Is There a Latitudinal Gradient in the Importance of Biotic Interactions?

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Abstract

Biotic interactions are believed to play a role in the origin and maintenance of species diversity, and multiple hypotheses link the latitudinal diversity gradient to a presumed gradient in the importance of biotic interactions. Here we address whether biotic interactions are more important at low latitudes, finding support for this hypothesis from a wide range of interactions. Some of the best-supported examples are higher herbivory and insect predation in the tropics, and predominantly tropical mutualisms such as cleaning symbioses and ant-plant interactions. For studies that included tropical regions, biotic interactions were never more important at high latitudes. Although our results support the hypothesis that biotic interactions are more important in the tropics, additional research is needed, including latitudinal comparisons of rates of molecular evolution for genes involved in biotic interactions, estimates of gradients in interaction strength, and phylogenetic comparisons of the traits that mediate biotic interactions.

INTRODUCTION

The latitudinal diversity gradient is one of the most striking biogeographic patterns on Earth (Fischer 1960). For virtually all taxonomic groups, species richness is highest in equatorial regions and declines toward the poles. This pattern holds for marine and terrestrial organisms, for living and extinct taxa (Crame 2002, Jablonski et al. 2006), for ectotherms and endotherms, and for taxa that differ in body size, mode of dispersal, and trophic level (Hillebrand 2004). Hypotheses for the latitudinal gradient fall into four main categories: (*a*) geometric constraints on range size and distribution (Arita & Vázquez-Dominguez 2008, Colwell & Hurtt 1994), (*b*) biogeographic history (Fine & Ree 2006, Ricklefs 1987, Wallace 1878, Wiens & Donoghue 2004), (*c*) ecological mechanisms of species coexistence (Connell 1971, MacArthur 1969, Valentine et al. 2008), and (*d*) evolutionary mechanisms of adaptation and speciation (Dobzhansky 1950; Fischer 1960; Rohde 1992; Schemske 2002, 2009). Despite considerable effort to understand the origin and maintenance of the latitudinal diversity gradient, no overriding explanation has emerged (Mittelbach et al. 2007).

The role of biotic interactions is a pervasive theme in efforts to understand the latitudinal diversity gradient (Schemske 2009). Wallace (1878) suggested that escape from glaciation at low latitudes allowed biotic interactions to flourish in tropical regions, leading to high species richness. Dobzhansky (1950) proposed that the severe, variable climate in temperate regions resulted in the evolution of a few, generalized species, whereas the benign, predictable climate in the tropics led to a greater importance of biotic interactions. As a result, tropical species are more specialized and tropical communities attain greater species diversity. Similarly, Fischer (1960) suggested that the stable climate in the tropics allowed for a wider range of morphological and physiological adaptations than in temperate regions.

Schemske (2002, 2009) revisited Dobzhansky's views on the importance of biotic interactions at low latitudes and proposed a mechanism whereby biotic interactions may increase rates of adaptation and speciation. He suggested that strong biotic interactions in the tropics promote coevolution, and as interacting species coevolve the optimum phenotype constantly changes, which might result in faster adaptation and speciation. In temperate populations, he proposed that the primary selective pressures are abiotic factors, which vary in space and time but do not evolve. Furthermore, stochastic changes in community composition following geographic isolation could promote rapid adaptation and speciation in the tropics (Schemske 2009). This process is analogous to Thompson's (1994) geographic mosaic theory, where spatial variation in species interactions facilitates local coevolution. Finally, where biotic interactions are important, each new species may introduce novel resources and interactions and, hence, expand the number of niche dimensions available within the community (MacArthur 1969, Vermeij 2005). In this way, a greater role of biotic interactions in the tropics may catalyze speciation and promote further diversification (Schemske 2009, Vermeij 2005).

Several ecological hypotheses suggest that biotic interactions can maintain high species richness (Pianka 1966). Paine (1966) proposed that the greater stability of annual production in the tropics sustains a disproportionate number of predator species that enhance diversity by ameliorating competitive exclusion among prey. Other ecological hypotheses specifically link herbivory with the maintenance of plant species diversity in tropical forests (Marquis 2005). Perhaps the best known of these is the Janzen-Connell hypothesis. Janzen (1970) and Connell (1971) independently proposed that high density-dependent predation on seeds and seedlings of tropical trees prevents competitive exclusion, and Leigh et al. (2004) regard this as a major mechanism for the maintenance of high tropical diversity.

Anecdotal evidence supports Wallace's (1878, p. 122) view that high tropical diversity is a consequence of the "complex influences of organism upon organism." Indeed, tropical regions

provide many striking examples of biotic adaptations and highly specialized species interactions (**Figure 1**; also see **Supplemental Figure 1 Expanded Caption**. Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Specialized biotic interactions also occur in extratropical regions, e.g., yucca moths and their hosts (Godsoe et al. 2008), pollen-collecting bees with extreme host specialization (Praz et al. 2008), and pines and their avian seed predators/dispersal agents (Benkman et al. 2003). However, quantitative analyses of how the importance and nature of biotic interactions change with latitude remain scarce. Here we review the existing literature and ask, Is there a latitudinal gradient in the importance of biotic interactions?

▶ Supplemental Material

A number of approaches have been proposed for estimating interaction strengths (Wootton & Emmerson 2005). The ideal metric for evaluating the importance of biotic interactions would be to estimate the proportion of the total variation in fitness that is due to biotic interactions in different geographic regions (Schemske 2009). Not surprisingly, such a comprehensive study has never been done. We thus enumerated the importance of biotic interactions in several ways, including (*a*) the "strength" of biotic interactions, e.g., bird nest predation, (*b*) the expression of traits involved in biotic interactions, e.g., chemical defense against predators, and (*c*) the frequency of different biotic interactions, e.g., seed dispersal by animals versus wind. We grouped studies into four broad categories: (*a*) predation, herbivory, parasitism, and disease, (*b*) defenses against predators, herbivores, parasites, and disease, (*c*) mutualisms, and (*d*) other indicators of biotic interactions (e.g., sex and recombination, sexual selection, density dependence, etc.).

