Inverse latitudinal gradients in species diversity

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Introduction

No single pattern of biodiversity has attracted ecologists more than the observed increase in species richness from the poles to the tropics (Pianka, 1966; Rohde, 1992; Rosenzweig & Sandlin, 1997; Gaston & Blackburn, 2000; Willig, Kaufman & Stevens, 2003; Hillebrand, 2004). An obstacle in the search for the primary cause of this latitudinal gradient is the ever-increasing number of hypotheses (Pianka, 1966; Rohde, 1992; Clarke, this volume), their interdependence (Currie, 1991; Gaston & Blackburn, 2000) and lack of rigorous falsification (Currie, Francis & Kerr, 1999; Currie, this volume). However, a general decline in species richness with latitude is commonly observed (Pielou, 1977; Colwell & Hurtt, 1994; Willig & Lyons, 1998; Colwell & Lees, 2000; Zapata, Gaston & Chown, 2003; Colwell, Rahbek & Gotelli, 2004).

Some groups of organisms, however, show an opposite trend: a strong latitudinal decline in species diversity towards the tropics. These trends have been almost neglected in the literature and little is known about their underlying ecological and evolutionary causes. Therefore, the ecological explanations proffered are usually specific to the group in question. Here an account of the most important cases of inverse latitudinal gradients is given. The existing hypotheses explaining this phenomenon are summarized and the evidence that tends to favor one of these is presented.

Groups showing inverse latitudinal gradients
North American breeding birds
Cook (1969) in his detailed study of gamma diversity in North American breeding birds revealed that a transect through central and eastern North

America showed an unambiguous decrease in regional diversity with decreasing latitude within the boundaries of the United States. This decrease was most marked in deciduous forests of the eastern United States, in which regional diversity declined sharply from New England toward the southeastern United States.

The pitcher plant mosquito

Buckley *et al.* (2003) studied geographical variation in species richness of the entire food web of invertebrates, protozoa and bacteria that inhabit the water-filled leaves (pitchers) of the purple pitcher plant, *Sarracenia purpurea* L. Species richness at the site scale (data collected from 39 undisturbed populations, randomly distributed throughout the range of *S. purpurea*, across North America) increased linearly with latitude; more species were recorded at the northern sites. Pitcher richness was *c.* 30% of the site richness and also increased linearly with latitude. A separate analysis of each taxonomic group (invertebrates, protozoa and bacteria) at the site scale showed that the increase in species richness with latitude was because of an increase in protozoan and bacterial richness; invertebrate richness exhibited no significant relationship with latitude. At the pitcher scale, the relationships between richness and latitude were slightly different: richness of all three components of the community increased with latitude and the abundance of the top predator in the system, the pitcher plant mosquito (*Wyeomyia smithii*), decreased significantly with latitude.

Shallow-water molluscs

Molluscs are the most diverse group of ocean-shelf macrobenthos, for which good comparative taxonomic data are available. Valdovinos, Navarrete and Marquet (2003) quantified latitudinal diversity gradients of Prosobranchia, Bivalvia and Placophora, from northern Peru (10° S) to Cape Horn (55° S), in particular their relationship to temperature and shelf area, and compared their results with the trends documented for both the northwestern Atlantic and northeastern Pacific Oceans. They analyzed the diversity and distribution of 629 species of shelled molluscs, including only those known to live in waters shallower than 200 m. Strong latitudinal changes in mollusc species diversity were evident along the Peru–Chilean shelf, for all major mollusc taxa studied, especially for Prosobranchia, the most diverse group within molluscs. However, the change in species diversity was not monotonous across latitudes. Diversity of prosobranch species remained relatively low and constant around a value of 100 species/latitudinal band between 10 and 40° S, and then sharply increased to the south, reaching *c.* 300 species/band around Cape Horn. This general pattern was similar for all taxonomic groups, but stronger for shelled species inhabiting

mostly hard substrates (Prosobranchia and Placophora), than for Bivalvia, which inhabit mostly soft substrates. Unlike temperature, shelf area explained a significant portion of the variance (59%) in species diversity south of the equator.

Marine benthic algae

On the Atlantic coast of Europe, the seaweed flora shows the classical pattern, with species richness increasing towards the equator (van den Hoek, 1975). However, in temperate Pacific South America, the number of species increases between 10° S to 55° S (Santelices, 1980).

Ichneumonids

The next unexpected decline in diversity towards the tropics is that observed in Ichneumonidae (first published by Owen & Owen, 1974), which belong to the largest insect families (Townes, 1969). The anomalous latitudinal gradient in ichneumonid diversity is a composite of separate trends in distinct lineages, some of which are more, and some less, species-rich in tropical than in temperate latitudes (Janzen, 1981; Gauld, 1986). Ichneumonid subfamilies with increasing diversity towards the tropics are usually generalists, with low potential growth rates (measured in terms of the number of eggs laid), or – if they are specialists – they attack exposed hosts. Ichneumonid subfamilies scarcer in the tropics are usually specialists, often attacking concealed hosts, and have high growth rates (Janzen, 1981; Gauld, 1986; Noyes, 1989; Askew, 1990; Gaston, 1991; Stork, 1991; Gauld, Gaston & Janzen, 1992; Hawkins, 1994).

