

The organization of phytophagous guilds in Cardueae flower heads: conclusions from null models

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ABSTRACT

Rich and diversified assemblages of larval stage phytophagous insects exploit the flower heads of the thistle tribe Cardueae. As these insects form communities within a shared resource unit with well-defined spatial boundaries, they offer a good opportunity to study the guild organization of communities of endophytic insects. We used random combinations of members of phytophagous taxa, which radiated on hosts of the subtribes Centaureinae and Carduinae, as species pools for null models to determine whether and to what extent the composition of the guilds in Cardueae flower heads follows predictable assembly rules. We tested two hypotheses and found that in both cases the null model can be rejected. *Assembly rule 1*: species assemblages in flower heads follow the rule of intra-generic isolation (i.e. each guild member belongs to a different genus) significantly more often than random combinations of Cardueae insects. We show that, where violations of this rule occur, they are almost exclusively due to the occurrence of a combination of those congeners of the genera *Urophora*, *Larinus* and *Cerajocera*, whose larval activities differ to some extent temporally and/or spatially. *Assembly rule 2*: the composition of guilds tends to develop towards a maximum of intra-guild differentiation – the three complementary trophic types (e.g. gall and callus feeders, receptacle and ovary chewers, omnivores and intra-guild predators) co-occur in guilds significantly more often than in random combinations. Our results show that the organization of phytophagous guilds in Cardueae flower heads is mainly a result of invasions due to host shifts. We suggest that in addition to larval competition for space and food, constraints such as the availability of enemy-free space and/or ‘free rendezvous arenas’ have shaped the structure of the guilds investigated.

Keywords: assembly rules, Cardueae flower heads, competition, enemy-free space, guild structure, invasions, rendezvous arenas.

INTRODUCTION

Since Goureaux's (1845) detailed description of the insect community in the heads of the nodding thistle (*Carduus nutans*), many authors (e.g. Varley, 1947b; Mellini, 1952; Redfern, 1968; Goeden and Ricker, 1986; Zwölfer, 1987) have investigated the inhabitants of the

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flower heads of ‘thistles’ and knapweeds (i.e. Asteraceae species belonging to the Cardueae and related tribes). These flower heads form discrete microhabitats, which allow the study of biological details such as oviposition, resource utilization, and the larval and pupal development of their inhabitants as well as their inter- and intraspecific interactions (Zwölfer, 1979) and the food web structures that they form (Zwölfer, 1994). The phytophagous larvae in Cardueae heads form a ‘community detachment whose members share resources that are exploited in a similar way’ (Root, 2001) and can therefore be treated as guilds. The species-rich tribe Cardueae offers an opportunity to compare groups of such guilds, which are associated with groups of related host plant species. As the host relationships of most members of the insect fauna of Cardueae are well known, a comparative analysis of these guilds can be performed to gain insight into their structure and evolution.

Any diversity of communities results from a combination of speciation, immigration and extinction rates (Rosenzweig, 1995). Thus, phytophagous guilds may accumulate species by speciation events – that is, the splitting and multiplication of resident guild members – or by invasions of foreign species, which originate from guilds associated with other host plants. They may lose species by extinction events. The expectation is that if guilds emerge from speciation events, a high proportion of the guild members should belong to the same genera. Alternatively, if guilds include a majority of species belonging to different genera, invasions into existing guilds must have been prevalent. The success of invasions obviously depends on the physiological and ecological preadaptations of the invader, but it may also be influenced by features such as the degree of species packing (Zwölfer, 1987), the presence of ‘empty niches’ or enemy-free space (Zwölfer, 1975). The relative importance of speciation and invasion processes and the relative importance of these processes for structuring guilds can be estimated by comparing the results of null models – that is, random combinations of species from the species pool (Gotelli and Graves 1996) – with real guilds.

A crucial question involved in null models is the selection of a species pool, the members of which should reflect their potential for belonging to the guilds under study. For our species pools, we selected phytophagous taxa that specialized in the exploitation of flower heads of the Cardueae during their evolution, and which include species that contain biotypes (*sensu* Diehl and Bush, 1984) and host races (*sensu* Bush, 1992). These host races provide models of how new host affiliations can evolve within the Cardueae subtribes and genera. Such host shifts, which are dependent on the simultaneous occurrence of both the original and the new host, must occur in sympatry or parapatry (Feder, 1998). Host shifts with disruptive selection can provide ‘ecological templates’ for Cardueae insects (Zwölfer and Romstöck-Völkl, 1991) for eventual speciation processes. The latter may be facilitated by a period of allopatry (Kondrashov and Mina, 1986), but the important point is that the initial differentiation is due to selective forces and not to genetic drift, as in classical allopatric speciation (Via, 2001).

The results of previous analyses of the phytophagous guilds in Cardueae flower heads (Zwölfer, 1982, 1986) suggest some degree of organization. Here we attempt to test this hypothesis statistically, and to specify with a set of null models to what extent this organization differs from mere random patterns. In particular, we seek to identify the potential constraints and structuring forces in flower head community composition, and discuss our results in connection with the available information on the biology of Cardueae insects and their intra-guild interactions.

METHODS, MATERIALS AND ASSEMBLY RULES

Field data

In 1961, one of us (H.Z.) started a systematic inventory of the phytophagous insect fauna associated with Cardueae, Carlineae and Echinopeae host plants (Zwölfer, 1965), a study which has continued for more than 40 years. For the comparison with null models we use the data on 72 Cardueae species whose flower heads have been investigated. Appendix 1 provides a list of the plant species and regions from which the samples were taken. We assessed the local guilds in various ways – by combining field observations on ovipositing insects, dissections of samples of immature and mature flower heads, and rearings of insects from mature heads (Zwölfer, 1965). At present we have at our disposal data from 2183 field-collected samples of Cardueae flower heads. Potential sources of sampling error may have been introduced because the sample size of flower heads was too small to cover all local guild members. Moreover, phytophagous species may have been underrepresented in the particular host population sampled. We accounted for these inaccuracies by aggregating the guilds of our field samples according to species numbers into size classes, which are compared with the corresponding size classes of the null models. We treated the members of the sub-tribes Carduinae and Centaureinae separately, because the host relationships of clusters of biotypes and species show that most host shifts took place within and between related genera – that is, within the Cardueae sub-tribes (Zwölfer and Romstöck-Völkl, 1991). Appendices 2 and 3 give the names and code numbers of the phytophagous insects associated with the Carduinae and Centaureinae flower heads used for the null models. A comparison of null models with the complete lists of phytophagous species associated with single Cardueae species (i.e. with gamma-diversity) would lead to erroneous conclusions, as much variation in their guild composition exists if the same host plant is collected over larger areas. Moreover, many Cardueae insects show distinct differences in their host relationships if they are studied along latitudinal or altitudinal gradients (Zwölfer and Romstöck-Völkl, 1991). Also, phenomena such as the ecological character displacement in certain *Larinus* species, which avoid co-occurrence in the same host plant populations by a geographically changing pattern of host races (Zwölfer, 1979), underline the importance of our null models being compared with alpha-diversity – that is, that the single samples collected from a local host plant population are taken as independent units.

