

PREFACE

Biogeography is the study of the geographic distribution of taxa and their attributes in space and time. Investigating biogeographic patterns and processes requires considerable amounts of data collected over large spatial and/or temporal scales. Evolutionary biogeography integrates distributional, phylogenetic, molecular and paleontological data in order to discover biogeographic patterns and assess the historical changes that have shaped them, following a step-wise approach. This book aims to understand the biogeography of the Drosophilidae in Africa and in other regions. This book also examines the development of preventive and educational components of conservation biogeography. The relevance of biogeographical evolutionary analyses for conservation science is discussed as well. In addition, the general methods that can be applied to prioritize areas for protection at regional global scales are also briefly commented on and exemplified with Mexico as a case study.

Chapter 1 - Evolutionary biogeography integrates distributional, phylogenetic, molecular and paleontological data in order to discover biogeographic patterns and assess the historical changes that have shaped them, following a step-wise approach. Although most of the authors involved in the theoretical development of biogeography or that apply specific methods usually conceive them as representing alternative "schools", they can be used to answer different questions. This review introduces the steps of this integrative approach and details the available methods. An evolutionary biogeographical analysis involves five steps: (1) recognition of biotic components (sets of spatio-temporally integrated taxa due to common history), through panbiogeography and methods used to identify areas of endemism; (2) contrastation of the biotic components and identification of the vicariant events that fragmented them, through cladistic biogeography and comparative phylogeography; (3) establishment of a hierarchic arrangement of the components in a biogeographic system of realms, regions, dominions, provinces and districts; (4) identification of cenocrons (sets of taxa with similar origins and ages), dated using intraspecific phylogeography, molecular clocks and fossils; and (5) formulation of a geobiotic scenario, that explains the evolution of the biotic components and cenocrons, integrating geological and tectonical information.

Chapter 2 - Three of the most recognized biogeographic paradigms on earth are the latitudinal gradients of species richness (the decreased richness in biological diversity from equatorial to polar regions), Bergmann's rule (the increase of body size in cold climates) and the unimodal pattern of diversity with depth (species richness peaking at intermediate depths). Understanding the causes of such patterns is still one of greatest contemporary challenges for biogeographers and ecologists. Moreover, though the generality and causal predictors of the

first two paradigms have been fully debated in the terrestrial biome, their relevance in marine systems is still poorly understood. In this chapter, the author reviews the present knowledge of these broad-scale biogeographic patterns in the marine systems and use cephalopod molluscs as a case study. Latitudinal gradients of species richness are present in coastal cephalopod fauna and both climate and area extent predict much of the diversity variation. Yet, in the open ocean, diversity does not decline monotonically with latitude and is positively correlated to the availability of oceanic resources. Therefore, a much stronger linkage between patterns of cephalopod diversity and bottom-up processes is found in the pelagic ecosystem. Additionally, cephalopod diversity does not show the classical hump-shaped response to depth. It declines sharply from sub-litoral and epipelagic zones to the slope and bathypelagic habitats and then steadily to abyssal depths. This suggests that higher thermal energy availability and productivity in shallow habitats promote diversification rates, and rejects hypotheses such as biome area, environmental stability and mid-domain effect. Climate also seems to play the most important role in structuring the latitudinal distribution of body size in these marine ectotherms. This evidence holds up to the concept of the "temperature-size rule" but does not support hypotheses for Bergmann's rule relating to resource availability, seasonality (or fasting endurance) and competition. Thus, it is evident that species-area-energy theories that have been formulated for the terrestrial biosphere also apply to the marine systems. In fact, although the phyletic composition and life-history characteristics of terrestrial and marine fauna are quite distinct, there is no reason to assume that the causal predictors behind these widespread biogeographic patterns will differ between these two realms.

