



Community structure and diversity of vegetation and flower-visiting wild bees (Hymenoptera: Apoidea) in sandy dry grassland: are there congruent characteristics?

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With 6 figures and 6 tables

Abstract: We studied community structures of mainly threatened types of sandy dry grassland, and those of flower-visiting wild bees, in successional, non-ruderal or ruderal gradients in the Upper Rhine Valley (Germany).

We searched for congruent characteristics in the floristic/faunistic structure of plant and bee species, and for differences between two study years. We also asked which vegetation type or complex plays the most important role as a pollen or nectar resource for wild bees, and what conclusions can be drawn for nature conservation. The vegetation types or complexes range from basiphytic pioneer stages to consolidated basiphytic to slightly acidophytic grasslands (classes Koelerio-Corynephoretea and Festuco-Brometea): Koelerion glaucae complex (1), Armerio-Festucetum trachyphyllae (2a, typical; 2b, ruderalized), ruderalized ex-arable field (3), and Allio-Stipetum capillatae (4).

We used a plot-based approach for recording vegetation data and flower-visiting wild bees. Relevés were sampled and flower-visiting bees netted on defined flower resources (2004, 2005). Data were analyzed by ordination, mixed linear models and regression analysis.

Phytosociological table and DCA show clear floristic differentiations between the vegetation types and complexes. For the bee data there were weaker species-based differentiations. In the year 2004 there were two bee assemblages, in the year 2005 this differentiation was not detectable. The most species- and individual-rich wild-bee populations were detected in the vegetation types 2b, 3 and 4. These types were characterized by a high diversity of entomophilous plant species in combination with high flower density. Although ruderalized sandy grasslands have only moderate conservation value based on vegetation characteristics, they offer remarkable resources for species-rich populations of wild bees. Important flower resources for endangered wild-bee species are, among others, *Centaurea stoebe* s.l., *Berteroa incana* and *Carduus nutans*.

The diversity characteristics of the studied vegetation types or complexes do not always correspond to those of the flower-visiting bees, which should be taken into account in developing conservation strategies.

Keywords: Biocoenology; Festuco-Brometea; Koelerio-Corynephoretea; Natura 2000 network; Plant-animal interactions; Ruderalization

Nomenclature: Vascular plant species: Wisskirchen & Haeupler (1998), with the exception of *Elytrigia campestris* (Godr. & Gren.) Kerguelen x *Elytrigia repens* (L.) Nevski; Bryophytes: Koperski et al. (2000); Lichens: Scholz (2000). Bee species are indicated with author names in Table 3.

Abbreviations: A = Armerio-Festucetum trachyphyllae, AS = Allio-Stipetum capillatae, EF = ex-arable field, FFH = Fauna-Flora-Habitat, K = Koelerion glaucae, rud. A = ruderalized Armerio-Festucetum trachyphyllae.

Introduction

Vegetation types of sandy dry grasslands are known to be rich in rare plant species, which are often entomophilous, e.g. Koelerion glaucae (Koelerio-Corynephoretea) with *Silene otites*, Armerio-Festucetum trachyphyllae (Koelerio-Corynephoretea) with *Armeria maritima* subsp. *elongata*, and Allio-Stipetum capillatae (Festuco-Brometea) with *Helianthemum nummularium* subsp. *obscurum* and *Dianthus carthusianorum*. These plant communities are restricted to nutrient-poor habitats, and are severely threatened throughout Central Europe, especially by fragmentation, which often leads to decreases of population sizes of

plants and animals and therefore to reduced gene flow (Schwabe & Kratochwil 2009, Exeler et al. 2010, Süß et al. 2010, Faust et al. 2012). Especially invertebrates may act as vectors between remnants of these habitats (for a wild-bee species in acidic sandy habitats, see Exeler et al. 2010).

In the past 15 years we have studied many ecological aspects of these sandy grasslands and their pioneer stages in the Upper Rhine Valley in Germany, including vegetation structure, productivity, nutrient dynamics, successional trends, grazing impact, and seed dispersal (Eichberg et al. 2006, 2007, Süß & Schwabe 2007, Süß et al. 2007, Faust et al. 2011a, Schwabe et al. 2013). We also developed scientific approaches to restore sandy habitats

and to reverse fragmentation (Stroh et al. 2002, Wessels et al. 2008, Eichberg et al. 2010, Freund et al. 2014).

However, biocoenological studies in sandy grassland of Central Europe are still rare, especially concerning wild bees (see e.g. Exeler et al. 2009 in Northern Germany). Wild bees (Hymenoptera: Apoidea) are target organisms of nutrient-poor sandy habitats (Kratochwil 2003), and are main pollinators of threatened and common plant species of the plant communities in question. Wild bees exhibit diverse resource utilization: in addition to flowering entomophilous plant species (sometimes belonging only to one plant family or genus) most of them need bare ground, because they have their nesting sites in open sand patches in the pioneer vegetation or along sand paths. For all these reasons a diverse wild-bee and plant network indicates intact landscape structures with unimpaired biodiversity (Oertli et al. 2005). According to experiments of Fründ et al. (2013) functional complementarity of bee species (e.g. complementary pollination niches) is especially important.

In the sand ecosystems of the Upper Rhine valley we have so far determined pollen loads of wild-bee species (Beil et al. 2008) and analyzed the structure of plant-bee interaction networks in different years (Kratochwil et al. 2009). Furthermore a preliminary study shows community structures of vegetation and bee species in the area Griesheimer Düne (Beil & Kratochwil 2004). Here we try to fill the gap of biocoenological wild-bee studies by analyzing sandy grasslands and their pioneer stages with the aim to combine data on vegetation and flower-visiting bee species.

In most unforested ecosystems of the temperate zone wild-bee species are considered as key pollinators (Cane 2001, Kratochwil 2003), and as essential for the existence of many entomophilous plant species (Batra 1995, Kevan 1999). During the past decades, the number of wild-bee species has considerably decreased in many countries worldwide ('pollination crisis', Kearns et al. 1998), which is attributed to habitat fragmentation, changes in land use, application of pesticides, bee diseases and climatic factors (Osborne et al. 1991, Kearns et al. 1998, Brown & Paxton 2009). Losses of pollinator diversity and thus pollination have severe consequences for plant reproduction (Garibaldi et al. 2013, Tylianakis 2013) and vegetation dynamics, since many plant species depend on diverse pollinator communities (Klein et al. 2003, Kremen et al. 2004, Biesmeijer et al. 2006). In general, many wild-bee communities are characterized by the presence of only a few abundant (mostly social) species, whereas many other species only occur in small individual numbers (Minckley et al. 1998, Kratochwil & Schwabe 2001, Potts et al. 2003, Oertli et al. 2005).

The community structure of these bee species may be influenced by different factors: plant diversity (Tscharntke et al. 1998, Potts et al. 2003), flower density (Viana & Kleinert 2006), diversity of nectar and pollen resources

(Potts et al. 2006), land-use intensity (Weiner et al. 2011), as well as availability of nesting sites (Potts et al. 2005, Murray et al. 2009) and specific surrounding landscape matrices (Ricketts 2001, Steffan-Dewenter et al. 2002, Chacoff & Aizen 2006).

Steffan-Dewenter & Tscharntke (2001) and Carvell et al. (2004) compared different successional stages of vegetation and detected changes in bee-species diversity. For conservation management it is important to know which habitat types (successional stages, ruderalized, non-ruderalized types) are characterized by the highest wild-bee diversity and richness in threatened species. Calcareous grasslands are known to be very rich in wild-bee species (Kratochwil 2003), although in Europe probably the highest values are reached in Mediterranean dry grassland and scrub within traditionally managed cultural landscapes (studies in Greece of Phrygana and olive groves by Nielsen et al. 2011). Generally the warm xeric areas of the Mediterranean basin have the highest bee diversity in Europe (Patiny et al. 2009). Westphal et al. (2008) detected 122 wild-bee species in calcareous grassland near Göttingen (ca. 1 ha) in central Germany, while Kratochwil (1984) found 132 wild-bee species in fallow Mesobrometum vegetation of 0.4 ha (pan traps: 83 spp., netting of flower-visiting bees in observation plots: 104 spp.) in the Kaiserstuhl area (southwestern Germany). Beil & Kratochwil (2004) detected 75 wild-bee species in the sandy area Griesheimer Düne which is characterized by calcareous sand and relatively dry conditions (12 ha, included in the present study).

Many wild-bee species of these sandy areas are known to be restricted to this type of substrate; they need gaps in the vegetation or open places as nesting sites (mostly ground-nesting bees). Nesting sites of many species are open sandy sites, but females, e.g. of *Dasygaster hirtipes*, gather pollen at other sites, rich in flowering plants (Celary 2005). This is true also for many other wild-bee species (Kratochwil 2003, Beil et al. 2008). So far many analyses have shown that the number of wild-bee species is much higher than the number of visited plant species, which results in asymmetric networks (Blüthgen et al. 2007, Kratochwil et al. 2009).

The questions to be answered by this study are as follows:

1. Are there congruent characteristics in the community structure of plant and bee species in the studied vegetation?
2. Which vegetation types or complexes support the highest numbers of plants and wild bees?
3. Are there differences between the floristic/faunistic structures of vegetation and flower-visiting bee species in the studied years?

