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## Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity?

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**Abstract** Two hypotheses of bottom-up control that predict that the species richness of Carabidae will depend either on the taxonomic diversity of plants (“taxonomic diversity hypothesis”) or on the structural heterogeneity of the vegetation (“structural heterogeneity hypothesis”) were tested. Plant species were classified into nine plant structural groups through cluster analysis of morphological traits (e.g. total height) at 30 early successional temporary wetlands in the east-German agricultural landscape. In a linear regression analysis, the heterogeneity of vegetation structures explained 55% of the variation in carabid beetle diversity. According to a partial correlation analysis, plant taxonomic diversity did not have a significant effect, consistent with the “structural heterogeneity hypothesis,” and contradicting previous studies which concluded that plant taxonomic diversity would be the most important factor in early successional habitats. An experimental study was used to test hypotheses on the processes underlying this bottom-up control by vegetation structure: the “hunting efficiency hypothesis,” the “enemy-free space hypothesis,” and the “microhabitat specialization hypothesis.” The composition of plant structural groups in 15 vegetation plots (1 m<sup>2</sup>) was manipulated, creating a gradient from dense vegetation to open plots. Subsequent pitfall catches revealed significant differences in the activity-abundances of the carabid species. Large species preferred dense vegetation plots, consistent with the enemy-free space hypothesis that large species are more vulnerable to predation on the open plots and prefer dense vegetation to escape from natural enemies. The results indicate that bottom-up

control is not mediated only by plant taxonomic or functional group diversity and that vegetation structures may be more important than previously suggested.

**Keywords** Biodiversity · Species richness · Spatial heterogeneity · Enemy-free space

### Introduction

Ecologists have taken many approaches to examining the relative importance of bottom-up and top-down forces in natural communities [review in Hunter and Price (1992)]. According to bottom-up models, the abundance or diversity of lower trophic levels controls the diversity of higher trophic levels (Hunter and Price 1992; Siemann 1998; Siemann et al. 1998). The patterns and processes of bottom-up effects are less well documented than those of top-down effects. It has been suggested that a more diverse resource base supports a more diverse community of consumers, but there is a fundamental disagreement over which characteristics define resource diversity. It has been hypothesized that the taxonomic diversity of plant species is directly correlated with the diversity of herbivores (the “taxonomic diversity hypothesis”) because each additional plant species can have specialized consumers (Murdoch et al. 1972; Siemann et al. 1998). These effects might cascade up from plant diversity via herbivore diversity to predator diversity (Hunter and Price 1992). As the physical structure of the environment, mediated by plant communities, influences the distribution and interactions of species [reviews in Lawton (1983) and McCoy and Bell (1991)], the structural heterogeneity of the vegetation might enhance the diversity of higher trophic levels (the “structural heterogeneity hypothesis;” Murdoch et al. 1972; Uetz 1991; Dennis et al. 1997, 1998). Although there is empirical support for both hypotheses of bottom-up control of diversity, few studies compare their relative importance (Murdoch et al. 1972; Southwood et al. 1979). Southwood et al. (1979) demonstrated the importance of the habitat’s successional age:

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while insect diversity increased with plant taxonomic diversity in early successional stages, plant structural heterogeneity determined insect diversity in the later stages. The amount of structural heterogeneity in their early successional study sites, however, was low, which indicates a potential correlation of structural heterogeneity with successional age in this study. Therefore, the question remains open whether it was the relative importance of structural heterogeneity for insect diversity or the structural heterogeneity itself that increases during succession.

Experiments investigating the underlying processes of bottom-up control were documented at a spatial scale of a few square meters (the “plot scale”). There are several potential explanations for a direct relationship between predaceous arthropod assemblages and structural aspects of the vegetation: (1) the potential for vertical or horizontal zonation due to evolved microhabitat specialization is higher in architecturally complex plant communities that offer various microsites for oviposition, hibernation and shelter (the “microhabitat specialization hypothesis;” Lawton 1983; Uetz 1991); (2) vegetation structure changes the efficiency of different hunting strategies and, consequently, large predators may be more efficient in sparse vegetation (the “hunting efficiency hypothesis;” Morse 1980; Heck and Crowder 1991); and (3) vegetation structure affects the vulnerability of prey species that have more chance of escaping from natural enemies in dense vegetation (the “enemy-free space hypothesis;” Price et al. 1980; Lawton 1983; Provencher and Vickery 1988). As the predators of the Carabidae preferably forage on large species because of reduced foraging time required and a higher nutritive value per biomass (Kaspari and Joern 1993), the large Carabidae should prefer dense vegetation plots as enemy-free space.

