

**ECOLOGICAL BIOGEOGRAPHY: A REVIEW WITH EMPHASIS ON
CONSERVATION AND THE NEUTRAL MODEL**
*BIOGEOGRAFÍA ECOLÓGICA: REVISIÓN CON ÉNFASIS EN CONSERVACIÓN Y EL
“MODELO NEUTRAL”*

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RESUMEN

La biogeografía ecológica estudia los factores que definen la actual distribución espacial de los organismos. Esta revisión resume los aportes más recientes en este campo, en el cual . la mayoría de los artículos recientes informan que factores ambientales como temperatura, humedad y salinidad son elementos clave en la biogeografía ecológica de muchas especies (seguidos de interacciones con otros organismos, y características genéticas). La biología molecular está develando que algunas "distribuciones incomprensibles" son en realidad el resultado de identificaciones taxonómicas incorrectas en que varias especies eran consideradas una sola especie. La teoría de biogeografía de islas a menudo es aplicable a la conservación, pero el nuevo modelo neutralista de biogeografía ecológica no calza con algunos de los organismos a los cuales se ha aplicado. El calentamiento planetario probablemente producirá ampliaciones de ámbito, dispersiones y nuevas invasiones. Hasta ahora, la mayoría del trabajo experimental en este campo se ha hecho en ecosistemas templados, por lo que en el siglo XXI, la biogeografía tropical debe hacer contribuciones significativas mediante simulaciones y experimentos de campo y de laboratorio, sobre los ámbitos de distribución geográfica y la biogeografía de comunidades.

PALABRAS CLAVE: revisión, biogeografía ecológica, templada versus tropical, calentamiento global, productividad científica por país.

ABSTRACT

Ecological biogeography studies the factors that define the spatial distribution of species in the present time. This review summarises recent contributions on ecological biogeography. Most recent articles report environmental factors such as temperature, humidity and salinity as key elements in the ecological biogeography of many species (followed by other organisms and genetic characteristics). Molecular data indicate that some "unexplainable" ranges are artifacts caused by taxonomic misidentification (several species erroneously classified as a single species). Island biogeography theory is often adequate for conservation management, and the new neutral model of ecological biogeography does not fit all species on which it has been tested. Global warming leads to range expansions, dispersal events, and new invasions. Until now, most experimental work has been done on temperate ecosystems. In the 21st century, tropical biogeographers should do landmark contributions by doing field, laboratory and simulation experiments about species ranges and community biogeography.

KEY WORDS: review, ecological biogeography, temperate versus tropical, global warming, scientific productivity by country.

INTRODUCTION

Biogeography studies the geographic distribution of organisms. Some of the key questions that this branch of biology attempts to answer are: How did organisms reach their current habitats? Why do not they expand their current ranges? Why does an ecosystem have a particular number of species?

Historical biogeography addresses the first question: past causes of organismic distribution, and was reviewed in a previous Gayana article (Monge-Nájera 1999). The other branch, ecological biogeography, studies the factors that define the spatial distribution of species in the present time. These factors are mainly ecological, and include other organisms and genetic characteristics (biotic factors) as well as environmental factors such as temperature, humidity and salinity (abiotic factors). An important recent contribution quantified the role

of historical versus ecological biogeographic factors: in Mediterranean rivers, 21% of the distribution of caddisflies is explained by ecological factors, 3% by historical processes, 0.3% by both factors, and the rest is unaccounted for (Bonada *et al.* 2005).

Recent general papers on biogeography deal with the need for complementary ecological and historical approaches (Wiens & Donoghue 2004, Biswas & Pawar 2006); a general review with emphasis on the Chinese biota (Chen & Song 2005); the interface between taxonomy and biogeography (Williams & Reid 2005), and history (Lyell's view: Bueno-Hernández & Llorente-Bousquets 2006).

This review summarises recent contributions on ecological biogeography, considering the application of island biogeography theory to ecology and conservation, and the application of the new neutral model of ecological biogeography.

Ecological factors that explain organic distribution on land

Until recently, deep ignorance of the number of bacterial species in any single place has prevented work on the ecological biogeography of bacterial communities. The cause of this limitation is that the methods developed in the 19th century, and still in use today, only allow identification of bacteria that can be cultured, and there are no culture methods for most species. New genetic techniques, however, have begun to overcome such limitations, and it is now known, for example, that the only ecological variable that clearly correlates with bacterial distribution on soils worldwide is pH (Fierer & Jackson 2006). The idea that bacteria show no biogeographic patterns has been rejected on the basis of soil bacteria distribution in Mexico, where, furthermore, the number of individuals per species can be graphically described by a hollow curve, just like in vertebrate communities (Noguez *et al.* 2005).