Study area, stages of succession and ruderalization

The study was conducted in the Hessian Upper Rhine Valley near Darmstadt (southwestern Germany). The nature-conservation areas 'Ehemaliger August-Euler-Flugplatz von Darmstadt' (70 ha, 8°35'E, 49°51'N) as well as 'Griesheimer Düne und Eichwäldchen' (45 ha, 8°34'E, 49°50'N) are part of the Natura 2000 network (Fauna-Flora-Habitat = FFH areas). They were chosen because they are characterized by different successional stages (without or with ruderalization) of sandy dry grasslands including pioneer stages. These are (1) Koelerion glaucae vegetation complex, (2a) Armerio-Festucetum, (2b) ruderalized Armerio-Festucetum, (3) ex-arable *Asparagus* fields and the area Griesheimer Düne which is dominated by the (4) Allio-Stipetum capillatae. The vegetation types and their long-term dynamics are introduced in Süß et al. (2010), Faust et al. (2011b) and Schwabe et al. (2013). Before 1945 the two areas were part of one large sand ecosystem complex (Griesheimer Sand; Zehm & Zimmermann 2004).

There is some knowledge about the successional and ruderalization processes in the sandy grasslands studied. Permanent plot research showed that the Koelerion stage can last more than 15 years without marked change (Hach et al. 2005, Süß et al. 2010), but scattered plants of *Stipa capillata*, e.g. at the Euler-Flugplatz, indicated that there is a development towards Type 4. According to Süß et al. (2010), Koelerion glaucae and Allio-Stipetum are clearly successional stages. If soil dynamics are absent, the development leads to top-soil acidification (from pH 7.5 to 5.4, see Faust et al. 2011b), and the resulting vegetation is an Armerio-Festucetum typicum. Vegetation types 2b and 3 reflect a ruderalization gradient. An ex-arable field can serve as a model for a restoration site without abiotic and biotic improvement (Eichberg et al. 2010). Here extractable phosphate-P values are still > 100 mg/kg dry soil (C. Storm, unpubl. data), i.e. quite similar to cultivated fields.

Our investigations have shown that ruderalization of sandy grasslands is favoured by high phosphate values (Süß et al. 2004, 2010). This ruderalization path was also induced by experimental nutrient addition in the same study area (Faust et al. 2012). If such a site remains unmanaged, competitive graminoids such as *Calamagrostis epigejos* will become dominant (Stroh et al. 2007, Süß et al. 2010, Schwabe et al. 2013). These data from related studies on the same sites are the basis for assignment of the following results to certain stages of succession without and with ruderalization.

Materials and methods

Study design

The study was conducted within the sites Euler-Flugplatz and Griesheimer Düne from early April to early September 2004 and 2005. Both areas were extensively grazed mainly by sheep (episodically by donkeys) in both years (Beil & Kratochwil 2004, Faust et al. 2011b).

Altogether we studied the following five vegetation types or complexes of basiphytic to slightly acidophytic sand according to a vegetation map published by Zehm & Zimmermann (2004) and the classification of the Natura 2000 areas of the study area:

1. Koelerion glaucae vegetation complex; vegetation complex of FFH priority type 2330: Open grassland with *Corynephorus* and *Agrostis*; 6120: Xeric and calcareous grasslands (Koelerion glaucae), Fig. 1a;
- 2a. Armerio-Festucetum trachyphyllae typicum; FFH priority type 6214: Central European calcaro-siliceous grasslands, Fig. 1b;
- 2b. Armerio-Festucetum trachyphyllae, ruderalized; FFH type as 2a, but rich in ruderal plant species;
3. Ex-arable *Asparagus* field, fallow since 1950–1960, Fig. 1c; and
4. Allio-Stipetum capillatae; FFH type 6240: sub-continental steppic grassland, Fig. 1d.

The whole area used for the study had a size of ca. 60 ha. Types 1, 2a, 2b and 3 were located at the Euler-Flugplatz, type 4 at the Griesheimer Düne. For each type, we used an area of ca. 150 m * 300 m within nearly homogeneous stands. Within each of these five stands we established nine circular permanent plots for vegetation and bee studies. The plots were selected in a systematic design, i. e. they were equally spaced as far as possible, excluding disturbed or inhomogeneous parts of the stands (see Fig. 2.1. in Beil 2007).

By means of vegetation relevés (80 m²) using the differentiated Braun-Blanquet scale according to Barkman et al. (1964), we described the floristic composition and obtained different structural data of the plots, including cover of forbs, graminoids and open soil. We chose this large relevé size already in the year 2000 to establish a monitoring system for the whole area, which covers large proportions of the areas and is an excellent basis for invertebrate studies. Other approaches employ smaller plot sizes (Zehm & Zimmermann 2004, Faust et al. 2011b), which are not adequate for bee studies.

Weekly relevés of the flower resources present in each permanent plot were made according to the method of Kratochwil (1984) and completed by additional estimations of the cover of flowers of entomophilous plant species. Thus, the average cover of the total number of flowering plant species as well as the average number of flowering plant species in each vegetation type or complex

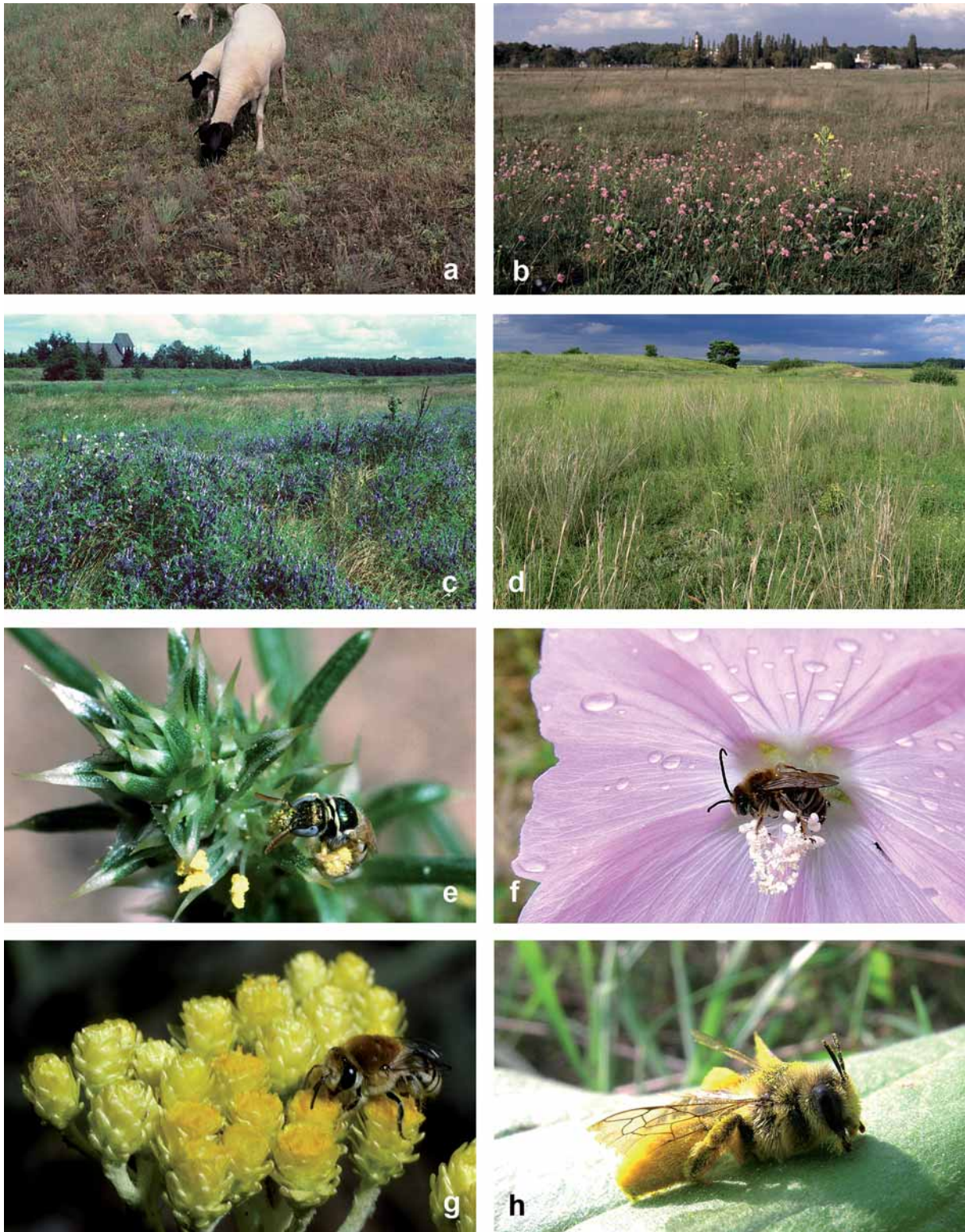


Fig. 1a–h. Vegetation types or complexes and selected wild-bee species.

a–d: Vegetation types or complexes: *Koelerion glaucae* complex (with last flowers of *Sedum acre*), *Armerio-Festucetum typicum* (with flowering *Armeria maritima* subsp. *elongata*, ex-arable field (with flowering *Vicia villosa* s.l.) and *Allio-Stipetum capillatae*. **e–h:** Characteristic wild-bee species: **e.** *Nomioides minutissimus* visiting *Salsola kali* subsp. *tragus*; **f.** *Eucera macroglossa*, oligolectic species Malvaceae (here *Malva alcea*); **g.** *Colletes fodiens* visiting *Helichrysum arenarium*; **h** *Dasygaster hirtipes*, target species in sandy habitats. Photos: Beil (h), Kratochwil (e, g), Schwabe (a–d, f).

was determined. In the following, ‘flowering plant species’ always refers to ‘flowering entomophilous plant species’, excluding for example graminoids and wind-pollinated forbs.

Bees were observed or caught in the same permanent plots by sweep nets from flowering plant species (examples see Fig. 1e, f, g), using a standardized protocol mainly once a week (but always with identical intensity in all plots) during a period of 15 min. under similar weather conditions (sunny, only slight winds, temperatures > 12 °C) in varying order. Due to negative experience with very small observation plots of only few square meters (e.g. Westphal et al. 2008), it was necessary to make our observation plots relatively large. We used the circular plot area of the vegetation relevés, and additionally a surrounding circle (all in all 200 m²). This approach is a compromise between observation and transect method; the latter is recommended by Westphal et al. (2008). The bee species which could clearly be determined in the field were only observed (among them *Eucera macroglossa* and *Dasypoda hirtipes*; Fig. 1f, h), whereas all other bee individuals were collected and frozen for later identification (−20 °C). The semi-domesticated honey bee (*Apis mellifera*) was excluded from the investigations. ‘Parasite’ refers to bee species practising nest parasitism (cuckoo bees, cleptoparasites).

