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Flower-visiting behaviour and habitats of the taxa of the *Andrena wollastoni* group (Hymenoptera, Anthophila, *Micrandrena*) on the Canary Islands compared to the Madeira Archipelago *

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Abstract: In a taxonomical study, the taxa of the *Andrena wollastoni* group (Madeira Archipelago, Canary Islands) were newly revised (KRATOCHWIL 2020). In the frame of the fieldwork for this taxonomical publication, we also enlarged the knowledge of the flower-visiting behaviour and the habitats of these wild-bee taxa on the Canary Islands. They inhabit Gran Canaria, La Gomera, La Palma, and Tenerife. For the Madeira Archipelago, we already published a bee-plant network (KRATOCHWIL et al. 2019).

It was possible to assign 69 bee-flower interactions (from the literature, revised museum material, and a private collection) to the species and the subspecies of the *A. wollastoni* group of the Canary Islands and the closely related *A. lineolata*. Additionally, we found 216 new interactions in the field.

We assigned (in the case of new observations georeferenced) data to vegetation series and vegetation complexes of the Canary Islands, defined by RIVAS-MARTÍNEZ (1987), which reflect the bioclimatic conditions. All taxa of the Canary Islands (*Andrena acuta acuta, A. a. tenoensis, A. a. wildpreti*, *A. catula, A. gomerensis gomerensis, A. g. palmae*, and *A. lineolata*) are (almost) not present in the hot arid-semiarid infracanarian zone (Kleinio neriifoliae-Euphorbio canariensis sigmion). They occur mainly in the thermo-infracanarian zone (semiarid to dry: Mayteno canariensis-Junipero phoeniceae sigmion) and especially in the subhumid thermo-mesocanarian zone (Ixantho viscosae-Lauro azoricae sigmion). Further, the dry mesocanarian zone (Cisto symphytifolii-Pino canariensis sigmion) is colonised especially in Gran Canaria (*A. catula*) and Tenerife (*A. a. wildpreti*). *A. lineolata*, the close relative of the species of the *A. wollastoni* group, is restricted to the dry supracanarian zone in the Teide area from 2000 to about 3000 m a.s.l. (Spartocytiso supranubii sigmion). In the Madeira Archipelago, *A. wollastoni* and *A. dourada* were detected in all vegetation zones.

Regarding the visited plant families, the females of *A. wollastoni* (Madeira Island) and *A. catula* (Gran Canaria) showed mainly flower visits on Asteraceae. Females of the other taxa of the *A. wollastoni* group (islands: Porto Santo, La Gomera, La Palma, and Tenerife) and *A. lineolata* (Tenerife) prefer Brassicaceae as the main pollen resource. With the exception of *A. wollastoni* (Madeira Island), all the other taxa of the *A. wollastoni* group, including *A. lineolata* (Tenerife), are no supergeneralists. Remarkable is the high number of interactions between the endemic plant species *Descurainia lemsii* (Tenerife) and the females of the endemic *A. a. wildpreti* (both restricted to the 'Cordillera Dorsal'), and between *Descurainia bourgaeana* and *A. lineolata* (both endemic species of the Teide area, *A. lineolata* between 2000 and around 3000 m a.s.l.).

The habitats of the taxa of the *A. wollastoni* group on the Canary Islands are mostly characterised by ruderal vegetation (margins of crop fields, road margins, and fallows with often dominant populations of *Hirschfeldia incana*). There are models for the habitats in the natural landscape, e.g., gaps in the laurel forest zone with *Pericallis streetzii* or in disturbance zones of barrancos. *A. a. wildpreti* and especially *A. lineolata* are almost restricted to natural habitats (for the former, rocky slopes in the *Pinus canariensis* vegetation complex but also secondary habitats on road edges, and for the latter, the subalpine vegetation complex). For the supergeneralist *A. wollastoni* (Madeira Island), there are no preferences in habitat selection; for *A. dourada* (Porto Santo), there are not enough data yet.

Key words: Andrenidae, Canary Islands, endemism, euryanthy, flower visitor, habitat preferences, Hymenoptera, Madeira Archipelago, vegetation series, vegetation complexes.

Introduction

The Madeira Archipelago and the Canary Islands are well-known examples of oceanic islands with staggered ages as well as different competitive conditions concerning species numbers. They show many examples of radiations in plant and animal taxa (e.g., KIM et al. 2008) and interactions between plant species and flower-visiting animal species (e.g., DELGADO 2000, VALIDO et al. 2004, VALIDO & OLESON 2010, RODRÍGUEZ-RODRÍGUEZ et al. 2013). This is also true for a neglected group of small wild-bee species (6.5-8 mm) of the *Andrena wollastoni* group (Anthophila, *Micrandrena*), which has been newly revised (KRATOCHWIL 2020). For the Madeira Archipelago, we already published a bee-plant network, considering also the species of the *A. wollastoni* group. In connection with taxonomical studies of the group and of related taxa (KRATOCHWIL 2020), we studied the flower-visiting behaviour and the habitat requirements for the taxa of the *A. wollastoni* group, and assigned the individual species to defined flower resources and vegetation series, reflecting bioclimatically characterised habitat types. Especially for the *A. wollastoni* taxa of the Canary Islands (they inhabit Gran Canaria, La Gomera, La Palma, and Tenerife), there was little knowledge about the habitats used by these taxa. The study by HOHMANN et al. (1993) with many data of the first author and the second author, Francisco La Roche, was an important basis for distribution data, and also gave some information about the flower visits. Regarding the whole data set, we will ask the following questions:

a. Are the considered wild-bee species restricted to specific thermoclimatic conditions and to specific habitats?
b. Which plant species have great importance as pollen and nectar resources for the taxa of the *A. wollastoni* group, and to which plant families do these plant species belong?
c. Are there models for bee-plant interactions in habitats without or with weak anthropogenic impact?

Material, methods, abbreviations, nomenclature

Most of the flower-visiting data of the Canary Islands are own data (n = 216); additionally, there are valuable data from HOHMANN et al. (1993), from revised museum material, and from the private collection of H. R. Schwenninger (Stuttgart, Germany) (in total, n = 69). Many new observation data for the Teide region from 2000 to more than 3000 m a.s.l. were available for the related taxon *A. lineolata*. These specimens of the Teide region were only observed but not collected, and there was no differentiation between females and males (LARA-ROMERO et al. 2019). The checked collections from museums (KRATOCHWIL 2020) gave more information about the distribution but only exceptionally about flower visits. The specimen-based data (in the case of new data, all georeferenced) were reported in KRATOCHWIL (2020).

The assignment of flower-visiting data to vegetation series and vegetation complexes followed the maps in RIVAS-MARTÍNEZ (1987). The vegetation series reflect the thermoclimatic conditions as well as the aridity/humidity, as shown by the defined vegetation complexes. For the Canary Islands, the following complexes can be distinguished:

I infracanarian zone: arid to semiarid (Kleinio neriifoliae-Euphorbio canariensis sigmion)
II thermocanarian zone
IIA thermo-infracanarian zone: semiarid to dry (Mayteno canariensis-Junipero phoeniceae sigmion)
IIB thermo-mesocanarian zone: subhumid (Ixantho viscosae-Lauro azoricae sigmion)
III mesocanarian zone: dry (Cisto symphytifolii-Pino canariensis sigmion)
IV supracanarian zone: dry (Spartocytiso supranubii sigmion).

