# Latitudinal and longitudinal barriers in global biogeography

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# Latitudinal and longitudinal barriers in global biogeography

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†*This paper is dedicated to the memory of my grandmother, Elisabeta Vilt (1921–2005) who brought me up in a world of colourful maps*

**Due to changes in climate and continental arrangement, plant and animal assemblages faced different dispersal barriers at different moments in Earth's history. It is generally accepted that groups which diversified during times of Gondwanan–Laurasian separation show different distribution patterns from those of more recent origin. Here I present principal component-derived maps for two globally distributed groups, with *ca* 1000 species each. Gymnosperm assemblages perfectly illustrate the existence of southern and northern components, corresponding to the Gondwanan and Laurasian temperate floras at the time when angiosperms started becoming dominant in the tropics, thus imposing a latitudinal barrier. Bat (chiropteran) assemblages indicate that the major biogeographical barrier in their Cenozoic dispersal was the longitudinal separation between the Old and New World.**

**Keywords:** bats; biogeography; Gondwanaland; gymnosperms

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## 1. INTRODUCTION

Earth's biogeographical regions were traditionally defined on the basis of having distinctive faunas and floras, and their number and delimitation are confirmed to some extent by modern analytical methods (Smith 1983; Procheş 2005). However, few borders between regions correspond to abrupt changes in animal or plant assemblages, and most fall in the middle of broad species replacement gradients (Williams 1996). Real demarcation lines are only evident where sharp barriers exist between two regions. The most obvious example is represented by oceanic basins that prevent frequent dispersal between terrestrial systems, but areas with unfavourable climate, interposed between two regions, can also represent barriers in the dispersal of organisms.

For organisms with good dispersal abilities, the Neogene arrangement of continents allows for free movement within the Old World and within the New World, but generally prevents movement between the two, with the exception of cold-tolerant taxa, which can make use of the intermittent opening of the Bering corridor (Sanmartín *et al.* 2001). The global positioning of land masses was different during much of the Mesozoic, when most of world's dry land was interconnected, but temperate assemblages in the north and south were separated by a broad, relatively uniform band of warm climate (Anderson *et al.* 1999; Scotese *et al.* 1999).

It is broadly accepted that numerous animal and plant groups conserve Gondwanan or Laurasian distribution patterns, and that such elements can lend Gondwanan/Laurasian character to regional faunas and floras (Good 1974; Sequeira & Farrell 2001). Likewise, it is acknowledged that in numerous 'modern' groups the most striking difference is that between the Old and New World assemblages (Cristoffer & Peres 2003). However, there has been no attempt to quantify in a spatially explicit manner variation in assemblage composition in cosmopolitan groups of different ages (the widespread, but not cosmopolitan genus *Bombus* being the closest call; Williams 1996). Here I show that, in bats and gymnosperms, the signal from past and present biogeographical barriers is strong enough to be analytically illustrated.

## 2. MATERIAL AND METHODS

The distributions of two large (*ca* 1000 species each), cosmopolitan taxa (bats, as an example of a modern, Cenozoic group, and gymnosperms, as an ancient, Mesozoic group) were used to illustrate global patterns of variation in generic assemblage composition. In the case of gymnosperms, the Gnetales were omitted, as some recent phylogenies place them as sister taxon to the angiosperms (and, under this hypothesis, their inclusion would have made gymnosperms paraphyletic; see Schmidt & Schneider-Poetsch 2002). While gymnosperm phylogeny is not definitively agreed on (Hill 2005), the inclusion of Gnetales (or the exclusion of Ginkgoales and Cycadales, included here) would not seriously alter the observed patterns, which are almost entirely due to conifer (Pinales) distributions. The distribution of each species was digitized at the 15° scale, based on comprehensive treatments (Corbett & Hill 1991; Farjon 2001; Jones 2002 and references therein). Fifteen degree squares make a rough cell size, but sufficient to illustrate patterns at a continental scale (for a discussion on the advantages and limitations of this cell size see Procheş 2005). To minimize errors resulting from the slightly unequal cell area, only cells between 60° N and 45° S with at least five species were considered in either analysis. (There are no bat or gymnosperm species endemic at higher latitudes.) Principal component analyses (PCAs) were conducted on the presence/absence of genera for either group (STATISTICA 6.1, copyright StatSoft, Inc. 1984–2003). Each factor (component) identified in the analyses thus corresponded to an assemblage of taxa of a certain geographical affinity, i.e. richly represented in a particular set of regions (cf. Barbujani 2000). The purpose of the study being to identify the single most important global-scale barrier in either group of organisms, only the first two factors derived from each analysis (cumulatively accounting for *ca* 50% of the variation in either group) were retained. The value of each factor was quantified as colour intensity (cyan and yellow, respectively; cf. Brewer 1994; Andrienko *et al.* 2003). The hues resulting from the combination of colour intensity on the two axes were used to map assemblage variation globally, cells shown in more similar colours thus having more similar bat/gymnosperm assemblages.

