

ZOOGEOGRAPHY: AN ECOLOGICAL PERSPECTIVE

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Contents

1. What is ecological zoogeography
 2. Ecogeographical "rules"
 - 2.1. Bergmann's rule
 - 2.2. Allen's rule
 - 2.3. Rapoport's rule
 3. Distribution of animals: patterns and causal factors
 - 3.1. Species conceptualization and delimitation: their importance for zoogeography
 - 3.2. Patterns of distribution
 - 3.3. Endemisms and relicts
 - 3.4. Abiotic ecological factors influencing species distribution
 - 3.5. Biotic ecological factors influencing species distribution
 - 3.6. Animal migration
 - 3.7. Basics of modeling species presence
 4. Animal distribution in a rapidly changing world: the effects of global change
 - 4.1. What is meant by global change?
 - 4.2. Extinction and reintroduction
 - 4.3. The effects of global warming on animal distribution
 - 4.4. The Lessepsian "migration"
 5. Concluding remarks
- Acknowledgements
Glossary
Bibliography
Biographical Sketch

Summary

Zoogeography studies distribution patterns of animal species and processes. This chapter presents some of the main topics covered by ecological zoogeography, involving analysis of the specific ecology of organisms on relatively small spatial and temporal scales. It begins by examining some of the most intriguing zoogeographical patterns concerning animal body size, for which Bergmann and Allen formulated two famous "ecogeographical rules" which, despite being heavily criticized, are now being re-evaluated; and also cover Rapoport's rule, stating that that species' latitudinal ranges are generally smaller at lower than at higher latitudes. It then highlights that understanding the observed distribution of animal species is a key task for

zoogeographers. Species conceptualization and delimitation are vital to reach that goal. Recent advances in DNA studies have revealed previously undetected species, profoundly changing our view of animal distribution. Some species (endemisms) have narrow ranges, others are widespread. Factors such as biogeographical corridors, isolation history, glacial or postglacial events, abiotic and biotic ecological factors and also human impact all influence distribution patterns. Active movement of organisms over short temporal scales also influences the composition of animal assemblages. Migration, one of the most striking phenomena in the animal world, implies a seasonal change in species occurrence in many regions of the world. Science is gradually making important steps forward in identifying the factors that trigger and control migration and orientation. Not only is zoogeography intellectually exciting, it also has important conservation applications because it is vital to understand species ranges for biodiversity management. Besides recording species distribution, state-of-the-art modeling techniques can help predict species range even when little observational information is available, thus aiding species management and conservation. We conclude the chapter by summarizing the biogeographical implications of the massive species extinction occurring on Earth, and discuss global warming as one of the main factors impacting biodiversity and altering species occurrence and distribution. Finally, we use the case of Lessepsian colonization, i.e. the colonization of the Mediterranean Sea by tropical species following the opening of the Suez Canal, as a striking example of human influence on zoogeographical patterns.

1. What Is Ecological Zoogeography

Biogeography studies the patterns of distribution of biological systems, processes or characteristics at several spatial and temporal scales. Spatial scales under analysis span over a wide range, including genes, organisms or groups of organisms and ecosystems or biomes.

Likewise, temporal scales examined in biogeography also vary greatly. Temporal patterns relevant for biogeographical studies span from million years to seasonal movements.

Large-scale phenomena such as continental drifts, today explained by modern plate tectonics, have had undoubtedly a huge effect on biodiversity patterns and species distributions, both those currently observed and those occurred in the past and inferred from fossils. Macroevolutionary patterns, mass extinctions or adaptive radiations leading to many taxonomical groups can only be interpreted when a long temporal scale is considered.

Today we also know that evolutionary processes can be much faster than previously thought; besides, on smaller scales distributional patterns of organisms are often influenced by changes occurred in historical times (such as e.g. land use change, or current human-driven climate change), or natural cycles covering short times such as seasonal or daily migrations.

Classically, biogeography is split into two main branches, historical biogeography and ecological biogeography (Cox and Moore, 2010).

Historical biogeography examines long-term processes, taking place over evolutionary or geological times, in often large geographical areas, concerning large taxonomical groups or taxa that are now extinct. The historical factors leading to the current distribution of a certain taxon, its history of radiation and colonization, the identification of the taxon's closest relatives and the analysis of their occurrence all form aspects analyzed by historical biogeographers. In most cases their interpretation would be impossible if long-term processes such as continental drift or the alternation of glacial and interglacial phases were not taken into account.

The scale of analysis of ecological biogeography, instead, is generally smaller in time and space. It often looks at species, or populations, rather than larger taxonomical units, and is more concerned with shorter times and intracontinental, landscape or habitat scales. Ecological biogeography looks at how abiotic and biotic forces can shape, or influence, a species' range, species replacements along altitudinal or latitudinal gradients, species richness in different habitats, etc.

