Correlated evolution of the association between aphids and ants and the association between aphids and plants with extrafloral nectaries

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The evolution of extrafloral nectaries (EFN) and the evolution of ant-aphid associations may have influenced each other. Published records allowed me to determine whether aphid species are associated with ants and whether they are associated with host plant species with EFNs. On the basis of these results a comparative phylogenetic study was conducted on a subgroup of monoeocious aphid species living above the soil surface. As aphid phylogeny was unresolved below the family level, I analysed two families – Aphididae and Drepanosiphidae – separately. Within each family, a large number of random phylogenies were generated and each random tree was analysed with a standard phylogenetic approach. The results suggest, on the one hand, that being tended by ants increases the likelihood that an aphid species will evolve an association with host plants that produce EFNs, or on the other hand, that aphid species associated with host plants carrying EFNs were more likely than other species to evolve an association with ants. I present two new hypotheses – the host-selection hypothesis and the host-sharing hypothesis – to explain these evolutionary patterns. The hypothesis that ant-attended homopterans may function as EFNs is rejected by the evolutionary patterns found in this study.

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Many aphids are associated with ants. Numerous but not all aphid and ant species are involved in these interactions and single species within either guild can in most cases interact with several species from the other guild. The association is based on what is generally assumed to be mutual beneficial services. Aphids excrete carbohydrate rich honeydew, which serves as a valuable energy source for ants. In return ants can provide a wide range of services for their aphid partners, the best described being protection from natural enemies. Further details on ant-Homoptera associations are provided in reviews by Nixon (1951), Way (1963), Beattie (1985) and Buckley (1987).

However, this simple view of an interaction between two partners may be complicated by a larger network of interactions with other partners. Thus, for example, apart from tending aphids, ants are also associated with plant species possessing extrafloral nectaries (EFN) (see review by Bentley 1977). These nectaries excrete carbohydrate rich nectar and are accessible by ants (in contrast to most floral nectaries); they thus serve as a valuable source of energy for ants (Zimmermann 1932, Elias 1983, Keeler 1989). In return ants protect the plants against herbivores (Inouye and Taylor 1979, O'Dowd 1979, Stephenson 1982, Barton 1986, Smiley 1986). This mutualism leads one to expect that ants are more likely to be associated with plants bearing EFNs than with those without EFNs (O'Dowd 1979, Barton 1986, Oliveira et al. 1987). Beattie (1985) and Keeler (1989) provide further details on interactions between ants and plants with EFNs.

Considering both the interaction between ants and aphids and the interaction between ants and plants, four hypotheses can be postulated. 1) Aphids tended by ants get a benefit from EFNs, since ants are already there to protect them, while aphids that are not adapted to ant-association do not benefit from ant presence. Ants may be detrimental to the aphids if the ants prey on them. This would lead to attended aphids being more likely to evolve associations with plants bearing EFNs. 2) If ants are tending aphids, then plants could evolve EFNs to distract ants from aphids (Becerra and Venable 1989, 1991). This would also lead to attended aphids being more likely to be associated with plants with EFNs. 3) On the other hand, aphids on plants with EFNs are perhaps more likely to get preyed on by ants. Therefore, they should either move to other plants or evolve mechanisms to make interactions with ants less damaging, i.e. evolve towards ant tending. This would lead to aphids living on plants with EFNs being more likely to evolve ant tending. 4) If ants that are tending aphids also provide indirect protection to the host plants of the aphids (Messina 1981, Beattie 1985, Gullan 1997), then plants associated with attended aphids would not need to evolve/produce EFNs to attract beneficial ants. This would lead to attended aphids being more likely to be associated with plants without EFNs. The first three ideas will result in a positive correlation between ant-association and association to EFN-plants and lead to two phylogenetic patterns: 1) the first two ideas mean that phylogenetic branches with ant-association will be more likely to evolve new associations with EFN-plants, and 2) the third idea means that phylogenetic branches with EFN-associations will be more likely to evolve ant-tending. The fourth hypothesis will lead to a negative correlation between ant-association and EFN-association. I here present a comparative study of aphid species occurring in Denmark and Fennoscandia to investigate possible correlations between associations with ants and associations with host plant species with EFNs.

