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The influence of matrix type on flower visitors of *Centaurea jacea* L.

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Abstract

The structure of invertebrate communities is impacted by landscape variables. Here we present a study on the influence of the surrounding matrix on pollinating flower visitors of the knapweed *Centaurea jacea* in a small-scale agricultural landscape (Central Hesse, Germany). The study was carried out in late summer 1998 by monitoring visits of 24 insect taxa at 15 *C. jacea* patches. The following matrix types were studied: (i) arable land only, (ii) arable land close to grassland (<50 m), (iii) a mosaic of arable land, grassland and forests, and (iv) grassland only.

More than half of the flower visitors were bees, with honeybees (*Apis mellifera*) and bumblebees being the dominant taxa. The matrix type did not affect either the mean frequency of total flower visits or the mean richness of all taxa. The same applied to different size classes. Significant matrix effects were confined to five large taxa of the Apoidea: *Bombus lapidarius*, *B. pascuorum*, the *B. terrestris* group, large wild bees (other than bumblebees) and *A. mellifera*. *A. mellifera* significantly preferred patches surrounded by grassland, while large wild bees preferred patches surrounded by a mosaic of arable land, grassland and forests. The flower visiting frequency of all three bumblebee species was high in patches surrounded by grassland, but only the *B. terrestris* group showed a clear-cut preference for this matrix type.

It is concluded that matrix effects on flower visitors of *C. jacea* are taxon- and body size-specific. Strong matrix effects on large pollinators suggest that these taxa are able to discriminate between patches. Considering the ecological services provided by pollinators, the preservation of large areas covered by interconnected grassland sites as well as by a mosaic of different land use forms should have high priority in future management strategies.

Keywords: Pollinators; Apoidea; Matrix effects; *Centaurea jacea*; Landscape ecology

1. Introduction

The composition of invertebrate communities is affected by a variety of landscape variables including patch conditions, length of ecotones and quality of the surrounding matrix (Aizen and Feinsinger, 1994; Webb, 1989; Ås, 1999; Duelli et al., 1999; Golden and Crist, 1999; Dauber and Wolters, 2000). However, results on the direction of these effects are conflicting. For example, while decreasing patch size reduced both the diversity and density of insects (Aizen and Feinsinger, 1994; Matter, 1997), patch size had no influence on the visitation rates of the pollinator communities investigated by Schmalhofer (2001). Such contradictory results can partly be explained by the fact that landscape effects on community structure are taxon specific, i.e. depend on habitat-specific responses of the organisms involved and on specific ecological processes that link landscape

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variation to population dynamics (Dunning et al., 1992).

The impact of landscape fragmentation on pollinators has been strongly underestimated in the past (Walther-Hellwig and Frankl, 2000). For this reason, we studied the influence of the surrounding matrix on pollinating flower visitors of the knapweed *Centaurea jacea* L., 1753. Agricultural management has a very strong isolating effect on this species, which makes it particularly well suited for the analysis of matrix effects. By selecting *C. jacea* patches that differ in the proportion of arable land in the surrounding area it is possible to systematically vary the degree of isolation. The following hypotheses were tested: (i) matrix effects on pollinating flower visitors of *C. jacea* are taxon- and body size-specific, and (ii) taxonomic richness and density of pollinating flower visitors decrease when the matrix of *C. jacea* patches is dominated by arable land, whereas both parameters increase when the matrix is dominated by grassland.

2. Methods

The study was carried out in late summer 1998 in the Lahn-Dill-Bergland (Central Hesse, Germany). All sites are situated in the rural districts of Hohenahr (Erda) and Biebertal (Frankenbach). A total of 15 *C. jacea* patches were selected by means of a GIS supported analysis (ArcInfo). Each patch was situated on sites that could be assorted to one of the following matrix types (Fig. 1): (A) arable land only (distance from the next grassland at least 200 m, $n = 4$), (AG) arable land close to grassland (distance from the next grassland less than 50 m; $n = 3$), (AGF) a small-scale mosaic of arable land, grassland and forest ($n = 4$), and (G) grassland only (distance from the next arable land at least 200 m, $n = 4$).