Aphids

Dixon *et al.* (1987) analyzed data on the area-adjusted regional species numbers of plants and aphids from 23 countries. They found a strong exponential decline in the ratio of the number of aphid to plant species, if plotted against the number of plant species. The regional species diversity of aphids was maximal at some intermediate latitudes, and declined in areas of high vegetation complexity – in the tropics. The paucity of aphids in the tropics and subtropics has been attributed to the aphids' adaptation to temperate conditions, which results in a reduced incidence of sexual reproduction in the tropics, causing reduced genetic recombination and therefore reduced speciation rate (Bodenheimer & Swirski, 1957). However, within the family Aphididae, the Aphidinae and Drepanosiphinae, which comprise 70% of modern aphids, are not restricted to a particular region, and the Greenideinae and Hormaphidinae, which comprise 7%, are restricted mostly to southern Asia and Australia (Eastop, 1977). Thus, some species from the major aphid subfamilies are endemic to the tropics and subtropics and are well adapted to the climatic conditions that prevail there (Hales, 1976;

Agarwala & Dixon, 1986). Although continuous parthenogenesis is more common in species living in the tropics and subtropics than in many temperate regions, sexual forms have been described for many of the endemic species in the tropical regions. In addition, the distribution of aphids does not appear to be restricted by the association with particular groups of plants, since most groups of vascular plants serve as hosts for aphids (Eastop, 1978); that is, at least 97% of the vascular flora of the world could potentially host aphids. Thus, because some species of aphids are able to survive and thrive in the tropics and subtropics and because their speciation is unlikely to have been limited by a lack of genetic recombination or of suitable host plants, it is difficult to understand why aphids as a group have not flourished on the rich tropical and subtropical floras.

General explanations of the inverse latitudinal trends in species diversity

In some cases species diversity of the group in question depends more strongly on some biotic or abiotic factor (for example, energy available, abundance of a "keystone" predator) than on latitude:

1. Southern parts of North America, for example, are considerably drier and have accordingly lower plant productivity, measured, for example, by the Normalized Difference Vegetation Index, NDVI, than more northern areas (see Hurlbert & Haskell, 2003). It is therefore not surprising that the species richness of North American breeding birds also declines towards the south, as – according to the species–energy relationship (Storch, Evans & Gaston, 2005) – there is a positive correlation between species richness and plant productivity.

2. One possible explanation for why species richness of invertebrates, protozoa and bacteria that inhabit the pitchers of *S. purpurea* generally increases with latitude, is that predation plays an important "keystone" role in structuring this community (Power *et al.*, 1996). As the abundance of the top predator, a filter-feeding mosquito, decreases, a greater number of taxa in lower trophic levels (protozoa and bacteria) were able to persist. This is supported by experimental studies on this system, which have shown that the pitcher-plant mosquito is a keystone predator regulating the species richness of protozoa and bacteria (Addicott, 1974; Cochran-Stafira & von Ende, 1998; Kneitel & Miller, 2002; Buckley *et al.*, 2003).

3. The inverted latitudinal pattern shown by seaweeds (Santelices, 1980) is the result of the coexistence along the coastlines of Peru and Chile of species with different geographic origins (Santelices, 1980). This region is characterized by high endemism (32.3% of the flora) and a very unequal contribution of tropical (3.4%) and sub-Antarctic (34.4%) species. The number of

tropical species decreases towards the South Pole, while the sub-Antarctic elements increase. The abundance of endemic species is relatively similar along most of the coastline, as is the abundance of the other two algal groups found there, namely the widely distributed (22.8% of the flora) and bipolar (7.1%) species.

However, sometimes the situation is more complicated and requires a more comprehensive explanation. This is especially the case for ichneumonids and aphids. Three hypotheses have been proposed:

The "**resource fragmentation hypothesis**" (RFH; Janzen & Pond, 1975; Janzen, 1981) has been used to explain the inverse latitudinal trends in species richness of Ichneumonidae. It assumes that as species richness becomes very high, the increasing number of potential host species does not support an increasing richness of parasitoid species because each of the additional potential host species is too rare to be exploited by specialist parasitoids. Below some threshold host density, parasitoids cannot find specific hosts, or cannot maintain viable population sizes over ecological time. The effect may be promoted by aspects of the lowland tropical climate: prey "bloom" of hosts that could support specialists, producing temporal fragmentation of resources (Janzen & Pond, 1975). To overcome resource fragmentation, tropical ichneumonids must be more polyphagous, or better at finding rare hosts (Janzen, 1981; Gauld & Gaston, 1994). Shaw (1994) proposed a related idea that fragmentation of hosts in the tropics affects speciation rates, so that radiations of parasitoids, particularly specialists, have not occurred in the tropics as extensively as in the temperate regions. When hosts are abundant and populations large, specialists can radiate by colonizing new hosts; smaller and more dispersed tropical populations present fewer opportunities for parasitoids to speciate in this manner. Further, predation may be more intense in tropical than in temperate ecosystems (Paine, 1966; Elton, 1973). Adult ichneumonids also suffer predation and, in the tropics, important predators such as birds, asiliid flies and dragonflies are abundant. If specialists spend more time searching for hosts, they will be more exposed to predators and thus would be more constrained than generalists in the tropics (Gauld, 1987).

The "**nasty host hypothesis**" (NHH) is based on the observations that toxicity is more common in tropical than in temperate plant communities (Levin, 1976; Coley & Aide, 1991; Basset, 1994) and that plant allelochemicals in host tissue can injure immature parasitoids (for example Duffey, Bloem & Campbell, 1986). Thus Gauld *et al*. (1992) proposed that increased toxicity, accompanied by great variety in the types of toxins, may make hosts in the tropics on average less accessible to parasitoids, leading to the observed decline in

species richness. To overcome host toxicity, a parasitoid lineage will have to become more specialized. As evidence, Gauld *et al.* (1992) noted that diversity is not lower among tropical parasitoids attacking life-stages of their hosts that are not chemically well-defended, such as eggs or pupae (except of the pupae of insects that sequester plant chemicals into adulthood), or attacking insects that feed on plant tissues containing few allelochemicals, such as sap or wood. Sime and Brower (1998) suggest that for parasitoids associated with the Papilionoidea, the NHH is the most and the RFH the least likely to explain their diversity patterns. Predation hypotheses may apply to parasitoid lineages whose hosts vary in concealment from predators. However, these mechanisms do not explain why this should have a disproportionately adverse effect on parasitoid diversity relative to host diversity.

*The "**common host hypothesis**"* (CHH). From Dixon *et al.* (1987) and Kindlmann (1988) it follows that inverse latitudinal trends in species richness should be found in groups, in which species are characterized by five main attributes: (1) host specificity, (2) necessity to look for the host periodically, (3) random host search, (4) short time available to find the host, and (5) the species richness of the group, to which their host belongs, increases towards the tropics. Host is understood here in the commonest sense, i.e. host for a parasite, plant for an herbivore etc. Actually, because of (1) and (2), the survival of the species is vitally dependent on periodical looking for the specific host. However, because of (3) and (4), the host of such species must be "relatively common" (that is, its abundance must exceed a certain critical value) – otherwise the individuals are not able to find it, as they have only a limited time for random search (Fig. 12.1). In the tropics, only a small proportion of the host species is "relatively common", as – because of (5) – there are many potential host species in the tropics, only few of them can therefore be "relatively common" (Fig. 12.1). In a sense, the CHH is a generalization and refinement of the RFH.
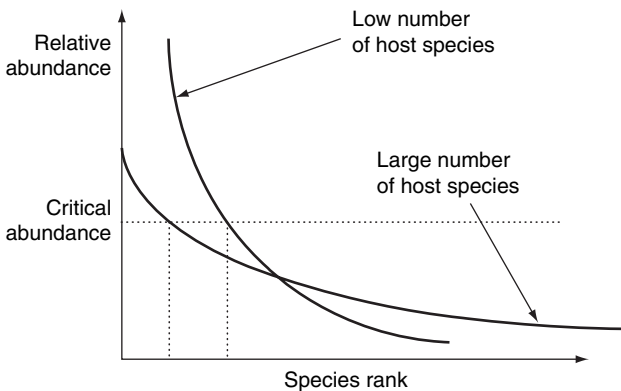

Figure 12.1 Illustration of the "common host hypothesis". Regionally present species from the host group are ranked here according to their relative cover. In communities where the total regional number of host species is large, the proportion of species whose relative cover (or abundance) exceeds the critical abundance is low.

Testing the common host hypothesis

Aphids are an ideal group, as they satisfy five main attributes. Most aphids feed on only one or a few species of plants, or commute between two plant species, a winter host and a summer host (host-alternating aphids) – (1). Because of their enormous population growth rates, they frequently overexploit their host plants and then it is advantageous for individuals to fly off and seek hosts elsewhere – (2). Because of their small size, they have little control of the direction of their flight, and therefore they look for their host plant at random – (3). It is advantageous for aphids to have high growth rates and short generation times. This is nicely illustrated by the parthenogenesis and telescoping of generations (a female has her own granddaughter developing in her gonads), characteristic of aphids. Thus migrant aphids have only a short time to search for a host plant – (4). The species richness of plants, the group they feed on, increases towards the tropics – (5).

