

## Phylogenetic Cascades and the Origins of Tropical Diversity

Matthew L. Forister<sup>1</sup>

Biology Department, MS 314, University of Nevada, Reno, Nevada 89557, U.S.A.

and

Chris R. Feldman

Department of Natural Resources and Environmental Science, MS 186, University of Nevada, Reno, Nevada 89512, U.S.A.

### ABSTRACT

For organisms involved in specialized ecological interactions, the potential exists to have congruent evolutionary histories, such that diversification within one lineage of organisms parallels diversification within another. This model of shared evolutionary history has most often been explored in a bitrophic context, particularly with plants and specialized herbivorous insects, though also with other ecological partners such as vertebrate hosts and their invertebrate parasites. Recently, the possibility has been raised that evolutionary histories might be shared across more than two trophic levels, a phenomenon that we term a phylogenetic cascade. We review previous work on tritrophic diversification and discuss outstanding questions, with an emphasis on plants, caterpillars, and parasitoids, in diverse tropical communities.

*Key words:* ecological speciation; host-associated differentiation; phylogenetic cascade; sequential radiation; sequential speciation; specialization; speciation.

MUCH OF LIFE ON EARTH IS CHARACTERIZED BY SPECIALIZED TROPHIC RELATIONSHIPS AMONG OFTEN DISTANTLY RELATED ORGANISMS (Futuyma & Moreno 1988, Thompson 2005). The diversity of these interactions exceeds what can be easily summarized, though notable examples range from the attine ants with their fungal gardens and associated antibiotic-producing bacterial symbionts (Currie *et al.* 2006) to physiological specializations of garter snakes that confer resistance to neurotoxins in their newt prey (Feldman *et al.* 2009). While these interactions are of inherent ecological interest, a fundamental evolutionary question is: to what extent do specialized relationships among contemporary species reflect shared or congruent evolutionary histories? Particularly for parasitic taxa that feed in or on the living tissues of other organisms, one can hypothesize that a specialized host preference might translate into a long history of association and even parallel evolutionary diversification (Futuyma & Mitter 1996). Fossil evidence has confirmed the antiquity of certain plant–herbivore interactions (Labandeira *et al.* 1994), and phylogenetic analyses have revealed histories of cospeciation, with patterns of diversification in one group being associated with patterns of diversification in a second group (Pellmyr & Leebens-Mack 1999, Becerra 2003, Page 2003, Light & Hafner 2007, McKenna *et al.* 2009). Because many parasitic taxa are actually parasites of parasites, there is the potential for evolutionary histories to be shared across multiple trophic levels, such that diversification at one trophic level (*e.g.*, plants) provides opportunities for the diversification of a second trophic level (*e.g.*, insect herbivores) which then opens up opportunities for diversification at a third level (*e.g.*, hymenopteran parasitoids).

Linked, multitrophic diversification can be termed a ‘phylogenetic cascade,’ and has also been called ‘sequential speciation’ and ‘sequential radiation’ (Abrahamson & Blair 2008, Feder & Forbes 2010). Stireman *et al.* (2006) also refer to ‘cascading host-associated differentiation’ with reference to plant-specific herbivorous insects and their specialized parasitoids. Although these terms can be used interchangeably, we prefer the term ‘phylogenetic cascade’ (and use it here) for its broad community-level connotation, because cascading dynamics in ecology typically involve large numbers of species across multiple trophic levels. Phylogenetic cascades have received relatively little attention in macroevolutionary studies of specialized groups, which have almost exclusively focused on bitrophic relationships (Futuyma & Agrawal 2009), despite the potential for relevant evolutionary dynamics across multiple trophic levels (Singer & Stireman 2005, Thompson 2005). When phylogenetic cascades have been studied, the focus has often been on very small suites of species. Even when systematic relationships have been assembled for more species-rich groups that could potentially be involved in cascading evolutionary dynamics, the ecological data is often lacking to match individual parasites with their hosts. However, ecological datasets are now being reported that provide an essential context for studying tritrophic evolutionary relationships (*e.g.*, Novotny & Basset 2005, Dyer *et al.* 2008, Janzen & Hallwachs 2008), and new methods are being developed for the quantification of ecological interactions that should greatly facilitate studies of the evolution of diversity (Janzen *et al.* 2005, Albrecht *et al.* 2007, Bascompte 2009, Dyer *et al.* 2010). This is an opportune time therefore, to review issues related to macroevolution within a tritrophic, community context.

