

The tri-trophic niche concept and adaptive radiation of phytophagous insects

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Abstract

A conceptual divide exists between ecological and evolutionary approaches to understanding adaptive radiation, although the phenomenon is inherently both ecological and evolutionary. This divide is evident in studies of phytophagous insects, a highly diverse group that has been frequently investigated with the implicit or explicit goal of understanding its diversity. Whereas ecological studies of phytophagous insects increasingly recognize the importance of tri-trophic interactions as determinants of niche dimensions such as host-plant associations, evolutionary studies typically neglect the third trophic level. Here we attempt to reconcile ecological and evolutionary approaches through the concept of the ecological niche. We specifically present a tri-trophic niche concept as a foil to the traditional bi-trophic niche concept for phytophagous insects. We argue that these niche concepts have different implications for understanding herbivore community structure, population divergence, and evolutionary diversification. To this end, we offer contrasting empirical predictions of bi- and tri-trophic niche concepts for patterns of community structure, the process of population divergence, and patterns of evolutionary diversification of phytophagous insects.

Keywords

Biodiversity, community structure, competition, enemy-free space, parasitoid, plant–insect interactions.

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INTRODUCTION

The great diversity of phytophagous insects is generally thought to have arisen through a coevolutionary process of adaptive radiation with respect to host plants (Ehrlich & Raven 1964; Mitter *et al.* 1988; Farrell *et al.* 1991; Thompson 1994; Farrell 1998; Schluter 2000). Most would agree that the radiations of host-plant use in several clades of phytophagous insects and of anti-herbivore defences in angiosperms satisfy Schluter's (2000) four criteria for adaptive radiation: common ancestry, phenotype–environment correlation, trait utility, and rapid speciation. Much indirect evidence supports the notion of coevolution between insects and plants (Cornell & Hawkins 2003), although the various coevolutionary mechanisms remain largely untested (reviewed in Thompson 1994, 1999). Palaeontological (Labandeira 2002) and phylogenetic (e.g. Farrell & Mitter 1998; Becerra 2003) evidence broadly support the view that phytophagous insects and plants (at higher taxonomic levels) have diversified in synchrony, suggesting that their antagonistic interaction

could have contributed to diversification. Furthermore, the observation that phytophagy is associated with enhanced species richness across insect taxa implies that feeding on plants, and angiosperms in particular, enhances rates of insect diversification (Mitter *et al.* 1988; Farrell 1998). The ecological mechanisms by which phytophagous insects have adaptively radiated, however, are not clear despite much work on the evolutionary ecology of particular herbivore–plant interactions.

The purpose of this article is to apply conceptual developments from the ecological literature to link mechanisms of community structure with those of adaptive radiation of host-plant use in phytophagous insects, which account for at least 25% of all macroscopic species on Earth (Strong *et al.* 1984). We specifically contrast the utility of bi-trophic (plant–herbivore) and tri-trophic (plant–herbivore–carnivore) views of herbivore niches because they have different implications for explaining evolutionary diversification and ecological coexistence. Although influences of the third trophic level on herbivore–plant interactions have been

recognized for decades (e.g. Hairston *et al.* 1960; Price *et al.* 1980; Jeffries & Lawton 1984), an explicit tri-trophic perspective has been lacking in attempts to link specific herbivore–plant interactions to a broader understanding of community structure and evolutionary diversification (Dicke 2000; Lill *et al.* 2002; Ferrari & Godfray 2003). By tri-trophic perspective, we mean conceptual and methodological approaches that consider the simultaneous relations of plants, herbivores, and carnivores, rather than either plant–herbivore (historical approach) or herbivore–carnivore (predator–prey) interactions alone. Here we consider carnivores to include predators, parasites, and pathogens of herbivores. We suggest that explicitly comparing bi- and tri-trophic perspectives and their consequences within particular study systems can provide critical insight in understanding the diversification of phytophagous insects as well as reconciling ecological theory of plant–insect interactions with empirical patterns.

