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Tritrophic interactions in tropical versus temperate communities

Introduction

The latitudinal gradient in diversity is one of the oldest (e.g., Wallace, 1878) and most obvious trends in ecology, and a wealth of literature is devoted to understanding both the causes and consequences of this gradient (Dobzhansky, 1950; also reviewed by Rohde, 1992). Given the enormous latitudinal differences in both diversity and productivity between temperate and tropical habitats, it is likely that relationships among trophic levels may also be fundamentally different. Although trophic interactions can be complex, a current research goal in community ecology is to determine which populations at different trophic levels are limited due to resource availability and which are limited due to consumption by higher trophic levels. In this chapter, we review the literature to determine if latitudinal trends exist for trophic controls. Identifying these patterns should help clarify whether ecological paradigms developed in temperate systems are useful for understanding tropical systems. Tropical ecologists, conservation biologists, and agricultural scientists have suggested that many ecological paradigms do not apply to tropical systems and should not be used to make management decisions or theoretical assumptions. Another advantage of identifying latitudinal gradients in tritrophic level interactions is that many of the hypotheses attempting to explain the latitudinal gradient in diversity are based on untested assumptions about the differences between tropical and temperate communities. For example, it is assumed that higher levels of specialization (for all consumers) in the tropics have allowed for greater numbers of species (Dobzhansky, 1950; Pianka, 1966; MacArthur and Wilson, 1967), but it is not at all clear that a latitudinal gradient in specialization exists (Price, 1991a; Marquis and Braker, 1994; Fiedler, 1998). Similarly, levels of predation are assumed to be higher in the tropics (Paine, 1966; Janzen, 1970), and these high levels are hypothesized as a factor that maintains higher levels of diversity (Pianka, 1966). Tests of these assumptions are an important part of understanding the latitudinal gradient in diversity.

In order to describe latitudinal gradients in terrestrial tritrophic interactions we focus on direct and indirect effects of predators and parasitoids on lower trophic levels, and effects of plant resources on upper trophic levels. Hairston *et al.*'s (1960) initial top-down hypothesis for herbivore regulation resulted in many theoretical and empirical studies on the effects of top-down and bottom-up forces on community structure (most recently reviewed by Pace *et al.*, 1999; Persson, 1999; Polis, 1999). However, there is still disagreement regarding which factors limit populations of different trophic levels. Currently, there are three prominent models that incorporate direct and indirect effects in tritrophic interactions (Fig. 4.1):

1. Top-down trophic cascades. In these models, predators and plants are resource-limited while herbivores are limited by their consumers. Thus, predators regulate their prey and indirectly benefit plants.
2. Bottom-up trophic cascades. These models suggest that both herbivores and enemies are regulated by plant biomass. Bottom-up hypotheses incorporate basic thermodynamics: energy is lost as it is transferred up the trophic chain, so the biomass of herbivores, then primary and secondary carnivores attenuates and is dependent on total primary productivity (Lindeman, 1942; Slobodkin, 1960).
3. The green desert. This also addresses bottom-up hypotheses but focuses on resource limitation as the factor determining community structure (Menge, 1992; Moen *et al.*, 1993). In this hypothesis it is assumed that herbivores cannot utilize most plant parts, either because they cannot digest the most common plant macromolecules (e.g., cellulose; Abe and Higashi, 1991) or because of toxic secondary metabolites (e.g., Murdoch, 1966; White, 1978).

Although the above models are not necessarily mutually exclusive, each one probably has better predictive power in specific ecosystems. Some authors have criticized these models and presented convincing arguments to dispose of trophic cascade theories (Polis and Strong, 1996) because of the ubiquity of factors such as omnivory and diet shifts and a general lack of demonstrable trophic structure in real communities. For example, many terrestrial predators eat both herbivores and plants,

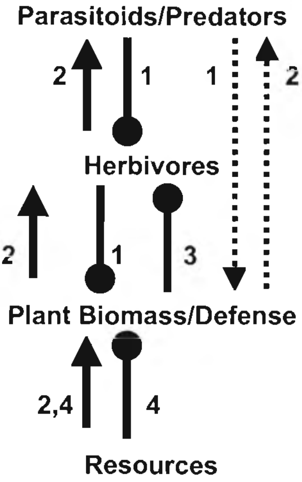

Fig. 4.1. Direct and indirect effects among three trophic levels and plant resources. Direct effects are indicated by a solid line between two trophic levels, and indirect effects (cascades) are indicated by a dashed line. A negative effect of one trophic level on the other is drawn with a bullet-head, and a positive effect is drawn with an arrowhead. The effect is on the trophic level nearest to the arrow- or bullet-head. The numbers closest to the lines refer to current models in ecology that examine trophic relationships: (1) top-down trophic cascades; (2) bottom-up trophic cascades; (3) the green desert model; and (4) resource availability models. The meta-analysis measured the strength of these interactions in tropical versus temperate systems.