We checked the conclusions derived from the null models based on our complete set of Cardueae insects (Appendices 2 and 3) by performing simulations with two subsets of phytophagous species originating from the Cardueae sampled in geographically restricted areas (Upper Frankonia in northern Bavaria and Provence in south-eastern France). For the calculation of χ^2 -values, we simply used the sums of guild sizes 2–7 in these additional tests, as, on the whole, the results were comparable to a pairwise comparison of individual guild sizes.

Assembly rules

Assembly rule 1: congeners are underrepresented in guilds

The absence of congeners – that is, of related phytophagous species in a guild – is an indication that the accumulation of species is the result of an invasion process (i.e. a shift

from another host plant species). Most phytophagous genera associated with Cardueae have similar biologies with regard to oviposition, larval biology and pupation, and congeners are often exploited by the same parasitoid species. Therefore, invaders belonging to a genus absent from the resident guild should be at an advantage. We tested to what extent the co-occurrence of congeners in real guilds of Cardueae flower heads deviate from random combinations drawn from the potential species pool associated with Cardueae host plants. From our field surveys, we know that possible deviations from assembly rule 1 might be due to the co-occurrence of those congeners whose larvae develop in the same host species, but which are temporally and/or spatially segregated. Therefore, we repeated our tests taking into account three special cases:

1. In the weevil genus *Larinus*, a large taxon the larvae of which exclusively exploit flower heads of Cardueae and related 'thistle-like' tribes (Zwölfer *et al.*, 1971), one subgroup (*Larinus planus*-type) is specialized in ovipositing into holes pierced into closed buds and exploits an early stage of the host. The other subgroup (*Larinus turbinatus*-type) oviposits into opened flower heads and uses a more advanced host stage (Zwölfer and Brandl, 1989). Members of both subgroups often co-occur in the same sample of flower heads of *Cirsium* spp., as was observed by Rabaud (1913) for *Cirsium arvense*.

2. As early as 1947, Varley showed that in flower head samples of *Centaurea* two tephritid species of the genus *Urophora*, *U. quadrifasciata* and *U. jaceana*, often co-occur (Varley, 1947a). The primitive gall inducer *U. quadrifasciata*, which exploits an advanced stage of immature heads of *Centaurea* spp., occasionally co-exists with other *Urophora* spp. with more complex galls, which are dependent on the early bud stage of flower heads (Myers and Harris, 1980; Burkhardt and Zwölfer, 2002).

3. In the tephritid genus *Cerajocera*, the sister species *C. ceratocera* and *C. plagiata* can be found in the same populations of *Centaurea scabiosa*. Hering (1935), who deals with both taxa as subspecies, discusses their ecological separation. In one form [according to Merz (1994) *C. ceratocera*] the larvae develop in the flower heads, whereas in the sister taxon [according to Merz (1994) *C. plagiata*] the larvae enter the peduncle from the flower head and mine within the stem.

To test the effects of these species pairs with different larval niches on assembly rule 1, we used the information on their distinct larval biology and treated them as if they were non-congeners – that is, we coded the '*Larinus turbinatus*-type', *U. quadrifasciata* and *C. plagiata* as separate units that are different from the remaining *Larinus*, *Urophora* and *Cerajocera* species.

Assembly rule 2: guilds contain combinations of three trophic strategies

The members of phytophagous guilds in Cardueae heads may be divided into three trophic subgroups (Zwölfer, 1987, 1994). Species in the first subgroup stimulate host plant tissues (Harris and Shorthouse, 1996) and induce different types of galls (members of the tephritid genus *Urophora* or the cynipid genus *Isocolus*) or growth of callus (certain members of the tephritid genus *Tephritis* and certain weevils (e.g. *Rhinocyllus*)). The larvae of these species exploit an early stage of the flower head as they need meristematic tissues. They almost always occur gregariously. The larvae of at least some of these species show an Allee effect, as they profit from their aggregation (Burkhardt and Zwölfer, 2002). Larvae of a second subgroup (tephritids, bruchids, weevils and chrysomelids) attack an intermediate

developmental stage of the host and feed on receptacle tissues, ovaries and immature achenes. This subgroup contains solitary as well as gregarious species. The larvae of the last subgroup (anobiids, tortricids, pyralids, gelechiids) live in maturing and mature flower heads where they may feed on achenes and, if there is an opportunity, also operate as intra-guild predators. Many of these species are cannibalistic and in most species only one larva per flower head reaches maturity. As these three trophic strategies form complementary subniches, we expect that in guilds with three and more phytophagous species all of the trophic subgroups should be represented. We tested this hypothesis by comparing the frequencies of occurrence of one, two and three trophic types in the guilds of our field samples with those of the simulated null communities.

The null models

Null models are now widely used in ecology to address questions on biodiversity, guild structure or biogeography (e.g. Manly, 1991; Gotelli and Graves, 1996; Gotelli, 2000). The purpose of a null model is to generate patterns based on the randomization of ecological data or random sampling from a known pool. It deliberately excludes biological mechanisms that may account for the observed patterns. We used the assembly rules described above to estimate constraints on how flower head communities assemble or organize themselves. In our null model, we organized the sequence of decisions in a hierarchical way. The data matrix comprised 49 species associated with Carduinae hosts and 57 species associated with Centaureinae hosts characterized by three parameters coding for genera, niche and trophic strategy (for details, see Appendices 2 and 3).

