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Bee-plant networks: structure, dynamics and the metacommunity concept

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Abstract

Wild bees play an important role within pollinator-plant webs. The structure of such networks is influenced by the regional species pool. After special filtering processes an actual pool will be established. According to the results of model studies these processes can be elucidated, especially for dry sandy grassland habitats. After restoration of specific plant communities (which had been developed mainly by inoculation of plant material) in a sandy area which was not or hardly populated by bees before the colonization process of bees proceeded very quickly. Foraging and nesting resources are triggering the bee species composition. Dispersal and genetic bottlenecks seem to play a minor role. Functional aspects (e.g. number of generalists, specialists and cleptoparasites; body-size distributions) of the bee communities show that ecosystem stabilizing factors may be restored rapidly. Higher wild-bee diversity and higher numbers of specialized species were found at drier plots, e.g. communities of Koelerio-Corynephoretea and Festuco-Brometea. Bee-plant webs are highly complex systems and combine elements of nestedness, modularization and gradients. Beside structural complexity bee-plant networks can be characterized as dynamic systems. This is shown by using the metacommunity concept.

Zusammenfassung: Wildbienen-Pflanzenarten-Netzwerke: Struktur, Dynamik und das Metacommunity-Konzept.

Wildbienen spielen eine wichtige Rolle innerhalb von Bestäuber-Pflanzen-Netzwerken. Ihre Struktur wird vom jeweiligen regionalen Artenpool bestimmt. Nach spezifischen Filterprozessen bildet sich ein aktueller Artenpool. Im Rahmen von Modellstudien (schwerpunktmäßig in Sandhabitaten) werden diese Prozesse untersucht. Nach einer Wiederherstellung von Pflanzengesellschaften (im Wesentlichen über Inokulation von Pflanzenmaterial) in einem zunächst weitgehend Wildbienen-freien Gebiet erfolgte die Kolonisation der Wildbienen außerordentlich schnell. Spezifische Nahrungs- und Nestressourcen selektieren die Artenauswahl der Wildbienen-Gemeinschaft. Ausbreitungsbarrieren und „genetische Flaschenhälse“ scheinen eine untergeordnete Rolle zu spielen. Funktionelle Gesichtspunkte (Anzahl Generalisten, Spezialisten, Kleptoparasiten; Körpergrößen-Verteilungen) innerhalb der Wildbienen-Gemeinschaft zeigen, dass ökosystem-stabilisierende Faktoren schnell etabliert werden. Eine höhere Wildbienen-Diversität und Abundanz spezialisierter Bienenarten existiert vorzugsweise an trockeneren Standorten (Gesellschaften der Koelerio-Corynephoretea und Festuco-Brometea). Bienen-Pflanzen-Netzwerke stellen hoch komplexe Systeme dar und verbinden Phänomene der Schachtelung, Modularisierung und Gradientenbildung. Darüber hinaus handelt es sich auch um höchst dynamische Systeme. Dies zeigt sich daran, dass eine Metacommunity-Struktur auch bei Bienen-Pflanzen-Netzwerken signifikant nachzuweisen ist.

1. Introduction

In ecological communities species are embedded in networks of interacting species (INGS et al. 2009). Mutualistic webs include interactions that are beneficial to both partners e.g. in pollinator-plant networks. In most cases the interactions between pollinators and vascular plant species are highly complex; there are diverse “pollination networks”, complex “polysystems” and highly dynamic systems (OLESEN et al. 2008), including numerous different pollinator and plant species (JORDANO 1987, BASCOMPTE & JORDANO 2007). Species in these networks vary in their degree of specialization between the interacting partners (MEMMOTT et al. 2004, VÁZQUEZ et al. 2009).

In pollinator-plant networks bee species play an important role. They are “keystone species” whose influence on ecosystem functions is essential (BOND 1993, KRATOCHWIL 2003). The loss of keystone species always causes serious consequences for the whole ecosystem concerning pollination, gene exchange and gene flow of wild plants (BAKER & HURD j1968, TEPEDINO 1979, WCISLO & CANE 1996, BIESMEIJER et al. 2006). Only a high diversity of bee species ensures pollination, the local long-term establishment of plant species and the variability and stability on plant community level. This is due to habitat and resource specialization of wild-bee species (KRATOCHWIL 2003).

The question arises: which factors determine structural and dynamical traits in bee-plant webs within ecological communities? There are different approaches explaining species coexistence and diversity on community level. One approach is the so-called “species-pool hypothesis”. This concept has its origin in island-biogeography theory (CORNELL & HARRISON 2014), combining e.g. geological, macroclimatic, landscape historical, evolutionary and population ecological processes. Following a deductive way, the biosphere can be divided into biomes (WALTER & BRECKLE 1999), vegetation complexes (different levels) and plant communities including their specific faunas (SCHWABE & KRATOCHWIL 2011). A “regional species pool” comprises all species available to colonize a focal site (CORNELL & HARRISON 2014). Different environmental filtering processes exist (e.g. abiotic and biotic frame conditions of the habitat site, dispersal capabilities of species) and “decide” regarding the potential of species structure within a local community. If species-specific adaptations in morphology, physiology and behavior (which evolved in the course of evolution) correspond to the site-specific abiotic and biotic environmental conditions, the ecological niche of a species can be identified.

Not all potential species occur in a local community (“dark diversity”; PÄRTEL et al. 2011, 2013) and not all species are available for creating a local web structure. One possible explanation can be proposed by the “metacommunity concept” (LEIBOLD et al. 2004), which explains the spatial and dynamic processes between subcommunities. Following our hypothesis, the metacommunity approach might be also occur in bee-plant networks.

In this review article mainly results of dry-grassland studies on sandy substrate in Germany are presented, asking the following questions:

- How long will the colonization process of wild bees take after restoration of specific plant communities in an area which was not or hardly populated by bee species?
- Which are the dispersal capabilities of bee species, are there any genetic bottlenecks and which role is played by stochasticity in contrast to deterministic constraints?
- Are there congruent characteristics in the community structure of plant and bee species, and which vegetation types (vegetation complexes) are suitable for a species-rich bee community?
- Are the network structures within a bee-plant web randomly distributed, nested, modularized or characterized by a gradient?
- In which way are bee-plant webs organized spatially and dynamically?

2. Species pools and habitat filtering

Level 1: Within the area of Germany, different bioregions can be distinguished. These bioregions are characterized by specific regional species pools (Fig. 1) with different percentages of floral and faunal geographic elements (e.g. central European, Eurosiberian, Subatlantic, Subcontinental, Submediterranean, alpine species). The occurrence of species of different geoelements within an area ("area type spectrum") can only be understood in Europe in the light of the postglacial re-immigration of plant and animal species from their glacial refugia (KRATOCHWIL 1988). The reduction of the species pool into regional species pools of different bioregions is the first filtering process.