All data concerning the ages of the islands refer to SCHMINCKE (1998), GALOPIM DE CARVALHO & BRANDÃO (1991), and GELDMACHER et al. (2000) for the Madeira Archipelago, and to FERNÁNDEZ-PALACIOS et al. (2011) and CARRACEDO (2011) for the Canary Islands.

Abbreviations: Mc = Macaronesia, M = Madeira Archipelago, MI = Madeira Island, PS = Porto Santo, C = Canary Islands, GC = Gran Canaria, G = La Gomera, P = La Palma, T = Tenerife, End = endemic, N = native, N? = native (doubtful), I = introduced.

Nomenclature: The included wild-bee taxa are *Andrena acuta acuta* WARNCKE, 1968 (Tenerife, Anaga region); *A. a. tenoensis* KRATOCHWIL, 2020 (Tenerife, Teno region); *A. a. wildpreti* KRATOCHWIL, 2020 (Tenerife, Dorsal Rift region); *A. dourada* KRATOCHWIL & SCHEUCHL, 2013 (Porto Santo); *A. catula* WARNCKE, 1968 (Gran Canaria); *A. gomerensis gomerensis* WARNCKE, 1993 (La Gomera); *A. g. palmae* KRATOCHWIL, 2020 (La Palma); and *A. wollastoni* WARNCKE, 1968 (Madeira Island). The taxonomically related *A. lineolata* WARNCKE, 1968 (Teide area, Tenerife) was also included in the analysis. Names of plant species and information about the status of the taxa follow the EURO+MED PLANTBASE (2006); the taxa of the Madeira Archipelago refer to the information in KRATOCHWIL et al. (2019). We use for ravines on the Canary Islands the term 'barranco'.

Previous results about the flower-visiting behaviour of *Andrena dourada* and *A. wollastoni* in the Madeira Archipelago

In two network publications, we have already studied the flower-visiting behaviour of *A. dourada* (Porto Santo, age 14.3 Ma, eight established wild-bee species) and *A. wollastoni* (Madeira Island, age 5.2 Ma., twelve established wild-bee species); KRATOCHWIL & SCHWABE (2018a) and KRATOCHWIL et al. (2019); for the vegetation series and complexes, see CAPELO (2004). There were no detections of individuals of the *A. wollastoni* group on the Desertas Islands until now (KRATOCHWIL et al. 2018). The flower-visiting data of the Madeira Archipelago were based on a database of collected or observed specimens of Hymenoptera Anthophila compiled by A. F. Aguiar, A. Kratochwil, A. Schwabe, and J.

Smit. We also included some data from the collections of the Laboratório Agrícola da Madeira, Camacha (ICLAM) (Kratochwil et al. 2019).

a) Porto Santo: *Andrena dourada*

Andrena dourada (photo: Fig. 2a in Kratochwil & Schwabe 2018a) was detected in the two thermozones that are present in Porto Santo (xeric/infra-Mediterranean zone and the only small subhumid zone). There are only low numbers of observed flower visits until now (n = 14), as follows. Asteraceae: *Calendula arvensis,* N (1♀), and *Leontodon taraxacoides* subsp. *longirostris,* N (2♀♀, 1♂). Brassicaceae: *Crambe fruticosa,* EndM (6♀♀); *Rapistrum rugosum* s.l., N (1♀); *Sinapis arvensis,* N (1♀). Frankeniaceae: *Frankenia laevis,* N (2♀♀).

Porto Santo is highly degraded especially by former anthropogenic impact. Due to the cessation of farming, even ruderal plant communities exist only as fragments. Some edge structures are present (road margins and margins of settlements) with ruderal plant species, offering pollen and nectar (*Rapistrum rugosum, Sinapis arvensis, Calendula arvensis, Leontodon taraxacoides*). Natural rocky habitats (*Crambe fruticosa*) and rocky/sandy habitats with partly episodic saltspray influence (*Frankenia laevis*) are also important. We suppose that *A. dourada* is currently endangered because it is restricted to small patches with probably low population sizes (Kratochwil & Schwabe 2018a).

b) Madeira Island: *Andrena wollastoni*

Compared to the eleven other wild-bee species, *Andrena wollastoni* is probably the species with the largest distribution area on Madeira Island. The species occurs in all thermozones (infra-/thermo-Mediterranean to meso-Mediterranean/temperate) from sea level to the highest mountains of the island (1750 m a.s.l.). An extremely dry thermozone, comparable to the arid-semiarid infracanarian zone, is not present. From more than 100 interactions of *A. wollastoni* (74♀♀, 43♂♂; Kratochwil et al. 2019 and the database of the Madeira Archipelago, compiled by A. F. Aguiar, A. Kratochwil, A. Schwabe, and J. Smit), females showed a preference for yellow- and white-flowering Asteraceae (35 interactions), and, to a lesser extent, Brassicaceae (n = 14). Half of the males visited yellow- and white-flowering Asteraceae as well. Species of all other plant families reached only five or fewer interactions per plant species. *Crepis vesicaria* subsp. *haenseleri* (N) was mostly visited by females (n = 11), followed by *Argyranthemum pinnatifidum* s.l. (EndM; n = 7); the males visited mostly *A. pinnatifidum* (n = 10).

Twelve different plant families were visited by males and females. *A. wollastoni* can be regarded as euryanthic. Regarding all wild-bee species and their interactions on Madeira Island (n = 637), Asteraceae (51%) and Brassicaceae (14%) were the most frequently visited plant families. The taxonomic revision and comparisons of all species of the *A. wollastoni* group (Kratochwil 2020) showed that compared to the other taxa of the group, *A. wollastoni* holds the top position concerning the length of the wings of the females.

Results

a) Gran Canaria: *Andrena catula*

Gran Canaria has an age of 14.6 Ma and 66 established wild-bee species (KRATOCHWIL & SCHWABE 2018b). With a few exceptions, nearly all specimens of *A. a. catula* from the museum collections, those summarised by HOHMANN et al. (1993), and all individuals we observed and collected in the field occurred mainly in the thermo- to mesocanarian zones. We detected most individuals especially in the subhumid vegetation complex (IIB) in the north of the island (Ixantho viscosae-Lauro azoricae sigmion and the substitution communities). Together with the museum material, more than 50 individuals/specimens were found there. In addition, there are occurrences in the thermo-infracanarian (semiarid to dry) zone (IIA), the Mayteno canariensis-Junipero phoeniceae sigmion, especially in the upper parts of southern and western barrancos. The species also occurs in the mesocanarian zone (III), Cisto symphytifolii-Pino canariensis sigmion (dry), such as open places near *Pinus canariensis* stands. The main habitat types are open sites with crops (Fig. 1a), fallows, fields, and road margins, margins of settlements, or edge structures of barrancos.