In a first step, we randomly drew from the potential species pool guilds comprising 3–8 species. Therefore, rule violations for different guild sizes were estimated. In each run, every species was drawn only once. According to assembly rule 1, we determined whether the species from a particular guild size belonged to different genera. Subsequently, we tested to what extent three congeneric species pairs with temporal and spatial niche differentiation caused violations of rule 1. Finally, we tested how often the randomly selected species belonged to different trophic strategies (rule 2) using the same Monte-Carlo procedure for species selection as above. All guild selection processes were repeated 1000 times and the relative frequencies of violations determined. Differences in the frequencies of rule violations for real and simulated assemblages were tested using the χ^2 -test. The tests of rule violations were implemented in a Turbo Pascal program.

RESULTS

The frequency of congeners in real and simulated guilds

Figure 1 shows that a considerable proportion (up to 50%) of our field samples of Centaureinae hosts (total = 695 guilds) do not follow assembly rule 1, as they contain congeners in guilds. These violations are, however, significantly less frequent than in the random combinations of the null model. Chi-square tests for observed and expected values for guild sizes 2–6 (d.f. = 1) give values of 59.9, 60.1, 27.5, 19.8 and 14.9, respectively, which show that here the null hypotheses can be rejected at $P < 0.001$. The statistical significance for the small sample of guild size class 7 ($n = 34$, $\chi^2 = 5.13$, $P = 0.024$) is weak and is absent in size class 8 ($n = 14$, $\chi^2 = 3.16$, $P = 0.075$). Generally, with increasing guild size, violations

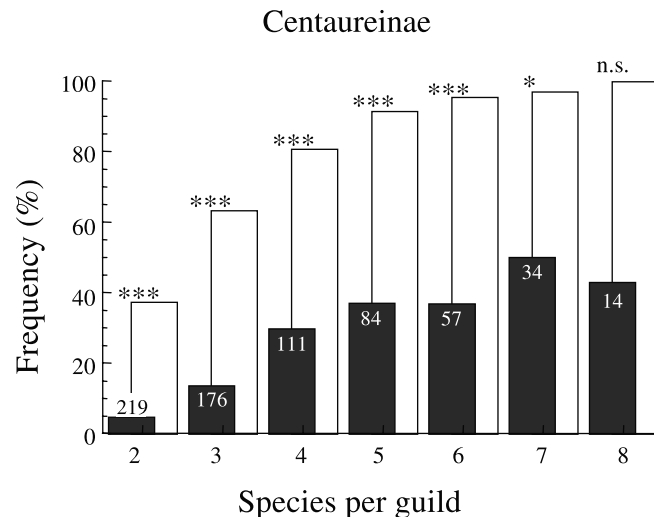


Fig. 1. The relative frequencies of violations of assembly rule 1 (no co-occurrence of congeners) in field data (■) and simulated guilds (□) for the Centaureinae. The frequency of violations increases with guild size. The numbers above the solid columns are the sample sizes. Simulations were run 1000 times. n.s. = non-significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

of rule 1 also increase. Corresponding results have been obtained with the regional Centaureinae faunas of Upper Frankonia ($\chi^2 = 69.3$; d.f. = 1; $P < 0.001$) and of Provence ($\chi^2 = 183.6$; d.f. = 1; $P < 0.001$).

We obtained similar results (Fig. 2) with 686 guilds from field samples of Carduinae host plants. Violations of assembly rule 1 occurred in 10–40% of the samples of individual guild size classes, but again in the majority of size classes there was either a highly significant deviation from the null model communities (class 3 and 6: $\chi^2 = 39.0$ and 16.1, each $P < 0.001$) or a significant deviation (class 2: $\chi^2 = 8.75$, $P = 0.003$; class 4: $\chi^2 = 8.51$, $P = 0.004$). No significant differences between actual and simulated rule violations were obtained with the small sample numbers of class 5 ($n = 26$, $\chi^2 = 3.27$, $P = 0.07$) and class 7 ($n = 6$, $\chi^2 = 1.57$, $P = 0.211$). Corresponding results have been obtained with the regional Carduinae faunas of Upper Frankonia ($\chi^2 = 182.6$; d.f. = 1; $P < 0.001$) and Provence ($\chi^2 = 85.0$; d.f. = 1; $P < 0.001$).

Exclusion of temporally and/or spatially separated congeners

If we take into account that in the genera *Larinus*, *Urophora* and *Cerajocera* there are three types of combinations of congeners whose larvae differ in how they exploit the host – that is, if we treat only species with homologous feeding niches as ‘congeners’ – the frequency of violations of assembly rule 1 in our field samples is drastically reduced. Figure 3 shows this effect for the Centaureinae. Here the χ^2 -values for all size classes of guilds (62.7, 94.7, 79.0, 67.6, 41.9, 26.7 and 13.8 for guilds 2–8, respectively) now indicate highly significant ($P < 0.001$) deviations from the random values of the null model for assembly rule 1. Corresponding results have been obtained with the regional Centaureinae faunas of Upper Frankonia ($\chi^2 = 150.9$; d.f. = 1; $P < 0.001$) and Provence ($\chi^2 = 307.0$; d.f. = 1; $P < 0.001$).