Invertebrates foraging at flowers of *C. jacea* were determined seven times during the period of investigation. All observation campaigns were performed under weather conditions that have proven appropriate for the community analysis of flower visitors (e.g. Schwenninger, 1992; Erhardt, 1985; Teräs, 1976; Pollard et al., 1975; Witsack, 1975; Matthews and Matthews, 1971). According to the method suggested by Aizen and Feinsinger (1994), the number and taxonomic composition of insects visiting flowers of *C. jacea* patches were recorded for 15 min on 15 flower heads per patch by one of five experienced entomologists at each date. Each study site was sampled

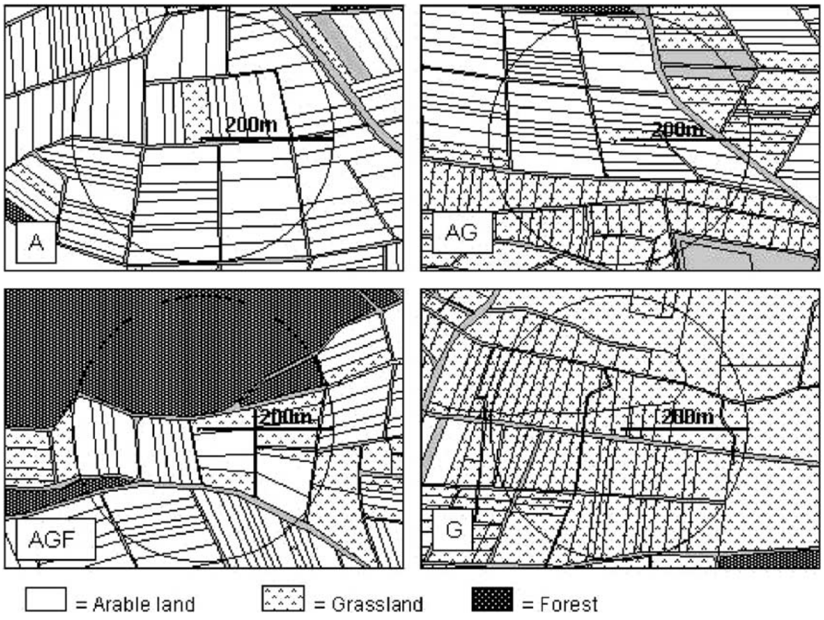

Fig. 1. Examples of the four matrix types.

Table 1

Mean frequency of flower visits and taxonomic richness monitored at *C. jacea* patches surrounded by four different matrix types in late summer 1998 (A: arable land only ($n = 4$), AG: arable land close to grassland (<50 m; $n = 3$), AGF: mosaic of arable land, grassland and forest ($n = 4$), and G: grassland only ($n = 4$))[a]

	A			AG			AGF			G		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Coleoptera	2.00 (1.15)	1.00 (2.00)	1.50 (2.38)	1.67 (2.08)	0.67 (1.15)	1.67 (2.89)	1.00 (0.82)	0.25 (0.50)	3.25 (2.75)	0.75 (0.50)	1.00 (1.41)	0.25 (0.50)
Diptera												
Syrphidae	0.00 (0.00)	1.50 (1.73)	1.00 (1.15)	0.33 (0.58)	0.67 (1.15)	2.67 (2.52)	0.00 (0.00)	3.50 (1.29)	3.00 (3.37)	0.00 (0.00)	1.50 (0.58)	5.75 (5.32)
E. balteatus			4.25 (3.30)			4.67 (3.21)			3.75 (1.71)			3.50 (1.00)
Other Diptera	0.50 (1.00)	0.75 (0.50)	2.25 (0.96)	2.00 (2.65)	7.00 (9.64)	0.33 (0.58)	0.25 (0.50)	1.50 (2.38)	2.75 (1.26)	0.00 (0.00)	1.75 (2.22)	1.00 (1.41)
Hymenoptera												
A. mellifera			11.50 (5.26)			12.67 (21.08)			6.00 (8.49)			66.25 (44.62)
B. lapidarius			7.25 (4.79)			4.00 (4.00)			6.00 (8.83)			5.75 (3.50)
B. terrestris association			0.25 (0.50)			1.33 (2.31)			0.50 (1.00)			4.25 (2.22)
B. pascuorum			6.75 (6.55)			1.67 (2.08)			1.25 (1.26)			5.75 (4.92)
Other *Bombus*			7.0 (5.72)			7.00 (7.27)			3.25 (1.71)			4.50 (3.11)
Wild bees (other than *Bombus*)	0.50 (0.58)	0.50 (0.58)	2.25 (2.22)	0.00 (0.00)	1.00 (1.00)	2.67 (1.15)	0.00 (0.00)	0.00 (0.00)	23.50 (21.49)	0.25 (0.50)	0.50 (0.58)	15.50 (15.44)
Other Hymenoptera	4.00 (2.94)	1.00 (0.82)	3.00 (0.82)	2.67 (2.08)	0.33 (0.58)	0.33 (0.58)	2.75 (3.59)	1.25 (1.50)	1.50 (1.29)	3.75 (2.87)	1.75 (1.71)	1.00 (2.00)
Lepidoptera									4.50 (5.26)			4.00 (3.16)
Maniola jurtina			0.25 (0.50)			0.33 (0.58)			1.50 (2.38)			2.50 (1.73)
Argynnis papia			0.00 (0.00)			0.00 (0.00)			1.00 (2.00)			1.00 (2.00)
Other Lepidoptera			0.81 (1.66)			0.33 (0.50)			2.00 (2.45)			0.50 (1.00)
Taxonomic richness	2. 50 (1.29)	1.26 (2.75)	12.25 (1.26)	2.67 (0.58)	2.67 (1.53)	8.00 (2.65)	1.75 (0.50)	3.25 (0.50)	11.00 (3.37)	2.00 (0.82)	3.75 (0. 96)	11.00 (2.58)
Total flower visits	7.00 (4.19)	4.75 (4.57)	48.06 (15.10)	6.67 (3.06)	9.67 (12.77)	39.67 (31.94)	4.00 (4.08)	6.50 (3.30)	63.75 (32.99)	4.75 (2.99)	6.50 (1.26)	121.50 (56.65)