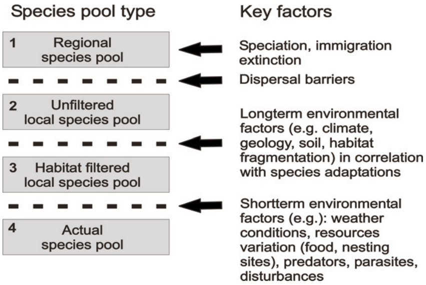

Fig. 1: Hierarchical relationship between regional and actual species pools, including key factors responsible for filtering processes (dotted line).

Level 2: The second process concerns dispersal barriers and leads to an unfiltered local species pool (Fig. 1).

Level 3: The third process is influenced by long-term environmental factors ("habitat filtering") in correlation with special adaptations of plant and animal species. In plant communities different habitat specificities of coexisting plant species can be shown e.g. by spectra of Ellenberg values or in a detailed phytosociologial analysis. Decisive environmental factors are climate, soil, geology (Fig. 1). Evaluating of literature reveals that about fifty percent of the 582 bee species of Germany (SCHEUCHL & SCHWENNINGER 2015) can be characterized as habitat specialists (KRATOCHWIL 2003). Most of these bee species are detected in communities of Festuco-Brometea, Artemisietea, extensively managed Molinio-Arrhenatheretea (dry) and Koelerio-Corynephoretea. The total of all *Salix*-dominated vegetation units (shrub formations: Salicetea purpureae, Salicion cinereae and Sambuco-Salicion) is ranked in fifth position followed by Stellarietea communities. These results hold true regardless of whether or not cleptoparasitic bees are included in the analysis (KRATOCHWIL 2003).

Concerning bee-species preferences, there are two main factors which determine the distribution and local dispersion of species: (1) Specificity in nesting and (2) nutrition (pollen, nectar). About two thirds of all bee species in Germany are ground-nesting bees preferring loose substrate (e.g. sand, loess); KRATOCHWIL (2003). About one third of all species show a high specificity in pollen collecting (oligolectic behavior), using only a few plant species (mostly on genus or family level). Oligolectic bee species were detected on species of 23 plant families but the dominance of two families for pollen collecting should be highlighted: Asteraceae and Fabaceae (KRATOCHWIL 2003). Most of all oligolectic bee species belong to mining bees (*Andrena*) and mason bees (*Osmia*). A quarter of the bee species in Germany are cleptoparasitic (e.g. *Nomada*, *Sphecodes*). Habitat-fragmentation as well as habitat mosaic structures can be also considered as important factors.

Level 4: Short-term environmental factors directly influence actual species pools: e.g., weather conditions, resource variation (food and nesting sites), predators, parasites, disturbances.

3. Model study 1: northwestern Germany, Hase valley

3.1 Wild-bee colonization after restoration of an alluvial vegetation mosaic

An alluvial vegetation mosaic along the River Hase (between Haselünne and Meppen, northwestern Germany) was developed by restoration management in the years 2000 and 2001 (STROH et al. 2005). After setting back the dikes, soil and sand were rearranged, creating a wetland-river dune complex low in nutrients. 67,000 m^3 of soil and sand material had been moved within an area of 37 ha. Only few plant species were present in the seed bank. The newly developed dune system has been inoculated with diaspores from mown and raked plant material taken from special source areas (Spergulo vernalis-Corynephoretum canescentis, Diantho deltoidis-Armerietum elongatae), serving also as reference sites (Nature reserve "Sandtrockenrasen am Biener Busch", Lingen). Low-lying areas (13.7 ha) were inoculated with commercial seed mixtures (plant species of *Festuca pratensis* grassland); STROH et al. (2005).

After the dikes had been set back in autumn 2001, flooding took place when the water table exceeded 290 cm. Floods did not reach the newly created sand dunes (REMY & ZIMMERMANN 2004). Moreover the habitat type spectrum of the restoration area is composed of fluviatile sand layer, extensively grazed pasture land (fresh to moist), permanent and periodical water holes and flood channels.

Colonization and succession of the bee community were studied by a pantrap method in the Spergulo-Corynephoretum and Diantho-Armerietum in the years 2003, 2005 and 2006 (EXELER & KRATOCHWIL 2009, EXELER et al. 2009). The analysis was conducted in the restored, primarily more or less wild bee-free habitats, in comparison with old, species-rich target sites. Ten permanent plots were established on the target and restoration sites in the Spergulo-Corynephoretum and Diantho-Armerietum.

8735 individuals belonging to 90 wild-bee species were detected at the target and restoration sites. In these four years, restoration and target sites correspond in having high species richness and abundance. The number of wild-bee species at restoration sites did not differ from the target sites in any study year. Differences between restoration and target sites were found only in the total abundance of bees and in the abundance of specialists, both of which were greater at the target sites. The community structure of bees at restoration sites converged only slightly to those of the target sites. The Renkonen index of similarity in wild-bee assemblage revealed a high similarity between restoration sites and target sites. Functional aspects (e.g. number of generalists, specialists, cleptoparasites, body-size distributions) of the bee communities show that ecosystem function may be restored rapidly. A remarkable aspect is that special target species (e.g. stenoecious species with preference for sandy habitats) become established in the restoration area very quickly (Tab. 1).

Tab. 1: Stenoecious colonizer species (target species) of bees (examples) in the restoration area within the first 4 years (according to EXELER & KRATOCHWIL 2009).

Andrena barbilabris (Kirby, 1802)	Dasypoda hirtipes (Fabricius, 1793)
Andrena clarkella (Kirby, 1802)	Lasioglossum sexnotatum (Kirby, 1802)
Andrena dorsata (Kirby, 1802)	Lasioglossum quadrinotatulum (Schenk, 1861)
Andrena vaga Panzer, 1799	Lasioglossum quadrinotatum (Kirby, 1802)
Colletes fodiens (Geoffroy, 1785)	Panurgus banksianus (Kirby, 1802)
Colletes cunicularius (Linnaeus, 1761)	Panurgus calcaratus (Scopoli, 1763

Using multivariate analyses (canonical correspondence analysis, CCA) a clear grouping of wild-bee assemblages of Spergulo-Corynephoretum in contrast to those of Diantho-Armerietum (target and restoration sites) were found (Fig. 2). At the Diantho-Armerietum sites, bee-species composition was determined by moisture, the number of entomophilous plant species and the cover of forbs, whereas at the Spergulo-Corynephoretum sites bare ground cover and drier conditions are decisive.

