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The evolution of generalization? Parasitoid flies and the perils of inferring host range evolution from phylogenies

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Abstract

It is widely assumed that high resource specificity predisposes lineages toward greater likelihood of extinction and lower likelihood of diversification than more generalized lineages. This suggests that host range evolution in parasitic organisms should proceed from generalist to specialist, and specialist lineages should be found at the 'tips' of phylogenies. To test these hypotheses, parsimony and maximum likelihood methods were used to reconstruct the evolution of host range on a phylogeny of parasitoid flies in the family Tachinidae. In contrast to predictions, most reconstructions indicated that generalists were repeatedly derived from specialist lineages and tended to occupy terminal branches of the phylogeny. These results are critically examined with respect to hypotheses concerning the evolution of specialization, the inherent difficulties in inferring host ranges, our knowledge of tachinid-host associations, and the methodological problems associated with ancestral character state reconstruction. Both parsimony and likelihood reconstructions are shown to provide misleading results and it is argued that independent evidence, in addition to phylogenetic trees, is needed to inform models of the evolution of host range and the evolutionary consequences of specialization.

Introduction

The remarkable degree of ecological specialization found in insects and other organisms has led many biologists to ponder the evolutionary consequences of specialized life histories. This is nowhere more true than in the study of plant–insect interactions, in which it has become apparent that most of the vast diversity of herbivorous insect species use a narrow range of host plants (Strong *et al.*, 1984; Futuyma, 1991; Thompson, 1994). One general paradigm that has emerged from studies of host range evolution in phytophagous insects is that specialization may limit opportunities for evolutionary diversification and increase the likelihood of population and species extinction (Simpson, 1944; Futuyma & Moreno, 1988; Moran, 1988; Jaenike, 1990; Siddall *et al.*, 1993). This general paradigm arises from arguments that intimate interactions with hosts should result in tradeoffs between performance on alternate hosts, limiting the ability of populations of parasites to expand their host ranges (Rausher, 1984; Jaenike, 1990; Joshi & Thompson, 1995). These tradeoffs in performance may include not just physiological efficiencies in utilizing a host but also the processes of host finding (Janz & Nylin, 1997; Bernays, 1998) and pressure from natural enemies (Bernays & Graham, 1988). Although this 'tradeoffs' hypothesis has received equivocal support from empirical studies (Via, 1984; Jaenike, 1990; Carriere & Roitberg, 1994; Fry, 1996), it remains one of the most prominent hypotheses to explain the remarkable degree of host specialization in phytophagous insects.

The increased susceptibility of specialized organisms to extinction, due in part to relatively restricted geographic ranges and small population sizes, is supported by analyses of background extinction rates as well as the susceptibility of taxa to mass extinction events (Jablonski, 1986; Smith & Jeffery, 1998; Purvis *et al.*, 2000; Labandeira *et al.*, 2002). I refer to this trend as the

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'extinction' hypothesis. Taken together, the 'tradeoffs' hypothesis (specialization limits opportunities for future diversification) and the 'extinction' hypothesis (specialized lineages are more prone to extinction) paint a bleak picture for the fate of specialized lineages and would suggest that these lineages, although possibly arising frequently, should be rather transient.

If specialized lineages are more prone to extinction and less likely to diversify than generalists, then it may be predicted that phylogenetic reconstructions of host range evolution should more often indicate transitions from generalists to specialists than the reverse. The prediction that host range evolution tends to proceed towards increased specialization, thereby limiting opportunities for diversification, has been supported by studies of a number of taxa including aphids (Moran, 1988), bark beetles (Kelley & Farrell, 1998), walking sticks (Crespi & Sandoval, 2000) and *Anolis* lizards (Losos *et al.*, 1994). Kelley & Farrell (1998) also point out that if specialized lineages are more prone to extinction they should tend to be phylogenetically derived, occupying the 'tips' of phylogenies, a pattern they discerned in their study of *Dendroctonus* bark beetles. However, other studies have demonstrated either no directionality in host range evolution [Futuyma *et al.*, 1995 (leaf beetles); Janz *et al.*, 2001 (butterflies)]; or patterns of derived generalist taxa arising from specialized ancestors (e.g. Muller, 1996; Scheffer & Wiegmann, 2000). In his recent analysis of phylogenetic studies of a variety of phytophagous insects, Nosil (2002) found that although transitions in host range occurred in both directions, the transition frequency across all taxa from generalist life histories to specialist was significantly higher than from specialist to generalist. Most of these studies of host range evolution, however, have relied almost entirely on parsimony or maximum likelihood (ML) methods to reconstruct the evolution of host range relative to a phylogenetic hypothesis. Thus, they all may suffer from both uncertainty in the phylogenetic reconstruction and inappropriate assumptions or artefacts of the character reconstruction methods (Cunningham *et al.*, 1998; Losos, 1999).

Insect parasitoids, like phytophagous insects, are often characterized by narrow host ranges (Godfray, 1994; Memmot *et al.*, 2000). This trend is most evident in endoparasitoids, which must develop inside a living, growing host. The intimate relationships between larval parasitoids and hosts suggests that parasitoids are also likely to experience tradeoffs in performance on alternate hosts (e.g. see Kraaijeveld *et al.*, 2001) and that specialization should have similar evolutionary consequences in these organisms to that predicted for phytophagous insects. Yet, the evolutionary consequences of specialization for parasitoids have not been well investigated. In this study, the predictions of the 'tradeoffs' and 'extinction' hypotheses are assessed by examining patterns of host range in a diverse clade of endoparasitoids, tachinid flies. These related predictions, that host range evolution tends to proceed from generalist to specialist and that specialists should occupy tips of phylogenies (i.e. be relatively young) because of increased extinction rates, were tested by reconstructing host range evolution using parsimony and ML methods on a phylogenetic reconstruction inferred with molecular sequence data. The results of these analysis are critically examined with respect to the limitations and assumptions of character evolution inference methods, possible biological interpretations of phylogenetic patterns of host range, and hypotheses concerning the evolution of specialization in tachinids and other parasitic organisms. In this regard, this system provides a case study for the assessing problems with inferring host range evolution and the caution that should accompany the acceptance and interpretation of ancestral state reconstructions on phylogenetic trees.