Before discussing the results, several data limitations need to be acknowledged. First, regrettably, the number of empirical studies relevant to this subject is limited. In an effort to identify all studies relevant to our topic, we made an extensive literature search using a variety of keywords (e.g., latitudinal gradient, biotic interactions, etc.) and reviewed hundreds of studies of interactions and taxonomic groups that we considered to be strong candidates (e.g., geographic patterns in bird nest predation, the incidence of animal pollination, drilling frequency in marine mollusks). Finally, we contacted numerous individuals with different taxonomic expertise. Thus, to the extent possible, our review was exhaustive. Second, relatively few studies have investigated biotic interactions along the entire latitudinal gradient. More common are studies that compare single localities from high and low latitudes, or that examine latitudinal patterns within a single geographic region. Because we are broadly interested in latitudinal patterns in biotic interactions and how they may explain the latitudinal diversity gradient, we included studies conducted across a substantial latitudinal range (>10° latitude) even if they did not include tropical regions. Nevertheless, 87% of the studies in our review spanned tropical or subtropical regions. Second, because some interactions are easier to study than others, e.g., herbivory and predation versus diffuse competition, our review does not cover all interactions expected in nature. Most notably, our literature search failed to turn up any direct comparisons of the strength of interspecific competition across latitude. Finally, as pointed out by Fischer (1960, p. 75), it is difficult to separate cause and effect: "... is the diversity of tropical biotas due to more intense competition, or is the more intense competition an outcome of the more diverse biota?" Our review does not attempt to distinguish between these alternatives.

PREDATION, HERBIVORY, PARASITISM, AND DISEASE

Avian Nest Predation

To examine the latitudinal pattern in nest predation rates, we compared tropical and temperate species (tropical data from Kulesza 1990 and Robinson et al. 2000, temperate data from Conway & Martin 2000). We found that tropical species have significantly higher predation rates (mean

proportion of nests destroyed by predators $= 0.64 \pm 0.17$, N $= 27$ species) than their extratropical counterparts (0.41 ± 0.14, N $= 65$ species) (Wilcoxon-Mann-Whitney test, $p < 0.01$). This result agrees with other studies employing direct observations of nesting success (Ricklefs 1969, Skutch 1949; but see Oniki 1979, Wesołowski & Tomiałojć 2005); however, additional tropical sites and species are needed to make this comparison more compelling.

A potentially powerful approach to this question is to make phylogenetically controlled comparisons between species residing at different latitudes. For example, Martin et al. (2000) measured predation rates for eight avian congeneric species pairs in Arizona and Argentina, and found higher rates in Arizona. However, both study sites were at similar latitudes (Arizona 34°N, Argentina 26°S), but outside the topics, and with only a single site at each latitude, one cannot rule out other potential causal factors. In another recent example, Martin et al. (2007) used phylogenetically independent contrasts in an examination of nest predation's potential effect on incubation time. Within this dataset, there are four study sites spanning tropical and temperate latitudes. It is

interesting to note that the site with the highest nest predation was a temperate site in South Africa (34°S); however this is also the only site of the four at sea level. The tropical site in Venezuela (9°N) experienced moderate levels of predation, but is in a high-elevation cloud forest (1400–2000 m). This example clearly illustrates the need for more data on nest predation collected across latitude from a variety of habitats in order to provide much-needed replication.

Several studies have employed artificial nests to measure predation rates in different habitats. In a review of 22 such studies ranging from 0°N to 53°N, Söderström (1999) found no relationship between predation rate and latitude. However, nest predation rates are often significantly underestimated on artificial nests compared to natural nests (Robinson et al. 2005). One possible explanation for the failure of artificial nests to predict natural nest predation is the lack of parental activity at artificial nests. Snakes are important nest predators in the tropics (Weatherhead & Bloun-Demers 2004), and they may rely heavily on these cues, as snake predation is extremely rare in artificial nests (S.K. Robinson, personal communication).

Insect Predation

Two studies have examined latitudinal differences in predation pressure on live insect baits. Jeanne (1979) measured ant predation of wasp larvae at five localities along a latitudinal gradient extending from 43°N to 2°S. The rate of ant predation increased toward the tropics and was not simply a direct result of this region's higher ant diversity (Jeanne 1979). A similar study by Novotny et al. (2006) showed that predation pressure (mostly from ants) on insect baits was significantly higher in a tropical versus a temperate forest, with an average of 28.3% predation in Papua New Guinea as compared to 1.6% in Moravia. These studies and similar experiments with marine fish and invertebrates (e.g., Bertness et al. 1981) are among the clearest examples of higher predation in tropical communities and provide a useful approach for investigating latitudinal trends in biotic interactions.

▶ Supplemental Material

Figure 1

Biotic interactions in the tropics. (For further description, see **Supplemental Figure 1 Expanded Caption**. Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org/**.) (*a*) Army ants (*Eciton burchelli*) and associated species in the New World tropics. Army ants form marauding swarms to flush their arthropod prey. *Left*: Army ant soldier (photo: © Jochen Bihn). *Middle*: Bicolored Antbird (*Gymnopithys leucaspis*), a "professional" ant follower that forages exclusively at army ant swarms (photo: Douglas Schemske). *Right*: Skipper (*Astraptes anaphus*: Hesperiidae, Eudaminae) feeding on bird droppings in Costa Rica (photo: Phil DeVries). Many male skippers feed on fresh bird droppings, often from birds that forage at army ant swarms. (*b*) Electric knife fishes (Gymnotiformes: Apteronotidae) from the Neotropics generate weak electric fields to electrolocate prey, predators, and conspecifics. *Left*: *Adontosternarchus nebulosus*, common in the Amazon and its tributaries (photo: Mark Sabjaj); *right*: *Magosternarchus raptor*, which feeds exclusively on the tails of other gymnotiform fishes. (photo: John Sullivan). (*c*) *Myrmecodia tuberosa* (Rubiaceae), an ant plant from Sarawak, Malaysia (photo: Christian Puff). Ants live in intricate chambers within the bulbous "tuber," and the plant extracts nutrients left by ants. (*d*) *Lambis scorpius*, of the family Strombidae (photo: Kaustuv Roy) from the tropical Indo-Pacific. The long apertural digits may deter predators and provide stabilization. (*e*) Bluestripe cleaner wrasses (*Labroides dimidiatus*) removing ectoparasites from a snapper (photo: Martyn Franklin). Cleaning behavior has evolved in a variety of tropical reef fishes. This mutualistic interaction has been co-opted by species of fangblennies, which mimic cleaners and nip pieces from client fishes. (*f*) *Rafflesia arnoldii* (Malpighiales) from Sumatra (photo: Kamarudin Mat-Salleh) possesses one of the largest flowers in the world, reaching 1 m in diameter. *Rafflesia* are specialized endoparasites of host vines in the genus *Tetrastigma* (Vitaceae). Flowers mimic the smell of rotting flesh, and are pollinated by carrion-feeding insects. (*g*) Oilbirds (*Steatornis caripensis*) in Trinidad (photo: Michael Oakley). This nocturnal species roosts in caves and cliffs, and feeds on large, lipid-rich fruits. Oil from nestlings was historically used to light torches, giving the species its name. Oilbirds are one of only two birds that use echolocation to navigate. (*h*) The hooded pitohui (*Pitohui dichrous*), an aposematically colored bird endemic to New Guinea whose skin and feathers contain a potent neurotoxin thought to defend against ectoparasites or predators (photo: Daniel Levitis). Such chemical defenses are rare in birds and are unknown outside of the tropics.