ADAPTIVE DIVERGENCE

As Schluter (2000) explains, the crux of ecological mechanisms of adaptive radiation is how divergent selection causes the genetic divergence of populations into different ecological niches. Here we define a niche in the broadest sense, as a species' ecological role in a community and the conditions allowing its persistence in a community (Chase & Leibold 2003). A general hypothetical mechanism for adaptive radiation is that divergent selection pressures in different populations cause adaptive phenotypic divergence among populations and reduced fitness of intermediate phenotypes (Schluter 2000). This 'adaptive divergence' hypothesis has been applied to phytophagous insects to suppose that adaptation to particular host-plants trades off with the ability to survive and reproduce on other kinds of host plants. It predicts the phenotypic divergence of different specialized host-plant races (occupying different niches) and their eventual genetic divergence (Rausher 1988; Jaenike 1990; Joshi & Thompson 1995; Funk 1998; Hawthorne & Via 2001; Fry 2003). Most explicit evolutionary or quantitative genetic tests of this hypothesis have taken a bi-trophic view, assuming that ecological and evolutionary responses to host-plant traits alone determine herbivore niches. In particular, it is the physiological response of herbivores to host-plant quality that is assumed to be an appropriate measure of fitness in one niche vs. another (e.g. Thompson 1996). The predicted trade-offs in physiological performance, however, have received limited empirical support (reviewed in Jaenike 1990; Thompson 1996; Strauss & Zangerl 2002). Although evolutionary trade-offs are likely to be transitory in nature and inherently difficult to detect (e.g. Fry 2003; Murphy 2004), a bi-trophic view of herbivore niches is likely to have limited the scope of detection from the outset (Janzen 1985; Bernays & Graham 1988; Dicke 2000).

THE TRI-TROPHIC NICHE CONCEPT

Ecological trade-offs in host use imposed by tri-trophic interactions must be considered along with bi-trophic trade-offs in testing models of adaptive divergence. Indeed, several studies have detected trade-offs in host use by considering tri-trophic interactions (e.g. Feder 1995; Berdegue *et al.* 1996; Stamp 2001; Mira & Bernays 2002; Singer *et al.* 2004). Adaptive divergence may be better understood in light of this work because the trade-off between physiological performance and susceptibility to carnivores is a recurring ecological theme within this plant–insect literature and more generally (e.g. McPeck 1996; Abrams & Chen 2002). For example, *Oreina elongata* leaf beetles perform better (physiologically) on the host plant *Adenostyles alliariae*, however, they prefer *Cirsium spinosissimum*, a host on which eggs experience lower levels of mortality in the field (Ballabeni *et al.* 2001). A similar relationship was found for pine sawflies (*Neodiprion sertifer*) relative to intraspecific host-plant variation: females preferred host trees on which physiological performance was relatively poor (and diterpenoid levels high), but vulnerability to parasitoids was low (Bjorkman *et al.* 1997). Gratton & Welter (1999) found that agromyzid leaf-miners transferred to novel, less suitable host plants exhibited significantly lower rates of parasitism, particularly by their more specialized parasitoids.

Together, these studies imply that the niches of phytophagous insects may be more profitably viewed as tri-trophic: population persistence in the community results from a balance of dietary performance benefits and host-plant associated refuges from or defences against various carnivores. This tri-trophic niche concept, while clearly within the confines of Hutchinson's (1957) theoretical niche concept, differs from operational definitions of niches based on single factors such as food, the physical environment (reviewed in Chase & Leibold 2003), or, more rarely, escape from predators (Ricklefs & O'Rourke 1975). Indeed, we see our tri-trophic niche concept as an application of the pluralistic niche concept espoused by Chase & Leibold (2003). Below, we contrast the consequences of bi- and tri-trophic views of herbivore niches for understanding the extant diversity and evolutionary diversification of insect herbivores. Furthermore, we present several empirical predictions that follow from each hypothesis.