potentially having no indirect positive effect on plants. Persson (1999) adds to these criticisms by pointing out that terrestrial studies of trophic cascades have not included appropriately scaled experiments with large vertebrate herbivores and predators and that there are many other indirect interactions that are equally important in structuring communities. Thus, the validity of these trophic models and their applicability to different habitats have been the target of much discussion. In this chapter, we compile information from the literature to assess the relative strength of top-down and bottom-up forces across a latitudinal gradient.

Specific predictions have been made about how aspects of tritrophic interactions differ between tropical and temperate systems. Below we review the evidence that suggests that in the tropics plants are better defended, herbivory is higher, and pressure from natural enemies is more intense. These patterns imply that tropical herbivore populations have adapted to pressures from intense bottom-up *and* top-down forces. In this chapter, we examine the literature relevant to the specific predictions of latitudinal differences and present a meta-analysis from 14 years of research in tropical and temperate communities. Using this analysis we evaluate the relative effects of top-down and bottom-up forces by directly comparing the suppression of herbivores by natural enemies versus by chemical compounds. We also assess the effects of plant resource availability on upper trophic levels via chemical defense or plant biomass.

Meta-analysis methods

The meta-analysis included data from January, 1985 through December, 1998. All papers in the journals *Oecologia*, *Biotropica*, and the *Journal of Tropical Ecology* were examined for quantitative measures of the following direct and indirect interactions: resources (light, nitrogen, phosphorus) on plant biomass or survivorship and on plant defenses; plant defenses (chemical defenses and leaf toughness) on percentage herbivory, herbivore biomass, or herbivore survivorship; herbivores (natural and artificial damage) on plant biomass or survivorship; natural enemies on prey biomass or survivorship; and natural enemies on plant biomass (see Fig. 4.1). The starting date was chosen because the first issue of the *Journal of Tropical Ecology* was published in that year. For the journal *Oecologia*, we used the same starting date but only included nine years of studies (1985–1993) because the work reported in that journal is mostly temperate, and we were attempting to collect a balanced sample of tropical and temperate work. A bibliography of the papers that were examined can be found on the internet along with the effect sizes from each study (http://www.caterpillars.org). Papers that were actually included in the meta-analysis were those that contained means, measures of dispersion, and sample sizes. We conducted a mixed model meta-analysis for temperate versus tropical systems to uncover potential latitudinal differences. We defined tropical studies as all those conducted in natural ecosystems below 2000 m within the tropics of Cancer and Capricorn or on organisms that live exclusively in those latitudes.

Equations in Gurevitch and Hedges (1993) were used to calculate combined effect sizes across all studies and 95% confidence intervals for the meta-analysis. Means and standard deviations were taken directly from tables or text, were calculated from other statistics, or were gleaned from figures (using a ruler). We calculated only one effect size per interaction per paper. If more than one effect size was available for an interaction, we randomly selected a value or used the last value in a series of measurements. In this chapter, we report all effect sizes along with the range of the 95% confidence intervals (after Gurevitch and Hedges, 1993); all other measures of dispersion reported here are ±1 standard error. Any effect sizes greater than 1.0 were considered to be large effects (Gurevitch and Hedges, 1993). We compared the strength of specific trophic interactions (Fig. 4.1) in tropical versus temperate systems by using the between class heterogeneity statistic, Q_B, which has approximately a χ^2 distribution (Gurevitch and Hedges, 1993).

Utilizing a meta-analysis for a review such as this one has notable advantages because the effect size calculated is independent of sample size, avoiding the problems arising from the positive correlation between sample size and likelihood of attaining a significant result. However, meta-analyses are subject to the same problems as any literature review based on vote-counting or more subjective narrative reviews of existing studies, including subjectivity of data collection from the literature, biases in collections of studies, and loss of system-specific details for the sake of generality (Gurevitch and Hedges, 1993). We attempted to minimize subjectivity of data collection by only including those studies that had distinct statistics reported in tables, figures, or text. The only obvious bias in the studies we examined was a tendency to examine specialist invertebrate herbivores when studying the effects of herbivory on plants. We discuss consequences of this bias below.