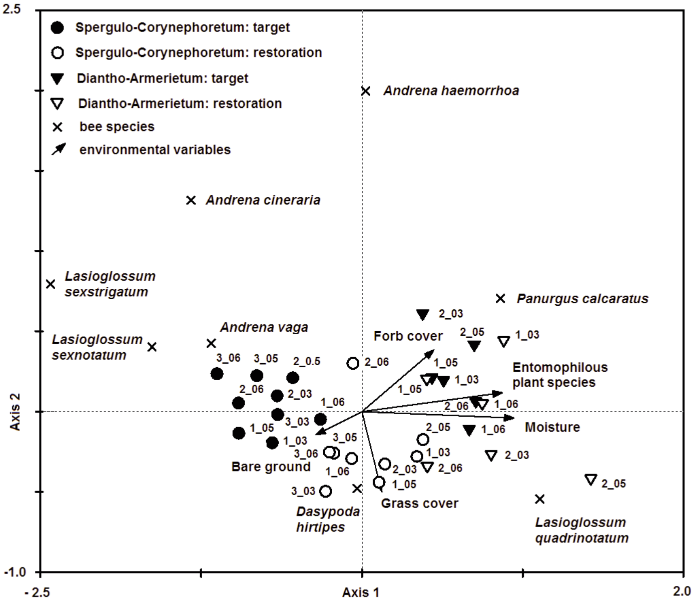

Fig. 2: Canonical correspondence analysis (PC-ORD 5.0) of bee species detections and the vectors of environmental variables in the years 2003, 2005, 2006 (according to EXELER et al. 2009): target area and restoration area of Spergulo-Corynephoretum and Diantho-Armerietum. Specific sites are annotated by the plot number and the year. First axis: eigenvalue = 0.26; second axis eigenvalue = 0.07.

The distribution and dispersion pattern of wild-bee communities, the quantity of pollen and nectar sources and the structure and composition of the vegetation in target and restored sites were studied in the same localities in a wider ecological scale (dry to moist habitats); EXELER (2008). The target area is characterized by both inland sand-dune vegetation (plot type "dry") and by seasonally flooded grasslands grazed extensively by cattle (plot type "moist") and riparian willow shrubs. In the restoration area sand-dune complexes (plot type "dry") and nutrient poor grasslands (plot type "moist") also exist. A grid-based system of permanent plots was established (distance 50 m); target area: 11 plots classified as "dry", 5 plots as "moist"; restoration areas: 12 plots "dry", 21 plots "moist".

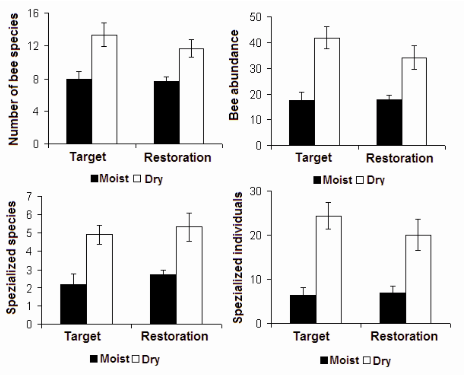

Fig. 3: Species number and abundances of bee species and of specialized bee species concerning dry and moist habitats in target and restoration sites (according to EXELER & KRATOCHWIL 2009).

A total of 1334 individuals belonging to 61 species were detected in the study areas. In both restoration and target plots, a higher diversity of wild bees was detected in dry plots than in moist plots. The number and abundance of wild-bee species differed significantly between restoration and target sites and among “dry” and “moist” plots (Fig. 3).

A significantly higher number of wild-bee species, total abundance, abundance of specialists and number of generalists were found at the target sites (Fig. 3). A multiple regression analysis shows the effects of environmental factors on different wild-bee response variables (EXELER 2008): Higher wild-bee diversity and the higher number of specialized species were found at drier plots (ANOVA “species”: $F_{1.45} = 24.1^{***}$; “individual numbers”: $F_{1.45} = 29.5^{***}$). The most important variables characterizing dry plots were a greater cover of bare ground and a high availability of Asteraceae species (e.g. *Hypochaeris radicata*, *Leontodon saxatilis*). In contrast, moist plots had a higher vegetation cover and were dominated by generalist wild-bee species (e.g. *Bombus* species). These results correspond to the knowledge that the majority of wild-bee species is heliophilous, preferring warm and dry conditions and bare ground nesting sites for endogaic nesting (KRATOCHWIL 2003).

3.2 Dispersal and genetic bottlenecks concerning wild-bee colonization

Foraging distance of wild bees have been discussed controversially. OSBORNE et al. (1999), GATHMANN & TSCHARNTKE (2002) and GREENLEAF et al. (2007) suggest a rather small flight radius for most species. ZAYED et al. (2005) and BEIL et al. (2008) characterize bees as having a large flight radius around their nest. But the question is not the foraging radius with a return to the nest. In contrast, dispersal for colonization refers to long-distance movements. Usually a female bee mates early in adult life and carries a lot of sperm cells for all of her reproductive life. Therefore a female is able to nest, reproduce and establish a population in a new area. But the long-distance dispersal rates of bees are not well known (RATHKE & JULES 1993).

It is assumed that the colonization takes place primarily from generalists followed later by specialists and species with limited dispersal ability (STEFFAN-DEWENTER & TSCHARNTKE 1997, TSCHARNTKE et al. 2002, MOIR et al. 2005). Some recent studies revealed therefore a reduced gene flow for populations of specialized species (PACKER et al. 2005, ZAYED et al. 2005, ZAYED & PACKER 2007), whereas PETERSON & DENNÖ (1998) found no difference between specialist and generalist bee species.

Population-genetic studies of two specialized bee species (*Andrena vaga*, *A. fuscipes*) were designed to analyze the gene flow within and among populations (EXELER et al. 2008, EXELER & KRATOCHWIL 2009, EXELER et al. 2010). *A. vaga* occurs naturally in sandy habitats and is specialized on willow (*Salix*) pollen as larval food and sandy soils as nesting sites. The habitats of *A. fuscipes* are heathlands strongly spezialized on heather (*Calluna vulgaris*) as larval food. In the case of *A. vaga* the genetic structure of 254 individuals (14 populations from northwest Germany, Lower Saxony, Rhineland to south Hesse; minimum distance 750 m, maximum distance 330 km), in the case of *A. fuscipes* (12 populations, geographical distance from less than 4 to 150 km) were analyzed using six to eight microsatellite loci (PAXTON et al. 1996, MOHRA et al. 2000). The data evaluations were carried out with the software GenAlEx (PEAKALL & SMOUSE 2006). The results for both species are similar. The populations are only slightly differentiated, that means that a relatively high gene flow between populations exists. For both species a high genetic diversity within populations and a low genetic differentiation among populations was found. Even in the case of great geographical distances (150 to 300 km), the genetic differences are low. Therefore it can be concluded that there is no genetic bottleneck concerning the tested species. The populations are well linked, the genetic separation and isolation effects are low.