This paper presents a study on bottom-up control of temporary wetland Carabidae species by plant communities. The study sites were in the first year of succession because they had been plowed, but they had substantial variation in vegetation structures. At the habitat scale, it was hypothesized that plant taxonomic diversity has a higher relative importance for the species richness of Carabidae than the structural heterogeneity of the vegetation. At the plot scale, I tested whether an experimental reduction in density and complexity of the vegetation enhances the activity-abundances of the large species as predicted by the hunting efficiency hypothesis, reduces activity-abundances consistent with the enemy-free space hypothesis, or reduces species richness consistent with the microhabitat specialization hypothesis.

## Material and methods

### Location and description of the study sites

The study was carried out in the agricultural landscape of northeast Germany (between 53° 22' N, 13° 34' E and 52° 22' N, 14° 15' E) in the years 1998–2000. Temporary wetlands are cultivated and typically produce crops in dry years. During years of average or

above-average precipitation, they retain surface water until spring or summer. The plant communities are dominated by annual therophytic species because the sites are plowed each year. Their physical structure varies between tall and dense vegetation dominated either by forbs (e.g. *Matricaria maritima* ssp. *inodora*, *Bidens tripartita*) or by grasses (*Elytrigia repens*) and sparsely vegetated dwarf-rush communities (*Peplis portula*, *Juncus tenagelia*). The temporary wetlands are inhabited by highly diverse communities of Carabidae consisting of a mixture of typical field species (e.g. *Carabus auratus*, *Pterostichus melanarius*) with numerous wetland species (e.g. *Agonum marginatum*, *Bembidion varium*). There is a gradient of species richness ranging from sites that have a species richness resembling those of conventional parts of the fields to highly diverse sites that can be characterized as diversity hot spots in the agricultural landscape.

### Species richness of Carabidae at the habitat scale

A total of 30 randomly chosen temporary wetlands were studied using pitfall trapping. The area of these temporary wetlands ranged between 50 m<sup>2</sup> and 2,400 m<sup>2</sup> (926±568 m<sup>2</sup>, mean±standard deviation). Habitat area and carabid species richness of the temporary wetlands were not correlated (Brose 2001a). The heterogeneity of flooding was included in the study as a predictor variable, because it was shown that it has a strong effect on plant species richness (Brose 2001b). For each temporary wetland, the maximum hydroperiod was recorded as the month when it completely dried out. The minimum hydroperiod was defined as the middle of March. The heterogeneity of flooding was coded as the number of months between the maximum and the minimum hydroperiod.

Five pitfall traps were placed on each study site in a stratified random design in which the habitats were stratified with respect to the hydroperiod. The traps (white cups: diameter 9.2 cm, 55% isopropanol with glycerin and detergent added) were covered with transparent plastic lids (10 cm above them) to avoid damage by animals or precipitation and were placed at a minimal distance of 4 m from each other. Each of the study sites was sampled between mid-April and mid-July and the beetles caught were removed every second week. After mid-July, harvesting and soil tillage began at the study sites. An autumn trapping season was not included in the study because after the sites were plowed, they lost their vegetation cover. The nomenclature follows Barndt et al. (1991).

The catches were pooled to give a total of observed species richness for each site. Because the species accumulation curves indicated that this sampling strategy underestimated the true number of species, particularly in the more diverse habitats (Brose 2002), I used second order jackknife estimates to obtain more accurate results of extrapolated species richness:

$$S_{\text{ext}} = S_{\text{obs}} + \left(\frac{2m-3}{m}\right)Q_1 - \left(\frac{(m-2)^2}{m(m-1)}\right)Q_2.$$

This non-parametric estimator is based on the observed number of species,  $S_{\text{obs}}$ , the number of species occurring in only one sample,  $Q_1$ , the number of species occurring in two samples,  $Q_2$ , and the total number of samples,  $m$  (Burnham and Overton 1979). It has been shown that these estimates accurately match the results of pitfall trapping studies with higher sampling intensity (Brose 2002). Although community evenness varied only moderately (range: 0.494–0.659), I chose second order jackknife estimates that are most robust concerning differences in community evenness.

