

# Spatial and temporal organisation of the pre-dispersal seed predator guild in a perennial legume, *Vicia tenuifolia*

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**Abstract.** 1. The variability of species combinations and membership assembly patterns in an insect pre-dispersal seed predator guild were studied at various spatial and temporal resolutions using presence/absence and abundance data in null models. The guild consists of seven beetle species (four bruchids and three curculionids) and one moth species that live on a perennial vetch, *Vicia tenuifolia* Roth (Leguminosae).

2. The seed predator guild varied considerably in the number of members and species combinations in space and time, and, contrary to expectations, there was no evidence of interspecific competition among guild members, supporting the view that other processes, including chance events, could contribute to guild formation.

3. It is concluded that, apart from the possibility of stochastic co-occurrence, it is the narrow host specialisation that constrains seed predator members to participate in the guild, and small differences in habitat preference can also lead to spatial and temporal variation.

**Key words.** Bruchids, coexistence, co-occurrence, C-score, curculionids, Leguminosae, lepidopterans, null model, species assembly.

## Introduction

Understanding the processes underlying assembly of ecological guilds and their organisation into higher level trophic systems is one of the major goals of community ecology (Gee & Giller, 1987). Variability in guild composition in space and time, guild constancy, proportionality, predictability, and seasonal and successional changes, all constitute special features of guild assembly that can assist in elucidating whether stochastic or deterministic forces contribute to the formation of guilds.

In a few cases spatio-temporal variations in arthropod guild composition have been demonstrated (Abbott *et al.*,

1992; Schonrogge *et al.*, 1995). Substantial local and regional spatial variation in species composition was found in a granivorous desert rodent guild (Brown, 1987). Whereas Lawton (1984a, b) demonstrated considerable spatial variability in the structure of herbivorous insect guilds living on bracken fern (*Pteridium aquilinum*), there was high similarity of composition of such guilds on *Quercus rubra* in Canada and the U.K. (Ashbourne & Putman, 1987). Relative spatial constancy in the proportions of herbivorous insect guilds inhabiting different tree types and biogeographical regions has also been found (Moran & Southwood, 1982; Southwood, 1996). However, constancy (predictability) of guilds was more probable at a local scale (Brown, 1987; Hendrix *et al.*, 1988). Constancy can be expected within guilds of herbivorous insects that specialise on a narrow range of hosts. Examples include chrysomelid beetles living on asparagus (*Asparagus officinalis*) (Kaszab, 1962), tephritid flies inhabiting flower heads of thistle species belonging to the tribe Cardueae (Zwölfer, 1988), and hispine beetles occupying scrolls of *Heliconia* leaves

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(Strong, 1984). Constancy of primary and secondary consumer guild species richness, abundance, and biomass was also demonstrated for six tropical *Acacia* species in comparison with a random model (Krüger & McGavin, 2001), but this did not mean taxonomical similarity. No such pattern was found in British arboreal arthropods classified into four guilds on 28 tree species; individual taxa were distributed idiosyncratically (Cornell & Kahn, 1989).

Whether communities are formed by random or deterministic processes, assembly rules can provide predictions of expected co-occurrence patterns. There is a set of such rules (Diamond's assembly rules, size relationships, guild proportionality, and others) (Weiher & Keddy, 1999) that invoke interspecific competition as a mechanism structuring communities. With few exceptions (Brown *et al.*, 1986; Brown, 1987), competition has not been experimentally demonstrated for guilds of seed predators. Lawton (1984a, b) found that not only were the herbivore communities organised by chance on bracken fern, but that significant interspecific interactions were lacking. On the basis of distributional data Zwölfer (1979, 1980) concluded that within the herbivorous communities of thistle heads competition produced the observed patterns. Still others (Rathcke, 1976; Strong, 1984; Jermy, 1985) did not find competition or considered it less likely to structure guilds of herbivorous insects. The lack of competition does not exclude the possibility of finding predictable guilds, e.g. due to narrow host-plant specialisation, or as a consequence of predation. Strengthening the above, Hawkins and Mills (1996) found great variability in guild composition of parasitoid communities reflecting historical events such as chance colonisation, hosts shifts, and specialisation.

Application of null models to analyse community organisational processes is based on the use of presence/absence data (Graves & Gotelli, 1993; Gotelli, 2000; Gotelli & McCabe, 2002; Feeley, 2003; Vázquez & Aizen, 2003; Zwölfer & Stadler, 2004), which, however, might be less powerful in detecting competitive relations. This is paradoxical, because population interactions are influenced by abundance, and members of a community can be represented by various frequencies that are not related to interactions (e.g. rarity, Gaston, 1994). In spite of the fact that the need to incorporate abundance data for detecting species association is not new (Schluter, 1984; Graves & Gotelli, 1993), such approaches are scarce.

In the present study the variability of a herbivorous insect pre-dispersal seed predator guild was examined by null models using both presence/absence and population density data and setting the hypothesis that the guild was organised by competitive forces. The extent of variability in guild composition and in the number of guild members can provide useful insight into possible constraints affecting species assembly. Different spatio-temporal resolution levels were applied at several arbitrary scales assuming that species interactions that occur with various intensities on different scales might be detectable (Levin, 1992). The following questions were addressed: how and to what extent does the species composition of the pre-dispersal

seed predator guild vary in space and time, and are the seed predator guild members assembled non-randomly or by chance?