IMPLICATIONS OF TRI-TROPHIC NICHES FOR DIVERSIFICATION

We are interested in adaptive divergence not only to understand the process itself, but also to learn about its consequences for patterns of biodiversity. Here again, we think bi-trophic and tri-trophic niche concepts may have profoundly different implications. Due to ecological oppor-

tunity alone (*sensu* Schluter 2000), the number of insect herbivore species predicted by the tri-trophic niche concept would exceed that predicted by a bi-trophic niche concept. This predicted difference follows from the notion that the potential diversity of niches increases dramatically with the addition of the third trophic level and its attendant complexity. For example, any set of resources (e.g. host plant species or tissue) can be used in multiple ways to acquire enemy-free space *from a particular set of enemies*, and several different strategies can coexist in the same plant-based feeding niche. Many such strategies exist within a community, including, at the very least, various feeding habits (e.g. leaf-mining, galling, feeding externally), defence types (e.g. crypsis, aposematism), phenological variation (e.g. early vs. late season), feeding preferences for particular hosts, and host ranges (e.g. monophagy vs. polyphagy). Each of these aspects of variation affects an herbivore's susceptibility to particular sets of carnivores: feeding habits (Hawkins 1994), defence types and diet breadth (Dyer 1995, 1997; Dyer & Gentry 1999; Gentry & Dyer 2002; Ferrari & Godfray 2003; Stireman & Singer 2003), phenology (Le Corff *et al.* 2000), and host identity as it relates to feeding preference (Barbosa *et al.* 2001; Lill *et al.* 2002; Singer *et al.* 2004).

This tri-trophic prediction of greater ecological opportunity assumes that competition for food will not limit herbivore coexistence because mortality from carnivores and plant defences is high, particularly in early life stages that consume little if any food. Life table studies generally support this assumption (Cornell & Hawkins 1995). In principle, many niches may be 'carved out' of plant-mediated, enemy-space because, unlike high quality food, it is not an easily exhaustible resource. We, therefore, predict that ecological opportunity should be particularly great for phytophagous insects because the diverse set of carnivores attacking them and mediating their interactions with diverse plant traits frequently limit competition for food (Strong *et al.* 1984, but see Denno *et al.* 1995). These diverse interactions can favour a multitude of evolutionary paths toward the acquisition of enemy-free space. The tri-trophic niche concept may, therefore, help explain the puzzling empirical observation in insects that phytophagy *per se* is associated with exceptional species richness (Mitter *et al.* 1988), whereas a parasitic life habit *per se* is apparently not (Weigmann *et al.* 1993).

Along with ecological opportunity, divergent selection pressure is the second major component of the process of adaptive radiation (Schluter 2000). Tri-trophic interactions may generate divergent selection on herbivores in at least one distinct way from plant-herbivore interactions: variation in enemy-free space. We envision natural selection mediated through enemy-free space as a possible initial stage in herbivore diversification. For example, some heritable

phenotypes in a population may be favoured by reduced enemy attack relative to other phenotypes. This situation would most likely cause divergence when different phenotypes (and selection regimes) predominate in different populations (*sensu* Thompson 1994). Murphy's (2004) study of *Papilio machaon* butterflies in Alaska clearly shows the importance of variation in enemy-free space associated with alternative host-plant species and microhabitats in the evolutionary ecology of host-plant use. Similarly, McPeck and colleagues have made a strong case for the role of enemy-free space in the divergent evolution of larval behaviour of damselflies living in lakes with different key predators (Stoks *et al.* 2003). As a testimony to the sheer diversifying force of enemy-free space, *Timema* stick insects have diverged into phenotypically distinct tri-trophic niches in the face of gene flow within local populations (Nosil *et al.* 2002).

In theory, variation in enemy-free space among different host-plant species may further facilitate herbivore divergence through enemy-mediated indirect competition ('apparent competition' *sensu* Holt 1977; Abrams 2000; Schluter 2000; Buckling & Rainey 2002). That is, high parasite loads or intense predation pressure on one herbivore species or population may elevate levels of mortality in other herbivore populations or species, thus favouring their divergence in host-plant use. Empirical measures of enemy-mediated indirect competition in nature have only just begun (Morris *et al.* 2004). However, it is important to note that enemy-mediated indirect competition among herbivore species may act oppositely as a limiting determinant of herbivore population size or community membership (e.g. Holt & Lawton 1993). If acting in the earliest stages of divergence, this process could inhibit the successful colonization of new niches. This outcome is particularly likely when indirect competition is mediated by host- or habitat-generalist carnivores, which would limit the acquisition of enemy-free space for herbivores colonizing new hosts or habitats.