Latitudinal trends in plant defenses

Plant defenses are an important component of tritrophic interactions over both ecological and evolutionary time-scales. Latitudinal differences in defenses among plant communities should influence population dynamics of plants, herbivores, and natural enemies, and these interactions shape the evolution of defenses. Several reviews and empirical studies indicate that there is a strong latitudinal gradient in chemical defenses, with tropical plants being better defended than temperate plants (Crankshaw and Langenheim, 1981; Langenheim *et al.*, 1986; Miller and Hanson, 1989; Coley and Aide, 1991; Basset, 1994; Gauld and Gaston, 1994; Coley and Kursar, 1996, in press a). Alkaloids are more common and toxic in the tropics (Levin, 1976; Levin and York, 1978). About 16% of the temperate species surveyed in these studies contained alkaloids, compared to more than 35% of the tropical species. Simple phenolics do not seem to vary between latitudes, but condensed tannins in mature leaves are almost three times higher in tropical forests (Becker, 1981; Coley and Aide, 1991; Turner, 1995). The diversity of secondary compounds is also much higher in tropical than temperate forests (Miller and Hanson, 1989; Gauld and Gaston, 1994). This may occur because plant diversity is far greater in the tropics, but it is also true that many sympatric closely related plants have different chemical defenses (Waterman, 1983; Gauld and Gaston, 1994). For many herbivores, leaf toughness is the most effective feeding deterrent (Coley, 1983; Lowman and Box, 1983; Langenheim *et al.*, 1986; Aide and Londoño, 1989). This defense increases threefold in the tropics across four different forest types, being lowest in temperate plants. Indirect plant defenses, such as domatia and extrafloral nectaries are also more common in the tropics (Koptur, 1991).

Another striking difference between tropical and temperate plant defenses is that young, expanding tropical leaves have the highest levels of investment in secondary compounds, while temperate plants invest in higher levels of chemical defense in mature leaves. In tropical trees, young leaves contain much higher concentrations of simple phenolics, condensed tannins, terpenes, and alkaloids compared to the concentrations found in mature leaves (Coley and Kursar, in press a). In temperate trees, young leaves contain half the concentration of condensed tannins as mature leaves (Coley and Kursar, in press a).

While the above data strongly indicate that both young and mature leaves of tropical species are substantially better defended than leaves from temperate species, our meta-analysis suggests that the negative impact of defenses on herbivores is similar in temperate and tropical regions (Fig. 4.2). There were large negative effects of plant defenses on herbivores for tropical (−1.06) and temperate (−1.32) systems, and there were no significant differences between the latitudes ($Q_B = 1.18$, df = 1, $P > 0.5$). These results are not inconsistent with the documented latitudinal gradient in plant defenses. In this case, herbivore response is not an adequate measure of severity of plant defense, since many of these studies examined specialist herbivores that are adapted to the defenses of their hosts. Temperate and tropical studies alike have demonstrated that specialists have evolved adaptations to detoxify or sequester the defensive compounds that are unique to their restricted array of host plants (Krieger *et al.*, 1971; Whittaker and Feeny, 1971; Feeny, 1976; Dyer, 1995; Camara, 1997). So, the similar magnitude of the