Methods

Aphids

The aphid species included in this study were restricted to species occurring in Denmark and Fennoscandia. A full record of these species and their biology with regard to ant-attendance and host plant species was available from the literature (Heie 1980, 1982, 1986, 1992, 1994, 1995). Each species was placed into one of four categories according to two binary traits: 1) whether the aphid has host plant species with EFNs (EFN-associated and non EFN-associated, respectively), and 2) whether the species is associated with ants (ant-associated and non ant-associated, respec-

tively). Species were categorised as ant-associated if Heie reports that the species is regularly visited by ants. Species reported as being visited only rarely or not being visited were categorised as non ant-associated. The plants with EFNs were found with an extensive literature search of species occurring in Denmark and Fennoscandia (see Appendix). Aphid species with at least one host plant species with EFNs were categorised as EFN-associated; the remaining species were categorised as non EFN-associated. In cases where the host plants were only resolved to the level of the genus (higher), the aphids were categorised as non EFN-associated. If any of these aphids had EFN-plants among their hosts, this would only affect the analysis if there exist a correlation between ant-tending and host plant resolution, which seems very unlikely.

Some aphid species are heteroeocious, i.e. alternate between primary and secondary host plant species (Heie 1980). As the association of the aphid with ants and with EFNs can differ between the primary and secondary hosts, these species were excluded from analysis.

Other aphids have a subterranean life style, feeding on roots and other plant structures below the soil surface. These may suffer less from natural enemies and thereby also experience less benefit from ant protection than aphids living above the soil surface. Furthermore, subterranean aphids are more likely to be associated with exclusively subterranean ants, which do not forage on plant parts above the soil surface where potential EFNs are located (Zimmermann 1932, Elias 1983). Thus, the selection pressures described in the introduction disappear. Subterranean aphids were therefore also excluded from analysis.

Analysis

The evolution of two binary characters on a phylogenetic tree can be analysed with the Contingent States Test performed by CoSta 1.02 (Sillén-Tullberg 1993, Lindenfors 1997). This test treats one character as independent and the other as dependent, according to the hypothesis being examined. From one node to the next in a phylogenetic tree, the dependent binary character has four possible transitions: if the two states are referred to as one and two, it can remain in state one, it can change from state one to state two, it can remain in state two, or it can revert from state two to state one. The number of these transitions in the phylogenetic tree is calculated for each of the two states of the independent character. The test then calculates the state of the independent character, in which the dependent character is more likely to change from the first to the second state. The statistical significance is calculated with Fisher's exact test. More details of the test can be found in Sillén-Tullberg (1993).

However, the true phylogeny of the aphids in this study is not known below the family level (Heie 1980, 1987). Therefore I adopted an approach, suggested by Martins (1996), to perform phylogenetic comparative studies where the phylogeny is unknown. With this approach one should ideally analyse all possible phylogenies to ensure that the true phylogenetic tree is among them. Since this is not possible, a large random sample of all possible trees should be analysed. If all random trees then show a significant association between the traits under study, then it is most likely that so does the true tree.

The aphid species were split into seven families according to Heie (1980). Only two families were analysed, as the others did not contain enough species or variability to allow an analysis. I then constructed 100 random phylogenetic trees within each family. The random trees were generated with MacClade 3.0 (Maddison and Maddison 1992), with the assumptions (1) that states are unordered, i.e. that either states within a trait could evolve from the other, and (2) that trees are equiprobable, i.e. the probability of picking any given tree out of all possible dichotomous rooted trees are equal. Each random tree represented a random phylogeny as character states were estimated for all ancestral nodes according to the states of the randomly related terminal branches (the character states of the observed aphid species).

With CoSta I tested the association between the two parameters in question on each random phylogeny. A basic assumption using this test is the equiprobability of state transitions for all branches since branch length is ignored. In analysing the patterns resulting from analysis of the random trees, I modified the method proposed by Martins (1996) avoiding parameter estimates from the distribution of statistics obtained from individual trees, but instead basing the interpretation on the probabilities obtained from the least significant trees.

In the present study, I treat two hypotheses by treating either the association with ants or the association with EFNs as the independent character and examining how the other trait evolves.

Results

Out of the original record of 621 aphid species, 447 were left after having excluded host-alternating and subterranean species. These 447 species constituted the basis of further analysis.