Climatic conditions in the study periods

In the study years 2004 and 2005, the mean annual temperatures were 10.7° C and 11.0° C, respectively, and the annual rainfall 556 mm and 524 mm. The mean annual sunshine duration was 1635 and 1770 hours (data from Frankfurt/Main Airport). In both years the weather conditions were average and no extraordinary climatic event occurred such as, e.g. in the dry year 2003.

Data analyses

We prepared a presence table with the vegetation data for both years, ordered according to diagnostic species. The bee data (individual numbers) were summarized in a table for each vegetation type or complex and each year. The assignment of bee species as specific to sandy habitats and dry grassland, or as generalists of dry habitats with broader habitat amplitude, was done based on Kratochwil (2003) and expert knowledge.

Multivariate analyses were made with different approaches (DCA, Polar Ordination, NMDS), using PC-ORD 6.11 (McCune & Mefford 2011). Detrended Correspondence Analysis reflected the studied gradients for the vegetation in a clear way. There was only low variation between the two years concerning the qualitative data of the floristic structure (as shown in the phytoso-

biological table); therefore we depicted the data of the two years in one DCA diagram. The DCA was run under ‘downweight rare species’, ‘rescale axes’ and ‘number of segments = 26’. For the analysis of vegetation the Braun-Blanquet scale was transformed to a nine-stage ordinal scale. In the case of the bees there was much variation between the years, therefore we show the results in one DCA diagram for each year. In 2005 one outlier had to be removed. The data set of the bees was log₁₀(x+1) transformed to prevent undue influence of dominant species.

The statistical analyses were made with mixed linear models (SAS 9.1, proc mixed, Littell et al. 2000), analyzing the following structures of co-variance and choosing those which showed the best AKAIKE results (AIC): autoregressive (1), heterogeneous autoregressive (1), autoregressive moving averages (1.1), unstructured compound symmetry and Huynh-Feldt. For multiple mean-value analyses the Tukey test was used.

Multiple linear regressions were chosen to assess those factors which had the most distinct effects on the presence of wild bees. In order to achieve a normal distribution of the data, the studied variables were transformed to log-normal distribution (log₁₀ x+1) whereas percentages were converted by angular transformation (arc sin). The availability of resources was analyzed concerning the abundance as well as the cover of flowering plant species. Additionally, the following independent habitat parameters were included: absolute species numbers of plants and cover of open soil. Due to the high correlation coefficients of the cover of forbs and graminoids, these values were not included in the regression analysis.

Results

Floristic structure and flower resources of the vegetation

Table 1 shows the floristic structure of the five vegetation types or complexes (see also Fig. 1a–d). Type 1 is characterized by the Koelerion glaucae vegetation complex with *Koeleria glauca* and others, intermingled with *Corynephorretalia* pioneer species such as, e.g. *Phleum arenarium* and *Veronica praecox*. Especially *Koeleria glauca*, *Veronica praecox* as well as *Tortella inclinata* indicate the base-rich conditions of this vegetation complex. Type 2a (Armerio-Festucetum trachyphyllae) is characterized by species which indicate slightly acidic conditions: *Armeria maritima* subsp. *elongata*, *Koeleria macrantha*, *Cerastium arvense* and others are diagnostic species. Partly they are also diagnostic species of the ruderalized type 2b; additionally, entomophilous species as *Berteroa incana* and *Centaurea stoebe* s.l. (both also in 3, 4) are present as well as competitive graminoids (*Cynodon dactylon*) and more mesophytic species (*Plantago lanceolata*). The ex-arable field (Type 3) is situated in the

Table 1. Vegetation of the five vegetation types or complexes for the two study years (presence table); relevés sampled in permanent plots. Column R: Red List plant species Hesse (HMULV 2008), Column F: fr = Flower resources used by wild-bees in the whole study period; mr = Main flower resources used by wild bees in the whole study period, defined after the key species of the bee-flower networks in the study area according to Kratochwil et al. (2009).

Habitat type		1		2a		2b		3		4		
		Koelerion glaucae complex		Armerio-Festucetum trachyphyllae		Armerio-Festucetum ruderalized		ex-arable field		Allio-Stipetum capillatae		
Number of relevés		9	9	9	9	9	9	9	9	9	9	
R	F	Year	Year	Year	Year	Year	Year	Year	Year	Year	Year	
Diagnostic species, type 1												
3		Silene otites	100	100	22	22	44	44	56	56	44	.
		Myosotis stricta	67	100	56	44	11	11	.	.	11	.
3		Corynephorus canescens	89	89	56	44	11	11
		Saxifraga tridactylites	100	100	22	22	22	22
3		Peltigera rufescens	67	56	22	11	11	11
		Poa bulbosa	100	100	67	33	11	.
		Erophila verna	56	22	.	.	11	.	.	.	11	11
2		Cetraria aculeata	100	78	44	22
		Cladonia rangiformis	100	89	44	56
3		Phleum arenarium	100	100	11	.	.
2		Koeleria glauca	78	78	11	.
3		Veronica praecox	78	78
		Carex praecox	33	22
		Tortella inclinata	44	33
Diagn. species, type 1, 2a (Salsolion species)												
		Psyllium arenarium	78	100	78	44	11	11	.	.	.	11
		Setaria viridis	89	78	11	22	11	11
	fr	Salsola kali subsp. tragus	78	78	33	33	11	.
Diagnostic species, type 1,4												
3	fr	Helichrysum arenarium	100	100	56	11	100	89
	fr	Senecio vernalis	89	78	67	22
Diagnostic species, type 2 a, b												
		Festuca brevipila (= trachyphylla)	33	33	100	100	100	100	33	44	22	22
	fr	Cerastium arvense	11	11	78	67	100	100	11	11	33	22
	fr	Potentilla argentea agg.	11	11	89	89	89	100	.	44	78	78
3	fr	Armeria maritima subsp. elongata	.	.	78	78	67	89	11	11	11	22
		Agrostis capillaris	.	.	44	78	22	22	.	.	22	11
Diagnostic species, type 2 a												
3		Koeleria macrantha	33	22	100	100	56	67	44	67	56	56
		Rumex acetosella s.l.	44	56	89	78	22	33	.	.	22	22
		Elytrigia campestris x Elytrigia repens	.	.	78	78	11	.
	fr	Hieracium pilosella	.	.	33	44	11
		Agrostis vinealis	.	.	22	22
		Galium verum agg.	.	.	22	22
		Scleranthus annuus agg.	.	.	11	11
Diagnostic species, type 2 b												
		Silene latifolia subsp. alba	11	.	44	11	89	78	33	44	22	11
		Cynodon dactylon	33	33	22	22	89	89	44	33	.	.
		Plantago lanceolata	.	.	33	33	89	89	22	33	11	11
		Festuca rubra	.	.	11	11	67	67	22	33	.	.
Diagnostic species, type 3 (4)												
	fr	Vicia angustifolia agg.	33	22	.	11	11	11	67	67	11	.
		Bromus sterilis	22	11	.	.	11	.	89	67	11	11
	fr	Tragopogon dubius	11	11	.	.	44	.	89	78	44	11
		Convolvulus arvensis	.	.	11	.	11	11	67	67	22	.
		Artemisia campestris	56	22	11	11
	fr	Campanula rapunculoides	56	44	33	44
		Vicia hirsuta	67	67	22	22
	fr	Vicia villosa s.l.	89	78	22	22
	fr	Papaver rhoeas	56	33	22	.
Diagnostic species, type 2 b, 3, 4												
mr		Berteroa incana	22	11	33	33	100	100	100	89	100	89
mr		Centaurea stoebe s.l.	67	33	11	.	100	100	89	100	89	100
Diagnostic species, type 4												
3		Stipa capillata	11	11	11	11	100	100
	fr	Senecio jacobaea	.	.	11	.	11	.	.	.	100	56
3		Phleum phleoides	.	.	.	11	78	67
		Asperula cynanchica	33	11
	fr	Helianthemum nummularium subsp. obscurum	33	33
		Helictotrichon pubescens	22	33
	fr	Salvia pratensis	33	33
	fr	Potentilla tabernaemontani	22	22
	fr	Dianthus carthusianorum	11	22
3		Thymus serpyllum	11	11
3		Allium sphaerocephalon	11	.
Add. Koelerio-Corynephorotea species												
		Arenaria serpyllifolia agg.	100	100	100	100	100	100	100	100	100	100
		Cerastium semidecandrum	89	100	100	100	89	100	56	89	89	89
	fr	Echium vulgare	56	67	89	67	44	33	33	11	89	67
	fr	Erodium cicutarium	100	100	100	100	78	78	44	44	89	67
3	fr	Medicago minima	100	100	100	100	100	100	100	89	100	67
		Petrorhagia prolifera	78	22	56	22	56	56	89	67	100	89
3		Silene conica	100	100	100	67	100	78	100	100	78	67
	fr	Trifolium campestre	44	33	100	78	100	100	100	100	22	22
3		Veronica verna	100	100	67	89	22	22	11	22	33	56
3		Vicia lathyroides	67	78	100	100	89	89	44	44	33	56
	fr	Trifolium arvense	11	11	56	.	44	22	78	33	33	22

Table 1. cont.