Plant species richness of the habitats was obtained by transect searches in each temporary wetland [details in Brose (2001b)]. The data were compiled once a month from March to July each year. Transect searches were performed on each study site until no additional vascular plant species were found. The results of the transect searches were pooled to give the total plant species richness at each site.

**Table 1** Traits recorded for the plant species

Plant traits	
Leaf type	
1	Graminoid
0	Forb
Growth type	
1	Supine
0	Erect
Organization of leaves	
1	Tussock or rosette
0	Others
Breadth in lower section (0–20 cm height)	
0	0–1 cm
1	1.01–3 cm
2	>3 cm
Breadth in upper section (20.01–70 cm height)	
0	0–5 cm
1	5.01–10 cm
2	10.01–20 cm
3	>20 cm
Total height (cm)	
0	0–5 cm
1	5.01–15 cm
2	15.01–40 cm
3	40.01–80 cm
4	>80 cm

#### Classification of plant structural groups and heterogeneity of vegetation structures

Each pitfall trap of the present study was associated with a plot (0.25 m<sup>2</sup>), and the vegetation was recorded by proportional cover. Thirty individuals of each plant species, collected from as many plots as possible, were chosen at the end of June for further analysis. Individuals were defined as the plant tissue originating from a single point of the root system. Accordingly, they were represented in some cases by genets (annual therophytes) and in other cases by ramets (clonal geophytes). Six structural traits were recorded for every individual plant (Table 1). Due to the structural focus of the analyses, forbs with long and thin leaves that bear resemblance to grasses (e.g. *Butomus umbellatum*) were classified as the graminoid leaf type. The maximum breadth of each individual was determined as the greatest extent from one leaf tip to another. Species with a height below 20 cm were recorded with a breadth of zero in the upper section.

The data matrix of the plant species and their six standardized trait variables was entered in an agglomerative cluster analysis using average linkage based on the squared Euclidian distances. The resulting nine species groups will subsequently be referred to as “plant structural groups” (Table 2). For each vegetation plot, the proportional covers of the species were summed to arrive at the proportional covers of the plant structural groups.

To measure the heterogeneity of the plant structural groups, the squared Euclidian distance of the plant structural groups’ proportional covers was calculated for each study site. This measure of the range of vegetation structures was used to define their heterogeneity at the habitat scale.

#### Community composition of Carabidae at the plot scale

An additional temporary wetland with a habitat area of 1,460 m<sup>2</sup> in a conventionally managed field of sugar beets was selected in 2000 for the experimental study (53° 22’ N, 13° 34’ E). While the upper sections of the site dried out in the beginning of April, the lowest areas were flooded until July. Fifteen experimental plots were placed in the section that dried out by the end of April. This study site was selected for two reasons: (1) the habitat contained a wide range of vegetation types and thus, potentially, a wide range of Carabidae communities; and (2) the study section extended over a large area, so the plots could be installed at least 4 m apart to avoid mutual influence of the treatments.

The duration of flooding and the distance to the shoreline were equal for the 15 plots. The vegetation of this section, dominated by the tall forb species *M. maritima inodora* and the smaller species *Juncus bufonius*, represented the most widespread vegetation type of the temporary wetlands. As the vegetation was uniform, there were no differences among the plots before the experiment was started. Three treatments with five replicates each were applied to the vegetation: (1) plots with removal of the tall forbs *M. maritima inodora* and *Bidens tripartita* (shoots were clipped to the ground; the “*Juncus*-plots”); (2) plots with complete removal of the above-ground vegetation (“open plots”); and (3) control plots without removal of vegetation (“*Matricaria*-plots”).

