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Bernhard Stadler · Pavel Kindlmann · Petr Šmilauer ·
Konrad Fiedler

A comparative analysis of morphological and ecological characters of European aphids and lycaenids in relation to ant attendance

Abstract Ants are a major environmental factor for many insect species. For example, aphids and lycaenids have evolved an array of associations with ants ranging from obligate myrmecophily to the avoidance of contact. Here we (1) analyze the predictive power of different ecological and morphological traits for explaining the strength of the association between ants and aphids/lycaenids and (2) contrast different taxonomic levels with respect to the variance explained by ant attendance. Data come from a literature survey including 112 species of aphids and 103 species of lycaenids from Europe. For aphids, feeding on woody plant parts is positively associated with ant attendance, while a high degree of mobility, feeding in isolation, and the possession of wings in the adult stage are negatively associated with ant attendance. In lycaenids, feeding on inflorescences and feeding on Fabaceae host plants is closely associated with ant attendance, while living in forests bears a smaller likelihood to establish mutualistic relationships. Body size always appeared to be a poor predictor for the degree of ant attendance. Overall, in both insect groups less than 10% of the variation in the ecological traits recorded is explained by the different modes of ant association. When decomposing the variance in traits explained by ant attendance at different taxonomic levels, aphids and lycaenids show contrasting results. In aphids, most variance in the degree of ant attendance is explained at the subfamily level and least at the species level. The opposite is true for lycaenids, where most variance is explained at the lowest taxonomic level. Possible mechanisms explaining these different patterns of associations with ants are suggested.

Keywords Aphids · Lycaenids · Ant–myrmecophile interactions · Mutualism · Comparative analysis

B. Stadler (✉)
Bayreuth Institute for Terrestrial Ecosystem Research,
University of Bayreuth,
95440 Bayreuth, Germany
e-mail: bernhard.stadler@bitoek.uni-bayreuth.de
Fax: +49-921-555799

B. Stadler
Harvard University, Harvard Forest,
P.O. Box 68, Petersham, MA 01366, USA

P. Kindlmann · P. Šmilauer
Faculty of Biological Sciences,
University of South Bohemia,
Branišovská 31, 370 05 České Budějovice, Czech Republic

K. Fiedler
Department of Animal Ecology I,
University of Bayreuth,
95440 Bayreuth, Germany

Introduction

Ants have developed close associations with very different organisms from different kingdoms. For example, they have developed mutualistic interactions with more than 465 plant species from over 52 families (Jolivet 1996), with fungi cultivated in gardens (Mueller et al. 1998), and with insects from which the ants may collect honeydew or nectar (Hölldobler and Wilson 1990). Frequently, however, closely related species within each of these groups of organisms exhibit quite different degrees of associations with ants. The reasons for these divergent developments are still largely unknown. Among homopteran species, which feed on the same host plant and even on the same plant organ, some species may be closely attended, while others are never visited by ants. For example, different aphid species of the genus *Cinara* feeding on spruce, pine or larch have developed different associations ranging from obligate myrmecophily to the absence of any interactions on each of their respective host plants (Scheuer 1964). Closely related lycaenid species usually show a less pronounced variability (Fiedler 1991a), although exceptions exist (*Drupadia/ Cheritra* group, Seufert and Fiedler 1996; *Ogyris*, Braby 2000). These different degrees of associations with ants indicate that there are many solutions to respond to an omnipresent predacious group of organisms like ants.

The meaning of the term "obligate" interactions differs slightly between aphids and lycaenids. While "obligately" myrmecophilous aphids are always attended by ants, but the identity of mutualistic partners may vary (Hölldobler and Wilson 1990), obligately myrmecophilous lycaenids are bound to associate with a few species nested within one ant genus. In that way, following the terminology of Cushman and Beattie (1991), ants are hosts rather than visitors of obligately myrmecophilous lycaenid larvae (Fiedler 2001). For the purpose of our analysis, we term all aphids and lycaenids as "steadily myrmecophilous" if they are (almost) constantly ant attended, thus including both obligately and steadily myrmecophilous lycaenids as defined in earlier work (Fiedler 1991a). Although certain mutualistic associations are amazingly old (Pellmyr and Leebens-Mack 1999; Machado et al. 2001), the conflicts of interest inherent in all such interactions (Hoeksema and Bruna 2000) suggest that, once evolved, outcome and evolutionary stability of mutualistic interactions are strongly shaped by environmental conditions. As a consequence, a number of ecological variables have been suggested to correlate with the expression of mutualism (Table 1).