## Materials and methods

### *The plant host*

*Vicia tenuifolia* Roth (Leguminosae) is an abundant perennial, stoloniferous plant species preferring sunny to half-shade habitats at (mostly oak) forest edges in Central Europe and forms homogeneous stands. Pods ripen by the end of July at most localities.

### *The pre-dispersal seed predator insects*

At least eight seed-predator species use *V. tenuifolia* with various frequencies: *V. tenuifolia* pods are utilised by four bruchid (*Bruchus venustus* Fährreus, *B. libanensis* Zampetti, *B. occidentalis* Lukjanovitsh and Ter-Minasjan, and *B. brachialis* Fährreus; Coleoptera, Bruchidae), three curculionid (*Oxystoma cerdo* Gerstäcker, *O. ochropus* Germar, and *Tychius 5-punctatus* Linnaeus; Coleoptera, Curculionidae) and one lepidopteran (*Etiella zinckenella* Treitschke; Lepidoptera, Phycitidae) pre-dispersal seed predator species.

In this study Root's guild definition is used (Root, 1973; p. 101): 'An ecological guild is a group of species that exploits the same resource in a similar way.' The bruchid sub-guild associated with the immature (green) pod of *V. tenuifolia* consume seeds from inside during development; the curculionids and the lepidopteran species chew seeds within the pods from the outside, one by one.

### *Sampling and identification of species*

Pods from a total of 80 *V. tenuifolia* stands (patches of plants within a distance of 500 m) were collected throughout Hungary within a 13-year interval (1991–2003) with the exception of 2000 when there was no pod crop because of drought. The number of sampled *V. tenuifolia* stands was  $6.7 \pm 3.7$  ( $\pm$  SD) per year. Only indehiscent pods were collected. Efforts were taken to collect comparable sample sizes. If a *V. tenuifolia* stand was small, all pods were collected. From larger stands at least 30 pods were taken randomly from different stems. Pods from the same stand were put into glass jars closed with linen and regarded as a sample unit (i.e. basic collection unit). All bruchid adults emerging or in seeds were removed and identified and their numbers were used for analyses based on abundance.

Seeds showing signs of lepidopteran or curculionid larval boring or consumption were examined for the presence of pre-dispersal seed predator developmental stages of all species (fertile eggs, first larval instars tunnelling in pod wall or entering seeds, shed skins and head capsules, etc.). As the

infestation by curculionids and lepidopterans could not be expressed in number of individuals, the number of *infested seeds* was used as the response variable for abundance-based analyses.

Consequently, the guild analyses were performed at two levels of taxonomic resolution. In the first each of the four individual bruchid species was involved, whereas in the second one only the major pre-dispersal seed predator groups (bruchids, curculionids, and lepidopterans) were considered. Hence the former constituted a taxon guild (Schoener, 1986) of related species, whereas the latter formed a guild at a higher level of taxonomic organisation.

#### *Spatio-temporal analysis of the guild*

In addition to the taxonomic resolution, guild analyses were also performed at six spatio-temporal levels of resolution (Table 1). There were four spatial levels distinguished: raw, fine, intermediate, and coarse. At the raw (stand) level, each sample unit (jar of pods) was regarded as a sample. At the fine spatial level, sample units that were from *V. tenuifolia* stands within 1 km of each other were pooled to form a sample. At the intermediate spatial level, sample units coming from the same village were pooled into a sample. Coarse depicts the level when space is not considered for analyses. Hence, raw, fine, and intermediate spatial levels form a spatial hierarchy. Thus, analyses that were performed included these spatial levels as well as time (year of sampling: considered–not considered) (Table 1).

The number of samples of the bruchid sub-guild at different spatio-temporal levels ranged from 12 to 65, whereas those used for analyses at higher taxa level varied between 11 and 76 (Table 1).

#### *Measuring the variability of guild organisation*

In order to express the variability in pre-dispersal seed predator guild organisation, two terms are introduced: guild variation and guild combination. Guild variation is

defined as the number of guild members (species) in a sample. For example, all samples with two guild members belong to the same guild variation (two-member guild variation) regardless of which two species are present. In contrast, guild combination means a unique species combination (Pielou & Pielou, 1968) of the guild members in a sample.

The expected frequencies of the guild variations were compared with those of the observed ones. The expected frequency of a guild variation was calculated by the binomial coefficient

$$\frac{n!}{(n-m)!m!},$$

where  $n$  is the total number of guild members, and  $m$  is the number of guild members (i.e. 0, 1, 2 ...  $n$ ) in the sample. The coefficient indicates which guild variation is the most frequent. For bruchids two-member guild variations ( $n = 4$ ,  $m = 2$ ) were expected to be most frequent (frequency = 6) at all spatial levels. The expected and observed frequencies, based on presence/absence data, were compared in graphs and by  $\chi^2$ -tests. This analysis was performed for the bruchid sub-guild only.

The number of possible guild combinations is given by  $2^n$  (Pielou & Pielou, 1968), which for bruchids is 16, and 8 for the higher level taxa pre-dispersal seed predators. The expected maximum number of guild combinations was compared with the observed values.