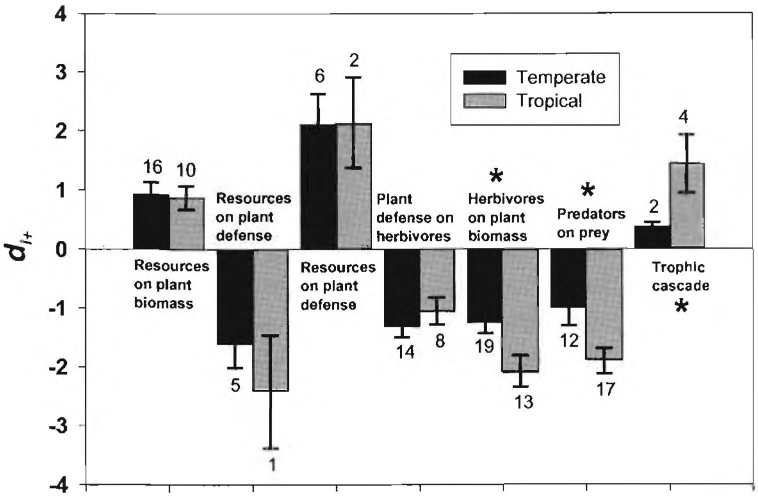

Fig. 4.2. Accumulated effect sizes across studies (d_{i+}) in tropical and temperate systems and 95% confidence intervals. The dependent variables included measures of biomass, defense, survivorship, and percentage damage. Any effect sizes greater than 1.0 were considered to be large effects. An asterisk indicates a significant difference ($P < 0.05$, based on the between class heterogeneity statistic, Q_B) for that interaction across lattitudes. The numbers above or below each bar indicate the number of studies included for the meta-analysis.

negative effect of defenses on herbivores across latitudes may result from coevolutionary interactions, where elevated defenses in the tropics are countered by elevated modes of tolerance or detoxification by specialist herbivores.

A more appropriate test of latitudinal differences in the effectiveness of plant defenses was recorded by Miller and Hanson (1989), who conducted experiments and literature reviews to compare development of a naïve generalist herbivore (*Lymantria dispar*) on 658 species of tropical and temperate food plants. Their results were consistent with the hypothesis that tropical plants are better defended: plant chemistry was a good predictor of suitability of host plants, and when tropical plants were added to their assay, the proportion of host plant rejections increased. A more extensive meta-analysis than the one reported here might allow for distinguishing the effects of plant defenses on adapted specialists versus generalists or naïve herbivores; in that case, we predict a greater negative effect of tropical versus temperate plants on the generalist or naïve herbivores.

Plant responses to resource availability

A number of studies on anti-herbivore defenses of plants have proposed relationships between resource availability, plant growth rates, plant vigor, and plant defense relevant to the three models of community structure that we present in our introduction (e.g., Bryant *et al.*, 1983; White, 1984; Larsson *et al.*, 1986; Nichols-Orians, 1991a; Price, 1991b; Herms and Mattson, 1992; Shure and Wilson, 1993; Fig. 4.1). However, in order to make sense of plant responses to resource availability, we must distinguish between interspecific trends, where we compare species that have evolved adaptations to different habitats, and intraspecific trends, where we compare phenotypic responses of plants to short-term changes in resources. These inter- and intraspecific responses are frequently opposite. For example, in chronically resource-poor communities, such as those with low light or poor soils, plants grow slowly and are selected to invest heavily in defenses (Janzen, 1974; Grime, 1979; Coley *et al.*, 1985). This in turn would limit herbivore populations, as predicted by the green desert hypothesis. However, in a given system, changing the availability of resources could either enhance or confound traditional hypotheses of bottom-up control. This is because plastic responses of plants reflect source–sink imbalances (not optimal solutions), and some resources increase growth, while others increase defenses. An example of enhancement of thermodynamic bottom-up control would be under lowered nitrogen conditions: levels of carbon-based defenses will increase, and herbivores will decline because of increased plant defense as well as lower plant biomass. The opposite situation (i.e., contradicting bottom-up predictions) could also result from variation in nitrogen or light availability. Kyto *et al.* (1996) found that despite predictions by bottom-up models, folivore populations did not increase in response to nitrogen additions, perhaps because of increases in nitrogen-based defenses. Similarly, under low light availability, herbivore populations might be expected to decline because of reduced plant productivity, but they are just as likely to increase because of lower levels of carbon-based defenses (Bryant *et al.*, 1983). Variation in light availability might also affect nitrogen-based defenses (Bryant *et al.*, 1983), which would alter effects of enhanced plant biomass on upper trophic levels. The few studies that have examined associations between resource availability, plant biomass, plant chemistry, and herbivory have yielded inconsistent results (Waterman *et al.*, 1984; Larsson *et al.*, 1986; Bryant *et al.*, 1987; Briggs, 1990; Dudt and Shure, 1994); thus the relationships between these variables need to be examined more closely. This type of work will enhance bottom-up models by improving our understanding of how communities adapt to different resource levels and how they respond to short-term fluctuations.

