Chapter 16

TROPICAL TRITROPHIC INTERACTIONS: NASTY HOSTS AND UBIQUITOUS CASCADES

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OVERVIEW

In the tropics, the high diversity of species at all trophic levels combined with increased chemical defense and predation intensity create ideal opportunities for interesting research in community ecology. Two particularly useful themes in the realm of tropical tritrophic interactions are trophic cascades and coevolution, and prominent hypotheses generated by these ideas should continue to provide guidance to empirical studies in tropical communities. Trophic cascades and coevolutionary interactions are expected to be different in tropical communities simply because of the increased diversity for most taxa at all trophic levels. However, many of the assumptions about how tropical communities are different from their temperate counterparts are not well tested and could be incorrect. Thus, a major goal of understanding tropical tritrophic interactions is to thoroughly document latitudinal patterns in community attributes such as consumer specialization, plant chemical defense, and intensity of predation.

There are no adequate syntheses of trophic cascades and coevolutionary hypotheses for the tropics due to a lack of focused research programs. To explicitly test these hypotheses, tropical ecologists should focus on model systems and must utilize phylogenetic data combined with creative experimental, correlational, observational, and modeling approaches. Myrmecophytes are good candidates as model systems for such a synthetic approach, given the diversity and importance of ant plants in most tropical communities. Tritrophic interactions in tropical communities are usually part of a more complex web with highly variable interaction strengths, yet with the right approaches and study systems, we can determine which interactions are the strongest for particular taxa and ecosystems.

INTRODUCTION

The interactions between myrmecophytes and their associated arthropods are perhaps the most distinctively tropical of all documented tritrophic interactions. These diverse tropical plants, which have evolved in over 100 genera (Heil and McKey 2003), are likely the result of millions of years of strong tritrophic interactions (e.g., Itino et al. 2001, Quek et al. 2004, Tepe 2004, McKey et al. 2005) and are just one of the many genres of intricate tritrophic stories that have yet to be fully investigated. Tropical ant plants have provided a convincing affirmative answer to the question of whether or not natural enemy impact on herbivores exerts strong enough selection pressure to modify plant traits, which is a central question for tritrophic studies. In fact, a thorough research program that utilizes a tropical myrmecophyte as a model system should produce advances for major issues in tritrophic interactions, including trophic cascades (Schmitz et al. 2000), evolution of specialization (Yu and Davidson 1997), multitrophic mutualism (Gastreich and Gentry 2004),...
interactions between living and detrital food webs (Dyer and Letourneau 2003), induced defenses (Fi diarrhea et al. 1989), genetic variation (Dalecky et al. 2002), plant defense theory (Heil et al. 2002), and chemical ecology (Rehr et al. 1973).

In this chapter I present challenges for understanding tritrophic interactions in the tropics. Because the field is quickly growing into an unwieldy topic worthy of its own volume (e.g., Tscharntke and Hawkins 2002, Burslem et al. 2005), I focus on two particularly important issues: trophic cascades and the evolution of feeding specialization. The trophic cascades hypothesis is a focus because the regulation of prey populations by natural enemies and the indirect effects on other trophic levels are focal research topics for community ecologists, population ecologists, conservation biologists, and applied scientists in agriculture and forestry. Specialization as a consequence of coevolution between hosts and parasites (which include herbivorous insects) is a key concept in tropical community ecology, and coevolutionary interactions could potentially generate a large percentage of the great diversity of plants and animals in tropical communities (Ehrlich and Raven 1964, Raven 1977, Farrell et al. 1992, Scott et al. 1992). But 40 years of theoretical development and hundreds of empirical studies still have not produced a comprehensive theoretical framework, and as a result there are no cohesive research approaches, especially for tropical taxa. In particular, coevolutionary theory has rarely considered the roles of other selective forces that could modify or enhance coevolution, such as predators and parasitoids of the herbivores (Singer and Stireman 2005).

Are tritrophic interactions in a tropical forest or agricultural system empirically distinguishable from temperate tritrophic interactions? Trophic cascades and coevolutionary interactions are expected to be different in tropical communities simply because of the increased diversity for most taxa at all trophic levels. Increased diversity at a given trophic level can weaken the effect of consumption on lower trophic levels, due to increases in interference competition (including intra-guild predation), diet shifts, omnivory, and other buffering mechanisms that are enhanced by greater complexity (Polis and Strong 1996). Increased diversity can also weaken the effect of resource availability on upper trophic levels due to increases in exploitation competition, decreased host availability for specialists, and changes in chemical defenses (Hunter and Price 1992, Dyer and Coley 2001). If true, these ecological changes could also make coevolution a less likely outcome, since top-down and bottom-up selective forces could be weakened via the same mechanisms that weaken cascades. There are plenty of additional attributes specific to tropical communities that lead to different predictions about selective pressures between trophic levels and associated indirect effects (e.g., increased primary productivity, see Oksanen et al. 1981). But how many of these additional attributes are rigorously documented and how many are simply part of tropical lore? Before examining coevolution and trophic cascades in the tropics, it is worth reviewing some of the assumptions about how tropical communities are different from their temperate counterparts.

TOUGHER PREDATORS, NASTIER PLANTS, MORE SPECIALIZED CONSUMERS?