A previous review on ant–myrmecophiles interactions involving aphids, coccids, membracids, and lycaenids showed that most of these myrmecophiles face very similar costs and benefits, i.e., in terms of life-history traits or with respect to the spatial distribution and availability of the ant partner (Stadler et al. 2001). These similarities exist in spite of the fact that the mode of attracting ants is quite different for these ant partners and that they live in different environments. Generally, for any myrmecophile the quality and quantity of honeydew/nectar are likely to play a crucial role for successfully attracting ants (Völkl et al. 1999; Pierce et al. 2002). Producing large amounts and a better quality of honeydew/nectar, however, bears costs for aphids and lycaenids when attended (Baylis and Pierce 1992; Fisher and Shingleton 2001; Pierce et al. 2002; Yao and Akimoto 2001, 2002). Yet, honeydew is essentially a waste product, which should be cheaper to produce compared to myrmecophilous butterfly larvae, which have to synthesize nectar in specialized glands for attracting ants. Depending on the environmental situation, an association with ants might be established if there are net benefits or given up if there are net costs. Therefore, at any time, honeydew producers may maintain a continuum of associations with ants. In contrast, nectar producers should be less flexible in modifying an established association, mainly because their morphological and physiological investment in ant attendance is larger. As a consequence, at the species level we expect a higher

Table 1 Variables selected and hypotheses associated with ant attendance

Variable	Hypothesis	Reference
Size	Larger insects produce more honeydew/nectar and are likely to attract more ants	Sudd (1983), Bristow (1991)
Feeding site on host plants	Aphids that feed on woody plant structures need more time to penetrate and withdraw their stylets and thus should use the protection function of ants; lycaenids on inflorescences are likely to attract more ants due to better nutrient conditions	Dixon (1998)
Colony structure	Dense aggregations should be easier to sample for honeydew/nectar than solitary-feeding individuals	Pierce et al. (1987), Hayamizu (1982)
Host specificity	Polyphagous insects are likely to occur in many different habitats and thus might come into contact with ants; in lycaenids polyphagy is often associated with ant-dependent oviposition	
Abundance	Abundant species should be more likely to tolerate ant attendance and should provide a more rewarding resource to ants	Dixon (1958)
Mobility	Mobile insects are less dependent on the protection service provided by ants	Dixon (1958), Stadler (2002)
Other defense structures	Species covered with wax wool and winged aphids should depend less on protection services provided by ants	Bristow (1991)
Host alternation	Host-alternating species (e.g., from trees to grasses) are more likely to come into contact with ants in a variety of habitats and therefore should develop mechanisms to tolerate ant attendance	
Exposition	Species feeding while exposed are more likely to come into contact with ants than are concealed feeders	Bristow (1991)
Size of distribution	Species with a wide distribution should be more likely to contact ants	
Fabaceae	Feeding on N-rich plants favors the production of high-quality nectar and thus facilitates ant attendance	Pierce et al. (1987), Pierce (1985)
Life form of host	The accessibility for the ant partner might affect the degree of ant attendance	Southwood (1986), Harley (1991)
Habitat	Insects on plants growing in open/disturbed habitats have a higher probability of being ant attended, because these habitats are more favorable for ants in their abiotic conditions (at least in northern and central Europe)	Punttila (1996)

variability in the degree of ant attendance for aphids compared to lycaenids.

The specific objectives of our analyses were (1) to rank the ecological and morphological variables, which were suggested in the literature to influence the degree of associations with ants, for each of our model insect groups separately; (2) to compare the ranks obtained in order to see the differences between aphids and lycaenids in this respect; and (3) to rank different taxonomic levels within each of these insect groups with respect to variance decomposition in these traits. We restricted our analyses

to aphids and lycaenids from Europe for which detailed information is available.