For this reason, we hypothesize that enemy-free space mediated by relatively host- or habitat-specific carnivores is most likely to impose divergent natural selection on herbivores while allowing opportunities to colonize new niches, whereas host- or habitat-generalist carnivores are most likely to promote host specificity *per se* (Bernays & Graham 1988) with more variable and complex effects on the processes of divergence and ecological opportunity. Such generalist carnivores may, for example, enforce the evolutionary conservation of particular defensive strategies (aposematism, crypsis, etc.) on particular host plants, rather than spur the colonization of novel tri-trophic niches. By contrast, host-specific carnivores, such as specialist parasitoids, themselves experience natural selection to use reliable (i.e. specific) cues to efficiently locate phytophagous

hosts (Vet & Dicke 1992). This, in turn, would give a selective advantage to potential host populations that acquire enemy-free space by diverging in characteristics used as specific cues by parasitoids (Lawton 1986; Vet & Dicke 1992; Dicke 2000; De Moraes & Mescher 2004). These specific cues may frequently result from the herbivore–plant interaction itself (e.g. plant volatiles released by specific herbivore–plant interactions, De Moraes *et al.* 1998), as several studies show that the particular ways herbivores use host plants explain variation in parasitism rates of hosts in natural communities (e.g. Hawkins 1994; Barbosa *et al.* 2001; Gentry & Dyer 2002; Lill *et al.* 2002; Stireman & Singer 2003). As parasitoids track their herbivore hosts in evolutionary time, the temporal window of enemy-free space for herbivores (i.e. ecological opportunity) is likely to be transitory. As this process continues over time, the expected outcome is rapid divergence of herbivore and parasitoid lineages via escape-and-radiate coevolution, as expected for plant–herbivore coevolution (Thompson 1999). The great species richness of interacting herbivore and parasitoid taxa is consistent with this idea.

EMPIRICAL PREDICTIONS

The implications of the tri-trophic niche hypothesis may be made most apparent and useful by contrasting its predictions with those of the bi-trophic niche hypothesis that is implicit in much of the plant–insect herbivore literature. We see at least three empirical predictions for which bi- and tri-trophic niche concepts differ. These include expectations for herbivore community structure, genetic divergence among populations, and diversification patterns. Below we describe unique predictions of each hypothesis, but also note cases in which bi- and tri-trophic hypotheses offer different explanations for the same previously documented pattern.

Herbivore community structure

Herbivore communities might be structured either by bi-trophic or tri-trophic niches. Although they did not explicitly recognize the distinction between bi-trophic and tri-trophic niches, Strong *et al.* (1984) made a convincing case for the importance of tri-trophic interactions in the community structure of phytophagous insects. Here we elaborate on a few key points and recent developments. The bi-trophic niche concept hypothesizes that the number of available feeding niches in a community limits the assemblage size of herbivores (species richness in the community). Thus, it predicts that the species richness of phytophagous insects depends on host-plant richness at a regional scale. Although this seems intuitively true and has received empirical support (Strong *et al.* 1984), a recent, intensive

study of California butterflies and plants did not support this prediction (Hawkins & Porter 2003).

The tri-trophic alternative is that herbivore assemblage size depends on the number of ways herbivores use plants for food and defence or refuge from carnivores. This will often be correlated with host-plant richness as host-plant species often differ in potential refuge and defensive properties (e.g. secondary chemistry, architecture), but it is not necessarily so. To test this idea, it would be helpful to subdivide herbivore assemblages according to defensive strategy. For herbivores that sequester toxins for defence, for example, herbivore assemblage size among particular plant species should positively associate with phytotoxin diversity (e.g. different classes of secondary metabolites) among those plant species (Fig. 1a). According to a strict bi-trophic view, toxin sequestration functions primarily to safely store toxins that could otherwise harm the herbivore. Thus, it predicts a negative association between herbivore assemblage size and phytotoxin diversity because, as a manifestation of the escalating chemical arms race between plants and herbivores, increasing phytotoxin diversity would present an increasingly formidable barrier to herbivore colonization (Ehrlich & Raven 1964) (Fig. 1a).