At the heart of all multitrophic issues in tropical community ecology are many assumptions that remain largely untested. Aside from obvious correlates of the increases in diversity, such as more reticulate food webs, the most prominent assumptions for tropical communities are: (1) tropical consumers are more specialized (Dobzhansky 1950, Pianka 1966, MacArthur and Wilson 1967); (2) predation is more intense in the tropics (Paine 1966, Janzen 1970); (3) chemical defenses are more abundant and toxic in the tropics (reviewed by Dyer and Coley 2001); and (4) multitrophic mutualisms are more important for tropical communities (Price 1991). It may seem that the only tenable generalization about latitudinal gradients in community ecology is the gradient in species richness, but a close examination of complex trophic interactions should reveal other strong gradients. The first job for tropical ecologists is to determine the taxa, ecosystems, and conditions for which the tropical paradigms...
of specialization, strong predation, toxic food, and indirect mutualisms are true. This is a prerequisite to addressing any questions in tritrophic interactions, including hypotheses on the evolution of specialization and trophic cascades. The best way to accomplish this is to ensure that improved natural history is a priority in all research on tropical tritrophic interactions.

Within the tropics, there are also complex patterns of tritrophic interactions. For example, altitudinal gradients create ecosystems in close proximity and extreme differences in overall diversity, productivity, and ant abundance—all of which decline with altitude (Janzen 1967). However, altitudinal gradients in ecological interactions have not been formally examined in the tropics (Novotny and Basset 2005). Perhaps the most striking pattern of interactions within the tropics is seen along the climate gradient from dry deciduous to wet evergreen forests in the tropics. As total annual rainfall increases and climatic variability decreases, tropical forests have higher plant diversity (Hall and Swaine 1976, Huston 1980, Gentry 1982, 1988), greater primary productivity and stem turnover (Philips et al. 1994), and lower seasonal production of new foliage and reproductive parts (Opler et al. 1980, van Schaik et al. 1993). In addition, plants living in wetter tropical forests appear to be better defended against herbivores, because their leaves are typically tougher, with higher concentrations of secondary compounds and lower nutritional value (Coley and Aide 1991). These changes in plant characteristics along tropical rainfall gradients should have important effects on tritrophic interactions. For example, it is possible that both the top-down impact of natural enemies and the bottom-up effect of plant defenses increase with greater rainfall and climate variability, leading to lower annual herbivore densities in wetter tropical forests (Coley and Barone 1996, Stireman et al. 2005). To document such a relationship between climate and herbivory based on the differences between tropical dry and wet forests, three general hypotheses should be tested: (1) in dry forests herbivore populations are limited by the bottom-up effect of plant availability (since leaves are largely deciduous and absent during the dry season) and direct abiotic effects of the severe dry season (Janzen 1988, 1993); (2) parasitoids, predators, and plant secondary compounds have a relatively low impact on herbivore populations in climatically variable dry forests; and (3) the effect of the dry season is small in wetter, less seasonal, tropical forests but herbivore populations are strongly influenced by the bottom-up effect of greater plant defenses and the top-down impact of higher enemy densities.

Tropical community ecologists have failed to provide sufficient support for the generalizations about differences between tropical and temperate communities and have not tested any hypotheses about tritrophic trends across tropical forests. There are a number of reasons that appropriate investigations have not been completed, perhaps the most significant being lack of resources to support the necessary research. Assuming that funding is available for such work in the future, careful tests of hypotheses that examine the evolution of specialization and trophic cascades will generate data that help establish the strength of these putative patterns and the relative importance of underlying mechanisms.

**EVOLUTION OF DIETARY SPECIALIZATION**

**Tritrophic view of feeding specialization**

Most current studies on tritrophic interactions are directly or indirectly influenced by the coevolution paradigm, in which the evolution of dietary specialization is a result of increasingly specialized adaptations for secondary metabolites in one plant taxon (Dethier 1954, Fraenkel 1959, Ehrlich and Raven 1964). This hypothesis was preceded by an explicitly tritrophic idea that specialized diets represent enemy free space for herbivores, because monophasic insects are better able to utilize chemical, morphological, and phenological attributes of their host plants to defend against predators and parasitoids (Brower 1958). Multiple authors have proposed the hypothesis that plant availability/apparency (sensu Feeny 1976, Rhoades and Cates 1976, including plant chemistry) and pressure from enemies shape herbivore diet breadth together (Hassell and
Southwood 1978, Dyer 1995, Camara 1997a, Singer et al. 2004a). In tropical wet forests, if herbivores really are trapped between more toxic plants and higher rates of predation and parasitism, it is likely that herbivore specialization has evolved in response to one or both of these strong forces and is maintained by one or both. The trick is trying to determine the relative roles of these selective forces. For a given herbivore clade, did specialization evolve as herbivores developed mechanisms to enhance plant availability (e.g., overcoming chemical defenses via specific enzymes) and then enemies maintained that specialization, or vice versa? Or were plant availability and natural enemies irrelevant? These questions can only be addressed by combining strong phylogenetic approaches with experimental approaches (e.g., Farrell and Mitter 1990, Futuyma and McCafferty 1990, also see Blackburn 2004) that examine the effects of herbivore diet on levels of parasitism and predation (reviewed by Hunter 2003). The high concordance between the cladogram of the chrysomelid genus Phyllobrotica and that of its host plants (Farrell and Mitter 1990) implies diversification in parallel as envisioned by the coevolutionary scenario, but is it possible that enemies were an additional selective force maintaining specialization in these beetles?