R	F	Habitat type	1	1	2a	2a	2b	2b	3	3	4	4
	fr	<i>Sedum acre</i>	67	78	67	89	44	78	.	11	78	67
		<i>Vulpia myuros</i>	89	89	100	89	78	100	44	56	.	11
		<i>Myosotis ramosissima</i>	67	78	67	56	11	33	11	56	.	78
	fr	<i>Alyssum alyssoides</i>	.	.	11	.	56	56	11	11	56	44
		<i>Acinos arvensis</i>	11	.	.	.	11	11
		<i>Ornithopus perpusillus</i>	.	.	.	11
		<i>Scleranthus perennis</i>	.	.	.	11
		<i>Herniaria glabra</i>	11	.
		Add. Festuco-Brometea species										
	mr	<i>Medicago falcata</i> (incl. <i>M. x varia</i>)	11	11	100	100	100	100	89	78	67	78
	mr	<i>Ononis repens</i> s.l.	56	56	56	56	78	78	.	11	89	89
3		<i>Festuca duvalii</i>	11	11	11	11	.	.	11	22	33	44
	fr	<i>Euphorbia cyparissias</i>	100	100	44	44	78	89	.	.	100	89
	fr	<i>Stachys recta</i>	11	11
		<i>Arabis hirsuta</i> agg.	11	.
		Add. competitive graminoids										
		<i>Carex hirta</i>	89	89	78	78	67	67	11	11	100	100
		<i>Poa angustifolia</i>	56	67	89	89	100	100	100	100	100	100
		<i>Elymus repens</i>	44	22	33	33	89	78	89	100	44	11
		<i>Calamagrostis epigejos</i>	11	11	67	56	78	78
		Add. species										
		<i>Bromus hordeaceus</i>	22	22	89	78	100	100	100	100	78	67
		<i>Bromus tectorum</i>	100	100	100	89	67	44	100	100	100	100
		<i>Conyza canadensis</i>	100	89	67	44	89	67	67	67	100	100
	mr	<i>Crepis capillaris</i>	22	11	44	56	89	89	89	89	89	78
	fr	<i>Geranium molle</i>	56	67	100	100	100	100	33	44	89	44
		<i>Oenothera biennis</i> s.l.	33	33	67	67	11	33	33	44	67	100
		<i>Rumex thyrsiflorus</i>	22	11	22	22	33	33	33	67	44	67
	mr	<i>Sisymbrium altissimum</i>	78	78	89	11	100	33	100	44	89	67
	fr	<i>Verbascum phlomoides</i>	56	89	100	100	100	100	100	100	100	100
		<i>Veronica arvensis</i>	89	89	89	100	89	100	78	89	100	78
	fr	<i>Hypochaeris radicata</i>	.	11	11	11	11	33	78	89	67	22
		<i>Cynoglossum officinale</i>	22	33	44	67	.	11	11	22	67	33
		<i>Arabidopsis thaliana</i>	56	33	11	11	22	.	33	44	67	33
		<i>Asparagus officinalis</i>	44	33	44	44	33	22	.	56	56	22
		<i>Chenopodium album</i> s.l.	78	33	67	11	22	22	11	11	.	11
	fr	<i>Hypericum perforatum</i>	33	33	11	11	.	.	11	11	22	11
		<i>Achillea millefolium</i> agg.	.	11	11	.	56	56	44	67	33	44
	fr	<i>Papaver dubium</i> s.l.	.	11	11	11	33	.	44	22	78	33
	fr	<i>Carduus nutans</i>	.	.	100	78	67	67	33	44	67	67
		<i>Taraxacum officinale</i> agg.	.	.	11	11	.	22	22	33	44	67
	fr	<i>Diploaxis tenuifolia</i>	11	11	22	22	56	56
		<i>Prunus serotina</i> juv.	.	11	.	11	.	.	.	22	11	11
		<i>Saponaria officinalis</i>	.	.	22	11	11	.	.	.	22	33
		<i>Crepis tectorum</i>	11	22	11	11
		<i>Rubus caesius</i>	.	.	.	11	11	22
	fr	<i>Thymus pulegioides</i>	.	.	11	11	11	11
		<i>Apera spica venti</i>	11	.	11	.	22	22
		<i>Capsella bursa-pastoris</i>	.	.	11	.	56	11
		<i>Polygonum aviculare</i> agg.	.	.	11	11	.	11
		<i>Galium album</i>	11	22	22
		<i>Malva alcea</i>	11	22	22
		<i>Fallopia convolvulus</i>	11	11	.	.
		<i>Solanum nigrum</i>	.	.	11	11
		<i>Silene vulgaris</i>	44	22
		<i>Carex spicata</i>	11	11
		<i>Erigeron annuus</i>	11	.	.	33	.	.
		<i>Daucus carota</i>	22	33	.	.
		<i>Cirsium arvense</i>	11	11	.	.
	fr	<i>Anchusa officinalis</i>	22	22
		<i>Arabis glabra</i>	11	11
		<i>Arrhenatherum elatius</i>	11	11
		<i>Reseda lutea</i>	11	11
		<i>Tripleurospermum perforatum</i>	11	11
		<i>Populus x canadensis</i> juv.	11
		<i>Cerastium holosteoides</i>	.	.	11
		<i>Geranium pusillum</i>	11
		<i>Lepidium densiflorum</i>	11	.	.	.
		<i>Dactylis glomerata</i>	11	.	.
		<i>Anchusa arvensis</i>	33	.
		<i>Agrimonia procera</i>	11	.
		<i>Viola arvensis</i>	11	.
		<i>Chondrilla juncea</i>	11	.
		<i>Crataegus monogyna</i> juv.	11
		<i>Holcus lanatus</i>	11
		<i>Rosa canina</i> s.l.	11
		Add. lichens										
		<i>Cladonia furcata</i> s.l.	89	100	67	67	33	33
		<i>Cladonia rei</i>	22	11	11	.	.
		<i>Cladonia pyxidata</i>	33	33
		Add. bryophytes										
		<i>Tortula ruraliformis</i>	100	100	67	67	56	56	56	44	56	44
		<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	100	100	100	100	100	100	44	44	100	100
		<i>Brachythecium albicans</i>	44	22	56	56	78	89	100	100	33	44

western part of the Euler-Flugplatz in the landscape matrix of neighbouring Armerio-Festucetum stands. Some species of the Armerio-Festucetum are present, but still there is a ruderal pattern with the entomophilous species *Vicia villosa* s.l. and the above-mentioned flower resources (*Centaurea*, *Berteroa*). Type 4 characterizes a medium successional stage of base-rich sites with the Allio-Stipetum capillatae. It is well characterized by *Stipa capillata* and some other Festuco-Brometea species such as *Dianthus carthusianorum*, *Helianthemum nummularium* subsp. *obscurum* among others. *Helichrysum* shows a high presence and characterizes the ‘type on sandy substrate’ of the Allio-Stipetum. Especially the types 1, 2 and 4 are rich in Red List plant species (13–15 species according to HMULV 2008); the ruderalized types show lower values (7–9), see Table 1, column R.

The important flower resources for bees in these vegetation types or complexes are added in column F in Table 1, according to the network study of Kratochwil et al. (2009, same study site). The most important resources are mainly concentrated in the more ruderalized types (e.g. *Berteroa incana*, *Sisymbrium altissimum*). Also common Asteraceae-species such as *Centaurea stoebe* s.l. and *Crepis capillaris* play an important role. A remarkable pollen resource is *Salsola kali* subsp. *tragus*, which is frequently visited by the endangered bee species *Nomioides minutissimus*.

DCA results and further vegetation data

Vegetation types are represented from the left to the right side in the ordination diagram (Fig. 2). According to the eigenvalues especially Axis 1 is far more relevant than Axis 2. The medium successional stage type 4 (Allio-Stipetum) is separated on the left side, compared to the open

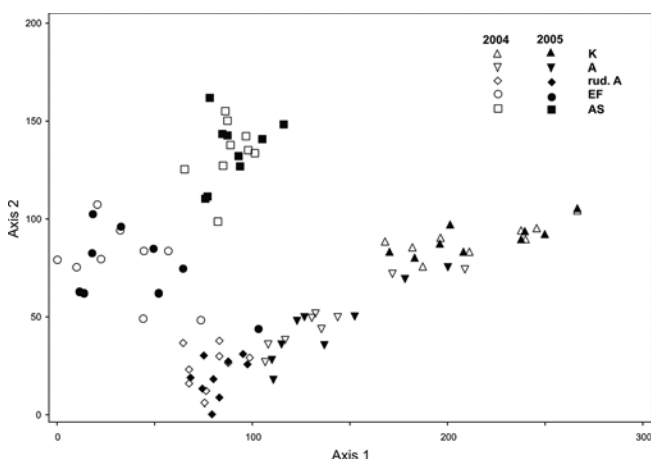


Fig. 2. DCA of the ordinal plant species data of the five different vegetation types or complexes for two years (2004 and 2005; 9 plots each). Eigenvalues: axis 1: $\lambda = 0.32$, axis 2: $\lambda = 0.14$; gradient length: 100 = 1 SD.

Koelerion glaucae complex on the right side. Within the types 1, 2a there are gradients in the diagram from open plots to more developed ones, reflecting the amplitude of these types. Types 2b to 3 represent the ruderalized types.

Fig. 3a–f and Table 2 show characteristics of the vegetation types in some more detail.

Concerning the mean number of plant species (Fig. 3a), there were only slight differences between the vegetation types, merely 2004 (not 2005) was characterized by minor but significant differences between the types (the ex-arable field showed lower values than the Allio-Stipetum and Koelerion glaucae complex). Concerning the factor ‘year’, significant decreases were observed in the Armerio-Festucetum and the Allio-Stipetum. The number of flowering plant species (Fig. 3b) was significantly lower in the Koelerion glaucae complex and Armerio-Festucetum than in the ruderalized Armerio-Festucetum and the ex-arable field. The highest number of flowering species was detected in type 4 (Allio-Stipetum). In this type, the total species number significantly decreased from 2004 to 2005 ($p = 0.027$).