Plasticity in plant defenses

In an earlier section, we discussed evidence for a latitudinal trend in defenses that results from selection. The data suggest that the optimal level of defense is greater in the tropics. Here we examine plastic responses of plants to variation in light and mineral resources (Bryant *et al.*, 1983; White, 1984; Larsson *et al.*, 1986; Nichols-Orians, 1991a; Price, 1991b; Herms and Mattson, 1992; Shure and Wilson, 1993). Not surprisingly, data from our meta-analysis showed that plants respond to an increase in resources by increasing growth (Fig. 4.2). In addition, there were defense responses consistent with the theory of carbon–nutrient balance (Bryant *et al.*, 1983). This hypothesis suggests that resources in excess of baseline requirements for growth and defense are invested in defenses. Thus, under conditions of high light, carbon-based defenses (e.g., tannins and terpenes) should increase, whereas under nitrogen fertilization, nitrogen-containing compounds (e.g., alkaloids) should increase. In our analysis, increases in nitrogen, phosphorus, and light availability had strong effects on plant defenses. Depending on the resources and the defenses, both positive and negative effects were seen in approximately equal numbers of studies (Fig. 4.2). For example, Nichols-Orians (1991b) found that increased light availability was correlated with increased concentrations of condensed tannins (positive effect of resources), while Mihaliak and Lincoln (1985) found that increased levels of nitrate (from fertilizing) led to decreased concentrations of volatile terpenes (negative effect of resources). Although resource levels clearly influenced plant growth and levels of defense, there were no differences between tropical and temperate systems in the magnitude of effect (resources on plant biomass, $Q_B = 0.19$, df = 1, $P > 0.5$; resources negatively affecting plant defense, $Q_B = 2.16$, df = 1, $P > 0.1$; resources positively affecting plant defense, $Q_B = 0.0016$, df = 1, $P > 0.9$).

Herbivory

Levels of herbivory are variable at many different scales of time and space at all latitudes. For example, herbivores generally prefer young leaves over mature ones, but the difference is most dramatic in the tropics (Coley and Aide, 1991). In addition, within the tropics, leaf damage is significantly less in wet than in dry tropical forests (Barone, in press a), pioneer species have higher levels of herbivory than understory species (Coley, 1988; Nuñez-Farfan and Dirzo, 1989; Marquis and Braker, 1994), and understory plants suffer more herbivory than canopy plants (Lowman, 1985; Barone, in press b).

Despite this variation within latitudes, there is a detectable latitudinal pattern of herbivory. A review of herbivory in tropical versus temperate systems reported that mean folivory was 7% ($n = 13$ studies) in the temperate zone versus 16.6% ($n = 29$ studies) in the tropics (Coley and Barone, 1996). The effect sizes calculated in the meta-analysis support the hypothesis that herbivory is more intense in the tropics and has a greater negative effect on plant biomass and survivorship than herbivory on temperate plants (Fig. 4.2; $Q_B = 31.0$, df$=1$, $P < 0.0001$). Despite this difference, the effects of herbivory on plants were large for both temperate (-1.25) and tropical (-2.1) studies.

Differences in herbivory on young versus mature leaves create a latitudinal pattern that mirrors the pattern of chemical defenses (Coley and Kursar, 1996). In the temperate zone, most of the damage occurs on mature leaves, while in the shade-tolerant species of the tropical wet forests, approximately 75% of the lifetime damage occurs during the short period of leaf expansion. The concentration of herbivores on ephemeral young leaves allows rapid herbivore development and might also select for efficient host-finding abilities in parasitoids.

Because physical and chemical defenses are higher in the tropics, the higher levels of herbivory suggest that herbivore pressure or specialized adaptations to specific plant defenses must also be greater. Our meta-analysis indicates that tropical herbivores probably are better adapted to defenses because the increased levels of tropical defenses do not have a greater negative effect on tropical herbivores when compared to the effect of weaker temperate plant defenses on their herbivores (Fig. 4.2). Some diversity hypotheses suggest that increased levels of specialized herbivory in the tropics help maintain the high diversity of trees (Janzen, 1970; Leigh, 1999). These authors suggest that if the herbivores are specialized, the intense levels of tropical herbivory will keep their host plant rare, allowing other species to coexist. Again, our meta-analysis supports this hypothesis since the tropical herbivores are more likely to suppress overall biomass of superior plant competitors. For example, one of the papers in our meta-analysis (Letourneau and Dyer, 1998b) uncovers a dramatic increase in the density of one understory plant (*Piper cenocladum*) when specialist herbivores are suppressed. Since *P. cenocladum* can occur at very high densities (Letourneau and Dyer, 1998b), forests where the plant is suppressed should be able to support higher species richness of understory plants.