Studies of feeding specialization are actually focused on the “realized niche” of an animal’s diet – the suite of resources that it is known to consume under natural conditions. Feeding efficiency is an additional component of specialized consumption (at any trophic level) and consumers that can efficiently consume only a narrow range of resources are referred to as “functional” specialists (Ferry-Graham et al. 2002, Irschick et al. 2005). Many ecologists have assumed that such functional specialization should be positively correlated with narrow diet breadths observed in nature. This assumption, however, is not appropriate (Fox and Morrow 1981, Camara 1997b) because enhanced feeding performance can evolve independently of dietary specialization. Furthermore, Fox and Morrow (1981) found that specialist insects effectively metabolize plant chemicals from plants that they rarely use in nature. The dichotomy between ecological specialization and functional specialization is more obvious when herbivores specialize on plants with defenses that decrease feeding efficiency (bad for the herbivore) while simultaneously deterring enemies (good for the herbivore). Despite the fact that the herbivore is a specialist, it does not perform better (physiologically) on its diet of choice, but it may enjoy lower mortality. In such a case, classic laboratory and field rearing experiments designed to detect trade-offs between feeding performance and diet (e.g., Camara 1997b) do not successfully detect negative genetic correlations because the herbivores are not functional specialists – in other words there are no genotypes that perform better on one diet versus another, but they are still limited to one diet due to pressure from enemies.

**Tests of the tritrophic view in temperate and tropical systems**

Explicit tests of the coevolutionary (bottom-up) scenario for dietary specialization in herbivores have been conducted primarily with temperate taxa (e.g., at this writing, only 23 of 750 studies that cite Ehrlich and Raven’s 1964 paper are focused on tropical taxa). A prominent exception is the well-documented synchronous evolution of Blepharida beetles and their host plants, Bursera spp. (e.g., Becerra and Venable 1999). The leaf beetles in this relationship have developed a wide array of behavioral and physiological mechanisms for circumventing each new defense of the host leaves, including squirting resins and complex mixtures of terpenes. There is no reason to assume that this and other well-documented examples of strong coevolution between host plant and herbivores are the rule in tropical communities, especially in light of the fact that several studies have also found low congruence between plant and herbivore phylogenies (e.g., Anderson 1993, Funk et al. 1995, Weintraub et al. 1995, Brandle et al. 2005). A rigorous coevolutionary theory for tropical systems awaits more tests of parallel phylogenies following the examples of existing work (Farrell and Mitter 1990, Mitter et al. 1991, Farrell et al. 1992, Futuyma et al. 1995, Becerra and Venable 1999) that encompass only a few clades.

The specific top-down view outlined above and also described by Singer and Stireman (2005) has
been tested in the tropics with predators (Dyer and Floyd 1993, Dyer 1995, 1997) and parasitoids (Gentry and Dyer 2002). The results for predators mirrored temperate studies (Bernays and Graham 1988, Bernays and Cornelius 1989), with specialists being better protected against predators than generalists. However, patterns of parasitism are very different. Gentry and Dyer (2002) found that tropical specialists were not better protected than generalists, and in fact some parasitoid taxa (e.g., Braconidae) prefer specialists and chemically defended caterpillars (Dyer 2001), perhaps because these hosts represent enemy free space, since chemically defended specialists are avoided by many distinct guilds of predators (Dyer 1997). This is in striking contrast to studies in temperate systems that demonstrate anti-parasitoid defensive value of sequestered secondary compounds (Barbosa et al. 1986, 1991, Turlings and Benrey 1998, Sime 2002) and it provides evidence against the “nasty host hypothesis” (Gauld et al. 1992), which argues that parasitic hymenopterans are less diverse in the tropics because their hosts have high levels of chemical defense. For all of these studies, a major problem with comparing defenses of specialist versus generalist herbivores against their enemies is that the original selective advantages of specializing could be lost, especially for anti-parasitoid mechanisms, since parasitoids could evolve mechanisms that allow them to overcome chemical defenses sequestered by herbivores (Dufley et al. 1986, Barbosa 1988, Hunter 2003). Whenever possible, a phylogenetic approach should be utilized to examine the evolution of diet breadth in association with adaptations that allow use of phytochemicals as anti-predator and anti-parasitoid defenses (Termonia et al. 2001, Kuhn et al. 2004).