Strains from decaying wood in Veracruz, Mexico, have evolved substrate selectivity: in this case, the direct ecological limitation to their spatial distribution is the availability of proper substrates (Pinzón-Picaseno & Ruiz-Rodriguez 2004).

The abiotic factors that define the ecological biogeography of plants on land, have been shown to be climate in the case in the vegetation of the Tibetan Plateau (Chen *et al.* 2005) and the Australian Euphorbiaceae (Hunter 2005); and soil characteristics for the grassland communities of Europe (Dengler 2005) and the Aizoaceae “stone plants” of South Africa

(Ellis *et al.* 2006). Two important biotic factors are dispersal and predation. Dispersal ability explains the ranges and abundance of forest plants in Panama (Chust *et al.* 2006) and of rice (*Oryza*) in Southeast Asia and New Guinea (Vaughan *et al.* 2005). The presence of grazers defines the spatial distribution of grassland species (Tallowin *et al.* 2005), and herbivory by deer defines the metapopulation ecology of plants on the Florida Keys (Barrett & Stiling 2006).

Invertebrate distribution can be explained by a combination of abiotic and biotic factors. In some groups, like subterranean crustaceans, temperature is an overriding factor (Issartel *et al.* 2005). In others, single biotic factors explain most of their distribution, for example, the chemical exclusions of other parasites in Rickettsiaceae (Kocan *et al.* 2004), predation in soil mites (Ruf & Beck 2005) and phylogenetic constraints in New Zealand land snails (Barker 2005). Finally, for most species, a larger combination of factors explains their ecological biogeography (*e.g.* Vargas *et al.* 2004).

There are several recent contributions about abiotic factors defining vertebrate ranges. Moisture and temperature define the ranges of Plethodontidae (“lungless”) salamanders (Marshall & Camp 2006), and also defined the ranges of Saurischian and Ornithopod dinosaurs in East Asia (Matsukawa & Lockley 2006). Other key abiotic factors are water, for the lizard *Uma inornata* in California (Chen *et al.* 2006); longitude, for birds in the North American riparian habitats (Skagen *et al.* 2005); light, for Tropical forest birds in Panama (Berg *et al.* 2006), and temperature for Madagascan lemurs (Lehman *et al.* 2006). Like in other groups, overriding biotic factors are less frequently cited, but examples include birds (wood warblers in North America) and dwarf chameleons in South Africa, whose spatial distribution is clearly defined by vegetation (Kelly & Hutto 2005, Tolley *et al.* 2006).

Ecological factors that explain organic distribution in aquatic habitats

In freshwater ecosystems, water level and temperature often affect organismic distributions. The recent increase in temperature has allowed nonindigenous and invasive water plants to expand their ranges in Sweden (Larson 2006). In Mediterranean rivers, 21% of the distribution of caddisflies is explained by a combination of ecological factors (Bonada *et al.* 2005). Wetland bird distribution in Canada is strongly defined by the water level

(Desgranges *et al.* 2006), and temperature draws the limits for the range of *Trachemys scripta* turtles (Willette *et al.* 2005).

The sea is probably the biome where the ecological biogeography of organisms has been more intensively studied. Maybe the reason is that, in comparison with forests and other terrestrial ecosystems, the ocean is a physically simpler medium. Abiotic factors known to define organismic regions in the ocean are temperature, substrate, currents, light and nutrients, among others. For example, temperature explains the distribution of fish larvae in Jalisco, Mexico (Navarro-Rodríguez *et al.* 2004); Archaeobacteria in North America and Crimea (Knittel *et al.* 2005); seabirds in the Pacific (Smith & Hyrenbach 2003); sea stars in the Gulf of California (Cintra-Buenrostro *et al.* 2005); dinoflagellates cysts in the Arctic (Matthiessen *et al.* 2005); coccolithophores worldwide (Baumann *et al.* 2005) and red tide precursor organisms in the Pacific (Sierra-Beltrán *et al.* 2004).