[a] The species of each taxon where assorted to different size classes: small (<5 mm), medium (5–10 mm), and large (>10 mm). Standard deviation is given in parenthesis.

only once or twice by the same expert to reduce individual bias (Haeseler and Ritzau, 1998; Hermann, 1996). The following taxa were recorded: Coleoptera (pollinating taxa only), Syrphidae, other Diptera (pollinating taxa only), Hymenoptera (other than Apoidea), Apoidea (other than *Bombus* (Latr., 1802) and *Apis mellifera* L., 1758), *Bombus*, *A. mellifera*, and Lepidoptera. The genus *Bombus* was further separated into five taxonomic categories (four species and *Bombus* spp.), Lepidoptera were separated into seven taxonomic categories (six species and 'other Lepidoptera'), and the species *Episyrphus balteatus* (DeGeer, 1776) was separated as an extra taxonomic unit from the Syrphidae. Moreover, all taxa were assigned to one of three size classes: small (<5 mm), medium (5–10 mm), and large (>10 mm). Because not all taxa cover all size classes, a total of 24 taxonomic units could be differentiated (Table 1). Several coarse parameters of community composition were additionally determined: (i) total frequency of flower visits per hour, (ii) total taxonomic richness (i.e. the sum of all taxonomic units), and (iii) frequency of flower visits of the three size classes, and (iv) taxonomic richness of the three size classes. Thus, a total of 32 dependent variables were available for further analyses.

Statistical analyses were carried out using the program STATISTICA for Windows 5.0 (Statsoft, 1995). Small Syrphidae had to be excluded because of their low density. A one-way analysis of variance (ANOVA) was applied to test the effect of matrix type (independent variable) on the flower visiting frequency of the dependent variables listed above. Data were log-transformed prior to analysis. To eliminate a bias caused by patch-specific variations in the density of flower heads, the number of flower heads within a radius of 10 m of both *C. jacea* and other flowering plants was included in the ANOVAs as a co-variable. Differences between means were tested using the Tukey HSD test ($P < 0.05$).

Table 2
Results of the one-way ANOVA on the effect of matrix type on the frequency of flower visits per hour by and taxonomic richness of pollinators of *C. jacea* (significant results are marked with an asterisk, $P < 0.05$; data transformation: $x' = \ln(x + 1)$)

	F-value		
	Small	Medium	Large
Coleoptera	1.33	0.46	1.56
Diptera			
E. balteatus	–[a]	–	0.28
Other Syrphidae	–	0.87	1.34
Other Diptera	0.68	2.65	1.81
Hymenoptera			
A. mellifera	–	–	3.49*
B. lapidarius	–	–	2.83*
B. terrestris s. l.	–	–	3.10*
B. pascuorum	–	–	3.01*
Other *Bombus*			1.14
Other Apoidea	1.19	2.09	2.91*
Other Hymenoptera	0.47	0.84	1.04
Lepidoptera	–	–	
Maniola jurtina	–	–	2.23
Argynnis papia	–	–	0.72
Other Lepidoptera			0.54
Taxonomic richness	1.20	0.10	2.13
Total flower visits	0.90	0.89	0.95

[a] Not found or less than 10 individuals recorded.