#### *Methods of guild analyses*

Based on a null model approach (Gotelli & Graves, 1996), the purpose of co-occurrence and coexistence analyses is to detect competition. First, co-occurrence analyses were applied to detect non-random patterns using presence/absence data. It is insensitive to differences in species abundance. However, in this study, regardless of spatio-temporal resolution levels, the ratios of bruchid adults were 485 *B. venustus* to 260 *B. libanensis* to 18 *B. occidentalis* to 1 *B. brachialis*, therefore it was important to also use

**Table 1.** Spatio-temporal levels of guild analyses and the number of samples.

Temporal levels	Spatial levels	Number of samples			
		Both sub-guilds analysed by		Only endophagous sub-guild analysed by	
		presence/absence	abundance	presence/absence	abundance
Time is considered: $T(\text{year})$	Raw	NA	NA	NA	NA
	Fine	40	40	42	42
	Intermediate (im)	33	32	34	33
	Coarse	12	11	12	12
Time is not considered	Raw	63	76	65	65
	Fine	26	26	28	28
	Intermediate (im)	16	16	16	16
	Coarse	NA	NA	NA	NA

NA, not analysed.

abundance data. Thus, as a second step, coexistence analyses were performed with abundance data.

The null models of both co-occurrence and coexistence analyses consisted of three parts: (1) metric selection, (2) the application of a randomisation algorithm to produce the null distribution of the same metric, and (3) a comparison of the observed metric with the null distribution. Co-occurrence analyses were performed with *C*-score (Stone & Roberts, 1990). The *C*-score measures the average number of 'chequerboard units' between all possible pairs of species. Chequerboard units (CU) for each species pair is calculated as:

$$CU = (o_i - s)(o_j - s),$$

where  $o_i$  is the number of occurrences of species  $i$ ,  $s$  is the number of shared sites (sites containing both species) and  $o_j$  is the number of occurrences of species  $j$ .

In spite of the fact that coexistence analysis of whole communities can be executed by applying Schluter's variance ratio (Schluter, 1984), it is not used as a metric here because it is not an expansion of *C*-score based on species abundances, and its interpretation is rather problematic. Instead, the method of Osnas and Ankney (2003) was followed. Co-existence between pairs of species was examined using the following coexistence metric:

$$C_{ij} = \sum_{w=1}^N x_{iw}x_{jw},$$

where  $C_{ij}$  is the coexistence metric between taxa  $i$  and  $j$ ,  $x_{iw}$  is the abundance of taxon  $i$  in site  $w$ ,  $x_{jw}$  is the abundance of taxon  $j$  in site  $w$ , and  $N$  is the total number of sites.

A wide array of randomisation techniques is available (Gotelli & Entsminger, 2001a). In the present study, Gotelli's method was applied (Gotelli, 2000): row and column totals of the species  $\times$  site matrix of species presence/absence (co-occurrence analysis) or species abundance (coexistence analysis) were kept constant (fixed row and column) and the sequential swap algorithm was used with the former, but other options were also tried (Gotelli & Entsminger, 2001b). This is because the marginals themselves reflect competitive interactions in the case of co-occurrence analysis (Gotelli, 2000) or control the correlation between species richness and abundance in the case of coexistence analysis (Osnas & Ankney, 2003). Randomisation was repeated 5000 times.

Comparison of the observed metric with the null distribution was performed using a *P*-value. The *P*-value expresses the proportion of the randomised metric values that were more extreme or equal to the observed metric value (Manly, 1991). The observed value of the metric was defined as significant if its *P*-value was equal or less than 0.05. In a guild structured by competition the observed *C*-score should fall in the upper marginal tail of the null distribution. Similarly, the observed coexistence metric suggests competition if its value falls in the lower tail of the null distribution.

### Microhabitat preference of bruchids

From 1999 to 2003, at the same location (47°32'N, 18°56'E), the positions of *V. tenuifolia* patches on a  $\approx 5 \times 15$  m stand divided by a permanent  $1 \times 1$  m mesh grid were mapped. It was also recorded whether the patches were shaded most of the day or were in a sunny position. Individual racemes within patches were tagged with numbered labels at flowering ( $\approx 1000$  racemes yearly, the majority of which underwent heavy flower and pod abortion). Ripe pods were picked and pre-dispersal seed predators and their parasitoids were allowed to emerge. Pods were evaluated for pre-dispersal seed predator infestation as explained above. However, only 2 years' data (1999 and 2001, altogether 1577 pods) could be used, because of total or partial crop failures in other years. Bruchid and parasitoid infestation in sun and shade were tested against the null hypothesis that there was no difference in habitat preference among bruchid species.

### Statistical analysis

Co-occurrence was analysed using the EcoSim program (Gotelli & Entsminger, 2001b) and coexistence using a Microsoft Excel macro. For the comparison of expected and observed guild membership distributions  $\chi^2$  tests were used. The numbers of seeds infested by the pre-dispersal seed predator members were compared with Kruskal–Wallis ANOVA. One-way ANOVA was used to test for differences in habitat preference of the bruchids. These statistical tests were performed with the STATISTICA 6.0 software (StatSoft, 2003).