Phylogenetic cascades should be of interest to ecologists and evolutionary biologists for a number of reasons. First, they are of

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<sup>1</sup>Corresponding author; e-mail: mforister@unr.edu

fundamental importance as a logical extension of the idea, notably articulated by Simpson (1953), that the colonization of novel environments and resources promotes diversification. That idea has subsequently been explored by many authors, generally within a single lineage (*e.g.*, Darwin's finches) or within a bitrophic context (*e.g.*, plants and herbivores), and has since become a mainstay of evolutionary biology under the rubric of adaptive radiation (Schluter 2000, Via & Hawthorne 2005, Funk *et al.* 2006, Stireman *et al.* 2006, Fordyce 2010). In addition to the fundamental importance of natural selection in creating biodiversity, the study of phylogenetic cascades has the potential to contribute to the venerable problem of the latitudinal gradient in species richness. There is of course a diverse array of hypotheses that address the latitudinal diversity gradient (Pianka 1966, Mittelbach *et al.* 2007). The idea of phylogenetic cascades does not stand on its own as another explanation for the latitudinal diversity gradient. This is because the phylogenetic cascades hypothesis posits that diversity at higher trophic levels follows from diversity at lower trophic levels, which still leaves one needing to explain the origin of diversity at that first trophic level (assuming that phylogenetic cascades are driven from the bottom up; discussed below). By the same token, however, the phylogenetic cascades hypothesis has the potential to simplify the problem: inherently plant-specific hypotheses on the origin and maintenance of tropical diversity (Wright 2002, Kreft & Jetz 2007) could have broader consequences for the general evolution of diversity when considered in the context of phylogenetic cascades.

The goal of the present discussion is to broaden the consideration of phylogenetic cascades from small suites of species, which have often been the focus, to include more species-rich lineages. For convenience, we focus much of our discussion on tropical plants, herbivores, and parasitoids, and discuss the implications for other suites of taxa in our Conclusion. More specifically, this paper: (1) investigates expectations and analyses associated with the demonstration of phylogenetic cascades; (2) reviews previous research on phylogenetic cascades; and (3) discusses avenues for future work, with an emphasis on diverse tropical communities. Although natural selection is clearly implicated in host-associated speciation, we do not cover this topic in detail because thorough discussions of natural selection and the evolution of reproductive isolation within a tritrophic context have recently been given (Abrahamson & Blair 2008, Feder & Forbes 2010).

## INVESTIGATING AND INTERPRETING PHYLOGENETIC CASCADES

A phylogenetic cascade is a process by which diversification at one trophic level has a positive effect on diversification at two or more other trophic levels, resulting in a shared evolutionary history that is manifest as an association, or nonindependent relationship, between phylogenies of the ecologically interacting organisms. Non-independence between and among phylogenies can take different forms. One possibility is a perfect or nearly perfect correspondence such that patterns of diversification are paralleled at a species level across phylogenies (Fig. 1). Such a close phylogenetic correspondence might be associated with extremely host-specific parasites,