3. Results

A total of 1245 flower visitors belonging to 24 taxa were recorded (Table 1). The most abundant groups were Apoidea (>50%), followed by other Hymenoptera and Diptera. Honeybees and bumblebees had the highest share of Apoidea with 46 and 33%, respectively. The matrix type did not affect either the mean frequency of total flower visits ($F = 0.93$) or the mean richness of all taxa ($F = 1.01$). The same applied to the mean frequency of flower visits and the mean taxonomic richness of the different size classes (Table 2).

Significant matrix effects were confined to five large taxa of the Apoidea: *Bombus lapidarius* (L., 1758), *B. pascuorum* (Scop., 1763), the *B. terrestris* group (L., 1758), large wild bees and *A. mellifera* (Table 2). Though the significant effects revealed by the ANOVA suggest a decline of *B. lapidarius* in patches surrounded by the matrix type AG as well as a decline of *B. pascuorum* in patches surrounded by the matrix types AG and AGF, no significant difference between means could be established by the Tukey test (Fig. 2). The particularly high frequency of flower visits by individuals belonging to the *B. terrestris* group in patches surrounded by the matrix

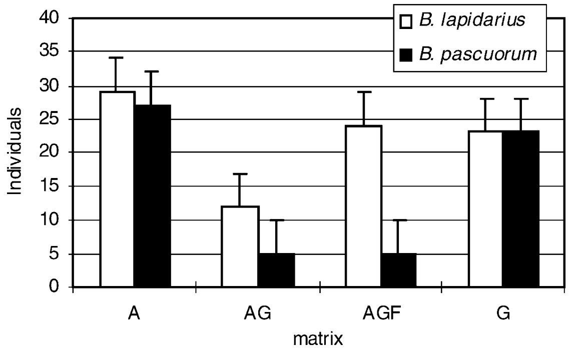

Fig. 2. Density of *B. lapidarius* and *B. pascuorum* (non-transformed data) in *C. jacea* patches surrounded by four different matrix types (A: arable land only ($n = 4$), AG: arable land close to grassland (<50 m; $n = 3$), AGF: mosaic of arable land, grassland and forest ($n = 4$), and G: grassland only ($n = 4$)).

type G, in contrast, was confirmed by significant differences between means (Fig. 3).

The flower visiting frequency of large wild bees (other than bumblebees) was significantly higher in patches surrounded by the matrix type AGF than in those surrounded by A and AG, while patches surrounded by G had an intermediate position (Fig. 4). Significantly more *A. mellifera* were recorded in patches surrounded by the matrix type G than in the other patches, without any significant difference between the matrix types A, AG, and AGF, respectively (Fig. 4).

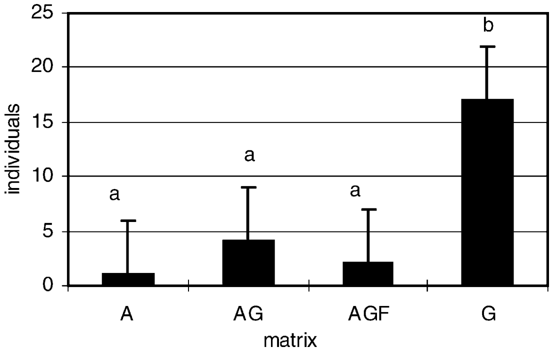

Fig. 3. Density of individuals belonging to the *B. terrestris* association (non-transformed data) in *C. jacea* patches surrounded by four different matrix types (see Fig. 2 for abbreviations; columns sharing identical letters are not significantly different according to the Tukey test ($P < 0.5$)).