## Results

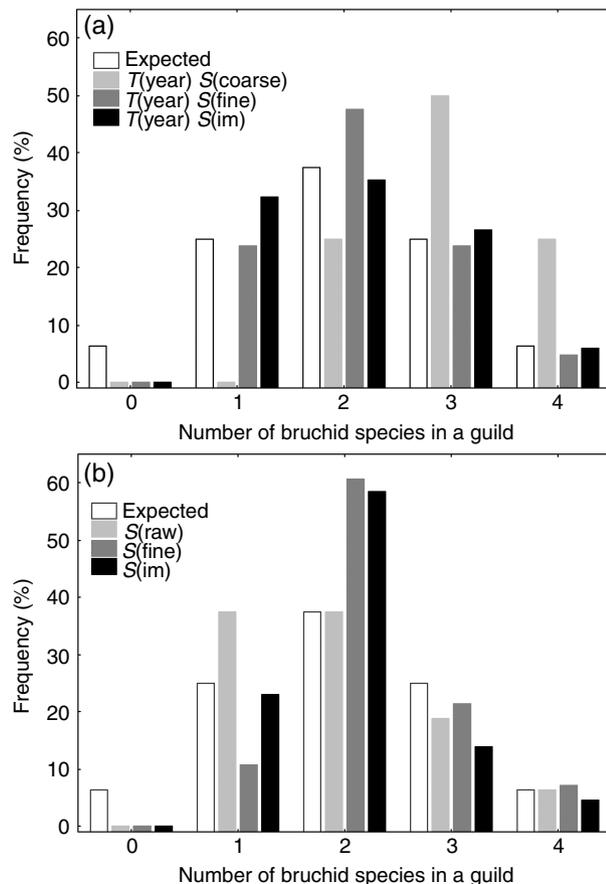
### Characterisation of the guild

Among the pre-dispersal seed predators, bruchids infested the greatest number of seeds (median: 22.5, lower and upper quartile: 7–67), followed by lepidopterans (10.0, 1.5–26) and curculionids (2, 0–6) when infestation was examined at raw sample level (i.e. jar of pods) (Kruskal–Wallis ANOVA for the number of infested seeds:  $H_2 = 69.43$ ,  $P < 0.001$ ). Within the endophagous sub-guild *B. venustus* was the most abundant (median: 11.0, lower and upper quartile: 3–43), followed by *B. libanensis* (5.0, 1–14), *B. occidentalis* (0, 0–1) and *B. brachialis* (0, 0–0) per sample (Kruskal–Wallis ANOVA for the number of bruchids:  $H_3 = 137.1$ ,  $P < 0.001$ ). When examined at the raw sample level, all four bruchid species were present in 4.6% of samples, three species in 13.9%, two species in 58.5%, and only one species in 23.1% of the samples. Mean guild variation was  $2.0 \pm 0.75$  ( $\pm$  SD) bruchid species per sample. *Bruchus venustus* was present in 90.8% of samples, *B. libanensis* in 76.9%, *B. occidentalis* in 26.2%, and *B. brachialis* in 6.2%. Of the higher taxa-level pre-dispersal

seed predators all three (bruchids, curculionids, and lepidopterans) were present in 50.8% of the samples, two in 34.9%, and one in 14.3%. There were  $2.4 \pm 0.73$  (mean  $\pm$  SD) pre-dispersal seed predators per sample. Bruchids were present in 100%, lepidopterans in 74.6%, and curculionids in 61.9% of samples.

#### Expected vs. observed membership frequencies of the guild

Observed frequencies of guild variations did not conform to expected distributions (Fig. 1a,b). Only in the case of 'year' was the observed distribution skewed to the right,



**Fig. 1.** Expected and observed membership frequencies of the bruchid guild at different resolution levels: (a)  $T(\text{year})S(\text{coarse})$ , Time + Space Course;  $T(\text{year})S(\text{fine})$ , Time + Space fine; and  $T(\text{year})S(\text{im})$ , Time + Space intermediate levels.  $\chi^2$  comparisons of expected ( $E$ ) and observed guild membership frequencies:  $E-T(\text{year})S(\text{coarse})$ :  $\chi^2 = 116.67$ , d.f. = 4,  $P < 0.0001$ ;  $E-T(\text{year})S(\text{fine})$ :  $\chi^2 = 9.44$ , d.f. = 4,  $P < 0.0507$ ;  $E-T(\text{year})S(\text{im})$ :  $\chi^2 = 8.65$ , d.f. = 4,  $P < 0.0704$  and (b)  $S(\text{raw})$ , Space raw samples without regards to resolution levels;  $S(\text{fine})$ , Space fine; and  $S(\text{im})$ , Space intermediate.  $\chi^2$  comparisons of expected ( $E$ ) and observed guild membership frequencies:  $E-S(\text{raw})$ :  $\chi^2 = 23.51$ , d.f. = 4,  $P < 0.0001$ ;  $E-S(\text{fine})$ :  $\chi^2 = 29.42$ , d.f. = 4,  $P < 0.0001$ ;  $E-S(\text{im})$ :  $\chi^2 = 14.06$ , d.f. = 4,  $P < 0.0071$ .

and the most frequent guild variation was three members. One- and two-member guild variations were less common, whereas the four-member variation was more frequent than was expected. At the fine and raw spatial resolutions there were higher frequencies of the two-member guild variation than predicted (Fig. 1b). Of the 16 possible bruchid guild combinations there was a maximum of eight (50%) observed with varying numbers (Tables 2 and 3). *Bruchus venustus* and *B. libanensis* formed 50.8% of the observed combinations. Of the possible eight higher taxa-level guild combinations only four were detected. All three participants formed 50.8% of possible combinations (Tables 4 and 5).