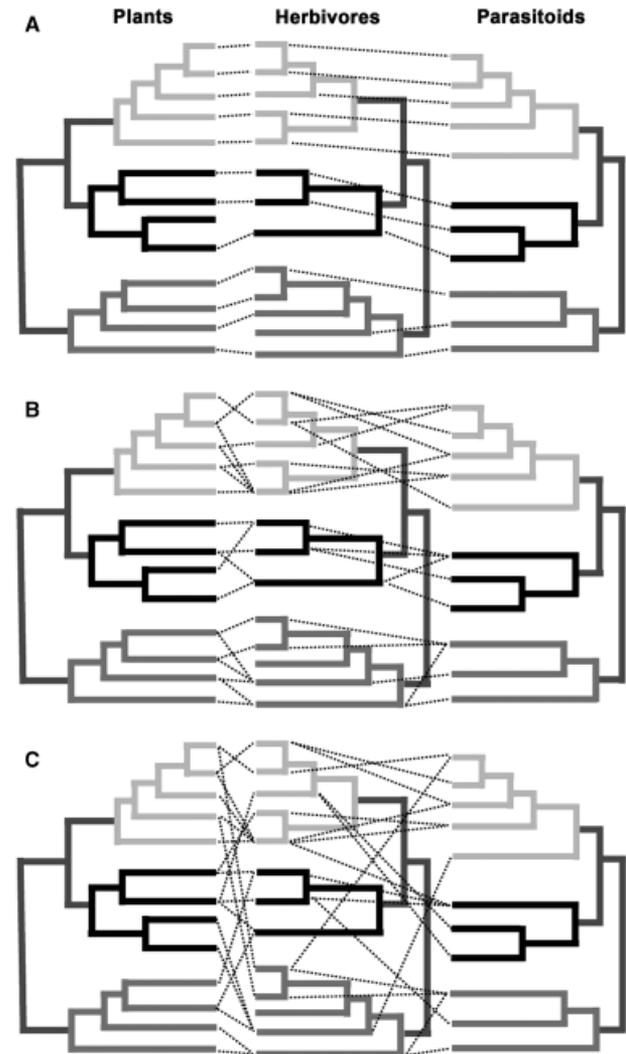


FIGURE 1. Hypothetical phylogenies illustrating: (A) species-level matching of relationships across trophic levels, (B) 'clade-for-clade' correspondence, and (C) independence across trophic levels. The first two represent phylogenetic cascades. For ease of visualization, different levels of shading are used for the major clades within each phylogeny.

particularly obligate parasites that spend their entire lives in or on a host, as with parasites of several birds and mammals where some of the most dramatic examples of shared, bitrophic evolutionary histories have been documented (Page 2003). For parasites with a dispersive life history stage, as with many herbivorous insects, phylogenetic patterns tend to correspond at a coarser scale, in particular at the level of clades: groups of related insects attacking groups of related plants (Mitter *et al.* 1991, Janz & Nylin 1998, Termonia *et al.* 2001, Percy *et al.* 2004, Berenbaum & Feeny 2008, Futuyma & Agrawal 2009). Here, a clade-for-clade, nonindependent relationship across phylogenies is expected, but with little phylogenetic matching within clades, suggesting some degree of ecological freedom as herbivorous clades evolve in association with specific plant clades (Fig. 1B).

The presence of a nonrandom association across phylogenies (Figs. 1A and B) does not necessarily imply temporally correlated diversification. One trophic level might diversify into the niches provided by a lower trophic level either contemporaneously with the lower trophic level, or at a much later date (*e.g.*, Farrell & Mitter 1998, Becerra 2003, Wheat *et al.* 2007). In the former case, coevolutionary dynamics might be involved, while in the latter case the second trophic level is 'tracking' the ecological opportunities presented by the lower trophic level, possibly without any coevolutionary interaction. Both cases are meaningfully considered a phylogenetic cascade in the sense that diversification at one trophic level affects diversification at other levels, thus the issues of contemporaneity and coevolutionary dynamics should be considered a subset of the phylogenetic cascades hypothesis. This framework is consistent with the interpretation put on many bitrophic systems, such as gophers and lice (Page 2003), in which the existence of shared history is of primary interest, and is treated as a separate question from coevolutionary dynamics associated with reciprocal selective pressures.

Nonindependence across two or more trophic levels might imply natural selection and diversification associated with the colonization of new resources (Stireman *et al.* 2006, Abrahamson & Blair 2008, Feder & Forbes 2010). However, this need not be the case, and there is at least one type of shared evolutionary history that is not a phylogenetic cascade. Consider a vicariant event that divides the range of a plant, while simultaneously fragmenting the ranges of associated herbivores and parasitoids. In geographic isolation on either side of a barrier, populations of the plants, herbivores, and parasitoids might all evolve incompatibilities that would prevent subsequent interbreeding with previously conspecific populations (Coyne & Orr 2004). Repeated vicariance or fragmentation directly affecting multiple trophic levels could then leave the signature of nonindependent phylogenetic histories, but should not be considered a cascade, since the diversification of one level is not driving the diversification of other trophic levels. This is not to say that vicariance (or allopatric speciation in general) cannot play a role in phylogenetic cascades, particularly if vicariance stimulates plant diversity, which then has a cascading effect on other trophic levels that subsequently diversify into open niches. Understanding the role of vicariance in phylogenetic cascades will be challenging, though insights might be gained from examining other, ecologically unrelated taxa in relevant geographic regions. If evidence is found for similar phylogenetic breaks in taxa that are not interacting ecologically with focal taxa, the possibility would have to be considered that congruent phylogenetic histories even among ecologically associated species are not the result of a phylogenetic cascade, but rather the result of a shared history of vicariance (associated, for example, with refugial areas; Bonaccorso *et al.* 2006). While this noncascading interpretation should always be considered a possibility for shared evolutionary histories, we assume throughout the rest of this paper that histories of parallel diversification will often involve ecological speciation (*i.e.*, host-associated divergence; Stireman *et al.* 2006, Abrahamson & Blair 2008, Feder & Forbes 2010). It is also entirely likely that different processes will operate at different spatial and temporal scales, such that both vicariance and

ecological speciation will contribute to shared phylogenetic patterns among lineages of interacting organisms.