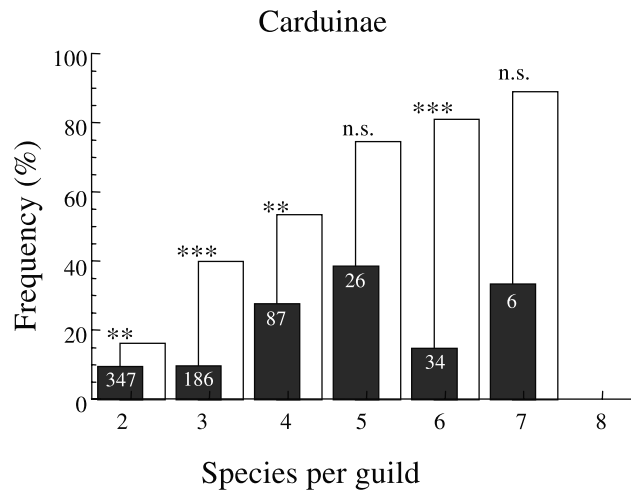


Fig. 2. The relative frequencies of violations of assembly rule 1 (no co-occurrence of congeners) in field data (■) and simulated guilds (□) for the Carduinae. The frequency of violations increases with guild size. The numbers above the solid columns are the sample sizes. Simulations were run 1000 times. n.s. = non-significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

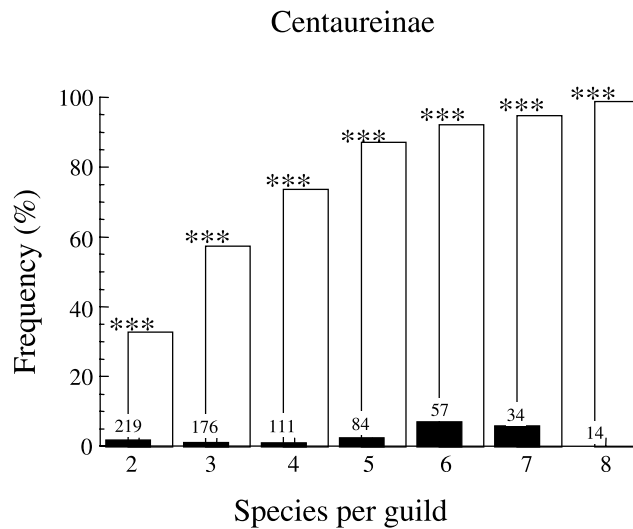


Fig. 3. The relative frequencies of violations of assembly rule 1 after the exclusion of three species pairs with different larval niches. Field data (■) and simulated guilds (□) for the Centaureinae. The numbers above the solid columns are the sample sizes. Simulations were run 1000 times. n.s. = non-significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

The fauna of the Carduinae field samples (Fig. 4) showed a similar pattern, with the exception of the classes with guild size 4 (7 violations in 87 samples) and guild size 5 (4 violations in 26 samples), where the proportion of violations is moderately higher. Size classes 2, 3, 4 and 6 (χ^2 -values of 50.0, 58.8, 27.3 and 21.0, respectively) allow the rejection of the null hypotheses with $P < 0.001$. For the small sample sizes in class 5

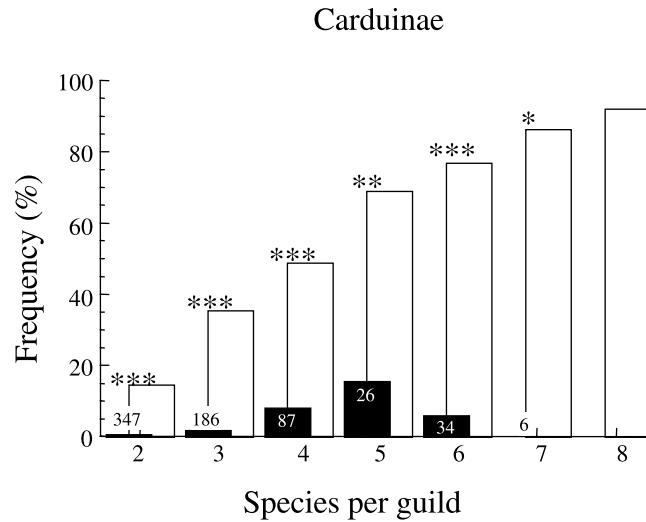


Fig. 4. The relative frequencies of violations of assembly rule 1 after the exclusion of three species pairs with different larval niches. Field data (■) and simulated guilds (□) for the Carduinae. The numbers above the solid columns are the sample sizes. Simulations were run 1000 times. n.s. = non-significant; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

($\chi^2 = 9.4$, $P = 0.002$) and class 7 ($\chi^2 = 5.8$, $P = 0.023$), the statistical significance is lower. Corresponding results have been obtained with the regional Centaureinae faunas of Upper Frankonia ($\chi^2 = 275.0$; d.f. = 1; $P < 0.001$) and Provence ($\chi^2 = 189.2$; d.f. = 1; $P < 0.001$).

Combinations of complementary trophic subgroups

According to assembly rule 2, the species composition of guilds should be balanced with respect to the three trophic subgroups. We therefore expected that in guilds with three or more members, a strong tendency would be found for all three trophic strategies to be present. Table 1 shows the results of tests of the distribution patterns of the frequencies of trophic subgroups in the null model with the results of 476 field samples of Centaureinae flower heads. Chi-square tests showed that for all size classes there was a highly significant

Table 1. Centaureinae, rule 2: proportion of subgroups, simulation with 1000 replicates

Guild size	n+%/ of field samples with:			Simulation (%)	χ^2	(P)
	1 subgroup	2 subgroups	3 subgroups			
3	6 (3.8%)	121 (69.8%)	49 (26.4%)	40.0–55.0–5.0	248	(0.000)
4	4 (3.7%)	37 (33%)	70 (63.3%)	24.0–62.9–13.1	246	(0.000)
5	0	16 (19%)	68 (81%)	13.6–62.8–23.6	154	(0.000)
6	0	6 (10.5%)	51 (89.5%)	8.6–57.3–34.1	85.7	(0.000)
7	0	1 (2.9%)	33 (97.1%)	4.0–48.5–47.5	30.8	(0.000)
8	0		14 (100%)	1.3–41.5–57.2	10.2	(0.001)

Table 2. Carduinae, rule 2: proportion of subgroups, simulation with 1000 replicates

Guild size	<i>n</i> +% of field samples with			Simulation (%)	χ^2	(P)
	1 subgroup	2 subgroups	3 subgroups			
3	34 (8.8%)	249 (64.1%)	105 (27.1%)	19.9–69.4–10.7	122	(0.000)
4	11 (5.5%)	68 (34.2%)	120 (60.3%)	11.2–64.9–23.9	145	(0.000)
5	0	32 (29.1%)	78 (70.9%)	6.9–59.8–33.3	59.1	(0.000)
6	0	8 (11.6%)	61 (88.4%)	3.4–55.4–41.2	59.1	(0.000)
7	0	1 (1.6%)	60 (98.4%)	2.4–51.4–46.2	53.1	(0.000)

difference ($P < 0.001$) between the null model and the empirical data, in which guilds with two and three trophic subgroups were distinctly overrepresented.