#### Guild analyses

Co-occurrence analyses with  $C$ -score, using presence/absence data, did not produce significant deviations from the null model, regardless of whether the bruchid guild or higher taxa pre-dispersal seed predator levels were examined or different kinds of row and column constraints were used (Tables 2 and 4). Moreover, none of the species pairs produced a significant coexistence metric predicting competition at any spatio-temporal resolution (Table 6).

#### Microhabitat preference of bruchids

The mean ( $\pm$  SD) number of *B. venustus* adults per pod was  $0.23 \pm 0.49$  in sunny patches, and  $0.22 \pm 0.50$  in shady ones ( $F_{1,1575} = 0.2235$ ,  $P = 0.6365$ ). The mean ( $\pm$  SD) number of parasitoids emerging from *B. venustus* was  $0.04 \pm 0.21$  per pod at the sunny, and  $0.10 \pm 0.31$  at the shady patches ( $F_{1,314} = 2.625$ ,  $P = 0.1062$ ). The mean ( $\pm$  SD) number of the three other bruchids per pod was  $0.11 \pm 0.34$  on sunny patches, and  $0.51 \pm 0.71$  on shady ones ( $F_{1,1575} = 175.1977$ ,  $P < 0.0001$ ). The mean ( $\pm$  SD) number of parasitoids emerging from the three other bruchids was  $0.04 \pm 0.19$  per pod at the sunny patches, and  $0.11 \pm 0.31$  at the shady patches ( $F_{1,216} = 4.062$ ,  $P = 0.0451$ ).

#### Discussion

Natural communities are open systems constantly changing in species composition and abundance. Guilds, as building blocks of communities, also change in space and time. The results of the present paper indicate that the pre-dispersal seed predator guild of *V. tenuifolia* exhibits considerable spatio-temporal change in variation and composition. Both number of members and composition might change due to factors that need more study, such as possible geographic differences, demographic stochasticity, overwintering losses, population dynamic processes, temporary shortage or local extinction of host plant, decreased

**Table 2.** Characteristics of the guild of the four bruchid species and the results of EcoSim analyses.

Resolution	No. of samples	No. of. guild combinations		The guild variation with the highest frequency (%)	C-score <sup>a</sup>		P-value
		Exp. max.	Obs.		Observed index	Mean of simulated indices	
<i>T(year)S(coarse)</i>	12	16	5	3 (41.7)	1.50	1.71	1.0000
<i>T(year)S(fine)</i>	42	16	7	2 (40.5)	20.17	21.92	0.7812
<i>T(year)S(im)</i>	34	16	6	2 (32.4)	7.83	8.29	1.0000
<i>S(fine)</i>	28	16	7	2 (32.1)	15.50	16.45	0.8134
<i>S(im)</i>	16	16	6	2 (31.2)	3.33	3.50	1.0000
<i>S(raw)</i>	65	16	8	2 (50.8)	60.17	59.79	0.4688

*T(year)S(coarse)*, Time + Space Course; *T(year)S(fine)*, Time + Space fine; *T(year)S(im)*, Time + Space intermediate; *S(fine)*, Space fine; *S(im)*, Space inter-mediate; *S(raw)*, Space raw. Exp. max., expected maximum; Obs., observed.

<sup>a</sup>Fixed row and column constraints were used.

suitability of host for one guild member, rate of predation and parasitisation, and microhabitat preference.

There were substantial deviations from the expected maximum values of guild combinations observed (Tables 2 and 4). Moreover, spatio-temporal resolution influenced the frequency distribution of guild variations (Fig. 1a,b): as the spatial resolution changed (from raw to coarse spatial level) the observed frequency distribution of guild membership skewed to the right (especially when time was considered, Fig. 1a). An explanation could be that the more detailed the resolution, the closer the observed number of guild combinations approaches the theoretically possible combinations (Gotelli & Entsminger, 2001b), because the finer spatio-temporal scale allows more stochasticity to occur (Levin, 1992; Noda, 2004). Thus, high resolution

favours detection of new combinations and vice versa; low resolution at the extreme results in only a single guild combination. On the other hand, analyses at a higher taxonomic level ensure a high probability that at least one species of any group will be present therefore the observed number of guild combinations will more closely approximate the maximum possible species combinations (Table 4). In the present study, the number of observed guild combinations reached half of the maximum possible. In contrast, relatively high numbers of more specific guilds (e.g. only bruchid species) do not include all species. The number of guild combinations was usually less than half of the possible combinations (Table 2). In the case of the bruchid guild, the most frequent variation (two species, Table 2) is due to the relatively high abundances of *B. venustus* and *B. libanensis*.