**ANALYTICAL APPROACHES.**—Determining whether ecological associates display evidence of congruent evolutionary history across three or more trophic levels can be distilled into two questions: (1) are the branching patterns concordant across phylogenies? and (2) are the shared branching patterns across phylogenies contemporary? The first question is central to documenting a phylogenetic cascade, whereas the second question can be considered a special case of the first, as discussed above. A rich variety of methods have been used to compare phyletic similarity between groups, from simple phylogenetic tests to focused analyses devised specifically for assessing patterns of co-speciation between ecological partners. Because most of these methods have been summarized elsewhere (Paterson & Banks 2001, Page 2003, Stevens 2004, Charleston & Perkins 2006), we do not attempt a comprehensive review. Rather, we highlight the most commonly used approaches, moving from analyses with more strict assumptions to those that are more flexible and perhaps most useful in plant–herbivore–parasitoid systems. Topology tests are routinely used to assess competing phylogenetic hypotheses in a number of areas of evolutionary biology. The null hypothesis of a topology test is that the 'true' tree (the best estimate of a phylogeny) and an alternative tree, though not necessarily identical, are statistically indistinguishable (Swofford *et al.* 1996). While topology tests can be quite flexible, these tests tend to be overly conservative: if host switches have occurred between major clades, a topology test is likely to reject the hypothesis of tree compatibility, even when overall congruence might be apparent (*e.g.*, Clark *et al.* 2000). Other phylogenetic techniques, such as the partition-homogeneity test (Farris *et al.* 1994), or the parametric bootstrap (Swofford *et al.* 1996) that have been proposed to assess co-divergence between groups (Huelsenbeck *et al.* 1997, Johnson *et al.* 2001) posit the same null hypothesis but might be overly strict (but see Takiya *et al.* 2006).

Another class of methods for investigating associations between phylogenetic trees are randomization or permutation tests. The most widely used of these is tree-reconciliation analysis (Page 1994a, b) implemented in TreeMap (Page 1995, Charleston & Page 2002) and CoRe-PA (Merkle *et al.* 2010). Here, the phylogeny of one species (*e.g.*, herbivorous insect) is mapped onto the phylogeny of another species (*e.g.*, host plant), and the number of co-divergence events obtained from 'reconciling' the trees is counted and compared with a random distribution of co-divergence events. However, if frequent host-shifts have occurred, as expected in plant–insect systems, then tree-reconciliation analysis might fail to identify significant relationships between phylogenies (Percy *et al.* 2004, Charleston & Perkins 2006). We also note that some investigators might find the newer program (CoRe-Pa) released by Merkle *et al.* (2010) easier to apply because it allows for multiple hosts per parasite as well as multifurcating phylogenies.

Two conceptually similar randomization methods that are somewhat less restrictive in their assumptions (also allowing for multiple hosts per parasite and multifurcating phylogenies) use simple matrix comparisons to detect nonrandom associations

between phylogenies. Both ParaFit by Legendre *et al.* (2002), and the permutation test by Hommola *et al.* (2009) use the phylogenetic distance matrices of two groups (percent differences from raw sequence data, patristic distances from branch lengths, etc.), rather than actual phylogenetic trees, as well as a simple matrix of associations between two ecological partners. These methods measure the observed correlation between the matrices, then compare the observed value with a null distribution of matrix correlations created through permutation (details of the randomization procedures differ slightly, see discussion in Hommola *et al.* 2009). Furthermore, ParaFit includes a procedure (analogous to a jackknife) that tests the importance of specific links between interacting species for the overall pattern of correlation. ParaFit has also been optimized for implementation on parallel processors that facilitates the analysis of large datasets (Stamatakis *et al.* 2007). Both procedures appear to perform well at detecting relationships between phylogenies, even when as much as 50 percent of the cladistic structure between groups is independent (Hommola *et al.* 2009).

All of the approaches that have been used to look at nonrandom associations between phylogenies operate in the framework of pair-wise comparisons (*i.e.*, between pairs of matrices). Given this pairwise framework, a hypothesis of a nonrandom association across multiple trophic levels should be investigated for each relevant pair, asking if there is a nonrandom association between plants and herbivores, between herbivores and parasitoids, and between plants and parasitoids. When the null hypothesis of independent association is rejected for each of those three comparisons, the conclusion can be drawn that diversification might have cascaded across trophic levels (alternative analyses are discussed below). It is necessary to test all three of those pairwise comparisons, since other scenarios (besides a phylogenetic cascade) might produce similar but distinct patterns. For example, evolutionary histories might exhibit nonindependence between plants and herbivores, and between plants and parasitoids, but not between herbivores and parasitoids. Although not a phylogenetic cascade, this interesting possibility is discussed further below in a review of the recent literature.

