara Expedition (1857-1859) by Georg von Frauenfeld on Madeira Island. The distribution of *L. p. phlaeoides* on Madeira Island was reported by Wakeham-Dawson & Aguiar (2002) and Wakeham-Dawson *et al*. (2002a) as widely spread at all altitudes up to 1,800 m *a.s.l*. The occurrence on Porto Santo is mentioned by Wakeham-Dawson *et al*. (2004).

Distribution patterns

The distribution patterns of 11 butterfly species of Porto Santo are summarised in Table 2 and Fig. 1. *Colias croceus* shows the widest distribution on the island (19 grids), followed by *Pieris rapae* and *Vanessa cardui* (11 and nine grids). All other species are characterised by a restricted distribution: *Vanessa vulcania* (one grid) and *V. atalanta* (three grids) are concentrated on sites with flowering *Echium*; *Leptotes pirithous* (five grids) and *Lampides boeticus* (three grids) prefer hot, dry, and sunny sites (Tshikolovets, 2011), in contrast to *Pararge aegeria* (four grids), which use shadow sites with trees or bushes (Tolman & Lewington, 1997). The migrant species *Danaus plexippus* and *Hypolimnas misippus* were detected on four grids and two grids respectively, while the newly detected *Macroglossum stellatarum* was found on three grids.

Flower visits and butterfly-plant network

Table 3 shows the visited plant species in March 2017, which were used as nectar resources. Butterflies could be detected on 15 plant species. The key species with the highest rates of visitation was *Echium nervosum*.

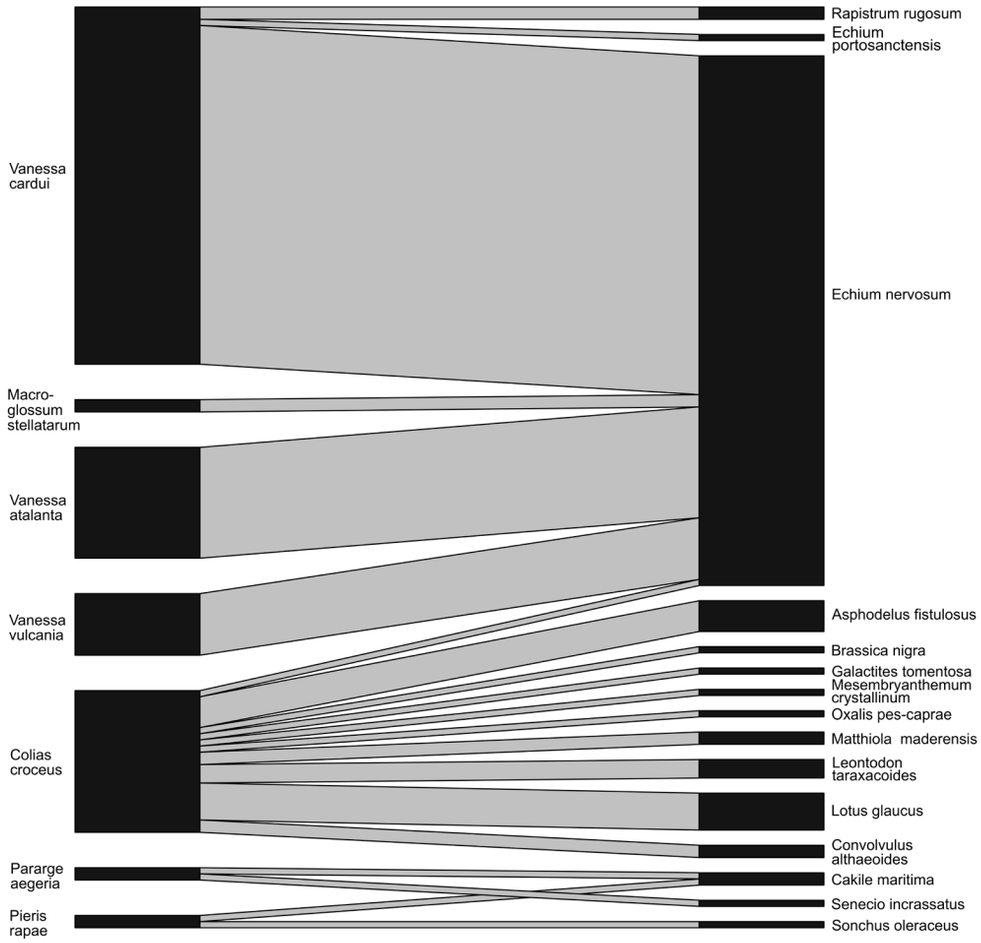

Fig. 2 – Bipartite graph of the butterfly-plant network of Porto Santo.