Marine Predation and Herbivory

Multiple studies have suggested that the intensity of predation by fish and crustaceans increases from temperate to tropical latitudes. Menge & Lubchenco (1981) showed that consumer pressure in the rocky intertidal (both predation and grazing) increased toward the equator along with a marked decrease in the abundance of prey. Tethering experiments using both soft- and hard-shelled crustacean prey have also found higher predation pressure at low latitudes (Heck & Wilson 1987, Peterson et al. 2001). Similarly, the incidence of shell-crushing predation on littoral gastropods in Panama is significantly higher than in Massachusetts (Bertness et al. 1981), although predation rates in Costa Rica were comparable to those in Massachusetts (Ortega 1986). For many of these studies, there is considerable variation within regions and among habitats (Heck & Wilson 1987).

Because drilling predation leaves a characteristic signature on the shell, its intensity can be quantified in modern death assemblages and the fossil record (Harper 2006). Turritellid gastropods from temperate oceans show lower drilling frequency than those from tropical habitats, suggesting higher predation pressure in the tropics (Allmon et al. 1990, Dudley & Vermeij 1978). In contrast, Miocene gastropod assemblages of central Europe show a decrease in drilling frequency from the Boreal province to the warmer Paratethys, although the trend is most pronounced only in certain habitats (Hoffmeister & Kowalewski 2001). Drilling frequency in modern bivalve death assemblages also tends to decrease toward the equator (Vermeij et al. 1989). A similar trend occurs in Cenozoic fossil assemblages, although some of the differences again tend to be habitat-specific (Hansen & Kelley 1995, Hoffmeister & Kowalewski 2001). In contrast, Alexander & Dietl (2001) reported a southward increase in drilling frequencies in two species of bivalves from New Jersey to the Florida Keys. Thus, drilling frequency across taxa does not show a consistent relationship with latitude.

Terrestrial Herbivory

Herbivory has received considerable attention in studies of terrestrial plant communities. Coley & Aide (1991) reviewed geographic patterns in rates of herbivory in broad-leaved forest trees and found significantly higher herbivory (average percent leaf damage per year) in tropical (10.9%) than in temperate (7.5%) regions. Leaf herbivory also varies among plant species in different tropical communities, with higher rates in gap specialists of wet forest (48.0%) than in dry forest (14.2%) or in shade-tolerant, wet forest (11.1%) species (Coley & Barone 1996). In a meta-analysis of studies of herbivory and plant defense in temperate and tropical communities, Dyer & Coley (2002) found significantly larger negative effects of herbivores on plant biomass and of predators and parasitoids on herbivores in the tropics.

Host-Parasite Interactions

Parasites can be important selective agents affecting the ecology and evolution of their hosts, and evidence suggests that parasitism and disease are more prevalent at low latitudes. The number of parasite or disease species found per host species often increases toward the tropics, including ectoparasites of marine fish (Rohde 2002, Rohde & Heap 1998), protozoan parasites of primates (Nunn et al. 2005), generalist parasites of carnivores (Lindenfors et al. 2007), and indirectly transmitted viruses and helminth, protozoan, and arthropod parasites of humans (Guernier et al. 2004). Groups showing no significant latitudinal variation are the endoparasites of marine fish (Rohde 2002, Rohde & Heap 1998), bacteria and fungi infecting humans (Guernier et al. 2004), and directly transmitted viruses of humans (Guernier et al. 2004) or other primates (Nunn et al.

2005). The intensity of parasitism (number of parasite individuals per host individual) also increases with decreasing latitude in partridge infected with helminths (Calvete 2003), in marine fish infected with ecto- (but not endo-) parasites (Rohde & Heap 1998), and in mosquito fish infected with pleurocercoid cestodes (Benejam et al. 2009). In Chile, the prevalence of blood parasites in birds increases toward lower latitudes (Merino et al. 2008), and the number of shorebirds infected with malaria declines with latitude in Europe and Africa (Mendes et al. 2005). Ricklefs & Sheldon (2007) caution, however, that blood parameters measuring infection in birds are often difficult to interpret in tests of regional effects.

Janzen (1970) and Connell (1971) predicted that the absence of seasonality in the tropics would result in higher parasite loads throughout the year and therefore stronger coevolution between parasites and hosts. Consistent with this prediction, Møller (1998) found that leukocyte concentrations in birds were significantly higher in tropical species compared to closely related temperate species, and relative spleen size (a measure of immune response) showed the same significant pattern. Subspecies of white-crowned sparrow (*Zonotrichia leucophrys*) also show higher levels of immune response at lower latitudes (Owen-Ashley et al. 2008). However, Møller et al. (2006) found that the immune response of altricial birds was significantly stronger in temperate Denmark than in subtropical Spain, and they concluded that higher bird densities in Denmark were responsible for the difference.

These studies document a general trend of greater parasite richness and prevalence at low latitudes. It has been hypothesized that this may be due to an increase in the abundance and diversity of vectors and/or climatic effects on vector behavior and parasite development at low latitudes (e.g., Guernier et al. 2004, Merino et al. 2008, Nunn et al. 2005). A stronger test of this hypothesis would be to compare rates of parasitism/disease in the same species across a range of latitudes. Surprisingly, such data appear to exist for only two species: the lizard *Eulamprus quoyii* (Salkeld et al. 2008) and humans (Cashdan 2001, Low 1990). In *E. quoyii*, blood parasite load was significantly and negatively correlated with latitude in Australia (Salkeld et al. 2008), and in humans, pathogen severity increases significantly with decreasing latitude (Cashdan 2001, Low 1990).

It is possible to indirectly assess a history of pathogen load in populations by examining genetic diversity of loci involved in immunity. For example, the major histocompatibility complex (MHC) codes for cell-surface proteins involved in binding pathogenic protein fragments and initiating an immune response (Klein 1986). MHC represents the highest expressed genetic diversity in humans and other vertebrates (Piertney & Oliver 2006) and is thought to result from balancing, frequency-dependent, and/or temporally or spatially variable selection imposed by pathogens (Hedrick 2002). Several studies have linked MHC diversity to pathogen pressure (summarized in Bernatchez & Landry 2003), but few have explicitly examined the relationship between latitude and MHC diversity. In a notable example, Dionne et al. (2007) found that after correcting for population history and neutral genetic diversity, MHC diversity in Atlantic salmon (*Salmo salar*) increased from 58° to 46°N latitude. In addition, bacterial communities in salmon habitat were more diverse at lower latitude, suggesting a causal link between increased pathogen richness and MHC diversity (Dionne et al. 2007).