We carefully checked all the zones of the island and screened thousands of flowers. Locally, there were higher population sizes, especially in Zone IIB (in the northern valleys near and above Teror and Santa Brígida, and in the south near San Bartolomé de Tirajana). *A. catula* is, also considering the whole data set, not very common. The main flight time is March and early April; according to HOHMANN et al. (1993) and our data, *A. catula* reaches mainly altitudes between 300 to 1200 m a.s.l.

Ruderal plant species play an important role as pollen and nectar resources, especially Asteraceae with yellow or orange flowers and Brassicaceae with yellow flowers.

The analysis of flower visits (44♀♀, 21♂♂) is based on our own data (n = 49), specimens of the Upper Austrian State Museum Linz, Austria (n = 4; see KRATOCHWIL 2020), and those of HOHMANN et al. (1993) (n = 12, partly only genus level of plants):

Females: Asteraceae (n = 18): *Calendula* spec. (n = 1); *C. arvensis*, N (n = 11); *C. officinalis*, I (n = 1); *Carduus* spec. (n = 1); *Sonchus bourgeaui*, N (n = 4). Boraginaceae (n = 4): *Echium decaisnei,* EndC (n = 1); *E. plantagineum*, N (n = 3). Brassicaceae (n = 15): *Descurainia* spec. (n = 1); *Hirschfeldia incana*, N? (n = 14). Euphorbiaceae (n = 5): *Euphorbia regis-jubae*, N (n = 5). Geraniaceae (n = 2): *Erodium chium*, N (n = 1); *Erodium moschatum*, N (n = 1).

Males: Asteraceae (n = 10): *Calendula arvensis,* N (n = 9); *Sonchus bourgeaui*, N (n = 1). Brassicaceae (n = 10): *Erysimum* spec. (n = 2); *Hirschfeldia incana*, N? (n = 8). Fabaceae (n = 1): *Cytisus proliferus*, EndC (n =1).

b) La Gomera: *Andrena gomerensis gomerensis*

La Gomera has an age of 9.4 Ma and 37 established wild-bee species (KRATOCHWIL & SCHWABE 2018b). *A. g. gomerensis* frequently occurs in high individual numbers in the thermocanarian zone (II): in the dry thermo-infracanarian zone (IIA), and in the subhumid thermo-mesocanarian zone (IIB).

The foraging habitats are open places in ruderal landscapes (Fig. 1b), fallows, road margins, edges of rocks, and gaps in the Laurisilva area. The visited plant species

(*Pericallis steetzii,* EndG) are partly restricted to places with higher humidity. The yellow-flowering *Hirschfeldia incana* is the most important pollen resource for the females. The main flight period is March and April, and the main altitudes are between sea level (mainly the northern coast) and 1200 m a.s.l.

The analysis of flower visits (36♀♀, 4♂♂) is based on our own data (n = 28) and data from HOHMANN et al. (1993) (n = 13):

Females: Asteraceae (n = 1): *Pericallis steetzii*, EndG (n = 1). Boraginaceae (n = 3): *Echium plantagineum,* N (n = 2), and *Echium strictum*, EndC (n = 1). Brassicaceae (n = 31): *Descurainia millefolia*, EndC (n =1); *Hirschfeldia incana*, N? (n = 29); *Sinapis* cf. *alba* (n = 1). Hypericaceae (n = 1): *Hypericum inodorum*, cultivar (n = 1).

Males: Asteraceae (n = 3): *Calendula arvensis*, N (n = 2); *Pericallis steetzii*, EndG (n = 1). Brassicaceae (n = 1): *Descurainia millefolia*, EndC (n =1).

c) La Palma: *Andrena gomerensis palmae*

La Palma has an age of 1.72 Ma and 33 established wild-bee species (KRATOCHWIL & SCHWABE 2018b). The occurrences of *A. g. palmae* are concentrated in the thermocanarian zone (II): the thermo-infracanarian zone (IIA) (Mayteno canariensis-Junipero phoeniceae sigmion; semiarid to dry), and the subhumid zone (IIB) (Ixantho viscosae-Lauro azoricae sigmion). In the mesocanarian zone (III) (Cisto symphytifolii-Pino canariensis sigmion), there were mainly detections in the transition from Zone IIB. One spectacular observation was made by F. La Roche, between 2050 and 2150 m a.s.l., with a flower visit of *Descurainia gilva* (HOHMANN et al. 1993). This endemic plant species is typical for the open upper pine forests (Zone III) and the transition zone to the supracanarian zone (IV). It is not clear whether *A. g. palmae* occurs in the supracanarian zone (IV). *D. gilva* is present up to 2300 m a.s.l.

There were no detections south of a line from Puerto Naos to Malpaises; these are the southern parts of La Palma, where the largest areas of the arid-semiarid Zone I are present.

The main habitats in Zones IIA and B are open places with ruderal vegetation and edge structures. The yellow-flowering *Hirschfeldia incana* and *Sinapis arvensis*, as well as the orange-flowering *Calendula arvensis*, are the most important pollen resources for the females. The main flight time is March to May, and the main altitudes reach from 400 to 900 m a.s.l. As an exception, one observation was made about 2100 m a.s.l. (see above).

The analysis of flower visits (34♀♀, 1♂) is based on our own data (n = 30), data from H. R. Schwenninger (n = 3, unpubl.), and data from HOHMANN et al. (1993) (n = 2):

Females: Asteraceae (n = 9): *Calendula arvensis*, N (n = 9). Boraginaceae (n = 2): *Echium plantagineum*, N (n = 2). Brassicaceae (n = 22): *Hirschfeldia incana*, N? (n = 9); *Sinapis alba*, N? (n = 2); *Sinapis arvensis*, N? (n = 10); and *Descurainia gilva*, EndP (n = 1). Geraniaceae (n = 1): *Geranium* spec. (n = 1).

Males: Euphorbiaceae (n = 1): *Euphorbia lamarckii*, EndC (n = 1).

d) Tenerife: *Andrena acuta*

Tenerife has an age between 6 and 11.5 Ma (Anaga 6 Ma, Teno 8 Ma, and Adeje 11.5 Ma; ages of special geological structures: Dorsal Rift 3.5-0.2 Ma, Las Cañadas 0.9 Ma; ANCOCHEA et al. 1990) and 66 established bee species (KRATOCHWIL & SCHWABE 2018b).

