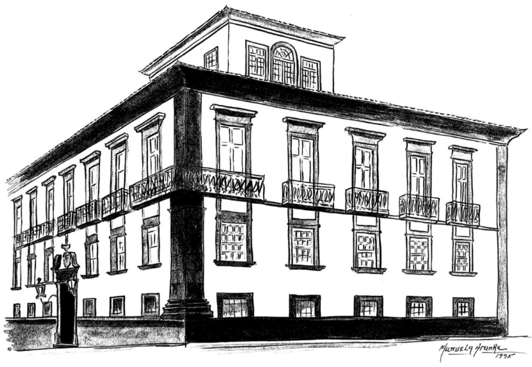


BOLETIM

MUSEU DE HISTÓRIA NATURAL DO FUNCHAL

Vol. LXIX (2019), Arts. 353-355

ISSN 2183-279X (online edition) | Available online at: http://boletim.cm-funchal.pt

Dezembro de 2019 - FUNCHAL - MADEIRA
Editado pela Câmara Municipal do Funchal

FICHA TÉCNICA // TECHNICAL INFORMATION

Título // Title:
Boletim do Museu de História Natural do Funchal
Vol. 69 (353-355), 2019

Editado por // Edited by:
Câmara Municipal do Funchal

Composição // Desktop publishing:
Ivelice Gonçalves
Museu de História Natural do Funchal

Arranjo gráfico // Layout:
Virgílio Gomes
Ivelice Gonçalves

Capa // Cover:
Desenho de contraste // Contrast mark:
Manuela Aranha
Fotografia // Photograph:
J. J. Gonçalves Silva
Oenothera rosea (ver // see art. 355, p. 35)

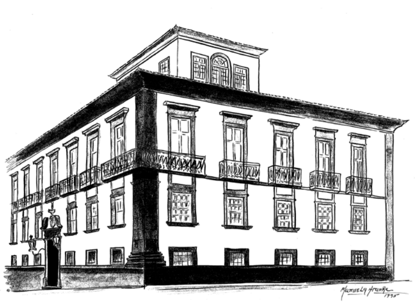
Secretariado e correspondência // Address:
Museu de História Natural do Funchal
Rua da Mouraria, 31
9004-546 Funchal
Madeira – Portugal
Telefone // Phone: (+351) 291 229761
Fax: (+351) 291 225180
E-mail: mmf.pubs@cm-funchal.pt

Website:
http://boletim.cm-funchal.pt

ISSN (edição online // online edition):
2183-279X

ISSN (edição impressa // printed edition): 0870-3876

Depósito legal // Legal deposit:
no. 228969/05



BOLETIM

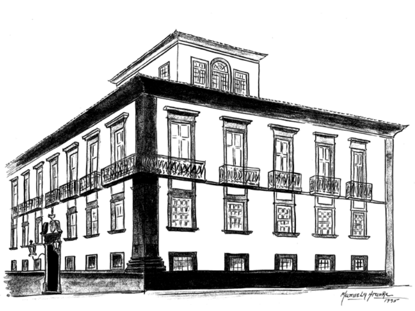
MUSEU DE HISTÓRIA NATURAL DO FUNCHAL

Vol. LXIX (2019), Arts. 353-355

ISSN 2183-279X (online edition) | | Available online at: http://boletim.cm-funchal.pt

Dezembro de 2019 - FUNCHAL - MADEIRA
Editado pela Câmara Municipal do Funchal

ÍNDICE // INDEX



BOLETIM

MUSEU DE
HISTÓRIA NATURAL DO FUNCHAL

Vol. LXIX (2019), Art. 353: 5-12

ISSN 2183-279X (online edition) | | Available online at: http://boletim.cm-funchal.pt

On the status of some nominal species of fishes described by Sarah Lee Bowdich in the account "Excursions in Madeira and Porto Santo during the autumn of 1823"

By Paolo Parenti [1] [*]

With 1 table

[1] *Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza, 1, 20126 Milano, Italy.*
[*] *E-mail: paolo.parenti@unimib.it*

ABSTRACT: The status of seven nominal species of fishes described by Bowdich in 1825 during a famous trip to Madeira and Cape Verde Islands is determined. Three nominal species have been discovered to represent senior synonyms of well-established taxa. They are: *Dentex diplodon*, *Dentex unispinosus*, and *Tetraodon laevissimus*. The Zoological Code of Nomenclature allows to maintain prevailing usage of the junior synonym by applying reversal of precedence. Therefore, a statement declaring the three Bowdich's nominal species as *nomina oblita* is included. The corresponding younger valid names, *Pomadasys perotaei* (Cuvier, 1830), *Lethrinus atlanticus* Valenciennes, 1830, and *Sphoeroides marmoratus* (Lowe, 1838) respectively, are here qualified as *nomina protecta*.

Keywords: senior synonyms, *nomina oblita*, reversal of precedence, fishes of Madeira, Bowdich.

RESUMO: O estatuto de sete espécies nominais de peixes descritas por Bowdich em 1825, no decurso da famosa expedição à Madeira e a Cabo Verde, é avaliado. Três espécies nominais representam sinónimos seniores de taxa bem estabelecidos. São elas: *Dentex diplodon*, *Dentex unispinosus*, e *Tetraodon laevissimus*. O Código Internacional de Nomenclatura Zoológica permite manter o uso prevalecente de sinónimos juniores, aplicando o princípio de precedência inversa. Em consequência, é apresentada uma declaração considerando estas três espécies como *nomina oblita*. Os correspondentes nomes válidos, mais novos, são: *Pomadasys perotaei* (Cuvier, 1830), *Lethrinus atlanticus* Valenciennes, 1830 e *Sphoeroides marmoratus* (Lowe, 1838), respectivamente e são aqui qualificados como *nomina protecta*.

Palavras-chave: sinónimos seniores, *nomina oblita*, precedência inversa, peixes da Madeira, Bowdich.

Received: 01 March 2019; Revised: 01 March 2019; Accepted: 26 March 2019; Available online: 26 August 2019; Published: 31 December 2019

INTRODUCTION

Sarah Lee Bowdich (née Wallis) (b. Colchester 1791-1866) was a British author, illustrator, zoologist, and botanist amongst the first European women to visit West Africa (Watkins, 1892). At the age of twenty-one she married the English explorer Thomas Edward Bowdich (1791-1823) and in 1822 she accompanied her husband in a travel to Madeira and Cape Verde Islands where they spent some months observing and describing the landscape and the creatures living on the islands and in the sea around them. Unfortunately, when they arrived at the mouth of River Gambia intending to explore the adjacent countries, Thomas caught malaria and died on 10 January 1824, leaving Sarah with three children. One year later Sarah decided to publish an account of the trip to Madeira and Cape Verde, which resulted in description of many animal and plant species (Beaver, 1999). Among fishes Sarah Bowdich is the authorship of 27 nominal species including eight species currently recognized as valid, 12 known to be junior synonyms, and seven currently unplaced (Fricke *et al.*, 2019). A careful examination of the text and the illustrations, when present, of these unplaced species revealed that they represent senior and junior synonyms of well-known fish species. In case older names predate long-established ones, the International Code of Zoological Nomenclature through the principle of priority promotes stability in order not to upset long-established names (Art. 23.9).

MATERIALS AND METHODS

All species described by Bowdich as new are not accompanied by type material (Fricke *et al.*, 2019). Therefore, conclusions about their positive identification are based on the original description and the illustration produced by the author, which are presented for all but one of the species discussed therein. On p. 121 of the book Sarah Lee wrote: “I had frequent occasion to lament the necessity of throwing away new and interesting objects, especially fishes, because no museum had furnished me with spirits and case to preserve them in.”.

RESULTS

In the account on the fishes recorded by Sarah Lee Bowdich in the *Excursions in Madeira and Porto Santo* thirty-six species were mentioned. Among these eight correspond to well-known species [*Esox sphyraena*, p. 124: *Sphyraena sphyraena* (Linnaeus, 1758); *Squalus carcharias*, p. 233: *Carcharodon carcharias* (Linnaeus, 1758); *Esox belone*, p. 234: *Belone belone* (Linnaeus, 1760); *Coryphaena novacula*, p. 235: *Xyrichtys novacula* (Linnaeus, 1758); *Sparus sargus*, p. 235: *Diplodus sargus* (Linnaeus, 1758); *Sparus chromis*, p. 235: *Chromis chromis* (Linnaeus, 1758); *Balistes punctatus*, p. 236: *Balistes punctatus* Gmelin 1789; *Vomer brownii* p. 237: *Selene brownii* (Cuvier, 1816)], one was not identified at the species level (*Hippocampus* sp., p. 233) and 27 were described as new species. Table 1 shows the present allocation of all these nominal species described as new. Seven nominal species are the object of the present study as they are currently unplaced in the Eschmeyer’s Catalog of Fishes on line (Fricke *et al.*, 2019). The positive identification of these nominal species lead to give status as junior or senior synonyms of well-established fish taxa. In particular, four nominal species are here recognized as junior synonyms: *Seleima aurata*, *Zeus childrenii*, *Labeo sparoides*, and *Chromis triacantha*, whereas three nominal species (*Dentex diplodon*, *Tetraodon laevissimus*, and *Dentex unispinosus*) are here regarded as senior synonyms of three well known marine fish species. The consequence of the discovery that nominal species predates well established names requires nomenclatural actions which are validated by the rules of the International Code of Zoological Nomenclature (Art. 23.9). In particular, in accordance with the principle of priority to promote stability of names in zoology, the application of reversal of precedence of two names allows to maintain the prevailing usage of a younger synonym over a senior synonym if two conditions are met. The first condition is that a name (senior synonym) has not been used as valid since 1899 and the second condition that a name (junior synonym) has been used as valid in at least 25 works, published by at least 10 authors during the past 50 years, encompassing a span of not less than 10 years. As both conditions are met, we can regard *Dentex diplodon*, *Dentex unispinosus* and *Tetraodon laevissimus* as invalid and *nomina oblita*, whereas the respective junior synonyms *Pomadasys perotaei* (Cuvier, 1830), *Lethrinus atlanticus* Valenciennes, 1830, and *Sphoeroides marmoratus* (Lowe, 1838) as *nomina protecta* and valid. In the following paragraphs information of the status of the aforementioned species is given in details.

Labeo sparoides Bowdich, 1825: 122, Fig. 29 (type locality, Madeira). This nominal species is another junior synonym of *Sarpa salpa* (Linnaeus, 1758) mainly on the

Table 1 – Fishes described as new species by Sarah Lee Bowdich and their present allocation.

Bowdich's nominal species	Page number, illustration and type locality	Present allocation	Reference
Amorphocephalus granulatus	238, Fig. 36, Boa Vista, Cape Verde Is.	*Xyrichtys novacula* (Linnaeus, 1758)	Parenti & Randall, 2000
Anomalodon incisus	237, Fig. 51, Gambia	*Pomadasys incisus* (Bowdich, 1825)	Roux, 1990
Balistes radiata	233, Fig. 45, St. Jago, Cape Verde Is.	*Balistes punctatus* Gmelin, 1789	Harmelin-Vivien & Quero, 1990
Bodianus maculatus	236, Fig. 39, Boa Vista, Cape Verde Is.	*Cephalopholis taeniops* (Valenciennes, 1828)	Smith, 1990
Chaetodon leachii	124, Madeira	*Pomacanthus paru* (Bloch, 1787)	Maugé, 1990
Chromis triacantha	235, Fig. 52, Gambia River	*Oreochromis niloticus* (Linnaeus, 1758)	this paper
Clupea fimbriata	234, Fig. 44, St. Jago, Cape Verde Is.	*Ethmalosa fimbriata* (Bowdich, 1825)	Whitehead, 1967
Dentex diplodon	235, Fig. 46, St. Jago, Cape Verde Is.	*Pomadasys perotaei* (Cuvier, 1830)	this paper
Dentex unispinosus	235, Fig. 42, St. Jago, Cape Verde Is.	*Lethrinus atlanticus* Valenciennes, 1830	this paper
Diastodon speciosus	238, Fig. 41, St. Jago, Cape Verde Is.	*Bodianus speciosus* (Bowdich, 1825)	Parenti & Randall, 2000
Julis squamimarginatus	234, Fig. 53, Gambia River	*Thalassoma pavo* (Linnaeus, 1758)	Parenti & Randall, 2000
Labeo sparoides	122, Fig. 29, Madeira	*Sarpa salpa* (Linnaeus, 1758)	this paper
Labrus iagonensis	234, Fig. 47, St. Jago and Gambia River	*Bodianus speciosus* (Bowdich, 1825)	Parenti & Randall, 2000
Lichia tetracantha	237, Fig. 49, St. Jago and Gambia River	*Trachinotus ovatus* (Linnaeus, 1758)	Daget & Smith-Vaniz, 1986
Mugil bispinosus	236, Fig. 38, Boa Vista, Cape Verde Is.	*Chelon bispinosus* (Bowdich, 1825)	Thomson, 1990
Phycis furcatus	122, Fig. 28, Madeira	*Phycis phycis* (Linnaeus, 1766)	Svetovidov, 1973
Pimelodus gambensis	234, Fig. 50, Gambia River	*Carlarius latiscutatus* (Günther, 1864)	Marceniuk & Menez, 2007
Pristipoma humilis	236, Fig. 40, St. Jago and Boa Vista	*Parapristipoma humile* (Bowdich, 1825)	Roux, 1973
Sciaena dux	236, Fig. 54, Gambia River	*Pseudotolithus typus* Bleeker, 1863	Trewavas, 1973
Sciaena elongata	236, Fig. 43, St. Jago, Cape Verde Is.	*Pseudotolithus elongates* (Bowdich, 1825)	Daget & Trewavas, 1986
Scorpaena kuhlii	123, Madeira	*Pontinus kuhlii* (Bowdich, 1825)	Eschmeyer, 1969
Seleima aurata	238, Fig. 37, Boa Vista, Cape Verde Is.	*Sarpa salpa* (Linnaeus, 1758)	this paper
Seriola picturata	123, Fig. 27, Madeira	*Trachurus picturatus* (Bowdich, 1825)	Hureau & Tortonese, 1973
Serranus rufus	122, Madeira	*Heteropriacanthus cruentatus* (Lacepède, 1801)	Hureau, 1973
Smaris royerii	123, Fig. 26, Madeira	*Centracanthus cirrus* Rafinesque, 1810	Tortonese *et al*., 1973
Tetraodon laevissimus	233, Fig. 48 [a], St. Jago, Cape Verde Is.	*Sphoeroides marmoratus* (Lowe, 1838)	this paper
Zeus childrenii	124, Madeira	*Capros aper* (Linnaeus, 1758)	this paper

[a] Misprinted as fig.18 on p. 233

ground that the fish is described having the body light silvery grey with ten golden stripes and all the fins are of a golden hue. The author mentions that the anal fin has 14 spines and 3 branching rays, but we assume she inverted the fin rays count.