The treatments were assigned to plots in a randomized block design with five blocks (replicates) that contained the three treatments in random distribution. This design was chosen to reduce the effects of other parameters, such as soil texture, on the Carabid beetle assemblages. The treatments started in mid-June and were repeated every second week. The pitfall traps (see description above) were placed in the center of the plots and sampling took place between mid-June and the end of July. After taxonomic determination, the mean body length of the species was obtained from Barndt et al. (1991). Species with a length of more than 9 mm were classified as large. The species activity-abundances were added up to arrive at small species, large species, and total activity-abundances. For each of the study plots, total species richness and the number of hygrophilous species [classification according to Barndt et al. (1991)] were calculated.

**Table 2** Characterization of the plant structural groups by the median of the trait variables; ranges are given in parentheses. The codes of the trait variables are given in Table 1.

Plant structural group	Leaf type	Height [cm]	Organization of leaves	Breadth low <sup>a</sup>	Breadth up <sup>b</sup>	Growth type
<i>Elytrigia</i> -group	1	4 (3–4)	0	0	0	0
<i>Alopecurus</i> -group	1	2 (2–3)	1	2	1 (1–2)	1
<i>Scirpus</i> -group	1	3 (3–4)	0	1 (1–2)	2	0
<i>Poa</i> -group	1	2 (2–2)	0	0	0	0
<i>Juncus</i> -group	1	2 (1–2)	1	2 (1–2)	0	0
<i>Plantago</i> -group	0	1 (0–2)	1	1 (1–2)	0	0
<i>Gnaphalium</i> -group	0	1 (0–1)	0	1 (1–2)	0	1
<i>Ranunculus</i> -group	0	2 (2–3)	0	1	1	0
<i>Matricaria</i> -group	0	3 (3–4)	0	1	2 (2–3)	0

<sup>a</sup> Breadth in lower section

<sup>b</sup> Breadth in upper section

## Data analyses

Consecutive univariate linear regression analyses were performed with the three independent variables (heterogeneity of flooding, plant species richness, and heterogeneity of vegetation structure) to see their influence on the extrapolated species richness of Carabidae. Simple one-tailed Pearson's product moment correlation and partial correlation analyses were used to determine the relationships between the variables.

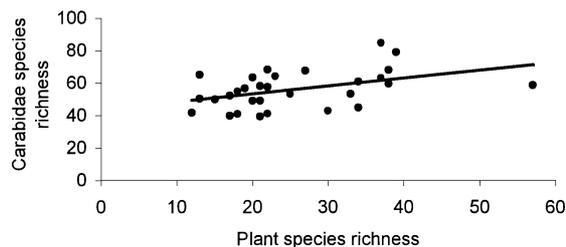
In the analyses of the experimental data at the plot scale, the activity-abundances of the small and the large species, the total activity-abundances, total species richness, and the number of hygrophilous species were used as dependent variables. As they fulfilled the requirements of normality and homogeneity of variances, their respective means in the three treatments were compared by analyses of variance using GLM (SPSS 8.0). In the case of significant results, post-hoc testing was done using LSD tests. Path analysis (RAMONA with GLS estimation; Systat 7.0) was used to test whether the effects of the treatments were mediated by changes in sampling efficiency. A model was tested in which the treatments influenced sampling efficiency, which influenced the activity-abundances of the small and the large species, and total species richness. Other dependent variables were excluded to avoid redundancy.

## Results

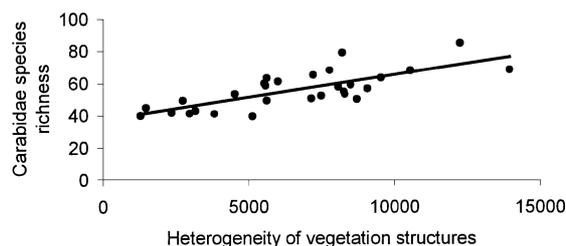
### Species richness of Carabidae at the habitat scale

In the 30 temporary wetlands studied, a total of 138 carabid species were recorded. The observed species richness of the study sites ranged between 28 and 58 with a mean of  $43 \pm 7$  (mean  $\pm$  standard deviation). The extrapolated species richness of the sites had a minimum of 39 and a maximum of 85 ( $56 \pm 11$ , mean  $\pm$  SD). On the vegetation plots, 92 plant species were recorded and classified into nine plant structural groups (Table 2). Dominating the vegetation on most plots, the *Matricaria* and the *Juncus* groups were the most widespread. The plant species richness of the study sites had a minimum of 12 and maximum of 57 ( $25 \pm 10$ , mean  $\pm$  SD). The heterogeneity of the vegetation structures ranged between 1,288 and 13,947 ( $6,587 \pm 3,097$ , mean  $\pm$  SD) and the heterogeneity of flooding ranged between 1 (partially flooded until mid-April) and 4 (partially flooded until mid-July).