Materials and methods

Data collection and coding

We collected information on different morphological and ecological variables from the literature for aphids and lycaenids, which might be important in determining the strength of an association with ants (Table 2). Data on aphids were collected from Börner

Table 2 Scores of ecological and morphological characters used in aphids and lycaenids. Notations in parentheses give a brief explanation of the categories. – indicates no corresponding category in the respective group of insects. Variable names and letters in bold were used as abbreviations in Fig. 2a,b and Fig. 3a–f

Variable	Category	Aphids	Lycaenids
Size	Continuous	Body length (mm); means if from different sources	Forewing length (mm); means if from different sources
Feeding **s**ite on host plants	1	**Leaves** (green plant parts)	**Leaves** (no preference for inflorescences)
	2	**Woody** parts	**Inflorescences** (preference for flowers, seeds)
Colony **s**tructure	1	**Dense** (with body contact)	Clumped (**dense**)
	2	**Scattered** (without body contact)	**Solitary** (larvae occur singly, often cannibalistic)
Host **specificity**	1	Monophagous	Monophagous (feeding on one or few plant species within the same genus)
	2	Oligophagous	Oligophagous (feeding on different genera of plants belonging to the same family)
	3	Polyphagous	Polyphagous (host ranges include ≥2 taxonomically unrelated plant families)
Abundance	1	Rare	Rare (individuals are recorded in low densities)
	2	Moderately abundant	Moderately abundant (larger numbers may be seen in favorable habitats or in some years)
	3	Very abundant	Very abundant (always in large numbers)
Ant attendance	1	Not attended	Not attended (always without ants)
	2	Facultative myrmecophile	Facultative (sometimes found with/without ants)
	3	Steady myrmecophile	Steady myrmecophile (almost always found in association with ants)
Exposition	1	**Exp**osed feeders	**Exp**osed feeders
	2	**Conc**ealed feeders (mostly in leaf rolls)	**Conc**ealed feeders
Mobility	1	Low (little movement when disturbed)	–
	2	Variable	–
	3	High (easily walk or drop off when disturbed)	–
Other **s**tructures	0	**None**	–
	1	**Wax**	–
	2	Leaf **curls**	–
	3	All adults are **alates**	–
Host **a**lternation	1	Host-alternating (**yes**)	–
	2	Non-host-alternating (**no**)	–
Localness	1	–	Very widely distributed (>75% of Europe)
	2	–	Widely distributed (>50% of Europe)
	3	–	Moderately distributed (10–50% of Europe)
	4	–	Regionally restricted (<10% of Europe)
	5	–	Very small range (local endemics)
Fabaceae	1	Fabaceae are not used as host plants	Not known to feed on N-fixing plants
	2	Fabaceae my be used by polyphagous species	Larval diet includes Fabaceae
	3	Fabaceae are used as host plants	Larvae restricted to Fabaceae
Life **f**orm of host	1	**Tree**/bush	**Tree**/bush (>2m)
	2	**Herb**aceous plants	Small woody shrubs (<2m)
	3	Grasses	**Herb**aceous plants
Habitat	1	**Open**/disturbed/pioneers	**Open**/disturbed/pioneers
	2	**Forested**/climax	Edges of woodland/**forest**

(1952), Thieme and Müller (2000), Kloft and Kunkel (1985), Blackman and Eastop (1994), and Heie (1986, 1987, 1992, 1994). Data on lycaenids came primarily from Higgins et al. (1978), Fiedler (1991b), Bink (1992), and Tolman and Lewington (1998). The literature survey was restricted to associations established above ground and to European species because at least aphids are better studied in this region. Aphids living in true galls were excluded from the analysis because they form a special type of environment. For butterflies, species delimitations follow Tolman and Lewington (1998). Lycaenids with parasitic ant associations (largely in the genus *Maculinea*; Fiedler 1998b) were excluded from analysis.

In total, ten variables were available for both taxa, while three variables could reasonably be coded for aphids, and one for lycaenids only (Table 2). These latter factors were suggested earlier to be of potential importance with respect to the strength of an association with ants. For example, feeding on nitrogen-fixing Fabaceae has been suggested to facilitate the production of nitrogen-rich nectar and thus increase the attractiveness of lycaenid larvae to ants (Pierce 1985; but, see Fiedler 1995).

For the classification of aphids we used *species*, *genera* and *subfamilies* following Heie (1980). For lycaenids we used *species*, *genera* and *tribes* as taxonomic units (Hesselbarth et al. 1995). Note that the taxonomic classification for aphids and lycaenids is not identical. For the purpose of the present study, this inconsistency is considered to be of minor importance since the focus is on variation in the degree of ant attendance at different relative levels of taxonomic hierarchies. Ongoing molecular studies reveal that most of the morphologically defined higher taxa within the Lycaenidae are indeed monophyletic (Pierce 2002).