Both historical and ecological biogeography take into account forces, events and processes which as a whole determine micro- and macroevolutionary changes: we might say that biogeography is the discipline analyzing the effect of space on evolutionary processes.

Zoogeography is the branch of biogeography dealing with distributional patterns of animals. In the past, animals have been often considered in historical analyses, whereas ecological biogeography has focused more on plants, though of course today this distinction has completely disappeared. As Cox and Moore (2010) put it, plants are static and their life traits more explicitly linked with the ecological features of the place where they live, a fact that helps ecological analyses. On the other hand, plants leave fossils more rarely than do animals, because the latter often possess bones (vertebrates), exoskeletons or other hard parts (from foraminifera to mollusks, crustaceans, insects, echinoderms, etc.) that are more likely to fossilize. The analysis of fossils has been a major approach to the study of historical biogeography.

The history of zoogeography includes the most prominent scientists of the last two-three centuries, scholars who gave an immense contribution to modern biology and ecology. Although no space is available here to even briefly review their work, it is important to remind the reader that modern zoogeography builds upon the outstanding work of people such as Alexander von Humboldt, Philip Sclater, Charles Darwin, George Simpson and Philip Darlington, to mention some; but it is Alfred Russel Wallace, the author in 1876 of *“The Geographical Distribution of Animals, With a Study of the Relations of Living and Extinct Faunas As Elucidating the Past Changes of the Earth's Surface”*, who deserves to be regarded as the “father” of zoogeography.

In this chapter we will focus on ecological zoogeography. The subject is so wide that it would be impossible to cover it thoroughly and a selection of topics is inevitable. Therefore, we will only focus on the main phenomena and processes regarding distributional patterns of animals based on the analysis scale typical of ecological zoogeography; among them, we will look at those that mostly contribute to the current scientific debate.

We will start our review by examining three of the best known “ecogeographical rules”. Although, as we will see, most of them are poorly supported by sufficient scientific data or remain largely controversial, the impact they have had on classical zoogeography is considerable. Particularly, the first two cases we will briefly cover are of special interest for the ecological zoogeographer because they look at the relationships between an animal’s size and the place where it occurs, i.e. the climatic constraints it faces.

2. Ecogeographical “Rules”

One of the most intriguing aspects of biogeography is represented by the recurrence of patterns concerning animal distribution or morphology which may be linked with factors such as latitude, altitude or climate. The fact that such patterns are found in a range of different organisms has often been interpreted as a general law, leading to the formulation of “rules”. However, when such rules were first proposed they relied on little empirical evidence, so that over time they have been questioned, corrected or revisited in the light of more robust, quantitative datasets and more effective analytical approaches (Olalla-Tàrraga, 2010). Several of these “rules” still remain anecdotal, rely on little evidence, or are at best largely controversial. Two of those that still attract the attention of many researchers concern the relationship between climate and body size, or size of certain body parts of animals, respectively Bergmann’s and Allen’s rules. We will also mention Rapoport’s rule, at least because it has had the merit to stimulate much research on species’ distributional patterns.

2.1. Bergmann’s Rule

This is a famous ecogeographical rule first formulated by Bergmann (1847): it originally stated that in cold climates endothermic species with a large body size are more frequent than in warmer areas (Figure 1). Note that the original formulation concerned species assemblages and was confined to endotherms. Studies on ectotherms have often failed to report this pattern. Pincheira-Donoso (2010) argues that this does not diminish the rule’s predictive power as far as the latter is only tested on endothermic organisms, i.e. according to its original formulation. Further reformulations soon shifted the scale of interest of this rule from interspecific to intraspecific variation, so that more evidence is now available for patterns of size variation observed within species, but studies verifying its validity for species groups (e.g. birds, mammals) also exist.

Imagine, for simplicity, a spherical animal. The area of its surface is calculated as $A = 4\pi r^2$ whereas its volume as $V = \frac{4}{3}\pi r^3$, r being the sphere’s radius. When the radius increases, the A/V ratio will decrease because A grows according to a quadratic exponential, V according to a cubic one. Animals dwelling cold climates vitally need to preserve as much heat as possible. Reducing the A/V ratio means reducing the surface available for heat loss per volume unit. Besides, larger animals also show thicker insulation layers (Blackburn et al., 1999). Logically, within a certain species the populations made of larger individuals should occur at higher latitudes / altitudes, i.e. in colder climates, whereas smaller-sized individuals should be found in lower latitudes or elevations.

Quite often this variation does not show abrupt changes in an animal's size, but rather a continuous pattern, called a cline.