Substrate characteristics define the distribution of gastropods in Britain (Grahame *et al.* 2006); polychaetes in Canada (Quijon & Snelgrove 2005); echinoderms in Colombia (Neira & Cantera 2005) and chondrichthyan fish in Britain (Ellis *et al.* 2005). Japanese ostracods match ocean currents in their distribution (Ogoh & Ohmiya 2005), and the same is true for sponges worldwide (Woerheide *et al.* 2005), and for bacterioplankton and nutrients in the Baltic Sea (Sipura *et al.* 2005).

An important biotic factor is food, for seabirds in Beringia (Piatt & Springer 2003), sea stars in the Gulf of California (Cintra-Buenrostro *et al.* 2005) and tintinnids in the Mediterranean (Krsinic & Grbec 2006). In the case of Indian Ocean Holothuroids, ranges correlate with dispersal ability (Samyn & Tallon 2005), and in South African ascidians, the correlation is with sociality (Primo & Vazquez 2004).

In contrast with the above examples, no abiotic or biotic factors have been found to explain the ecological biogeography of hydrothermal vent communities in the Pacific (Govenar *et al.* 2005).

Examples of geographic ranges reconsidered after molecular analysis

Molecular techniques are now frequently used to understand the ecological biogeography of all groups of organisms, and have shown that taxonomic misidentification originated some cases of unexplainable distributional ranges, for example in Alopiinae snails, whose

distribution fits genetics, not morphology (De Weerd *et al.* 2004). Unexplainable bird ranges also proved to result from misclassification of convergent taxa in woodpeckers (Moore *et al.* 2006) and Accipitridae hawks (Do Amaral *et al.* 2006).

Examples of novel genetic results include the finding that mycorrhizal fungi are not the host generalist, species-poor group that was previously believed (Fitter 2005) and the discovery of the strong host specialization of plant pathogenic fungi in North America (Johnson *et al.* 2005).

Genetics also show that the range recoveries of some groups, such as the red oaks of the USA, are endangered because recent populations growing on old pasture lands have low genetic diversity (Gerwein & Kesseli 2006). A similar problem affects damselflies in England (Watts *et al.* 2005), shrews in Tanzania (Stanley & Olson 2005) and prong horn antelopes in the USA (Stephen *et al.* 2005). In contrast, the ravens of the world appear to be one species with a climate-defined biogeography and large genetic variation (Omland *et al.* 2006).

Barriers are the defining element of ecological biogeography, and recent genetic work shows that barriers can be ethological in the case of the Arctic charr (Adams *et al.* 2006) and the Mallorcan midwife toad (Kraaijeveld-Smit *et al.* 2006), but also climatic (for marmots in the USA, Floyd *et al.* 2005) or topographic (for North American salamanders, Liu *et al.* 2006).

Genetics are also applied to understand the distribution of freshwater organisms. Physical barriers affect *Thioalkalivibrio* bacteria worldwide (Foti *et al.* 2006), and several fish species: the bass in the USA (Cooke & Philipp 2006), sardines in Brazil (Paiva *et al.* 2006), the Atlantic Salmon in Russia (Primmer *et al.* 2006) and Australian *Leiopotherapon* fish (Bostock *et al.* 2006). On the other hand, genetic barriers appear to define the ranges of brown trout in Norway (Heggenes *et al.* 2006) and bluegill sunfish in Japan and Korea (Kawamura *et al.* 2006). In the case of the Pearly Mussel in the USA, no isolation by distance has been found (Grobler *et al.* 2006). Molecular techniques have shown that the extraordinarily large and varied ranges of some species are produced by taxonomic misidentifications. In these cases, the ranges of several species were thought to be the range of a single species. Examples are snails in Japan and the Crystal Darter in the USA (Kamiya & Shimamoto 2005, Morrison *et al.* 2006).

On marine ecosystems, genetics have shown that ranges can be defined by both abiotic and biotic barriers. Abiotic barriers were identified in English snails, for which a cliff acts as the barrier (Grahame *et al.* 2006), and for Pacific snails (Meyer *et al.* 2005). Mussels in the Indian Ridge and the Atlantic Ridge are limited spatially by endosymbiosis (McKiness & Cavanaugh 2005); and again, as in vertebrates, strange ranges may also represent taxonomical misidentifications, for example in Atlantic amphipods (Kelly *et al.* 2006). In other cases, traditionally recognized “barriers” such as the East Pacific Barrier and the Bahamas barrier do not significantly impair gene flow for some fish species (Robertson *et al.* 2004, Taylor & Hellberg 2006).