Tachinidae

Tachinid flies are the most species rich group of parasitoids outside the hymenopteran Parasitica, with over 8000 described species (Wood, 1987). The taxonomic diversity of tachinids is matched by the immense range of hosts they use, from sawflies to scorpions (Williams *et al.*, 1990; Eggleton & Belshaw, 1993), and the wide variety of mechanisms by which they attack them (O'Hara, 1985). Tachinids are also extraordinary among endoparasitoids in the diversity of host ranges found in the family, from monophagy on a single host species to broad polyphagy across host orders. Thus, the family may be particularly useful for understanding the evolutionary implications of specialist and generalist life history strategies. Despite their taxonomic, morphological, and ecological diversity, tachinids have been subject to few modern analyses of the relationships between taxa or analyses of the evolution of their diverse life histories and range of host associations.

Materials and methods

Tachinid phylogeny

Phylogenetic reconstructions of the Exoristinae (the largest subfamily of Tachinidae) based on DNA sequence data from two genes, EF-1alpha and 28S rDNA (Stireman, 2002), were used to reconstruct the evolution of host range in tachinids in this study. This phylogenetic study involved 49 species in 43 genera, representing a small, but well-dispersed proportion of all taxa in the subfamily as well as several outgroup taxa from other tachinid subfamilies. Details of reconstruction of this phylogeny can be found in Stireman (2002). A Bayesian reconstruction using both genes (partitioned) was conducted in addition to these previous analyses using Mr Bayes (Huelsenbeck & Ronquist, 2001). This analysis employed the following parameters: GTR model with separate estimates of rates of change for each gene and codon position, 100 000 cycles, sampled every 100, burn-in 500 trees, all priors default.

Host range

Two measures of host range were used to examine the evolution of host-specificity: the number of host families and the number of host species from which a tachinid species was reared. Host range information was gathered from three primary sources: Arnaud's (1978) catalogue of tachinid-host associations, Strazanac *et al.* (2001), and data from the Lepidoptera rearing programme of Stireman & Singer (2003a,b). To minimize the inclusion of inaccurate host records, which are common in literature on parasitoid-host associations (Shaw, 1994), I ignored all host subspecies and unidentified species, unless they were the sole record for that host family, when tallying the number of families and species attacked.

Several of the species included in the phylogenetic analysis lacked information on host associations. If host ranges were known for other members of the genera to which these species belonged, they were assigned the average of these host ranges. If no information existed for any species in the genus, either no host range was assigned (no assumptions analysis), or they were assumed to be specialists (assumption analysis). The assumption of relative specificity for these taxa is likely to be true because if there are no rearing records in the literature, then it is likely that these species use a fairly restricted range of hosts.

Tachinid species were classified as 'specialists' and 'generalists' on the basis of the distribution of host ranges they exhibited. 'Specialists' which may be more aptly regarded as oligophagous, were defined by having mean range of three or fewer host families and 'generalists' were defined as using hosts in five or more families. As an alternative criterion, specialists were defined as attacking eight or fewer host species, while generalists used more than 10 host species. These values were chosen because they represented the greatest area of discontinuity in the host ranges of the taxa included (Fig. 1). Although, a categorization based more explicitly on the phylogenetic breadth of hosts used may be preferable, it is at this point not possible given the current state of lepidopteran systematics. It is often customary to restrict the term 'specialist' to enemies attacking hosts in only a single family, however this presupposes that host phylogenetic position is important in limiting host use. This does not appear to be the case with Tachinidae in which species often attack only a few, often distantly related, hosts and where ecological or life history traits of hosts may be more important in determining patterns of host use (Stireman & Singer, 2003a,b). In any case, the categorization used here is less artificial than arbitrarily dividing taxa upon whether they use one or more host families, and the predictions of the 'tradeoffs' and 'extinction' hypotheses should still apply given relative degrees of specialization. It should be stressed that any inferences made concerning how many times specialist or generalist strategies have evolved are underestimates, for there are many exoristine tachinid taxa not included in this analysis that possess host ranges belonging to both of these classes.

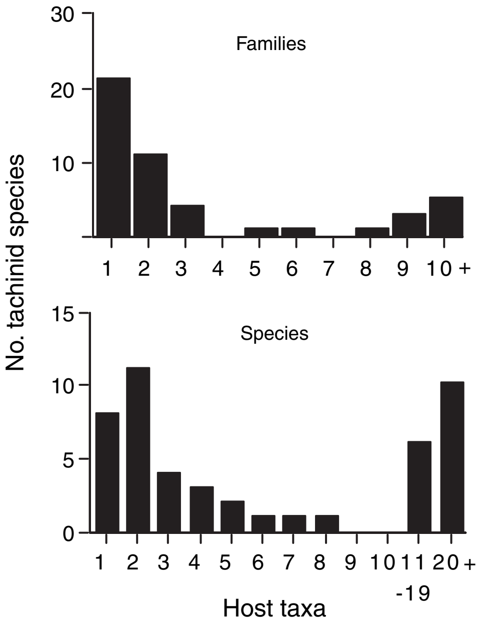

Fig. 1 The distribution of host ranges of tachinid species included in the present phylogenetic reconstruction(s) in terms of the number of host families (top) and host species (bottom). The number of tachinid species attacking 10 or more host families and from 11 to 19 and 20 or more host species are binned together.

Analysis

The most parsimonious scenarios of host range evolution were reconstructed on trees inferred by each of the inference methods (neighbour joining, parsimony, maximum likelihood) for each gene used in Stireman (2002), and on the parsimony and Bayesian inferred tree of the combined data set using MacClade (Maddison & Maddison, 2000). Taxa that were especially mobile between analyses were represented by unresolved nodes.