4. Model study 2: southwestern Germany, upper Rhine valley near Darmstadt

4.1 Units for plant and wild-bee networks: vegetation types or vegetation complexes

In the upper Rhine valley (Darmstadt region, Germany) characteristics in the floral and faunal structure of plant and bee communities were studied (BEIL et al. 2014). The vegetation types and complexes range from basiphytic pioneer stages to consolidated basiphytic to slightly acidophytic grasslands (Koelerio-Corynephoretea, Festuco-Brometea): Koelerion glaucae complex, Armerio-Festucetum trachyphyllae, ruderalized ex-arable field and Allio-Stipetum capillatae. The study was conducted using a permanent plot-based approach.

A total of 1714 individuals belonging to 84 wild-bee species were detected. The detrended correspondence analysis (DCA) of the vegetation types and complexes show clear differentiations in contrast to the bee-species assemblages (Fig. 4, Fig. 5). The most species- and individual-rich wild-bee populations were detected in the vegetation types: ruderalized Armerio-Festucetum trachyphyllae, ruderalized ex-arable field and Allio-Stipetum capillatae, which were characterized by a high diversity of entomophilous plant species in combination with high flower density. Important flower resources for the wild-bee species are, among others, *Centaurea stoebe* s.l., *Berteroa incana* and *Carduus nutans*.

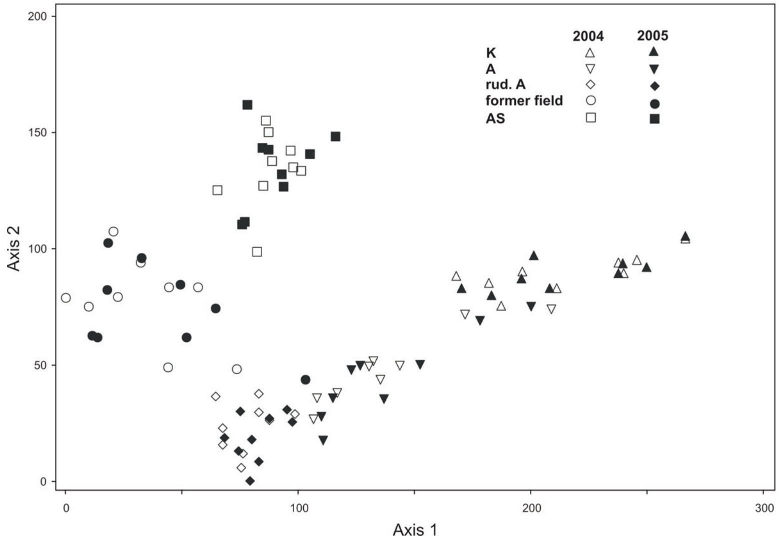

Fig. 4: DCA (PC-ORD 5.0) of the ordinal plant species data of the five different vegetation types and complexes for two years (2004, 2005; 9 plots each) according to BEIL et al. (2014). K: Koelerion glaucae vegetation complex, A: Armerio-Festucetum, rud. A: ruderalized Armerio-Festucetum, former field: ex-arable *Asparagus* fields, AS: Allio-Stipetum capillatae. Eigenvalues: axis 1: λ = 0.32, axis 2: λ = 0.14; gradient length: 100 = 1 SD.

4.2 Bee-plant networks

Many investigations have focussed on structures of flower-visitor webs (BASCOMPTE et al. 2003, OLLERTON et al. 2003, LEWINSOHN et al. 2006, OLESEN et al. 2008). BASCOMPTE et al. (2003), BASCOMPTE & JORDANO (2007) and others point out, that mutualistic networks are generally nested. This was primarily shown by the concept of the “Nested Temperature Calculator (NTC)”; PATTERSON & ATMAR (1986). Plant species may be regarded as “resource islands” for flower-visiting species, therefore a nested-subset analysis

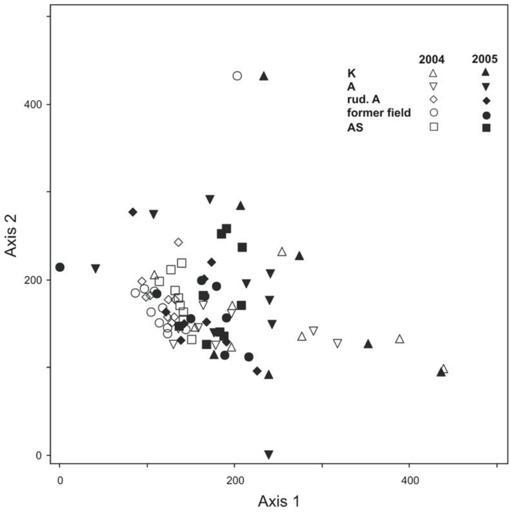

Fig. 5: DCA (PC-ORD 5.0) of the log (x+1) transformed bee abundances of the five different vegetation types or complexes for two years (2004, 2005; 9 plots each, abbreviations see Fig. 4) according to BEIL et al. (2014). Eigenvalues: axis 1: $\lambda = 0.51$, axis 2: $\lambda = 0.29$; gradient length: 100 = 1 SD.

of the network of flower-visiting species can be conducted (BASCOMPTE et al. 2003, DUPONT et al. 2003). In a presence-absence matrix bee species aligned in columns and plant species in rows (Fig. 6). If those species with fewer interactions are associated with a subset of species that interact with the most connected ones, networks are nested (BASCOMPTE et al. 2003). Specialized plant species are often associated with flower visitors widespread, abundant, and generalists. In contrast, specialized flower visitors (oligolectic species) are often closely connected with widespread and abundant plant species, visited by broad spectra of bees and characterized by a high degree of interaction. Moreover, bee and plant generalists tend to interact with other generalists (LEWINSOHN et al. 2006). In most of all parts of Europe asymmetric structures in flower-visitor interactions are the rule (ASHWORTH et al. 2004, VÁZQUEZ & AIZEN 2004, BLÜTHGEN et al. 2007; OLESEN et al. 2008). The matrix temperature T is a percentage that measures how much the presence-absence matrix departs from perfect nestedness. Besides nestedness, an interaction matrix can also be detected as a compartmented (modularized) or a gradient structure (KRATOCHWIL et al. 2009); Fig. 7.

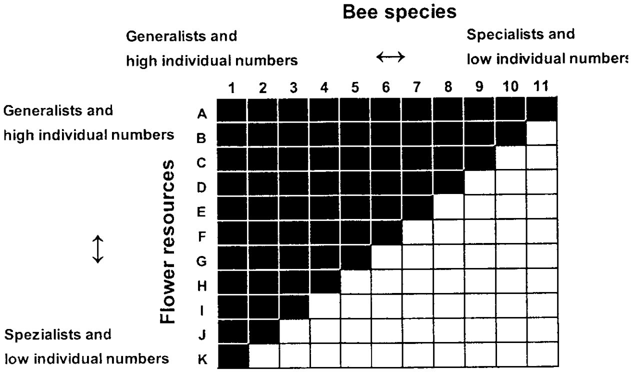

Fig. 6: Nested-subset matrix of bee species (1-11) and flower resources (A-K). Black boxes: present bee species and flower resource; white: absence.