Because the information comes from many different sources, it is unlikely that the same rigor of classification was used throughout these different studies, leading to potential blurring of effects. In addition, a classification of continuous variables such as the degree of ant attendance, or colony structure and mobility of myrmecophiles, might appear a rather crude approach, especially if there is temporal or spatial variability associated with these variables. Nevertheless, we suspect that if the differences are strong enough, they should show up in spite of these confounding effects.

It is obvious that limits in the knowledge on systematic information restrict the extent to which results can be generalized or used for identifying mechanisms that explain emerging patterns. A restriction of the analyses towards those species for which some information on the phylogenetic relatedness is available would severely reduce the dataset and introduce another form of bias. For example, molecular systematics of aphid species, which are of economic importance, is usually better studied than that of species living in natural habitats (Normak 2000; Martinez-Torres et al. 2001). Focusing on the former group would affect the ecological characters, which are likely shifted to, e.g., more open habitats, and many taxa would be underrepresented. Thus, we faced a tradeoff to restrict our analyses to a limited number of species, which are taxonomically characterized, or to select a broader spectrum of species for which sufficient ecological information was available. We focused on the second option, together with applying statistical procedures that take different degrees of relatedness among taxa into account.

Data analysis

We conducted two types of analyses to determine the association between ecological and morphological traits of aphids and lycaenids and their attendance by ants. First we analyzed the separate datasets of the two insect groups in terms of their relationship with different degrees of ant attendance. The relationship of the measured traits to ant attendance was summarized with a standard constrained ordination method [redundancy analysis (RDA)] using the program CANOCO (Ter Braak and Šmilauer 2002). RDA can be viewed as a method similar to multivariate linear regression, with additional reduction of dimensionality of the results (Ter Braak and Looman 1994). Qualitative traits (feeding site, colony structure, host plant life form, habitat type, etc.) were coded using binary dummy variables (as usual for predictors in ANOVA). Semi-quantitative descriptors with an ordinal nature (such as host specificity, abundance, or mobility) were treated as quantitative variables. Codes are presented in Table 2.

The multivariate analysis was supplemented by classical statistical tests based on fitting a linear regression model for each of the traits, using ant attendance as a predictor. We assumed that the individual species might have their trends correlated due to shared evolutionary history, especially if they are congeneric. Therefore, the fitted regression models, as well as the permutation test used for the constrained ordination analyses, did not draw on the original data for individual species but rather used the generic averages for the individual traits (and ant-attendance level).

The related multivariate hypotheses were tested using non-parametric permutation tests. Because individual species are not independent data points but are phylogenetically related, however in a largely unknown way, we had to account for this in the analyses. The permutation schemes used for testing hypotheses about the effects of ant attendance upon ecological and morphological traits at individual taxonomic levels had to take into account the hierarchical arrangement of those levels. We analyzed data averaged at the tested taxonomic level, and random permutations were restricted to the next higher taxonomic level. For example, when testing effects of ant attendance at the level of genera, the averages of ant attendance for individual genera were randomly permuted with respect to the averaged trait values, but only within individual subfamilies or tribes. In this way, our approach is comparable to the method of phylogenetically independent contrasts (PIC; Harvey and Pagel 1991), because we compare differences only among categories with a similar extent of phylogenetic relatedness. Additionally, we performed a hierarchical decomposition analysis of the variance in species traits, explained by ant attendance, using again the framework of RDA to evaluate the total variation in traits. Here we examined the distribution of variances across three different taxonomic levels (Harvey and Pagel 1991).

Results

Aphid species came from eight different subfamilies, with the Macrosiphinae as the most species-rich group (Fig. 1a). With the exception of the subfamily Drepanosiphinae, in which species appear not to be attended, species in most other subfamilies show a mixture of different degrees of associations with ants. In the lycaenids a similar pattern is apparent (Fig. 1b). Species from five tribes were included in the analysis, with the highest species number in the Polyommatini. Only the European Lycaenini are never ant attended.

The tests for individual species traits available for the two test taxa (Table 3) revealed a significant relationship of ant attendance with feeding site for both aphids ($P=0.0021$) and lycaenids ($P=0.0286$), with colony structure for aphids only ($P=0.0004$) and with legume host plants ($P=0.0023$) for lycaenids only. The relationship between ant attendance and host specificity was nearly significant ($P=0.068$) for lycaenids.