The value of analysing the evolution of characters on a phylogenetic reconstruction is strongly dependent on how accurately the reconstruction represents the true phylogeny or history of diversification of the organisms in question. An inaccurate reconstruction can easily result in misleading scenarios of character evolution. Although a number of relationships between taxa were well supported in my previous analysis of phylogenetic relationships among the Exoristinae, many nodes were supported by few characters and low bootstrap values, and placements of certain taxa were questionable (Stireman, 2002). In order to safeguard against inaccuracies in this reconstruction influencing the inferred history of host range evolution, 1000 parsimony bootstrap replicates were performed on the combined data set and all trees from each replicate were retained. For each of these (1250) trees the number of changes in host range classes and the frequency of transitions from specialist to generalist (S–G) and vice versa (G–S) were calculated using MacClade (Maddison & Maddison, 2000). This resulted in a distribution of the total number of changes required between host range states in either direction (S–G, G–S) across bootstrapped trees. These data were used to calculate distributions of the ratios of S–G to G–S transitions across bootstraps for both equivocal and unequivocal changes. All instances of zero transitions (in either direction) were replaced with 0.1 to avoid infinity and zero values in calculating the ratios of transitions. These analyses were repeated for host range classifications based on the number of host families used and the number of host species used, and also for trees assuming taxa with no known hosts were specialists and without this assumption.

Ancestral states and transitions between specialist and generalist strategies were also reconstructed on the combined evidence parsimony reconstruction using ML methods implemented in Mesquite (Maddison & Maddison, 2003a) and Compare 4.5 (Martins, 2003). Both symmetrical (equal rates of forward and backward transitions) and asymmetrical (forward and backward rates of transitions estimated independently via ML) models were used to reconstruct host range evolution as a dichotomous variable using the Ancestral States Module of Mesquite (Maddison & Maddison, 2003b) as well as Discrete (Pagel, 1999). A generalized (linear) least squares approach (GLS; Martins & Hansen, 1997) was used to estimate the number of host families and species of ancestral nodes as a continuous character using Compare 4.5 (Martins, 2003). These GLS estimates are identical to ML estimates assuming normally distributed error terms (Martins & Hansen, 1997). Maximum likelihood methods are useful because they take into account branch length information and quantify uncertainty in character state reconstruction (Pagel, 1994, 1999), however, is has been suggested that employing asymmetric transition rates can be problematic for small to medium sized data sets where change is relatively rare (Schluter *et al.*, 1997).

Results

Parsimony reconstructions of host range on the independently inferred trees and the bootstrap character analysis of the combined data set indicate that polyphagous lineages have arisen from more specialized lineages multiple times in exoristine tachinids (Table 1; Fig. 2). Each gene and analysis method indicates that polyphagy (mean families ≥5) has evolved at least four times among the taxa sampled, despite a reduced number of taxa (43 species) present in the 28S analyses (Table 1). In addition, the ratios of S–G transitions to G–S transitions are strongly biased in favour of the former in all parsimony reconstructions for both measures of host range (host families and host species; Table 1).

Maximum likelihood probabilities of ancestral states using a symmetrical model suggest a pattern of host range evolution very similar to that reconstructed using parsimony (Fig. 3a) as is expected when rates of change are relatively low. Ancestral state probabilities estimated with an asymmetrical model result in a similar pattern (Fig. 3b), with most internal nodes having a relatively higher probability of being specialist than generalist. However, the unconstrained estimates of transition rates for the asymmetrical ML model over the whole tree are highly biased towards generalist to specialist transitions (S–G: 0.254; G–S: 0.979); likely a consequence of the many extant specialists derived from nodes with small probabilities of being generalists. A likelihood ratio test indicates that this asymmetric model is significantly more likely than the symmetric model ($\chi_1^2 = 7.63$, $P < 0.01$).

Reconstructions of the number of host families and species as continuous characters using Compare's GLS estimates were consistent with the independent origin of several generalist lineages from more specialized ancestors, and bore a pattern similar to that of the discrete ML analyses (Fig. 3b, values above nodes). However, given that the ancestral state estimates are weighted averages, the root and internal nodes inevitably possess intermediate values as in the asymmetric ML reconstruction [e.g. root = 1.97 ± 3.42 (SE) host families and 7.69 ± 14.84 host species].

The combined bootstrap analysis indicates a range of six to 10 transitions between polyphagy and oligophagy for diet classifications based on the number of host families used and nine to 14 times for host species. Over 99% of replicates indicate at least seven and 10 changes in host specificity with regard to host families and species, respectively [mean for families: 8.14 ± 0.054 (SE); species: 11.8 ± 0.093]. The distribution of the ratios of G–S transitions to S–G transitions calculated for the bootstrap replicates are highly skewed towards specialist to generalist regardless of whether taxa without known hosts were assumed to be specialists, or without this assumption [Fig. 4; host families (assumption, no assumption, x ± SD) 0.078 ± 0.058, 0.089 ± 0.066; host species 0.115 ± 0.089, 0.134 ± 0.10].

The apparent pattern of generalist lineages repeatedly evolving from more specialized ancestors and occupying relatively terminal branches of the phylogeny demonstrated here is unlikely to be due merely to artefacts of taxon sampling. This is nonetheless at least possible given

Table 1 The ratios of changes from specialist to generalist to the reverse transition (S–G : G–S) with regard to the range of host families or host species across phylogenetic reconstructions (genes and inference methods) of exoristine tachinids (see Stireman, 2002).

		Host families		Host species	
Gene(s)	Inference method	Unambig	Ambig	Unambig	Ambig
Ef1α + 28S	Parsimony	7 : 0	7 : 0	8 : 0	10 : 1
Ef1α + 28S	Bayesian	5.3 : 0	7.5 : 0.4	8.9 : 0	11.4 : 0.6
Ef1α	Parsimony	5.8 : 0	7.6 : 0.6	9.8 : 0	11.6 : 0.6
Ef1α	NJ	8 : 0	8 : 0	9 : 0	11 : 2
Ef1α	ML	5 : 0	6.5 : 0.5	9 : 0	10 : 2
28SrDNA	Parsimony	5 : 0	5 : 0	7 : 0	7 : 1
28SrDNA	NJ	4 : 0	5 : 1	9 : 0	9 : 0
28SrDNA	ML	5 : 0	6 : 1	8 : 0	9 : 1

'Unambig' indicates unambiguous transitions and 'Ambig' indicates all transitions including ambiguous ones inferred through parsimony optimization. Not all taxa were present in analyses of the 28S rDNA data set, and the number of transitions inferred was averaged across equally parsimonious or equally likely trees. Estimates for the Bayesian analysis are average transitions across trees excluding the burn-in (see text). ML, maximum likelihood; NJ, neighbour joining.