The subfamilies of ichneumonids scarcer in the tropics are usually specialists – (1), they are parasitoids and have to search for hosts – (2), they often attack concealed hosts, which introduces a random element into their host search – (3), they lay many eggs and therefore they do not have much time for laying each egg – (4) and the diversity of their hosts increases towards the tropics – (5). Therefore it is not surprising that the diversity of these ichneumonids declines towards the tropics.

Janzen and Pond (1975) and Janzen (1981) suggest that low host population density acts as a barrier to ichneumonid species-richness by rendering certain species too scarce to serve as a specialist's host. The common host hypothesis (CHH) suggests that besides the absolute host density the relative one could also play a role.

Psyllids can serve as a counterexample. They are similar to aphids in terms of their host specificity (Hodkinson, 1974) and ability to find their host plants (Moran, 1968; Moran & Brown, 1973). Nevertheless they are most numerous in terms of species in the tropics (see for example Hodkinson, 1986). Psyllids can live for a long time as adults – for months, rather than only for days or weeks as do aphids – so they do not satisfy (4). Since they lay eggs and do not have to meet the high food demands of embryos developing within them, as aphids do, psyllids possibly survive for prolonged periods off their host plants. Long adult life combined with the ability to survive off the host plant for long periods greatly increase the probability of finding a host plant.

A similar situation occurs in coccids. They search for their host plants at random – they are passively dispersed by wind. But they have a lower growth rate than aphids, only completing one or two generations per year (Dixon, Hemptinne & Kindlmann, 1987). Their long life does not increase their probability

Table 12.1 *Reproductive success of orchids, measured as the percentage of flowers pollinated per plant, in various parts of the world*

Geographic area	Nectar bearing Rewarding		Nectarless Deceptive	
	% RS	(*N*)	% RS	(*N*)
North America	49.3	(11)	19.5	(9)
Europe	63.1	(8)	27.7	(29)
Temperate zones, southern hemisphere	74.4	(3)	41.4	(8)
Temperate zones of Asia	43.0	(3)	–	–
Temperate zones	**56.0**	**(25)**	**28.5**	**(46)**
Tropics	**24.9**	**(5)**	**11.5**	**(27)**

Numbers of species considered are in brackets.
Source: Neiland & Wilcock (1998)

of finding a host plant, as is the case for psyllids. However, due to their low growth rate they are less likely to overexploit their hosts. Consequently, for coccids there is less urgency to find another host plant of the same species – so they do not satisfy (2). That is, there is not such a great advantage in regularly dispersing and searching for more suitable hosts, and dispersal is less important for their survival. They can exploit even uncommon plants and therefore their species diversity may increase towards the tropics.

The CHH is supported indirectly by the following: if the CHH is correct, then the host plants of aphids should be common. Dixon *et al.* (1987) checked the percentage of plants of three plant families (Asteraceae, Ranunculaceae and Daucaceae) in Czechoslovakia that host aphids. This revealed that the common species of plants (as indicated by the Flora of Czechoslovakia, where each plant species is characterized as "common", "scattered" or "rare" by the authors) are five times more likely to have aphids associated with them than are scattered or rare species. Similarly, the most abundant species of the families Euphorbiaceae, Lamiaceae and Viciaceae are more likely to host aphids than the rarer species. Most of the plant species that host aphids, but are indicated as rare in the Flora of Czechoslovakia, are more abundant in adjacent countries (Dixon *et al.*, 1987).

Beyond the scope of species richness patterns is another application of the CHH: the reproductive success of orchids, measured as the percentage of flowers pollinated per plant, consistently declines towards the tropics (Table 12.1, Neiland & Wilcock, 1998). With respect to the assumptions of the CHH, for successful pollination, the insect pollinators have to transfer pollen from one

species to the same plant species – (1), they have to do it every flowering season – (2), they visit the plants at random – (3), the visitation sequence has to be short – otherwise they lose the pollinia they are carrying – (4), and the species richness in Orchidaceae increases towards the tropics – (5). Thus the CHH predicts the pattern observed in Table 12.1.

Conclusion

Certain taxonomic groups do not follow the usual trend of increasing species richness from the poles to the tropics. One explanation for this is that it is a consequence of the constraints imposed by the way of life of the group. In groups where dispersal from one host patch to another occurs frequently and the individuals look for hosts at random, the common host hypothesis suggests that their species diversity should be inversely related to the species diversity of their hosts. Any deviation from the above-mentioned assumptions results in the usual trend in the latitudinal gradient in species richness.

The empirical data for several groups indicate that the CHH can explain several inverse latitudinal gradients. Nevertheless, the very diversity of nature makes it likely that this is not the only explanation.

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