Temporal scales: from over 100 million years ago to current communities

The tropical patterns of parasitism on lepidopterans of varying diet breadths are potentially compatible with the view that enemies contributed to patterns of specialization, since pressure from parasitoids is relatively new compared with the long histories of specialized plant–herbivore relationships. For example, the Tachinidae is an estimated 20–40 million years old (Evenhuis 1994), and this family is usually the dominant source of lepidopteran mortality (Dyer and Gentry 2002, Gentry and Dyer 2002, Janzen and Hallwachs 2002, Stireman et al. 2005). In contrast, some genera of plants and herbivores have associations that go back almost 100 million years (Labandeira et al. 1994, Becerra 2003). Does this mean that selective pressures from tachinids that have arisen over the last 20 million years are driving diet breadths of herbivorous insects towards polyphagy because tachinids attack specialized herbivores? The question of evolution of generalized diet has been examined only sparingly in a phylogenetic context (for aphids, Moran 1988; for parasitoids, Stireman 2002). Singer and colleagues (2004a,b) have taken an interesting approach to understanding diet breadth of generalist arctiids. For two generalist arctiids (Estigmene acrea and Grammia geneura), a mixed diet provides benefits of increased growth due to including a high quality plant in the diet and increased defense due to including a toxic plant in the diet. For both of these arctiids, the value of enemy free space supersedes the value of enhanced larval performance due to better food quality.

Regardless of how the specialization evolved at any trophic level and whether or not it is adaptive, narrow consumer diet breadth should modify its ecological role in a community (e.g., herbivores of different diet breadth respond differently to resources, Long et al. 2003). Specialist herbivores are far more likely to present a consistent regulatory force on plants than are individual species of generalists (Strong et al. 1984, Carson and Root 2000, Dyer et al. 2004), and specialist parasitoids are traditionally thought to be more effective regulators of herbivores than generalist predators (Myers et al. 1989, Hawkins et al. 1997, Denoth et al. 2002). Putting diet breadth into a coherent ecological context should be an important goal of tropical community ecologists, given that many hypotheses about the origin and maintenance of tropical diversity make assumptions about the prevalence and consequences of consumer specialization (reviewed by Wright 2002).
TROPHIC CASCADES

Definitions

The term “trophic cascades” has been defined in many ways, which has created problems (Hunter 2001), but the most restrictive definition is: a measurable increase in primary productivity due to negative effects of predators on herbivore biomass (Paine 1980, Power 1990, Carpenter and Kitchell 1993). Defined as such, the trophic cascade hypothesis is also known as the “green world hypothesis” (Polis 1999) and was first proposed by Hairston et al. (1960: HSS, for Hairston, Smith, and Slobodkin). Here I use the HSS definition of a trophic cascade, but there are many other types of trophic cascades hypotheses that are potentially important forces in terrestrial systems and they fall under a more general definition provided in theoretical and empirical studies (Hunter and Price 1992, Carpenter and Kitchell 1993, Polis 1999, Halaj and Wise 2001, Dyer and Letourneau 2003, Letourneau et al. 2004, Schmitz 2004, Schmitz et al. 2004) — indirect effects of one trophic level on a non-adjacent level. This includes indirect effects among individual species or entire trophic levels, with the effects acting on densities, traits, or community parameters, such as species richness (Figure 16.1). Two additional cascades hypotheses that I consider here are the “trait-mediated cascade” and the “diversity cascade,” both of which could be important in tropical communities. A trait-mediated trophic cascade is a change in plant biomass caused by modifications in herbivore foraging behavior in the presence of predators (Schmitz et al. 2004). A diversity cascade is an indirect effect of diversity at one trophic level on a non-adjacent trophic level (Dyer and Letourneau 2003). No trophic cascade hypothesis has been fully tested in a tropical system (Dyer and Coley 2001).

Trophic cascades hypotheses have been extended to the ecosystem exploitation hypothesis (EEH), which incorporates variation in primary productivity and generalizes predictions for even and odd numbers of trophic levels that might result along a productivity gradient (Fretwell 1977, 1987, Oksanen et al. 1981, Oksanen 1991, Hairston and Hairston 1997). The HSS and EEH models of multitrophic interactions have endured numerous attacks. Some ecologists have dismissed trophic cascades as one of many indirect effects that are unlikely to be of great importance in terrestrial systems (Polis and Strong 1996, Menge 2000, Halaj and Wise 2001). The criticism most relevant to tropical systems is that diverse terrestrial systems are unlikely to contain linear trophic levels, thus direct effects of one trophic level on another are never likely to be strong enough to cascade in any direction (Polis and Strong 1996). Omnivory, intra-guild predation, interference competition, spatial heterogeneity, prey refugia, and other factors that putatively buffer

Figure 16.1 A simplified path diagram of selected direct and indirect effects that are examined in tropical food webs. Solid lines are direct effects, dashed lines are indirect effects, arrowheads are positive effects, and circle heads are negative effects. The letters next to the lines could be path coefficients or any other statistic of effect size, allowing comparisons between magnitudes of direct and indirect effects. The top-down cascade model predicts that B will be an important pathway. Plant defense (Moen et al. 1993) and resource availability (reviewed by Stamp 2003) hypotheses predict that A will be an important pathway. Resource limitation or bottom-up cascade models (Lindeman 1942, Slobodkin 1960, Hunter and Price 1992) predict that C will be an important pathway. This chapter focuses on pathways A and B.
ecological systems from strong top-down effects of predators (Strong 1992, Polis and Strong 1996, Polis et al. 2000) are found in most tropical communities. Both Strong (1992) and Polis (1999) have argued that trophic cascades should only be expected in systems characterized by low within-trophic level diversity, simple food webs, discrete habitats, and little spatial heterogeneity. These authors assert that complex communities contain “species cascades,” where the indirect positive effect of predators is demonstrated only for one species of plant, not for an entire community. In this view, predation can be important in diverse communities for particular imbedded food chains, but trophic cascades are not predicted to be important for an entire complex community.