In order to understand which ecological or morphological variables are associated with ant attendance, a separate analysis for aphids and lycaenids was performed using the full set of variables. For aphids (Fig. 2a), the overall relationship between the studied traits and ant attendance was significant ($F=3.9$, $P=0.002$). Feeding on woody plant parts is closely associated with ant attendance, while a high degree of mobility or the possession
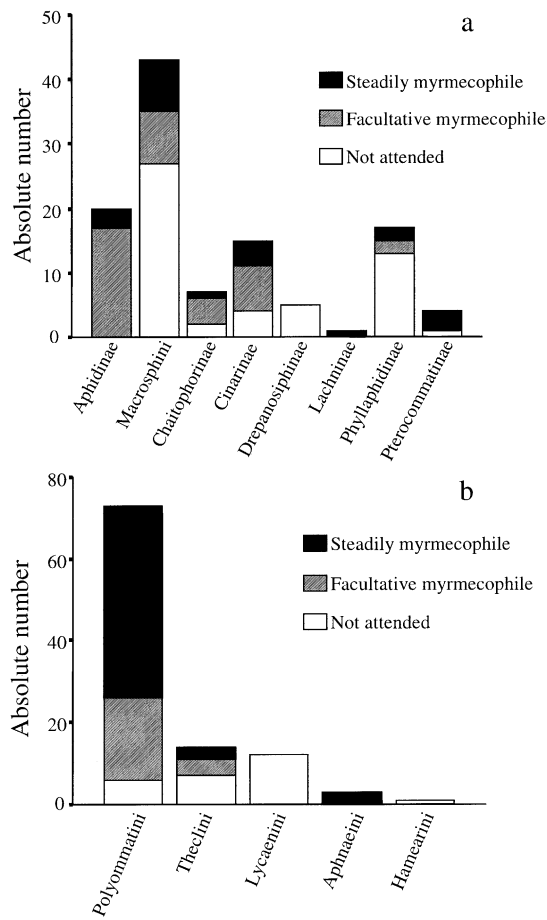
Fig. 1 Number of species of **a** aphids and **b** lycaenids showing different degrees of associations with ants. Aphids are represented in subfamilies, while lycaenids are shown in tribes. *Black columns* Steady myrmecophiles, *gray columns* facultative myrmecophiles, *open columns* unattended species

Fig. 2 Ordination diagram of redundancy analysis (RDA) displaying differences in traits explained by extent of ant attendance (*horizontal axis*) for **a** the aphid data and **b** the lycaenid data only. Categorial traits are shown as *dots* (with one dot for each factor level), (semi)quantitative traits are displayed as *arrows* pointing in the direction of increasing trait values (variable names are in italics). Variable names correspond to the categories given in Table 2

of wings in the adult stage is closely associated with not being attended by ants. Body size of a species, habitat type, and abundance are not associated with ant attendance. Living in dense colonies seems to be a trait associated with a higher probability of ant attendance. In total, the horizontal axis explains 8.7% of the total traits' variability and represents the fraction explained by ant attendance, while the variability explained on the other
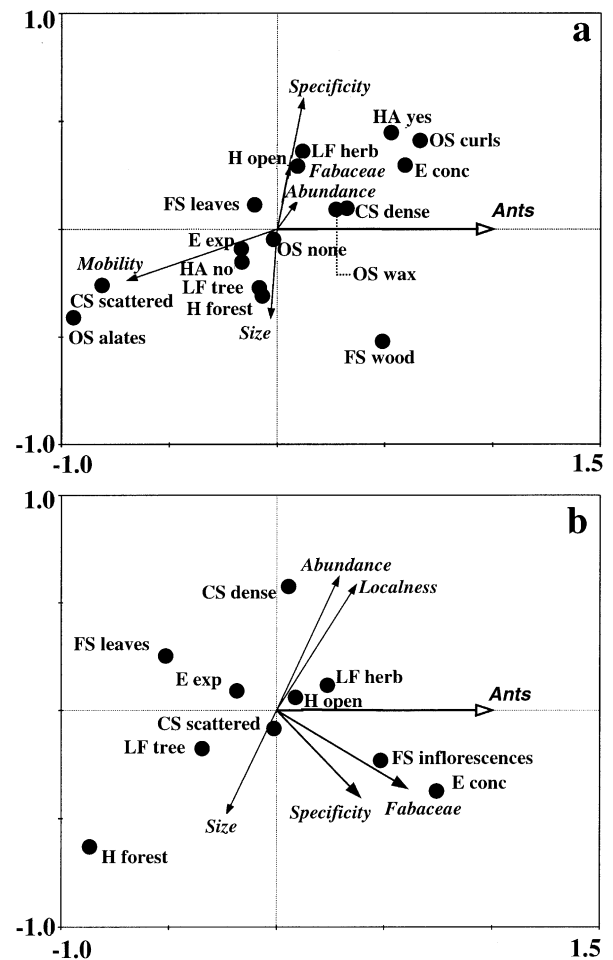
ordination axis (25.4%) represents part of the residual variability.