For relatively palatable, cryptic herbivores that rely on refuges provided by their host plants, assemblage size should positively associate with host-plant architectural complexity. Increasing architectural complexity would offer not only a greater diversity of refuges, but perhaps more effective refuges (e.g. Geitzenhauer & Bernays 1996). Thus, woody plants, with their greater architectural complexity, would be expected to harbour more chemically defenceless (tasty) herbivore species than would herbaceous plants in the same community, providing a specific interpretation of the empirical pattern observed in British insect communities (Strong *et al.* 1984). Unlike the bi-trophic niche concept, the tri-trophic niche concept does not predict this pattern for herbivores that rely on chemical defence (nasty), because they would not require such refugia (Fig. 1b). Note that this prediction is independent of whether there are more species of ‘nasty’ or ‘tasty’ herbivores because it concerns the relationship between herbivore species richness and plant complexity (slope) not the absolute richness (intercept). Testing our predictions requires a community ecology approach that incorporates information about mechanisms of species interactions.

Genetic divergence and speciation

Genetic divergence among conspecific herbivore populations would result from differing selective agents under the bi- and tri-trophic hypotheses. In the former case,

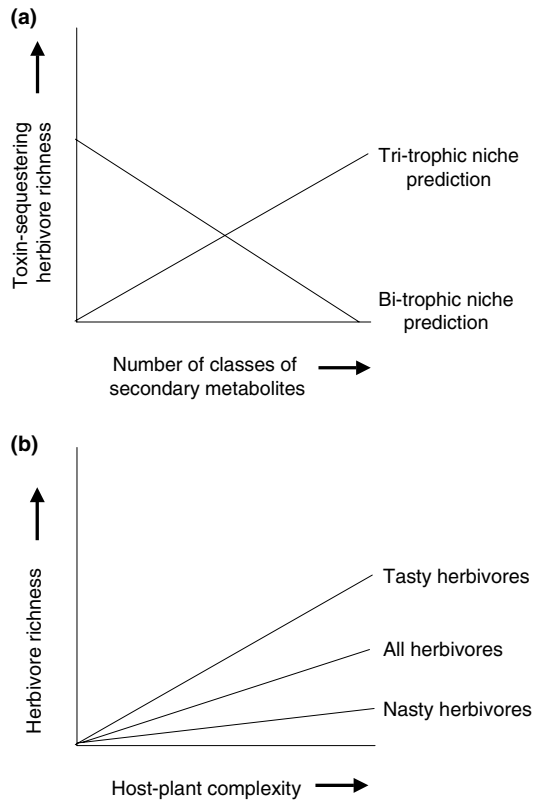


Figure 1 Predicted species richness of phytophagous insects on host plants according to bi-trophic and tri-trophic niche hypotheses. For herbivores that sequester phytotoxins for defence, the former predicts decreasing richness as the number of allelochemical classes increases, whereas the latter predicts the opposite (a). The bi-trophic niche hypothesis makes no distinction between herbivores that do or do not sequester toxins in explaining the increase of herbivore richness with increasing architectural complexity of host plants, whereas the tri-trophic niche hypothesis predicts this increase to be greater for the non-sequestering (tasty) species (b).

divergent selection on physiological performance would cause populations that differed in host-plant utilization to become reproductively isolated from one another (Hawthorne & Via 2001). However, this scenario assumes that genes influencing host-plant preference somehow become associated with genes for increased performance on the alternate host at the time of the host shift or shortly afterwards. Otherwise, viability selection against host-shifters should weed out genes associated with preference for the novel host. The frequent lack of preference–performance correlations in host use by phytophagous insects (e.g. Courtney & Kibota 1990) suggests that this genetic assumption is not generally true. By contrast, a tri-trophic scenario casts carnivores as additional agents of divergent selection for the acquisition of enemy-free

space. It follows that genetic divergence among populations using different host plants (or the same host plants in different defensive ways, e.g. Blair *et al.* 2005) should be positively associated with divergence in enemy-space (i.e. assemblage of enemies, frequency of mortality from shared enemies). Unlike the bi-trophic hypothesis, this perspective does not assume a preference–performance correlation because the benefits of enemy-free space may more than offset the physiological and developmental costs associated with using novel host plants (Brown *et al.* 1995; Murphy 2004) (Fig. 2a). Enemy-free space could also inhibit a host shift even when it would be favoured by host-plant quality (Fig. 2b), perhaps because other herbivores with shared enemies occupy the novel host plant.