**Trait-mediated cascades**

It is likely that the mechanism of trophic cascades is often trait mediated rather than density mediated (Schmitz et al. 2004), thus a distinction has been made between trait-mediated and density-mediated indirect interactions (TMII and DMII, respectively; Werner and Peacor 2003). In DMII, the cascade is mediated by a change in abundance of the intervening species or trophic level, while in TMII, the indirect effect is mediated by a change in behavior or defensive attributes of the intervening species (Gastreich 1999, Schmitz et al. 2004). DMII and TMII are not mutually exclusive; in fact it is likely that in trophic cascades, trait-mediated interactions are the most important mechanistic explanation for strong indirect effects on density (Schmitz et al. 2004). The best tropical example of a trait-mediated trophic cascade is reported by Gastreich (1999), who studied spiders, ants, and caterpillars associated with the ant plant *Piper obliquum*. Theridiid spiders altered the foraging of mutualist *Pheidole bicornis* ants, causing increased levels of caterpillar herbivory, while ant densities were unchanged (Gastreich 1999). Gastreich and Gentry (2004) argue that spiders are generally useful predators for examining DMII versus TMII, because they are ubiquitous enemies and have been shown to alter the density and behavior of their prey in many contexts (e.g., MacKay 1982, Gastreich 1999, Dukas and Morse 2003, reviewed by Wise 1994).

**Diversity cascades**

Diversity cascades are a complex set of interactions that are particularly relevant to tropical systems. The response variables in diversity cascades can be diversity indices, species richness, abundance, or some other metric related to diversity. The most straightforward diversity cascade involves the indirect effect of plant diversity on overall consumer diversity via increased herbivore richness and abundance (Figure 16.2, path A). This bottom-up cascade hypothesis is a subset of the major hypotheses explaining the latitudinal gradient in species diversity, and it is well tested, with results indicating that plant diversity usually explains a measurable portion of consumer diversity for many different ecosystems.
study taxa, and scales of study (reviewed by Rohde 1992, Waide et al. 1999, Mittelbach et al. 2001). Top-down diversity cascades are less intuitive and depend on the particular assemblage of species. For example, an increase in predator diversity can cause an overall increase in herbivore abundance due to greater intra-guild predation and omnivory among predators (Hochberg 1996, Denoth et al. 2002); in turn, this can cause decreases in plant abundance (Figure 16.2, path B). In this scenario, as more species of predators are added, overall predation rates on herbivores decline because predators are consuming each other, herbivory increases, and primary productivity declines. However, increased enemy diversity may be just as likely to cause decreases in herbivory if the enemies are more specialized – such as parasitic Hymenoptera. In this case, complementarity between predators or “sampling error” (i.e., the “right predator” is more likely to be sampled from a more diverse community of enemies) causes an increase in overall enemy-induced mortality of herbivores (Stireman et al. 2004). Two examples of more complex top-down diversity cascades are presented in Dyer and Stireman (2003) and Dyer and Letourneau (2003). In the latter example, addition of a predatory beetle that specialized on one ant species caused increases in diversity of predacious ants living in a tropical understory shrub. This increase in ant diversity caused lower diversity of herbivores but overall higher levels of herbivory and lower plant biomass (Dyer and Letourneau 2003).

Diversity cascades have been examined indirectly by ecologists testing the assertion that more diverse systems are less likely to exhibit classic top-down cascades. For example, Finke and Denno (2004) demonstrate in a temperate (Spartina dominated) marsh that increasing diversity of predators (spiders and mirid bugs) leads to an increase in herbivore (planthoppers) density and a decrease in plant biomass (Figure 16.2, path B), mostly via intra-guild predation – in the “higher predator diversity” treatments, the spiders consumed the mirid bugs. Their experiments were conducted to demonstrate that trophic cascades are weaker in more diverse communities, but the experiments were not a valid test of cascades along a diversity gradient, since only enemy diversity was manipulated; herbivore and plant diversity were low for all treatments. Natural ecosystems do not follow such a gradient, and increases in overall arthropod diversity, including herbivores, result in very different community dynamics than only small increases in predator richness (Dyer and Stireman 2003). Nevertheless, their results provide empirical evidence for one type of diversity cascade leading to a decline in plant biomass (Figure 16.2, path B). It is interesting to note that they were manipulating generalist predators – had the enemies in their studies been specialists, they may have found a diversity cascade that leads to an increase in plant biomass (Figure 16.2, path C).

### Problems and adjustments to trophic cascades theory

Trophic cascades theory is still spinning its wheels. There have been three major reviews (Polis 1994, Pace et al. 1999, Persson 1999) and four meta-analyses (Schmitz et al. 2000, Dyer and Coley 2001, Halaj and Wise 2001, Shurin et al. 2002), while the number of direct empirical tests of cascades in terrestrial systems is still relatively low (fewer than 50 by December 2005), with very few studies in tropical systems. The criticisms and interpretive modifications of putative trophic cascades (or species cascades) in terrestrial systems warrant closer inspection of the methods utilized to study tritrophic interactions in diverse communities. One reason why progress has been stymied is because trophic cascades have never been tested properly in terrestrial systems. Below I outline the major faults in empirical tests of trophic cascades in terrestrial systems.