Crude analysis

The distributions of aphids associated with ants and with EFNs among the families are given in Table 1. Overall 21.9% of the species were ant-associated and 6.3% were EFN-associated. Among the ant-associated species 14.3% were EFN-associated, whereas only 4% of the non ant-associated species were EFN-associated. Among the EFN-associated aphids, 50% of the species were associated with ants, whereas among the non EFN-associated aphids only 20.1% were associated with ants. The overall distribution of species shows a significant positive correlation between association with ants and with EFNs ($p = 0.0007$; Fisher's exact test). For details on individual families see Table 1.

Analysis of random trees

The distribution of p-values obtained from analysing individual random phylogenetic trees is summarised in Table 2.

Independent character: association with ants
On branches where aphids were associated with ants, there were more transitions than expected by random processes from not being associated with EFNs to being associated with EFNs. Among the Aphididae, all of the 100 trees were significant at the 0.001 level, with the highest p-value at 0.00018. The random trees constructed from Drepanosiphidae showed higher p-values than the trees constructed from Aphididae. However, none of the trees showed p-values exceeding 0.05 and only two trees exceeded 0.01. The highest p-value obtained from Drepanosiphidae was 0.01525.

Independent character: association with EFNs
On branches where aphids were associated with EFNs, there were more transitions than expected by random

Table 1. The distribution of aphid species associated with ants and with EFNs among families. Only monoeocious aphid species feeding above the soil surface are included. Numbers in the table are number of species within each family placed into each of the four possible categories. +ant = ant-associated; −ant = not ant-associated; +EFNs = EFN-associated; −EFNs = not EFN-associated.

		+ EFNs	−EFNs
Aphididae	+ant	8	52
	−ant	10	240
Drepanosiphidae	+ant	5	16
	−ant	3	76
Hormaphididae	+ant	0	1
	−ant	0	1
Lachnidae	+ant	1	12
	−ant	0	14
Mindaridae	+ant	0	0
	−ant	0	2
Pemphigidae	+ant	0	0
	−ant	1	1
Thelaxidae	+ant	0	3
	−ant	0	1
Overall	+ant	14	84
	−ant	14	335

Table 2. Distribution of *p*-values obtained from the analysis of individual random phylogenetic trees, (a) ant-association treated as the independent character, (b) EFN-association treated as the independent character. The *p*-value is obtained from Fisher's exact test performed on each random tree. One hundred random trees from each of the two families Aphididae and Drepanosiphidae were analysed. Numbers are the number of random trees within each aphid family showing a *p*-value higher than or equal to the corresponding *p*-value from the same row in the table.

| *p*-value | a | | b | |
	Aphididae	Drepanosiphidae	Aphididae	Drepanosiphidae
0.05	0	0	0	0
0.01	0	2	0	5
0.001	0	28	1	45
0.0001	10	100	27	100
0.00001	100	100	94	100
0.000001	100	100	100	100

processes from no ant-association to ant-association. All trees in both families had *p*-values below 0.05. The Aphididae again showed the lowest *p*-values; all trees had values below 0.005 and the highest *p*-value was 0.00199. Among the Drepanosiphidae, five trees had *p*-values exceeding 0.01 and 45 trees exceeded 0.001; the highest *p*-value was 0.01312.

Discussion

The present study showed a positive correlation between the likelihood that aphids are tended by ants and the likelihood that they are associated with plants that produce EFNs; this result held true for both the crude analysis and for the analysis taking into account the phylogenetic history with random phylogenies. In the latter case, the results suggest that an association with EFNs is more likely to evolve when ants already tend aphids, and that tending by ants is more likely to evolve in aphids previously associated with plants producing EFNs. However, when using the approach with totally random phylogenies there may be a tendency for both characters to evolve simultaneously, i.e. evolve on the same branches. Therefore, it is impossible to determine if ant-association or EFN-association evolved first on these branches, which again means that it cannot be stated that EFN-association is more likely to evolve in ant-associated aphids *and* that ant-association is more likely to evolve in EFN-associated aphids. From the present study one cannot separate between these two phylogenetic patterns. The association, then, between ant-tending and host plants bearing EFNs lend support to the three first ideas outlined in the introduction but is inconsistent with the fourth idea.