Island biogeography

One aspect of ecological biogeography, island biogeography, received much attention at the end of the 20th century, first on theoretical grounds, then on its potential application to the problem of conservation of organisms in "islands of protected nature" in an anthropologically changed world.

The MacArthur and Wilson model of island biogeography (MacArthur & Wilson 1967) was based on common sense principles: islands that are big and close to species sources should have more species, and diversity results from the equilibrium of species addition and extinction. Maybe for that reason, most recent literature reports that such principles hold for real islands. Examples include bacteria and shrubs in Spain (Maestre & Cortina 2005, Reche *et al.* 2005); diatoms in Antarctica (Van de Vijver *et al.* 2005); vascular plants in North America (McMaster 2005); calcareous grasslands in Belgium (Bisteau & Mahy 2005); forest and sedge land in Australia (Driscoll 2005); *Pinus* populations in China (Chiang *et al.* 2006); land snails in Greece and New Zealand (Barker 2005, Triantis *et al.* 2005); dung beetles in Namibia (Sole *et al.* 2005); fish in Hungarian streams (Eros & Grossman 2005); seabirds in Australia (Priddel *et al.* 2006); birds of prey, in the Mediterranean and Macaronesian Archipelagos (Donazar *et al.* 2005); birds in Britain and Ireland (Russell *et al.* 2006), and Howler Monkeys in Venezuela (Feeley & Terborgh 2006). By contrast, the model could not explain the island biogeography of Australasian land snails, possibly because it neglects *in situ* speciation (Cameron *et al.* 2005), and forest-savanna mosaics in Africa (Hovestadt *et al.* 2005).

General recent developments in island biogeography refer to the “z” index, curvilinear pattern, life history and leaf lifespan. Low “z” values correlate with high colonization ability; a multi-species metapopulation model indicated that the relationship of “z” with important parameters can be predicted only if either the dispersal ability or the power of establishment is known (Hovestadt & Poethke 2005). He *et al.* (2005) presented a new model for local-regional species richness in ecological islands that does not require species interactions to produce the curvilinear pattern. Using island biogeography theory, they found that a high extinction rate produces a curvilinear pattern of local-region relationships, while a high colonization rate produces a linear pattern. Equilibrium models need to consider life history traits, because one island can be in equilibrium and have barriers for one organism, but not for others (Shepherd & Brantley 2005). Finally, it has been stated that better biogeography models for vegetation should include leaf lifespan (Zhang & Luo 2004).

Island Biogeography and Conservation

Island biogeography is often applied in conservation for hypothesis testing, finding ways for wildlife-human coexistence, and prediction.

A long term (40 years) study in Japan found that biodiversity in “islands of habitat” in a matrix of “non-habitat” can be summarized with the phi-coefficient, which has the advantage, over other indices, that it can be combined with the Chi-square test to statistically test hypotheses (Yasuda *et al.* 2005).

Regarding coexistence, urban water reservoirs can conserve the bulk of tropical molluscan biota in Southeast Asia, especially when the pH is near 7.3 and the habitat includes rocks (Clements *et al.* 2006). Ecologically managed agri-environments ("agri-environment schemes") help the biota adapt to climate change, and slow the spread of alien and invasive species (Donald & Evans 2006). Similarly, a limited extraction of trees from African evergreen forests benefits understorey bird diversity and has little effect on canopy birds (Holbech 2005). A theoretical framework is now available to apply island biogeography models to temporary wetlands and their biota under anthropogenic stress (Angeler & Álvarez-Cobelas 2005)

The island biogeography model predicts 80% of butterfly fish biodiversity in 48 islands of the Western and central Pacific (Kulbicki *et al.* 2005), while regional heterogeneity and compositional turnover can predict the number of protected areas necessary to protect mammals in Canadian ecoregions (Wiersma & Urban 2005). However, the model failed when patch size and isolation were used to predict understory plant restoration success in a highly fragmented riparian landscape of California (Holl & Crone 2004).

The impact of species introductions is also studied by island biogeography. The introduction of Arctic foxes for fur production in the Aleutian and Kurile islands greatly decreased the population of Whiskered Auklets from the 1700's to 1900's. Foxes began to be eradicated after 1948, and these birds have now recovered (Williams *et al.* 2003). Island biogeography can also be successfully combined with molecular analysis and conservation, as when DNA analysis showed that Asian badgers are closely related to the endangered population in Crete Island, so that they can be used for a reintroduction program (Marmi *et al.* 2006).