Zeus childrenii Bowdich, 1825: 124. This species is described in Chapter 5 of the book, entitled *Zoological, Meteorological, and Barometrical Observations – Flood of Madeira*. In the main text Bowdich mentions the presence of a *Zeus* among the fish specimens brought to her by fishermen and peasantries. The fish is said to be lacking the long filaments typical of *Zeus faber* and having a brilliant red colour. The scientific name is given in the footnote. Lowe (1838) regarded this nominal species as a synonym of the boarfish *Capros aper* (Linnaeus, 1758). A similar species occurring in the area is *Antigonia capros* Lowe, 1843, but this species has an extremely deep body (0.8–1.2 SL vs 1.7–1.9 of *C. aper* or *Z. faber*). The generic name *Zeus* has been erected by Linnaeus (1758) to accommodate *Z. aper* and three additional species (*vomer*, *gallus*, and *faber*) and *Z. aper* was diagnosed as *Z. cauda equali*, *corpore rubente* (caudal fin truncated, body reddish). Next the generic name *Zeus* was used by early ichthyologists for different kind of fishes other than *Z. aper* and eight nominal species of the family Zeidae. In particular it has been used for several species of Carangidae and for three Lampridae, two Leiognathidae, one Menidae, one Kurtidae, one Cichlidae and one Cyttidae (Fricke *et al*., 2019). Based on these considerations and the short description of *Z. childrenii* the identity with *Capros aper* (Linnaeus, 1758) is confirmed.

Tetraodon laevissimus Bowdich, 1825: 233, Fig. 48 misprinted 18 (see p. xii) (type locality, Port Praya, St. Jago Island, Cape Verde Islands). The fish is described having "the back and the sides of a beautiful rose colour irregularly marked with deep black; the pectoral fin has 13 rays and the anal, dorsal and caudal fins, each with 7 rays". A good illustration is provided by Bowdich misprinted on p. 223 as Fig. 18 instead of Fig. 48. Based on the description and illustration, this species is clearly identified as a senior synonym of *Sphoeroides marmoratus* (Lowe, 1838). *Tetraodon laevissimus* has never been used in ichthyological literature and conditions exist to allow prevailing usage of *Sphoeroides marmoratus* as claimed in the previous paragraph. *Sphoeroides marmoratus* (Lowe, 1838) is thus regarded as valid, qualifying as a *nomen protectum*, while the name *Tetraodon laevissimus* Bowdich, 1825 is recognized as invalid, qualifying as a *nomen oblitum*.

As evidence that the conditions of Article 23.9.1.2 have been met the following list of publications is included: Lowe-McConnell, 1962; Arnoult *et al.*, 1966; Almeida, 1986; Schneider, 1990; Shipp, 1990; Hureau, 1991; Wirtz, 1994; Galeote & Otero, 1996; Reiner, 1996; Arruda, 1997; Santos *et al.*, 1997; Afonso *et al.*, 1999; Wu *et al.*, 1999; Morato *et al.*, 2000; Ebert, 2001; Galeote, 2001; Louisy, 2001; Mendiola, 2005; Vacchi *et al.*, 2007; Wirtz *et al.*, 2008; Bañón & Santás, 2011; Psomadakis *et al.*, 2012; Brito *et al.*, 2013; Wirtz *et al.*, 2013; Matsuura, 2016; Guedes-Alonso *et al.*, 2017.

Chromis triacantha Bowdich, 1825: 235, Fig. 52 (type locality, Gambia). Briefly described in the zoological section of the appendix of the book, this species is named on the basis of the presence of three spines in the ventral fins. No fish species is known having this feature, confirming that fin rays count made by Bowdich are quite unreliable, as already noticed by Valenciennes in the Histoire naturelle des Poissons (1830: 275). The fish is described as silvery grey, except the fins which are orange. Dorsal fin XV, 11 and anal fin III, 9 complete the description. It is concluded that *C. triacantha* is a junior synonym of *Oreochromis niloticus* (Linnaeus, 1758).

Dentex unispinosus Bowdich, 1825: 235, Fig. 42 (type locality Port Praya, St. Jago Island, Cape Verde Islands). Valenciennes (1830: 275) was the first to recognize *D. unispinosus* as a junior synonym of his *Lethrinus atlanticus* even though fin ray count reported by Bowdich contains several errors such as a single free spine in the dorsal fin followed by 21 soft rays and the anal fin with 4 spines and 8 soft rays. The fish is reported as silvery, slightly tinged with red. *Dentex unispinosus* is here regarded as a senior synonym of *L. atlanticus*; however, conditions exist to allow "prevailing usage" of *Lethrinus atlanticus* Valenciennes, 1830, as provided by Article 23.9.1 of the International Code of Zoological Nomenclature (ICZN, 1999): (1) *Dentex unispinosus* has not been used as valid since 1899 (Article 23.9.1.1) and (2) *Lethrinus atlanticus* has been used as valid name in at least 25 works, published by at least 10 authors during the past 50 years, and encompassing a span of not less than ten years (Article 23.9.1.2). *Lethrinus atlanticus* Valenciennes, 1830 is thus regarded as valid, qualifying as a *nomen protectum*, while the name *Dentex unispinosus* Bowdich, 1825 is recognized as invalid, qualifying as a *nomen oblitum*. As evidence that the conditions of Article 23.9.1.2 have been met the following list of publications is included: Bauchot & Blanc, 1961; Ricker, 1973; Beck, 1976; Sato, 1978; Maigret & Ly, 1986; Ofori-adu, 1988; Carpenter & Allen, 1989; Roux, 1990; Schneider, 1990; Grabda & Heese, 1991; Hureau, 1991; Sanches, 1991; Coppola *et al.*, 1994; Vakily, 1994; Diouf, 1996; Reiner, 1996; da Silva Monteiro, 1998; Afonso *et al.*, 1999; Wu *et al.*, 1999; Zuev & Boltachev, 2000; Sédzro, 2003; Wirtz *et al.*, 2007; Cheung *et al.*, 2013; Wirtz *et al.*, 2013; Oliveira *et al.*, 2015.

Dentex diplodon Bowdich, 1825: 235, Fig. 46 (type locality Port Praya, St. Jago Island, Cape Verde Islands). This fish is briefly described in the zoological section of the appendix of the book: it is characterized by small teeth set in a double row, dorsal fin with 10 spines and 16 soft rays, anal fin with 3 spines and 10 soft rays, body silvery grey with a yellow spot on the opercle; fins yellow tinged with red. *Dentex diplodon* is here regarded as a senior synonym of *Pomadasys perotaei* (Cuvier, 1830) often misspelled as *peroteti* in literature (*e.g.* Roux, 1986; Diouf & Toguebaye, 1993; Bandowe *et al.*, 2014). However the combination *Dentex diplodon* has never been used in literature and conditions exist to allow "prevailing usage" of *Pomadasys perotaei*, as provided by Article 23.9.1 of the International Code of Zoological Nomenclature (ICZN, 1999): (1) *Dentex diplodon* has not been used as valid since 1899 (Article 23.9.1.1) and (2) *Pomadasys perotaei* has been used as valid name in at least 25 works, published by at least 10 authors during the past 50 years, and encompassing a span of not less than ten years (Article 23.9.1.2). *Pomadasys perotaei* (Cuvier, 1830) is thus regarded as valid, qualifying as a *nomen protectum*, while the name *Dentex diplodon* Bowdich, 1825 is recognized as invalid, qualifying as a *nomen oblitum*. As evidence that the conditions of Article 23.9.1.2 have been met the following list of publications is included: Osório, 1898; Breder & Rosen, 1966; Maigret & Ly, 1983; Bellemans *et al.*, 1988; Roux, 1986, 1990; Negedly, 1990; Schneider, 1990; Grabda & Heese, 1991; Hureau, 1991; Sanches, 1991; Vivien, 1991; Lesnoff & Damiano, 1993; Diouf, 1996; Reiner, 1996; Caverivière & Andriamirado, 1997; Afonso *et al.*, 1999; Wu *et al.*, 1999; Bauchot, 2003; Albaret *et al.*, 2004; Wirtz *et al.*, 2007, 2013; Snoeks & Vreven, 2008; Bandowe *et al.*, 2014; Carpenter & de Angelis, 2016.

Seleima aurata Bowdich, 1825: 238, Fig. 37. This fish is described in the zoological section of the appendix of the book. The name is based on a specimen that has been collected at Boa Vista, Cape Verde Islands and the vernacular name *Seleima* used by Portuguese fishermen for the sea bream *Sarpa salpa* (Linnaeus, 1758) has been taken by Bowdich as genus name for her specimen. The description of the specimen, in particular fin ray count and the presence of eight orange longitudinal stripes, together with the illustration given by the author leaves no doubt that *Seleima aurata* is a junior synonym of the sparid *Sarpa salpa*.

REFERENCES

AFONSO, P., F. M. PORTEIRO, R. S. SANTOS, J. P. BARREIROS, J. WORMS & P. WIRTZ:

1999. Coastal marine fishes of São Tomé Island (Gulf of Guinea). *Arquipélago*, **17** (A): 65-92.

ALBARET, J.-J., M. SIMIER, F. S. DARBOE, J.-M. ECOUTIN, J. RAFFRAY & L. T. DE MORAIS:

2004. Fish diversity and distribution in the Gambia estuary, West Africa, in relation to environmental variables. *Aquatic Living Resources*, **17**: 35-46.

ALMEIDA, A. J.:

1986. Présence des poissons *Syngnathus rostellatus* (Syngnathidae), *Clinitrachus argentatus* (Clinidae) et *Sphoeroides spengleri* (Tetraodontidae) sur la côte du Portugal. *Ciência Biológica – Ecology and Systematics* (Portugal), **6**: 1-7.

ARNOULT, J., F. d'AUBENTON, M. L. BAUCHOT & M. BLANC:

1966. Poissons Téléostéens. In: Résultats scientifiques des Campagnes da la "Calypso". *Annales de l'Institut Océanographique du Monaco*, **44**: 1-22.

ARRUDA, L. M.:

1997. Checklist of the marine fishes of the Azores. *Arquivos do Museu Bocage*, Nova Série **3** (2): 13-162.

BANDOWE, B. A. M., M. BIGALKE, L. BOAMAH, E. NYARKO, F. K. SAALIA & W. WILCKE:

2014. Polycyclic aromatic compounds (PAHs and oxygenated PAHs) and trace metals in fish species from Ghana (West Africa): Bioaccumulation and health risk assessment. *Environmental International*, **65**: 135-146.

BAÑÓN, R. & V. SANTÁS:

2011. First record of *Lagocephalus laevigatus* (Tetraodontiformes, Tetraodontidae) from Galician waters (north-west Spain), a northernmost occurrence in the north-east Atlantic Ocean. *Journal of Fish Biology*, **78** (5): 1574-1578.

BAUCHOT, M.-L. & M. BLANC:

1961. Poissons Marins de l'Est Atlantique tropical. Téléostéens Perciformes. II. Percoidei. *Atlantide Report*, **6**: 43-101.

BAUCHOT, M.-L.:

2003. Haemulidae. In: *Faune des poissons d'eaux douce et saumâtres de l'Afrique de l'Ouest*, Tome 2. *Faune et Flore tropicales*, **40** (eds.: C. Lévêque, D. Paugy & G. G. Teugels). Pp. 495-503. Musée Royal de l'Afrique Centrale, Tervuren, Belgique; Museum National d'Histoire Naturalle, Paris, France and Institut de Recherche pour le Développement, Paris, France.