The same results were obtained for the Carduinae, for which data from 827 field samples were available (Table 2). Again, we obtained corresponding results with the regional Centaureinae faunas of Upper Frankonia ($\chi^2 = 102.7$; d.f. = 2; $P < 0.001$) and Provence ($\chi^2 = 124.1$; d.f. = 2; $P < 0.001$) and with the regional Carduinae faunas of Upper Frankonia ($\chi^2 = 92.2$; d.f. = 2; $P < 0.001$) and Provence ($\chi^2 = 28.2$; d.f. = 2; $P < 0.001$).

DISCUSSION AND CONCLUSIONS

Rule 1: no co-occurrence of congeners

Our tests show that congeners may occasionally co-occur in individual samples of Cardueae flower heads. Nevertheless, the null model according to which congeners occur in random combinations in the endophytic guilds in Cardueae flower heads can be rejected for both subtribes. Congeners are significantly underrepresented in real guilds. As multiplicative speciation of resident species should have resulted in much higher rates of congeners, our tests indicate that the accumulation of species in the flower head guilds must have occurred mainly by host shifts and/or a host-determined specialization of originally oligophagous species. Host shifts take place between different but related host taxa and may result in speciation events, leading to new host associations while usually maintaining general biological traits such as oviposition and larval feeding behaviour. Mamaev (1975) comes to a similar conclusion with regard to phytophagous gall midges, where species formation is most often associated with the passage of the initial plant species to a new host.

Only a small proportion of Cardueae insects radiated by changing the oviposition and larval feeding sites while maintaining their association with their hosts (Zwölfer, 1982). The latter group is mainly represented by the cynipid genus *Isocolus*, whose members induce galls in the achenes, bracts, stem and root crown of *Centaurea* spp. Stone (2002) points out that this type of speciation is widespread among cynipids. An interesting case is a pair of sibling species of the tephritid genus *Cerajocera*, *C. ceratocera* and *C. plagiata*, which presumably originated from an ancestor already associated with flower heads of *Centaurea scabiosa* (Hering, 1935). Here, not a shift to other hosts but partial niche separation took place. Both species oviposit into the flower heads, but whereas the larvae of *C. ceratocera* feed on the receptacle and the ovaries, the larvae of *C. plagiata* mine the peduncle and the stem. Hering (1935) discusses this phenomenon as a case of ecological (= sympatric) speciation, but one cannot, of course, exclude the possibility that temporal allopatry reinforced

the speciation process. A similar phenomenon has been observed in the tephritid genus *Blepharoneura* on Cucurbitaceae hosts (Condon, 1997).

The cases of co-occurrence of congeners of the tephritid genus *Urophora* in flower heads of *Centaurea* spp. always involves *U. quadrifasciata*, a primitive, oligophagous species with non-lignified ovary galls, and a monophagous *Urophora* spp. with specialized lignified galls. As *U. quadrifasciata* attacks a more advanced stage of the flower heads than the monophagous *Urophora* spp., there is a partial temporal separation of the ecological niches of these congeners (Varley, 1947b). Within the genus *Urophora* these co-occurring congeners belong to different species groups associated with Centaureinae host plants (White and Korneev, 1989). The differentiation of their life histories might well have been combined with minor host shifts within this subtribe.

The great majority of violations of assembly rule 1 in the subtribe Carduinae (Fig. 2) are caused by the co-occurrence of a pair of oligophagous weevil species of the genus *Larinus* in flower heads of *Cirsium* spp., *L. planus* and *L. turbinatus*. They belong to the same subgenus *Larinodontes* with genetic distances (Nei's *D*) of over 1 (Jensen and Zwölfer, 1994), indicating a low relatedness, and are frequently found in the same *Cirsium arvense* population. As early as 1913, Rabaud described the partial niche separation of these two *Larinus* spp., which one finds frequently in the same *Cirsium arvense* population. Females of *L. planus* drill a hole through the wall of closed flower head buds and deposit their eggs with a slender and curved rostrum, whereas females of *L. turbinatus* use a conical and blunt rostrum, pushing their eggs from the top into the florets of opened flower heads. The larva then feeds on the tissues of a more advanced stage of the flower head. *Larinus turbinatus* avoids ovipositing into flower heads already occupied by *L. planus*. Since both species have a rather broad host range within the Carduinae, it is questionable whether host shifts have been involved in the evolution of their different oviposition and feeding niches.

With this biological information included in our null model, we obtain a marked contrast between the patterns resulting from random selections of species and those from empirical surveys (Figs. 3 and 4). This corroborates our conclusion that the structure of guilds in the Centaureinae and Carduinae flower heads is characterized by a distinct underrepresentation of species with a homologous way of resource utilization. Our analysis suggests that, as far as guilds are the results of invasions, the success of an invader depends at least partially on synecological characteristics – that is, on the absence of resident species which have similar demands on their environment, which use their resources in a similar way and which are exposed to similar mortality factors.

Rule 2: balanced distribution of trophic subgroups

Our analysis shows that the guilds in Centaureinae and Carduinae flower heads are not random aggregations with respect to the distribution of trophic subgroups. The strong tendency to accumulate species belonging to different trophic subgroups points to a structure that must have resulted from constraints during their phase of species accumulation. As each of the three trophic subgroups has a different functional profile and uses a different subset of the common resource, the affiliation with different subgroups reduces the overlap of the larval niches, which is a particular problem for the endophytic larvae confined to the limited space of flower heads.

The early growth phase of flower heads is exploited by species with gregarious larvae, which, as gall formers, are able to import nutrients via a newly generated vascular system

(Harris, 1980; Harris and Shorthouse, 1996) or which, as callus feeders, stimulate the tissues to produce calluses. At least some of these species show a marked Allee effect – that is, they benefit from a certain degree of crowding (Burkhardt and Zwölfer, 2002). The larvae of the second subgroup, which often consists of solitary feeders, concentrate their activity on a slightly later developmental phase of the flower head, where they mine the receptacle and immature achenes. High densities may lead to competitive interactions between the first and second subgroups (Zwölfer, 1979). The third subgroup contains the larvae of phytophagous species, which, on contact with other guild members, become carnivorous. These species are cannibalistic and usually only one larva survives in a flower head. As a consequence, within the flower head guilds, species of this subgroup are potential intra-guild predators and are competitively superior to the other two subgroups.