Several cases of host races or cryptic sibling species in which enemy-free space is implicated in facilitating host shifts have appeared in recent years (Feder 1995; Dopman *et al.* 2002; Nosil *et al.* 2002; Thomas *et al.* 2003; Murphy 2004). For example, the *Solidago gigantea* race of galling fly

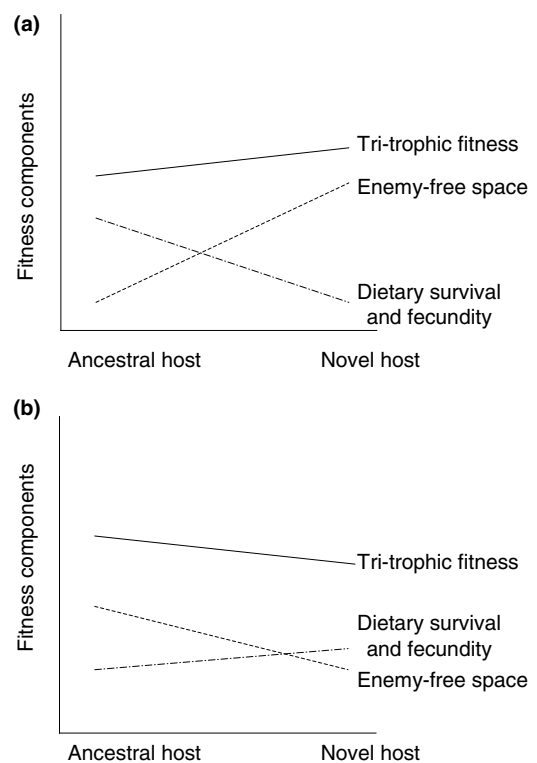


Figure 2 Cases showing how relative differences in enemy-free space among ancestral and novel host plants can take precedence over relative differences in host plant quality in determining the evolutionary ecology of host-plant use. In the former case (a), natural selection favours the use of the novel host because the relative survival benefit from enemy-free space outweighs the relative survival and fecundity costs from host quality. In the latter case (b), natural selection opposes a host-plant shift for the same reason.

Eurosta solidaginis exhibits lower levels of parasitism than the presumed ancestral sympatric race on *S. altissima* (Brown *et al.* 1995). Transplant experiments with genetically differentiated lineages of the gall-forming gelechiid moth *Gnorimoschema gallaesolidaginis* between *S. altissima* and *S. gigantea* show no evidence of trade-offs in performance, instead suggesting a trend towards increased performance (survival and mass) of all individuals on the ancestral host (*S. altissima*; Seehawer 2002). Another gall-maker, *Epiblema scudderiana* (Tortricidae) that utilizes these same host plants but does not exhibit host races, also performs better on *S. altissima* (J. Stireman, S. Heard, unpublished data), which is more frequently used than *S. gigantea*. In both of these cases, there is evidence that mortality from parasitism can vary widely relative to host-plant identity, suggesting that enemy-free space may have facilitated initial host shifts (*Gnorimoschema*) and maintained the use of physiologically sub-optimal host plants (*Epiblema*; J. Stireman, S. Heard, unpublished data). More studies along these lines are clearly needed, as they are central to resolving the relative importance of bi- and tri-trophic mechanisms of diversification.