Chapter 3 - The Drosophilidae is one of the most evolutionary successful muscomorphan families, with nearly 4,000 species showing astonishing morphological and ecological diversity. It is also unique in biological sciences thanks to the wealth of over 100 years of genetic and ecophysiological research, culminated in the sequencing of the complete genomes of 12 of its species. The aim of this Chapter was to trace the evolution of the Drosophilidae in the Afrotropical region in light of the accumulated faunistic and ecological observations and recent advances in the family phylogenetics and African paleoenvironmental studies. First, a reanalysis of the geographical distribution of 527 species belonging to 31 genera and two subfamilies revealed three main centers of endemism: West Africa (WA), East and South Africa (ESA) and the Insular Indian Ocean (IIO). Species richness shows a longitudinal cline in WA and a latitudinal cline in ESA, with Upper Guinea and South Africa being the most speciose, respectively. However, there are only four endemic genera in Africa, showing its old affinities with other continents. We have thus reviewed the origin and evolution of major drosophilid genera and species groups by reanalyzing recently published sequences of the nuclear gene *Amyrel* in the Schizophora, the Drosophilidae and the Afrotropical subgenus *Zaprionus*. Relative rate test showed no departure from the assumption of strict molecular clock, and thus *Amyrel* evolutionary rate was calibrated using the fossil record. The results show the family to have originated in the Early Eocene (50 MYA) and diversified in the Middle to Late Eocene. We also suggest that the Drosophilidae may be of Euramerican origin. Although Africa was an isolated continent from the Cretaceous to the Early Miocene, it may have been inhabited by early drosophiline radiations (*Chymomyza* and the *latifasciaeformis* group of *Scaptodrosophila*) in the Late Eocene. These taxa are associated with palm trees, a dominant feature of the African Eocene environment. Molecular dating of the basal genus *Lissocephala* whose species breed early in premature fig fruits (syconia) show

the genus to start diversification in the Oligocene. More 'derived' lineages (*Zaprionus* and Old World *Sophophora*) breed later on mature and ripening syconia. This ecological succession may recapitulate a phylogenetic trend towards an increase in alcohol tolerance and the utilization of sweet resources. Neogene climatic and tectonic changes have proposed many speciation models of Afrotropical drosophilids: the ecotonal and refugial hypotheses. A reanalysis of *Amyrel* divergence and geographical distribution in three clades (*Drosophila melanogaster* subgroup, *D. montium* group and the genus *Zaprionus*) showed that no single mode of speciation has prevailed. Although in an analysis at both the family and continental scales only general patterns are relevant, the authors hope that their review will serve as a lightening rod for future integrative research aiming to understand the biogeography of the Drosophilidae in Africa and in other regions.

Chapter 4 - Conflicting opinions regarding the relative importance of dispersal versus vicariance in understanding Caribbean biogeography continue to stimulate lively debate, despite recent advances in regional tectonics, geology, palaeogeography and palaeontology. The Greater Antilles are young geographical features, probably mid-Miocene and Hispaniola has a rich terrestrial invertebrate fossil record in the form of Dominican Republic amber inclusions. Spiders are common in Dominican amber and all fossil species belong in extant families. The island is unique in terms of its known spider fauna, in that a similar number of families have described species recorded on Hispaniola from both fossils in amber and from the extant fauna. It is also the region of the world where the amber fauna is most similar to the Recent fauna, and Miocene Hispaniolan spider biodiversity was presumably similar to that at present.

Fossils form empirical data with both phylogenetic and temporal implications and are of paramount importance for understanding historical biogeography. They can play a decisive role in falsifying hypotheses proposed solely on the distributions of extant taxa. It is also possible to generate hypotheses for both fossil and extant faunas that are ultimately falsifiable through the discovery of new Hispaniolan taxa. The amber spider fauna has clear affiliations to the present South American fauna, so how did they colonize the island from the mainland: dispersal or vicariance? The high Miocene biodiversity (including taxa with poor dispersal capabilities) on a geologically young island would seem to add more weight in favour of the vicariance model for explaining on-island spider lineages, although dispersal cannot be excluded for some of the highly dispersive taxa. However, a case-by-case approach is required in order to determine the relative contributions of the different models. The future research direction for understanding the biogeographical patterns will lie in the application of cladistic and phylogenetic biogeographical approaches. It is interesting to note that preliminary observations based on pedipalp morphology suggest some fossil taxa are more derived than extant forms. The contribution that the Dominican (and Mexican) amber fossil fauna can make to our understanding of the origins of Hispaniolan biodiversity, and Caribbean biogeography in general, should not be underestimated.

Chapter 5 - The distribution and abundance of bird species along a rural-urban gradient placed in Comunidad Valenciana (Spain) was examined. At a regional scale (2800 km²) I used data on presence-absence of breeding bird species in 10 x 10 km squares in order to determine the patterns of bird species' richness along the rural-urban gradient. Such squares were grouped into four sectors according to a decreasing degree of urbanization and they represent: Mediterranean transitional woodland shrub, mostly woody crops, mostly permanently irrigated land, and mostly urban areas. At a local scale (Valencia, 76 Km²) I used