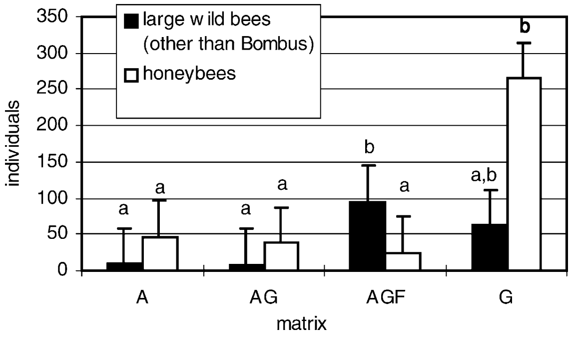

Fig. 4. Density of large wild bees and *A. mellifera* (non-transformed data) in *C. jacea* patches surrounded by four different matrix types (see Fig. 2 for abbreviations; columns of the same shading sharing identical letters are not significantly different according to the Tukey test ($P < 0.5$)).

4. Discussion

The significant response of five large Apoidea taxa to differences in matrix type revealed in this study confirms our first hypothesis: matrix effects on pollinating flower visitors of *C. jacea* are taxon- and body size-specific. However, our results also show that coarse parameters of community structure such as total frequency of flower visits or taxonomic richness do not provide suitable indicators of matrix effects on flower visitors of *C. jacea*. Moreover, most taxonomic units investigated in our study did not respond to changes in matrix composition. This contrasts results reported in the literature (e.g. Jeanneret and Charmillot, 1995; Pfaff and Wolters, 1999 for Lepidoptera; Knecht et al., 2000 for flower visiting Coleoptera). Considering that the matrix types chosen in our study can be related to different degrees of isolation (A > AG > AGF > G), our data on the other hand confirm the findings of Steffan-Dewenter and Tscharntke (1999) and Schmalhofer (2001), who could not establish any relationship between the degree of isolation and the total number of flower visitors.

The strong matrix effect on large bees found in our study seems to contradict the finding of a positive correlation between the degree of isolation and the mean body size of insects visiting flowers (Gathmann et al., 1994; Steffan-Dewenter and Tscharntke, 1999). Because of the fact that large bees are able to forage much greater ranges than small- and medium-sized bees (Gathmann et al., 1994), one might conclude that matrix effects on large taxa are leveled out by their high flight capacity. However, the studies cited above were carried out in landscapes with widely separated flower patches (up to 1000 m), while our study focused on a small-scale mosaic landscape with distances about 200 m. We hypothesize that, under conditions in which the ability to overcome long distances does not play a role, large flower visitors use their high flight capacity to discriminate between patches and are thus able to select the most appropriate resources. Large social insects such as bumblebees and honeybees, which have much higher energetic costs than small solitary bees (Heinrich, 1976), can best fulfill their nutritive requirements by foraging in comparatively large, connected *C. jacea* patches situated in grassland sites (Agren, 1996; Sih and Baltus, 1987; Pleasants, 1981). Solitary bees, in contrast, depend much more on the availability of a small-scale mosaic of microhabitats suitable for both nesting and food provision (Westrich, 1989). This would explain why the highest number of large wild bees was found in patches surrounded by a mosaic of grassland, arable land and forests.

The hypothesis that taxonomic richness and density of flower visitors decreases when the matrix of *C. jacea* patches is dominated by arable land, but increases when the matrix is dominated by grassland is not confirmed by our results. However, we did find a positive effect of a grassland matrix on honeybees and on the *B. terrestris* group. These bees show forage constancy not only for certain flowers, but also for the foraging area (e.g. Osborne and Williams, 2001). Especially honeybees have large foraging ranges and preferentially recruit discrete vegetational patches of high nutritional quality (Ginsberg, 1983; Aizen and Feinsinger, 1994). Honeybees thus tend to explore other plant species or patches than wild bees (Aizen and Feinsinger, 1994; Ginsberg, 1983). Though the density of all three investigated bumblebee species was high in *C. jacea* patches surrounded by grassland, only the individuals of the *Bombus terrestris* group showed a clear-cut preference for this matrix type. The species-specific response patterns confirm that bumblebees differ in foraging strategies and range (Hedtke and Schricker, 1996; Walther-Hellwig and Frankl, 2000).

5. Conclusion

All the flower visitors monitored in our study are pollinators (Allen-Wardel et al., 1998; Kevan, 1999), with bees probably being particularly effective (Batra, 1995; Kevan, 1999). Though our results suggest that the pollinator community of *C. jacea* as a whole is quite robust against matrix effects, the significant response of large Apoidea points to the important role of the surrounding landscape in modulating the association between pollinating insects and flowering plants. Considering the ecological services provided by pollinators in agricultural landscapes, our study indicates that the preservation of large areas covered by interconnected grassland sites as well as by a mosaic of different land use forms should have high priority in future management strategies.

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