Diseases in plants are less studied than in animals, but the data available suggest that plants in the tropics experience greater pathogen pressure. For crop plants grown across a range of latitudes, diversity of disease increases toward the equator (Wellman 1968, Yang & Feng 2001), though it is unclear whether incidence of disease increases accordingly. In cultivated oats and wild relatives grown in Australia, plants at lower latitudes are more resistant to stem and crown rusts (Burdon et al. 1983), and rust pathogens (genus *Puccinia*) appear more virulent at low latitudes (Oates et al. 1983).

Parasitoids of Herbivorous Insects

The immature stages of nearly all herbivorous insects are host to an extraordinary variety of insect parasitoids. The broad geographic distribution of this biotic interaction makes this an interesting system for the study of latitudinal patterns. In a review of Lepidopteran rearing programs conducted from Canada to Brazil, Stireman et al. (2005) found a significant negative correlation between attack rates (parasitoid wasps and tachinid flies) and variation in annual precipitation, but no effect of latitude. The four highest parasitism rates were all observed in tropical forest, but the two lowest rates were also from tropical sites. If the analysis is restricted to forest communities, there is a much higher level of parasitism in the tropics (L.A. Dyer, personal communication). Compilations from other rearing studies also suggest that levels of parasitism are higher in tropical (32.5%) than temperate (17%) forests (Dyer & Coley 2002). In contrast, a meta-analysis found that the mean maximum percentage parasitism did not change along a climatic temperature gradient suggesting that peak parasitoid rates are, on average, no different in temperate versus tropical regions (Hawkins 1994). The mixed pattern for parasitism may in part be because Hymenopteran parasitoids do not show a striking latitudinal gradient in species richness (e.g., Sime & Brower 1998).

DEFENSES AGAINST PREDATORS, HERBIVORES, PARASITES, AND DISEASES

Chemical Warfare in the Ocean

Chemical defense against consumers is widespread among marine algae and invertebrates (Bakus et al. 1986, Cimino & Ghiselin 1998, Hay & Fenical 1988, McClintock & Baker 2001) and the production of these chemicals may be more common in tropical taxa. For example, tropical and subtropical genera of algae produce most of the secondary metabolites, with the exception of phlorotannin-producing brown algae, which show no clear latitudinal trend (Hay & Fenical 1988; Targett et al. 1992, 1995). Similarly, Bakus (1974) and Bakus & Green (1974) showed in laboratory experiments that tropical sponges and holothurians were more toxic to certain fish than were temperate species. Few studies have tested whether latitudinal differences in secondary metabolites are due to increased consumer pressure in the tropics (Becerro et al. 2003, Kicklighter & Hay 2006). Using feeding assays, Bolser & Hay (1996) showed that sea urchins consumed about twice the number of algal species offered from North Carolina compared to congeners from the Bahamas. Similarly, a palatability survey of 81 marine worm species found that the frequency of unpalatability was 2.6 times higher in tropical species compared to warm temperate ones (Kicklighter & Hay 2006). The proportion of species with chemical defense in Arctic marine communities, where predation pressure is low, is also much lower compared to tropical or temperate communities (Lippert et al. 2004), but in Antarctica chemical defenses in sponges are common (Amsler et al. 2001; McClintock 1987, 1989).

Some tropical herbivores are more resistant to seaweed defenses than are their temperate counterparts. In laboratory assays, herbivorous fishes and sea urchins from North Carolina were deterred by lower concentrations of secondary metabolites of the tropical brown algae *Dictyota acutiloba* compared to their counterparts from Guam (Cronin et al. 1997). In no case was a tropical herbivore more deterred by these chemicals than a temperate one.

Exceptions to these general trends also exist. For example, Becerro et al. (2003) showed that chemical defenses of sponges from tropical and temperate regions were similar, and that they

were equally effective in deterring fish predators. Another interesting exception is Antarctica, where toxicity of invertebrates such as asteroids and sponges appears to be unusually high (Amsler et al. 2001; McClintock 1987, 1989). Clearly much remains to be learned about latitudinal and geographic variation in chemical defenses in marine organisms. Nonetheless, there is some support for the idea that regions with high consumer pressure such as the tropics have a larger proportion of marine species with well-developed chemical defenses. Antarctica remains a major exception to this pattern and the reason is unclear (Amsler et al. 2001, Aronson & Blake 2001, Clarke et al. 2004).

Defenses in Marine Mollusks

Geographic trends in antipredatory morphologies have been documented for many species of mollusks. Shell thickness, shell shape, and ornamentation reduce predation by fish and crabs (e.g., Palmer 1979; Vermeij 1978, 1987), and the proportion of intertidal and subtidal gastropod species with such traits is negatively correlated with latitude (e.g., Palmer 1979; Vermeij 1978, 1987; Zipser & Vermeij 1978). Middle Paleozoic brachiopod fossils also show a latitudinal gradient in such antipredatory traits (Dietl & Kelley 2001; Leighton 1999). Frequency of repaired injuries of the shell also decreases at higher latitudes in the gastropod family Terebridae (Vermeij 1980). However, repaired injuries can reflect breakage other than by predation (Harper 2006).

Consumer-Prey Interactions in Salt Marsh

Latitudinal variation in plant-herbivore interactions has been quantified for salt marshes along the Atlantic coast of the United States. Herbivores given a choice of northern or southern conspecifics of ten plant species usually preferred those from the north (Pennings et al. 2001). Preference was correlated with a number of plant traits, e.g., toughness, palatability of polar extracts, and nitrogen content (Siska et al. 2002). Furthermore, preferences persisted in a common garden experiment, suggesting genetic control of the differences in palatability (Salgado & Pennings 2005). In the case of *Spartina alterniflora*, southern plants also suffer more herbivore damage, although the diversity and density of dominant leaf-chewing consumers changed little with latitude (Pennings & Silliman 2005). Trends similar to those observed in the United States were also found in European salt marshes (Pennings et al. 2007).