BEAVER de B. D.:

1999. Writing natural history for survival – 1820-1856: the case of Sarah Bowdich, later Sarah Lee. *Archives of Natural History*, **26**: 19-31.

BECK, V. U.:

1976. Die Zusammensetzung der Erträge aus der Küstenfisherei Togos. *Meeresforschung*, **25**: 37-45.

BELLEMANS, M., A. SAGNA, W. FISCHER & N. SCIALABBA:

1988. Fiches FAO d'identification des espèces pour les besoins de la pêche. Guide des ressources halieutiques du Sénégal et la Gambie (Espèces marines et d'eaux saumâtres). FAO, Rome.

BOWDICH, S. L.:

1825. Fishes of Madeira. In: *Excursions in Madeira and Porto Santo during the autumn of 1823, while on his third voyage to Africa* (by Bowdich, T. E.), pp. 121-125 and 233-238. George B. Whittaker, London.

BREDER, C. M. & D. E. ROSEN:

1966. *Modes of reproduction in fishes*. T. F. H. Publications, Neptune City, New Jersey. 941 pp.

BRITO, A., R. FREITAS, F. ESPINO, C. FERNÁNDEZ-GIL, A. BOYRA, & J. A. GONZÁLEZ:

2013. Fishes. In: *Espécies marinhas de Cabo Verde* (eds.: C. Fernández Gil, J. A. González & N. González-Henriquez), pp. 32-73. Oceanográfica, Las Palmas, Spain.

CARPENTER, K. E. & G. R. ALLEN:

1989. *FAO species catalogue. Vol. 9. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date*. FAO Fisheries Synopsis, FAO, Rome, pp. v + 118, viii Pls.

CARPENTER, K. E. & N. de ANGELIS (eds.):

2016. *The living marine resources of the Eastern Central Atlantic. Volume 4. Bony fishes part 2 (Perciformes to Tetradontiformes) and Sea turtles*. FAO Species Identification Guide for Fishery Purposes, Rome, FAO, pp. xiii + 2343-3124.

CAVERIVIÈRE, A. & G. A. R. ANDRIAMIRADO:

1997. Minimal fish predation for the pink shrimp Penaeus notalis in Senegal (West Africa). *Bulletin Marine Sciences*, **61** (3): 685-695.

CHEUNG, W. L., R. WATSON & D. PAULY:

2013. Signature of ocean warming in global fisheries catch. *Nature*, **497**: 365-368.

COPPOLA, S. R., W. FISCHER, L. GARIBALDI, N. SCIALABBA & K. E. CARPENTER:

1994. *SPECIESDAB: Global species database for fishery purposes. User's manual*. FAO Computerized Information Series (Fisheries) No. 9, FAO Rome, 103 pp.

CUVIER, G. & A. VALENCIENNES:

1830. *Histoire naturelle des poissons. Tome Sixième*, Levrault, Paris, pp. xxiv + 6 + 559, Pls. 141-169.

da SILVA MONTEIRO, V. M.:

1998. *Peixes de Cabo Verde*. Ministério do Mar, Gabinete do Secretário de Estado da Cultura. M2-Artes Gráficas, Lda., Lisbon. 179 pp.

DAGET, J. & W. F. SMITH-VANIZ:

1986. Carangidae. In: *Check-list of the freshwater fishes of*

Africa (CLOFFA), Vol. II (eds.: J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde), pp. 308-322. ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris.

DAGET, J. & E. TREWAVAS:

1986. Sciaenidae. In: *Check-list of the freshwater fishes of Africa (CLOFFA)*, Vol. II (eds.: J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde), pp. 333-337. ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris.

DIOUF, J. N. & B. S. TOGUEBAYE:

1993. Studies of coccidian parasites of fish from the coast of Senegal (West Africa): new species of the genus Goussia (Apicomplexa, Eucoccidiida, Calyptosporidae). *Zoologica Scripta*, **22** (2): 117-126.

DIOUF, P. S.:

1996. *Les peuplements de poissons des milieux estuariens de l'Afrique de l'Ouest: L'exemple de l'estuaire hyperhalin du Sine-Saloum. Université de Montpellier II*. Thèses et Documents Microfiches No.156. ORSTOM, Paris. 267 pp.

EBERT, K.:

2001. *The puffers of fresh and brackish waters*. Aqualog Verlag, Rodgau (Germany). 96 pp.

ESCHMEYER, W. N.:

1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpaenidae). *Occasional Papers California Academy of Sciences*, **79**: i-iv + 1-143.

FRICKE, R., W. N. ESCHMEYER & R. van der LAAN (eds.):

2019. Eschmeyer's catalog of fishes. Electronic version accessed: 26 02 2019.

GALEOTE, M. D. & J. G. OTERO:

1996. Primera cita en aguas peninsulares españolas de *Sphoeroides marmoratus* (Lowe, 1839) (Pisces, Tetraodontidae). *Zoologica baetica*, **7**: 3-10.

GALEOTE, M. D.:

2001. Primera cita para las costas europeas de *Canthigaster rostrata* (Bloch, 1796) (Pisces, Tetraodontidae). *Boletín Instituto Español de Oceanographía*, **17** (3 & 4): 313-315.

GRABDA, E. & T. HEESE:

1991. *Polskie nazewnictwo popularne kraglouste i ryby. Cyclostomata et Pisces. Wyzsza Szkola Inzynierska w Koszalinie*. Koszalin, Poland. 171 p. (in Polish).

GUEDES-ALONSO, R., Z. SOSA-FERRERA & J. J. SANTANA-RODRÍGUEZ:

2017. Determination of steroid hormones in fish tissues by microwave-assisted extraction coupled to ultra-high performance liquid chromatography tandem mass spectrometry. *Food Chemistry*, **237**: 1012-1020.

HARMELIN-VIVIEN, M. L. & J.-C. QUÉRO:

1990. Balistidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), p. 1055-1060. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

HUREAU, J.-C.:

1973. Priacanthidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2.* (eds.: J.-C. Hureau & T. Monod), p. 364. Unesco, Paris.

1991. La base de données GICIM: Gestion informatisée des collections ichthyologiques du Muséum. In: *Atlas Préliminaire des Poissons d'Eau Douce de France*, pp. 225-227. Conseil Supérieur de la Pêche, Ministère de l'Environnement, CEMAGREF et Muséum national d'Histoire naturelle, Paris.

HUREAU, J.-C. & E. TORTONESE:

1973. Carangidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2.* (eds.: J.-C. Hureau & T. Monod), pp. 373-384. Unesco, Paris.

ICZN:

1999. *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature c/o The Natural History Museum, London, U. K. 306 pp.

LESNOFF, M. & A. DAMIANO:

1993. *Guide de reconnaissance des principales espèces d'intérêt commercial de la ZEE guinéenne*. Centre Nationale des Sciences Halieutiques de Boussoura, Conakry, Ghana, 26 pp.

LOUISY, P.:

2001. *Guide d'identification des poissons marins*. Europe et Méditerranée. Eds. Eugène Ulmer, Paris, 512 pp.

LOWE, R. T.:

1838. A synopsis of the fishes of Madeira; with the principal synonyms, Portuguese names, and characters of the new genera and species. *Transactions of the Zoological Society of London*, **2** (pt. 3, art. 14): 173-200.

LOWE-McCONNELL, R. H.:

1962. The fishes of the British Guiana continental shelf, Atlantic coast of South America, with notes on their natural history. *Zoological Journal of the Linnean Society*, **44** (301): 667-700.

MAIGRET, J. & B. LY:

1986. *Les poissons de mer de Mauritanie*. Science Nat, Compiègne (France), 213 pp.

MARCENIUK, A. P. & N. A. MENEZES:

2007. Systematics of the family Ariidae (Ostariophysi, Siluriformes), with a redefinition of the genera. *Zootaxa*, **1416**: 1-126.

MAUGÉ, A. L.:

1990. Pomacanthidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), p. 841. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

MENDIOLA, C.:

2005. Presencia de *Sphoeroides marmoratus* (Lowe, 1838) y *Sphoeroides pachygaster* (Müller & Troschel, 1848) (Osteichthys, Tetraodontidae) en el Mediterráneo occidental (bahía de Santa Pola, Sureste de España). *Revista de la Societat Paleontològica d'Elk, Seccíon*

Vertebrados Actuales, **7**: 1-11.

MORATO, T., R. S. SANTOS & J. P. ANDRADE:

2000. Feeding habits, seasonal and ontogenetic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic. *Fishery Research*, **49** (1): 51-59.

NEGEDLY, R.:

1990. *Elsevier's dictionary of fishery, processing, fish and shellfish names of the world*. Elsevier Science Publishers, Amsterdam, The Netherlands, 623 pp.

OFORI-ADU, D. W.:

1988. List of fishes, shellfishes and other marine food resources in the Ghanaian coastal waters. *Marine Fishery Research Technical Paper*, **1**: 1-43.

OLIVEIRA, M. T., M. N. SANTOS, R. COELHO, V. MONTEIRO, A. MARTINS & P. G. LINO:

2015. Weight-length and length-length relationships for reef fish species from the Cape Verde archipelago (tropical north-eastern Atlantic). *Journal of Applied Ichthyology*, **31** (1): 236-241.

OSÓRIO, B.:

1898. Da distribuição geográfica dos peixes e crustáceos colhidos nas possessões portuguesas da África Occidental e existentes no Museu Nacional de Lisboa. *Jornal do Sciências Mathemáticas, Physicas e Naturaes, Lisboa* (sér. 2), **5** (19): 185-202.

PARENTI, P. & J. E. RANDALL:

2000. An annotated checklist of the species of the Labroid fish families Labridae and Scaridae. *Ichthyological Bulletin of the J. L. B. Smith Institute of Ichthyology*, **68**: 1-97.

PSOMADAKIS, P. N., S. GIUSTINO & M. VACCHI:

2012. Mediterranean fish biodiversity: an updated inventory with focus on the Ligurian and Tyrrhenian seas. *Zootaxa*, **3263**: 1-46.

REINER, F.:

1996. *Catálogo dos peixes do arquipélago de Cabo Verde*. Publicações avulsas do IPIMAR vol. 2, Instituto Português de Investigação Marítima, Lisboa, 339 pp.

RICKER, W. E.:

1973. *Russian-English dictionary for students of fisheries and aquatic biology*. Fisheries Research Board of Canada, Ottawa, 428 pp.

ROUX, C.:

1973. Pomadasyidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2*. (eds.: J.-C. Hureau & T. Monod), pp. 391-395. Unesco, Paris.

1986. Pomadasyidae. In: *Check-list of the freshwater fishes of Africa (CLOFFA)*, Vol. II (eds.: J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde), pp. 327-330. ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris.

1990. Haemulidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), pp. 783-788. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

SANCHES, J. G.:

1991. *Catálogo dos principais peixes marinhos da República de Guiné-Bissau*. Instituto Nacional de Investigação das Pescas, Lisboa, 429 pp.

SANTOS, R. S., F. M. PORTEIRO & J. P. BARREIROS:

1997. Marine fishes of the Azores: annotated checklist and bibliography. *Bulletin University of the Azores*. Supplement 1. Universidade dos Açores, Ponta Delgada (Açores) Portugal, 244 pp.

SATO, T.:

1978. A synopsis of the sparoid fish genus Lethrinus, with the description of a new species. *Bulletin of the University Museum, University of Tokyo*, **15**: i-v + 1-70, Pls. 1-12.

SCHNEIDER, W.:

1990. *FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea*. FAO, Rome, 268 pp.

SÉDZRO, K. M.:

2003. Names of marine fishes of Togo in the Ewe language. In: *Fish biodiversity: Local studies as basis for global inferences* (eds.: M. L. D. Palomares, B. Samb, T. Diouf, J. M. Vakily & D. Pauly.), pp. 230-233. ACP-EU Fishery Research Report, 14.

SHIPP, R. L.:

1990. Tetraodontidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), pp. 1069-1072. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

SMITH, C. L.:

1990. Serranidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), pp. 695-706. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

SNOEKS, J. & E.J. VREVEN:

2008. Haemulidae. In: *The fresh and brackish water fishes of Lower Guinea, West-Central Africa. Volume II. Collection Faune et Flore tropicales 42* (eds.: M. L. J. Stiassny, G. G. Teugels & C. D. Hopkins), pp. 424-431. Institut de Recherche pour le Développement, Paris, France, Muséum National d'Histoire Naturelle, Paris, France, and Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

SVETOVIDOV, A. N.:

1973. Gadidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2*. (eds.: J.-C. Hureau & T. Monod), pp. 303-320. Unesco, Paris.

THOMSON, J. M.:

1990. Mugilidae. In: *Check-list of the fishes of the eastern tropical Atlantic (CLOFETA)*, Vol. II (eds.: J. C. Quero, J. C. Hureau, C. Karrer, A. Post & L. Saldanha), pp. 855-859. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

TORTONESE, E., T. SERTORIO & M.-L. BAUCHOT:
1973. Centracanthidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2*. (eds.: J.-C. Hureau & T. Monod), pp. 417-419. Unesco, Paris.