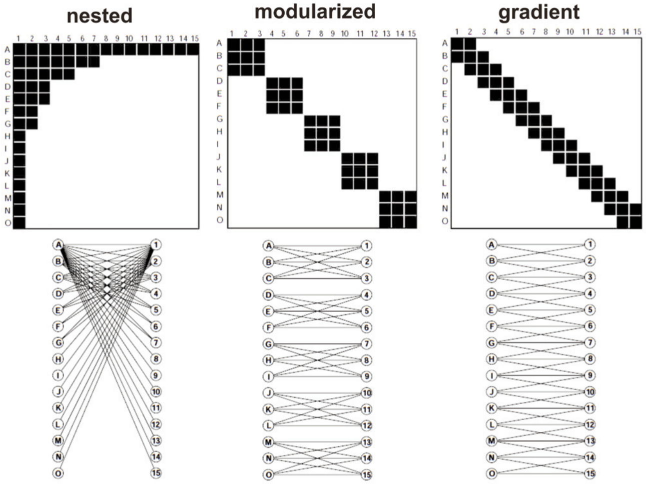

Fig. 7: Network structures: nested, modularized and with gradient (according to LEWINSOHN et al. 2006); upper row: presence-absence diagrams, lower row: bipartite graphs.

The interaction web of a plant-bee pollinator community was studied in 2004 and 2005 on 45 circular permanent plots with radius 8 m in the northern upper Rhine Valley near Darmstadt (Germany), in two nature protection areas ("Ehemaliger August-Euler-Flugplatz": 70 ha; "Griesheimer Düne und Eichwäldchen": 45 ha), comprising five vegetation types and complexes: (1) Koelerion glaucae vegetation complex; (2) Armerio-Festucetum trachyphyllae typicum; (3) Armerio-Festucetum trachyphyllae, ruderalized; (4) ex-arable *Asparagus* field; (5) Allio-Stipetum capillatae. In total, 1714 individual bees were recorded (2004: n = 1172; 2005: n = 542); KRATOCHWIL et al. (2009).

Nestedness

It is possible to quantify the pattern of nestedness of a bee-plant web with different programs, such as "Nested Temperature Calculator (NTC)" (ATMAR & PATTERSON 1995), "Binmatnest" (RODRIGUÉZ-GIRONÉS & SANTAMARÍA 2006), "Nestedness" (ULRICH 2006). Further other methods were compared in KRATOCHWIL et al. (2009). NTC and Binmatnest reveal in our datasets significant nestedness (Tab. 2). In contrast, it was only after masking (singletons of plant-bee interactions were removed from columns and rows), that weakly significant nestedness was indicated by the software "Nestedness", and then only for one year and without singletons (Tab. 2). The temperature values determined by "Binmatnest" were always lower than those of NTC. The results of NTC in 2004 are shown in Fig. 8, differentiated in interactions with more than one partner and singletons with data occurring only once in a matrix. Linkage levels characterize the number of interactions per species.

Tab. 2: Nested-Subset Analysis calculated via "NTC", "Binmatnest" and "Nestedness", T= temperature in degrees, Tsim = randomized mean temperature (1000 iterations), N = degree of nestedness, p = level of significance.

	year	bee species	plant species	Interactions	T	T_{Sim}	N	p
NTC	2004	69	42	225	6.6	24.3 ± 2.0	0.933	**< 0.001**
	2005	60	33	171	9.2	25.2 ± 2.4	0.908	**< 0.001**
BINMATNEST	2004	69	42	225	4.2	13.8 ± 1.8	0.958	**< 0.001**
	2005	60	33	171	5.7	14.7 ± 2.2	0.943	**< 0.001**
NESTEDNESS	2004	69	42	225	5.2	4.1 ± 0.6	0.948	0.8925
	2005	60	33	171	6.5	5.5 ± 0.7	0.935	0.9147
NESTEDNESS	2004	35	30	181	18.4	17.5 ± 1.3	0.816	0.7642
without singletons	2005	31	18	128	18.9	21.5 ± 1.6	0.811	**0.0505**

Nestedness can also be documented by bipartite graphs presenting species in columns or rows facing each other (Fig. 7). The same data sets were also used for bipartite plot analyses. The interactions are drawn as links and grouped by the number of interactions in decreasing order. Figures of bipartite plots for 2004 and 2005 were published in KRATOCHWIL et al. (2009). The bipartite graphs of 2004 and 2005 demonstrate a highly asymmetric pattern. In 2004, 42 plant species were visited by 69 bee species (225 interactions); in 2005, 33 plant species were used by 60 bee species (171 interactions). The analyses revealed that the most common species show the most frequent interactions with other species. Plant species with high interaction numbers were correlated with almost all bee species and vice versa. Polylectic bee species dominated in the group of species with many interactions and high distribution frequency. Oligolectic species showed a low number of interactions; the same was true for cleptoparasites. Plant species with low interaction number and frequency were visited mostly by those bee species with higher connectivity and wider distribution in the study area. These features correspond to nestedness.

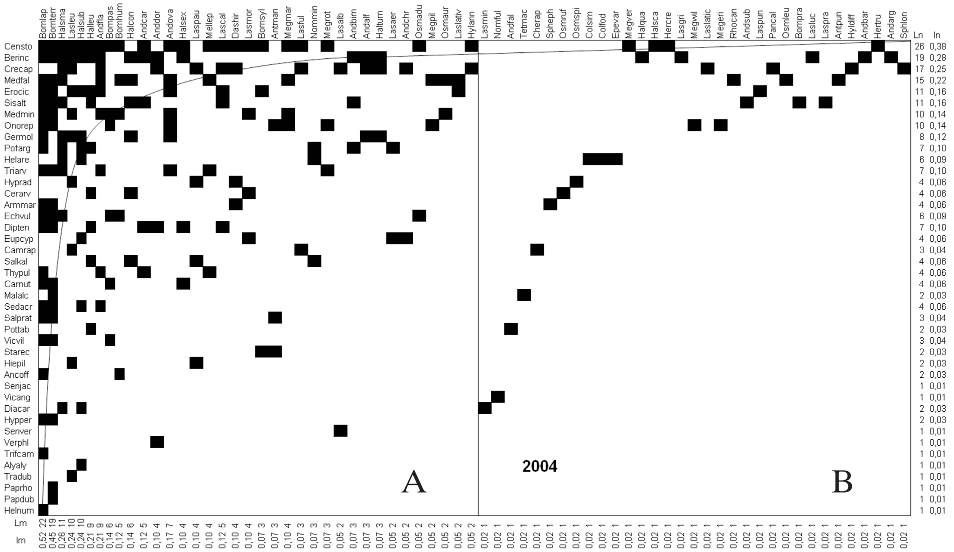

Fig. 8: Nested-subset analysis with "NTC" in 2004. A: Interactions with more than one partner; B: singletons (data occurring only once in a matrix). Abbreviations see Appendix. The data analysis of 2005 is characterized in KRATOCHWIL et al. (2009); (linkage level Lm of a bee species m is the number of plant species visited by m, linkage Ln of a plant species n is the number of bee species visiting n).