The phenomenon is especially evident for some endothermic species. Grey wolves inhabiting northern latitudes, for example, such as arctic tundra populations, are clearly larger in size than those found at lower latitudes, e.g. in Mexico or the Mediterranean.



Figure 1. A comparison between skulls of white tailed deer, *Odocoileus virginianus*, respectively from Mexico (up) and Canada (bottom). The clear difference in size can be explained in terms of Bergmann's rule. Image courtesy of Terra Nova Genomics Inc – Dr Steven Carr.

Patterns apparently contradicting Bergmann's rule are found even among endotherms, however. Palearctic shrews follow the converse to the rule, i.e. size decreases at higher latitudes (Ochocińska and Taylor, 2003; Yom-Tov and Yom-Tov, 2005), possibly because of other dominating effects such as character displacement or food availability.

Although more studies have addressed intraspecific variation (e.g. Ray, 1960; Ashton *et al.*, 2000; Meiri *et al.*, 2004), patterns occurring across species have also been analyzed (e.g. Blackburn and Gaston, 1996; Gaston and Blackburn, 2000; Rodríguez *et al.* 2006). More recent research showed the existence of non-linear relationships between body size and temperature. In mammals, for instance, gradients of body size are more influenced by temperature in colder climates than those in warmer because the selective pressure posed by conserving heat is only significant in the former (Rodríguez *et al.*

2006; 2008). In the warmer areas of southern Nearctic and the Neotropics, both local and broad-scale patterns of variation in the body size of mammals are influenced by climatic gradients occurring in mountainous areas, possibly because the extent of habitat in mountains is limited and counters the occurrence of species of a larger size (Rodríguez *et al.* 2008).

2.2. Allen's Rule

This rule (Allen, 1877) states that in endotherms protruding body parts, such as tail, ears, bill, extremities, and so forth, are relatively shorter in the cooler parts of the range of a species than in the warmer parts. The rule follows the same logic as Bergmann's, because shorter protruding parts minimize the A/V ratio of an animal's body, thus countering heat loss. Although widely mentioned in textbooks, the available evidence is limited to few validations for single species. Again, the rule is often extended to ectotherms, with no significant supporting evidence, which in thermally heterogeneous habitats would benefit by slowing down changes in body temperature thus improving their performance. Few studies have verified this rule across species. One studies focused on seabirds (Nudds and Oswald, 2007) whereas a recent one (Symonds and Tattersall, 2010) comprised birds from several taxonomic groups and showed that direct association between beak length and temperature occurs in parrots, galliforms, penguins and gulls, whereas support for the rule in leg element lengths was weak (i.e. beaks would be more constrained by temperature).

There is scientific evidence (Serrat *et al.* 2008) that mammal limbs and ears may grow longer under warmer ambient temperature, as seen in mice in lab conditions, because the latter would prompt cartilage proliferation. This might explain Allen's patterns in terms of phenotypic plasticity rather than by advocating strict genetic control for the development of appendages in different climates, but prudence is needed before drawing conclusions from a single case study.

2.3. Rapoport's Rule

Rapoport's rule states that organisms living at lower latitudes show narrower latitudinal ranges than those occurring at higher latitudes; the rule would also apply to elevation (organisms at higher elevation would have narrower altitudinal ranges). The rule was first enunciated by Stevens (1989) and is named after E.H. Rapoport who provided the first evidence for the phenomenon. It has been employed as a possible explanation for tropical species diversity (narrower ranges granting coexistence to more species).

There is little consensus on the rule's validity – in fact studies confuting it are more numerous than those supporting it. Clearly, species that have evolved recently in the tropics may show narrower ranges because they have not yet had the time to spread, vice versa for species with a longer evolutionary history (Rohde, 1998).

3. Distribution of Animals: Patterns and Causal Factors

3.1. Species Conceptualization and Delimitation: Their Importance for Zoogeography

The analysis of animal species distribution, with the identification of its proximate and remote causes, is a central issue in zoogeography. Clearly, understanding (and agreeing on) what a given species actually is constitutes a fundamental condition for analyzing its geographical range. Although this may seem obvious, the ever growing number of species recognized by scientists, often resulting from the splitting of taxa previously described as valid “species”, may make the task anything but easy. Besides describing new species, scientists often revise taxonomy, and this complicates biogeographical analyses even further.

In fact, the concept of species itself is a widely debated issue, raised in a wealth of scientific literature and leading to almost 30 different definitions. As De Queiroz (2007) puts it, in all the different concepts, species is recognized as a separately evolving metapopulation lineage, but the concepts differ as to which properties manifest divergence. However, a discussion of the various species concepts goes well beyond the scope of this chapter, and the interested reader is invited to consult the numerous sources covering this important topic.