Defenses in Terrestrial Plants

Herbivory is ubiquitous in terrestrial systems, and a number of studies have examined latitudinal patterns in plant defenses. These studies typically find evidence of greater investment in defenses in tropical plants, consistent with evidence that herbivore pressure is higher in the tropics (see above). Basset (1994) used native insect herbivores to compare the palatability of woody plant foliage from temperate and tropical regions (Switzerland and New Guinea) and found that temperate species were significantly more palatable (by 2.3 times, on average). Dyer & Coley (2002) found that tropical plants invest in greater chemical, biological and structural defense, and extensive feeding trials with the temperate generalist herbivore *Lymantria dispar* demonstrated that tropical plants were less palatable (Miller & Hanson 1989). Levin (1976) found that the percentage of alkaloid-producing plants is negatively correlated with latitude. Furthermore, the alkaloids found in tropical genera occur in higher concentrations and are more toxic (Levin & York 1978). Latex, another widespread defense against herbivores, is also more common in tropical plants (Lewinsohn

1991). Coley & Aide (1991) found that tropical plants produce tougher leaves of lower nutritional quality and with a higher concentration of condensed tannins.

The comparisons discussed above are based on pooled samples of entire floras; thus differences in the taxonomic composition of temperate and tropical communities may be confounded with patterns of defense. Levin (1976) compared the defenses of temperate and tropical taxa within lineages in the Compositeae and the Leguminoseae and observed a negative correlation between latitude and the percentage of alkaloid-producing plants. Furthermore, Hallam & Read (2006) examined defenses in five evergreen species of *Eucryphia* in eastern Australia and found an increase in total phenolics and tannin activity and a decrease in nutritional quality with decreasing latitude. In a study of a single, widespread species of *Acacia* in Australia, Andrew & Hughes (2005) found no relationship between latitude and herbivory and no consistent pattern of increasing plant defenses toward tropical latitudes.

The fossil record shows that intensity of plant-herbivore interactions in terrestrial ecosystems also changes with temperature when latitude is held constant. In southwestern Wyoming, a humid subtropical climate prevailed during the early Eocene, and plants had more types of insect damage per host species as well as higher attack frequencies as compared to the late Paleocene when a humid temperate to subtropical climate prevailed (Wilf & Labandeira 1999, Wilf et al. 2001).

Other Latitudinal Comparisons of Defenses

Laurila et al. (2008) found that antipredator defenses in *Rana temporaria* tadpoles decreased with increasing latitude along a 1500-km transect in Sweden, a pattern consistent with lower predator densities at high latitudes. Parchman et al. (2007) found that pine cones from Hispaniola have evolved thicker scales than those from northern latitudes and that the bills of Hispaniolan crossbills are deeper than those of their North America counterparts. They attribute these differences to greater opportunities for predator-prey coevolution at lower latitudes, perhaps due to escape from Pleistocene climatic disturbances.

Aposematic Coloration and Aspect Diversity

Wallace (1878, p. 98) probably provided the first evidence of latitudinal differences in traits associated with biotic interactions, with the observation that warningly colored (aposematic) insects are more common in the tropics: "It is in the tropics that we find most largely developed, whole groups of organisms which are unpalatable to almost all insectivorous creatures, and it is among these that some of the most gorgeous colours prevail." Gauld et al. (1992) also note that the number, and sometimes the proportion, of aposematic insects are higher in the tropics. Surprisingly, to our knowledge there are no rigorous tests of this proposal. Extensive surveys in caterpillars did not find a close association between coloration and chemical defenses, suggesting that factors other than predation may play a role in the evolution of caterpillar color patterns (Dyer 1995, Gentry & Dyer 2002).

Higher predation and selection for predator avoidance in the tropics may cause an increase in the diversity of cryptic prey phenotypes ("aspect diversity"). Consistent with this hypothesis, Ricklefs & O'Rourke (1975) observed a greater variety of sizes, patterns, and shapes in tropical species than in temperate moth species. However, recent studies failed to replicate this pattern, leading Ricklefs (2009) to conclude, "Either frequency-dependent (apostatic) selection is not a powerful force in diversifying moth appearance, or it does not vary with latitude, or potential resting backgrounds and cryptic strategies are similarly constrained in temperate and tropical regions."

MUTUALISM

Pollination and Seed Dispersal

Regal (1982) classified plants as animal- or wind-pollinated, and found that the frequency of animal-pollinated plants was much higher in tropical regions. Although consistent with the hypothesis of stronger biotic interactions in tropical regions, the factors responsible for this pattern are poorly understood. Using a phylogenetic approach, Friedman & Barrett (2008) found no evidence that ecological conditions in extratropical regions favored the evolution of wind pollination. However, their study examined only higher taxonomic levels, with samples obtained from a few species per family and a single species per genus. It would be valuable to examine the incidence of shifts in the mode of pollination at lower taxonomic levels as well.

Seed production in animal-pollinated species is often pollen-limited, due largely to inadequate pollinator visitation (Knight et al. 2005). The magnitude of pollen-limitation can be viewed in part as a product of competition for pollinator service and is estimated by comparing the seed production of flowers receiving supplemental pollen to that of open-pollinated flowers (Knight et al. 2005). In a comprehensive review of supplemental pollination studies, Vamosi et al. (2006) found a significant positive relationship between the magnitude of pollen limitation and regional species richness, with latitude treated as a covariate, suggesting that competition for pollinators is indeed highest in diverse communities. If both species richness and latitude are considered together in a model of pollinator limitation, there is a significant effect of richness, no effect of latitude, and a significant richness × latitude interaction, with greater pollen limitation observed in diverse communities at low latitudes (J.C. Vamosi, personal communication). Thus, only in diverse plant communities is competition for pollinator service higher at low latitudes.

Moles et al. (2007) found that the fraction of animal-dispersed plants increased from high to low latitude regions, and Jordano (2000) observed that >90% of tropical plant species rely on animals for seed dispersal.

Mutualistic Defenses in Terrestrial Plants

The percentage of plant families that produce extrafloral nectaries, an adaptation for ant defense against herbivores, is higher in tropical (39%) than in temperate (12%) communities (Coley & Aide 1991). Moreover, ant-plant symbioses in which protective ants live within specialized plant structures are restricted to the tropics and involve >100 plant genera and >40 ant genera (Davidson & McKey 1993). Endophytic fungi provide protection from pathogens in some plant hosts (Arnold et al. 2003, Herre et al. 2007), and the incidence of infections from endophytes increases from <1% in the arctic to >99% in the tropics (Arnold & Lutzoni 2007).