The most obvious difference between the vegetation types or complexes was the cover of forbs (Fig. 3c), which was lowest in the Koelerion glaucae complex and significantly higher in the ex-arable field, with medium values in the other vegetation types. There was a general tendency of decrease in cover of the flowering plants from 2004 to 2005 (Fig. 3d), which was significant in the ruderalized Armerio-Festucetum as well as the ex-arable field. Here, the highest cover values of flowering plant species on all study sites were assessed in 2004. The extremely low cover values in the ex-arable field in 2005 were an exception (see Discussion). The Allio-Stipetum was characterized by a higher graminoid cover than the other vegetation types (Fig. 3e). There were no significant differences concerning the mean cover value of open-soil (Fig. 3f) due to a large variation.

Community structure of wild-bee species in the different vegetation types or complexes

According to Table 3 and the DCA (Fig. 4a, b), the different vegetation types or complexes showed especially in the year 2004 two main bee assemblages. Types 1 and 2 of the vegetation types or complexes were negatively characterized by the (near) absence of species such as *Andrena pilipes*, *Melitta leporina* and others. The other vegetation types or complexes showed a more diverse group of target bee species for dry habitats and the group of ‘other species’. A typical combination of sand- and dry-grassland specific bees could be observed in all vegetation types or complexes (e.g. *Halictus leucabeneus*, *H. smaragdulus*). *Nomioides minutissimus* was observed mainly in the Koelerion glaucae type with the main local pollen source *Salsola kali* subsp. *tragus* (Koelerion com-

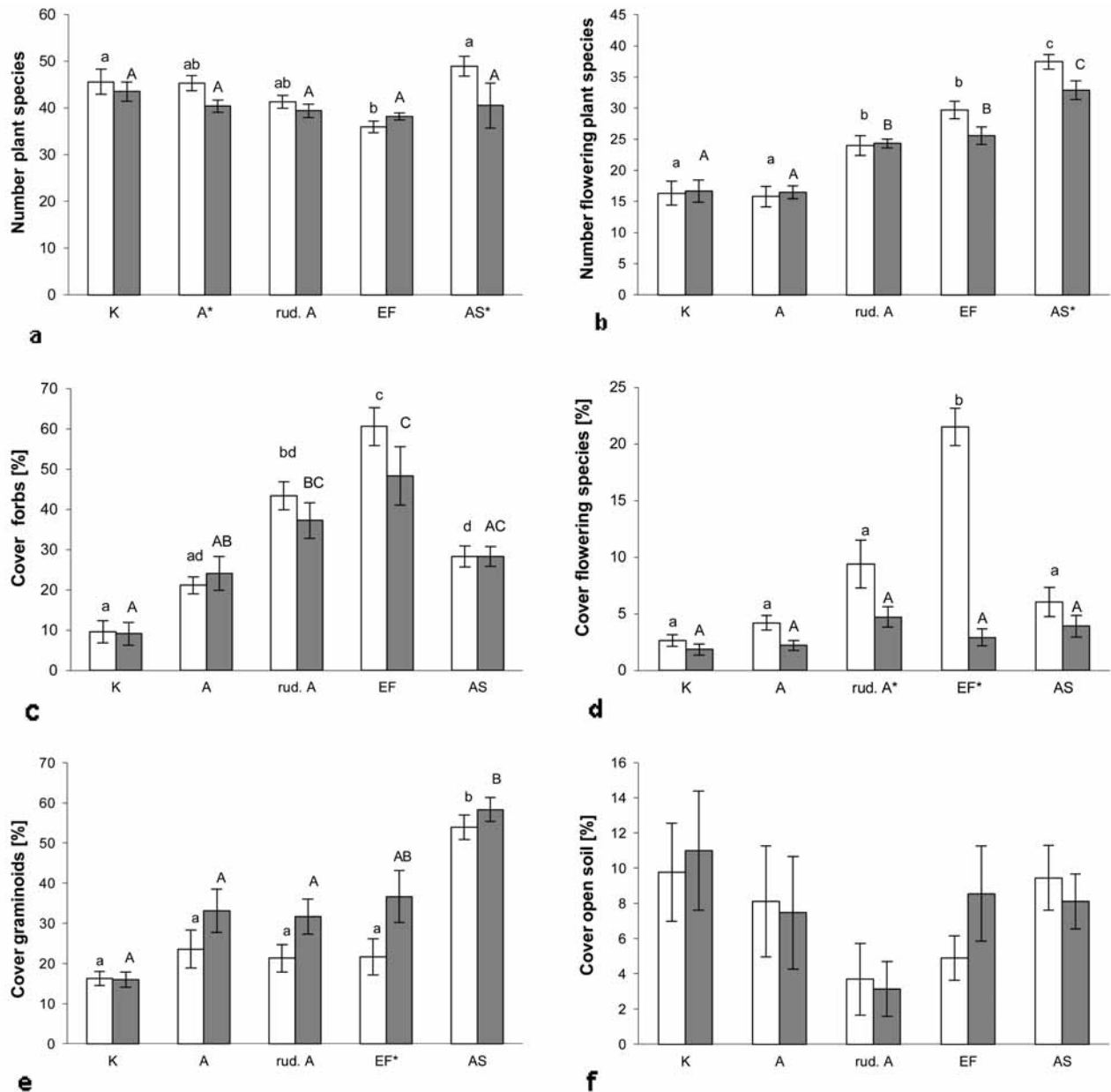


Fig. 3a–f. Characterization of the different vegetation types or complexes in the permanent plots (9 for each type and year). Plant species: all species of the relevés, flowering plant species: entomophilous species. K = *Koelerion glaucae* complex, A = *Armerio-Festucetum typicum*, rud. A = ruderalized *Armerio-Festucetum*, EF = ex-arable field, AS = *Allio-Stipetum*. Significant differences within vegetation types or complexes between 2004 and 2005 are marked by “*”, between the vegetation types or complexes of one year: lower-case letters for 2004 and capital letters for 2005. f open soil: no significance. Significance was set at $p < 0.005$. Error bars = standard errors.

plex). Red List species (following Tischendorf et al. 2009) occurred in all vegetation types or complexes in similar numbers (Table 3). Concerning the numbers of wild-bee species and individuals (Table 4), significant differences were observed among the vegetation types or complexes, the different study years as well as their interaction (type*year), regardless of whether *Bombus* and parasites are taken into consideration or not. Only concerning *Bombus* was the interaction not significant.

The specific vegetation types or complexes are characterized by significantly different species numbers of bees (Fig. 5a–f). Highest species diversity (Fig. 5a) was reached in the ruderalized *Armerio-Festucetum*, the ex-arable field site as well as in the *Allio-Stipetum*. In 2005, the study sites became more similar due to the significantly decreasing species numbers in the ex-arable field (see Discussion). The categories ‘wild bee species without *Bombus*’ and ‘*Bombus* species’ (Fig. 5c, e) showed the

Table 2. Results of the mixed linear model of the studied vegetation types or complexes; degrees of freedom (numerator, denominator): habitat type (4, 40), year (1, 40), habitat type*year (4, 40); F: F value; p = statistical significance; ns = not significant.

	F	p
Mean number plant species		
Habitat type	3.5	0.0162
Year	15.7	0.0003
Habitat type*year	5.0	0.0024
Mean number flowering plant species		
Habitat type	32.3	< 0.0001
Year	6.8	0.0136
Habitat type*year	4.3	0.0057
Mean cover herbs		
Habitat type	22.7	< 0.0001
Year	2.7	ns
Habitat type*year	2.0	ns
Mean cover flowering plant species		
Habitat type	16.0	< 0.0001
Year	97.9	< 0.0001
Habitat type*year	33.5	< 0.0001
Mean cover graminoids		
Habitat type	14.1	< 0.0001
Year	22.2	< 0.0001
Habitat type*year	2.5	0.0586
Mean cover open soil		
Habitat type	1.2	ns
Year	0.3	ns
Habitat type*year	1.1	ns

same tendency. Only the Armerio-Festucetum was characterized by an increase of bee species diversity (without *Bombus*) in the year 2005.

Concerning the bee abundance (Fig. 5b), in 2004 only the ex-arable field site significantly differed from the Koelerion complex, Armerio-Festucetum and ruderalized Armerio-Festucetum due to a higher abundance of *Bombus* as well as other wild-bee species (Fig. 5d, f). Except for the wild bees (without *Bombus*) in the Armerio-Festucetum all types were characterized by generally decreasing numbers of individuals in 2005, although these differences are only significant in the ex-arable field. This can be attributed to the decreasing *Bombus* abundance of up to 95 %. Rare plant species were not frequently visited by wild-bee species; only the endangered *Medicago minima*, *Armeria maritima* subsp. *elongata* and *Helichrysum arenarium* were visited at all, and only two or three Red List bee species were detected (Table 5). On the other

hand, plants with mainly ruderal occurrence such as *Centaurea stoebe* s.l., *Berteroa incana* and *Carduus nutans* were visited by five to nine Red List bee species (Table 5).

Factors influencing the community structure of wild bees

Regression analysis was used to assess specific factors influencing the occurrence of wild bees in the study sites (Fig. 6). Concerning species numbers the results of the multiple regression analysis (Table 6) show a high adjusted degree of determination of $r^2 = 0.69$. The number of flowering plant species shows a highly significant correlation with numbers as well as abundance of wild-bee species (Fig. 6a, b). There are also close positive correlations between bee species and abundance and cover of flowering plant species (Fig. 6c, d). The cover of open soil does not show any significant correlation with bee occurrence (Table 6).

Discussion

In the following we discuss the questions 1–3 which were highlighted in the Introduction.