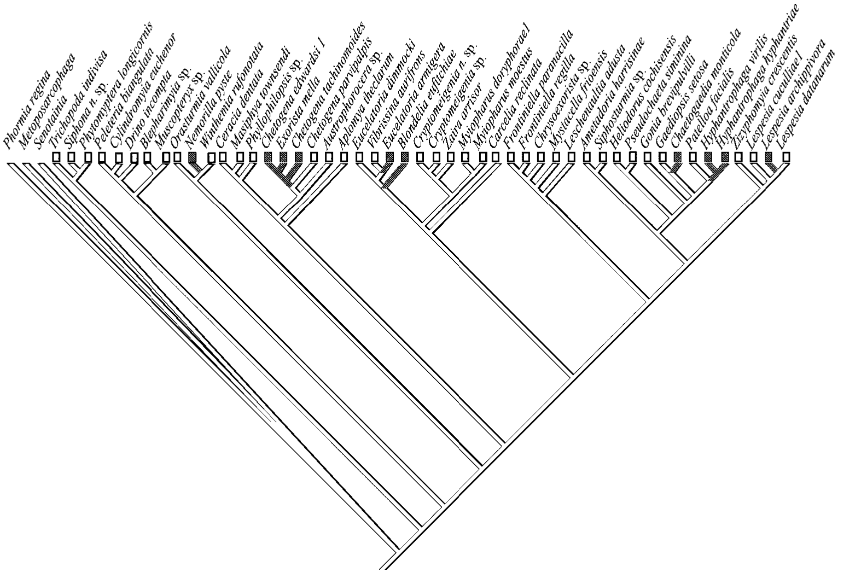

Fig. 2 A phylogenetic reconstruction (parsimony) of exoristine tachinids based on both 28SrDNA and EF1α from Stireman (2002) illustrating the dispersed distribution and most parsimonious history of polyphagy (five or more host families) in grey. It should be noted that the reconstructed placement of *Drino incompta* is very unlikely.

the sparse sampling of taxa within the diverse Exoristinae. However, this possibility becomes even more remote when one considers that each of the genera that contain polyphagous species also contains several relatively specialized taxa (e.g. *Lespesia*; Sabrosky, 1980). This is illustrated by the distribution of host ranges (number of host families) within tachinid genera from Lepidoptera-parasitoid associations drawn from Arnaud (1978) and Strazanac *et al.* (2001) (Fig. 5). In each of these genera containing five or more species, there is a recurring pattern of predominantly specialized species with one or a few polyphagous species. Phylogenetic information on the relationships of these species is lacking for the most part, but it is unlikely that the generalists are the basal lineages in each of these cases. The two genera with more than two species represented in the phylogenetic reconstruction examined here both suggest that the generalist species are not basal (see Fig. 2).

Discussion

The results for both classifications of host range (host families and species) and analysis methods (parsimony and symmetric ML) suggest that polyphagy has evolved numerous times within the Tachinidae, that these polyphagous lineages tend to occupy the tips of the reconstructed phylogenies, and that evolutionary transitions from specialist to generalist life histories have occurred more frequently than the reverse. The pattern of derived generalists indicated here is the opposite of that predicted under the assumptions that specialized lineages are prone to extinction and are unlikely to