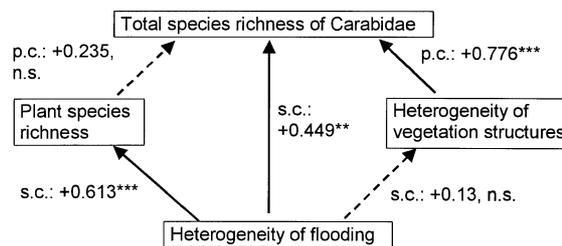
In a linear regression analysis, plant species richness explained 18% of the variation in extrapolated species richness of Carabidae (Fig. 1). Excluding the outlying study site with the highest plant species richness did not cause major changes in the regression model. A further regression analysis revealed that the heterogeneity of vegetation structures explained 55% of the total variation in extrapolated species richness of Carabidae (Fig. 2). The heterogeneity of flooding significantly influenced the total species richness of Carabidae ( $r^2=0.2$ ;  $P<0.05$ ,  $n=30$ ,  $y=5.23x+37.87$ ). The heterogeneity of flooding was significantly correlated with plant species richness and total Carabidae species richness, but it was not correlated with the heterogeneity of vegetation structures (Fig. 3). Furthermore, plant species richness and the heterogeneity of vegetation structures were not correlated. Partial correlation analyses with the heterogeneity of flooding



**Fig. 1** Linear regression of extrapolated species richness of Carabidae on plant species richness ( $r^2=0.18$ ;  $P<0.05$ ,  $N=30$ ,  $y=0.46x+41.42$ )



**Fig. 2** Linear regression of extrapolated species richness of Carabidae on the heterogeneity of vegetation structures ( $r^2=0.55$ ;  $P<0.001$ ,  $N=30$ ,  $y=0.003x+35.86$ )



**Fig. 3** Path diagram with significant and non-significant (dotted arrows) correlations. s.c. Simple correlation, p.c. partial correlation with heterogeneity of flooding as control variable, \*\*\*  $P<0.001$ , \*\*  $P<0.01$ , n.s. not significant

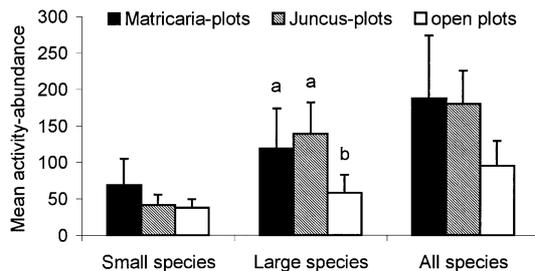
as a control variable indicated a highly significant relationship with the heterogeneity of vegetation structures, but no conditional independence of the correlation between plant species richness and the total species richness of Carabidae (Fig. 3).

### Community composition of Carabidae at the plot scale

The vegetation of the experimental plots consisted of 17 species (Table 3). While the mean total cover of the *Matricaria*- and the *Juncus*-plots did not differ significantly, the treatments reduced the mean total cover of the open plots. The vegetation of the *Matricaria*-plots was dominated by the tall forb *M. maritima inodora*, which produced a dense vegetation layer in the upper section. On the *Juncus*-plots, this vegetation layer was absent and only the lower section vegetation was dense. The *Juncus*-plots represented a treatment in which the complexity of

**Table 3** Mean proportional covers of the plant species on the experimental plot types at the end of the experiment (the end of July)