Marine Endosymbiosis

The tissues of marine invertebrates often contain photosynthetic dinoflagellates (zooxanthellae), which promote the growth and survival of their host and, in turn, receive nutrients and protection (Muscatine 1990). Such associations might increase under the more intensely competitive, predator-rich conditions of tropical waters. For example, Yonge (1957) concluded, "Although symbiosis is exceptional in temperate waters, almost every species of coelenterate in tropical waters contains zooxanthellae. For instance, on a coral reef, not only do reef-building corals (Madriporaria) contain zooxanthellae, but also anemones (Actiniaria), soft corals (Alcyonacea), sea fans (Gorgonacea), and hydroid corals (Hydrocorallinae), as well as Scyphozoa and members

of other smaller groups." Quantitative comparisons of how the frequency of zooxanthellae-host associations changes with latitude are needed to confirm this observation. In addition, evidence that the association evolved more than once would strengthen the argument that biotic interactions are imposing strong selection on symbiosis.

Cleaning Symbiosis

Cleaning symbiosis, where the cleaner species removes ecotoparasites and other material (skin, mucus) from the body surfaces of "client" species, has evolved in a variety of taxa (e.g., fish, shrimp, birds, lizards) and occurs most often in aquatic habitats (Côté 2000, Grutter 2002). This mutualism is especially well developed in coral reef fishes, where species establish cleaning stations at particular reef sites that are repeatedly visited by client species. Cleaning symbioses occur in both temperate and tropical systems, but far more are described in tropical waters (Grutter 2002). Quantitative comparisons of cleaning symbiosis across latitude are lacking.

INDIRECT INDICATORS OF BIOTIC INTERACTIONS

Geographic Patterns in Sexual Systems and Recombination Rates

Strong biotic interactions and coevolution create a continually shifting pattern of selection that favors sex and recombination (Bell 1982). If the importance of biotic interactions increases toward the tropics, we might also expect an increase in the relative frequency of reproductive systems that promote recombination in tropical regions.

Indeed, Levin (1975) concluded that herbivore and pathogen pressures are highest in the tropics, and that tropical plants display a higher frequency of sexual systems that promote outcrossing, e.g., dioecy, than is found in extratropical communities. Schuster (1988) noted that the frequency of asexuality in liverworts was lower in the tropics, whereas Mishler (1988) reported that there was no latitudinal pattern in moss sexual systems. Dorken & Eckert (2001) found a significant negative correlation between latitude and most measures of sexual reproduction for the aquatic plant *Decodon verticillatus*. Glesener & Tilman (1978, p. 669) reviewed geographic patterns in animal parthenogenesis and found that sexual forms are prevalent at lower elevation and at lower latitudes, and that these represent regions of higher "biotically imposed stress." The frequent observation that asexual reproduction is less common in the tropics is consistent with the hypothesis that strong biotic interactions favor sexual reproduction.

For sexual species, the proportion of offspring produced by outcrossing provides a measure of the opportunity for recombination. In plants, analyses conducted with and without phylogenetic correction find a significant, negative correlation between latitude and outcrossing rate, but this may be explained by temperate regions having a higher frequency of annuals, which are often highly self-pollinating (D. Moeller, personal communication). However, the selection of plant species for mating system studies is probably biased, with relatively few estimates from self-incompatible or dioecious species, both of which are disproportionately represented in tropical communities (Bawa 1974, Vamosi et al. 2003). Hermaphroditic animals also show a weak negative correlation between mean outcrossing rate and latitude, but the sample size is small, and the relationship is not significant (J. Auld, personal communication).

Sexual Selection

Sexual selection is a potent biotic interaction that can potentially lead to speciation (Ritchie 2007), but empirical evidence for a geographical pattern in sexual selection is limited. In an analysis

of 69 phylogenetically independent species pairs of birds separated by at least 10° of latitude, Cardillo (2002) found no increase in sexual dimorphism or dichromatism at lower latitudes. The relationship between latitude and sexual size dimorphism (SSD) has been analyzed across several additional taxonomic groups. In a comparative study including 98 temperate species of vertebrates and invertebrates, SSD was significantly higher toward lower latitudes (Blanckenhorn et al. 2006). SSD must be approached cautiously as a proxy for sexual selection however, as it could alternatively result from factors such as sex-specific natural selection (Cox et al. 2003).

Latitudinal Gradients in Ectotherm Mortality and Body Size

Mortality rates decrease at higher latitudes in freshwater fish and other ectotherms and may reflect lower predation rates in temperate regions. Heibo et al. (2005) examined juvenile and adult mortality as a function of latitude in 75 populations of Eurasian perch (*Perca fluviatilis*) over a latitudinal range from about 40–70°North. Juvenile and adult mortality rates were positively correlated, and both declined significantly with increasing latitude. European freshwater fish generally show increased life span, age at maturity, and adult body size with increasing latitude (Blanck & Lamouroux 2007). North American freshwater fish similarly show an increase in maximum age with latitude, but no significant effect of latitude on maximum length (Belk & Houston 2002). However, two species in their survey (*Esox lucius*, *Micropterus dolomieu*) exhibited large, positive correlations between latitude and maximum body size. Juvenile survival in Sceloporine lizards in North America also increases at higher latitudes, along with an increase in adult size and a delay in sexual maturity (Angilletta et al. 2004). Although direct evidence for the causes of increased survival of fish and lizards at higher latitudes is lacking, most mortality in juvenile and adult fishes is generally attributed to predation (e.g., Hixon & Carr 1997, Post et al. 1998), and Angilletta et al. (2004) hypothesize that reduced lizard survival at lower latitudes is due to higher predation rates. Angilletta et al. (2004) also suggest that the tendency for intraspecific body size to increase with increasing latitude in ectotherms (a variant on Bergmann's rule; Blackburn et al. 1999) may arise due to delayed reproduction in response to lower mortality at higher latitudes.

Herbivorous Insect Life Tables

Life tables provide information on age-specific survival and sources of mortality at different developmental stages and, thus, allow evaluation of the factors that regulate populations living in different ecological conditions. If biotic interactions prevail in the tropics, then the mortality spectrum of tropical species should include biotic factors such as natural enemies or competition rather than climatic factors. A comprehensive synthesis of 124 life tables detected a small, non-significant tendency for enemy-induced mortality to decrease at higher latitudes and a tendency for weather-induced mortality to increase (Cornell & Hawkins 1995, their Figure 6). A more powerful statistical analysis detected significantly higher enemy-induced mortality in tropical/subtropical habitats compared to temperate habitats, but only for the egg and pupal stages (Hawkins et al. 1997).