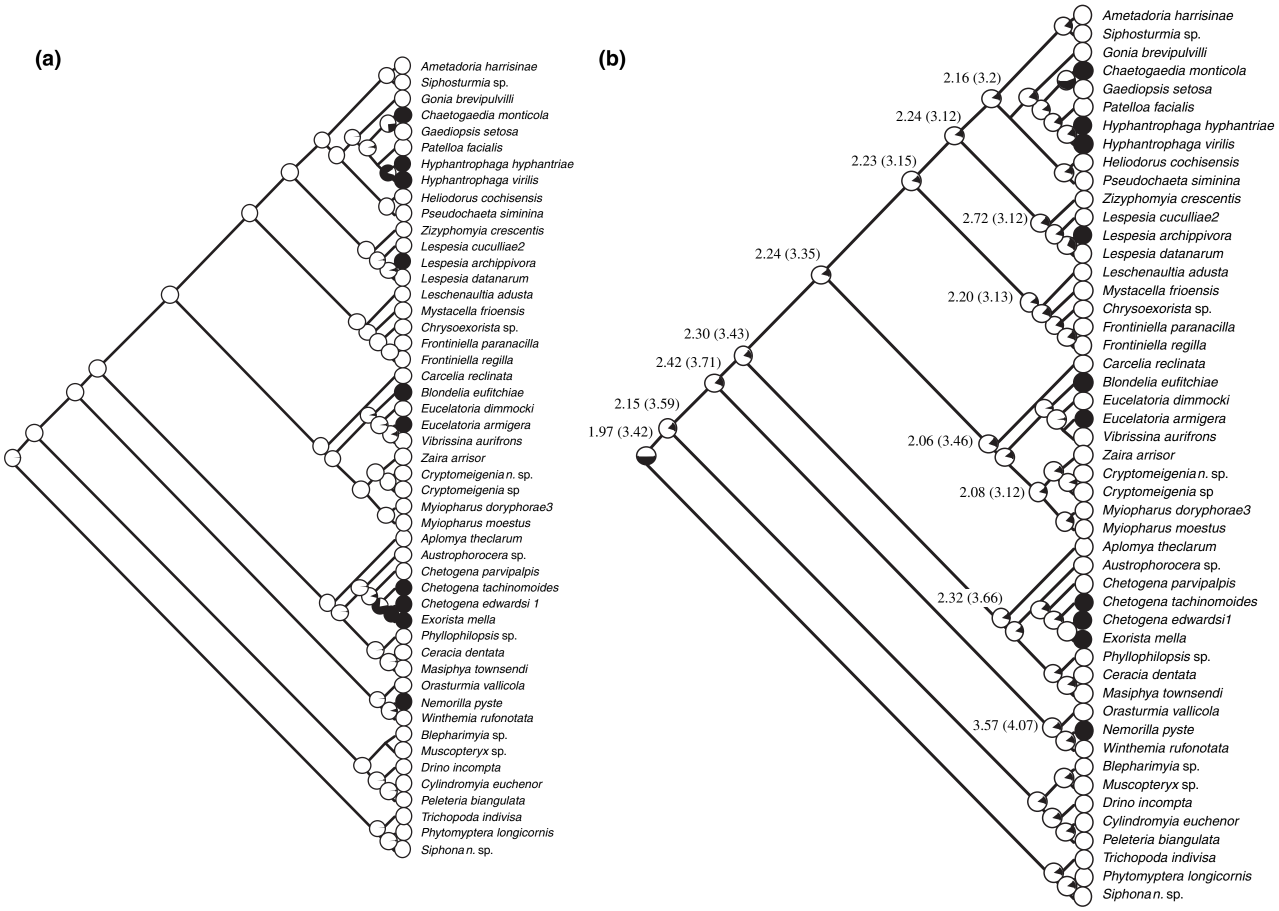

Fig. 3 Maximum likelihood reconstructions of ancestral host range employing symmetrical [i.e. equal rates of gain and loss (a)] and asymmetrical [i.e. unequal rates of gain and loss (b)] likelihood models. Pie diagrams (circles) at nodes indicate the likelihood of specialist (1–3 host families, white) or generalist (5+ families, black) states. Numbers in (b) above or to the right of major internal nodes indicate estimates of ancestral states (±SE) of the number of host families as a continuous character using a generalized least squares method (see text).

diversify over evolutionary time. Rather, the current reconstructions suggest that specialization has no inhibitory effect on diversification in tachinid flies and that, if anything, generalist lineages are more transient over evolutionary time. Thus, either the general 'generalist to specialist' paradigm is incorrect (or has limited application to only certain kinds of parasitic organisms), or it is more or less correct but not fully discernable with the phylogenetic approach employed here. Below, these results are examined more carefully and a number of possible explanations for this pattern ranging from artefacts of the methods used to reconstruct character evolution to refutation of the traditional 'tradeoffs' and 'extinction' arguments are briefly explored.

Artefacts of character reconstruction

It may be noted that the one of the conclusions above, that evolutionary transitions from specialist to generalist life histories have occurred more frequently than the reverse, is not strongly supported by the asymmetric ML and GLS continuous character analysis. However, unconstrained (asymmetrical) ML methods have been shown to perform poorly when change is rather rare, as it appears to be in the present case (Schluter *et al.*, 1997). Under such conditions, unique or rare character states located at the tips of phylogenies may acquire undue weight and be assigned to basal nodes (Mooers & Schluter, 1999). In the present case, even when only a single derived generalist was retained (e.g. *Chetogena edwardsi*; and all other generalists coded as specialists) ML transition rates over the whole tree were still strongly biased towards G–S transitions (S–G: 0.047; G–S: 2.47), a seemingly unlikely conclusion. For this reason models with equal transition rates are often considered to lead to more realistic estimates and are preferred (Schluter *et al.*, 1997). The potential for conflict in using these methods can also be witnessed in a recent phylogenetic study of

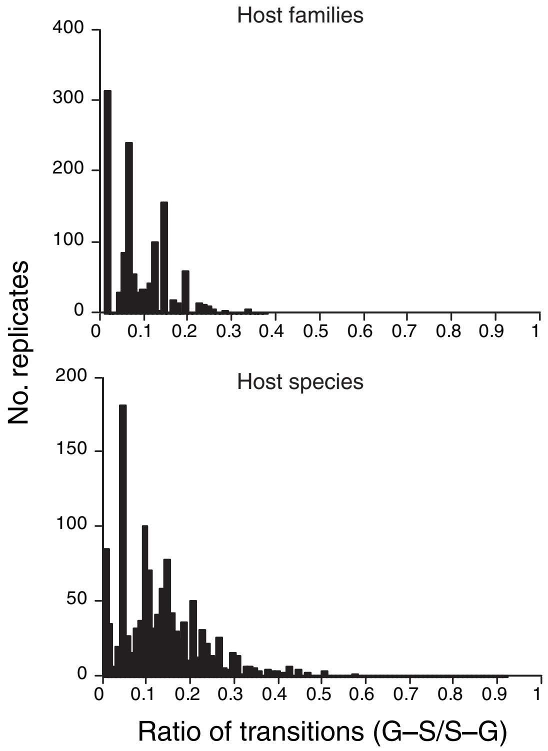

Fig. 4 The distribution of ratios of G–S to S–G transitions reconstructed for 1000 parsimony bootstraps (1250 trees) of the combined data set (both genes) for host families (top) and host species (bottom).

Dendroctonus bark beetles, in which initial parsimony optimization of host range provided evidence for the evolution of increasing specialization (Kelley & Farrell, 1998). Yet, results from this study were subsequently used as an example of strong bias towards increasing generalization based on asymmetric ML estimated transition rates by Nosil (2002).

For continuous traits, ancestral state estimates are weighted averages and thus their values tend to be intermediate between values in the extant taxa (Schluter *et al.*, 1997; Pagel, 1999). Thus basal nodes are rarely reconstructed as highly specialized regardless of the true history, and specialized terminal taxa are almost always reconstructed as descending from more generalized ancestors. In addition, standard errors of ancestral estimates are so large (for host species averaging over 200% of the estimates themselves) that it is difficult to identify significant patterns.

Another methodological problem is that the ‘ tradeoffs’ hypothesis implies that it is difficult for specialized lineages to ‘revert’ to more generalized life histories. However, neither asymmetric ML nor GLS models of ancestral state reconstruction inherently assume ‘restraining’ forces that conserve host range over evolutionary time. Such constraining forces can easily be incorporated into the models, but without independent evidence suggesting what biologically plausible levels of this constraint should be, it would seem inappropriate to artificially assign such parameters.