Species	Open	<i>Juncus</i>	<i>Matricaria</i>
<i>Agrostis stolonifera</i> L.	0	0.25	0
<i>Alopecurus geniculatus</i> L.	1.25	16.75	3.5
<i>Apera spica-venti</i> (L.) P.B.	0	1.5	11.75
<i>Bidens tripartita</i> L.	0.5	0.5	0.5
<i>Gnaphalium uliginosum</i> L.	0	2.25	0
<i>Juncus bufonius</i> L.	1.5	31.25	1.75
<i>Matricaria maritima inodora</i> (L.) Dostál	0	4	68.75
<i>Peplis portula</i> L.	3.25	2.5	0
<i>Plantago intermedia</i> Gilib.	3	17	1.5
<i>Polygonum aviculare</i> L.	0.75	17.75	9.5
<i>Polygonum lapathifolium</i> L.	0	0.25	0
<i>Rorippa palustris</i> (L.) Besser	0	0.5	0
<i>Rumex maritimus</i> L.	0.25	2.75	0.5
<i>Scleranthus annuus</i> L.	0	0	0.25
<i>Spergularia rubra</i> (L.) J. et C. Presl	0.25	0.25	0.25
<i>Trifolium hybridum</i> L.	0.25	1	1.25
<i>Vicia hirsuta</i> (L.) S.F. Gray	0	0.5	0.5
Mean total cover	11	99	100

**Fig. 4** Activity-abundances (mean±SD) of the groups of small, large (>9 mm) and all species on the *Matricaria*-plots, *Juncus*-plots and open plots. Significant differences were recorded for the large species (GLM,  $F=4.867$ ,  $P=0.018$ ,  $r^2=0.448$ ). Significant differences of the means are indicated with different letters

the vegetation was reduced by the removal of the upper vegetation layer, but the aboveground density of the vegetation was the same as in the *Matricaria*-plots (Table 3). The vegetation of the open plots was not completely absent (Table 3). This was due to the bi-weekly timing of the treatments, which allowed some quickly growing species (e.g. *Peplis portula*) to appear on these plots. However, the structural differences with the other plot types were large.

A total of 34 carabid species was caught by pitfall trapping in the experimental plots. The assemblage consisted of 22 small and 12 large species. While the mean activity-abundances of the large species did not significantly differ between the *Matricaria*- (119±55, mean±SD) and the *Juncus*-plots with reduced vegetation complexity (139±43, mean±SD), their values on the open plots with reduced vegetation complexity and density (58±24, mean±SD) were significantly lower (Fig. 4). In contrast to this, there were no significant effects of the treatments on the activity-abundances of the small species

and the total activity-abundances (Fig. 4). In the 34-species carabid beetle assemblage, 12 species were classified as hygrophilous. There were no significant differences between the three treatments in total species richness or in the number of hygrophilous species (GLM,  $P>0.05$ ). A path analysis indicated that the treatment effects were not mediated by sampling efficiency ( $F_0=0.456$ , RMSEA=0.276,  $P[\text{RMSEA}\leq 0.05]=0.063$ ).

## Discussion

The results do not support the hypothesis that plant taxonomic diversity has a higher relative importance for the species richness of Carabidae than the structural heterogeneity of the vegetation. Although the temporary wetlands were in an early successional stage, the structural heterogeneity of the vegetation was the most important predictor variable. It was shown that an experimental reduction in density and complexity of the vegetation reduced the activity-abundances of the large species as predicted by the enemy-free space hypothesis. The predictions of the hunting efficiency hypothesis and the microhabitat specialization hypothesis were not supported by the experiment.

### Species richness at the habitat scale

There was a significant impact of plant species richness on total species richness of Carabidae at the habitat scale, but the coefficient of determination was relatively low. The results of partial correlation analyses indicate that: (1) the heterogeneity of flooding influenced plant species richness as well as the total carabid species richness; and (2) the significant correlation between the diversity of plants and Carabidae in the univariate regression analysis might be caused by a co-linearity with the effects of the heterogeneity of flooding. Accordingly, the “plant taxonomic diversity hypothesis” must be rejected, corroborating Siemann et al. (1998). There is evidence that the correlation between plant and predator diversity is limited to a regional or global level (Southwood 1978). The present results support the hypothesis that at local scales the species composition of plants determines arthropod diversity by influencing interactions (Siemann 1998).