#### Entire trophic levels have not been deleted in diverse systems

In a complete, diverse community, it is not possible to experimentally remove all predators and parasitoids, nor is it possible to find a diverse terrestrial community from which all enemies have been removed. Thus, there are no direct experimental or correlational tests of trophic cascades in terrestrial communities, which is why
the existing evidence is weak and easy to criticize. The exceptions, where a large percentage of individuals in an upper trophic level is removed (e.g., Carson and Root 2000), usually result in large indirect effects. One such exception is the case noted by Terborgh et al. (2001), where islands formed by hydroelectric impoundments in Venezuela were devoid of vertebrate predators. These islands experienced dramatic levels of herbivory, 10 to 100 times greater than comparable areas on the mainland, with corresponding reductions in plant seedlings and saplings. However, even in this example of “ecological meltdown” important enemies of invertebrates were not excluded; perhaps such an additional exclusion would lead to “ecological catastrophe,” or the first convincing demonstration that trophic cascades are very strong stabilizing forces in tropical forests.

**Insufficient natural history**

All syntheses of trophic cascades and trophic interactions point to the lack of detailed knowledge of food webs as major limitations in testing hypotheses. Thus, some authors have made a strong argument that future studies need to document more details about species associations, strengths of connections between species, and other basic natural history of food webs (Cohen et al. 1993; Wootton 1997, Schmitz et al. 2000). The situation is exacerbated in tropical systems, since natural history is typically scant. A perfect example of this lack of information is the fact that actual trophic levels of predators or parasitoids are unknown. In fact, some authors acknowledge that they have lumped fourth trophic levels with third trophic levels for analyses (Halaj and Wise 2001), which results in a smaller effect size for cascades.

**Temporal and spatial scales are very small**

In the meta-analysis by Schmitz et al. (2000), almost all of the 60 studies examined were done for only one season using individual plants or very small plots (0.1–0.5 m²). Unsurprisingly, there were no effects of study duration on the magnitude of the trophic cascade. Valid tests of indirect predator regulation of plant populations would require decades or even centuries of study (Holt 2000, Hunter 2001), but even tests that simply demonstrate density effects consistent with regulation or control may require a large number of years (Letourneau and Dyer 1998, Carson and Root 2000). The existing experimental spatial scales are also biased towards showing no traditional trophic cascade, since none of the very small-scale manipulations that are usually conducted could conceivably cause a change in ecosystem productivity. Furthermore, this bias towards only studying smaller spatial scales is unlikely to lead to a unified understanding of tritrophic community patterns (Levin 1992).

**Meta-analyses are incomplete**

A simple tabulation of all the literature utilized in recent meta-analyses that test similar hypotheses allows one to calculate percent overlap of studies used in pairs of meta-analyses. The mean literature overlap between current paired meta-analysis publications (Schmitz et al. 2000, Dyer and Coley 2001, Halaj and Wise 2001, Shurin et al. 2002) is 5.7 ± 1.8%, which means that each analysis left out most of the studies that other authors deemed important. In addition, most meta-analyses do not restrict the number of studies used from single papers to avoid effect size biases, which results in amplified effect sizes for studies that report more results. This practice meets the criteria outlined by Hurlbert (1984) for pseudoreplication, since multiple results from a single study are used as independent observations in calculating the effect size statistic, increasing the relative contribution and associated biases of the selected studies. Before meta-analysts produce the complete, properly replicated quantitative summary, many more thorough empirical studies are necessary at appropriate spatial and temporal scales, especially in tropical systems where they are lacking (Dyer and Coley 2001).

**The current paradigm is premature**

Many authors have concluded that trophic cascades are not important in more diverse terrestrial systems (reviewed by Schmitz et al. 2000, Dyer
and Coley 2001, Shurin et al. 2002, Letourneau et al. 2004, Stireman et al. 2004), and Halaj and Wise (2001) concluded this particular indirect effect is simply a trickle in most terrestrial systems. It is now assumed by many ecologists that only the simpler communities are likely to demonstrate cascades— aquatic versus terrestrial systems, grasslands versus forests, agricultural versus natural systems, and temperate versus tropical systems. While there is some limited support for this paradigm, trophic cascades, diversity cascades, trait-mediated indirect effects, and species cascades cannot be rejected as major forces in determining diversity, primary productivity, and number of trophic levels in tropical communities. In fact, the trophic cascade is one of the most useful theoretical frameworks for testing hypotheses about regulation of herbivore populations. Through tests of these and related hypotheses, ecologists will uncover the degree to which trophic cascades are weaker in more diverse terrestrial ecosystems and are likely to discover important community processes.