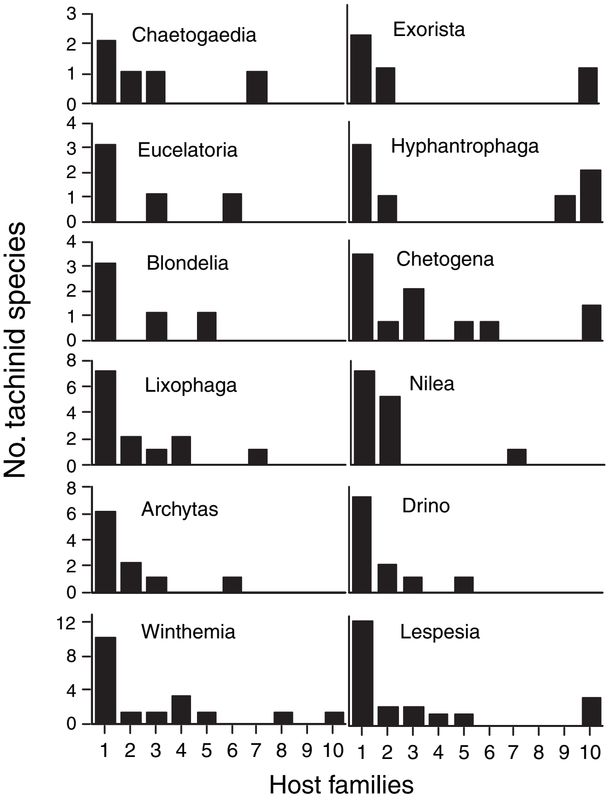

Fig. 5 Distributions of host ranges of tachinid species within genera from Arnaud (1978) in terms of the number of host families attacked illustrating the dominance of specialized species, but presence of generalist species in each genus. Tachinid species attacking more than 10 host families are grouped.

The limitations of parsimony methods of character reconstruction have been pointed out by several authors who have tended to focus on the inability of parsimony methods to deal with branch lengths and rapid evolution (multiple changes along branches), and the inherent assumption of equal rates of gains and losses (Schultz *et al.*, 1996; Cunningham *et al.*, 1998; Losos, 1999). Perhaps one of the most pervasive problems with character state reconstruction is that results are often taken at face value with little exploration of how they may be biased by the reconstruction method. In this study, the bias towards specialist to generalist transitions for parsimony reconstructions appears quite striking and is apparently robust to phylogenetic uncertainty (Fig. 4). However, a similar and overlapping range of ratios can be obtained for character state transitions reconstructed on 1000 randomly generated trees (for the same taxa) and for 1000 randomly shuffled character sets on the parsimony consensus tree (Fig. 6), with mean ratios of the bootstrap reconstructions falling well within the 95% confidence intervals of these random data sets ($P > 0.3$ in all cases). Because there are relatively few 'generalists' and branch lengths are ignored, even these simple random trees or randomly shuffled character states can easily result in similar biases (although on average these are not as extreme as those found for the hypothesized tree and associated bootstraps).

Thus, it is unclear whether a strong bias towards specialist to generalist transitions in tachinids actually exists, and neither reconstruction method appears to provide much insight into this problem. Nevertheless, a bias towards 'generalization' is still suggested by ML and parsimony, the generalist lineages are rather widely dispersed on the tachinid phylogeny and across tachinid genera (Fig. 5), and they seem to occupy relatively terminal positions. If we assume these patterns do exist and are not merely artefacts of character reconstruction methods, what do they imply about the evolution of host range?

Generalism as a dead end?

First, it may be that the general paradigm is truly flawed. There may be no overarching bias in the likelihood of specialist or generalist lineages diversifying or facing extinction. This has been argued by several researchers who have failed to identify phylogenetic patterns of derived and/or short lived specialized lineages (e.g. see Nosil, 2002). However, the present case would suggest that not only are the predictions of the paradigm not upheld, but in fact evolution in the present group of taxa proceeds in the opposite direction: generalists are repeatedly derived from specialists. In some groups of organisms (especially those that are vagile such as tachinids), generalist lineages may be less likely to diversify because it is more difficult to achieve conditions of genetic isolation (Jablonski & Roy, 2003). This is suggested by the relatively large geographic distributions, broad phenologies, and the variety of habitats occupied by generalist species. In more specialized organisms genetic isolation may be achieved via phenological, chemosensory, physiological or other adaptations to particular hosts (e.g. sympatric/ecological speciation, Bush, 1975, 1994; Funk *et al.*, 2002) in addition to more traditional allopatric means that may be facilitated by specialization on a particular host.

It is also possible, although seemingly unlikely, that polyphagous lineages could be relatively more prone to extinction than more specialized taxa. This could be due either to intense competition with more efficient specialists or to high levels of mortality exerted by natural enemies. Among phytophagous insects, generalists tend to be taxonomically rare (aside from certain groups, e.g. Acrididae; Bernays & Chapman, 1994), and there is some evidence that generalist exophytic Lepidoptera tend to experience higher rates of parasitism than more specialized species (Stireman & Singer, 2003a). Although these scenarios appear reasonable, the paucity of evidence supporting them and the diversity of empirical and theoretical studies that support more traditional views of relative extinction risks, ecological tradeoffs, and biases in diversification suggest that alternative hypotheses