These results corroborate the structural heterogeneity hypothesis, consistent with a study on the effects of grazing management in grassland ecosystems that related the diversity of epigeal beetles to vegetation structure (Dennis et al. 1998). In recent years, the influence of plant functional group diversity on the diversity of higher trophic levels has been outlined (Symstad et al. 2000). In their experimental study, however, Symstad et al. (2000) raised questions about the underlying mechanisms that remained unanswered. In particular, the positive correlation between the presence of forbs and the species richness of the mainly graminivorous Homoptera was unexplained. A possible explanation arises from the fact

that the addition of forbs to a vegetation plot of graminoids increases its structural complexity. Accordingly, the effects of vegetation structure might have a considerable influence in experiments on the relationship between plant functional diversity and arthropod species richness.

Although the temporary wetlands in the present study are habitats in an early successional stage, the structural heterogeneity of the vegetation was a better predictor of carabid beetle species richness than plant taxonomic diversity. This contradicts the results of Southwood et al. (1979). There are two possible explanations: (1) the results depend on the taxonomic group studied; and (2) in contrast to young fields, the vegetation structures of the temporary wetlands vary considerably. Studies on herbivorous insects support the first hypothesis because the importance of plant taxonomic diversity increases with the degree of specialization in the taxonomic group studied (Siemann et al. 1998). However, with respect to polyphagous predators like Carabidae, the second explanation might be more important, and the actual amount of structural heterogeneity is more important than the successional stage of the habitat. While in some habitat types structural heterogeneity increases slowly on the successional trajectory (e.g. fallow fields), structural heterogeneity in other habitat types depends less on the successional stages (e.g. wetlands).

#### Community composition of Carabidae at the plot scale

It was mainly the reduction in vegetation density on the open plots, but not the reduction in vegetation complexity on the *Juncus*-plots, that influenced the activity-abundances of the large species. These results are in accordance with other experimental studies relating structural aspects of the vegetation to the community composition of ground-dwelling beetles and spiders (Hatley and MacMahon 1980, Rypstra 1983, Dennis et al. 1997, Costello and Daane 1998). A possible complication arises from the fact that the treatments of vegetation structure might have influenced the sampling efficiency of the pitfall traps. Accordingly, sampling efficiency might have been responsible for the changes in activity-abundances. A path analysis, however, indicated that this indirect effect is not likely to be responsible for the present results. Furthermore, the density of the vegetation influences the ease of movement of ground beetles, which might cause the efficiency of the pitfall traps to increase on the open plots. In the present study, however, the opposite pattern was detected: the total activity-abundances were lower on the open plots. In conclusion, the problem of indirect effects of the treatments via sampling efficiency appears to be negligible in the present study.

Although none of the hypotheses about the processes mediating the influence of vegetation structure on carabid beetles can be eliminated from consideration, some are better supported by these results. According to the hunting efficiency hypothesis, large predators should

prefer sparsely vegetated microhabitats. However, the results for the carabid beetles in the present study indicated the opposite distribution of large species. This is consistent with the enemy-free space hypothesis holding that large species, in particular, are more vulnerable to predation on the open plots and, should prefer dense vegetation to escape from natural enemies. This interpretation is supported by data showing that the activity-abundances of the small species that generally have a lower vulnerability were not affected by the treatments. There was no decrease in species richness or in the number of hygrophilous species in the plots with reduced vegetational complexity. Furthermore, the experimental reduction in vegetation complexity did not affect the activity-abundances. These results indicate that the microhabitat specialization hypothesis must be rejected with respect to vegetation complexity at the plot scale. However, it is known that carabid species respond to a variety of abiotic variables [e.g. Blake et al. (1994)] that might also contribute to different microhabitats. The constancy in the number of hygrophilous species indicates that potentially higher moisture in the plots with dense vegetation is not likely to have an impact on the results of the experiment. However, there was still considerable variation in the activity-abundances within the treatments, indicating that other environmental variables have an additional influence. Although the potential impact of abiotic factors has been reduced by the experimental design chosen, small variations in soil texture or moisture might offer distinct oviposition microsites, and thus the microhabitat specialization hypothesis cannot be rejected completely. Considering a larger spatial scale, the amount of horizontal complexity of the vegetation, measured by the heterogeneity of vegetation structures, is more important. As this variable has been shown to influence the diversity of carabid beetle communities, the support for the microhabitat specialization hypothesis in the present study is scale dependent.

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