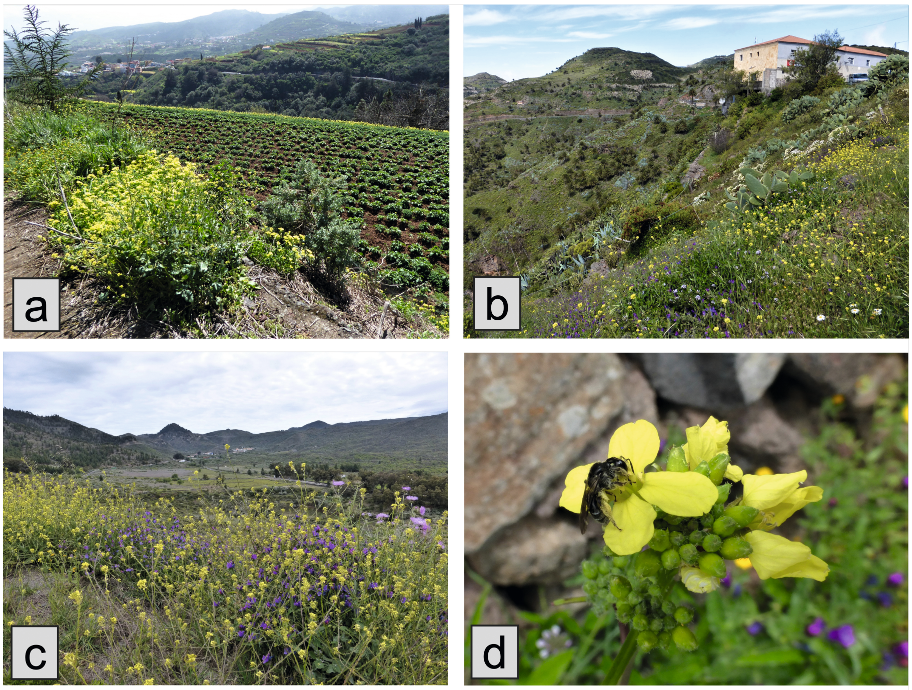

Fig. 1: (**a**) Typical crop-field margin with *Hirschfeldia incana* and *Calendula arvensis*, both frequently visited by *Andrena catula* (northern part of Gran Canaria, Zone IIb, 12th March 2018); photo: A. Schwabe. (**b**) Slope with ruderal vegetation (*H. incana*, frequently visited by *A. g. gomerensis*; additionally, *Echium plantagineum* and *Psoralea bituminosa* can be seen) with a grazed vegetation complex in the background (La Gomera, Zone IIb, 24th April 2016); photo: A. Schwabe. **c:** Road margin in the Teno area, with *H. incana* (frequently visited by *A. a. tenoensis*; additionally, *E. plantagineum* and *Galactites tomentosus*) (Tenerife, Zone IIA, 21st April 2016); photo: A. Schwabe. (**d**) *A. a. tenoensis* (female), collecting pollen on *H. incana* (margin of a small trail in the Teno area) (Tenerife, Zone IIA, 21st April 2016); photo: A. Schwabe.

In the following, we will introduce the results for the three newly described subspecies.

Andrena acuta acuta

This subspecies occurs in the Anaga region, in the area of the formerly separated Anaga Island. *A. a. acuta* was detected in the subhumid vegetation complex Ixantho viscosae-Lauro azoricae sigmion (IIB) and in the barrancos on the northeastern slope of the Anaga mountains, as well as on the northwestern slope (IIA: Mayteno canariensis-Junipero phoeniceae sigmion). According to the data, the main period of activity is March and April, and the main altitudes reach from about 100 to 900 m a.s.l. Actually, the area in the laurel forest zone has only a few occurrences of pollen and nectar resources for *A. a. acuta*. The classical site, e.g., of the holotype and one of the paratypes (Cruz del Carmen), has been modified by soil sealing and building of touristic infrastructures.

The analysis of flower visits (10♀♀, 3♂♂) is based on data from Hohmann et al. (1993) (n = 9) and our own data (n = 4):

Females: Asteraceae (n = 2): *Calendula arvensis*, N (n = 1); *Calendula* spec. (n = 1). Boraginaceae (n = 1): *Echium plantagineum*, N (n =1). Brassicaceae (n = 6): *Hirschfeldia incana*, N? (n = 6). Fabaceae (n = 1): *Spartium junceum*, I, after MUER et al. (2016) (n = 1).

Males: Asteraceae (n = 1): *Calendula arvensis*, N (n = 1). Brassicaceae (n = 1): *Descurainia millefolia*, EndC (n = 1). Fabaceae (n = 1): *Spartium junceum*, I, after MUER et al. (2016) (n = 1).

Andrena acuta tenoensis

This newly described subspecies (KRATOCHWIL 2020) occurs in the formerly separated Teno Island. We observed individuals mainly north and west of Santiago del Teide and in the surroundings of Erjos; other data were gathered from specimens of different collections after determination of the subspecies status (KRATOCHWIL 2020). *A. a. tenoensis* occurs in the thermocanarian zone (II). Most of the detections were made in Zone IIa: thermo-infracanarian, semiarid to dry (Mayteno canariensis-Junipero phoeniceae sigmion). Some are situated in Zone B (thermo-mesocanarian: subhumid Ixantho viscosae-Lauro azoricae sigmion).

The foraging habitats are open places, especially edge structures and fallows with ruderal plant species (Fig. 1c). Pollen and nectar resources are especially yellow-flowering Brassicaceae, mainly *Hirschfeldia incana* (Fig. 1d). The main altitude range is 100-1000 m a.s.l., and the flight time is mainly from March to May.

The analysis of flower visits (26♀♀, 2♂♂) is based on our own data (n = 25) and data from HOHMANN et al. (1993) (n = 3):

Females: Asteraceae (n = 3): *Andryala pinnatifida*, N (n = 1); *Calendula arvensis*, N (n = 2). Brassicaceae: (n = 23): *Hirschfeldia incana*, N? (n = 22); *Sinapis alba*, N? (n = 1).

Males: Asteraceae (n = 2): *Andryala pinnatifida*, N (n = 1); *Reichardia* spec. (n = 1).

Andrena acuta wildpreti

This newly described subspecies (KRATOCHWIL 2020) has an extraordinary distribution. It occurs in the Dorsal Rift zone ('Cordillera Dorsal') between 1000 and nearly 2000 m a.s.l., including the northwestern slope (e.g., Aguamansa, 1000 m a.s.l., no flower visits), and the upper southeastern slope about 1500 m a.s.l. (no flower visits) (KRATOCHWIL 2020). The occurrences are linked to the mesocanarian zone: Cisto symphytifolii-Pino canariensis sigmion (Type III). *A. a. wildpreti* can mainly be found on sites with rocky substrates or on margins or gaps of the pine forest. The main pollen and nectar resource is *Descurainia lemsii* (20 observations of females, additionally one from HOHMANN et al. 1993), a Tenerife endemic plant species, restricted to the 'Cordillera Dorsal' (Fig. 2a, b). All observations of interactions between *A. a. wildpreti* (Fig. 2c) and *D. lemsii* were made between 1900 and nearly 2000 m a.s.l. on rocky substrates. According to D. & Z. BRAMWELL (1990), *D. lemsii* occurs in the upper pine forest area, north of Pico Teide, between 1600 and 2000 m. It is a 'Cordillera Dorsal' species similar to *Sideritis oroteneriffae* (D. & Z. BRAMWELL 1990). *Hirschfeldia incana* is a pollen and nectar resource, especially in lower altitudes, mainly of the Esperanza Forest (1000-1200 m a.s.l.). The observed flight period of *A. a. wildpreti* is mainly April and May.