Lycaenid larvae showed a somewhat different picture (Fig. 2b) yet also showed an overall significant relation-

Table 3 Relationships between different ecological traits and ant attendance for aphid and lycaenid species, calculated at the generic level. Only those traits with a significant result for at least one of the two insect groups are listed

Trait	Aphids	Lycaenids
Feeding site	Higher attendance of species feeding on woody plant parts ($P=0.0021$)	Higher attendance of species feeding on inflorescences ($P=0.0286$)
Colony structure	Higher attendance of species with dense colonies ($P=0.0004$)	n.s.
Host specificity	n.s.	Higher attendance of species with higher host specificity ($P=0.0677$)
Fabaceae	n.s.	Higher attendance of species with stronger preference for Fabaceae ($P=0.0023$)

Fig. 3 Ordination diagrams summarizing the hierarchical decomposition of the variance in traits, explained by ant attendance for **a–c** aphids and **d–f** lycaenids. Variance is shown for the subfamily/tribe level (**a, d**), generic level (**b, e**) and species level (**c, f**). Categorial traits are shown as *dots* (with one dot for each factor level), (semi)quantitative traits are displayed as *arrows* pointing in the direction of increasing trait values (variable names are in italics). Note that the values for the percentage of explained variance refer only to the horizontal (constrained) ordination axis. Variable names correspond to the categories given in Table 2
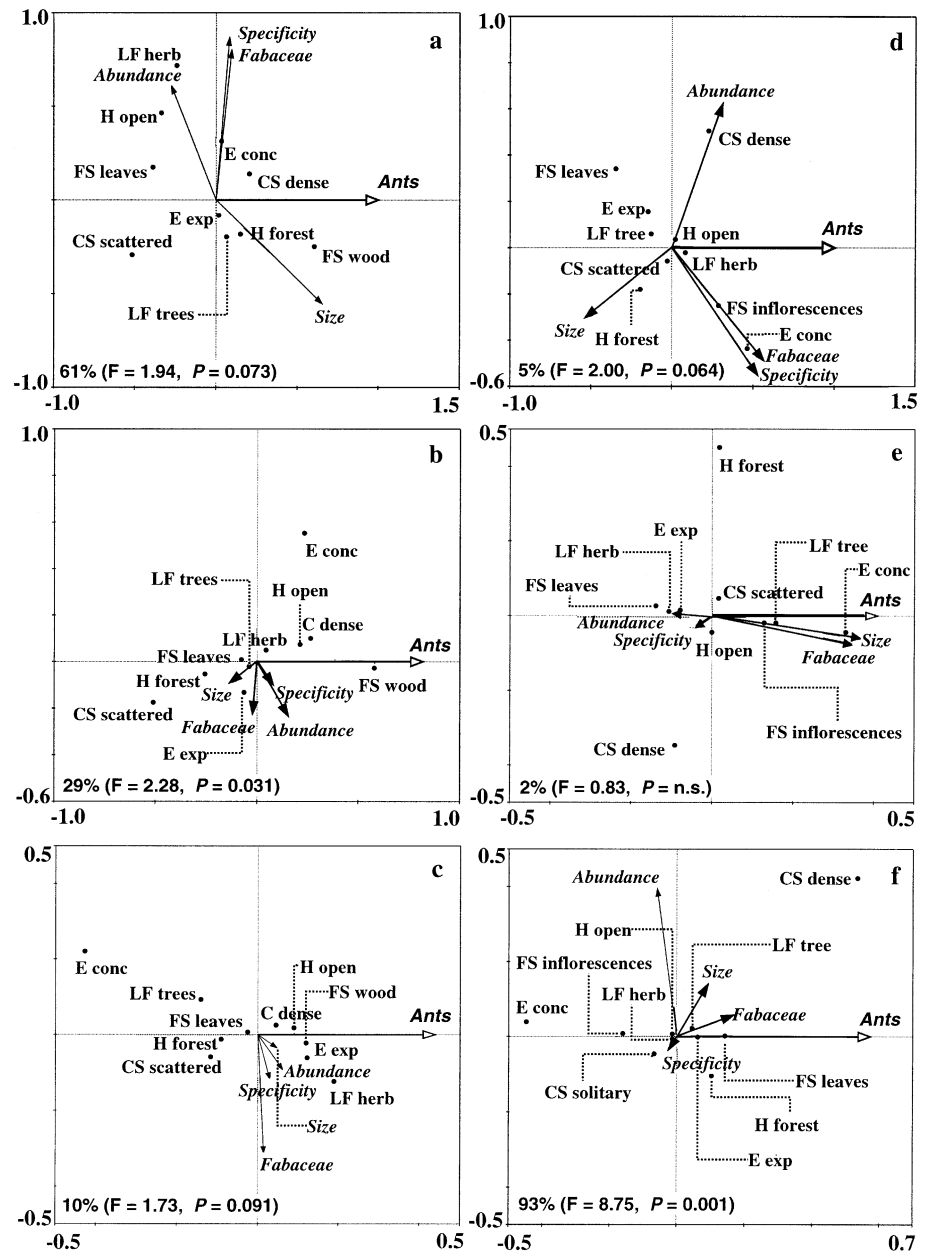
ship between ecological traits and ant attendance (F=2.4, P=0.017). Feeding on inflorescences and on Fabaceae is strongly associated with ant attendance, while living in forested habitats decreases the likelihood of being attended for European species of lycaenids. Most other morphological and ecological traits cluster in the central region of the canonical (horizontal) axis. In total, this axis (and, therefore, ant attendance) explains 4.0% of the total variability, and the second, non-canonical axis explains 23.5% of the total variability in trait values.