The pairwise framework for investigating phylogenetic cascades is not completely satisfying, and there is considerable room for analytical innovation. At the very least, it would be useful to have a single test for nonindependence across three or more phylogenies. Legendre and Lapointe (2004) and Campbell *et al.* (2009) have developed a method to test for congruence among several distance matrices (CADM) though this method has not been applied to host-parasite data, and the randomization method of Hommola *et al.* (2009) could be extended to more than two phylogenies (W. Gilks, pers. com.). Beyond a test for nonindependence across more than two phylogenies, path analysis (or structural equation modeling; Grace 2006) might provide a useful framework for investigating cause and correlation among phylogenetic matrices (see Legendre & Legendre 1998 and Goslee *et al.* 2005 for a discussion of distance matrices and path analysis). With paths specified between plants and herbivores, between herbivores and parasitoids, and between plants and parasitoids, one could examine partial correlation coefficients and discover (as a hypothetical example), that most of the structure shared across phylogenies was driven by the

relationship between plants and herbivores, a conclusion that would be difficult in a pair-wise framework. Ives and Godfray (2006) have discussed these issues and developed statistical tools for an objective that is slightly different from but relevant to the cophylogenetic perspective. Focusing on communities rather than specific, interacting lineages, they investigated patterns of host association across trophic levels while accounting for phylogenetic signal, asking, for example, if a particular host is likely to be attacked by a suite of related parasites.

We have not yet addressed the issue of temporal correlation, which is an important sub-question of the larger phylogenetic cascades issue. Particularly if diversification is associated with coevolutionary dynamics, we expect roughly contemporaneous diversification across lineages. This temporal hypothesis can be tested with a highly resolved fossil record. For example, the first appearance of a lineage of plants should be closely followed by its insect herbivores (*e.g.*, McKenna *et al.* 2009). Of course, the fossil record is rarely so generous, thus molecular genetic data have been used to test the hypothesis of contemporaneous diversification. Assuming that the molecular data used to construct our phylogenies are behaving in a roughly clock-like manner (that is, evolving with some rate-constancy) then we can estimate the time at which lineages have diverged (*e.g.*, Hedges & Kumar 2009). This is best accomplished when we can ‘calibrate’ the pace of molecular evolution with one or more fossil or biogeographic data points for both ecological partners. We can then independently estimate the divergence dates of co-diverged taxa to see how closely they match (*e.g.*, Percy *et al.* 2004, Sorenson *et al.* 2004). When one taxon lacks a sufficient fossil record, we might use the calibration points of the other taxon (*e.g.*, Sorenson *et al.* 2004, Reed *et al.* 2007). However, this approach is circular (Light & Hafner 2008), and we could instead force the divergence dates of one phylogeny onto the second to see if this creates an unrealistic rate of molecular evolution in the second (*e.g.*, Feldman & Spicer 2006). If no reliable calibration points exist, then we can adopt a published substitution rate, preferably from closely related taxa, to once again estimate divergence times. In a similar vein, we might also compare the branch lengths of co-diverged taxa, expecting to find a tight correlation between co-diverged pairs (Page 1991, 1996; Light & Hafner 2008). Another simple approach would be to use the ultrametric distances produced by time-calibrated tree analysis (chronophylogram) for the matrix comparisons in ParaFit or the permutation test of Hommola *et al.* (2009). If these analyses demonstrate significant relationships between matrices, then the phylogenies could be said to match in both temporal and topological structure. Further still, comparisons of analyses done with ultrametric vs. patristic distances might highlight temporal disagreement between co-divergences. Finally, coalescent models could be useful in this context (Page 1996), but have yet to be explored in these systems.

All of these points need to be considered with the caveat that molecular dating can be thorny; the assumptions of a molecular clock are often violated, fossil calibration points are often misused, error around divergence estimates can be so large that the dates obtained are of questionable use, and published rates of molecular evolution are frequently unreliable (Graur & Martin 2004, Parham

& Irmis 2008). There is also the issue of how closely co-divergence is expected to match for coevolving lineages. We might expect divergence in the higher trophic levels to lag behind divergence in the lower trophic levels (Light & Hafner 2008), but how much of a lag should we still consider to represent temporal concordance and co-evolution? Understanding the temporal component of phylogenetic cascades (or any co-speciation) is certainly an area of research where additional conceptual and analytical improvements are needed.