TREWAVAS, E:
1973. Sciaenidae. In: *Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean. CLOFNAM. Volume 2*. (eds.: J.-C. Hureau & T. Monod), pp. 396-401. Unesco, Paris.

VACCHI, M., S. BUSSOTTI, A. M. MIGLIETTA & P. GUIDETTI:
2007. Presence of the Guinean puffer Sphoeroides marmoratus (Lowe, 1838) in the Mediterranean Sea. *Journal of Fish Biology*, **71** (4): 1215-1219.

VAKILY, J. M.:
1994. *Sierra Leone Fishery Surveys Database System (FisDas)*. Vol. 1: User manual. Vol. 2: Technical Reference Handbook. IMBO, Freetown (Sierra Leone) and ICLARM, Manila (Philippines).

VIVIEN, J.:
1991. *Faune du Cameroun. Guide des mammifères et des poissons*. GICAM et Ministère de la Coopération et du Développement, Paris, 271 pp.

WALKINS, M. G.:
1892. Sarah Lee. In: *Dictionary of National Biography* (ed.: S. Lee). Volume 32 (Lambre to Leigh), p. 379. Smith, Elder, and Co., London.

WHITEHEAD, P. J. P.:
1967. The West African shad, *Ethmalosa fimbriata* (Bowdich, 1825): synonymy, neotype. *Journal of Natural History*, **1** (4): 585-593.

WIRTZ, P.:
1994. *Underwater Guide. Fish of Madeira, Canary Islands and Azores*. Verlag Stephanie Naglschmid Stuttgart, 126 pp.

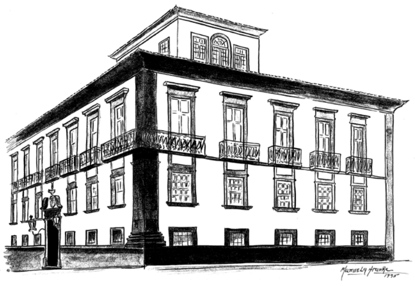
WIRTZ, P., A. BRITO, J. M. FALCÓN, R. FREITAS, R. FRICKE, V. MONTEIRO, F. REINER & O. TARICHE:
2013. The coastal fishes of the Cape Verde Islands – new records and an annotated check-list. *Spixiana* (München), **36** (1): 113-142.

WIRTZ, P., C. E. L. FERREIRA, S. R. FLOETER, R. FRICKE, J. L. GASPARINI, T. IWAMOTO, L. A. ROCHA, C. L. S. SAMPAIO & U. SCHLIEWEN:
2007. Coastal fishes of São Tomé and Principe Islands, Gulf of Guinea (Eastern Atlantic Ocean) – an update. *Zootaxa*, **1523**: 1-48.

WIRTZ, P., R. FRICKE & M. J. BISCOITO:
2008. The coastal fishes of Madeira Island – new records and an annotated check-list. *Zootaxa*, **1715**: 1-26.

WU, H. L., K.-T. SHAO & C. F. LAI:
1999. *Latin-Chinese dictionary of fish names*. The Sueichan Press, Taiwan. 1028 p.

ZUEV, G. V. & A. R. BOLTACHEV:
2000. Demersal fish communities on the Guinea Shelf (West Africa). *Journal of Ichthyology*, **40** (4): 312-319.



BOLETIM

MUSEU DE
HISTÓRIA NATURAL DO FUNCHAL

Vol. LXIX (2019), Art. 354: 13-32

BOLETIM
MUSEU DE HISTÓRIA NATURAL DO FUNCHAL

ISSN 2183-279X (online edition) | | Available online at: http://boletim.cm-funchal.pt

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

By A. Kratochwil [1] *, A. Schwabe [2], J. Smit [3] & A. F. Aguiar [4]

With 7 figures and 5 tables

[1] Department of Biology/Chemistry, Ecology Section, University of Osnabrück, Barbarastr. 13, D-49069 Osnabrück, Germany.
[*] Corresponding author: anselm.kratochwil@biologie.uni-osnabrueck.de
[2] Department of Biology, Technische Universität Darmstadt, Schnittspahnstr. 10, D-64287 Darmstadt, Germany.
[3] Voermanstraat 14, NL-6921NP Duiven, The Netherlands.
[4] Entomology Lab, Laboratório de Qualidade Agrícola, Secretaria Regional de Agricultura e Pescas, Caminho Municipal dos Caboucos, 61, 9135-372 Camacha, Madeira, Portugal.

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

Received: 26 July 2019; Available online: 26 August 2019; Published: 31 December 2019

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 km^2 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.

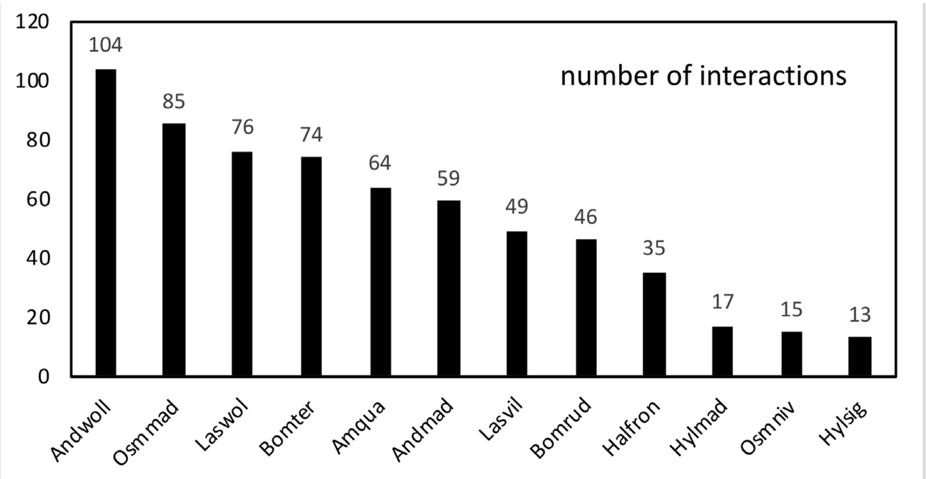


Fig. 1 – Number of wild-bee interactions concerning different bee species (Abbreviations in Table 1).

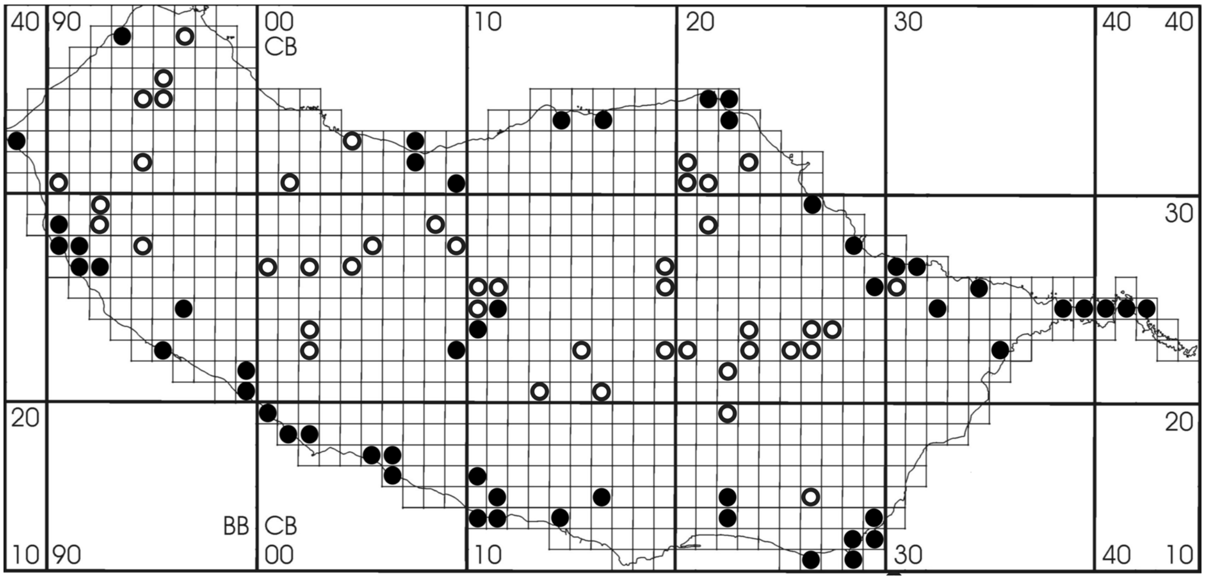


Fig. 2 – Grid elements (1 km x 1 km), based on the 1/25000 scale military map of the Madeira Archipelago (2004). Madeira Island comprises 826 raster elements. Bee-plant interactions were detected in 98 grid elements (179 localities). Black points: 54 grids of the infra- / thermo-Mediterranean zone; White 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).

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 Lm of a bee species m is the number of plant species visited by m. The linkage level Ln 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 lm = Lm/P (P = total number of bee species). Species with high linkage levels utilise more species than do species with low linkage levels.

RESULTS AND DISCUSSION

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.

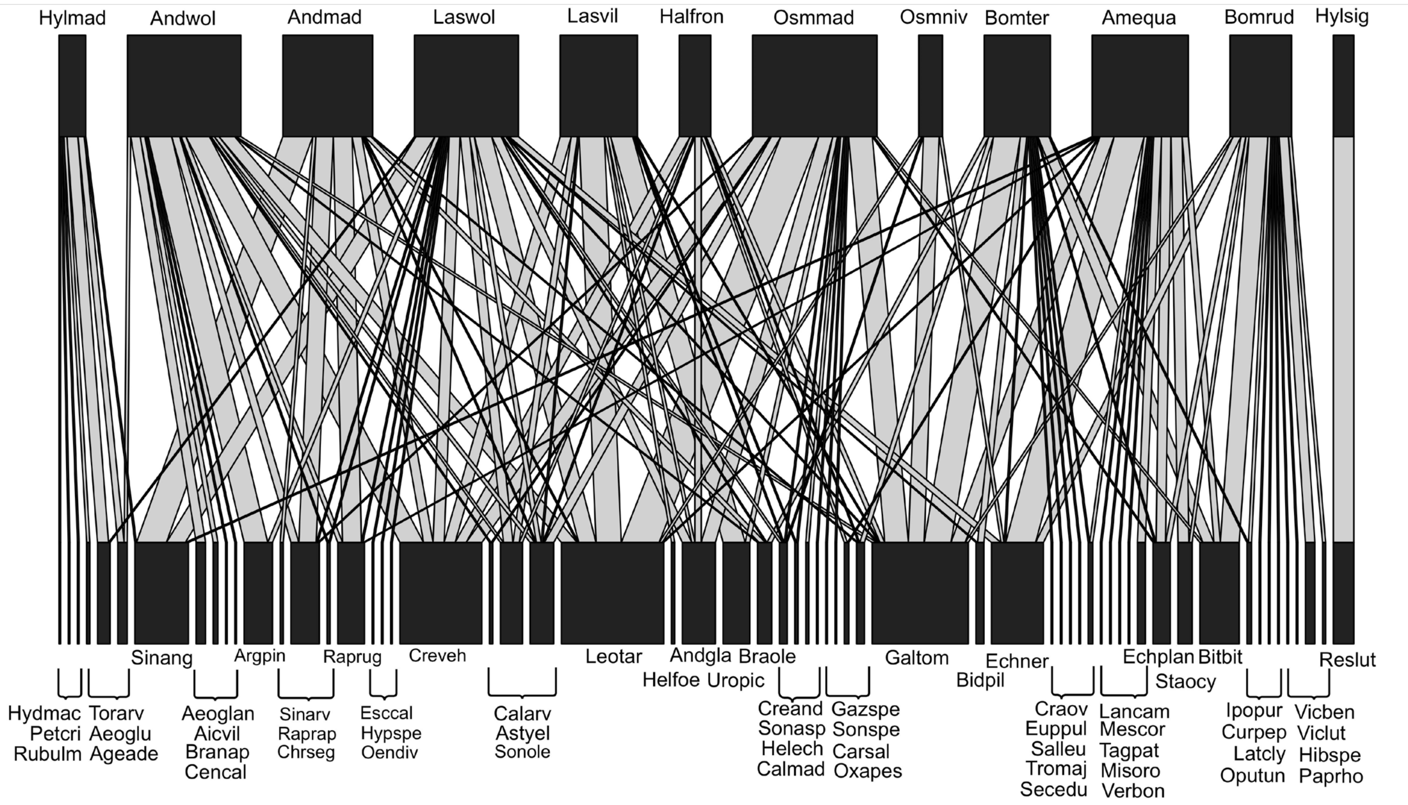


Fig. 3 – Bipartite graph of the bee-plant network of the infra- / thermo-Mediterranean zone of Madeira Island: the top row shows bee species and the bottom row shows plant taxa. For abbreviations see Tables 1 and 2.