Species conceptualization and delimitation are actually separate problems, although they are frequently confused. The latter task is linked to which operational procedure is adopted to recognize species, and certainly complicated by the fuzzy nature of species boundaries (De Queiroz, 2007). In their review, Sites and Marshall (2004) show how virtually no method can effectively delimit species boundaries *in all cases* and that conflicting results can derive from the adoption of different approaches. Moreover, some qualitative judgment is inevitable whatever method is adopted. Overall, a degree of prudence should always be adopted in species delimitation. It should be noted that far from being a sophisticated intellectual activity, describing new species has important practical consequences, first of all from the conservation point of view. To manage a species effectively we have to be able to delimit it unambiguously. One attempt to overcome the problem is the formulation of “Evolutionary Significant Units” (ESUs), namely a set of populations that are morphologically and genetically distinct from others and show a distinct evolutionary history (Ryder, 1986).

Since the 1990s, the advances in DNA analysis have revealed the existence of a lot of previously unsuspected species whose morphology is so similar as to make separation based on the assessment of external characters difficult or impossible. Such species, known as cryptic species, may in many cases be recognized only from molecular analysis. Morphological stasis in speciation – i.e. the process in which external morphology remains stable during species evolution – appears to be a common phenomenon in animals, for it is estimated that up to 30% of all existing animal species are cryptic. The discovery of cryptic species typically consists of splitting a previously described taxon into two or more “good” (i.e. scientifically valid) species. Clearly, once a taxon is split, its formerly described distribution has little meaning, being a “mixture” of the geographical ranges covered by the newly separated species. Recent studies suggest that cryptic species occur evenly among animal groups and biogeographical regions (Pfenninger and Schwenk, 2007).

An interesting example is provided by a butterfly in the HesperIIDae family occurring in Costa Rica, *Astraptēs fulgerator*. According to molecular studies, it is in fact a complex

of at least 10 largely sympatric cryptic species (Hebert *et al.*, 2004). Although all these species feed on different plants and have different caterpillars and ecological requirements, adult morphology is of little help in separating them effectively. In the European bat fauna, it was only in the 1990's that zoologists realized that one of the commonest bats found throughout the continent, the common pipistrelle (formerly known as *Pipistrellus pipistrellus*) actually consists of two species, one of which retained the former name *P. pipistrellus* while the other was named *P. pygmaeus*. In this case the molecular validation only occurred after a lot of evidence had been gathered on the two separate species, including echolocation (the maximum energy frequency of *P. pygmaeus* calls is ca. 10 kHz higher than those of *P. pipistrellus*), social call structure, morphological details, and ecology.



Figure 2. Left: parapatric distribution of the two sibling salamanders, northern spectacled salamander, *Salamandrina perspicillata* (northern range) and spectacled salamander *S. terdigitata* (southern range). Right: *S. perspicillata*. Image courtesy of Luca Cistrone

The two pipistrelles largely occur in sympatry, but in other cases, cryptic species may occur on separate territories. For example, in Italy salamanders in the genus *Salamandrina* were until recently regarded as a single monotypic endemic species, *S. terdigitata*, the spectacled salamander (Zuffi, 1999). DNA analysis has shown that the taxon actually consists of two cryptic entities, *S. perspicillata* (northern spectacled salamander) and *S. terdigitata*, whose speciation dates back to 4.5-10 Ma). The two species occur in the Italian Apennines and hilly areas and occupy adjoining geographical ranges (i.e. they are parapatric; Figure 2), *S. terdigitata* replacing *S. perspicillata* south of the Volturno River, in Southern Italy. Noticeably, where the two species ranges come into contact, hybridization does occur (Hauswaldt *et al.*, 2011). There must still be many undiscovered cryptic taxa, meaning that the biological diversity of many animal groups, and their inter-relationships in ecosystems, is still largely underestimated, and this certainly affects the appropriateness of conservation strategies. From what has been said so far, it should be clear that biogeographers are waiting for taxonomists to identify actual distributional ranges and analyze the causal factors which have delimited them.

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Biographical Sketch

Danilo Russo is an animal ecology scientist based at the University of Naples Federico II, Italy. He obtained his PhD in zoology at the University of Bristol (U.K.) in 2002 and is still honorary member of that academic institution. He is a well-recognized specialist in bat ecology and conservation biology. His scientific interests also cover the effects of land use change on animal distribution patterns and the ecology of management-dependent long-horned beetles.

Since 2007 Danilo has been teaching conservation biology and nature reserve management at the University of Naples Federico II. He also teaches zoology (University of Salerno, Italy) and applied zoology (Second University of Naples).

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