Patterns of diversification

To date, evolutionary diversification has mostly been considered from a bi-trophic view via escape-and-radiate coevolution (e.g. Ehrlich & Raven 1964; Mitter *et al.* 1988; Farrell 1998). According to this hypothesis, herbivore diversification depends on the acquisition of specific counter-adaptations to specific plant defences, which allows exploitation of vacant, potential niches provided by diversifying host-plant lineages. It is the specificity of such interactions along with trade-offs in host use ability that would cause herbivore divergence in colonizing such underexploited plant lineages over time. A central bi-trophic prediction, then, is that diversification should be positively associated with host specificity in herbivore lineages. A caveat is the specialization as a dead-end argument (discussed in Thompson 1994): for example, extreme host specificity could lead to reduced diversification rates because of elevated extinction rates for herbivore species using host plants with high extinction rates. This bi-trophic prediction could be tested by comparing diversification rates of herbivore lineages that vary in host specificity but use the same host lineages (e.g. herbivore fauna of oaks). Because host plant specialization may often be associated with diversification of defensive strategies, a positive association between host specificity and herbivore diversification may also be expected under the tri-trophic niche hypothesis.

However, the tri-trophic hypothesis predicts more specifically that diversification will be particularly high in lineages for which divergent selection pressure imposed by

carnivores is high, and ecological opportunity in tri-trophic niche space is great. Divergent natural selection imposed by carnivores is likely to be highest in herbivore lineages subjected to relatively high attack rates by host- or prey-specific carnivores (e.g. parasitoids, as discussed above). Ecological opportunity in tri-trophic niche space is likely to be greatest in herbivore lineages subjected to a relatively low degree of interspecific competition. Therefore, herbivore lineages are expected to increase their diversification rates as this specific predation/competition 'ratio' increases. This prediction could be tested by comparing the diversification rates of herbivore lineages with different feeding strategies, which show variation in these parameters and serve as phylogenetically controlled replicates (Fig. 3). Externally feeding folivores, for example, experience relatively high frequencies of mortality from parasitoids compared with herbivores with the most concealed feeding strategies (e.g. rootivores, borers) (Hawkins 1994). Similarly, free-living folivores show less evidence of interspecific competition than these concealed strategists (Denno *et al.* 1995). On this evidence, the tri-trophic niche hypothesis predicts systematically higher diversification rates in external folivore lineages relative to lineages of such concealed feeders (Table 1, Fig. 3).

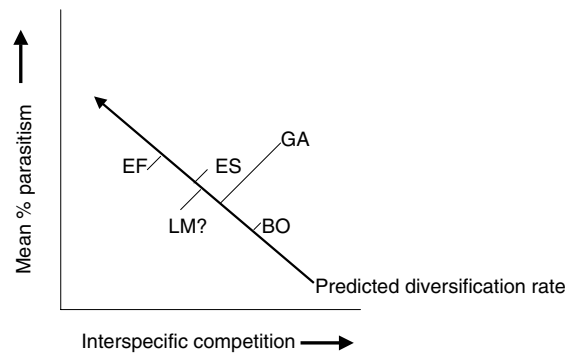


Figure 3 Relative differences in mean frequency of parasitism and documented frequency of interspecific competition among feeding strategies of phytophagous insects (EF, external folivore; ES, external sap feeder; LM?, leaf miner; GA, gall maker; BO, stem or wood borer). Parasitism rankings are derived from Hawkins (1993) and competition rankings are interpreted from Denno *et al.* (1995) and more recent studies on interspecific competition that cited Denno *et al.* 1995 ($n = 25$). Leaf miner parasitism is uncertain because the mean frequency of parasitism by specialists is likely to be considerably less than published total frequencies of parasitism. In Denno *et al.* (1995) there are limited data for certain feeding strategies (i.e. galls, leaf-miners), rendering our interpretation tentative. The tri-trophic niche hypothesis predicts the diversification rates in insect lineages to be positively associated with the frequency of mortality from specialist parasitoids and negatively associated with the frequency of interspecific competition.