Natural enemies

In addition to facing a diverse array of plant toxins, herbivores in the tropics may also be subjected to more intense pressure from natural enemies. It has long been thought that predation is more intense in tropical compared to temperate ecosystems (Paine, 1966; Elton, 1973; Rathcke and Price, 1976; Gauld and Gaston, 1994). There are some data that support this hypothesis (Jeanne, 1979) along with some indirect evidence, but very few appropriate comparisons have been made. The most cited indirect evidence that predation is more intense is that important predatory taxa are more diverse in the tropics. Ants provide a clear example of an important group of predators that are more species-rich and abundant in tropical versus temperate systems (Kusnezov, 1957; Fischer, 1960; Wilson, 1971). Jeanne (1979) tested the hypothesis of a latitudinal gradient in ant predation by offering wasp larvae to ants at five locations along a latitudinal gradient and found that rates of predation were significantly greater in the tropics. Our meta-analysis also confirms that natural enemies have strong negative effects on herbivores at all latitudes, but the magnitude of the effect is significantly higher in tropical (−1.89) versus temperate (−1.0) systems (Fig. 4.2; $Q_B = 21.3$, df = 1, $P < 0.0001$).

Overall levels of parasitism are either the same in tropical and temperate systems (Hawkins, 1994) or are slightly higher in tropical systems, despite the fact that for some parasitoid groups diversity is lower and assemblage sizes are smaller in the tropics compared to temperate systems. Hawkins (1994) examined levels of parasitism for over 1200 hosts all over the world and found no latitudinal gradient in mortality, and while he did document a positive relationship between parasitoid species richness and mean parasitism rates, the lower levels of diversity in the tropics were not associated with lower levels of parasitoid-induced mortality. Other rearing studies indicate that levels of parasitism are slightly higher in tropical versus temperate forests. G. Gentry and L. A. Dyer (unpublished data, but also see http://www.caterpillars.org and Dyer and Gentry, 1999) have compiled a five-year database of over 200 species of tropical Lepidoptera and have found that mean yearly levels of parasitism for 55 well-sampled species (17 families) were 32.5% ± 3%. In contrast, mean levels of parasitism across 98 species (13 families) of temperate caterpillars (from a long-term database published in Schaffner and Griswold, 1934 and used by Sheehan, 1991 then by Dyer and Gentry, 1999) were 17% ± 2%. Even if pressure from parasitoids is higher in the tropics than in the temperate zone, it is likely that predation is a more important source of mortality than parasitism in tropical systems while parasitism is more important source of mortality in temperate systems. Hawkins *et al.* (1997) quantified enemy-induced mortality for 78 species of herbivores and found that predators represent the dominant natural enemy in the tropics, whereas parasitoids are dominant in temperate systems.

An examination of latitudinal trends in plant defenses provides additional indirect evidence for higher pressure from natural enemies in tropical systems. Mature leaves of rainforest species have extremely high concentrations of condensed tannins as compared to temperate ones (Coley and Aide, 1991). Tannins as defenses present a paradox, because they cause herbivores to grow more slowly but also to consume more leaf tissue (Price *et al.*, 1980; Coley and Kursar, in press a). The paradox is solved if prolonged larval development makes herbivores susceptible to predation for longer, as the removal of larvae, particularly in the early instars, will reduce damage to the plant (Benrey and Denno, 1997). Therefore, we would only expect tannins to evolve as a defense if, by slowing herbivore growth, they made larvae more vulnerable to predators. The high tannin levels in mature tropical leaves, and the low abundance of mature leaf feeders, suggests that natural enemies may be quite effective in reducing herbivory in tropical forests (Coley and Kursar, in press a).

Herbivore defenses

The large negative effects of plant toxins on herbivores are attenuated by the fact that many specialized herbivores utilize these toxins for their own defense. Studies comparing different defensive mechanisms of herbivores have found chemical defenses to be the most effective against a diverse suite of natural enemies (Dyer, 1995, 1997). Chemical defenses of tropical versus temperate herbivores potentially mirror the defenses found in their host plants: tropical herbivores are generally more toxic than their temperate counterparts. Both direct and indirect evidence has been accumulated to support this generalization. Sime and Brower (1998) presented direct evidence that tropical Lepidoptera are more toxic than those in temperate latitudes. They demonstrated that the latitudinal gradient in species richness of unpalatable butterflies is greater than the gradient for the Papilionidae, which they use as an average (in terms of palatability) butterfly family. These results should be viewed with caution, since many supposedly toxic groups have never been investigated for toxicity (DeVries, 1987, 1997), and many groups that were thought to be toxic were not toxic to several different invertebrate predators (Dyer, 1995, 1997). In addition, the assumption that the immatures of entire families or subfamilies of butterflies are unpalatable (Sime and Brower, 1998) is unrealistic and has not been supported by empirical data (Dyer, 1995).