Are there congruent characteristics in the community structure of plant and bee species in the studied vegetation?

Although there were clear floristic differences between the five vegetation types or complexes, gradients were observed, especially between types 2b and 3, which can be seen in the DCA diagram.

The DCA of the bee species, on the other hand, did not show such clear differentiations among the floristically pre-determined types, and there was only a weak differentiation into two assemblages in one of the study years.

Pollen analyses of 558 pollen loads of bee individuals (Beil et al. 2008) showed that the flight-distances and foraging ranges even of small bees are much larger than earlier supposed. We were able to prove by pollen of rare species in the study site (*Tilia*, *Aesculus* and other woody species) that the minimum linear distance between the nearest occurrence of the pollen resource and the observation plot was about 1200 m, e.g. in the case of the small *Lasioglossum fulvicorne* (6–7 mm body size). Apparently, a considerable proportion of the landscape around the study sites is used by the bee species studied. There are only a few specialized oligolectic species, e.g. *Eucera macroglossa*, using the pollen resource of *Malva alcea* in the Allio-Stipetum, and *Osmia adunca*, using *Echium vulgare*.

Table 3. Records of wild bees in the different vegetation types or complexes; bee target species according to Kratochwil (2003). Column A: Status Red List (Tischendorf 2009), B: Indication of parasites, C-E: Bee individuals in the different years and sum.

Habitat type					1	1	2a	2a	2b	2b	3	3	4	4	
A	B	C	D	E	Koelerion glaucae complex		Armerio- Festucetum trachyphyllae		Armerio- Festucetum ruderalized		ex-arable field		Allio- Stipetum capillatae		
Number of plots					9	9	9	9	9	9	9	9	9	9	
Year					2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	
Target species of sandy habitats and dry grassland															
G	38	56	94		Halictus leucaeneus Ebmer, 1972	1	3	4	8	8	17	11	16	14	12
	70	4	74		Andrena pilipes Fabricius, 1781	.	1	.	.	20	2	42	.	8	1
2	22	8	30		Nomioides minutissimus (Rossi, 1790)	16	6	6	1	1
	7	1	8		Andrena bimaculata (Kirby, 1802)	2	.	4	1	1	.
	2	3	5		Osmia adunca (Panzer, 1798)	1	.	2	.	.	.	1	1	.	.
G	2	3	5		Lasioglossum aeratum (Kirby, 1802)	.	.	1	.	.	1	.	.	2	1
	4	.	4		Megachile pilidens Alfken, 1924	1	3	.	.	.
G	2	2	4		Andrena barbilabris (Kirby, 1802)	1	2	1	.	.	.
3	1	1	2		Andrena argentata Smith, 1844	1	1	1	.	.	.
3	1	.	1		Rhopitoides canus (Eversmann, 1852)	1
P	.	1	1		Stelis punctulatisima (Kirby, 1802)	1
1	1	.	1		Lasioglossum prasinum (Smith, 1848)	1	.
Target species of dry habitats with broader habitat amplitude															
G	22	41	63		Halictus smaragdulus Vachal, 1895	1	4	6	10	8	12	2	4	5	11
	27	16	43		Dasygaster hirtipes (Fabricius, 1793)	4	5	10	7	13	4
	23	6	29		Melitta leporina (Panzer, 1799)	.	.	2	.	12	1	5	1	4	4
2	19	.	19		Megachile maritima (Kirby, 1802)	3	.	.	.	9	.	7	.	.	.
2	6	5	11		Eucera macroglossa Illiger, 1806	6	5
	1	4	5		Osmia spinulosa (Kirby, 1802)	2	1	2
	1	4	5		Halictus scabiosae (Rossi, 1790)	.	1	.	.	.	2	1	1	.	.
	2	.	2		Hylaeus annularis (Kirby, 1802)	1	.	1	.
P	1	.	1		Epeolus variegatus (Linnaeus, 1758)	1
2	P	.	1		Coelioxys conoidea (Illiger, 1806)	.	.	1
	1	.	1		Colletes fodiens (Fourcroy, 1785)	1	.
	1	.	1		Panurgus calcaratus (Scopoli, 1763)	1	.
	1	.	1		Anthidium punctatum Latreille, 1809	1	.
3	.	1	1		Anthidium nanum Mocsáry, 1881	1
3	.	1	1		Ceratina chalybea Chevrier, 1872	1
Other wild-bee species															
	401	145	546		Bombus lapidarius (Linnaeus, 1758)	27	18	25	4	67	72	208	8	74	43
	208	16	224		Bombus terrestris (Linnaeus, 1758)	7	.	7	1	25	8	125	5	44	2
3	37	16	53		Bombus humilis Illiger, 1806	2	.	1	8	7	13	2	14	6	
3	19	27	46		Halictus sexcinctus (Fabricius, 1775)	4	3	1	6	5	12	8	5	1	1
	30	9	39		Lasioglossum leucozonium (Schrank, 1781)	2	.	.	.	2	1	13	5	13	3
	37	1	38		Andrena flavipes Panzer, 1799	1	.	.	.	11	1	13	.	12	.
	19	18	37		Halictus subauratus (Rossi, 1792)	6	1	.	2	2	3	1	3	10	9
	18	18	36		Lasioglossum calceatum (Scopoli, 1763)	.	.	.	1	3	6	12	8	3	3
	24	5	29		Andrena ovata (Kirby, 1802)	4	1	4	.	6	1	5	1	5	2
	6	21	27		Lasioglossum fulvicorne (Kirby, 1763)	.	3	.	7	1	1	1	1	4	9
	24	1	25		Andrena dorsata (Kirby, 1802)	7	.	11	1	6	.
	13	10	23		Bombus pascuorum (Scopoli, 1763)	2	.	1	.	1	7	4	2	5	1
	12	10	22		Lasioglossum pauxillum (Schenck, 1853)	5	1	1	1	1	1	1	4	5	3
	6	13	19		Halictus confusus Smith, 1853	1	.	.	2	1	3	1	.	3	8
	4	12	16		Lasioglossum morio (Fabricius, 1793)	.	.	1	3	2	6	.	.	1	3
	2	11	13		Lasioglossum albipes (Fabricius, 1781)	.	1	.	.	2	.	4	.	2	4
G	5	6	11		Osmia crenulata (Nylander, 1856)	2	.	5	3	.	1
	3	7	10		Bombus sylvarum (Linnaeus, 1761)	2	.	1	2	2	3
	4	5	9		Halictus tumulorum (Linnaeus, 1758)	.	1	.	1	1	.	.	1	3	2
	5	2	7		Megachile rotundata (Fabricius, 1787)	.	.	1	.	1	2	3	.	.	.
	4	2	6		Andrena alfenella Perkins, 1914	.	.	1	.	3	1
	2	3	5		Megachile willughbiella (Kirby, 1802)	.	1	.	1	1	1	.	.	1	.
	2	3	5		Lasioglossum lucidulum (Schenck, 1861)	1	.	.	.	1	3
	3	2	5		Osmia aurentata (Panzer, 1799)	1	.	.	.	2	2
2	1	2	3		Halictus quadricinctus (Fabricius, 1776)	.	.	1	.	.	1
	2	1	3		Lasioglossum lativentre (Schenck, 1853)	.	.	.	1	.	.	1	1	.	.
	2	1	3		Andrena falsifica Perkins, 1915	1	.	.	.	1	1
	3	.	3		Anthidium manicatum (Linnaeus, 1758)	1	.	.	.	2	.
	.	3	3		Ceratina cyanea (Kirby, 1802)	1	.	1	.	1
	3	.	3		Osmia rapunculi (Lepelletier, 1841)	3	.	.	.
	1	1	2		Colletes similis Schenck, 1853	1	1
	2	.	2		Andrena chrysoceles (Kirby, 1802)	.	.	1	1	.
	1	1	2		Lasioglossum laticeps (Schenck, 1870)	1	1
	1	1	2		Lasioglossum punctatissimum (Schenck, 1853)	1	1	.	.	.
	1	.	1		Osmia truncorum (Linnaeus, 1758)	1
	.	1	1		Andrena synadelpha Perkins, 1914	.	1
	.	1	1		Colletes cunicularius (Linnaeus, 1761)	.	1
	.	1	1		Lasioglossum vilosum (Kirby, 1802)	.	1
	.	1	1		Andrena tibialis (Kirby, 1802)	.	.	.	1
	.	1	1		Halictus pollinosus Sichel, 1860	.	.	.	1
P	1	.	1		Nomada fulvicornis Fabricius, 1793	1
	1	.	1		Osmia bicornis (Linnaeus, 1758)	1
P	1	.	1		Sphecodes longulus Hagens, 1882	1
	1	.	1		Megachile ericetorum Lepelletier, 1841	1
	.	1	1		Hylaeus angustatus (Schenck, 1861)	1
	.	1	1		Andrena minutula (Kirby, 1802)	1
P	.	1	1		Sphecodes albilabris (Fabricius, 1793)	1
	1	.	1		Andrena subopaca Nylander, 1848	1	.	.	.
	1	.	1		Lasioglossum minutissimum (Kirby, 1802)	1	.	.	.
	1	.	1		Bombus pratorum (Linnaeus, 1761)	1	.	.	.
3	P	.	1		Sphecodes cristatus Hagens, 1882	1	.	.
	1	.	1		Hylaeus difformis (Eversmann, 1852)	1	.
	1	.	1		Megachile versicolor Smith, 1844	1	.
	1	.	1		Osmia leucomelana (Kirby, 1802)	1	.
P	1	.	1		Sphecodes ephippius (Linnaeus, 1767)	1	.
	.	1	1		Ceratina cucurbitina (Rossi, 1792)	1
P	.	1	1		Sphecodes monilicornis Kirby, 1802	1
Sum					87	49	60	57	223	189	523	91	279	156	
Number of Red Data species					6	4	4	8	7	9	9	6	7	10	