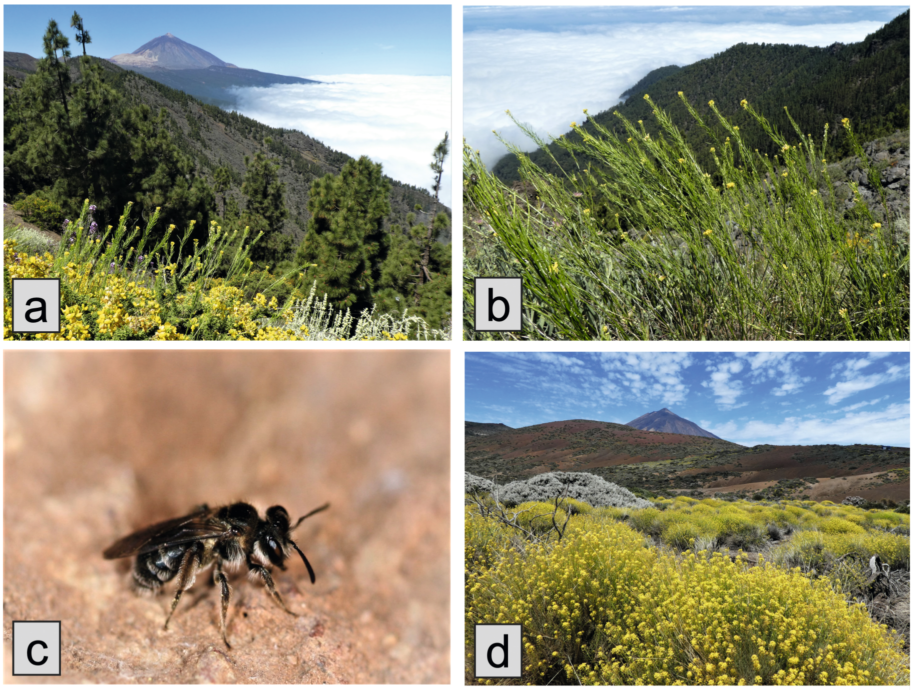

Fig. 2: (**a**) Habitat of the 'Cordillera Dorsal' species *Descurainia lemsii*, which is frequently visited by *A. a. wildpreti* (upper pine forest complex with rocky slopes, Zone III). Bottom right (not visited by *A. a. wildpreti*): *Sideritis oroteneriffae* ('Cordillera Dorsal' species); foreground: *Adenocarpus viscosus* (Tenerife, Montaña Ayosa; 22nd May 2019); photo: A. Schwabe. (**b**) Close-up of flowering and fruiting *D. lemsii* on a margin of rocky slopes in the *Pinus canariensis* forest complex (Tenerife, Montaña Ayosa; 26th May 2019); photo: A. Schwabe. (**c**) *A. a. wildpreti* (female, body length 7.7 mm); site and date of Fig. 2b; photo: A. Kratochwil. (**d**) Habitat of *A. lineolata*, visiting mainly *D. bourgaeana* (foreground) and *Cytisus supranubius* (white, background) (Tenerife, below Izaña, Teide area; Zone IV; 21st May 2019); photo: A. Schwabe.

The analysis of flower visits (30♀♀, 8♂♂) is based on our own data (n = 37) and one interaction from HOHMANN et al. (1993). *A. a. wildpreti* seems to be oligolectic on Brassicaceae. We carefully screened flowers of other families in the distribution area but did not detect any flower visit by *A. a. wildpreti.*

Females: Brassicaceae (n = 30): *Descurainia lemsii*, EndT (n = 21); *Hirschfeldia incana*, N? (n = 9).

Males: Brassicaceae (n = 8): *Descurainia lemsii*, EndT (n = 6); *Hirschfeldia incana*, N? (n = 2).

e) Tenerife: Related species *Andrena lineolata* WARNCKE, 1968

This remarkable species was already recognised by WARNCKE (1968) as a species on its own and separated from *A. wollastoni*. The habitat is restricted to the Teide region from about 2000 to 3300 m a.s.l. in Tenerife (Fig. 2d). The vegetation in the habitat of this wild-bee species is characterised mainly by *Descurainia bourgaeana* and *Cystisus supranubius* (Descurainio-Spartocytisetum supranubii Brullo et De Marco 2008; see Table 2 in BRULLO et al. 2008). It is restricted to the supracanarian Zone IV (Spartocytiso supranubii sigmion).

Two specimens from the northern Tenerife region (one male from Las Mercedes, March 1952, and one female from La Laguna, May 1928, each without altitude; see HOHMANN et al. 1993) are difficult to interpret (wrong determination?). One observation of a male, visiting *Retama raetam* in the Izaña area, 2200 m a.s.l. (HOHMANN et al. 1993), must be a wrong labelling, because *R. raetam* s.l. (now the endemic taxon *R. rhodorhizoides* for the Canary Islands) is a species of lower altitudes, occurring in the Echio aculeati-Retametum rhodorhizoidis (see RIVAS-MARTÍNEZ et al. 1993).

The main flight time of *A. lineolata* is May to July, but males are sometimes detected earlier and may also fly in a wider range. For this species, Brassicaceae play a remarkable role, especially the endemic *Descurainia bourgaeana* (yellow) and, with lower importance, *Erysimum scoparium* (white to pink colour change; OLLERTON et al. 2007), but there were also detections on Fabaceae (*Cytisus supranubius*: white to light pink). The habitat is extreme: open places with mainly *D. bourgaeana,* which are dry, stormy, and exposed to extreme temperature amplitudes. *A. lineolata* is the most specific endemic wild-bee species for the Spartocytiso supranubii sigmion in Tenerife. In addition, *Hylaeus canariensis* ERLANDSSON, 1983, is characteristic of this habitat (about 300 observations were made by LARA-ROMERO et al. 2019 between 2400 and 3300 m a.s.l.), but the species also occurs in the Dorsal Rift zone (DATHE 1993) (we detected one male of *H. canariensis* in the Dorsal Rift zone, La Crucita, 1990 m a.s.l., 21.05.2019, leg. A. Kratochwil, on *D. lemsii*). There are only two detections of *H. canariensis* in lower altitudes (1♂, Mercedes, Mirador Janina, 792 m a.s.l., 24.05.2019, leg. A. Kratochwil on *Hirschfeldia incana*; 1♀, Los Rodeos 600 m a.s.l., 18.07.1962, leg. J. M. Fernández, in DATHE 1993). Remarkable is that both wild-bee species are relatively small in body size (*A. lineolata*: 6.8 mm, *H. canariensis*: 3-3.5 mm). According to a study by LARA-ROMERA (2019) on the elevational gradient in the Teide area, the mean body sizes of pollinators should increase with elevation, and pollinators should be more generalists. In the context of the *A. wollastoni* group and *A. lineolata* on Tenerife, this is not the case: *A. a. acuta, A. a. tenoensis*, and *A. a. wildpreti* are significantly larger (7.3-7.7 mm) than *A. lineolata*. (KRATOCHWIL 2020).