The "nasty host hypothesis" (Gauld *et al.*, 1992; Gauld and Gaston, 1994) provides further indirect evidence for the elevated toxicity of tropical herbivores. Many taxa of parasitoid Hymenoptera are not more diverse in the tropics, and one explanation for this could be that tropical hosts are more toxic than extra-tropical hosts. The parasitoid groups that are negatively affected by "nasty" compounds are less diverse in the tropics. Furthermore, diversity of tropical parasitoids is not lower for egg or pupal parasitoids because these stages are usually not chemically defended; likewise diversity is high for tropical parasitoids of herbivores that eat non-toxic plant tissue (Gauld *et al.*, 1992; Gauld and Gaston, 1994). Gauld *et al.* (1992) also pointed out that the proportion of aposematic insects is higher for many taxa in the tropics and that the tissues of most of these insects are likely to be toxic.

Chemically defended herbivores are often dietary specialists (Duffey, 1980; Bowers, 1990; Dyer, 1995), therefore it is possible that the gradient in herbivore unpalatability (if it does exist) is correlated with a latitudinal gradient in specialization. Limited evidence has been provided in support of such a gradient (Scriber, 1973, 1984; Basset, 1994; Scriber *et al.*, 1995; Sime and Brower, 1998), although there are notable exceptions where chemical and phylogenetic constraints minimize any latitudinal gradients in host plant specialization (Fiedler, 1998). For those groups for which diet breadths are narrower in the tropics, the increased specialization may be a result of plant chemistry (Ehrlich and Raven, 1964) or pressure from natural enemies (Bernays and Graham, 1988), or a combination of these top-down and bottom-up forces (Dyer and Floyd, 1993).

Tritrophic interactions and trophic cascades

Tropical ecosystems are generally considered to be more complex, containing longer trophic chains and trophic webs that exhibit more omnivory, intraguild predation, and unpredictable indirect effects. Convincing arguments have been made suggesting that top-down and bottom-up trophic cascades are unlikely to occur in such complex ecosystems. However, studies that have focused on top-down forces have discovered recipient control in terrestrial systems with high diversity that include omnivory and opportunistic diets (Spiller and Schoener, 1994; Dial and Roughgarden, 1995; Floyd, 1996; Moran *et al.*, 1996; Letourneau and Dyer, 1998b; Dyer and Letourneau, 1999a, b; Pace *et al.*, 1999). The concept of distinct trophic levels that exert statistically detectable forces on other levels (whether they be donors or recipients) is useful for community ecology; rather than discarding this concept, more empirical tests are needed to examine the role of omnivory with respect to mediating or mitigating top-down and bottom-up forces. Alternatively, the concept of "effective" trophic levels, in which trophic levels are fractional rather than discrete integers (e.g., 3 = a predator with a 100% diet of herbivores, 2.5 = an omnivore with a 50% herbivores and 50% plant diet), could be utilized to enhance the predictive power of the major trophic cascades models (Christian and Luczkovich, 1999).

Using either the traditional concept of trophic levels or the new concept of functional trophic levels, very few terrestrial studies have documented clear top-down cascades (as actual indirect effects) anywhere (Letourneau and Dyer, 1998a). This is because it is difficult to control for direct effects of predators and parasitoids on plants (or top predators on herbivores). For example, many of the ant–plant systems in the tropics, which have been used to demonstrate the positive effects of predators on plants, have not measured clear indirect effects because the ants may have considerable positive direct effects on the plant (nutrient procurement), considerable negative direct effects (costs of producing food), or other indirect effects (see Bronstein and Barbosa, chapter 3, this volume). With this caveat in mind, the limited numbers of studies that do exist suggest that top-down cascades occur in terrestrial systems (reviewed by Pace *et al.*, 1999). In fact, the strong negative effects of enemies on herbivores and negative effects of herbivores on plants uncovered by our meta-analysis (Fig. 4.2) support the idea that enemies can have indirect positive effects on plants even if they do shift diets, eat plants, or compete with other consumers. The very few studies in our meta-analysis that directly documented a top-down cascade also support this idea (Fig. 4.2). Effects of enemies on plants were positive for both tropical (1.44) and temperate (0.38) systems, but the effects were significantly greater for the tropics ($Q_B = 6.03$, df = 1, $P < 0.025$).