**BOTTOM-UP OR TOP-DOWN?**—Cascades have directionality, by definition. A long-standing research program in ecology has been the investigation of trophic cascades, which can proceed both from the bottom-up (when primary productivity drives community dynamics) and from the top-down (driven by predation) (Hunter & Price 1992, Dyer & Letourneau 1999, Pace *et al.* 1999, Polis *et al.* 2000). We expect phylogenetic cascades to be bottom-up, since the lower trophic level is the niche into which the upper trophic levels diversify. Note that this is not the same as saying that selective pressures associated with coevolutionary dynamics cannot point in both directions (from herbivores to plants and from plants to herbivores, for example). Indeed, it is chemically mediated, coevolutionary pressures that Ehrlich and Raven (1964) hypothesized when they described ‘escape and radiate’ patterns in which plants are driven to ‘escape’ from selection pressures imposed by butterflies. However, in a phylogenetic context, the phylogenetic signal left by ‘escape and radiate’ dynamics is most usefully thought of as a bottom-up cascade, because the plants ultimately provided the ecological space associated with herbivore diversification.

Can phylogenetic cascades ever be top-down? For a phylogenetic cascade to be meaningfully called top-down, an upper trophic level would have to create ecological opportunities that affect the diversification of lower trophic levels. This might be possible, if pressure from natural enemies creates enemy-free space that facilitates the diversification of a plant lineage. In the long run, however, it might be difficult to distinguish this phenomenon from a bottom-up cascade if herbivores ultimately diversify onto novel plant species despite enemy pressure. Thus the phenomenon of enemies creating space into which plants diversify might best be thought of generally as a type of indirect evolutionary effect (skipping the intermediate herbivore level) and not a phylogenetic cascade.

## WHAT DO WE KNOW ABOUT PHYLOGENETIC CASCADES?

The relatively small number of studies that have investigated the potential for evolutionary histories to be shared across three or more trophic levels can at present be divided into two groups: (1) studies focusing on a very small number of focal taxa from each interacting group, and not necessarily in a phylogenetic, comparative context; and (2) studies involving multiple taxa involving comparisons of phylogenetic patterns across groups.

The first category of studies, involving nonsymbiotic relationships with an emphasis on focal taxa and population dynamics in mostly temperate groups has been well summarized by both Abrahamson and Blair (2008) and Feder and Forbes (2010). These

authors describe a small number of well-studied systems in which host-associated differentiation at the level of an herbivore has apparently been tracked by the differentiation of natural enemies. For example, the gall fly *Eurosta solidaginis* attacks two closely related goldenrod (*Solidago*) species, *Solidago altissima* and *Solidago gigantea*, and has formed isolated, sympatric races associated with the two hosts as a consequence of host-related selective pressures. A flower beetle that attacks the galls made by *E. solidaginis*, eating gall tissue and preying on the fly larvae, has similarly been found to experience host-specific selection associated with galls on the two *Solidago* species. Sympatric populations of the beetles associated with the different hosts (larval prey and plant species) show modest but significant levels of genetic differentiation. Similarly, host-associated diversification by the apple maggot fly, *Rhagoletis pomonella*, appears to have been tracked by the formation of distinct, host-associated populations of a specialized wasp parasitoid, *Diachasma alloeum* (Forbes *et al.* 2009, Feder & Forbes 2010). Like the flies, the wasps mate on fruits that they locate through the plant volatiles, which lead them to their prey. Thus a similar mechanism for reproductive isolation (plant-specific mating sites) is important for both the flies and the natural enemies, providing a clear possibility for a cascading effect and ultimately shared evolutionary histories.

The second category of studies, involving comparative phylogenetic analyses, is presently represented by a small body of work, involving relatively few species, particularly at the highest trophic level. Phylogenetic patterns among figs, galling moths (*Platyneura* spp.) and parasitoids (*Apocrypta* spp.), were documented by Silvieus *et al.* (2008) using five species of parasitoid wasps. They found a nonsignificant but suggestive association between parasitoids and their hosts. Lopez-Vaamonde *et al.* (2005) studied 15 parasitoid species and did not find evidence for co-speciation across all trophic levels, but did find conserved (nonrandom) associations between wasps (*Achrysocharoides* spp.) and associated plant genera.