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,

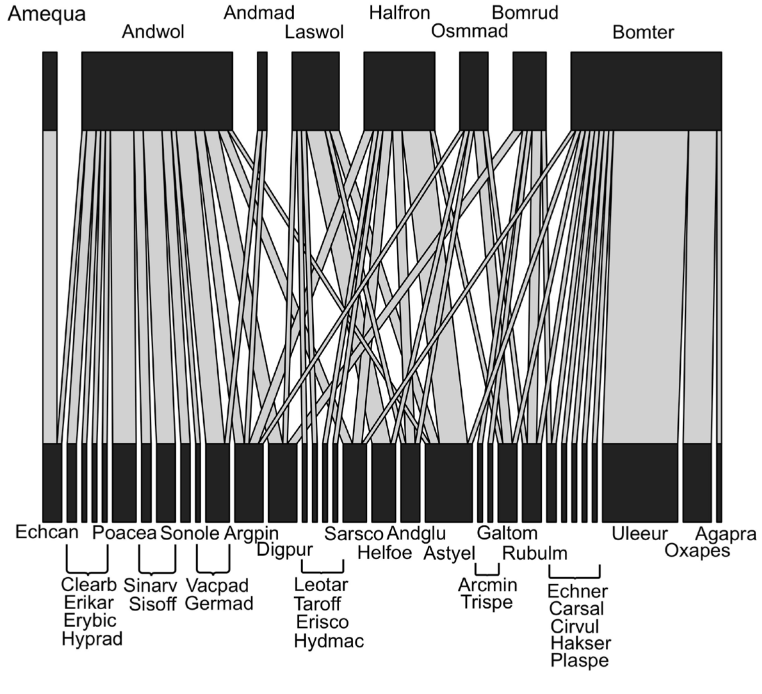


Fig. 4 – Bipartite graph of the bee-plant network of the temperate zone *s.l.* of Madeira Island: the top row shows bee species and the bottom row shows plant taxa. For abbreviations see Tables 1 and 2.

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

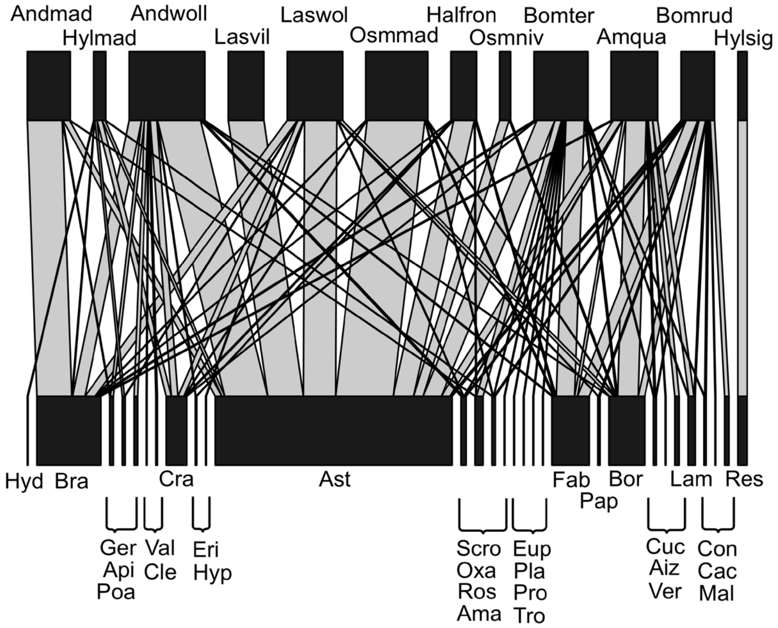


Fig. 5 – Bipartite graph of the whole bee-plant network of Madeira Island: the top row shows wild-bee species and the bottom row shows plant families. For abbreviations, see Table 1 and 2.

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

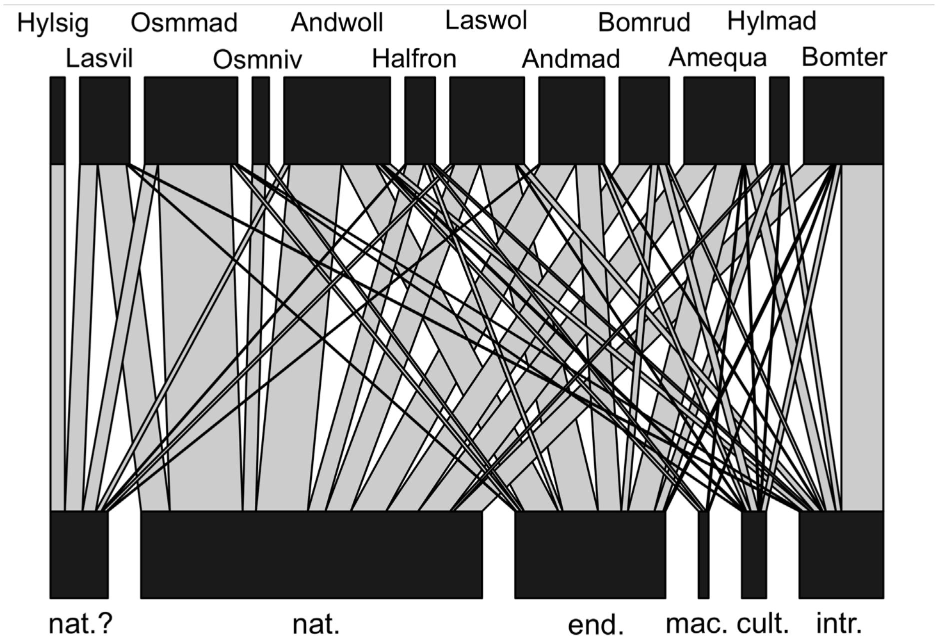


Fig. 6 – Bipartite graph of the bee-plant network of Madeira Island: top row shows wild-bee species and the bottom row shows the statuses of the visited plant taxa. For abbreviations, see Tables 1 and 2.

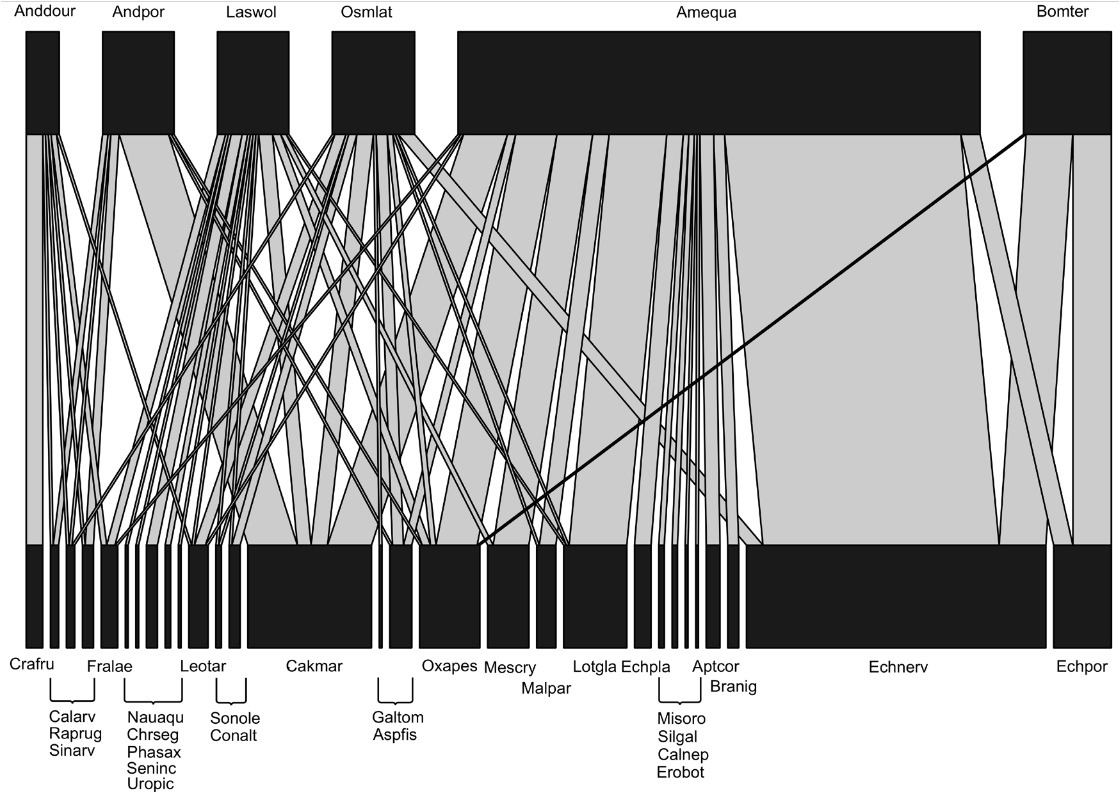


Fig. 7 – Bipartite graph of the bee-plant network of Porto Santo: the top row shows wild-bee species and the bottom rows shows the visited plant species. Abbreviations of wild-bee species: Amequa = *Amegilla quadrifasciata maderae*, Anddou = *Andrena dourada*, Andpor = *Andrena portosanctana*, Bomter = *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 km^2, while Porto Santo is only 42 km^2. 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 Im 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 Im 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 Im 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.

ACKNOWLEDGEMENTS

We cordially thank Ysabel Gonçalves (Museu de História Natural do Funchal, Madeira, Portugal) for cooperation and Miguel Andrade (Madeira, Portugal) for data concerning *Megachile pusilla*. Special thanks go to the authorities in the Madeira Archipelago for access and collection permits.

REFERENCES

ALDRIDGE, A. E.:
1981. Anatomy and evolution in Macaronesian *Echium* (Boraginaceae). *Plant Systematic and Evolution*, **138**: 9-22.

ARECHAVALETA, M., S. RODRÍGUEZ, N. ZURITA & A. GARCÍA:
2010. *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres*. 2009. Gobierno de Canarias, 579 pp.

BARRETT, S. C. H.:
1998. The reproduction biology and genetic of island plants. In: *Evolution on Islands* (ed.: P. R. Grant), pp. 18-34. Oxford University Press, Oxford.

BEIL, M., A. KRATOCHWIL, C. STORM & A. SCHWABE:
2014. Community structure and diversity of vegetation and flower-visiting wild bees (Hymenoptera: Apoidea) in sandy dry grassland: are there congruent characteristics? *Phytocoenologia*, **44** (3/4): 175-192.

BLÜTHGEN, N., J. FRÜND, D. P. VÁZQUEZ & F. MENZEL:
2008. What do interaction network metrics tell us about specialization & biological traits? *Ecology*, **89**: 3387-3399.

BORGES, P. A. V, C. ABREU, A. M. F. AGUIAR, P. CARVALHO, R. JARDIM, I. MELO, P. OLIVEIRA, C. SÉRGIO, A. R. M. SERRANO & P. VIEIRA (eds.):
2008. *Listagem dos fungos, flora e fauna terrestres dos arquipélagos da Madeira e Selvagens* [*A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*]. Funchal & Angra do Heroísmo: Direcção Regional do Ambiente da Madeira and Universidade dos Açores. 438 pp.

BREHM, A., J. JESUS, H. SPINOLA, C. ALVES, L. VICENTE & D. J. HARRIS:
2003. Phylogeography of the Madeira endemic lizard *Lacerta dugesii* inferred from mtDNA sequences. *Molecular Phylogenetics and Evolution*, **26**: 222-230.

CAPELO, J., J. C. COSTA, M. LOUSÃ, S. FONTINHA, R. JARDIM, M. SEQUEIRA & S. RIVAS-MARTÍNEZ:
1999. Notas do Herbário da Estação Florestal Nacional (LISFA): Fasc. X. *Silva Lusitana*, **7** (2): 257-290.

CAPELO, J., M. SEQUEIRA, R. JARDIM, J. C. COSTA & S. MESQUITA:
2004. Guia da Excursão Geobotânica dos V Encontros ALFA 2004 à Ilha da Madeira. *Quercetea*, **6**: 5-45.

CAPELO, J., M. SEQUEIRA, R. JARDIM, S. MESQUITA & J. C. COSTA:
2005. The vegetation of Madeira Island (Portugal). A brief overview and excursion guide. *Quercetea*, **7**: 95-122.

COSTA, J. C., C. NETO, C. AGUIAR, J. CAPELO, M. D. ESPERITO SANTO, J. HONRADO, C. PINTO-GOMEZ, M. MONTEIRO-HENRIQUES, M. SEQUEIRA & M. LOUSÃ:
2012. Vascular communities in Portugal (Continental, the Azores and Madeira). *Global Geobotany*, **12**: 1-180.

d'ANTONIO, C. & T. L. DUDLEY:
1993. Alien species: the insidious invasion of ecosystems by plants and animals from around the world has become a major environmental problem. *Pacific Discovery*, **1993**, summer: 9-11.

DAVY A. J., R. SCOTT & C. V. CORDAZZO:
2006. Biological flora of the British Isles: *Cakile maritima* SCOP. *Journal of Ecology*, **94**: 695-711.

de LIMA, M. I. P. & J. L. M. P. de LIMA:
2009. Investigating the multifractality of point precipitation in the Madeira Archipelago. *Nonlinear Processes in Geophysics*, **16**: 299-311.

DORMANN, C. F., B. GRUBER & J. FRÜND:
2008. Introducing the bipartite package: analysing ecological networks. *R News*, **8**: 8-11.

DORMANN, C. F., J. FRÜND, N. BLÜTHGEN & B. GRUBER:
2009. Indices, graphs and null models: Analysing bipartite ecological networks. *The Open Ecology Journal*, **2**: 7-24.