Host-selection hypothesis

In this scenario, EFNs evolved to attract ants by offering extrafloral nectar; in return ants have provided these plants with protection by preying on, deterring, or

disturbing potential herbivores. Because of the high prevalence of ants on plants with EFNs, aphids that can benefit from ants (see introduction) will therefore select host plant species that produce EFNs. Thus, aphids that had already evolved mechanisms allowing attendance by ants were more likely to switch to plants that produce EFNs (Table 1). This view is supported by numerous experimental studies showing the protective role of ants patrolling plants with EFNs, and the protective role of ants tending honeydew producing Homoptera (Nixon 1951, Way 1963, Beattie 1985). This aphid strategy, however, might have some evolutionary consequences for the ant-plant interaction, as the presence of ant-attended aphids might change the presence of ants from a benefit to a cost to the plant. Thus, ant-attended aphids might disrupt the mutualistic interaction that had previously evolved between ants and plants. Buckley (1983) investigated such a tripartite interaction (though the ant-attended Homoptera was a membracid and not an aphid species) and found that the homopterans, when not associated with ants, decreased the growth and seed set of their host plant. This detrimental effect of homopterans on the plants was further amplified when their ant partners tended the homopterans. Thus, ant-tended homopterans may actually exploit the interaction between ants and plants with EFNs; not only will aphids "steal" the resource (carbohydrates from the phloem sap) with which the plant "pays" its ant partner, they may also steal the protective service experienced by the plant. This may be accomplished by distracting the ants away from the nectaries (to the honeydew) and thereby lessen the protective effect of the ants to the plant (Buckley 1983). In other words, the aphids may be parasitising a mutualism.

Ant-distraction hypothesis

However, this evolutionary pattern – that aphids tended by ants are more likely to select plants producing EFNs (Table 1) – could also be explained by

arguing that EFNs may have specifically evolved as a defence against ant-homopteran mutualisms by attracting ants to EFNs (Becerra and Venable 1989). This would lead to a decreased benefit to homopterans because ants switch from tending aphids to 'tending' EFNs. Therefore predators are more likely to attack the aphids, so that producing EFNs has reduced the cost due to homopterans. Thus, if plants have been able to develop EFNs in response to ant-aphid mutualisms, then the increased likelihood for the evolution of an association to plants with EFNs in already ant-tended aphid species may have been due to the evolution of EFNs on plants (hosting ant-aphid associations). The pattern may not necessarily appear because ant-tended aphid species have changed host to a plant species with EFNs. However, it seems unlikely that plant species actually should have evolved EFNs as a defence against ant-aphid mutualisms, as numerous studies provide evidence that ants protect plants with EFNs against non-homopteran herbivores (Inouye and Taylor 1979, O'Dowd 1979, Stephenson 1982, Barton 1986, Smiley 1986). Thus, the selection pressure for the evolution of EFNs seems more likely to originate from non-homopteran herbivory. It should also be noted that, from the present study, it is not possible to conclude that plants have evolved EFNs in response to ant-aphid associations, since such a conclusion would require a simultaneous investigation of plant phylogeny.

Host-sharing hypothesis

The second pattern – that aphids on plants producing EFNs are more likely to become associated with ants (Table 1) – may be formulated as an extension of the host-selection hypothesis. As plants with EFNs are more likely to be attended by ants, any aphid species that has selected a host plant species with EFNs will be more likely to interact intimately with ants than if it had selected a host plant species without EFNs. This increased proximity between ants and aphids in time and space due to host sharing may increase the probability for the evolution of an association between the two, in particular if the ants occasionally prey on aphids they do not usually tend. In this scenario, adaptations allowing ants to tend the aphid may be seen as a defence mechanism of the aphid. This hypothesis underlines general ideas about the evolution of a mutualism. A prerequisite for a mutualistic association between species will be that the participants of the association at some time of their life will be located at the same place at the same time. This prerequisite is clearly enhanced when the species share a common host. Reliance on continued presence of an association partner, which is favoured under host sharing conditions, may also stabilise the evolution of the association. As Keeler (1985) writes in her presentation of

cost/benefit models of mutualism: "mutualism is favoured by a high probability of establishing the interaction (so that few individuals lack partners); and/or long duration of the interaction once it is established". Thus, the ant-plant mutualism may have facilitated the establishment of an ant-aphid mutualism. Whether the resulting tripartite interaction is beneficial to all participants must await further investigation.