As for the organisation of the pre-dispersal seed predator guild, significant deviations from the null models were not observed (Tables 2 and 4), suggesting that the guilds were not competitively structured. In a community where species co-occurrence is determined by competitive relations the C-score or checkerboard index should be significantly larger than expected by chance. It is probable that in the case of applying fixed row and column sums the analysis could not detect competition at higher taxa level, because substantial variability in null distribution is lost through pooling the data. It was found that the guild assembly, neither at the level of bruchid species nor at higher taxa, was affected by interspecific competition. In spite of this, the substantial overlap in resource use between *B. venustus* and *B. libanensis*, the two most abundant bruchid species, might still indicate competitive relations. However, quantitative analyses of resource use have revealed that, although these species live on a common resource, many pods and seeds remain unused (Á. Szentesi and T. Jermy, unpubl. data). Similarly to parasitoid communities (Hawkins & Mills, 1996), the bruchid pre-dispersal seed predator guild functions among undersaturated niche conditions, and whether individual resource units (pods or seeds) are utilised or not is largely a chance event. Even if competition is

**Table 3.** The possible guild combinations and their obtained frequency of endophagous sub-guild members.

Guild combinations				Occurrence number (%) <sup>a</sup>
Ven	Lib	Occ	Bra	
1	1	1	1	3 (4.6)
0	1	1	1	0
0	0	1	1	0
0	0	0	1	0
0	0	1	0	1 (1.5)
1	0	1	1	0
1	0	0	1	0
1	0	0	0	9 (13.8)
1	1	1	0	8 (12.4)
1	1	0	0	33 (50.8)
1	1	0	1	1 (1.5)
1	0	1	0	5 (7.7)
0	1	0	1	0
0	1	1	0	0
0	1	0	0	5 (7.7)
0	0	0	0	0

Ven, *B. venustus*; Lib, *B. libanensis*; Occ, *B. occidentalis*; Bra, *B. brachialis*.

<sup>a</sup>Refers to raw spatial resolution.

**Table 4.** Characteristics of the guild of the three major pre-dispersal seed predator groups and the results of EcoSim analyses.

Resolution	No. of samples	No. of. guild combinations		The guild variation with the highest frequency (%)	C-score <sup>a</sup>		
		Exp. max.	Obs.		Observed index	Mean of simulated indices	P-value
<i>T(year)S(coarse)</i>	12	8	3	3 (83.3)	NA	NA	NA
<i>T(year)S(fine)</i>	40	8	4	3 (52.5)	12.00	42.50	0.9998
<i>T(year)S(im)</i>	33	8	4	3 (54.5)	9.33	25.41	0.9966
<i>S(fine)</i>	26	8	4	3 (50.0)	6.00	18.96	0.9988
<i>S(im)</i>	16	8	4	3 (56.3)	2.00	5.51	0.9752
<i>S(raw)</i>	63	8	4	3 (50.8)	35.00	109.54	1.0000

*T(year)S(coarse)*, Time + Space Course; *T(year)S(fine)*, Time + Space fine; *T(year)S(im)*, Time + Space intermediate; *S(fine)*, Space fine; *S(im)*, Space intermediate; *S(raw)*, Space raw. Exp. max., expected maximum; Obs., observed.

<sup>a</sup>As fixed row and column calculations are not applicable (see explanation in Discussion), the results of analyses using equiprobable constraints are presented instead. NA, not analysed.

demonstrated it does not necessary follow that this force governs community assembly (Simberloff *et al.*, 1999). The explanation for the patterns should be found elsewhere.

Co-occurrence patterns may appear to result from competition when some guild members are rare or very specialised on a different host. This must be taken into consideration when assigning species to guilds. Three bruchid species (*B. venustus*, *B. libanensis*, and *B. occidentalis*) are almost completely monophagous, because they overwhelmingly occur in *V. tenuifolia* and only rarely use another host plant, *V. cracca* L. (Jermy & Szentesi, 2003) whose temporal occurrence is substantially different. The fourth species, *B. brachialis*, is very rare in *V. tenuifolia*, its major host plant being *V. villosa* Roth, and its presence/absence can substantially modify the number of guild combinations. To some extent, the same is true for *B. occidentalis* due to its relative rarity. Thus, on the one hand, the absence of a rare species (due to either monophagy on a different host or low abundance) might falsely appear to indicate competition between it and the other species of the guild. On the other, rarity does affect the results of this study, because spatio-temporal resolution levels determine which species combinations are included in the samples, and the probability of the presence of a rare

species could have been increased by more extensive sampling only.

It is suggested that members in taxon guilds, being close relatives and having a very restricted host spectrum (monophagy or narrow oligophagy) are obligatory guild-forming species. These species are constrained by their use of the same resource and participate in guilds according to their relative abundances. The number of such guilds must be substantial given the proportion of specialised insect species, which is close to 80% (Schoonhoven *et al.*, 1998). As an example, for oligophagous species the similar but specific chemical profiles of plant species in the Brassicaceae was an important factor in the formation of phytophagous guilds (Frenzel & Brandl, 1998), whereas common leaf chemical constituents (nitrogen, water, cellulose, and lignin) did not affect arboreal guild composition (Peeters, 2002). Guild members, however, do not necessarily compete (Rathcke, 1976; Lawton, 1984b; Strong, 1984; Kaszab, 1962). Hawkins and MacMahon (1989) emphasise that generalist members may often destabilise guilds. Even in a case where competition was found important among phytophagous insect guild members, it was not the sole organising force (Zwölfer & Stadler, 2004).

One of the factors that produces variability in guild composition can be microhabitat requirements of members (Joern & Lawlor, 1981). It was found that *B. venustus* preferred sunny and shady *V. tenuifolia* patches equally, whereas the other three species were significantly more abundant in shady patches. Furthermore, it was not the parasitoid activity that produced the skewed distribution of bruchid infestation, because it was even higher on shady patches.

This study indicates that factors other than competitive interactions among guild members influence organisational processes, and that guild members probably assemble by chance. No interactions between bruchid species were detected, whereas food specialisation and habitat requirements seemed to explain guild membership sufficiently. The potential importance of competitive interactions in guild organisation is not denied; however its role might depend on the type of community examined.