The guild structure with three complementary trophic strategies can be found in most Palearctic Cardueae taxa, as shown by our records from Europe, Pakistan and Japan. But such a structure does not exist in the Nearctic *Cirsium* species (Goeden and Ricker, 1986, 1987a,b; Zwölfer, 1988). The Nearctic thistle fauna is not only much poorer in endophytic genera and species; it also lacks members of the highly specialized first subgroup. This contrast is probably due to the fact that the Nearctic Cardueae taxa (*Cirsium*, *Saussurea*) are a relatively young group (originating in the Pliocene or early Pleistocene; Steck, 1981), whereas all available evidence shows that most of the radiation of the Palearctic Cardueae took place earlier in the Miocene (Steck, 1981; Zwölfer, 2000). This suggests that the evolution of the ‘balanced’ guild structure of the Cardueae required a time span of 15–40 million years.

The Palearctic Cardueae, with their high diversity of phytophagous species and a well-adjusted guild structure with three complementary subgroups, are a rare and possibly unique phenomenon in the plant family Asteraceae. One of the authors (H.Z.) did not find such assemblages in samples of flower heads of the European members of the thistle tribes Carlineae (genera *Carlina*, *Xeranthemum*, *Stachelina*) and Echinopeae (genus *Echinops*), and Clark (1989) did not find them in his study of South African members of the thistle tribe Arctoteae (*Berkheya*). In an extensive analysis of the rich insect fauna of goldenrod (*Solidago*), Root and Cappuccino (1992) also state that there exists no integrated community structure. On the other hand, Goeden (1997), based on his rich rearing records of florivorous tephritids in Southern California, shows that the flower heads of the Heliantheae and Helenieae (two other Asteraceae tribes) may contain at least partially organized guilds.

Preconditions and mechanisms structuring Cardueae guilds

In comparison with studies dealing with assembly rules for animal groups such as bird communities (e.g. Diamond, 1975), we profit in our study from the fact that direct observations on species interactions within the flower head communities are relatively easy (Varley, 1947a,b; Zwölfer, 1979, 1994). Moreover, the results of biological control projects conducted against weedy Cardueae (i.e. of attempts to assemble guilds in an ecological large-scale experiment) provided additional information on the different competitive powers of individual phytophagous species and their interactions [e.g. *Urophora affinis* and *U. quadrifasciata* (Harris, 1980; Myers and Harris, 1980); *Terellia virens*, *Urophora* spp. and *Larinus minutus* (Groppe and Marquardt, 1989); *Metzneria paucipunctella* and *Urophora* spp. (Story *et al.*, 1991)].

The taxonomic diversity of the phytophagous fauna associated with the Cardueae is largely due to the fact that the different species with their flower heads served as a 'radiation platform' (Zwölfer, 1988) for many tephritids (e.g. the genera *Urophora*, *Chaetorellia*, *Terellia*, *Tephritis*), but also for the gelechiid genus *Metzneria* or the large weevil genus *Larinus*. During these radiation processes, the great majority of the phytophagous species have been more conservative in the plant structures exploited, their way of oviposition, and their larval feeding and pupation behaviour than in their association with a particular Cardueae host plant species. Where members of a guild belong to different genera, this continuation of many genus-specific biological features provided the basis for an at least partial niche separation. This niche separation may reduce interspecific larval competition for food and space (Stewart, 1996), but it is obviously not sufficient to exclude antagonistic interactions. In many Cardueae species, such interactions can be directly observed, when large samples of flower heads are dissected (e.g. Varley, 1947a; Zwölfer, 1994). In addition to the almost ubiquitous occurrence of intra-guild predation, interference with pupation sites may occur; lignified gall tissue can function as 'scorched earth' for other competitors, or the structure of the flower head may be modified to prevent further use by other species. However, our data suggest that the patterns of guilds in Cardueae flower heads are not exclusively structured by competition for larval resources.

A crucial point in the evolution of guilds in Cardueae flower heads appears to be the initial phase of an invasion into guilds by host shifts (Zwölfer and Romstöck-Völkl, 1991). For invading congeners of those phytophagous groups which use their particular Cardueae host plants as a specific rendezvous arena for courtship and mating, a first hurdle may be seen in an interference with the mating system of the resident congener. Thus, for all tephritid species associated with Cardueae species, their specific host is an important element in partner recognition. This can be demonstrated by the relatively simple induction of interspecific mating of congeneric partners, if males and receptive females are confronted without their hosts in Petri dishes (Zwölfer, 1974a,b). Also in the field, occasional interspecific courtship and mating errors have been observed on *C. nigra* [exploited by both *U. quadrifasciata* and *U. jaceana* (Varley, 1947b)] and on *C. aspera* [exploited by both *U. quadrifasciata* and *U. affinis* (unpublished data, H.Z.)]. As no hybrids of *Urophora* species are known, such interspecific mating errors do not result in viable offspring. We therefore assume that species invading guilds which lack congeners have the advantage of 'free' rendezvous arenas and avoid interference with the wrong sex partners. That the prevention of hybridization (i.e. the reinforcement of reproductive barriers) can be one of the important functions of niche segregation is a conclusion to which Rohde (1977, 1979) and Simkova *et al.* (2002) have come with regard to a quite different group of guilds (monogenean platyhelminths parasitizing the gills of marine fishes).

Larval and pupal parasitoids exploiting hosts in Cardueae flower heads can be assigned to two groups (Capek and Zwölfer, 1990): the 'habitat-specific' parasitoids are primarily associated with flower heads of a particular host plant in which the host insects belonging to different genera and even to different families and orders can be attacked. In contrast, the 'taxon-specific' group is in many cases restricted to host species belonging to the same genus. Such more or less 'genus-specific' parasitoids have been reared by us from the cynipid genus *Isocolus* (Baumann and Vidal, 1992), the weevil genera *Rhinocyllus* (Zwölfer and Harris, 1984), *Bangasternus* (Sobhian and Zwölfer, 1985) and *Larinus* (Zwölfer, 1975), the tephritid genus *Urophora* (Zwölfer and Arnold-Rinehart, 1992) and the gelechiid *Metzneria* (H. Zwölfer and W. Englert, unpublished). Assuming that these taxon-specific parasitoids

are significant mortality factors, this implies that the fitness of an invader into a guild with a resident congener is negatively affected from the very beginning because of the encounter with resident parasitoid species (Brown *et al.*, 1995; Feder *et al.*, 1995). In contrast, an invader of a guild without congeners may profit from a more or less enemy-free habitat during the initial phase of host switching (Jeffries and Lawton, 1984).