DUPONT, Y. L., D. M. HANSEN & J. M. OLESEN:
2003. Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, **26**: 301-310.

ESFELD, K., M. A. KOCH, T. V. D. NIET, M. SEIFAN & M. THIV:
2009. Little interspecific pollen transfer despite overlap in pollinators between sympatric *Aeonium* (Crassulaceae) species pairs. *Flora*, **204**: 709-717.

FELLENDORF, M., C. MOHRA, S. ROBERTS, P. WIRTZ & G. van der ZANDEN:
1999. The bees of Madeira (Hymenoptera, Apoidea). *Bocagiana*, **197**: 1-17.

FLACHER, F., A. HANSART, E. MOTARD, A. M. FOFANA, O. VINCENT, B. GESLIN, I. DAJOZ & X. RAYNAUD:
2017. Does competition with wind-pollinated species alter *Echium plantagineum*'s attractiveness to a common pollinator *Bombus terrestris*? *Ecological Entomology*, **42**: 617-628.

GALOPIM de CARVALHO, A. M. & J. M. BRANDÃO:
1991. Geologia do Arquipélago da Madeira. *Museu Nacional de História Natural (Mineralogia e Geologia) da Universdidade de Lisboa*, pp. 1-170.

GARCÍA, J. D. D.:
2000. Patterns of insect flower visitation in *Lavandula bucchii* Webb (Lamiaceae), an endemic shrub of Tenerife (Canary Islands). *Journal of Natural History*, **34** (11): 2145-2155.

GARCÍA-TALAVERA, F.:
1999. La Macaronesia: consideration geológicas, biogeográficas y paleoecológicas. In: *Ecología y cultura en Canarias. Musea de la Cienca y el Cosmos, Cabildo Insular de Tenerife, Spain* (eds.: Fernández-Palacios J. M., J. J. Bacallado & J. A. Belmonte), pp. 41-63.

GELDMACHER, J., P. van der BOGAARD & H.-U. SCHMINCKE:

2000. The 40 Ar/39 Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems*, **1**: Paper number 1999GC000018.

GODMAN, F. du CANE:

1870. *Natural History of the Azores, or Western Islands*. J. Van Voorst, London. 377 pp.

GROOM, S., S. HAYES, H. NGO, M. STEVENS & M. SCHWARZ:

2014a. Recipe for disruption: Multiple recent arrivals of megachilid bees in Pacific archipelagos. *Journal of Insect Conservation*, **18**: 613-622.

GROOM, S., H. NGO, S. REHAN & P. SKELION:

2014b. Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems. *Biological Invasions*, **16**: 2293-2302.

GROOM, S., M. STEVENS, T. RAMAGE & M. SCHWARZ:

2016. Origins and implications of apid bees (Hymentopera: Apidae) in French Polynesia. *Entomological Science*, **20** (1): 65-75.

INOUE, K.:

1993. Evolution of mutualism in plant-pollinator interactions on islands. *Journal of Bioscience*, **18**: 525-536.

JARDIM, R. & M. MENEZES DE SEQUEIRA:

2008. Lista das plantas vasculares (Pteridophyta and Spermatophyta). In: *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos* (eds.: P. A. V. Borges, C. Abreu, A. M. F. Aguiar, P. Carvalho, R. Jardim, I. Melo, P. Oliveira, C. Sérgio, A. R. M. Serrano & P. Vieira), pp. 179-208. Funchal and Angra do Heroísmo: Direcção Regional do Ambiente da Madeira and Universidade dos Açores.

JOHANSON, L. G., A. HOFFMANN, L. WALKER & M. A. NASH:

2018. Bees of the Victorian Alps: Network structure and interactions of introduced species. *Austral Ecology*. doi:10.1111/aec.12669.

KRAEMER, M. & U. SCHMITT:

1997. Nectar production patterns and pollination of the Canarian endemic *Echium wildpretii* Pearson ex Hook. fil. *Flora*, **192**: 217-221.

KRATOCHWIL, A.:

2003. Bees (Hymenoptera: Apoidea) as keystone species: specifics of resource and requisite utilisation in different habitat types. *Berichte der Reinhold-Tüxen-Gesellschaft*, **15**: 59-77.

KRATOCHWIL, A. & E. SCHEUCHL:

2013. *Andrena (Micrandrena) dourada* nov. sp. from Porto Santo, Madeira Archipelago, Portugal. *Linzer biologische Beiträge*, **45** (1): 755-774.

KRATOCHWIL, A. & S. KRAUSCH:

2016. Bee-plant networks: structure, dynamics and metacommunity concept. *Berichte der Reinhold-Tüxen-Gesellschaft*, **28**: 23-40.

KRATOCHWIL, A. & A. SCHWABE:

2018a. Wild bees (Anthophila) of Macaronesia – biogeographical and evolutionary aspects. *Berichte der Reinhold-Tüxen-Gesellschaft*, **30**: 149-162.

2018b. Wild bees (Anthophila) of Porto Santo (Madeira Archipelago) and their habitats: species diversity, distribution patterns and bee-plant network. *Linzer biologische Beiträge*, **50** (2): 1219-1247.

KRATOCHWIL, A., M. BEIL & A. SCHWABE:

2009. Complex structure of pollinator-plant interaction-webs: random, nested, with gradients or modules? *Apidologie*, **40** (6): 634-650.

KRATOCHWIL, A., A. SCHWABE, & E. SCHEUCHL:

2014. *Andrena (Suandrena) portosanctana* Cockerell, 1922 and *A. (Suandrena) maderensis* Cockerell, 1922 – new taxonomical and ecological data for two closely related endemic bee species of the Madeira Archipelago, Portugal. *Linzer biologische Beiträge*, **46** (2): 1535-1567.

KRATOCHWIL, A., A. SCHWABE & A. F. AGUIAR:

2018a. Comments on the butterfly fauna of Porto Santo (Madeira Archipelago): species list, distribution patterns and butterfly-plant network. *Boletim do Museu de História Natural do Funchal*, **68** (349): 5-20.

KRATOCHWIL, A., J. SMIT & A. F. AGUIAR:

2018b. Updated checklist of the wild bees of the Madeira Archipelago (Hymenoptera: Apoidea: Anthophila). *Linzer biologische Beiträge*, **50** (2): 1213-1228.

LANDI, P., H. O. MINOARIVELO, A. BRÄNNSTRÖM, C. HUI & U. DIECKMANN:

2018. Complexity and stability of ecological networks: A review of the theory. *Population Ecology*, **60** (4): 319-345.

LINSLEY E. G. & R. L. USINGER

1966. Insects of the Galápagos Islands. *Proceedings of the California Academy of Sciences*, **33**: 113-196.

MAGNACCA, K. & C. KING:

2013. Assessing the Presence and Distribution of 23 Hawaiian Yellow – Faced Bee Species on Lands Adjacent to Military Installations on O'ahu and Hawai'i Island, and appendix. Pacific Cooperative Studies Unit, University of Hawaii at Manoa: Honolulu, HI, USA, 26 pp.

MESQUITA, S., J. CAPELO & J. de SOUSA:

2004. Bioclimatologia da Ilha da Madeira: abordagem numérica. *Quercetea*, **6**: 47-59.

MOTTEN, A. F.:

1982. *Pollination Ecology of the Spring Wildflower Community in the Deciduous Forests of Piedmont North Carolina*. PhD thesis, Duke University, Duhram, North Carolina, USA.

NATIONAL DIRECTORATE FOR THE ENVIRONMENT:

2015. *Fifth National Report on the Status of Biodiversity in Cabo Verde*. https://www.cbd.int/doc/world/cv/cv-nr-05-en.pdf, 95pp.

OBERDORFER, E.:

1975. Bemerkungen zur Vegetation Madeiras. *Anales del Instituto Botánico A. J. Cavanilles*, **32** (2): 1315-1332.

OLESEN, J. M. & P. JORDANO:

2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, **83**: 2416-2424.

OLESEN, J. M. & A. VALIDO:

2003a. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution*, **18**: 177-181.

2003b. Bird pollination in Madeira Island. *Ardeola*, **50** (1): 67-69.

OLESEN, J. M., L. I. ESKILDSEN & S. VENKATASAMY:

2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, **8**: 181-192.

OLESEN, J. M., M. ALARCÓN, B. K. EHLERS, J. J. ALDASORO & C. ROQUET:

2012. Pollination, biogeography and phylogeny of oceanic island bellflowers (Campanulaceae). *Perspectives in Plant Ecology, Evolution and Systematics*, **14**: 169-182.

OLLERTON, J., S. P. JOHNSON, L. CRANMER & S. KELLIE:

2003. The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany*, **92**: 807-834.

OLLERTON, J., L. CRANMER, R. STELZER, S. SULLIVAN & L. CHITTKA:

2009. Bird pollination of Canary Island endemic plants. *Naturwissenschaften*, **96**: 221-232.

PÉREZ, A. J. & N. MACÍAS-HERNÁNDEZ:

2012. Presencia de *Bombus (Megabombus) ruderatus* en Canarias. *Revista de la Academia Canaria de Ciencias*, **24**: 103-114.

PRESS, J. R. & M. J. SHORT:

1994. *Flora of Madeira*. The Natural History Museum London. St. Edmundsbury Press, Suffolk, 574 pp.

R CORE TEAM:

2018. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.

RASMUSSEN, C., A. L. CARRION, R. CASTRO-URGAL, S. CHAMORRO, V. H. GONZÁLEZ, T. L. GRISWOLD, H. W. HERRERA, C. K. MCMULLEN, J. M. OLESEN. & A. TRAVESET:

2012. *Megachile timberlakei* Cockerell (Hymenoptera: Megachilidae): Yet another adventive bee species to the Galápagos Archipelago. *The Pan-Pacific Entomologist*, **88** (1): 98-102.

RIVAS-MARTÍNEZ, S.:

1996. *Bioclimatic map of Europe*. Servicio de Publicaciones de la Universidad de Granada, Granada.

2009. Ensayo geobotánico global sobre la Macaronesia. In: *Homenaje al Prof. Wolfredo Wildpret de la Torre* (eds.: E. Beltrán Tejera, J. Alfonso-Carrilo, A. Garcia Gallo & O. Rodríguez Delgado. Inst. Est. Canarios, La Laguna, Tenerife: pp. 255-296.

RIVAS-MARTÍNEZ, S., D. SÁNCHEZ-MATA & M. COSTA:

1999. North American boreal and western temperate forest vegetation (syntaxonomical synopsis of the potential natural plant communities of North America II). *Itinera Geobotanica*, **12**: 5-316.

RUSSO, L.:

2016. Positive and negative impacts of non-native bee species around the World. *Insects*, **7**: 1-22.

SCHAEFER, H., O. J. HARDY, L. SILVA, T. G. BARRACLOUGH & V. SAVOLAINEN:

2011. Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters*, **14**: 389-396.

SCHLEUNING, M, J. FRÜND, O. SCHWEIGER, E. WELK, J. ALBRECHT, M. ALBRECHT, M. BEIL, G. BENADI, N. BLÜTHGEN, H. BRUELHEIDE, K. BÖHNING-GAESE, M. DEHLING, C. F. DORMANN, N. EXELER, N. FARWIG, A. HARPKE, T. HICKLER, A. KRATOCHWIL, K. KUHLMANN, I. KUHN, D. MICHEZ, S. MUDRI-STOJNIK, M. PLEIN, P. RASMONT, A. SCHWABE, J. SETTELE, A. VUJIC, C. WEINER, M. WIEMERS & C. HOF:

2016. Mutualistic networks are more sensitive to plant than to animal loss under climate change. *Nature Communication*, **7**: 13965.

SCHMID-HEMPEL, R., M. ECKHARDT, D. GOULSON, D. HEINZMANN, C. LANGE, S. PLISCHUK, L. R. ESCUDERO, R. SALATHE, J. J. SCRIVEN & P. SCHMID-HEMPEL:

2014. The invasion of Southern South America by imported bumblebees and associated parasites. *Journal of Animal Ecology*, **83**: 823-837 [first published 21 November 2013].

SJÖGREN, E.:

1972. Vascular plant communities of Madeira. *Boletim do Museu de História Natural do Funchal*, **26** (14): 45-125.

SMIT, J. T. & J. SMIT:

2003. *Hylaeus signatus* (Panzer, 1798) new for the fauna of Madeira (Hymenoptera: Apidae), with notes on its feeding behaviour. *Entomofauna*, **24** (11): 165-167.

SNELLING, R.:

2003. Bees of the Hawaiian Islands, exclusive of *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society*, **76**: 342-356.

SOCHOR, M., R. J. VAŠUT, T. F. SHARBEL & B. TRÁVNÍČEK:

2015. How just a few makes a lot: Speciation via reticulation and apomixis on example of European brambles (*Rubus* subgen. *Rubus*, Rosaceae). *Molecular Phylogenetics and Evolution*, **89**: 13-27.

TAVARES, C. N.:

1965. Ilha da Madeira o meio e a flora. *Revista Faculdade de Ciências da Universidade de Lisboa*, Ser. 2, **13** (1): 51-175.