Most of the used plant species are endemic or native; therefore, they were already present about 500 years ago, before the beginning of the strong human impact. Most of the endemic or native plant species are common and widely distributed on Porto Santo. The plant species with the highest butterfly visitation rates is *Echium nervosum*, endemic to the Madeira Archipelago, and distributed in dry microforests, open rocky and dry habitats. *Echium nervosum* is also planted on roadsites. Also visited by butterflies is *Echium portosanctensis*, endemic to Porto Santo, growing in open rocky habitats of the subhumid zone and planted locally on roadsides in the northern part. Hybrids of these *Echium* species also exist.

A higher number of visits was observed on *Lotus glaucus* (endemic to Macaronesia) in sandy habitats and on *Cakile maritima* in driftline habitats. Butterflies were also observed on *Matthiola maderensis*, endemic to the Madeira Archipelago and growing on coastal rocks and cliffs, which are partly influenced by salt-spray.

Apart from these endemic plant species, there is a second group comprising native species with a wider distribution in the Mediterranean region or in North Africa that grow on Porto Santo, *e.g.*, on roadsides and fallows: *Asphodelus fistulosus*, *Brassica nigra*, *Convolvulus althaeoides*, *Galactites tomentosa*, *Leontodon taraxacoides*, *Rapistrum rugosum*, and *Sonchus oleraceus*.

The bipartite graph of the butterfly-plant network of Porto Santo (Fig. 2) shows the flower-visiting butterfly species on the left-hand side and the visited plant species on the right-hand side, both connected by interaction links. The butterfly-plant network is asymmetric: seven butterfly species versus 15 plant species.

The butterfly-plant network shows that the most abundant butterfly species on flowers is *Vanessa cardui* with a preference for *Echium nervosum*. *Vanessa atalanta* and the endemic *V. vulcania* also show a preference for the *Echium* species (*E. nervosum*, endemic for the Madeira Archipelago, and *Echium portosanctensis*, endemic for Porto Santo, including hybrids). In contrast, *Colias croceus* has a diversified flower-visiting behaviour (observed on ten plant species of different plant families).

CONCLUSIONS

Porto Santo, a relatively old and small volcanic island in the Atlantic Ocean, is a model area for the colonisation of islands by insect species of different areageographical origins. Regarding bee species, Porto Santo served as an important colonisation source for Madeira Island (Kratochwil & Schwabe, 2018).

Porto Santo has only two butterfly species which are endemic to archipelagos of Macaronesia or parts of it: *Vanessa vulcania*, endemic to the Madeira Archipelago and the Canary Islands, which can be considered a relict species on Porto Santo, and, at a subspecies level, *Lycaena phlaes phlaeoides* (endemic to the Madeira Archipelago). In contrast, many other butterfly species are endemic to Madeira Island: *Hipparchia maderensis* (Bethune-Baker, 1891), *Pararge xiphia* (Fabricius, 1775), *Gonepteryx maderensis* Felder, 1862, and *Pieris wollastoni* (Butler, 1886). These species do not occur on Porto Santo, because there are no habitat conditions of higher mountain zones. The endemic butterflies of Madeira Island prefer vegetation mosaics of forest sites with forest edges and forest islands (*Pararge xiphia* and *Gonepteryx maderensis*) or live generally at higher altitudes (*Hipparchia maderensis*, 800-1,800 m *a.s.l.*; *Pieris wollastoni*, 400-1,110 m *a.s.l.*). Whether these species ever existed on Porto Santo is a question that cannot be answered.

A possible exchange of butterfly individuals between Madeira Island and Porto Santo is facilitated by the small distance of 45 km between the islands (*e.g.*, in the case of *Danaus plexippus*, *Vanessa atalanta*, and *V. cardui*, but also of other butterfly species, *e.g.*, *Colias croceus*, which are migratory and good flyers).

The butterfly-plant network of Porto Santo shows asymmetry: Seven butterfly species used 15 different plant species, but not as marked as the bee-plant network with six wild-bee species and 27 different plant species (Kratochwil & Schwabe, 2018).

Like the wild-bee species, the woody *Echium* species *E. nervosum* (endemic to the Madeira Archipelago) and *E. portosanctensis* (endemic to Porto Santo), including hybrids, are key species as resources for *Vanessa atalanta*, *V. cardui* and *V. vulcania*.

V. vulcania is not common. This endemic butterfly species was found only within one grid in the north of the island at an altitude of 235 m *a.s.l.* *Vanessa vulcania* is a remnant of an earlier time period of the island, when (due to lack of human impact) areas with microforests and *Apollonias barbujana* laurisilva vegetation still existed. *Vanessa vulcania* show a similar preference for the subhumid zone as the bumblebee *Bombus terrestris lusitanicus* (Kratochwil & Schwabe, 2018).

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NOMENCLATURE

The nomenclature for plant species names follows Jardim & 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).