An answer to the question, ‘what do we know about phylogenetic cascades?’ can be summed up at this point as follows: (1) mechanisms involved in ecological speciation (such as reproductive isolation as a pleiotropic consequence of mate location behavior) certainly have the potential to cascade across trophic levels, as demonstrated by the case studies above involving the flies *Eurosta* and *Rhagoletis*; and (2) although at least two cases have been investigated in a comparative, phylogenetic context (Lopez-Vaamonde *et al.* 2005, Silvieus *et al.* 2008), convincing cases involving large numbers of species, particularly at the highest trophic level, have yet to be reported.

## PHYLOGENETIC CASCADES IN DIVERSE COMMUNITIES

Tropical communities provide excellent opportunities for investigating phylogenetic cascades, for at least two reasons: high species richness and high levels of specialization relative to higher-latitude communities. Although the latter issue (a latitudinal gradient in specialization or niche breadth) has been the subject of debate and ongoing investigation (MacArthur 1972, Ollerton & Cranmer 2002, Vazquez & Stevens 2004, Novotny *et al.* 2006), there is no

doubt that tropical communities contain very large numbers of specialized taxa; and, at least for Lepidoptera in the New World, there does indeed appear to be a latitudinal gradient in specialization (Dyer *et al.* 2007). Large numbers of species can manifest a richer or more complex phylogenetic signal, which should increase power to reject the null hypothesis of no association or independent histories across phylogenies. Furthermore, narrow host ranges associated with large numbers of specialized interactions make it more likely that parasite speciation events will be associated with host shifts, which makes it particularly likely that patterns of diversification will be shared across trophic levels. Similar to insect herbivores, tropical parasitoids might also be extremely specialized. Average host ranges reported from a recent survey suggest that many tropical parasitoids might have host ranges that consist of one or a very small number of herbivore hosts (Smith *et al.* 2008). Beyond the basic need for more extensive investigation into phylogenetic cascades, which is well suited by rich, tropical communities, below we discuss a few more specific questions that could be addressed.

HOW WILL PATTERNS AT THE HOST-HERBIVORE LEVEL CORRESPOND TO PATTERNS AT THE HERBIVORE-PARASITOID LEVEL?—As discussed above, patterns of nonindependent phylogenetic association across trophic levels can take at least two distinct forms, illustrated in Figs. 1A and B; we can refer to these two patterns as species-matching (Fig. 1A) and clade-matching (Fig. 1B). From a large number of studies examining phylogenetic patterns shared by plants and herbivores, we can say that herbivorous insects often exhibit clade-matching (Farrell & Mitter 1990, 1998; Becerra 2003), though exceptions have been documented, and more comparative phylogenetic studies are needed of parasitoids and their hosts (Stireman 2005). Furthermore, we can ask if patterns will be similar across trophic levels. For example, in groups where herbivores tend to exhibit stricter species-matching, will those herbivores also be associated with parasitoids that exhibit similar species-matching? Or are patterns at different levels in a sense independent?

ARE THE PARASITOID MORE LIKELY TO TRACK THE HERBIVORES OR THE PLANTS THROUGH EVOLUTIONARY TIME?—As has been found for one of the few published studies of phylogenetic cascades (Lopez-Vaamonde *et al.* 2005), a parasitoid phylogeny might show independence with respect to a herbivore phylogeny but a nonindependent relationship with a plant phylogeny. The mechanism explaining this pattern might be that parasitoids can use plant volatile cues to locate prey, and thus might diversify more directly in response to the diversification of plants than of the herbivores (Price *et al.* 1980, Dicke & van Loon 2000).

WILL PHYTOCHEMICAL PATTERNS OR PHYLOGENETIC RELATIONSHIPS AMONG HOSTS BE A BETTER PREDICTOR OF HERBIVORE AND PARASITOID PHYLOGENIES?—Ehrlich and Raven (1964) envisioned phylogenetic patterns of insect herbivores as often being shaped or constrained by chemical similarities and dissimilarities among different lineages of plants. It is often difficult to test the extent to which phytochemistry *per se* drives patterns of herbivore evolution, because phytochemical patterns can be confounded with phylogenetic

relationships. However, phytochemical and phylogenetic similarities need not always be correlated (Becerra 1997, Wahlberg 2001, Winkler & Mitter 2008), and situations when they are not provided opportunities for testing the importance of phytochemical traits. Becerra (1997) investigated associations between plant and herbivore phylogenies and between herbivore phylogenies and a cladogram of hosts based on phytochemical traits, and found the latter (phytochemical relationships) was more predictive of the phylogenetic history of the herbivores. Given a system, such as the one Becerra (1997) studied, in which patterns of phytochemical similarity are not completely correlated with patterns of phylogenetic relatedness (among plants), one could then ask not only if phytochemistry is associated with herbivore diversification, but also if phytochemical associations predict parasitoid diversification. This question is of course complementary to the question posed above (regarding the diversification of parasitoids tracking plants) and the results reported by Lopez-Vaamonde *et al.* (2005).