**FUTURE DIRECTIONS**

Research on tritrophic interactions in the tropics is still in its infancy. One problem that could prevent significant progress is a trend towards jumping from one hot topic to another. In fact, it has become popular to declare hypotheses “dead” without an appropriate arsenal of tests (e.g., coevolution: Rausher 1988; carbon–nutrient balance hypothesis: Hamilton et al. 2001; terrestrial trophic cascades: Polis and Strong 1996). This gives a false sense of progress. For tritrophic interactions in the tropics, the focus should be on utilizing a combination of the best available methods to create a broader synthesis and an improved understanding of important mechanisms behind trophic cascades and coevolutionary interactions. For example, Irschick et al. (2005) review studies of the evolution of specialization and provide a solid framework for future investigation, using a combination of modern approaches. On the other hand, ecologists should avoid the temptation to conduct short-term experiments at spatial scales that fail to rigorously test the relevant hypotheses, are often contradictory, and yield few theoretical advances.

Here I propose hypotheses relevant to coevolution and trophic cascades. I also provide recommendations for approaches to testing these and related hypotheses. Since interaction strengths and corresponding statistics can vary a good deal (reviewed by Wootton and Emmerson 2005), it is relevant to differentiate between strong and weak effects within a community. For example, Halaj and Wise (2001) argue that trophic cascades are actually “trickles,” which are weak effects as quantified by meta-analyses. Wootton and Emmerson (2005) provide important guidance on how to detect “strong” interactions in a community utilizing experimental, correlational, and modeling approaches. Here, I use “strong effects” to indicate where persistent additions (Yodzis 1988) or deletions (Paine 1980) of a population cause statistically significant and biologically important changes in major community parameters: productivity, diversity, number of functional trophic levels, and presence or absence of keystone species. In quantitative summaries of empirical data, strong effects would include all those that are mathematically equivalent to “large” meta-analysis effect sizes (sensu Gurevitch and Hedges 2001).

**Future research: Hypotheses**

1. **Top-down and bottom-up forces have had strong effects on the evolution of diet breadth.**
2. **Strong consumer–resource relationships can lead to tight coevolution.**
3. **Diversity cascades are a strong component of tropical systems.**
4. **As consumer specialization increases, the strength of cascades and other indirect effects increase.**
5. **Top-down forces are more effective at controlling specialist herbivores while bottom-up forces are more important for generalists.**

There are many appropriate alternatives to these general hypotheses. For example, in many systems narrow diet breadth may be a result of genetic drift or other non-adaptive forces, but a research program designed to test Hypothesis 1
above (e.g., as outlined by Irschick et al. 2005) should obviously consider this alternative. Each investigative approach outlined below allows for thorough tests of these and other alternative hypotheses.

**Natural history**

While ecologists have made great advances in recent decades by focusing on experimental approaches and utilizing cutting edge molecular techniques, it is still natural history and correlational data that form the basis of our most important theories and new hypotheses. Perhaps the greatest contemporary tropical tritrophic dataset is the Janzen–Hallwachs plant–caterpillar–parasitoid dataset, which provides basic natural history data for lepidopteran host plant affiliations and the parasitoid fauna that they support (Janzen and Hallwachs 2002). These data provide the raw materials for a thorough approach to interesting questions in community ecology and evolution and have already been used to guide experimental (Sittenfeld et al. 2002) and molecular (Hebert et al. 2004) approaches to testing complex hypotheses. Similar databases are being developed throughout the tropics (e.g., Dyer and Gentry 2002, Novotny et al. 2002). These databases have been used to test and generate numerous hypotheses, including subsets of the general hypotheses outlined above (see Lill et al. 2002, Barbosa and Caldas 2004, Janzen et al. 2005, Novotny and Basset 2005, Singer and Stireman 2005, Stireman et al. 2005).

**Phylogenetic approaches**

Advances in molecular systematics and comparative methods have provided a relatively new set of tools for ecologists to examine classic ecological questions. Farrell et al. (1992) present a useful outline for using phylogenies to test for tight coevolution between plants and herbivores. There are other research foci within tropical tritrophic interactions that would benefit from a phylogenetic approach. For example, Heil et al. (2004) used a phylogenetic approach to demonstrate that herbivore-induced extraloral nectar in *Acacia* myrmecophytes is a plesiomorphic state while constitutive flow of nectar is derived. Thus, plant rewards became more readily available for specialized ants that kill herbivores, indicating that a tritrophic interaction has driven recent coevolutionary relationships between plants and insects: this result is directly relevant to Hypotheses 2 and 3 above.

The phylogenetic approach is clearly necessary for testing hypotheses about specialization at any trophic level (e.g., Hypothesis 1 above) by utilizing phylogenetically controlled comparisons between specialist and generalist consumers and examining phylogenetic trends within taxa towards narrower or broader diet breadths (outlined by Irschick et al. 2005). This approach should be combined with a concerted effort to document ecological and functional specializations. First, tropical ecologists must establish the actual diet breadth of different species within a clade, despite the large amount of descriptive work involved. Second, a better integration of field and laboratory observations within the same taxon will allow for rigorous tests of how resource use is related to performance, thus differentiating between ecological and functional specialization (Irschick et al. 2005). For example, experiments could reveal the relative performance of specialized consumers when placed on more generalized diets or when exposed to alternative food items.