In summary, the organization of phytophagous guilds in Cardueae flower heads appears to result primarily from invasions due to host shifts. The available evidence allows the conclusion that not only direct larval competition for limited resources is important, but also indirect effects that determine the successes and failures of host shifts. Enemy-free space and 'free rendezvous arenas' appear to operate as additional filters impeding the invasion of flower heads in the presence of congeners.

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APPENDIX 1

Cardueae species investigated for flower head insects

Carduinae	<i>Onopordum acanthium</i> WE, CE
<i>Arctium lappa</i> CE	<i>O. illyricum</i> WM, EM
<i>A. minor</i> CE	<i>O. tauricum</i> EM
<i>A. nemoralis</i> CE	
<i>A. tomentosum</i> CE	<i>Cynara cardunculus</i> WM
	<i>C. scolymus</i> WM
<i>Cirsium acaule</i> CE	
<i>C. arvense</i> WE, CE, WM	<i>Jurinea mollis</i> CE
<i>C. brachycephalum</i> CE	
<i>C. candelabrum</i> EM	Centaureinae
<i>C. canum</i> CE	<i>Centaurea alba</i> EM
<i>C. eriophorum</i> WE, CE	<i>C. arenaria</i> EM
<i>C. erisithales</i> CE	<i>C. aspera</i> WM
<i>C. ferox</i> WM	<i>C. collina</i> WM
<i>C. heterophyllum</i> CE	<i>C. calcitrapa</i> WM
<i>C. matsumura</i> J	<i>C. cyanus</i> CE, EM
<i>C. monspessulanum</i> WM	<i>C. diffusa</i> EM, BS
<i>C. oleraceum</i> C, CE	<i>C. iberica</i> WM
<i>C. palustre</i> WE, CE	<i>C. jacea</i> WE, CE
<i>C. pannonicum</i> CE	<i>C. maculosa</i> CE
<i>C. rivulare</i> CE	<i>C. melitensis</i> WM
<i>C. setosum</i> S	<i>C. montana</i> CE
<i>C. spinosissimum</i> CE	<i>C. napifolia</i> WM
<i>C. tuberosum</i> WE	<i>C. nicaeensis</i> WM
<i>C. vulgare</i> WE, CE, WM	<i>C. nigra</i> WE, CE
<i>Carduus acanthoides</i> WE, CE	<i>C. nigrescens</i> CE, EM
<i>C. carlinifolius</i> WM	<i>C. paniculata</i> WM
<i>C. crispus</i> CE	<i>C. pratensis</i> WE
<i>C. defloratus</i> CE	<i>C. pseudophrygia</i> CE
<i>C. defloratus glaucus</i> CE	<i>C. scabiosa</i> WE, CE
<i>C. edelbergi</i> P	<i>C. solstitialis</i> WM, EM, BS
<i>C. nigrescens</i> WM	<i>C. spinulosa</i> CE
<i>C. nutans</i> WE, CE,	<i>C. triumfetti</i> CE
<i>C. personata</i> CE	<i>C. vallesiaca</i> CE
<i>C. pycnocephalus</i> WM	
<i>C. sanctaebalmae</i> WM	<i>Carthamus caeruleus</i> WM
<i>C. tenuiflorus</i> WE	<i>C. lanatus</i> WM, EM
	<i>C. tinctorius</i> WM
<i>Galactites tomentosa</i> WM	<i>Serratula tinctoria</i> CE, WM
<i>Silybum marianum</i> WM, EM	<i>Microlonchus salmanticus</i> WM

Regions: WE = Western Europe, CE = Central Europe, WM = Western Mediterranean, EM = Eastern Mediterranean, BS = Black Sea region, S = Siberia, J = Japan.

APPENDIX 2

A list of phytophagous insects in Carduinae flower heads used for the null models

No.	Genus and species	Order	Code A	Code B	Code C
1	<i>Homeosoma binaevellum</i>	Lep.	1	1	3
2	<i>H. nebulellum</i>	Lep.	1	1	3
3	<i>Thalpochares purpurina</i>	Lep.	20	1	3
4	<i>Myelois cribrumella</i>	Lep.	25	1	3
5	<i>Lobesia fuligana</i>	Lep.	21	1	3
6	<i>Epiblema scutulana</i>	Lep.	22	1	3
7	<i>E. luctuosana</i>	Lep.	22	1	3
8	<i>Cochylis posterana</i>	Lep.	3	1	2
9	<i>Aethes rubigana</i>	Lep.	26	1	3
10	<i>Eucosma cana</i>	Lep.	4	1	3
11	<i>E. fulvana</i>	Lep.	4	1	3
12	<i>E. cf oblongana</i>	Lep.	4	1	3
13	<i>Metzneria neuropterella</i>	Lep.	5	1	3
14	<i>M. lappella</i>	Lep.	5	1	3
15	<i>Pyroderces argyrogrammos</i>	Lep.	12	1	2
16	<i>Urophora stylata</i>	Dipt.	6	1	1
17	<i>U. solstitialis</i>	Dipt.	6	1	1
18	<i>U. congrua</i>	Dipt.	6	1	1
19	<i>U. terebrans</i>	Dipt.	6	1	1
20	<i>Tephritis conura</i>	Dipt.	23	1	1
21	<i>T. cometa</i>	Dipt.	23	1	2
22	<i>T. bardanae</i>	Dipt.	23	1	2
23	<i>T. hyoscyami</i>	Dipt.	23	1	2
24	<i>T. postica</i>	Dipt.	23	1	2
25	<i>T. heiseri</i>	Dipt.	23	1	2
26	<i>T. frauenfeldi</i>	Dipt.	23	1	2
27	<i>Chaetostomella cylindrica</i>	Dipt.	8	1	2
28	<i>Acanthiophilus helianthi</i>	Dipt.	9	1	2
29	<i>Xyphosia miliaria</i>	Dipt.	24	1	2
30	<i>Terellia longicauda</i>	Dipt.	13	1	2
31	<i>T. serratulae</i>	Dipt.	13	1	2
32	<i>T. nigripalpis</i>	Dipt.	13	1	2
33	<i>T. fuscicornis</i>	Dipt.	13	1	2
34	<i>T. lappae</i>	Dipt.	13	1	2
35	<i>T. tussilaginis</i>	Dipt.	13	1	2
36	<i>T. ruficauda</i>	Dipt.	13	1	2
37	<i>T. winthemi</i>	Dipt.	13	1	2
38	<i>Larinus turbinatus</i>	Col.	11	2	2
39	<i>L. scolymi</i>	Col.	11	2	2
40	<i>L. sturnus</i>	Col.	11	1	2
41	<i>L. jaceae</i>	Col.	11	1	2
42	<i>L. carlinae</i>	Col.	11	1	2
43	<i>L. latus</i>	Col.	11	1	2
44	<i>L. cynarae</i>	Col.	11	1	2
45	<i>L. onopordi</i>	Col.	11	1	2
46	<i>Rhinocyllus conicus</i>	Col.	28	1	1
47	<i>Lasioderma cf serricorne</i>	Col.	14	1	3
48	<i>Psylliodes chalcomera</i>	Col.	27	1	2