HOW WILL THE STUDY OF PHYLOGENETIC CASCADES AFFECT OUR UNDERSTANDING OF OTHER COMMUNITY-LEVEL PATTERNS AND PROCESSES?—There has been a long-standing interest in the application of phylogenetic concepts to issues in community ecology (Johnson & Stinchcombe 2007). One of the key questions in this area has been: is there phylogenetic structure in community composition (in other words, are the species in a given community a phylogenetically random sample of the regional species pool) (Webb *et al.* 2002, Hardy & Senterre 2007, Kraft *et al.* 2007)? For example, Lessard *et al.* (2009) compared disturbed and undisturbed communities to ask if invasion alters the extent to which communities include taxa representing a diversity of evolutionary lineages. Communities that contain multiple lineages involved in phylogenetic cascades will clearly have a structure that is biased toward a phylogenetically nonrandom assemblage of species.

A number of researchers have recently taken an explicitly network perspective on communities, which involves a graph-theoretic approach to examine patterns of interaction among large suites of species (Proulx *et al.* 2005, Lewinsohn *et al.* 2006, Bascompte & Jordano 2007, Ings *et al.* 2009). Among the findings of network research is an apparently ubiquitous pattern of nestedness, analogous to the nestedness of island communities (Brown & Lomolino 1998), in which more specialized species tend to interact with increasingly generalized sets of species (just as smaller islands tend to contain more widespread taxa). Within a network context, we might ask: will a community characterized by many lineages involved in phylogenetic cascades, be characterized by a higher or lower level of nestedness? Phylogenetic cascades could reduce the overall level of nestedness in a community, as they essentially involve an amplification of the diversity of fairly specialized interactions. Similarly, we might ask how the stability of community composition through time could either affect or be affected by phylogenetic cascades. On the one hand, a certain level of stability, at least environmental stability, seems essential for the evolution and persistence of species-rich, specialized lineages. On the other hand, specialized lineages associated with phylogenetic cascades could make a community more prone to disruption, because a

disturbance (or extinction) at a lower trophic level will potentially remove a large number of interacting lineages at higher trophic levels. Although this issue of specialization and extinction is not, of course, novel (Vázquez & Simberloff 2002), the idea of phylogenetic cascades does put the topic in a new light by providing a framework for thinking about the evolution of communities characterized by high levels of species richness and specialization.

## CONCLUSIONS

In summary, we have much to learn about the possibility that evolutionary histories can be shared across trophic levels as lineages at higher levels diversify into the open niches provided by lower trophic levels. We have focused here on plants, herbivores, and parasitoids only for convenience, and not to imply that such systems necessarily provide the most fruitful systems in which to study phylogenetic cascades. Opportunities abound for investigations involving other ecological interactions that could involve cascading dynamics in surprising directions. For example, one could investigate fungal endophytes and other intracellular organisms associated with plants and the possibility that phytochemical diversity created by the diversification of endophyte lineages could drive cascading phylogenetic dynamics (Saikkonen *et al.* 1998).

Another avenue of research is to consider the many unrelated but potentially competing lineages of herbivores that are often specialized to use the same lineage of plants, but which might interact with different lineages of natural enemies. At higher trophic levels, hyperparasitoids could be included in analyses, as well as symbiotic organisms (*e.g.*, *Wolbachia* bacteria) within the herbivores, parasitoids, and hyperparasitoids (Heath *et al.* 1999, Shoemaker *et al.* 2002, Takiya *et al.* 2006, Noda *et al.* 2007). Finally, the comparative perspective on phylogenetic cascades could be applied at a population or phylogeographic level, involving comparisons among populations of interacting species (Thompson 2005). While it is easy to imagine possibilities that extend the phylogenetic cascades idea in unusual directions (*e.g.*, cascading coevolution due to so called 'keystone molecules'; Zimmer & Ferrer 2007), clearly the first task should be the accumulation of more case studies involving phylogenetic histories of species-rich groups and well-documented ecological interactions that span multiple trophic levels. Trophic cascades and diversity cascades have played a central role in ecological studies (Pace *et al.* 1999, Dyer & Letourneau 2003). Answers to the questions posed here could suggest an equally important role for phylogenetic cascades in evolutionary biology.

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