the abundance of wintering and breeding bird species recorded in 118 squares of 700 x 700 m. Such squares were grouped into four classes depending on the cover of rural and urban landscapes: permanently irrigated land, mixed, mostly urban, and urban landscape. At regional scale, breeding bird richness did not show significant changes along the gradient, whereas data at the local scale revealed a decreasing number of bird species with increasing urbanization. Patterns at the regional scale were presumably related with: (i) the spatial variation of bird richness which increased from inland to the coastal fringe; (ii) a greater diversity of habitats because of development; (iii) a moderate level of urbanization; (iv) the use of a grain large enough to sample different habitats many of them sufficiently large to fulfil the requirements of many species. At the local scale, the following factors were apparently important: (i) a higher degree of urbanization; (ii) the smaller grain employed which sampled a less diverse set of habitats, and the extent of them was in many cases too small to fulfil habitat requirements of sensitive species; and (iii) the fact that urban parks were rarely suitable to open-field bird species of the surrounding habitat. The proportion of threatened species showed some variation along the gradient depending on the spatial scale and criterion employed, but overall the number of threatened species increased with increasing urbanization. The study area is a very developed region, where conservation strategies can not be designed without a full consideration of the intricate set of socio-economic processes which have driven most of the changes in the landscape. Currently, efforts should be orientated to conserve the biological communities and the ecological role of the agricultural land which still constitutes the landscape matrix at many spatial scales and administrative boundaries.

Chapter 6 - The extinct charophyte family Clavatoraceae was a significant component of the early Cretaceous lacustrine macrobenthos before the radiation of aquatic angiosperms. The most plesiomorphic and oldest representatives of this family occurred during the Late Jurassic and were scattered in a few localities in the central part of the Peri-Tethyan domain (Western Europe and Northern Africa) and on the margins of the North American Interior Seaway (Morrison Formation). In the beginning of the Early Cretaceous (Berriasian-Barremian), clavatoraceans were dominant in the Peri-Tethyan region and expanded eastwards, reaching the Chinese basins during the Valanginian and Hauterivian. During Barremian and Aptian times clavatoraceans reached their maximum diversity in the Peri-Tethyan region and their maximum palaeogeographic extension worldwide. Two species achieved a cosmopolitan distribution (Eurasia, North and South America and Northern and Eastern Africa), while four species were subcosmopolitan, mainly in the Northern Hemisphere. In contrast, the remaining clavatoracean species showed a marked endemic distribution in specific areas of the Tethyan region, which at that time was an archipelago of large islands enhancing allopatric speciation. During the Albian, the clavatoraceans began to decline. After a significant gap in the fossil record, Late Cretaceous clavatoraceans were either relict forms of previous cosmopolitan species in Northeast Asia or belonged to newly evolved species of endemic distribution in Southern Europe. The family Clavatoraceae became extinct near the Cretaceous-Tertiary boundary.

A historical biogeographic analysis of the clavatoraceans shows that the Tethyan region was a main focus of speciation for the family. A few species that originated in the Peri-Tethyan archipelago migrated elsewhere, sometimes reaching a worldwide distribution contemporaneous with the palaeogeographic extension of wetlands. Certain adaptations, such as the conjoint disposition of gametangia or the capability to colonise new biotopes provide

keys to understanding the worldwide migration of particular species. The dispersal of most Tethyan species required substantial time spans - usually several million years - to achieve a cosmopolitan biogeographic range. The animal vectors of clavatoracean propagules are unknown, but may include ancestral birds and dinosaurs. The decline of the family Clavatoraceae in the Albian was marked by the extinction of many endemic species and by significant biogeographic range restrictions for cosmopolitan species. In the Latest Cretaceous, only two completely isolated species remained prior to extinction.

Chapter 7 - Investigating biogeographic patterns and processes requires considerable amounts of data collected over large spatial and/or temporal scales. Availability of such large datasets has recently increased thanks to the rapid developments of geographical information systems, satellite images, and data accessibility through the Internet. But beyond these technical advances, many biogeographic studies are now based on data collected by volunteers from the general public, so-called citizen scientists. The shared principles of these programs most likely to improve large-scale investigations have hardly been highlighted. In this chapter, the authors first browse existing citizen-science monitoring programs particularly useful for biogeography. They then highlight whether and how these data are valuable to address current challenges in biogeography and large-scale conservation targets. Using concrete examples, the authors further explain why these data should be particularly efficient to develop the preventive and educational component of conservation biogeography.

Chapter 8 - The relevance of biogeographical evolutionary analyses for conservation science is discussed and highlighted. The general methods that can be applied to prioritize areas for protection at regional global scales are briefly commented and exemplified with Mexico as a case study. The authors conclude that a biogeographical atlas, representing a synthesis of distributional patterns of taxa from a country or area, may help determine priorities for the selection of areas for conservation.