Decomposition of the variance in ecological and morphological traits, which is explained by ant attendance on different taxonomic levels, performed separately for the aphid and lycaenid data, should offer an indication on potential phylogenetic constraints associated with ant attendance. In aphids, 61% of the variance is explained at the subfamily level, 29% at the generic level, and 10% at the species level (Fig. 3a–c). The F statistics and significance values shown in the figures refer to the test of the null hypothesis of no effect of ant attendance on the studied traits at the particular taxonomic level. Feeding on woody plant parts is always strongly correlated with ant attendance, whereas the positions of other variables in the ordination varied across the levels of analysis and mostly fall into the central range. Little of the variation is explained at the species level. In contrast, in lycaenids only 5% of the variance is explained at the tribal level, 2% at the generic level, and 93% at the species level (Fig. 3d–f).

Discussion

Mutualistic associations between ants and their partners can be viewed like any other mutualistic interaction: as reciprocal exploitations that provide net benefits for both partners (Bronstein 1994, 2001; Cushman et al. 1994; Thompson 1994; Herre et al. 1999). Such interactions are often analyzed from the ants' perspective, which are supposed to drive the system, mostly because they are able to prey on their partner (Way 1963; Buckley 1987; Sakata 1995; Rosengren and Sundström 1991; Offenberg 2001). However, whether predation is a good indicator for determining the direction of selection pressures for organisms with high population growth rates is not clear. In addition, the range of the realized degrees in the strength of mutualistic interactions deserves a closer inspection. Recent studies suggest that partners of ants adopt very finely tuned strategies to respond to ant attendance (Fiedler and Hölldobler 1992; Fiedler and Hummel 1995; Burghardt and Fiedler 1996; Flatt and Weisser 2000; Fisher and Shingleton 2001; Stadler et al. 2002; Pierce et al. 2002; Yao and Akimoto 2002). For example, the aphid *Tuberculatus quercicola* excretes smaller droplets of honeydew more frequently in ant-attended colonies than in ant-excluded colonies, which results in no significant differences in total sugar concentration and total volumes of honeydew excreted between attended and unattended aphids (Yao and Akimoto 2001). Given that ant partners are actively responding to ant attendance, it is reasonable to ask what environmental factors are likely to affect the strength of ant–myrmecophile interactions and what are the likely mechanisms that promote or constrain adaptations.

Overall, only a small fraction of the total variance in ecological traits (<10%) was explained by different degrees of ant attendance. This might indicate that many of the ecological variables that have been suggested to affect the expression of ant–herbivore interactions are of little importance or act only at small scales and therefore do not show up in a broad comparative analysis. However, despite the heterogeneity of data and the inevitably coarse scoring to make data comparable between the two insect groups, some variables turned out to have significant relationships with ant attendance (Table 3).