## 3. RESULTS

The two groups considered here showed contrasting patterns in global assemblage variation. In bats, the first factor (explaining 32.56% of the variation) ranged from −0.8 in the temperate regions of the Old World to 0.2 in the tropical New World (the most species-rich region globally). The second factor (explaining 14.56% of the variation) had values of −0.4 (in tropical Southeast Asia, with the most species and genus-rich fauna in the Old World) to 0.7 in the tropical New World. Therefore, globally, the clearest distinction was that

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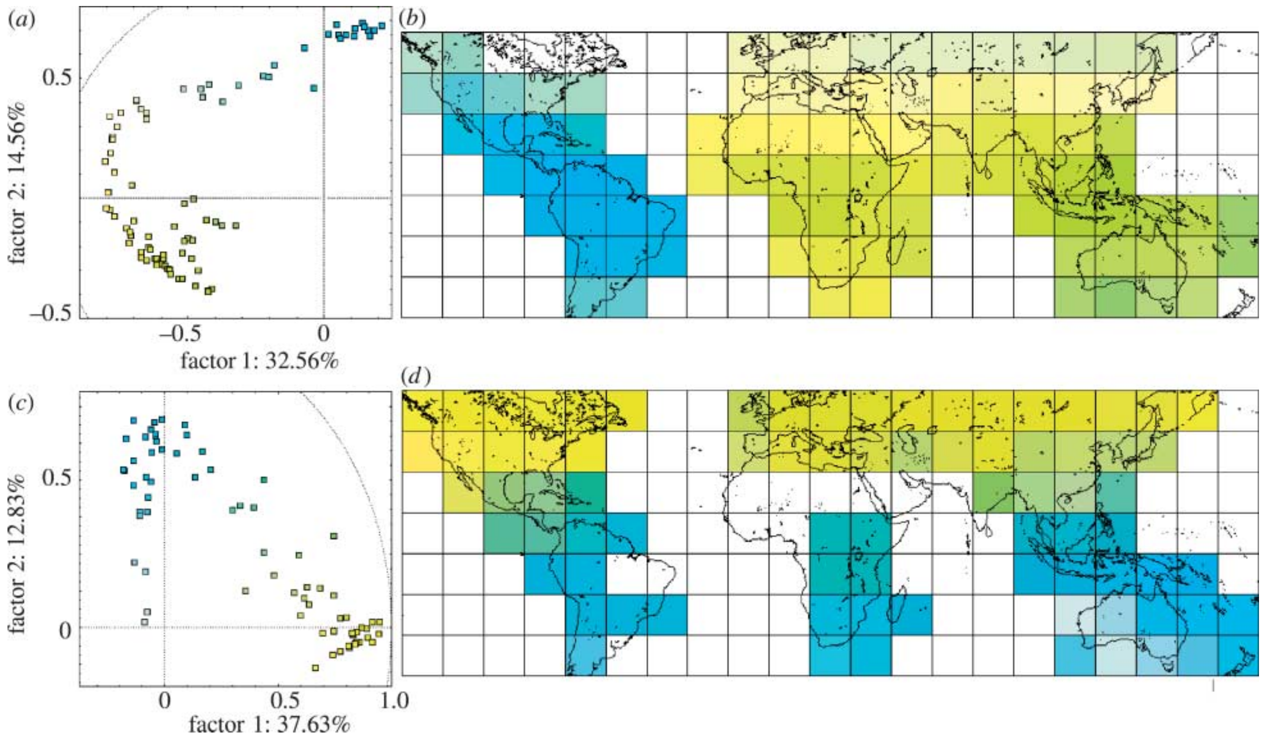

Figure 1. Principal component analyses (*a*, *c*) and maps showing global variation in assemblage composition (*b*, *d*) for bats (*a*, *b*) and gymnosperms (*c*, *d*). Only 15×15° cells with more than five species in either group were included in the analyses.

between the tropical regions of the New and Old worlds. In the south, the temperate regions were entirely separated, but there was a smooth transition between the northern temperate regions of America and Eurasia (where several bat genera are shared; figure 1*a*,*b*).