The bipartite web pattern was analyzed with the Bipartite Package 0.73 of DORMAN et al. (2008) using different null models to test significance. The observed nestedness of the real bee-plant web has a significantly lower temperature (<0.001) than the value reproduced by null model 1 (Patefield algorithm); KRATOCHWIL et al. (2009).

Modules

Modularity was tested with the software "Net-Cutter 1.0" (MULLER 2008) individually modified by H. Muller (Milan, Italy) for our tasks. "Edge-betweenness clustering" was used as proposed by GIRVAN & NEWMAN (2002). To prove significance, a randomization was conducted by "edge-swapping" as null model (1000 iterations). The graph structure and the presence of communities are visualized with "CircleLayout".

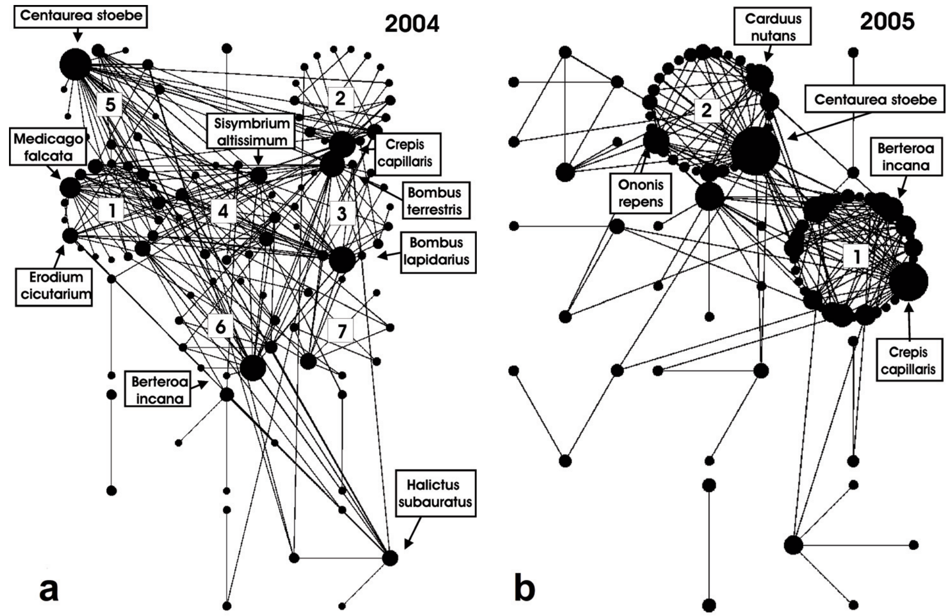

Fig. 9: Modularity graph of 2004 (a) and 2005 (b) based on edge-betweenness clustering according to KRATOCHWIL et al. (2009); 1-7: module number; plots: species; lines: interactions.

The analysis of co-occurrence networks showed a modularized pattern of five to seven in 2004 and two modules in 2005 (Fig. 9a,b). The species were connected within modules by hub species, between modules by connector species fixing the modules within a network. Our network is characterized by four to six dominant connector plant species, changing partly between years but representing four important flower types: in 2004: *Berteroa incana* (actinomorphic), *Centaurea stoebe* (Asteroideae type), *Medicago falcata* (zygomorphic), *Sisymbrium altissimum* (actinomorphic); in 2005: *Centaurea stoebe* (Asteroideae type), *Crepis capillaris* (Cichorioideae type), *Cerastium arvense* (actinomorphic), *Ononis repens* (zygomorphic). The number of modules and the pattern of hub-plant species showed high between-year variability. The same is true concerning bee species. The module pattern in both years was significantly modularized (Tab. 3).

Tab. 3: Modularity degrees of the data sets (2004, 2005), of the 50 randomized graphs by "edge-swapping" (1000 iterations) with NetCutter 1.0 (MULLER 2008); according to KRATOCHWIL et al. 2009); P: level of significance.

modularity	2004	2005
Actual value	0.4121	0.4452
Expected value	0.3785	0.3959
Standard deviation	0.0014	0.0166
Z-score	2.3384	2.9610
P	< 0.01	< 0.002

Key hub and key connector species are characterized by a high flower density and a specific flower type (actinomorphic, zygomorphic, Asteroideae-, and Cichorioideae type). This circumstance guarantees that all bee species regardless of their body size or their pollen collecting behavior will have resources available.