**Large-scale, long-term experiments**

The temporal and spatial scales of many experiments in the tropics are generally very small (Schmitz et al. 2000, Halaj and Wise 2001). Larger and longer experiments may cast light on the generality of the copious studies done in small plots for 1 year or less. Eventually, meta-analyses will provide direct quantitative comparison. Since some large-scale experiments are not possible, mensurative experiments, such as the formation of islands or fragments free of vertebrate predators (Crooks and Soule 1999, Terborgh et al. 2001), provide a viable alternative. Experiments should also be integrated in cohesive research programs that utilize or acknowledge models, correlational data, observational data, and phylogeny.
Modeling approach

Many theoretical components of trophic cascades in diverse communities have not been examined. Lotka–Volterra models have been used to demonstrate that adding a third trophic level to a community with four species (i.e., going from three plants and one herbivore to two plants, one herbivore and one predator) decreases herbivore population growth (Pimm and Lawton 1977). Does increasing the number of players at each trophic level (i.e., constructing a complex terrestrial community) alter this important predator control? If so, by what mechanism does it alter the response of herbivore populations to predators, and is there a threshold of this effect of diversity on predator–prey dynamics? Although these are not explicit tests of diversity cascades, such theoretical investigations could generate hypotheses and guide experimental, correlational, and observational studies. For example, several models suggest that the overall impact of parasitism on herbivore population size in biocontrol should decline with the number of parasitoid species (Kakehashi et al. 1984, Hassell and May 1986, Godfray and Waage 1991, Briggs 1993), whereas Hochberg (1996) showed that if individual parasitoids attack different hosts (as is typically the case with predation versus parasitism), multiple parasitoids should increase overall natural enemy impact. Hence, the specific assumptions employed in complex food-web models can radically alter predictions and warrant more careful consideration than in models of simpler systems.

Mesocosm/component-community approach

A mesocosm is a contained, usually experimental, assemblage of species with known physical and biotic dimensions that is a subset of a larger ecosystem (Odum 1984). Relative to microcosm studies, mesocosm studies typically utilize semi-controlled aquatic environments, and more natural assemblages that are designed to mimic natural communities (Boyle and Fairchild 1997). A similar concept is the component community (Root 1973), which is an assemblage of species associated with a particular resource: this is an example of a natural terrestrial mesocosm. If the component community is contained and easy to manipulate, it is a useful terrestrial mesocosm for testing hypotheses in community ecology. In natural terrestrial mesocosms, such as the endophytic insect fauna associated with a particular plant species, multitrrophic manipulations are relatively easy. An entire trophic level can be deleted to test for trophic cascades – this is analogous to how mesocosms have been utilized in numerous studies of aquatic trophic cascades (Carpenter and Kitchell 1993). Some component communities have more than 50 species and thousands of individuals of interacting animals distributed among fewer than 100 discrete replicates (Dyer and Letourneau 2003). Fragments and islands are also mesocosms where it is possible to delete trophic levels or find systems with very few predators (Schoener and Spiller 1995, 1996, Terborgh et al. 2001). Small agricultural fields may also be treated as mesocosms if they provide enough complexity, such as an alfalfa field (Dyer and Stireman 2003). Are the cascades in these communities strong or are they trickles because of the buffering of other interactions? The limited number of studies to date suggest they are pervasive forces (Terborgh et al. 2001, Dyer and Letourneau 2003).

Species cascade approach

One could easily take experimental data that focus on a trophic chain and extrapolate out to the full web. The trophic cascades uncovered by Schoener and Spiller (Spiller and Schoener 1994, Schoener and Spiller 1999) focus on lizards and spiders as predators and on the relatively narrow trophic structure associated with them. If the same studies were conducted on the same islands with other taxa of predators and the results were consistent, it would provide strong evidence for effects of the entire predator trophic level on primary productivity of the island. This simple approach could be incorporated into any existing research program. A fixed number of tree species from a tropical forest could be selected randomly from the list of all available trees. For each tree species, all predators could be excluded using established methods (e.g., Floyd 1996) and
the leaf biomass monitored for an appropriate period of time (Holt 2000). If a species cascade is demonstrated for the majority of species, it suggests that top-down forces of natural enemies are likely to result in community-wide effects. In addition, this approach provides a theoretical link to the issues about specialization discussed earlier in this chapter. Tropical communities could be modeled as parallel chains of species cascades with coevolved specialized consumers and their host plants. These chains could be connected by generalist consumers and detrital webs. Such a modeling approach would provide a framework for connecting these two bodies of tritrophic research.

CONCLUSION

Specialization and trophic cascades hypotheses should continue to provide guidance to empirical studies in tropical communities. To test these hypotheses, tropical ecologists must utilize solid phylogenetic data combined with creative experimental, correlational, observational, and modeling approaches. A concerted effort by tropical research programs that utilize these approaches to study focal communities or other model systems (e.g., Schoener and Spiller 1999, Schoener et al. 2001, Janzen and Hallwachs 2002, Dyer and Palmer 2004) will allow for fruitful synthesis and development of a useful theoretical framework for tropical specialization and trophic cascades. Such a synthetic approach would be an improvement over the existing cacophony of experiments, observations, and phylogenetic work across the geographic and taxonomic landscape of the tropics. Tritrophic interactions in tropical communities are usually part of a convoluted web with highly variable interaction strengths, yet with the right approaches and study systems we can determine which interactions are the strongest for particular taxa and ecosystems.

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