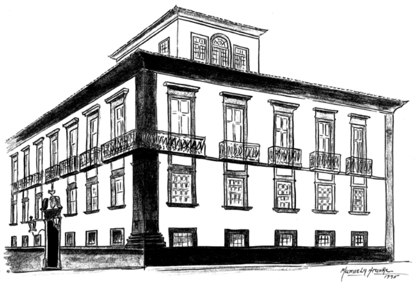
TRAVESET, A. & D. M. RICHARDSON:

2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution*, **21**: 208-216.

TRAVESET, A., R. HELENO, S. CHAMORRO, P. VARGAS, C. K. MCMULLEN, R. CASTRO-URGAL, M. NOGALES, H. W. HERRERA & J. M. OLESEN:
2013. Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society London B*, **280**: 20123040.

VALIDO, A. & J. M. OLESEN:
2010. Pollination on islands: examples from the Macaronesian archipelagos. In: T*errestrial arthropods of Macaronesia. Biodiversity, Ecology and Evolution* (eds.: A. R. M. Serrano, P. A. V. Borges, M. Boieiro, P. Oromí). Sociedade Portuguesa de Entomologia, Lisbon, pp. 249-283.

WEISSMANN, J. A., A. PICANÇO, P. V. A. BORGES & H. SCHAEFER:
2017. Bees of the Azores: an annotated checklist (Apidae, Hymenoptera). *ZooKeys*, **642**: 63-95.



BOLETIM

MUSEU DE
HISTÓRIA NATURAL DO FUNCHAL

Vol. LXIX (2019), Art. 355: 33-38

ISSN 2183-279X (online edition) | | Available online at: http://boletim.cm-funchal.pt

First record of the Rose Evening Primrose *Oenothera rosea* L' Hér. ex Aiton (Onagraceae) on the island of Madeira (Portugal)

By J. J. Gonçalves Silva [1] * & J. P. Ferreira [1]

With 5 figures

[1] *Museu de História Natural do Funchal, Rua da Mouraria, 31, 9004-546 Funchal, Madeira, Portugal.*
[*] *Corresponding author: juan.silva@cm-funchal.pt*

ABSTRACT: *Oenothera rosea* L' Hér. ex Aiton is reported for the first time for the island of Madeira. In Portuguese territories, nine *taxa* of the genus *Oenothera* L. (Onagraceae) are recorded. The species *Oenothera rosea* is present in mainland Portugal and in the Azores, as well as in the Canary Islands (Spain) and in the archipelago of Cape Verde (Republic of Cabo Verde). Similar to what is happening in other parts of the world, the presence of *O. rosea* on the island of Madeira, as well as other species introduced and properly reported over the last 10 years as naturalized, may pose a new potential threat to endemic flora and vegetation.

Key words: *Oenothera*, Onagraceae, new record, Madeira.

RESUMO: É assinalada pela primeira vez na ilha da Madeira, a ocorrência da espécie *Oenothera rosea* L' Hér. ex Aiton. Em território português, estão assinalados nove *taxa* do género *Oenothera* L. (Onagraceae). A espécie *Oenothera rosea* está presente em Portugal Continental e no arquipélago dos Açores, assim como nos arquipélagos das Canárias e de Cabo Verde. À semelhança do que está a acontecer noutras partes do mundo, a presença de *O. rosea* na ilha da Madeira, tal como de outras espécies introduzidas e devidamente assinaladas nos últimos 10 anos como naturalizadas, pode implicar uma potencial nova ameaça para a flora e vegetação endémicas.

Palavras-chave: *Oenothera*, Onagraceae, novo registo, Madeira.

Received: 26 August 2019; Revised: 27 August 2019; Accepted: 03 September 2019; Available online: 20 September 2019; Published: 31 December 2019

INTRODUCTION

The archipelago of Madeira is located in the North Atlantic, approximately 630 km northwest from the West African coast (Casablanca, Morocco) and 900 km southwest from Europe (Lisbon, Portugal). It comprises the islands of Madeira, Porto Santo and the Desertas and together with the Selvagens, Canary Islands, Azores and Cape Verde archipelagos, makes up the biogeographical zone of Macaronesia. The Madeira climate is Mediterranean and deeply influenced by the northeast trade wind system, with weather conditions varying considerably between the south and north coasts and according to altitude. This climate, along with the high volume of traffic in people and goods that the island experiences, means the island is very vulnerable to new introductions of alien species.

The flora of the archipelagos of Madeira and Selvagens, according to Menezes de Sequeira update (*pers. comm.*, 2018), comprises 1,268 *taxa* of vascular plants (species and subspecies). Of these, 29 *taxa* are 'possible introduced' and 402 to 441 *taxa* are 'introduced'.

The willowherb or evening primrose family (Onagraceae) totals ten *taxa*, native and introduced, in the archipelago of Madeira (Turland, 1994; Jardim & Sequeira, 2008). Besides these, *Oenothera fruticosa* L. is also present on the island of Madeira, as ornamental, according to Quintal (2007).

One hundred and twenty-one species of the genus *Oenothera* occurs in open, often disturbed habitats in temperate to subtropical areas of North, Central, and South America, with the centre of diversity in southwest North America (Raven, 1981; Efloras, 2019).

In Portugal, Menezes de Sequeira *et al*. (2012) recognise nine *taxa* belonging to the genus *Oenothera*, including the species *O. rosea* L' Hér. ex Aiton occurring, as introduced and naturalized, in mainland Portugal (Franco, 1971; Domingues de Almeida & Freitas, 2006) and in the Azores (islands of Flores, Faial, Pico, Terceira, São Miguel and Santa Maria) (Palhinha, 1966; Rostanski, 1992; Hansen & Sunding, 1993; Schäfer, 2005; Silva *et al*., 2010). Until the present, this species hasn't been recorded for the island of Madeira (Lowe, 1831, 1856, 1864; Menezes, 1894, 1899, 1905, 1914, 1922a, 1922b, 1926a, 1926b, 1927; Eriksson *et al*., 1979; Hansen & Sunding, 1993; Short, 1994; Vieira, 2002 and Jardim & Sequeira, 2008).

Concerning the other Macaronesian Archipelagos, the species *O. rosea* L' Hér. ex Aiton has been introduced in the Canary Islands and is present on the islands of La Palma, Tenerife, Gran Canaria, Fuerteventura and Lanzarote (Hansen & Sunding, 1993; Acebes Ginovés *et al*., 2010). In the archipelago of Cape Verde, it was introduced and occurs on the island of Santo Antão (Hansen & Sunding, 1993; Sánchez-Pinto *et al*., 2005).

MATERIAL AND METHODS

The specimens of *Oenothera rosea* L' Hér. ex Aiton reported herein were identified according to Raven (1981); Dietrich (1997), Schäfer (2005) and García (2016), and are deposited in the herbarium of the Natural History Museum of Funchal (MADM). Coordinates were obtained using Garmin GPSMAP 78 series GPS and plotted in Google Earth (Fig. 1).

Fig. 1 – Geographical locations where *Oenothera rosea* L' Hér. ex Aiton was collected on the island of Madeira.

Studied material

Oenothera rosea L' Héritier ex Aiton, Hort. Kew. 2: 3. 1789. Sect. Hartmannia (Spach) Endl.

Portugal, Madeira:

On road to chapel of São Francisco de Borja, Cruz da Guarda, Porto da Cruz, Machico, 26.VII.2019, João Ferreira *leg*., 32º 45' 15.5'' N 16º 49' 38.3 W (MADM 7108);

On a garden area along João Abel de Freitas Road, São Vicente, 31.VII.2019, Juan Silva & João Ferreira *leg*., 32º 47' 42.7'' N 17º 02' 22.4'' W, 92 m *a.s.l.* (MADM 7117);

On road to Queimadas, at roadside, Santana, 26.VIII.2019, Juan Silva *leg*., 32º 48' 33.0'' N 16º 53' 14.4'' W, 339 m *a.s.l.* (MADM 7118).

General description

The following description is based on the one given by Efloras (2019):

Herbs ascending to decumbent, perennial, rhizomatous and sometimes suffrutescent from woody caudex, rarely with basal rosette. Stems 7-65 cm, simple or branched, strigillose, sometimes with longer spreading hairs. Leaves green, with inconspicuous veins, glabrous to sparsely strigillose; petioles 3-20 mm; basal blade 2-5 x 0.5-2 cm; cauline blade elliptic to oblanceolate or oblong-ovate, 1-6 x 0.4-2.5 cm, base attenuate, margin subentire to coarsely dentate, sometimes sinuate-pinnatifid at leaf base, apex acute to obtuse. Inflorescence a lax open simple raceme. Flowers open near sunrise; floral tube 4-10 mm. Sepals 5-10 mm, with free tips 0.4-1 mm. Petals pink to rose-purple, 5-12 mm. Anthers 2-3.5 mm; pollen ca. 50% fertile. Ovary usually densely strigillose; stigma surrounded by anthers. Capsules clavate or narrowly obovoid, 4-12mm, valves angled or weakly winged, attenuate to slender sterile stipe (pedicel) 5-20 mm. Seeds in several indistinct rows per locule, brown with dark spot at each end, obovoid, 0.5-1.2 mm, finely papillose.

Flowering: V-XI. (Fig. 2A, B, C, D).

Fig. 2 – *Oenothera rosea* L' Hér. ex Aiton: **A)** general aspect; **B)** flower; **C)** leaves; **D)** flower and capsules.

Key for the Madeiran species of the genus *Oenothera* (adapted from Short, 1994 and Efloras, 2019):

1. Petals white, pink or purple; capsules clavate or obovoid, valves sharply angled, winged or ridged, pedicelled --------- 2
Petals yellow, at least before fading; capsules cylindric, unwinged, sessile -- 3

2. Petals 16-38 mm, white, fading to rose-purple; sepals 16-32 mm; leaf margin weakly serrate to sinuate-pinnatifid, often with large terminal lobe -- ***tetraptera***
Petals 5-12 mm, pink to rose purple; sepals 5-10 mm; leaf margin subentire to coarsely dentate, sometimes sinuate-pinnatifid at leaf base -- ***rosea***

3. Hypanthial tube 6-8(-10) cm; leaves densely pubescent --- ***longiflora***
Hypanthial tube c.1 cm; leaves with ciliate margins, otherwise subglabrous --- ***stricta***

CONCLUSIONS

Several new introductions and consequent naturalizations were reported by Hansen (*e.g.* 1968, 1969, 1970, 1971, 1973, 1974, 1978, 1987 and 1992) and compiled by Vieira (2002) during the second half of the last century. This new discovery adds to many others introduced *taxa* on the island of Madeira, that have been noticed in recent years, such as, *Solidago chilensis* Meyen, *Viburnum tinus* L., *Andryala integrifolia* L., *Billardiera heterophylla* (Lindl.) L. Cayzer & Crisp, *Cobaea scandens* Cav. and *Silene latifolia* Poir. subsp. *latifolia* (Gonçalves Silva *et al.*, 2008, 2009; Ferreira *et al.*, 2011; Benedito & Menezes de Sequeira, 2014; Pupo-Correia & Menezes de Sequeira, 2014 and Gonçalves Silva & Paz Rúben, 2016).

As indicated previously, the centre of diversity of the genus *Oenothera* is in southwest North America, from where its representatives have spread over time to several continents and islands either naturally (such as by the wind), or for the most part, introduced by man (such as being cultivated in gardens as ornamental plants, or by accident in ballast earth, corn seed, hay, fodder or other cargo) (Rostanski, 1991). Nowadays, this genus represents one of a few genera alien to Central Europe whose representatives largely differ in their invasive success, from widespread to rare (Mihulka *et al.*, 2003). According to DAISIE [Delivering Alien Invasive Species Inventories for Europe (http://www.europe-aliens.org/)], *Oenothera rosea* is a South American neophyte considered an alien species in Austria, Belgium, Italy, Sardinia and Sicilia (not established) and in the Azores, Baleares, France, Portugal and Spain (established), while in Israel its alien status (established or not established) is unknown. *O. rosea* is first mentioned in northern Africa (Algeria) by Hamel (2016). In South Africa, the rose evening primrose, has invaded grassland, mountain and coastal vegetation habitats (Frean *et al.*, 1997).

The biology of *O. rosea* suggests a high potential for invasiveness; Meiyu *et al.* (2009) note its high reproductive and adaptive abilities, with it readily producing seed banks (the seed quantity of an individual plant reaches 2.6 x 10^5) and having small, light, round seeds that disperse up to 100 cm, with a germination rate reaching 85%. These qualities of *O. rosea* give it the possibility of invasiveness and installation in surrounding areas (as observed during our field work) to quickly become the single dominant species.

Despite being an invasive plant in some parts of the world, *O. rosea* has also been shown to have pharmacological potential. A large number of phytoconstituents have been isolated and identified from different parts of this plant, showing its medicinal properties (Kaur *et al.*, 2017; Munir *et al.*, 2017 and Calva-Candelaria *et al*, 2018).

ACKNOWLEDGEMENTS

Thanks are due to Francesca Zino and Manuel Biscoito for useful comments and language revision on a first version of the manuscript.