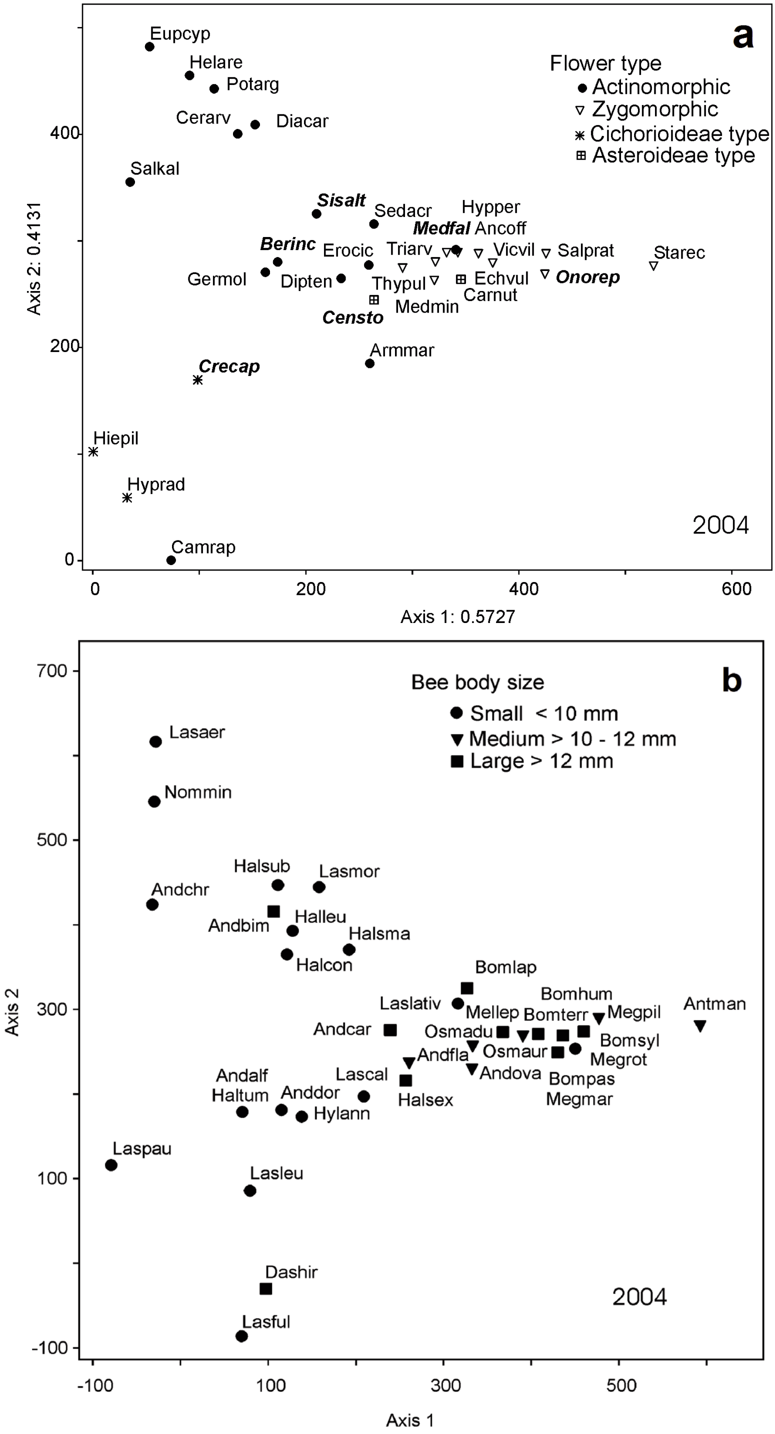

Fig. 10: DCA (PC-ORD 5.0) analysis of the plant-bee web 2004 with plant species (a) and bee species (b) and characterization by flower types and bee body sizes (key hub and connector plant species in bold and italics); according to KRATOCHWIL et al. (2009). For abbreviations of species, see Appendix.

Gradients

The DCA diagrams (PC-ORD 5.0) are based on the same datasets which were used for web analyses (here: 2004; for 2005 see KRATOCHWIL et al. 2009) for plant (Fig. 10a) and bee species (Fig. 10b). Both diagrams can be projected of each other. Fig. 10a revealed two main and two further traits of plant species with different flower types. The left side of the graph represents plant species with relatively small, actinomorphic flowers (e.g.: *Berteroa incana*, *Geranium molle*, *Alyssum alyssoides*, *Salsola kali*) or inflorescences easily accessible for bees (*Euphorbia cyparissias*). Bees (Fig. 10b, left side) were composed of those bees with small body sizes (*Andrena*, *Lasioglossum*, *Halictus*) characterized by hind legs (coxa, femur) bearing hairs for pollen collecting. Fig. 10a right side is dominated by plant species with zygomorphic flowers (*Stachys recta*, *Ononis repens*, *Salvia pratensis*, *Echium vulgare*). Their flower-visiting bee species (Fig. 10b) are of larger body size, with longer proboscises and other pollen-collecting structures (*Bombus*: hind-leg corbiculae; *Megachile*: hair brushes on abdominal tergites). *Halictus* species with larger body sizes also occur (*Halictus quadricinctus*, *H. sexcinctus*). The group with medium body size comprises species of *Andrena*, *Osmia* and *Megachile* with an intermediate position in the DCA. Pseudanthia of the Cichorioideae are grouped on the left side of the DCA (Fig. 10a) preferably visited by smaller bee species or, in the case of *Dasypoda hirtipes* and *Osmia spinulosa,* by Asteraceae specialists (Fig. 10b). Species visiting the Asteroideae type were grouped in the center. The DCA analysis shows the existence of a gradient (partly compartmented) concerning flower type, body size of bees and pollen-collecting structures. These parameters are important features on the structure of the bee-plant web.

5. Model study 3: southwestern Germany, upper Rhine valley near Heidelberg

Metacommunity approach

Habitat-fragmentation and habitat-mosaic structure is an important factor for analyzing web structures. Not all potential species occur in a local community, but beyond that circumstance bee species are able to change between local communities (subcommunities) within the habitat mosaic if the distance between the local sites is appropriate. Following our hypothesis, the metacommunity approach might be realized in bee-plant networks too.

The studies were conducted in 2008 in the upper Rhine valley (Sandhausen/Heidelberg, Germany) in a linear gradient of eight study sites characterized by inland sand dune vegetation (KRAUSCH 2013). The distance of the sites of group A to group B is 6 km, within group A 0.08 up to 4 km (on average 1.4 km), within group B 0.15 km. The vegetation complex includes a mosaic of Koelerio-Corynephoretea und Festuco-Brometea communities (*Festuca guestfalica*-community, *Corynephorus canescens*-community, *Helianthemum nummularium-Asperula cynanchica* community, Jurineo cyanoidis-Koelerietum glaucae), partly ruderalized with communities of the Stellarietea mediae, Artemisietea und Agropyretea (KRAUSCH 2013). The size of the plots reached from 0.4 to 4.8 ha. A total of 1402 individuals belonging to 101 bee species were detected (KRAUSCH 2013). The metacommunity structure on web level was tested with “Nestedness” (ULRICH 2006), the modularity with “Net-Cutter 1.0” (MULLER 2008).

Hypothesis 1: Significance in nestedness of a bee-plant web is a precondition for the existence of a metacommunity including subcommunities. All bees of all sites together demonstrate no nestedness, the group A without group B significant nestedness (Tab. 4).

Tab. 4: "Nestedness" analysis: T: temperature, Tsim: temperature simulation, SD: standard deviation, N: Nestedness-value, P: level of significance.

group	method	T	Tsim	SD	z-value	N	P
A and B (all bees)	Nestedness	24.5°	25.25°	± 0.94°	-0.79	0.76	0.2148
A (all bees)	Nestedness	22.85°	26.22°	± 1.15°	-2.92	0.71	0.0018***
A and B (only flower visitors)	Nestedness	16.83°	18.66°	± 1.05°	-1.74	0.83	0.0409
A (only flower visitors)	Nestedness	18.51°	19.4°	± 1.38°	-0.64	0.82	0.2611

*** P≤0.001

Hypothesis 2: Bee-plant webs of small habitats (< 50 plant and bee species) show no significant nestedness or modularity (BOSCH et al. 2009, OLESEN et al. 2007). The hypothesis is corroborated (Tab. 5).