According to HOHMANN et al. (1993) and our results, *D. bourgaeana* is a key species for the flower-visitor network of the Cañadas and, according to LARA-ROMERO et al. (2019), also for an elevational gradient up to 3300 m a.s.l. (Refugio de Altavista). Seventeen different wild-bee species have been recorded as flower visitors until now (HOHMANN et al. 1993, LARA-ROMERO et al. 2019, and our data). Between 2400 and 3300 m a.s.l., there were observations of *Hylaeus canariensis* ERLANDSSON, 1983 (n > 100); about 50 individuals of *Lasioglossum morio cordiale* (PÉREZ, 1907) sensu EBMER (1976, 1988) (= L. *collopiense* [PÉREZ, 1907] sensu PAULY [2016]), and a few individuals each of *L. a. arctifrons* (SAUNDERS, 1903), *Andrena c. chalcogastra* (BRULLÉ, 1938), and *Colletes d. dimidiatus* (BRULLÉ, 1939)*,* visiting *D. bourgaeana* (observation data of LARA-ROMERO et al. 2019).

The publication of DUPONT et al. (2003) with the aim of studying the plant-flower-visitor network of the subalpine desert of Tenerife (one study area, 1 km SSW of Paradores, 2050 m a.s.l.) does not cover stands of *D. bourgaeana* but *Cytisus supranubius. A. lineolata* was not present.

The analysis of flower visits (32♀♀, 33♂♂) is based on our own data (n = 43) and HOHMANN et al. (1993) (n = 22):

Females: Brassicaceae (n = 29): *Descurainia bourgaeana*, EndT (n = 29). Fabaceae (n = 3): *Cytisus supranubius*, EndC (n = 3).

Males: Brassicaceae (n = 27): *Descurainia bourgaeana*, EndT (n = 26); *Erysimum scoparium*, End C (n = 1). Fabaceae (n = 6): *Cytisus supranubius*, EndC (n = 6).

Additionally, there are observations of LARA-ROMERO et al. (2019), without separation of males and females. On an elevational gradient of the Teide area (2350 m to 3200 m a.s.l.) they observed *A. lineolata* on *D. bourgaeana* EndT (n = 39); *Cytisus supranubius*, EndC (n = 59); *Erysimum scoparium*, EndC (n = 11); *Echium auberianum*, EndT (n = 4).

Comparison of the taxa and discussion

We will follow the questions of the introduction section.

a) Are the considered wild-bee species restricted to specific thermoclimatic conditions and to specific habitats?

Comparing all the taxa of the *A. wollastoni* group on the Canary Islands, it is remarkable that they do not live in the extremely dry and xeric habitats of the lowlands of the Canary Islands (Kleinio neriifoliae-Euphorbio canariensis sigmion, Zone I) but more in the thermozones with more humidity or in the higher mesocanarian zone (Fig. 3). There were only a very few exceptions detected in Zone I, mainly older data from museums (KRATOCHWIL 2020) without information about habitats; possibly they were found in more humid special sites. The avoidance of extremely hot and arid habitats may also be the reason why there were no successful colonisations of the islands Fuerteventura, Lanzarote, and La Graciosa, with almost exclusively Zone I. In the Madeira Archipelago, the climatic conditions are generally not so extreme. On Madeira Island, *A. wollastoni* was detected in all vegetation zones (this is also true for *A. dourada* in Porto Santo) (KRATOCHWIL & SCHEUCHL 2013, KRATOCHWIL & SCHWABE 2018a, KRATOCHWIL et al. 2019). Both islands do not have such extreme climatic conditions comparable to the infracanarian zone. *A. wollastoni* is the most successful species of the *A. wollastoni* group in colonising a large spectrum of areas on Madeira Island and habitats. With 7.6 mm in females, it is one of the largest species of the group (together with *A. a. tenoensis* and *A. a. wildpreti*), but the females have also the largest wing length of all species (KRATOCHWIL 2020), and is therefore probably a successful coloniser.

b) Which plant species have great importance as pollen and nectar sources for the taxa of the A. *wollastoni* group, and to which plant families do these plant species belong?

Regarding the visited plant families (Table 1), females of *A. wollastoni* (MI) showed mainly flower visits of Asteraceae; the same is true for *A. catula* (GC). For all the other taxa and islands (PS, G, P, T), and for *A. lineolata* (T), Brassicaceae species are the main pollen resources for the females. Regarding all the Canary Islands, Asteraceae species represent 15%, and Brassicaceae species only 5% (WELß & LINDACHER 1994); therefore, Brassicaceae have a high proportion of flower visits. For the Madeira Archipelago, Asteraceae represent 11%, and Brassicaceae 5%; therefore, the flower visits of *A. wollastoni* represent this proportion.

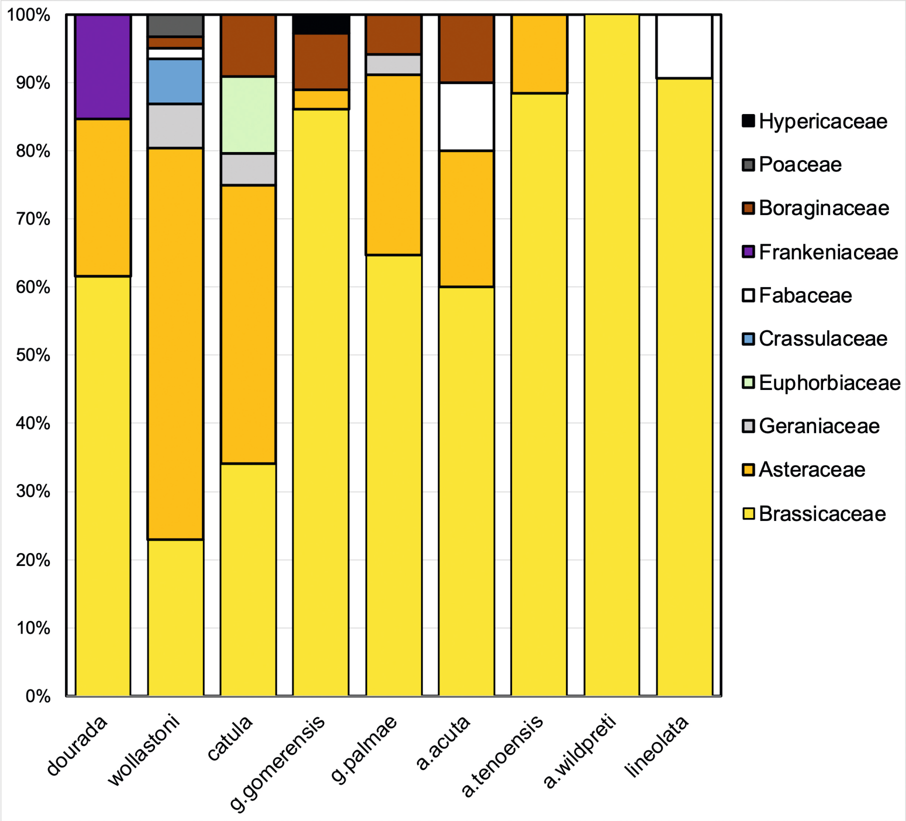

Fig. 3: Plant family preferences of the taxa of the *A. wollastoni* group and *A. lineolata* in the Madeira Archipelago and the Canary Islands (only flower-visiting interactions by females are shown); for specific numbers of interactions, see text.