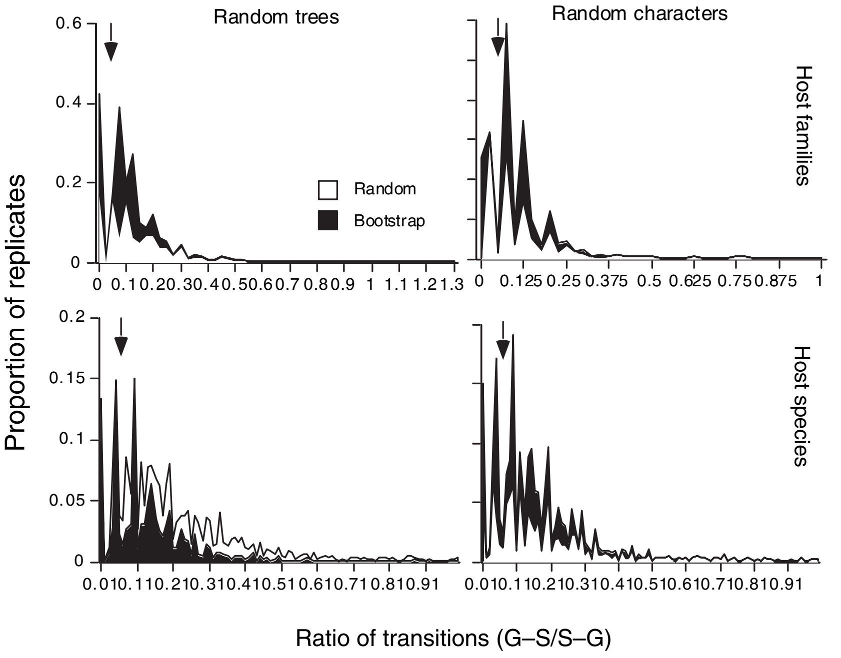

Fig. 6 Distributions of the ratio of G–S to S–G transitions inferred by parsimony for bootstrap trees (black) and random trees (white, at left) and randomly shuffled characters on the combined parsimony tree (right). Top panels are for host families and bottom panels are for host species. Arrows indicate ratios of transitions indicated on the combined parsimony tree with nonrandomized host ranges (i.e. Fig. 2).

which do not call for throwing out an entire paradigm should be explored.

There are no generalists

It is possible that truly generalized tachinids may be rare, and most species identified as generalists are actually complexes of closely related and relatively specialized taxa. Thus, the apparent generalist lineages occupying the tips of the phylogeny may just represent clusters of recently diverged and relatively specialized lineages. Tachinid flies (and other parasitoids) are notoriously difficult to identify due in part to the great diversity of morphologically similar species (Crosskey, 1976). In addition, there is a complete absence of studies on this group employing allozymes or DNA based molecular markers to examine population differentiation or the potential for cryptic speciation. At least one tachinid species, *Euclytia flava* (and perhaps others, e.g. *Trichopoda pennipes*) appears to be comprised of host races that cue in on particular sexual pheromones of hemipteran hosts belonging to different genera (Aldrich & Zhang, 2002; J. Aldrich, USDA, pers. comm.). Thus, it seems possible that many generalist species could be comprised of cryptic species or genetically differentiated populations that exhibit narrower host ranges. However, local ecological sampling programs suggest that many species of tachinids (e.g. *Chaetogaedia monticola*, *Lespesia aletiae*, *L. archippivora*, *C. tachinomoides* and *C. scutellaris*) are polyphagous even at local scales (Stireman & Singer, 2003a,b), and some species introduced for biological control have had widespread impacts on nontarget pests (e.g. *Compsilura concinnata* Boettner *et al.*, 2000). Thus, at least some generalist tachinids truly appear to be generalists. However, the degree to which increased resolution of cryptic species or host races may alter observed patterns of derived generalist lineages at the tips of the tachinid phylogeny is unclear and could be appreciable. It also has the potential to influence inference of host range evolution in other parasitic taxa suspected to be to be rife with cryptic lineages such as phytophagous insects and hymenopteran parasitoids.

Evolutionary advantages of oligophagy

In a somewhat contrasting view from the cryptic-species argument, it is possible that there are relatively few truly specialized tachinids that attack a single host species or a few related species (Eggleton & Gaston, 1992; Belshaw, 1994), and such lineages are likely to become evolutionary dead ends as theory would predict. The primarily oligophagous lineages considered here to be ‘specialists’ might be striking an optimal balance between the masterful craftsman and the jack of all trades. Their host ranges may not be too limited to force them into an evolutionary *cul de sac* of small population sizes and strong dependence on the population dynamics of a single or limited set of hosts, and yet not too large to severely limit the efficiency of host location and larval development or inhibit the ability to compete with more specialized species. It thus may be taxa with host ranges intermediate between extreme specialists and extreme generalists that are most likely to avoid extinction over the long-term and to generate daughter lineages. The evolutionary offspring of these oligophagous lineages, consisting in part of more specialized or more generalized species, may then be more sensitive to the ecological forces that lead to extinction.

This hypothesis is difficult to evaluate because of the problems inherent in ascertaining the complete host range of a parasitoid (or a phytophagous insect; Shaw, 1994). In the extreme view, one can never know whether or not additional host species are used by a parasitoid without large samples of all potential host species. However, rearing data, geographic distribution, and taxonomic evidence would suggest that at least some species of tachinids are quite specialized such as *Lespesia rileyi* (*Papilio* butterfly specialists), *Aplomyiopsis epilachnae* (Coccinellidae beetles in the genus *Epilachnus*), *Belvosia borealis* (sphingid moths in the genus *Ceratomia*), *Ametadoria harrisinae* (zygaenid moths in the genus *Harrisina*), and *Cholomyia inaequipes* (weevils in genus *Conotrachelus*). However, the species in this study that have been recorded from only one or two host species (12 species, most of which have been reared rarely and thus their narrow host ranges are suspect) do not exhibit any pattern suggesting that they are young lineages. Although incomplete sampling makes it difficult to gauge relative ages of taxa, these species do not tend to occupy branches far removed from the base of tachinids on the combined data set tree (average nodes from root ± SE: 6.36 ± 0.97, vs. all taxa: 7.98 ± 0.42).

Can reconstruction methods test the generalist to specialist model?