Hosts can also be considered islands, colonized by parasites. For example, protozoans use two zones of an octopus digestive tract and develop different life history strategies in each (Ibañez *et al.* 2005). Mexican freshwater fish parasites conform to the historical and ecological biogeography of their hosts, both taxonomically and biogeographically (Perez-Ponce de León & Choudhury 2005). Parasites of five Goby Fish species from the Baltic sea studied by a combination of island biogeography theory, and the “theory of screens”, show that colonization by parasites has three types of “distance” to the island-hosts: genetic, phylogenetic and ecological (Zander 2005). The composition of parasitic species in fish and mammalian hosts, suggests that parasitisation follows predictions from the island biogeography model (*e.g.* larger hosts have more parasite species) and from epidemiological theory (*e.g.* parasite transmission increases with host density) (Poulin 2004).

Plants can also be considered islands to be reached by herbivores, but only herbivores that can recognize a host whilst in flight, align on patches of vegetation according to island biogeography models (Bukovinszky *et al.* 2005).

The neutral theory of ecological biogeography

The neutral model of ecological biogeography is an outstanding and controversial point of 21st century biogeography. It was presented in book length by Hubbell (2001).

The neutral model is a good null hypothesis to explain fires in natural habitats, which are basically stochastic processes. Real data show that topography, fuel, and other factors, affect natural fires (McKenzie *et al.* 2006). The model also predicts genetic diversity in the annual plant complex “*Mercurialis annua*”, in which monoecy predominates over other reproductive options when colonization is frequent (Obbard *et al.* 2006). A neutral model was also used to develop a formula for the joint likelihood of observing a given species abundance dataset in a local community with dispersal limitation (Etienne 2005).

The model has failed to predict community structure in many cases. These include aquatic invertebrates in rock pools monitored over a 13-year period (Fuller *et al.* 2005); Indo-Pacific coral communities (Domelas *et al.* 2006); experimental grassland communities (Harpole & Tilman 2006), herbaceous plants on serpentine soil (Harrison *et al.* 2006), perennial grass and shrubs in a semi-arid habitat (Armas & Pugnaire 2005), shifting mosaic habitats (Wimberly 2006) and dispersal-limited communities (Etienne & Alonso 2005).

Nevertheless, both neutral and non-neutral explanations fit data for marine diatoms (Pueyo 2006), some trees in tropical forests (Volkov *et al.* 2005), rotifers (Beres *et al.* 2005), and stream invertebrates (Thompson & Townsend 2006). Gravel *et al.* (2006) believe that traditional and neutral models are extremes of a continuum: when niche and competitive exclusion are important, non neutral theory applies. When immigration plays an important role in the community, there is stochastic species exclusion and the neutral model applies.

The future of ecological biogeography: global warming and conservation

Global warming and its effects on organisms is a key subject at the time of writing this review. Climatic change is a constant of the planet's history, and the past holds the key to understanding the effects of future climate change. The ecological biogeography of fossil crustaceans indicates that a Devonian global warming led to sea-level rises, resulting in range expansions, dispersal events, and species invasions. Simultaneously, opportunities for vicariant speciation were reduced (Rode & Lieberman 2005). The same could be true for

marine species in a currently warming Earth. Nonindigenous and invasive water plants from warm habitats are expected to expand their ranges in temperate areas (Larson 2006); and on land, some barriers will disappear (Floyd *et al.* 2005), specially because range edges may not be physiologically more stressful, as previously believed (Sagarin & Somero 2006).

The latest available studies indicate that, on the basis of a sample composed of 1198 species, the minimum viable population size is 1377 individuals (90% probability of persistence over 100 years) and persistence is more related to habitat than to species characteristics (Brook *et al.* 2006). To prevent the effects of climatic change, Cardillo *et al.* (2006) studied 4000 mammal species and used ecological theory to predict sites where they will need protection in the future, allowing early protection measures.

Conclusion

I want to finish this review by stating that ecological biogeography is now mature enough for intensive experimentation (Pennings & Silliman 2005). Until now, most experimental work has been done on temperate ecosystems. In the 21st century, tropical biogeographers should do landmark contributions by doing field, laboratory and simulation experiments about species ranges and community biogeography. I hope that this review inspires you to stop reading and do your first experiment on ecological biogeography.

ACNOWLEDGMENTS

I thank Andrés Angulo for the invitation to write this review and Guillermo D'Elía for valuable suggestions to improve an earlier draft. Mónica Chaves helped with the library research.

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