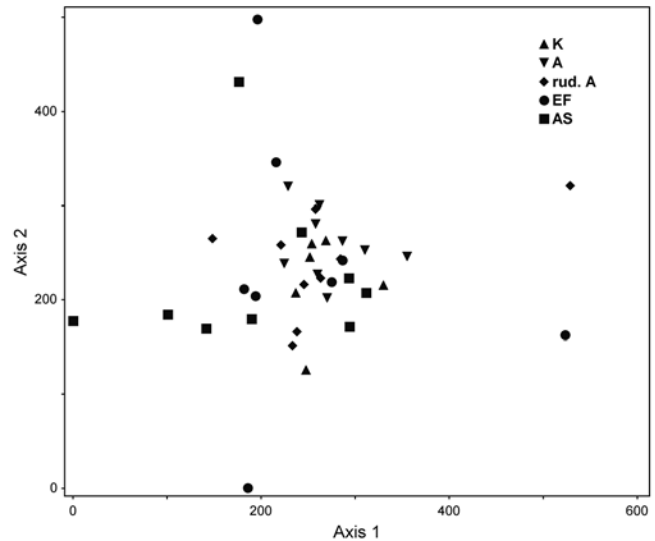
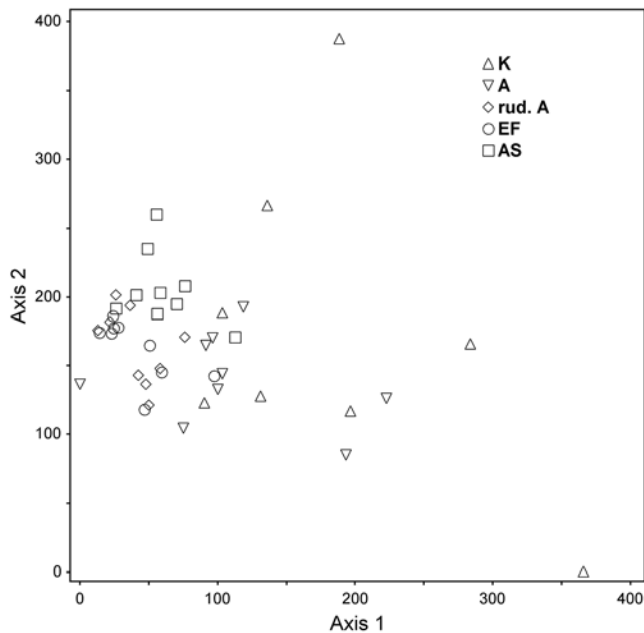


Fig. 4a. DCA of the log ($x+1$) transformed bee abundances in 2004 of the five different vegetation types or complexes (9 permanent plots each). Eigenvalues: axis 1: $\lambda = 0.45$, axis 2: $\lambda = 0.20$; gradient length: 100 = 1 SD.

Fig. 4b. DCA of the log ($x+1$) transformed bee abundances in 2005 of the five different vegetation types or complexes (9 permanent plots each). One outlier (plot C8) was deleted for this analysis. Eigenvalues: axis 1: $\lambda = 0.43$, axis 2: $\lambda = 0.28$; gradient length: 100 = 1 SD.

In contrast to these results on wild bees distinct invertebrate communities according to definable types of vegetation were described for orthopterans, e.g. Zehm (1997) for the study area, and Poniatowski & Fartmann (2008) for other dry grasslands.

Which vegetation types or complexes support the highest numbers of plants and wild bees?

The diversity characteristics of vegetation and bees differed in the study sites. The number of plant species was relatively similar in the studied gradient. If a fine-scale approach is used (2 m² plots instead of 79 m² plots) there is even a peak in the *Koelerion glaucae* complex (Süss et al. 2007), while there is a remarkably high number of wild-bee species in the more ruderalized (2b, 3) and mid-successional vegetation types (4). This is astonishing, because the *Allio-Stipetum* already has high cover of graminoids. The special tussock growth form of the dominant *Stipa capillata* and low shading effects probably allow both high *Stipa* cover and high numbers of flowering plant species. The ruderalization gradient (2b, 3) is characterized by high cover-percentages of forbs and high numbers of flowering plant species (e.g. *Centaurea stoebe* s.l., *Vicia villosa* s.l.). If such types are not managed in the long run, competitive graminoids such as *Cynodon dactylon* and *Calamagrostis epigejos* will become dominant, while the diversity of flowering plant species will decrease (Stroh et al. 2007, Süss et al. 2010, Schwabe et al. 2013).

Steffan-Dewenter & Tscharnke (2001) described highest abundance of wild bees in transitional stages of fallow-land areas where pioneer stages are passing into early succession stages of vegetation dominated by perennial plant species, which is in line with our results. As seen in Fig. 3f the vegetation type ex-arable field still has open soil conditions but already perennial plant species, especially Fabaceae species as e.g. *Vicia villosa* s.l. Potts et al. (2003) stated that, in Mediterranean regions, higher bee diversity depends primarily on the existing plant diversity, but for our study this is only true if the diversity of flowering entomophilous plant species is emphasized. A very important parameter which determines assessment of wild-bee diversity is probably the species richness of flowering plant species. This is in accordance with the results of Steffan-Dewenter & Tscharnke (2001).

All vegetation types showed a heterogeneous pattern of bare-soil gaps, while also sand trails (partly by livestock, see Eichberg et al. 2008), small tracks and slopes provided nesting places for ground-nesting wild-bee species. As an example colonies of *Andrena pilipes* occurred on sandy paths in the *Koelerion* area of the Euler-Flugplatz, and important flower resources are used in the vegetation types 2b and 3.

In other studies we were able to show that the types 1, 2a, 2b and 3 also reflect a gradient of increasing soil-nutrients (see Section 'Study area, stages of succession and ruderalization'). According to Burkle & Erwin (2010) low nitrogen levels favour forbs, and therefore also flower production of mostly entomophilous plant spe-

Table 4. Results of the mixed-linear model concerning the number of species and individuals of bees; degrees of freedom (numerator, denominator): habitat type (4, 40), year (1, 40), habitat type*year (4, 40); abbreviations see Table 2.

	F	p
Number wild-bee species		
Habitat type	13.5	< 0.0001
Year	17.6	0.0001
Habitat type*year	3.7	0.0117
Number wild-bee species without <i>Bombus</i>		
Habitat type	12.2	< 0.0001
Year	11.0	0.0019
Habitat type*year	5.2	0.0017
Number <i>Bombus</i> species		
Habitat type	7.7	0.0001
Year	24.4	< 0.0001
Habitat type*year	1.4	ns
Number wild-bee species without <i>Bombus</i> and parasites		
Habitat type	12.2	< 0.0001
Year	11.4	0.0017
Habitat type*year	5.3	0.0016
Abundance wild-bee species		
Habitat type	9.7	< 0.0001
Year	33.8	< 0.0001
Habitat type*year	13.3	< 0.0001
Abundance wild-bee species without <i>Bombus</i>		
Habitat type	8.2	< 0.0001
Year	22.8	< 0.0001
Habitat type*year	8.7	< 0.0001
Abundance <i>Bombus</i>		
Habitat type	7.7	0.0001
Year	27.5	< 0.0001
Habitat type*year	11.7	< 0.0001
Abundance wild-bee species without <i>Bombus</i> and parasites		
Habitat type	8.3	< 0.0001
Year	23.4	< 0.0001
Habitat type*year	8.9	< 0.0001

cies and pollinator visitation. This was not detected for our Koelerion glaucae complex (Type 1), which is characterized by low nitrogen levels (Bergmann 2004) but low cover percentages of forbs and graminoids. It is remarkable that the pioneer stages (Type 1) show such a high phytodiversity, which is not accompanied by high numbers of flowering entomophilous plant species, and therefore there is a relatively low bee diversity compared to

the other vegetation types or complexes. Nevertheless there was one plant species with high presence in the Koelerion complex, *Salsola kali* subsp. *tragus*, which is often assumed to be mainly wind-pollinated (Blackwell & Powell 1981). In our study *Salsola* was an important pollen resource for the endangered bee species *Nomioides minutissimus* (which also visits *Thymus serpyllum* and *T. pulegioides*).

The bee community of the five vegetation types or complexes formed a network conducted mainly by ruderal plant species or those with ruderal tendency such as *Centaurea stoebe* s.l., *Berteroa incana* or species which are ubiquists such as *Crepis capillaris* (Kratochwil et al. 2009). The great importance of ruderal species for wild bees was pointed out e.g. by Kratochwil & Klatt (1989) and Kratochwil (2003). Threatened plant species did not belong to the top species regarding bee visitation; on the contrary a common plant species (*Centaurea stoebe* s.l.) was visited by up to nine threatened bee species.

Are there differences between the floristic/faunistic structure of vegetation and flower-visiting bee species in the studied years?

The vegetation data show only slight differences in the structure of the two studied years. However, in extreme years with e.g. high temperature there are severe impacts, resulting in a decrease of mainly annual species, as was shown for the area Euler-Flugplatz by Faust et al. (2011b).

The resource parameters 'number of flowering plant species' and 'cover of flowering plant species' were key factors for the occurrence of high bee diversity. The present study revealed generally lower numbers of bee species and individuals in the year 2005. Fluctuations of bee species, their faunistic structure and their abundances between different years have already sufficiently been proven by several studies (among others by Herrera 1988, Oertli 2005, Larson et al. 2006). Annual changes in the number of bee individuals are common, as shown in other areas (e.g. Wilson et al. 2009, Tepedino & Stanton 1981), even when the flower resources are similar. Often no clear correlation with possible factors such as pesticide use or fragmentation (Patiny et al. 2009) is detectable. Our results emphasize the importance of studying bee communities for more than one vegetation period; mostly studies are made for only one year and often only for some weeks.