Finally, it is possible that the broadly believed impressions that specialized lineages tend to be derived from more generalized ancestors and that they are more prone to extinction and less prone to diversification are true, but this pattern remains hidden because of the way in which character evolution is reconstructed. This can be visualized in a simple verbal model with two primary assumptions. The first, and most important, assumption is that polyphagous lineages are less likely to become extinct than more specialized lineages, as is suggested by studies of fossil taxa (Smith & Jeffery, 1998; Labandeira *et al.*, 2002). Second, we assume that generalist lineages may be relatively more likely to diversify with a biased production of specialized descendents. That is, generalist lineages tend produce specialist daughter lineages much more frequently than additional generalist lineages. This corresponds to a scenario where selection pressures on local (perhaps peripheral) populations of a generalist species favour specificity of host use (e.g. via more efficient use of locally abundant host species). Given some barrier to gene flow, these specialized populations may diverge through rapid evolutionary changes in small populations and reinforcement of co-adapted gene complexes (allopatric; Mayr, 1963; Thompson, 1994), or through changes in phenology or cues used in host location that become associated with mating patterns (sympatric; Bush, 1994; Berlocher & Feder, 2002). More central (geographically and ecologically) polyphagous populations may be less likely to diverge from one another because of a lack of barriers to gene flow and weaker divergent selection pressures associated with hosts. Under these assumptions, evolution may take place as illustrated in Fig. 7 (left), where a persistent generalist lineage gives rise to many specialized daughter species, some of which become extinct. However, when we optimize host range evolution on this phylogeny using parsimony or ML (symmetrical model), it appears that the generalist lineage occupies a terminal branch and is descended from more specialized ancestors (Fig. 7, right). Rates of transitions must be biased 3 to 1 in favour of generalist to specialist transitions under parsimony to reconstruct the hypothesized history of host range evolution. Asymmetrical ML methods are more suggestive of a pattern of derived specialists (with more even probabilities of specialists and generalists at internal nodes). However, these models appear to be getting the 'right' answer for the wrong reasons. The relatively large probabilities of generalist ancestors inferred by asymmetric ML (~ 0.16) appear due to artefact, not due to more accurate ancestral state reconstruction (see previous discussion). Moreover, to achieve 95% confidence in generalism at ancestral nodes in this example, bias in transitions must be approximately 18-fold (significantly less likely than equal rates: $\chi_1^2 = 21.9$, $P < 0.001$). Most striking, is that the bias necessary to confidently reconstruct ancestors as generalists in this example is towards specialist to generalist transitions, exactly the opposite of the verbal model proposed.

It is difficult to judge the accuracy of the model of host range evolution proposed here because it requires knowledge of processes that take place over large time scales and it is largely invisible to standard methods of character reconstruction. However, the assumptions have some support in the literature (above), and are likely robust with regard to the assumption that specialists are relatively less likely to diversify. Bayesian methods of character reconstruction will also be likely to fail to reconstruct host range evolution accurately under this scenario. Although these methods are better at incorporating information on the relative probabilities of transitions from specialist to generalist life histories or vice versa, this 'prior' information is extremely difficult to gather from phylogenetic reconstructions in a nontautological manner. If the assumptions set forward here are commonly met, the frequency of transitions from specialist to generalist life histories and the diversification of specialized lineages will be vastly overestimated.

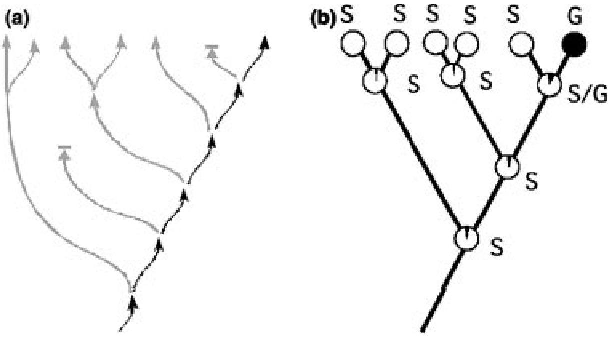

Fig. 7 (a) A hypothetical phylogenetic scenario in which generalists (black) persist through evolutionary time (low extinction) and repeatedly give rise to more specialized descendents (grey) that are relatively more prone to extinction. (b) The most parsimonious (letters) and most likely (symmetric model, pie diagrams as in Fig. 3) reconstructions of host range using the extant taxa from A (S, specialist; G, generalist; S/G, equivocal).

Conclusions

It is unclear whether the patterns found in Tachinidae are representative of other 'parasitic' groups such as parasitic wasps or phytophagous insects. Nosil's (2002) analysis of phylogenetic studies of phytophagous insects found an overall bias towards specialists being derived from generalists, although there was a large degree of variation and several studies tended towards the opposite pattern. It is clear, however, that all of the arguments presented here concerning difficulties in inferring host range evolution could be applied to other groups as well, whether they be parasitoids, herbivores, mutualists or predators. Perhaps most alarming is the potential for artefacts in phylogenetic character reconstruction using both parsimony and ML. Potential explanations for the distribution of generalists observed here are far from exhausted, but it should be noted that at least two of the hypotheses presented suggest that the relationship between host range and the demography shaping species birth and death processes cannot be properly tested using only current uninformed phylogenetic comparative methods.

Testable hypotheses can be generated from each of the explanations outlined above. For example, fossil data could be used to test whether lineages with intermediate levels of specialization tend to be more successful than those at more extreme ends of the spectrum. In addition, the relative advantages of parasitic organisms with varying levels of host specificity could be tested in ecological time in terms of host location efficiency, development on hosts, avoidance of natural enemies, and the longer term population demographic consequences of these traits. The extent to which generalist species represent independent cryptic lineages and the degree to which parasitic organisms are composed of genetically differentiated 'host races' can also be relatively easily assessed with the diversity of molecular markers and genetic analysis techniques that are currently available.

Continued accumulation of phylogenetic data from different groups of organisms with parasitic lifestyles will greatly aid in our understanding of the relationship between specialization and evolutionary stability and diversification. Such data for host groups will also allow better assessment of host ranges by enabling the incorporation of phylogenetic relationships into these estimates. However, given the limited amount of historical information that it is possible to obtain for groups with poor fossil records (such as most insects) and the potential for bias in character reconstruction, more studies focusing on patterns of host use and host range at the interface of ecology, population genetics and phylogeny are needed. To understand the evolutionary consequences of host range we need continued investigation of the ecological forces that predispose populations to diverge genetically and the forces that cause host range contractions, expansions and shifts in parasitoids and other organisms with parasitic lifestyles. These studies need to explicitly consider the ecological phenomena and interactions that are driving the evolution of these traits and make use of careful records of taxonomically accurate host associations. Such ecological and microevolutionary analyses can then be used to parameterize phylogenetic character reconstruction with realistic probabilities of transitions that may be extrapolated to inform processes occurring over deeper evolutionary time.

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