For aphids an important variable that seems to be associated with ant attendance is living in groups. It is unclear what the causal factor for aggregation is, but it is likely that ants can gain more honeydew from aggregated individuals. In addition, if the production of honeydew and nectar bears costs (e.g., Yao and Akimoto 2002), the costs for an individual might be reduced if there are longer intervals between visitations. Interestingly, larval aggregation did not emerge as a significant correlate of myrmecophily among European lycaenids, in contrast to the positive effects of group living documented in obligately ant-associated butterflies (Axén and Pierce 1998) and the frequent occurrence of large larval aggregations in such species (e.g., Fiedler and Maschwitz

1989). However, in Europe most lycaenid larvae do not show the close associations with ants that are typical for tropical species. In aphids, a high mobility and the production of winged adults tend to be associated with the absence of ant attendance (Fig. 2a). These characters can be viewed as alternative defense strategies if the protection service of ants is not used or is unavailable. When feeding on woody parts it might be more difficult for aphids to quickly withdraw their stylets upon attack (Dixon 1998), making the use of the protection services of ants more likely.

For European lycaenids, living in forests is associated with a lower likelihood of being myrmecophilous. In temperate zones, herbivores inhabiting open and warmer habitats are more likely to encounter ants, since ant communities of such successionary habitats tend to be more diverse and foraging activities more concentrated in the herb or shrub layer (Punttila 1996). In contrast to aphids, lycaenids are significantly more likely to be associated with ants when feeding on inflorescences or leguminous host plants. This might be due to the fact that nitrogen-rich plant material allows for the production of more attractive nectar (Pierce 1985), while phloem sap quality is not associated with N-fixing abilities of the host plants. Here intracellular midgut symbionts of aphids that provide their hosts with essential amino acids seem to play a more crucial role (Sandström and Moran 1999).

The relationship between host plant specificity and ant attendance was close to being significant, yet in an opposite way from that suggested in Table 1. Generally, polyphagy is positively associated with myrmecophily in lycaenid larvae (Fiedler 1998a). This pattern is largely mediated by the oviposition behavior of females, where the presence of ants takes precedence over host plant choice (Pierce and Elgar 1985). Most other tested variables cluster in the central region of the ordination (Fig. 2) and are likely to indicate either multidirectional selection pressures with respect to costs and benefits of ant attendance or that these characters are not at all related to ant attendance. To summarize this aspect, the strength of an association with ants developed in European species of aphids and lycaenids is affected by the feeding sites in both groups, while colony features were good predictors for aphids and Fabacean hosts for lycaenids.

Similar patterns appear to exist in terms of costs and benefits for different taxa of myrmecophiles. In aphids, coccids, membracids, and lycaenids, similar direct effects, such as a prolongation or shortage of the development time, as well as indirect costs, were reported when the ant partner was not available to a myrmecophile. For a recent review of the available information, see Stadler et al. (2001). Nevertheless, the investment in different groups of insects for developing or maintaining an association with ants is likely to be different. Lycaenids have to invest in specialized nectar organs to produce nectar, while aphids tap into the phloem bundles passing surplus energy through the gut system. Therefore, a change in morphological structures might be less easy to achieve than a

change in honeydew quality or quantity if selection pressures are operating in different directions in different habitats or at different times. Figure 3a–f indicates that lycaenids are indeed more conservative in establishing or abandoning associations with ants than aphids, thereby quantitatively supporting previous suggestions made on the grounds of qualitative comparisons (Fiedler 1991a). For example, at the species level aphids were found to develop an array of associations with ants from unattended species to obligate myrmecophiles. Consequently, the explained variance in this trait is rather low at the species level. The opposite is true for lycaenids, with most species of specific genera expressing very similar degrees of association with ants.

In summary, our analysis shows that the relationships between ants and ant partners are only to a small extent explained by coarse-grained (environmental) traits. It seems more likely that the effects on net costs and benefits in life-history characters (growth rates, developmental time, number of offspring) are more critical for the evolution of an association with ants (Stadler et al. 2002) than is a specific environmental setting. Currently, however, we lack sufficiently precise data for a comprehensive analysis of life-history traits to appropriately address such a suggestion. Moreover, a better understanding of phylogenetic relationships that would allow for more rigorous tests of phylogenetic effects seems desirable. The fact that aphids show much more flexibility in their associations with ants at the species level than do lycaenids argues in favor of the conclusion that variation in the degree of ant attendance, despite all the striking parallels between both groups of herbivorous myrmecophiles (Stadler et al. 2001), may not be explained by ecological characters alone.

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