**Table 5.** The possible guild combinations and their obtained frequency of pre-dispersal seed predator guild members.

Guild combinations			Occurrence, number (%) <sup>a</sup>
Bruchids	Lepidopterans	Curculionids	
1	1	1	32 (50.8)
1	1	0	15 (23.8)
1	0	0	9 (14.3)
1	0	1	7 (11.1)
0	1	1	0
0	1	0	0
0	0	1	0
0	0	0	0

<sup>a</sup>Refers to raw spatial resolution.

**Table 6.** Results of the coexistence analyses: the probability values of receiving equal or smaller coexistence metric in a chance event.

Taxonomical resolution	Co-existence		Spatio-temporal resolution						
	Taxon 1	Taxon 2	<i>T</i> (year) <i>S</i> (coarse)	<i>T</i> (year) <i>S</i> (fine)	<i>T</i> (year) <i>S</i> (im)	<i>S</i> (raw)	<i>S</i> (fine)	<i>S</i> (im)	
Major pre-DSPs	Bru	Lep	1.000	1.000	1.000	0.783	1.000	1.000	
	Bru	Cur	1.000	1.000	1.000	1.000	1.000	1.000	
	Lep	Cur	1.000	1.000	1.000	1.000	1.000	1.000	
Bruchid species	B. ven.	B. lib.	0.999	1.000	1.000	1.000	1.000	1.000	
	B. ven.	B. occ.	0.741	1.000	1.000	1.000	1.000	0.997	
	B. ven.	B. bra.	0.390	0.660	0.908	1.000	0.994	0.638	
	B. lib.	B. occ.	0.869	1.000	1.000	1.000	1.000	1.000	
	B. lib.	B. bra.	0.419	0.545	1.000	1.000	1.000	0.362	
	B. occ.	B. bra.	1.000	1.000	1.000	1.000	1.000	1.000	

*T*(year)*S*(coarse), Time + Space Course; *T*(year)*S*(fine), Time + Space fine; *T*(year)*S*(im), Time + Space intermediate; *S*(raw), Space raw; *S*(fine), Space fine; *S*(im), Space intermediate; pre-DSPs, pre-dispersal seed predator; Bru, Bruchidae; Lep, Lepidoptera; Cur, Curculionidae. B. ven., *Bruchus venustus*; B. lib., *B. libanensis*; B. occ., *B. occidentalis*; B. bra., *B. brachialis*.

## Acknowledgements

The authors are indebted to Joseph A. Veech for valuable comments and for substantial English editing of the manuscript. The study was supported by grants from the Hungarian Research Fund Agency (OTKA) nos 1434 and 13300, as well as by the János Bolyai Scholarship of the Hungarian Academy of Sciences to D.S.

## References

- Abbott, I., Burbidge, T., Williams, M. & Vanheurck, P. (1992) Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in Mediterranean forest of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. *Austral Journal of Ecology*, **17**, 263–274.
- Ashbourne, S.R.C. & Putman, R.J. (1987) Competition, resource-partitioning and species richness in the phytophagous insects of red oak and aspen in Canada and the U.K. *Acta Oecologica*, **8**, 43–56.
- Brown, J.H. (1987) Variation in desert rodent guilds: Patterns, processes, and scales. *Organization of Communities. Past and Present* (ed. by J. H. R. Gee and P. S. Giller), pp. 185–203. Blackwell Scientific, Oxford.
- Brown, J.H., Davidson, D.W., Munger, J.C. & Inouye, R.S. (1986) Experimental community ecology: the desert granivore system. *Community Ecology* (ed. by J. Diamond and T. J. Case), pp. 41–61. Harper & Row, New York.
- Cornell, H.V. & Kahn, D.M. (1989) Guild structure in the British arboreal arthropods: is it stable and predictable? *Journal of Animal Ecology*, **58**, 1003–1020.
- Feeley, K. (2003) Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. *Oecologia*, **137**, 104–113.
- Frenzel, M. & Brandl, R. (1998) Diversity and composition of phytophagous insect guilds on Brassicaceae. *Oecologia*, **113**, 391–399.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Gee, J.H.R. & Giller, P.S. (1987), eds. *Organization of Communities. Past and Present*. Blackwell Scientific, Oxford.
- Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.
- Gotelli, N.J. & Entsminger, G.L. (2001a) Swap and fill algorithms in null model analysis: rethinking the knight's tour. *Oecologia*, **129**, 281–291.
- Gotelli, N.J. & Entsminger, G.L. (2001b) *Ecosim: Null Models Software for Ecology, Version 7.0*. <http://www.garyentsminger.com/ecosim/ecosim.htm>. Acquired Intelligence Inc. & Kelsey-Bear, Jericho, Vermont.
- Gotelli, N.J. & Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press, Washington.
- Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.
- Graves, G.R. & Gotelli, N.J. (1993) Assembly of avian mixed-species flocks in Amazonia. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 1388–1391.
- Hawkins, C.P. & MacMahon, J.A. (1989) Guilds: the multiple meanings of a concept. *Annual Review of Entomology*, **34**, 423–451.
- Hawkins, B.A. & Mills, N.J. (1996) Variability in parasitoid community structure. *Journal of Animal Ecology*, **65**, 501–516.
- Hendrix, S.D., Brown, V.K. & Dingle, H. (1988) Arthropod guild structure during old field succession in a new and an old world site. *Journal of Animal Ecology*, **57**, 1053–1065.
- Jermey, T. (1985) Is there competition between phytophagous insects? *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **23**, 275–285.
- Jermey, T. & Szentesi, Á. (2003) Evolutionary aspects of host plant specialisation – a study on bruchids (Coleoptera: Bruchidae). *Oikos*, **101**, 207–215.
- Joern, A. & Lawlor, L.R. (1981) Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos*, **37**, 93–104.
- Kaszab, Z. (1962) *Levélbogarak – Chrysomelidae*. Fauna Hungariae, no. 63. Akadémiai Kiadó, Budapest [In Hungarian].
- Krüger, O. & McGavin, G.C. (2001) Predator–prey ratio and guild constancy in a tropical insect community. *Journal of Zoology*, **253**, 265–273.
- Lawton, J.H. (1984a) Herbivore community organization: general models and specific tests with phytophagous insects. *A New Ecology. Novel Approaches to Interactive Systems* (ed. by