All the taxa of the *A. wollastoni* group on the Canary Islands are no supergeneralists in the sense of Valido & Oleson (2010), compared to, e.g., *Anthophora a. alluaudi* with visits of 18 plant families (Canary Islands: Gran Canaria and Tenerife) or *Lasioglossum loetum* with visits of 30 plant families (Canary Islands) (Hohmann et al. 1993 and our own data). On Madeira Island, *A. wollastoni* (males and females) visits (according to the actual knowledge) taxa of 11 different plant families, and can be classified as the supergeneralist of this island (*Amegilla quadrifasciata maderae* visits nine, and *Lasioglossum wollastoni* eight different plant families; Kratochwil et al. 2019).

On the Canary Islands, *Hirschfeldia incana* (Brassicaceae) is the most important plant species for the taxa of the *A. wollastoni* group, with the exception of *A. a. wildpreti* (see below). *H. incana* is a generalistic plant species concerning flower visitors, with visits from

46 different wild-bee taxa, which is nearly the top position (Hohmann et al. 1993 and our own data). The top position, with 68 wild-bee species, is held by the native *Launaea arborescens*, Asteraceae, with main occurrences in the arid-semiarid Zone I. It is doubtful whether *H. incana* is a native species (Euro+Med Plantbase 2006). The plant species that also has great importance for wild-bee species is *Calendula arvensis*, which is classified as native by the Euro+Med Plantbase (2006). Ruderal habitats are frequently characterised by *H. incana* and *C. arvensis*, especially in the zones with more humidity. Ruderal habitats are well presented in Zones II-III in GC, G, P, and T, with the exception of nearby Laurisilva areas, core areas of cities, and areas with huge hotel complexes or other buildings with ground sealing. Roadsides and edges of crop fields or settlements are important habitats, where the individuals of the wild-bee species group occur (Fig. 1a-d). In the study by Arévalo et al. (2005) about roadside vegetation in GC and T, *C. arvensis* and *H. incana* belong to the most frequent species on both islands. Arévalo et al. (2005) classified them as alien plants but not as ‘transformer species’ among the aliens.

Table 1: Assignment of *Andrena catula, A. gomerensis, A. acuta*, and *A. lineolata* to different vegetation series of the Canary Islands (Rivas-Martínez 1987, see section ‘Material and Methods’). In the Madeira Archipelago, *A. wollastoni* (Madeira Island) and *A. dourada* (Porto Santo) are distributed in all vegetation series.

		catula	*g. gomerensis*	*g. palmae*	*a.acuta*	*a.tenoensis*	*a. wildpreti*	*lineolata*
		GC	G	P	T	T	T	T
I	infracanarian	–	–	–	–	–	○○	○○
IIA	thermo-infracanarian	x	x	x	x	x	○○	○○
IIB	thermo-mesocanarian	x	x	x	x	x	○○	○○
	transition	x		x				
III	mesocanarian	x	○○	x	○○	○○	x	○○
	transition			x			x	
IV	supracanarian	○○	○○	?	○○	○○	○○	x

–	bee taxon not present (exceptions partly occur)
x	bee taxon present in this zone
○○	zone is not present on the specific island or in the distribution area of the taxon
?	no data

Remarkable is the high number of interactions between *Descurainia lemsii* and *A. a. wildpreti. D. lemsii* is one of the seven endemic *Descurainia* species of the Canary Islands. All these species are woody perennials, have relatively large flowers compared to other species of the genus, and are self-incompatible (GOODSON et al. 2006). Molecular studies have shown that all species derived from a single colonisation event, followed by inter-island colonisations and species diversifications. Probably, shifts occurred from the ancestral habitat of the woody *Descurainia* in the lower zones into the pine forest and into high-altitude zones (GOODSON et al. 2006). A further 'Cordillera Dorsal' plant species is *Sideritis oroteneriffae*, which also developed after a single colonisation event. *Sideritis* subgenus *Marrubiastrum* is characterised by 24 species distributed among the Canarian Islands and the Madeira Archipelago (BARBER et al. 2000).

D. lemsii is an attractor for different wild-bee species. HOHMANN et al. (1993) detected, besides *A. a. wildpreti*, three other species and three interactions (1♂ *Colletes d. dimidiatus,* 1♀ *Lasioglossum loetum*, and 1♀ *Melecta curvispina*); our data show additionally six further interactions (1♀ *Andrena c. chalcogastra*, 1♀ *Colletes d. dimidiatus,* 2♀♀ *Hylaeus ater* [SAUNDERS, 1903], 1♂ *H. canariensis*, and 1♀ *Lasioglossum loetum*). There are also interactions of the honeybee (*Apis mellifera* LINNAEUS, 1758).

As in many other cases, especially in the higher mountains of the Canary Islands, honeybees are frequent visitors and often cause a mutualistic disruption (VALEDO & OLESON 2010). *Hirschfeldia incana* (which is visited by *A. a. wildpreti* and other taxa of the bee group) is frequently visited by honeybees. Melissopalynological studies have shown even unifloral honey with *Hirschfeldia* pollen (LA SERNA RAMOS & GÓMEZ FERRERAS 2011). There is a strong competition with smaller wild-bee species.

D. gilva occurs on La Palma in similar habitats as *D. lemsii* on Tenerife (upper zones of the pine belt and the transition zone to the supracanarian zone). There is also a similarity in morphological features in *D. gilva* compared to *D. lemsii*, which was interpreted as a convergent development by GOODSON et al. (2006). Unfortunately, there is only one interaction known until now: *D. gilva – A. g. palmae* (HOHMANN et al. 1993). It should be studied whether there are regular interactions: *D. gilva* and *A. g. palmae*, corresponding to *D. lemsii* and *A. a. wildpreti. D. gilva* was also visited by three other wild-bee species, with three interactions of females (1♀ *A. chalcogastra palmaensis* WARNCKE, 1968; 1♀ *A. vulcana zumboa* WARNCKE, 1968; and one specimen of *Anthophora a. alluaudi*; HOHMANN et al. 1993). The endemic *D. millefolia*, too, is frequently visited by wild-bee species (twelve species according to HOHMANN et al. 1993).

c) Are there models for bee-plant interactions in habitats without or with weak anthropogenic impact?

The degree of anthropogenic influence is mostly moderate to high in the habitats of the taxa of the *A. wollastoni* group. Therefore, the question arises, where did the bees live before human impact? In the following, we give examples of potential habitats in the natural landscape.

- Madeira Archipelago: For *A. dourada* (PS), we found interactions with *Crambe fruticosa* (EndM) on undisturbed rocky substrates. For *A. wollastoni* (MI), there are data about interactions with *Argyranthemum pinnatifidum* s.l. and subsp. *succulentum*, e.g., on undisturbed cliffs, on rocks, and in weakly disturbed ravines.