REFERENCES

ACEBES GINOVÉS, J. R., M. C. LEÓN ARENCIBIA, M. L. RODRÍGUEZ NAVARRO, M. del ARCO AGUILAR, A. GARCÍA GALLO, P. L. PÉREZ de PAZ, O. RODRÍGUEZ DELGADO, V. E. MARTÍN OSORIO & W. WILDPRET de la TORRE:

2010. Pteridophyta & Spermatophyta. *In*: Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). M. Arechavaleta, S. Rodríguez, N. Zurita & A. García (coord.). Gobierno de Canarias. Pp. 119-172.

BENEDITO, M. & M. MENEZES de SEQUEIRA:

2014. First record of *Cobaea scandens* Cav. (Polemoniaceae) as naturalized plant in Madeira Island (Portugal). *Silva Lusitana*. N.º Especial Floramac 2012. Ano XXII: 131-135.

CALVA-CANDELARIA, N., M. E. MELÉNDEZ-CAMARGO, H. MONTELLANO-ROSALES, A. R. ESTRADA-PÉREZ, M. C. ROSALES-HERNÁNDEZ, M. J. FRAGOSO-VÁZQUEZ, M. MARTÍNEZ-ARCHUNDIA, J. CORREA-BASURTO & Y. K. MÁRQUEZ-FLORES:

2018. *Oenothera rosea* L' Hér. ex Ait. attenuates acute colonic inflammation in TNBS-induced colitis model in rats: *in vivo* and *in silico* myeloperoxidase role. *Biomedicine & Pharmacotherapy*, **108**: 852-864.

DAISIE (European Invasive Alien Species Gateway):

2008. *Oenothera rosea* L' Hér. ex Aiton. Available from: http://www.europe-aliens.org/speciesFactsheet.do?speciesId=10019# [accessed 08th August 2019].

DIETRICH, W.:

1997. *Oenothera* L. *in* Castroviejo, S., Aedo, C., Benedi, C., Laínz, M., Muñoz Garmendia, F., Nieto Feliner, G. & Paiva, J. (eds.), *Flora Ibérica*. Vol. **8**. Real Jardín Botánico, CSIC. Madrid: 90-100.

DOMINGUES de ALMEIDA, J. & H. FREITAS:

2006. Exotic naturalized flora of continental Portugal – A reassessment. *Botanica Complutensis*, **30**: 117-130.

EFLORAS:

2019. Published on the Internet:
http://www.efloras.org [accessed 08th August 2019]. Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.

ERIKSSON, O., A. HANSEN & P. SUNDING:

1979. *Flora of Macaronesia, checklist of vascular plants*. Part I. Revised Edition. 93 pp.

FERREIRA, M. Z., I. A. FERNÁNDEZ, R. JARDIM & M. M. SEQUEIRA:

2011. *Andryala integrifolia* L. (Asteraceae), a new alien species for the island of Madeira (Portugal). *Silva Lusitana*, **19** (1): 114-125.

FRANCO, J. A.:

1971. *Nova Flora de Portugal (Continente e Açores), Lycopodiaceae – Umbelliferae*. Vol. I, Edição do Instituto Superior de Agronomia, Lisboa, Portugal. 648 pp + 2 mapas.

FREAN, M., K. BALKWILL, C. GOLD (NEE ANDERSON) & S. BURT:

1997. The expanding distributions and invasiveness of *Oenothera* in southern Africa. *South African Journal of Botany*, **63** (6): 449-458.

GARCÍA, X.:

2016. *Guía das plantas de Galícia* (3.ª ed.). Vigo: Xerais De Galicia Edicions. 509 pp.

GONÇALVES SILVA, J. J., J. C. SEMPLE, R. LOPEZ LAPHITZ & M. MENEZES de SEQUEIRA:

2008. First record of La Plate River Goldenrod *Solidago chilensis* Meyen (Asteraceae), in the island of Madeira (Portugal). *Boletim do Museu Municipal do Funchal (História Natural)*, **58** (320): 31-36.

GONÇALVES SILVA, J. J., R. BARONE & M. MENEZES de SEQUEIRA:

2009. First record of naturalized *Viburnum tinus* L. (Caprifoliaceae), in the island of Madeira (Portugal). *Boletim do Museu Municipal do Funchal (História Natural)*, **59** (323): 5-15.

GONÇALVES SILVA, J. J. & F. PAZ RÚBEN:

2016. First record of the White Campion *Silene latifolia* Poir. subsp. *latifolia* (Caryophyllaceae), in the Island of Madeira (Portugal). *Boletim do Museu de História Natural do Funchal*, **66** (343): 13-17.

HAMEL, T.:

2016. Première observation d'une xenophyte *Oenothera rosea* L' Hér. ex Aiton (Onagraceae) en Afrique du Nord. *Acta Botanica Malacitana*, **41**: 287-289.

HANSEN, A.:

1968. Floristische beobachtungen auf der insel Madeira (nebst biographischen notizen über einige ältere sammler von Madeira – Pflanzen). *Bocagiana*, **15**: 1-11.

1969. Weitere beiträge zur flora der insel Madeira. *Bocagiana*, **19**: 1-11.

1970. Beiträge zur Flora der Inseln Madeira, Porto Santo und Ilhéu Chão (Desertas). *Bocagiana*, **25**: 1-18.

1971. Contributions to the flora of the Madeira Archipelago. *Bocagiana*, **27**: 1-14.

1973. Contributions to the flora of Madeira. *Bocagiana*, **32**: 1-13.

1974. Contributions to the flora of Madeira and Porto Santo. *Bocagiana*, **36**: 1-37.

1978. Contributions to the flora of the Archipelago of Madeira. *Bocagiana*, **45**: 1-18.

1987. Contributions to the flora of the Archipelago of Madeira. *Bocagiana*, **109**: 1-11.

1992. Contributions to the flora of the Azores, Madeira, P. Santo and the Canary Islands. *Boletim do Museu Municipal do Funchal (História Natural)*, **44** (242): 157-179.

HANSEN, A. & P. SUNDING:

1993. Flora of Macaronesia. Checklist of vascular plants. 4th revised edition, *Sommerfeltia*, **17**: 295 pp.

JARDIM, R. & M. M. SEQUEIRA:

2008. As plantas vasculares (Pteridophyta e Spermatophyta) dos arquipélagos da Madeira e das Selvagens. *In*: Borges, P. A. V., Abreu, C., Aguiar, A. M. F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A. R. M. & Vieira, P. (eds.), *Listagem dos fungos flora e fauna terrestre dos arquipélagos da Madeira e Selvagens*, pp. 157-208. Direcção Regional do Ambiente da Madeira and Universidade dos Açores. Funchal and Angra do Heroísmo.

KAUR, R., M. ALI, S. S. DAHIYA, S. K. SHARMA, S. SULTANA & S. R. MIR:

2017. Phytochemical Investigation of *Oenothera rosea* L' Hér. ex Aiton. *International Journal of Research in Pharmacy and Biosciences*, **4** (4): 24-31.

LOWE, R. T.:

1831. Primitiae Faunae et Florae Maderae et Portus Sancti; sive species quaedam novae vel hactenus minus rite cognitae animalium et plantarum in his insulis degentium breviter descriptae. *Transactions of the Cambridge Philosophical Society*, **4** (1): 1-70.

1856. Species Plantarum Maderensium quaedam Novae, vel hectenus ineditae, breviter descritae. *Hooker's Journal of Botany and Kew Garden Miscellany*, **8**: 289-302.

1864. *A manual Flora of Madeira and the adjacent Islands of Porto Santo and the Desertas*. Vol. **1**. Part: III: 275-276. London.

MEIYU, W., C. SHIJUN & L. LIPING:

2009. Reproductive biology characteristics of invasive alien plant *Oenothera rosea*. *Guangxi Zhiwu / Guihaia*, **29** (2): 227-230.

MENEZES, C. A.:

1894. *Catálogo das Phanerogamicas da Madeira e do Porto Santo não indicadas na Flora d'estas ilhas, do Revd.º Padre Richard Thomas Lowe*. Typ. do "Direito do Funchal". Funchal. 69 pp.

1899. *Notice sur Les Phanérogames de Madère et Porto Santo non indiquées dans la flore de ces îles de Richard Thomas Lowe*. Imprimerie "Academica". Funchal. 23 pp.

1905. Catálogo das Phanerogamicas e Cryptogamicas Vasculares do Archipelago da Madeira (Madeira, Porto Santo e Desertas). Annaes de Sciencias Naturaes, 9: 119-144.

1914. *Flora do Archipelago da Madeira (Phanerogamicas e Cryptogamicas Vasculares)*. Typ. Bazar do Povo. Funchal. 282 pp.

1922a. Uma antiga Lista de Plantas da Madeira. *Brotéria. Série Botânica*, **20** (1): 12-25.

1922b. Subsídios para o estudo da Flora do Arquipélago da Madeira. *Brotéria. Série Botânica*, **20** (3): 113-119.

1926a. Novos subsídios para o estudo da flora do Arquipélago da Madeira. *Brotéria. Série Botânica*, **22** (1): 20-27.

1926b. Nota acerca de algumas plantas da flora do Arquipélago da Madeira. *Jornal de Sciências Matemáticas, Físicas e Naturais*, **96**: 1-7.

1927. Mais algumas notas sobre a Flora Madeirense. *Brotéria. Série Botânica*, **23** (2): 73-77.

MENEZES de SEQUEIRA, M., D. ESPÍRITO-SANTO, C. AGUIAR, J. CAPELO & J. HONRADO:

2012. *Checklist da Flora de Portugal (Continental, Açores e Madeira)*. Associação Lusitana de Fitossociologia. Lisboa, p. 33.

MIHULKA, S., P. PYÄEK & J. MARTÍNKOVÁ:

2003. Invasiveness of *Oenothera* congeners in Europe related to seed characteristics. *In*: Child, L. E., Brock, J. H., Brundu, G., Prach, K., Pyäek, P., Wade, P. M. and Williamson, M. (eds.), *Plant Invasions: Ecological Threats and Management Solutions*, pp. 213-225. Backhuys Publishers, Leiden, The Netherlands.

MUNIR, R., N. SEMMAR, M. FARMAN & N. S. AHMAD:

2017. An updated review on pharmacological activities and phytochemical constituents of evening primrose (genus *Oenothera*). *Asian Pacific Journal of Tropical Biomedicine*, **7** (11): 1046-1054.

PALHINHA, R. T.:

1966. *Catálogo das plantas vasculares dos Açores*. Edição da Sociedade de Estudos Açoreanos Afonso Chaves, Lisboa, Portugal, 186 pp.

PUPO-CORREIA, A. & M. MENEZES de SEQUEIRA:

2014. *Billardiera heterophylla* (Lindl.) L. Cayzer & Crisp (Pittosporaceae) as naturalized plant in Madeira Island (Portugal). *Silva Lusitana*. N.º Especial Floramac 2012. Ano XXII: 27-33.

QUINTAL, R.:

2007. *Quintas, Parques e Jardins do Funchal – Estudo Fitogeográfico*, pp.615-665. Esfera do Caos Editores Lda. Lisboa.

RAVEN, P. H.:

1981. *Oenothera* L. *In*: Tutin, T. G., Burges, N. A., Heywood, V. H., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds.), *Flora Europaea*. **2**. (Rosaceae to Umbelliferae). Reprinted. Cambridge University Press. Pp. 306-308.

ROSTANSKI, K.:

1991. The representatives of the genus Oenothera L. in Portugal. *Boletim da Sociedade Broteriana*, **64**: 5-33.

1992. The *Oenothera* species in the collection of Prof. Dr. A. Hansen in Copenhagen (CO). *Boletim da Sociedade Broteriana*, **2** (65): 91-92.

SÁNCHEZ-PINTO, L., M. L. RODRÍGUEZ, S. RODRÍGUEZ, K. MARTÍN, A. CABRERA & M. C. MARRERO:

2005. Spermatophyta. *In*: Arechavaleta M., Zurita, N., Marrero, M. C. & Martín, J. L. (eds.), *Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres)*. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias, pp. 40-57.

SCHÄFER, H.:

2005. *Flora of the Azores, a field guide*. 2nd enlarged edition. Margraf Publishers. Weikersheim, Germany. 346 pp.

SHORT, M. J.:

1994. *Oenothera* L. *In*: Press, J. R. & Short, M. J. (eds.), *Flora of Madeira*, pp. 235-236. The Natural History Museum. London.

SILVA, L., M. MOURA, H. SCHAEFER, F. RUMSEY & E. F. DIAS:

2010. List of vascular plants (Tracheobionta) *In*: Borges, P. A. V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A. F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R. S., Silva, L., Vieira, P. & Vieira, V. (eds.), *A list of the terrestrial and marine biota from the Azores*. Pp. 117-146, Princípia, Cascais, 432 pp.

TURLAND, N. J.:

1994. Onagraceae. *In*: Press, J. R. & Short, M. J. (eds.), *Flora of Madeira*, pp. 233-237. The Natural History Museum. London.

VIEIRA, R.:

2002. Flora da Madeira. Plantas vasculares naturalizadas no arquipélago da Madeira. *Boletim do Museu Municipal do Funchal (História Natural)*, Supl. no **8**: 5-281.