- P. W. Price, C. N. Slobodchikoff and W. S. Gaud), pp. 329–383. John Wiley & Sons, New York.
- Lawton, J.H. (1984b) Non-competitive populations, non-convergent communities, and vacant niches: The herbivores of bracken. *Ecological Communities. Conceptual Issues and the Evidence* (ed. by D. J. Strong Jr, D. Simberloff, L. G. Abele and A. B. Thistle), pp. 67–99. Princeton University Press, Princeton, New Jersey.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–67.
- Manly, B.J.F. (1991) *Randomisation and Monte Carlo Methods in Biology*. Chapman & Hall, New York.
- Moran, V.C. & Southwood, T.R.E. (1982) The guild composition of arthropod communities on trees. *Journal of Animal Ecology*, **51**, 289–306.
- Noda, T. (2004) Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. *Population Ecology*, **46**, 105–117.
- Osnas, E.E. & Ankney, C.D. (2003) Null models of North American prairie duck communities: local habitat conditions and temporal scale influence community patterns. *Evolutionary Ecology Research*, **5**, 913–932.
- Peeters, P.J. (2002) Correlation between leaf constituent levels and the densities of herbivorous guilds in an Australian forest. *Austral Ecology*, **27**, 658–671.
- Pielou, D.P. & Pielou, E.C. (1968) Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology*, **21**, 202–216.
- Rathcke, B.J. (1976) Competition and coexistence within a guild of herbivorous insects. *Ecology*, **57**, 76–87.
- Root, R.B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.
- Schluter, D. (1984) A variance test for detecting species associations, with some example applications. *Ecology*, **65**, 998–1005.
- Schoener, T.W. (1986) Overview: kinds of ecological communities – ecology becomes pluralistic. *Community Ecology* (ed. by L. Diamond and T. J. Case), pp. 467–479. Harper & Row, New York.
- Schonrogge, K., Stone, G.N. & Crawley, M.J. (1995) Spatial and temporal variation in guild structure: parasitoids and inquiline of *Andricus quercuscalicis* (Hymenoptera: Cynipidae) in its native and alien ranges. *Oikos*, **72**, 51–60.
- Schoonhoven, L.M., Jermy, T. & van Loon, J.J.A. (1998) *Insect–Plant Biology: From Physiology to Evolution*. Chapman & Hall, London.
- Simberloff, D., Stone, L. & Dayan, T. (1999) Ruling out community assembly rule: The method of favoured states. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (ed. by E. Weiher and P. Keddy), pp. 58–74. Cambridge University Press, Cambridge.
- Southwood, T.R.E. (1996) Natural communities: structure and dynamics. *Philosophical Transactions of the Royal Society of London B*, **351**, 1113–1129.
- StatSoft (2003) *Statistica (Data Analysis Software System), Version 6*. StatSoft Inc., Tulsa, Oklahoma.
- Stone, L. & Roberts, A. (1990) The checkerboard score and species distributions. *Oecologia*, **85**, 74–79.
- Strong, D.R. Jr (1984) Exorcising the ghost of competition past: phytophagous insects. *Ecological Communities. Conceptual Issues and the Evidence* (ed. by D. J. Strong Jr, D. Simberloff, L. G. Abele and A. B. Thistle), pp. 28–41. Princeton University Press, Princeton, New Jersey.
- Vázquez, D.P. & Aizen, M.A. (2003) Null model analyses of specialization in plant–pollinator interactions. *Ecology*, **84**, 2493–2501.
- Weiher, E. & Keddy, P. (1999), eds. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge.
- Zwölfer, H. (1979) Strategies and counter-strategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschritte der Zoologie*, **25**, 331–353.
- Zwölfer, H. (1980) Distelblütenköpfe als ökologische Kleinsysteme: Konkurrenz und Koexistenz in Phytophagenkomplexen. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, **2**, 21–37.
- Zwölfer, H. (1988) Evolutionary and ecological relationships of the insect fauna of thistles. *Annual Review of Entomology*, **33**, 103–122.
- Zwölfer, H. & Stadler, B. (2004) The organization of phytophagous guilds in Cardueae flower heads: conclusions from null models. *Evolutionary Ecology Research*, **6**, 1201–1218.

Accepted 15 July 2005