Homopterans as EFNs

The association between ant-tending and host plants producing EFNs seen in aphids in this study is in contrast to what would be expected according to the hypothesis (Messina 1981, Beattie 1985, Gullan 1997) that ant-attended homopterans may function as EFNs. According to this hypothesis ant-tended homopterans should provide indirect protection to their host plant by attracting ants, which, apart from tending the homopterans, also provide protection to the homopteran host plant. A study conducted by Messina (1981) showed that goldenrods with ants and membracids grew taller and produced more seeds than goldenrods with only membracids. This effect was probably due to the ants disturbing a herbivore beetle. Beattie (1985) and Gullan (1997) provide discussions and additional references on Homoptera acting as indirect protectors of their host plants. If, however, this interaction outcome were the norm for such interactions, EFNs should be more likely to evolve on plants where ants do not tend the aphids, as plants associated with ant-tended aphids already experience ant protection. This would result in a negative correlation between tending by ants and host plants producing EFNs, the opposite of the pattern seen in this study.

Conclusion

The positive correlation between ant-association and association to plants with EFNs in aphids, found in this study, lends support to the host-selection, the ant-distraction and the host-sharing hypotheses. The random phylogenetic analysis, though, is not able to separate between the pattern that aphids associated with ants are more likely to evolve an association to plants with EFNs and the pattern that aphids associated with EFN-plants are more likely to evolve an association to ants. Therefore, further phylogenetic studies within the aphid families are needed before it will be possible to distinguish between support for, on the one hand, the host-selection and the ant-distraction hypotheses, and on the other hand, the host-sharing hypothesis. A rule of thumb, though, suggests that the most widespread character, in this case ant-association (Table 1) is most likely to evolve first on the phylogenetic tree. Thus,

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most support is found for the pattern that ant-associated aphids are more likely to evolve an association to plants with EFNs. However, this evolutionary pattern is explained by two mutually exclusive hypotheses – the host-selection hypothesis and the ant-distraction hypothesis. The latter, though, lacks empirical support since numerous ecological studies show that ants protect EFN-plants against non-homopteran herbivores (Inouye and Taylor 1979, O'Dowd 1979, Stephenson 1982, Barton 1986, Smiley 1986). I conclude that the observed association between ant-association and EFN-association in aphids is best explained by one of the two hypotheses advanced in this paper: 1) the host-selection hypothesis, or 2) the host-sharing hypothesis. In contrast, this association rejects the hypothesis that homopterans may function as EFNs.

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Appendix

Record of Danish and Fennoscandian plant species possessing EFNs. The record was constructed by an extensive literature search. Numbers indicate references to literature where species have been mentioned, or illustrated, as possessing EFNs. 1 = Pemberton and Vandenberg (1993); 2 = Hansen (1991); 3 = Elias (1983); 4 = Zimmermann (1932).

Family	Species	Reference	Family	Species	Reference
Amygdalaceae	*Prunus padus*	1,2	Oleaceae	*Ligustrum vulgare*	4
	P. avium	1,2,4		*Syringa vulgaris*	4
	P. cerasus	1,2,4	Poaceae	*Eragrostis minor*	4
Asteraceae	*Helianthus annuus*	1		*E. megastachya*	4
	H. tuberosus	4	Polygonaceae	*Polygonum convolvulus*	4
	Centaurea cyanus	4		*P. cuspidatum*	4
	C. jacea	1		*P. dumetorum*	4
	C. montana	4		*P. sacchalinense*	4
Balsaminaceae	*Impatiens glandulifera*	4	Polypodiaceae	*Pteridium aquilinum*	1
			Salicaceae	*Salix alba*	1
	I. parviflora	4		*S. fragilis*	2,4
Caprifoliaceae	*Sambucus ebulus*	4	Salicaceae	*Populus × canadensis* cv. *Serotina*	2,4
	S. nigra	1,4		*P. × candicans*	2,4
	S. racemosa	1,4		*P. nigra*	4
	Viburnum opulus	1,4		*P. tremula*	4
Cucurbitaceae	*Cucurbita pepo*	4		*P. tremuloides*	4
Euphorbiaceae	*Ricinus communis*	1,4		*P. trichocarpa*	2,4
Fabaceae	*Vicia sepium*	4	Scrophulariaceae	*Melampyrum arvense*	4
	V. angustifolia	1		*M. nemorosum*	4
	V. faba	1,4		*M. pratense*	3,4
	V. villosa	1	Tiliaceae	*Tilia platyphyllos*	4
	V. cracca	1			
	V. sativa	1,4			