Leaf mining may be instructive as an apparent ‘exception that proves the rule’. Parasitoid assemblages of leaf miners are typically diverse and attack rates very high (Hawkins 1994). However, parasitoid assemblages of leaf-miners are frequently dominated by generalists (Lewis *et al.* 2002) that may limit opportunity for escaping to enemy-reduced space. Under such circumstances, indirect competition mediated by parasitoids may limit leaf-miner community membership (Holt & Lawton 1993) rather than facilitate divergence. Consequently, the tri-trophic hypothesis predicts intermediate rates of diversification in leaf-mining lineages, whereas their diversification is predicted to be extremely rapid by the bi-trophic hypothesis on the basis of their high host specificity (Table 1, Fig. 3).

The predictions may also apply to patterns of variation within these feeding strategies. For example, as ‘extended phenotypes’ of the insects that cause them, galls are illustrative. Stone & Schonrogge (2003) conclude that in two relatively species-poor galling groups, aphids and thrips, gall structures have diversified primarily in response to selection for increased feeding area, whereas in the highly diverse gall midges and gall wasps (Cecidomyiidae and Cynipidae) defensive attributes are the most probable explanation for gall diversity. Both of these diverse families (several thousand described species per family) contain multiple examples of extensive adaptive radiations on single plant species and genera [e.g. *Asphondylia* on *Larrea tridentata* (Waring & Price 1989) and *Andricus* on Oak (Cook *et al.* 2002; Stone *et al.* 2002)]. These diverse gallers offer highly

Table 1 Comparison among different herbivore feeding strategies in the estimated importance of interspecific competition and mortality from parasitoids

Feeding strategy	% Frequent competition	% Mortality from parasitoids
EF	18 (9/50)	40
ES	69 (31/45)	40
LM	38 (3/8)	68
GA	73 (8/11)	53
BO	69 (20/29)	23
RF	? (1/1)	12

Feeding strategies are external folivores (EF), external sap feeders (ES), leaf miners (LM), gall makers (GA), stem and seed borers (BO), and root feeders (RF).

Interspecific competition is quantified as the percentage of studies reporting evidence of frequent competition among herbivore species [Denno *et al.* 1995 plus all more recent studies (through April 2005) on interspecific competition that cited Denno *et al.* 1995, $n = 25$]. Mortality from parasitoids is quantified as the average percentage of parasitism for each herbivore group (derived from Hawkins 1993, Fig. 1b).

apparent examples of how the interactions between host plants and natural enemies may shape herbivore niches and evolution.

One of the major challenges to testing the bi-trophic and tri-trophic diversification hypotheses is obtaining enough information to do so. There is still surprisingly little quantitative information, for example, on the host specificity of phytophagous insects generally (Novotny & Basset 2005). Similarly, we lack phylogenetic hypotheses for many lineages of insect herbivores, particularly at lower taxonomic levels where ecological information may be most meaningfully analysed in a phylogenetic context. However, several examples of this promising approach have begun to appear (e.g. Termonia *et al.* 2002; Lopez-Vaamonde *et al.* 2005; Weiblen *et al.* in press), and the use of phylogenetic comparative methods will be key to understanding the relationship between ecological niches and evolutionary diversification.

CONCLUSIONS

We have argued that an explicitly tri-trophic view of the community structure and diversification of phytophagous insects may explain general ecological and phylogenetic patterns that are currently unexplained or partially explained from a bi-trophic perspective. We see the tri-trophic niche as the critical conceptual link between ecological and evolutionary dynamics. Although our focus has been on phytophagous insects, the tri-trophic niche concept may apply to the diversification of other important coevolutionary players in tri-trophic interactions, such as plants and lineages of insect parasitoids, or other systems involving ecologically specialized organisms (e.g. some marine food webs). By offering three contrasting predictions of bi- and tri-trophic hypotheses for the evolutionary ecology of plant–insect interactions, we hope to introduce a useful framework for further theoretical and empirical investigation of these plant–herbivore–carnivore interactions, which involve a majority of the described macroscopic species on Earth. Refining and testing our general predictions requires the gathering of additional ecological, population genetic, and phylogenetic information on a diversity of systems. As this process will necessarily involve the use of diverse methods in ecology, quantitative and population genetics, and phylogenetic biology, we hope our framework will encourage intellectual ‘cross-pollination’ by giving a common goal to interested workers in these subdisciplines.

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