Tab. 5: "Modularity analysis" of the different plots with Netcutter ("edge-swapping", 50 simulations); P: level of significance.

group	A	A	A	A	A	A	B	B
plot	1	2	3	4	5	6	7	8
plant species visited	10	7	6	7	6	10	7	12
bee species	28	23	15	19	22	32	14	28
interactions	50	39	22	26	33	45	21	51
modularity value	0.48	0.44	0.48	0.46	0.47	0.64	0.51	0.61
excepted value	0.50	0.40	0.50	0.48	0.44	0.62	0.5	0.58
standard deviation	0.02	0.03	0.03	0.04	0.02	0.02	0.02	0.03
z-value	-1.05	1.44	-0.70	-0.55	1.17	1.14	0.63	1.08
modularity (P)	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.

Hypothesis 3: Significance in modularity is a precondition for the existence of a metacommunity. All bees of all sites together demonstrate no modularity; the same is true for group A without group B. The hypothesis is not corroborated (Tab. 6).

Tab. 6: "Modularity analysis" of group A and B, group A and group B with Netcutter ("edge-swapping", 50 simulations); P: level of significance.

	group A and B	group A	group B
plant species visited	36	31	16
bee species	78	70	35
interactions	226	175	68
modularity value	0.4	0.44	0.51
excepted value	0.02	0.02	0.02
standard deviation	1	-0,16	0,78
z-value	0.42	0.43	0.53
modularity (P)	n. s.	n. s.	n. s.

Hypothesis 4: Significance in modularity can only be realized if entomophilic plant and bee species show synchronicity. Therefore we differentiate in two phenophases: spring and summer. The hypothesis is corroborated that group A shows significance in modularity under spring and summer phenophases differentiation (Tab. 7).

Tab. 7: "Modularity analysis" of group A and B and group A separated in spring and summer phenophases with Netcutter ("edge-swapping", 50 simulations); P: level of significance.

	group A and B spring	group A and B summer	group A spring	group A summer
plant species visited	12	25	11	21
bee species	24	67	20	62
interactions	46	188	30	149
modularity value	0.55	0.39	0.56	0.44
excepted value	0.56	0.37	0.60	0.41
standard deviation	0.02	0.02	0.02	0.01
z-value	-0.52	0.75	-1.86	1.69
modularity (P)	n. s.	n. s.	0,031*	0,046*

* P ≤0.05

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Appendix: Abbreviations

Plant species: Alyaly*: Alyssum alyssoides,* Ancoff*: Anchusa officinalis,* Armmar: *Armeria maritima,* Berinc*: Berteroa incana*, Camrap: *Campanula rapunculus,* Carnut: *Carduus nutans,* Censto*: Centaurea stoebe,* Cerarv: *Cerastium arvense,* Crecap: *Crepis capillaris,* Diacar: *Dianthus carthusianorum,* Dipten: *Diplotaxis tenuifolia,* Echvul: *Echium vulgare,* Erocic: *Erodium cicutarium,* Eupcyp: *Euphorbia cyparissias,* Germol: *Geranium molle,* Helnum*: Helianthemum nummularium,* Helare: *Helichrysum arenarium,* Hiepil: *Hieracium pilosella,* Hypper: *Hypericum perforatum,* Hyprad: *Hypochaeris radicata,* Malalc*: Malva alcea,* Medfal: *Medicago falcata,* Medmin: *Medicago minima,* Onorep: *Ononis repens,* Papdub: *Papaver dubium,* Paprho: *Papaver rhoeas,* Potarg: *Potentilla argentea,* Pottab: *Potentilla tabernaemontani,* Salkal: *Salsola kali* subsp*. tragus,* Salprat: *Salvia pratensis,* Sedacr: *Sedum acre,* Senjac*: Senecio jacobaea,* Senver: *Senecio vernalis,* Sisalt: *Sisymbrium altissimum,* Starec: *Stachys recta,* Thypul: *Thymus pulegioides,* Tradub: *Tragopogon dubius,* Triarv: *Trifolium arvense,* Trifcam: *Trifolium campestre,* Verphl: *Verbascum phlomoides,* Vicang: *Vicia angustifolia,* Vicvil: *Vicia villosa.*

Bee species: Andalf: *Andrena alfkenella*, Andarg: *Andrena argentata*, Andbar: *Andrena barbilabris*, Andbim: *Andrena bimaculata*, Andcar: *Andrena carbonaria* agg., Andchr: *Andrena chrysosceles*, Anddor: *Andrena dorsata*, Andfal: *Andrena falsifica*, Andfla: *Andrena flavipes*, Andova: *Andrena ovatula*, Andsub: *Andrena subopaca*, Antman: *Anthidium manicatum*, Antpun: *Anthidium punctatum*, Bomhum: *Bombus humilis*, Bomlap: *Bombus lapidarius*, Bompas: *Bombus pascuorum*, Bompra: *Bombus pratorum*, Bomsyl: *Bombus sylvarum*, Bomterr: *Bombus terrestris*, Cherap: *Chelostoma rapunculi*, Colfod: *Colletes fodiens*, Colsim: *Colletes similis*, Dashir: *Dasypoda hirtipes*, Epevar: *Epeolus variegatus*, Halcon: Halictus *confusus*, Halleu: *Halictus leucaheneus*, Halqua: *Halictus quadricinctus*, Halsca: *Halictus scabiosae*, Halsex: *Halictus sexcinctus,* Halsma: *Halictus smaragdulus*, Halsub: *Halictus subauratus*, Haltum: *Halictus tumulorum*, Hercre: *Heriades crenulatus*, Hertru: *Heriades truncorum*, Hylann: *Hylaeus annularis*, Hyldiff: *Hylaeus difformis*, Lasaer: *Lasioglossum aeratum*, Lasalb: *Lasioglossum albipes*, Lascal: *Lasioglossum calceatum*, Lasful: *Lasioglossum fulvicorne*, Lasgri: *Lasioglossum griseolum*, Laslatic: *Lasioglossum laticeps*, Laslativ: *Lasioglossum lativentre*, Lasleu: *Lasioglossum leucozonium*, Lasluc: *Lasioglossum lucidulum*, Lasmin: *Lasioglossum minutissimum*, Lasmor: *Lasioglossum morio*, Laspau: *Lasioglossum pauxillum*, Laspra: *Lasioglossum prasinum*, Laspun: *Lasioglossum punctatissimum*, Megeri: *Megachile ericetorum*, Megmar: *Megachile maritima*, Megpil: *Megachile pilidens*, Megrot: *Megachile rotundata*, Megver: *Megachile versicolor*, Megwil: *Megachile willughbiella*, Mellep: *Melitta leporina*, Nomful: *Nomada fulvicornis*, Nommin: *Nomioides minutissimus*, Osmadu: *Osmia adunca*, Osmaur: *Osmia aurulenta*, Osmleu: *Osmia leucomelana*, Osmruf: *Osmia rufa*, Osmspi: *Osmia spinulosa*, Pancal: *Panurgus calcaratus*, Rhocan: *Rhophitoides canus*, Spheph: *Sphecodes ephippius*, Sphlon: *Sphecodes longulus*, Tetmac: *Tetralonia macroglossa*.

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