The strong top-down (direct and indirect effects) control demonstrated by tropical studies in our meta-analysis included large vertebrate predators and herbivores (e.g., Jedrzejewski *et al.*, 1992; Meserve *et al.*, 1993), which partially addresses Persson's (1999) criticism that trophic cascades studies have not been appropriately scaled. The results of these studies are also relevant to tropical conservation issues. Terborgh (1992) suggested that top-down cascades are important in Neotropical forests, and he hypothesized that the decline of large mammalian predators due to forest fragmentation and hunting could lead to an increase of mammalian seed predators and a decline in tree species with large seeds. Terborgh's specific predictions may be incorrect because a correlation between herbivore body size and seed size may not exist (Brewer *et al.*, 1997). However, it is clear that top-down control is important in tropical systems, and various cascading effects may cause tropical conservation problems similar to the negative cascading effects of disappearing coyotes (caused by habitat fragmentation) on bird diversity in temperate communities (Crooks and Soulé, 1999).

Conclusions

The main latitudinal trends noticed across the three trophic levels of plant, herbivore, and natural enemy indicate that with respect to temperate ecosystems, the tropics exhibit: (1) increased diversity for most taxa at all three trophic levels, with the exception of some parasitoids, (2) higher levels of plant defenses (mechanical, biotic, and chemical), (3) increased levels of herbivory, (4) more toxic herbivores, and (5) more intense pressure from natural enemies.

Examination of the effect sizes in the meta-analysis revealed that strong top-down and bottom-up forces were detectable in both temperate and tropical systems (Fig. 4.2). Despite the complex trophic structure of tropical communities, distinct trophic levels exert statistically detectable forces on other levels. There was no latitudinal difference in the effect of plant defenses on herbivores, however, top-down effects of predators on herbivores and herbivores on plants were significantly stronger in the tropics. Thus, if one looks at the relative importance of these forces on community structure, we see quite surprising and distinct patterns in the different systems. In temperate systems, plant chemistry appears to have a stronger ecological impact on herbivores than do natural enemies, even though levels of defense are relatively low. On the other hand, in tropical systems natural enemies seem to be more important than plant defenses. Thus, controls on community organization may follow different rules along a latitudinal gradient.

Why do we see these latitudinal differences, with top-down controls being relatively more important in the tropics? We offer several speculative suggestions. First, the exploitation ecosystem hypothesis posits that greater productivity should favor top-down control because when plant productivity is high, as in the tropics, sufficient resources will be available to allow natural enemies to act as "effective trophic levels" that control herbivore populations (Fretwell, 1977; Oksanen *et al.*, 1981). Second, because tropical climates are more favorable year round, populations of both herbivores and natural enemies do not suffer severe seasonal crashes. This should lead to a more reliable presence of an effective third trophic level in tropical communities. And finally, because natural enemies are predictable due to benign tropical climates, plants have had the evolutionary opportunity to enlist the help of natural enemies in controlling herbivores (Coley and Kursar, in press b). For example, tropical plants more frequently have extrafloral nectaries. They also have twice the levels of tannins and toughness, which slow herbivore growth and increase their susceptibility to natural enemies. Thus, we suggest that the high, year-round productivity of the tropics may be an important factor leading to the observed gradient in trophic controls.

Many aspects of trophic cascades models remain untested in tropical or temperate systems. Most studies have focused on biomass at different trophic levels, and very few studies have examined top-down effects of predators on plant community structure or bottom-up effects of plant resources on animal community structure (Persson 1999). Clearly, more empirical studies are needed to understand the scope of trophic cascades and the conditions under which they occur. Future studies should attempt to test the effects of top-down cascades on plant community structure and bottom-up cascades on consumer community structure, and investigators should utilize creative approaches, such as examining effective trophic levels (Christian and Luczkovich, 1999), to alleviate some of the problems pointed out by critics of trophic cascades theory (Polis and Strong, 1996). These studies will undoubtedly reveal some of the mechanisms driving the strong latitudinal gradient in species diversity.

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