Note: Code A = genus number; Code B = ecological differences between congeners if co-occurring species are assigned different numbers; C = trophic strategy: 1 = gall formers and callus feeders, 2 = larvae feeding on receptacle and ovaries, 3 = feeding on achenes and intra-guild predators.

APPENDIX 3

A list of phytophagous insects in Centaureinae flower heads used for the null models

No.	Genus and species	Order	Code A	Code B	Code C
1	<i>Homeosoma binaevellum</i>	Lep.	1	1	3
2	<i>H. nebulellum</i>	Lep.	1	1	3
3	<i>Thalpochares parva</i>	Lep.	18	1	3
4	<i>Stenodes straminea</i>	Lep.	2	1	3
5	<i>St. alternana</i>	Lep.	2	1	3
6	<i>St. dorsimaculana</i>	Lep.	2	1	3
7	<i>Cochylis posterana</i>	Lep.	3	1	2
8	<i>Eucosma hohenwartiana</i>	Lep.	4	1	3
9	<i>E. cana</i>	Lep.	4	1	3
10	<i>E. fulvana</i>	Lep.	4	1	3
11	<i>Metzneria metzneriella</i>	Lep.	5	1	3
12	<i>M. paucipinctella</i>	Lep.	5	1	3
13	<i>M. aprilella</i>	Lep.	5	1	3
14	<i>M. diffusella</i>	Lep.	5	1	3
15	<i>M. hilarella</i>	Lep.	5	1	3
16	<i>M. ehikella</i>	Lep.	5	1	3
17	<i>M. intestinella</i>	Lep.	5	1	3
18	<i>Pyroderces argyrogrammos</i>	Lep.	12	1	2
19	<i>Urophora quadrifasciata</i>	Dipt.	6	2	1
20	<i>U. jaceana</i>	Dipt.	6	1	1
21	<i>U. affinis</i>	Dipt.	6	1	1
22	<i>U. hispanica</i>	Dipt.	6	1	1
23	<i>U. cuspidata</i>	Dipt.	6	1	1
24	<i>U. jaculata</i>	Dipt.	6	1	1
25	<i>U. sirunaseva</i>	Dipt.	6	1	1
26	<i>Chaetorellia acrolophi</i>	Dipt.	7	1	2
27	<i>Ch. jaceae</i>	Dipt.	7	1	2
28	<i>Ch. hestia</i>	Dipt.	7	1	2
29	<i>Ch. loricata</i>	Dipt.	7	1	2
30	<i>Ch. succinea</i>	Dipt.	7	1	2
31	<i>Ch. australis</i>	Dipt.	7	1	2
32	<i>Chaetostomella cylindrica</i>	Dipt.	8	1	2
33	<i>Acanthiophilus helianthi</i>	Dipt.	9	1	2
34	<i>Terellia colon</i>	Dipt.	13	1	2
35	<i>T. virens</i>	Dipt.	13	1	2
36	<i>T. uncinata</i>	Dipt.	13	1	2
37	<i>T. zerovae</i>	Dipt.	13	1	2
38	<i>Ceriocera ceratocera</i>	Dipt.	16	1	2
39	<i>Isocolus jaceae</i>	Hym.	10	1	1
40	<i>I. areolata</i>	Hym.	10	1	1
41	<i>I. centaureae</i>	Hym.	10	1	1
42	<i>I. rogenhoferi</i>	Hym.	10	2	1
43	<i>Larinus obtusus</i>	Col.	11	2	2
44	<i>L. minutus</i>	Col.	11	2	2
45	<i>L. longirostris</i>	Col.	11	1	2
46	<i>L. sturnus</i>	Col.	11	1	2
47	<i>L. jaceae</i>	Col.	11	1	2
48	<i>L. australis</i>	Col.	11	2	2
49	<i>L. canescens</i>	Col.	11	2	2
50	<i>L. curtus</i>	Col.	11	2	2
51	<i>L. rusticanus</i>	Col.	11	1	2
52	<i>Bangastermus provincialis</i>	Col.	15	1	2
53	<i>B. orientalis</i>	Col.	15	1	2
54	<i>Eustenopus abbreviatus</i>	Col.	17	1	2
55	<i>Bruchidius tuberculatus</i>	Col.	19	1	2
56	<i>Lasioderma redtenbacheri</i>	Col.	14	1	3
57	<i>L. cf serricorne</i>	Col.	14	1	3

Note: Code A = genus number; Code B = ecological differences between congeners if co-occurring species are assigned different numbers; C = trophic strategies: 1 = gall formers and callus feeders, 2 = larvae feeding on receptacle and ovaries, 3 = feeding on achenes and intra-guild predators.