Conclusions for nature conservation

The results show that the high conservation value of vegetation and habitat types 1, 2a and 4 is not fully compatible with the structure of the bee community. The great

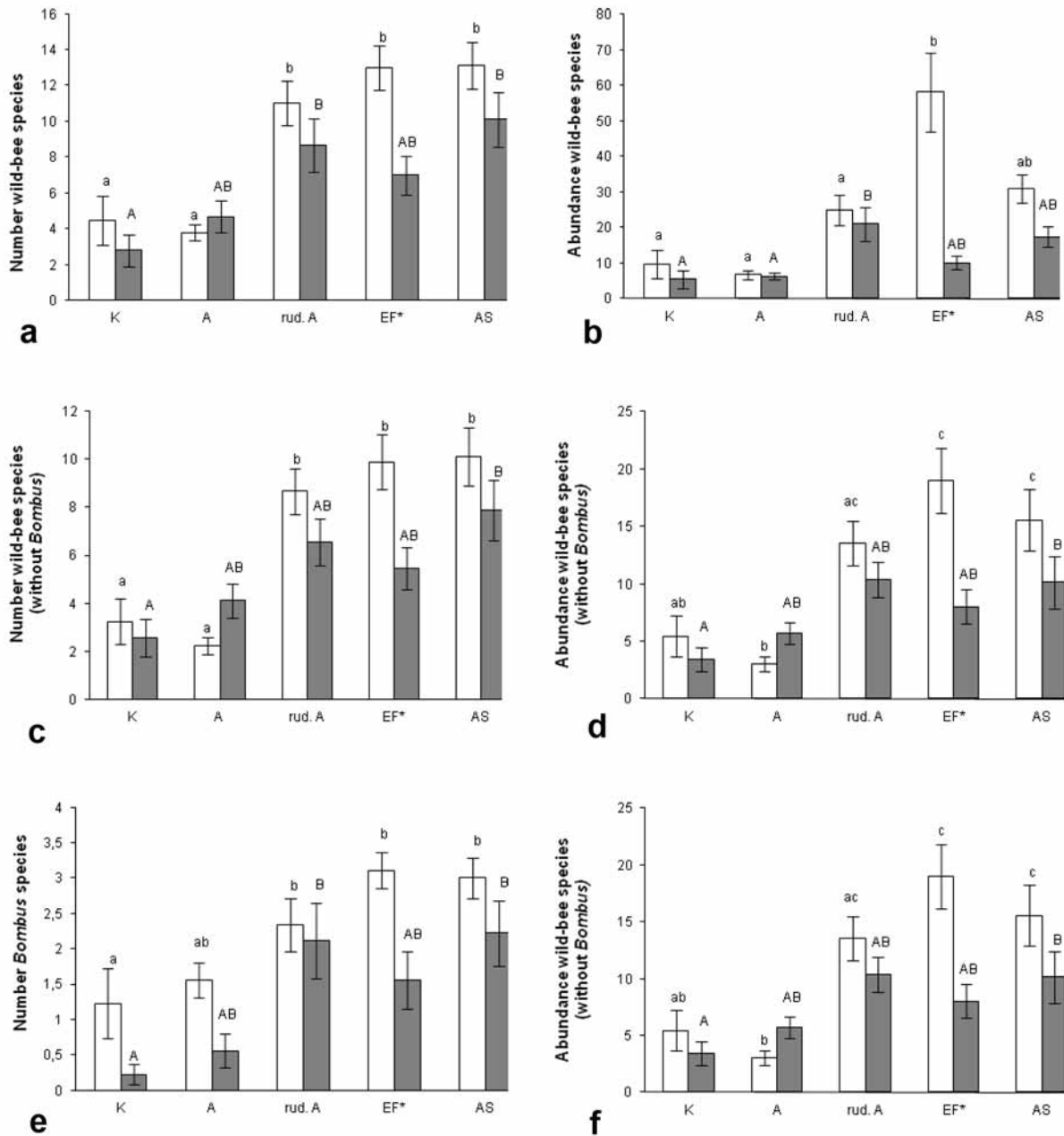


Fig. 5a–f. Diversity characteristics of wild bees in the studied vegetation types or complexes (permanent plots, 9 for each type and year); abbreviations, see Fig. 3.

importance of ruderal plant species for wild bees is well known (Kratochwil 2003) and was shown in this study. It should be taken into consideration that a flower-rich pattern must be guaranteed in grazed nature-protection areas. On one hand grazing is necessary to prevent further ruderalization with dominant graminoids, e.g. *Calamagrostis epigejos* (Süss et al. 2004, Schwabe et al. 2013), but on the other hand the grazing pattern should be differentiated to protect sufficient flower resources (Beil & Kratochwil 2004). Because of the high spatio-temporal variation of bee communities (Murray et al. 2009) it is impor-

tant to have large nature-conservation areas of semi-natural vegetation, for example, by re-uniting formerly large areas which are fragmented today with the help of restoration measures, and also to integrate fallows (Eichberg et al. 2010, Krausch 2011, 2012). This will secure pollination services for neighbouring agricultural fields as well (Klein et al. 2012).

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Table 5. Red-listed plant species and number of visiting bee species; additionally data on top-visited plant species and Red-listed bees (all data for the two study years).

Plant species Red-listed plant species	Species number all flower-visiting bees	portion red-listed bee species
Medicago minima	11	2
Armeria maritima subsp. elongata	8	3
Helichrysum arenarium	7	3
Top-five plant species according to number of flower visits (wild bees)		
Centaurea stoebe s.l.	35	9
Crepis capillaris	27	3
Berteroa incana	22	7
Medicago falcata	15	4
Ononis repens	15	3
Additional plant species with high proportion of red-listed bees		
Carduus nutans	12	5
Potentilla argentea	13	4

Table 6. Results of the multiple linear regression analysis. regr = regression coefficient (slope), SE = standard error, p = significance level, ns = not significant.

	regr	SE	p
Number wild-bee species			
Number plant species	0.03	0.05	ns
Number plant species in flower	0.34	0.05	< 0.001
Cover plant species in flower	14.39	2.86	< 0.001
Cover open soil	-3.27	2.10	ns
Abundance wild-bee species			
Number plant species	-0.001	0.004	ns
Number plant species in flower	0.026	0.004	< 0.001
Cover plant species in flower	1.76	0.24	< 0.001
Cover open soil	-0.32	0.18	ns

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tris x Elytrigia repens, and to Dr. A. Thorson (Oxford) for language revision. Financial support was provided by the ‘Deutsche Bundesstiftung Umwelt’ and the ‘German Federal Ministry for Education and Research’ (BMBF, No. 01LN0003). We also are very grateful to the reviewers for helpful comments on an earlier version of the manuscript. We thank the regional administration (Regierungspräsidium Darmstadt) for the permission to carry out our investigations in nature reserves and to collect bee specimens by selective methods.

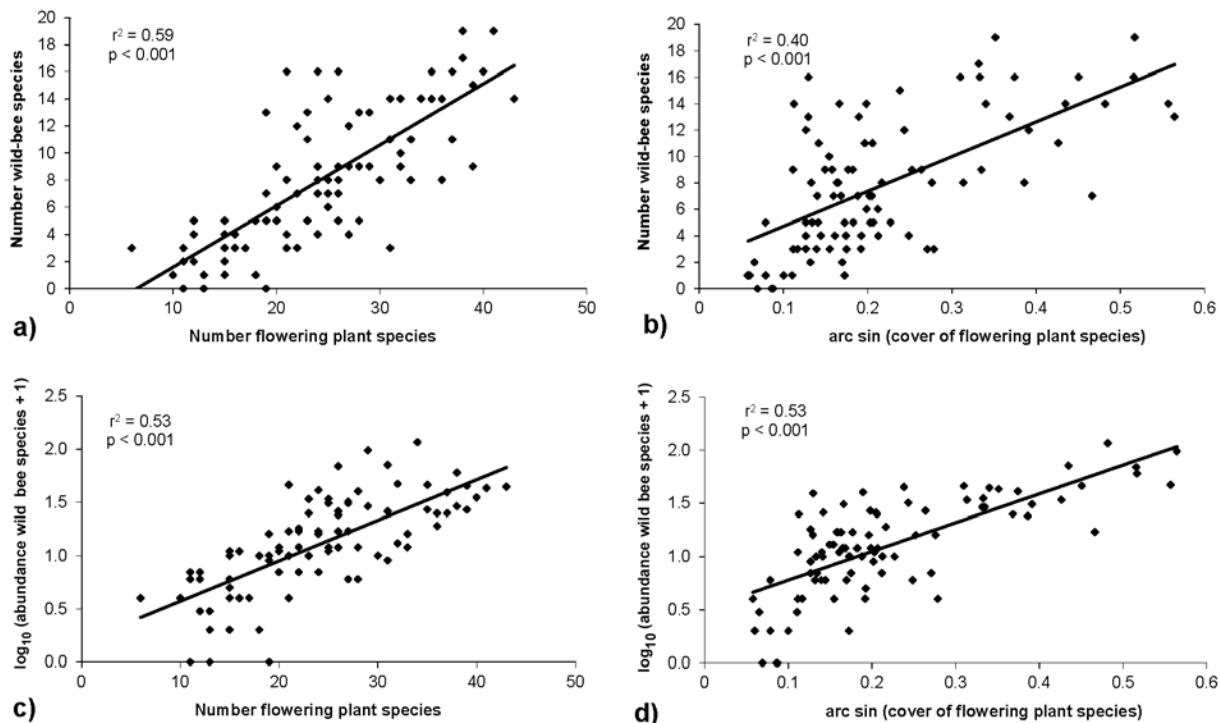


Fig. 6a–d. Scatterplot and regression of wild-bee species numbers and individuals in dependence on resources.

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