Density Dependence

If biotic interactions are stronger at lower latitudes, then density dependence should also become more apparent because biotic factors such as predation, interspecific competition, intraspecific competition, and disease are most likely to limit populations in a density-dependent manner. In contrast, harsh, unproductive environments at high latitudes may keep populations below their

biotically induced carrying capacities. Evidence for latitudinal gradients in density dependence comes from the cycling dynamics of small mammal populations in boreal environments. Mammal populations showing regular cycles are characteristic of boreal regions and none is known from the tropics (Sinclair & Gosline 1997). The tendency for mammal populations to cycle decreases with latitude (Hanski et al. 1991, Hansson & Hentonen 1985, Saitoh et al. 1998), and in at least two cases, the pattern correlates with decreasing strength of the density-dependent signal in time-series data (Bjørnstad et al. 1995, Saitoh et al. 1998). Increased density-dependent predation or increased reproduction, depending upon the species, was posited to account for the decrease (Bjørnstad et al. 1995, Hanski et al. 1991, Hansson & Hentonen 1985).

Large mammals also show a stronger signal of density dependence in time series data as latitude decreases. Post (2005) showed that density dependence increased and density independence decreased with decreasing latitude for 27 populations of caribou. They attribute this pattern to reduced overgrazing and, thus, decreased intraspecific competition at high latitudes where snow cover is higher during the winter. All of these studies were done at high latitudes and exclude truly tropical environments in the comparisons.

Latitudinal gradients in density dependence can also be examined using demographic techniques. If density dependence is greater in the tropics, then transition probabilities among critical life stages should depend more upon conspecific and heterospecific densities than in extra tropical regions. Hille Ris-Lambers et al. (2002) found that the proportion of forest tree species showing density-dependent mortality was similar in tropical and extratropical forests. Their review, however, did not evaluate the strength of density-dependent mortality.

SYNTHESIS

To assess latitudinal trends in the importance of biotic interactions, we grouped studies into categories representing different indicators of biotic interactions (**Table 1**). Each of these categories included a number of subcategories, with one to several individual studies per subcategory [e.g., bird nest predation represents a single subcategory under predation, but our assessment is based on multiple studies (**Table 1**)]. For each subcategory, we characterized the importance of biotic interactions as: (*a*) greater at low latitudes, (*b*) greater at high latitudes, or (*c*) no latitudinal pattern. We found only a single case of significantly stronger interactions in extratropical regions—bird immune response was stronger in Denmark than in Spain (Møller et al. 2006), but a similar study including tropical regions reported the opposite pattern (Møller 1998). Thus, for simplicity, we classified this subcategory as having "no difference." For all other subcategories, results from different studies were never contradictory, although in a few cases some studies found a significant pattern, whereas others did not (e.g., bird nest predation). In addition, we indicated the geographic scope of studies, that is, whether tropical or subtropical regions were included. We also gave a subjective ranking of the confidence in our assessment of biotic interactions (low, moderate, high) based upon such criteria as the statistical significance of geographic comparisons, the consistency of results from different studies, the number of studies available, etc.

This approach for summarizing the results is not ideal, yet we feel that the dataset has too many limitations to warrant a more detailed statistical analysis at this time. For example, although a meta-analysis would be valuable for comparing geographic patterns in the importance of biotic interactions (see Dyer & Coley 2002), for the most part, the studies now available are too limited in their sampling locations and response variables, and too heterogeneous in the metrics employed to provide meaningful measures of effect size.

We compiled data on 39 subcategories of biotic interactions, and most (87%) included data from studies conducted in low and high latitudes (**Table 1**; see also **Supplemental Table 1**). For the

Table 1   Latitudinal patterns in the importance of biotic interactions[a]

Indicators of biotic interactions	Higher at low latitudes[b]	Higher at high latitudes[b]	No difference[b]
Predation, herbivory, parasitism, disease			
Predation on bird nests	XX		
Insect predation by ants	XXX		
Marine invertebrates (shell crushing)	XXX		
Marine mollusks (drilling)			XXX
Marine herbivory (salt marsh)	XXX		
Terrestrial herbivory	XXX		
Ectoparasites of marine fish	XXX		
Endoparasites of marine fish			XXX
Blood parasites of birds and lizards	XXX		
Diseases of crop plants	XXX		
Vector-borne parasites and diseases of humans	XXX		
Parasitoid attack			XX
Defenses against predators, herbivores, parasites, disease			
Palatability of:			
-Marine worms	XXX		
-Marine algae			XX
-Marine invertebrates			XX
-Salt marsh plants	XXX		
-Leaves	XXX		
-Butterfly larvae	XXX		
-Frog larvae[c]	XX		
Coevolution of pines and crossbills	XXX		
Mimicry in insects	X		
Moth aspect diversity			XX
Immunological defense—bird leucocytes[d]			XX
Mutualisms			
Pollination by animals	XXX		
Seed dispersal by animals	XXX		
Ant-plant mutualisms	XXX		
Fungal endophytes	XXX		
Marine zooxanthellae	X		
Cleaning symbiosis (marine)	XXX		
Other			
Sex and recombination:			
-Plants	XX		
-Animals	XXX		
Sexual selection—sexual dichromatism in birds			XX
Sexual selection—sexual size dimorphism	XX		
MHC sequence diversity in Atlantic salmon[c]	XXX		
Life-history evolution			
Life expectancy in fish[c]	XXX		

(*Continued*)

Table 1 (*Continued*)

Indicators of biotic interactions	Higher at low latitudes[b]	Higher at high latitudes[b]	No difference[b]
Sources of mortality			
-Herbivorous insect life tables	X		
Density dependence			
-Small mammal cycles (food limitation)[c]	XX		
-Caribou (food limitation)[c]	XX		
-Forest trees (seedling survival)			X

[a]Citations for studies referenced are presented in **Supplemental Table 1**. See the **Supplemental Material link** in the online version of this article or at **http://www.annualreviews.org/**.
[b]Level of confidence in our assessment of the importance of biotic interactions: low (X), moderate (XX), or high (XXX).
[c]Studies confined to temperate regions; all others include either tropical or subtropical latitudes.
[d]The two studies of immunological defense in birds were conducted at different geographic scales and had different results. For the sake of simplicity, we place these findings under the category of "no difference"—see text and **Supplemental Table 1** for further discussion.

entire dataset, and considering three possible classes of interaction strength (low latitude higher, high latitude higher, no difference), there is a highly significant departure from the null expectation ($\chi^2 = 36.5$, DF = 2, p < 0.001). Low latitudes have stronger biotic interactions in 30 (77%) of the cases, as compared to 9 with no geographic difference; we found no case where interaction strengths were higher at high latitudes (**Table 1**). These results hold if the analysis is restricted only to subcategories that included tropical or subtropical regions (N = 34; $\chi^2 = 28.3$, DF = 2, p < 0.001), or to the subset of these for which we have high confidence in the pattern (N = 21; $\chi^2 = 31.1$, DF = 2, p < 0.001). Despite the great diversity of approaches used in the studies reviewed here, it seems clear that biotic interactions are frequently more important in tropical regions.