In gymnosperms, the first two factors (explaining 37.63 and 12.83% of the variation, respectively) corresponded to the northern (factor 1) and southern (factor 2) floras. There were clear clusters of cells at high values on either axis, with a series of transitional cells corresponding to Central America and Southeast Asia ranging between them (figure 1*c*,*d*).

## 4. DISCUSSION

The cells with high score on the principal component axes largely correspond to the areas with the richest and regionally most representative bat and gymnosperm assemblages (see Findley 1993; Contreras-Medina & Vega 2002), confirming that the first two factors do indeed capture the major global patterns in assemblage variation.

How do the patterns mapped here fit in with currently accepted phylogeographic scenarios? From the limited bat fossil record, it appears that extant lineages diverged soon after the Cretaceous–Paleogene boundary, and diversified mostly in the northern landmasses, where the most plesiomorphic forms and/or the oldest fossils are found (as is the case with Pteropodidae, Rhinolophoidea, Emballonuroidea, Vespertilionoidea). One lineage (Noctilionoidea), however, diversified in the Southern Hemisphere and its three families are currently endemic to New Zealand, Madagascar and tropical America, respectively (Teeling *et al.* 2005). As the distance between the southern continents increased, these became isolated from one another; and more recent imports from the north found themselves equally isolated from one another, with only one clear case of Atlantic crossing (Emballonuridae; Teeling *et al.* 2005). With a continuous warm climate belt from Africa to Asia and Australia, tropical bat assemblages in the Old World stayed fairly homogeneous. They were, however, separated from the New World by the Atlantic and Pacific oceans. On the other hand, cold-adapted lineages (Vespertilionidae, Molossidae) found it relatively easy to cross the narrower barriers between North America and Eurasia. This scenario is perfectly reflected in the highly dissimilar bat assemblages in the southern continents and in the tropics, with a gradual transition from the Old to the New World in the northern temperate band.

In the case of gymnosperms, conifers and cycads need to be discussed separately. The major extant conifer lineages are of Jurassic age (Anderson *et al.* 1999). At that time, some families, like the Araucariaceae, had a broad distribution (Sequeira & Farrell 2001). During the Cretaceous, recently diversified angiosperms largely out-competed slow-growing conifers from the tropical belt (Bond 1989), and different sets of taxa survived in the Northern and Southern Hemispheres (or, if the same taxa survived, they evolved further in complete isolation, resulting in different present-day genera, as may be the case in Cupressaceae and Taxaceae; see Hill & Brodribb 1999). Cooler climates during the Cenozoic allowed both northern and southern lineages to expand and diversify (LePage 2003; Quinn & Price 2003), and even to re-colonize to the tropical belt, where northern and southern lineages co-occur to a limited extent (in Central America, Southeast Asia, East Africa; see figure 1*d*). Therefore, it can be said that conifer assemblages are in the process of breaking the latitudinal barrier represented by tropical angiosperm forests—mainly, but not only, along longitudinal mountain ranges. However, figure 1*d* shows that the relictual patterns separating northern and southern assemblages are largely conserved, and the recent tropical intermixing is extremely limited.

Cycads and *Ginkgo* were included in the dataset, but their limited and fragmented distribution did not grant them an effect on the first two factors separated by the analysis. In cycads, a distinction between northern and southern taxa is not as clear (see Jones 2002). Owing to their mainly tropical modern distribution and long independent evolution in the New and Old Worlds, global cycad assemblages, when considered alone, show a pattern more similar to that observed in bats (data not presented), and given the potential paraphyly of the gymnosperms, this can be viewed as a third, independent analysis. However, the differences between Australia and Africa are much greater here (only one common genus: *Cycas*), making it more meaningful to talk of three, rather than two 'worlds', with three longitudinal barriers, represented by three oceans.

It can be argued that bats and gymnosperms represent ideal groups to show such contrasting hemispherical patterns, and that in most other groups global-scale barriers will not be nearly as clear. Indeed, most taxa of comparable diversity are likely to be either geographically restricted (e.g. completely absent from temperate regions, Australia or the New World) or at least imbalanced at higher taxonomic levels (Procheş 2005). Looking at the single most important barrier globally would be insufficient in such cases, and more than two PCA-derived factors would be needed to fully visualize variations in global assemblage composition.

Principal component analysis used in combination with colour cartography, as exemplified here, represents an attractive way of illustrating geographical barriers and gradients. This method and other spatially explicit techniques, such as neighbourhood turnover indices (Williams *et al.* 1999) or Monmonier's algorithm (Manni *et al.* 2004), can complement phylogeographic reconstruction by providing a powerful visualization tool.

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