- Canary Islands: For Gran Canaria, there are data about interactions of *A. catula* with *Euphorbia regis-jubae* and *Echium decaisnei* in the upper succulent shrub formation (in Zone IIA, thermo-infracanarian: semiarid to dry).

In La Gomera, there were proven interactions of *A. g. gomerensis* with *Pericallis steetzii* (the plant species is restricted to places with higher humidity, e.g., in the Laurisilva forest complex) and for *Descurainia millefolium* and *Echium strictum,* occurring on rocky substrates. In La Palma, *A. g. palmae* visited *Euphorbia lamarckii* in the upper succulent bush (Zone IIA) and *D. gilva* (upper pine forest complex with a transition to the open supracanarian Zone IV).

For Tenerife, there are nearly no data about natural habitats of *A. a. acuta*; only flower visiting of *D. millefolium* (see above) was proved. *A. a. tenoensis* visited *Andryala pinnatifida,* which occurs, e.g., on rocky slopes, in a complex with *Erica scoparia*/*E. arborea* stands. Only in special cases (e.g., wind exposition) may this be a natural habitat.

Regarding the whole *A. wollastoni* group, *A. a. wildpreti* is the taxon with the most detections in (near) natural habitats, especially as flower visitor of *D. lemsii* in the upper pine forest complex and on rocky slopes in this complex. Additionally, *D. lemsii* is also visited in habitats with human impact: roadsides and trail edges in the upper pine forest.

The near relative of the *A. wollastoni* group, *A. lineolata*, exclusively visits natural habitats in the supracanarian zone (IV) and endemic plant species; *D. bourgaeana* is mostly the pollen and nectar resource. It is noticeable that the taxa of higher altitudes, especially *A. a. wildpreti* and *A. lineolata*, are obviously more specialised in flower visiting than the taxa of lower altitudes.

In summary, there are models for habitats for species of the *A. wollastoni* group in the natural landscape of the Canary Islands and the Madeira Archipelago, but in many areas, moderate human impact has enlarged the diversity and quantity of resources for these in body size small *Andrena* taxa.

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Zusammenfassung

In einer taxonomischen Studie wurden die Taxa der *Andrena wollastoni*-Gruppe (Madeira Archipel, Kanarische Inseln) neu bearbeitet (KRATOCHWIL 2020). Im Rahmen von Geländearbeiten für diese taxonomische Publikation auf den Kanarischen Inseln konnten wir auch neue Daten über die Blütenbesuchs-Interaktionen und die Habitate dieser Wildbienen-Taxa gewinnen. Nur die Inseln Gran Canaria, La Gomera, La Palma und Teneriffa werden besiedelt. Für den Madeira Archipel

publizierten wir bereits ein Wildbienen-Pflanzen-Netzwerk (KRATOCHWIL et al. 2018). Für die Kanarischen Inseln konnten 69 Wildbienen-Blüten-Interaktionen aus der Literatur, von revidierten Museumsexemplaren und einer privaten Sammlung den Taxa der *A. wollastoni*-Gruppe zugeordnet werden sowie der nah verwandten *A. lineolata.* Zusätzlich war es möglich, 216 neue Interaktionen im Gelände festzustellen.

Wir ordneten die (im Falle der neuen Fundpunkte geo-referenzierten) Daten den von RIVAS-MARTÍNEZ (1987) für die Kanarischen Inseln beschriebenen Vegetationsserien und -komplexen zu, die die bioklimatischen Verhältnisse widerspiegeln. Alle Taxa der Kanarischen Inseln (*Andrena catula, A. gomerensis gomerensis, A. g. palmae, A. acuta acuta, A. a. tenoensis, A. a. wildpreti* und *A. lineolata*) fehlen weitgehend in der heißen arid-semiariden infracanarischen Zone (Kleinio neriifoliae-Euphorbio canariensis Sigmion). Sie kommen vorwiegend in der thermo-infracanarischen Zone vor (semiarid-trocken: Mayteno canariensis-Junipero phoeniceae Sigmion) und insbesondere in der subhumiden thermo-mesocanarischen Zone (Ixantho viscosae-Lauro azoricae Sigmion). Des Weiteren wird die trockene mesocanarische Zone besiedelt (Cisto symphytifolii-Pino canariensis Sigmion), insbesondere in Gran Canaria (*A. catula*) und Teneriffa (*A. a. wildpreti*). *A. lineolata*, eine nah verwandte Art der *A. wollastoni*-Gruppe, ist beschränkt auf die trockene supracanarische Zone in der Teide Region (2000 bis um 3000 m a.s.l), dem Spartocytiso supranubii Sigmion. Im Madeira Archipel wurden *A. wollastoni* und *A. dourada* in allen Vegetationszonen gefunden.

Betrachtet man die Pflanzenfamilien, besuchten Weibchen von *A. wollastoni* (Madeira Island) und *A. catula* (Gran Canaria) hauptsächlich Pflanzenarten der Asteraceae. Weibchen aller anderen Taxa der *A. wollastoni*-Gruppe der Inseln Porto Santo, La Gomera, La Palma, Teneriffa und auch *A. lineolata* (Teneriffa) besuchten bevorzugt Arten der Brassicaceae. Mit Ausnahme von *A. wollastoni* (Insel Madeira) sind alle anderen Taxa der *A. wollastoni*-Gruppe und auch *A. lineolata* (Teneriffa) keine Super-Generalisten im Blütenbesuch. Bemerkenswert ist die hohe Zahl an Interaktionen zwischen der endemischen Pflanzenart *Descurainia lemsii* und der endemischen Wildbienen-Unterart *A. a. wildpreti* (beide beschränkt auf die „Cordillera Dorsal“, Teneriffa) und zwischen *Descurainia bourgaeana* und *A. lineolata* (beides Endemiten des Teide-Gebietes, *A. lineolata* zwischen 2000 und um 3000 m ü.M.).

Die Habitate der Bienentaxa der *A. wollastoni*-Gruppe auf den Kanaischen Inseln sind zumeist durch ruderale Vegetation gekennzeichnet (Randstreifen von Äckern, Straßenränder, Brachen mit oft dominierender *Hirschfeldia incana*). Es gibt jedoch Modelle für Habitate in der Naturlandschaft, z.B. Lücken in der Lorbeerwald-Zone mit *Pericallis streetzii* oder in Störzonen von Barrancos. *A. a. wildpreti* und insbesondere *A. lineolata* sind weitgehend beschränkt auf natürliche bzw. naturnahe Habitate. Erstere besiedelt felsige Abhänge im *Pinus canariensis*-Vegetationskomplex, aber auch Sekundärhabitate an Straßenrändern, die zweite Art kommt im subalpinen Vegetationskomplex vor. Im Falle des Super-Generalisten *A. wollastoni* (Insel Madeira) konnten keine Präferenzen der Habitatwahl festgestellt werden, für *A. dourada* (Porto Santo) sind die Daten noch defizitär.

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