Implications for the Latitudinal Diversity Gradient

The general latitudinal trend of a greater importance of biotic interactions that emerged from this review supports (but does not prove) the hypothesis that biotic interactions contribute to the origin and maintenance of the latitudinal diversity gradient. The greater incidence of disease and of herbivory in tropical plants is consistent with the assumptions of the Janzen-Connell hypothesis, which is often regarded as an important mechanism for the maintenance of high tropical tree diversity (Leigh et al. 2004). Furthermore, a greater role of animal pollination in the tropics may promote rapid floral divergence and speciation (Kay et al. 2005), consistent with the idea that biotic interactions expand opportunities for the evolution of novel forms, and accelerate adaptation and speciation (Dobzhansky 1950; Schemske 2002, 2009). Nevertheless, considerable work is needed before the biotic interaction hypothesis for the latitudinal diversity gradient can be adequately tested.

FUTURE DIRECTIONS

There are countless opportunities for the study of latitudinal patterns in the absolute and relative importance of biotic interactions. We describe several possible directions for further research. The comprehensive, broad-scale approaches that we propose here pose a variety of challenges, and successful implementation will require considerable effort of time and resources. Nevertheless, given the long-standing interest in the latitudinal diversity gradient and the current lack of consensus on its cause, further research is justified.

(1)   Obtain comprehensive estimates of the absolute and relative importance of biotic and abiotic factors to major components of fitness. Such studies are required to evaluate the evolutionary hypothesis that the latitudinal diversity gradient is a consequence of stronger biotic interactions in the tropics (Dobzhansky 1950, Schemske 2009). To obtain a general picture of latitudinal patterns in biotic interactions, it will be important to place greater emphasis on interactions such as competition and diffuse mutualisms—these are poorly represented in the current literature, but have potentially strong effects on community composition (Schoener 1983; Hay et al. 2004).

(2)   Examine geographic patterns for traits involved in biotic interactions, particularly for taxonomic groups (e.g., genera, families) that span tropical and extratropical regions. Examples include latitudinal comparisons of the frequency of seed dispersal by wind versus animals, of structural or chemical defense against predators, or of vigilance in foraging birds. Studies of this kind may provide novel insights not revealed by more challenging investigations of interaction strength. For example, a history of strong predation may cause prey to evolve greater toxicity or crypticity, resulting in a reduction in interaction strengths. Thus, estimates of contemporary interaction strengths may sometimes reveal less about the history of interactions than do geographic differences in the relative frequency of the traits themselves.

(3)   Conduct comparative studies to directly estimate the magnitude of different biotic interactions across multiple localities that span polar, temperate, and tropical regions. Past research has focused mainly on one-to-few, widely spaced localities. Yet, identifying the causal factors that affect latitudinal difference in biotic interactions will require studies conducted along broad geographic gradients. Where possible, standardized experiments should be performed (e.g., Bertness et al. 1981, Jeanne 1979) to reduce the number of potential confounding factors and thereby allow direct comparisons across geographic regions that may differ in countless environmental features. It is also important that experimental designs be based on knowledge of the natural history of the interacting organisms, as exemplified by the failure of artificial bird nests to accurately measure nest predation (Robinson et al. 2005). Ultimately, observational and experimental studies should be designed to allow the estimation of effect sizes using meta-analysis (Nakagawa & Cuthill 2007), an approach used successfully by Dyer & Coley (2002) to evaluate geographic patterns in tritrophic interactions.

(4)   Expand studies of the importance of biotic interactions to other gradients, such as altitudinal gradients in terrestrial systems and bathymetric gradients in aquatic systems. These studies could determine whether the proposal that biotic interactions are more important in regions of low abiotic stresses can be generalized beyond latitudinal patterns, and would ultimately shed light on the factors contributing to the latitudinal diversity gradient.

(5)   Adopt phylogenetic approaches, such as comparisons of the kinds and strength of biotic interactions in representatives of tropical and extratropical sister clades, or in congeners distributed along the latitudinal gradient (e.g., Novotny et al. 2006). Note, however, that phylogenies will not be useful when the taxa comprising tropical and extratropical regions have distinct evolutionary histories, as is often the case. In these situations, studies across multiple independent groups will be required to overcome clade-specific effects.

(6)   Expand the examination of traits to include molecular evidence of biotic interactions, e.g., the allelic diversity of genes involved in disease/pathogen resistance. It should also be possible to conduct latitudinal comparisons of the rate of molecular evolution of housekeeping genes to those involved in biotic interactions.

(7)   Examine latitudinal patterns in the functional and taxonomic composition of species assemblages involved in biotic interactions. For example, are tropical pollinators, seed predators,

or herbivores more specialized to their host plants than their extratropical counterparts? Greater specialization has been suggested as a mechanism that contributes to the coexistence of species in the tropics, yet the few studies on this topic have found mixed results (Dyer et al. 2007, Novotny et al. 2006, Ollerton & Cranmer 2002).

(8) Consider whether latitudinal patterns in biotic interactions are caused by one or more underlying environmental factors (e.g., temperature or precipitation), or are in part a consequence of the diversity gradient itself. To distinguish cause from effect will require studies of the taxonomic composition of interactions, whereby interaction strengths could be weighted by such factors as (*a*) local species richness, (*b*) the relative abundance of potential interactors, or (*c*) the level of specificity of the interaction. The critical question is: Do the strength and variety of biotic interactions experienced by an individual increase with increasing species richness?

(9) Examine the energetic and physiological costs of adaptation to abiotic factors, such as cold temperature tolerance, that may constrain adaptation along biotic axes.

(10) Conduct paleontological studies to evaluate the importance of biotic interactions over long periods. Estimates of past climates combined with studies of biotic interactions that leave a signature in the fossil record, such as predation and herbivory, could be used to identify historical patterns in the importance of biotic interactions (Allmon et al. 1990, Dudley & Vermeij 1978).

PRÉCIS

As stated by Jablonski (2008, p. 716): "Despite the enormous literature on biotic interactions in modern and ancient systems, biotic factors are poorly understood as macroevolutionary agents." We suggest that a greater focus on geographic patterns in the importance of biotic interactions will ultimately contribute to a broader understanding of the mechanisms that generate gradients in biodiversity. Furthermore, the ongoing loss and degradation of natural biological communities in virtually all geographic regions make time of the essence if we are to understand the origin and maintenance of such striking biogeographic patterns as the latitudinal diversity gradient.

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Errata

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