L. A. S. JOHNSON REVIEW No. 4

Bridging historical and ecological approaches in biogeography

Jorge V. Crisci[A], *Osvaldo E. Sala*[B], *Liliana Katinas*[C] *and Paula Posadas*[D,E]

[A]Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, Paseo del Bosque,
B1900FWA La Plata, Argentina.
[B]Center for Environmental Studies, Brown University, Box 1943, Providence, RI 02912, USA.
[C]División Plantas Vasculares, Museo de La Plata, Paseo del Bosque, B1900FWA La Plata, Argentina.
[D]Museo Paleontológico Egidio Feruglio, Fontana 140, U9100GYO Trelew, Argentina.
[E]Corresponding author. Email: pposadas@mef.org.ar
All the authors contributed equally to this manuscript

Abstract. The practice of biogeography is rooted in disciplines that traditionally have had little intellectual exchange and yielded two complementary biogeographic approaches: ecological and historical biogeography. The aim of this paper is to review alternative biogeographic approaches in the context of spatial analysis. Biogeography can be used to set priorities for conservation of biological diversity, but also to design strategies to control biological invasions and vectors of human diseases, to provide information about the former distribution of species, and to guide development of ecological restoration initiatives, among other applications. But no one of these applications could be fully carried out until an integrative framework on biogeography, which bridges biogeographical historical and ecological paths of thinking, has been developed. Although we do not propose a new biogeographic method, we highlight the causes and consequences of the lack of a conceptual framework integrating ecology and history in biogeography, and how this required framework would allow biogeography to be fully utilised in fields such as conservation.

Introduction

No one who studies biogeography can fail to be impressed, or perplexed, by the recent increase in the diversity of approaches used to study the distribution of species in geographic space (Crisci 2001). This diversity is reflected in the variety of the subjects treated by recent biogeography books: analytical biogeography (Myers and Giller 1988), dynamic biogeography (Hengeveld 1990), historical biogeography (Crisci *et al*. 2000, 2003), cladistic biogeography (Humphries and Parenti 1999), island biogeography (Whittaker 1998; MacArthur and Wilson 2001), panbiogeography (Craw *et al*. 1999), phylogeography (Avise 2000), regional biogeography (Morain 1984), and vicariance biogeography (Nelson and Platnick 1981), among others.

One of the first principles in biogeography was Buffon's law in 1761: 'different areas have different species'. Since the time of Buffon until now, the history of biogeography may be divided in two parts: one dealing with the development of Buffon's law and the other dealing with the development of causal explanations of this law. Regarding causal explanations, biogeographers have recognised two research traditions, mostly isolated from each other, to which may be attached the labels 'ecological biogeography' and 'historical biogeography'. The Swiss botanist Agustin P. de Candolle in 1820 was the first to distinguish these two traditions (Nelson 1978), noting: 'the confusion of these two classes of ideas is one of the causes that have most retarded the science [biogeography] and that have prevented it from acquiring exactitude'. Although both subdisciplines of biogeography have the same objective (understanding the distribution of species in space and time), they use different epistemological approaches in addition to focusing on different spatio-temporal scales [i.e. evolutionary processes occurring over millions of years on a large often global scale *v.* ecological processes occurring over short temporal and small spatial scale (Myers and Giller 1988)]. The difference of scales is also one of organisation levels (taxa *v.* functional groups). Ecological biogeography is based on functional groups of species and environmental constraints whereas historical biogeography focuses on taxonomic groups and historical biogeographic events. Two locations in the world with similar abiotic characteristics (precipitation and temperature) may have identical functional groups of organisms and may be considered similar from an ecological point of view but they may have quite different species composition.

For example, climate conditions in the temperate arid and semiarid regions of North and South America are quite similar, since climatic patterns of North and South America are very similar (Paruelo *et al*. 1995), and consequently they look similar from an ecological point of view. However, North American prairies and steppes evolved under intensive grazing of bison (Mack and Thompson 1982) while large ungulates were absent from South America at that time (Marshall and Sempere 1993). Ecological biogeography on its own cannot account for the lack of large ungulates in South America, whereas historical biogeography on its own cannot explain the presence of arid and semiarid vegetation in Central North America. Both subdisciplines are needed in order to achieve a full understanding of biogeography.

As mentioned earlier, each of these two traditional biogeographic approaches uses different concepts, which are frequently explored in the literature, but attempts at integrative approaches are scarce (e.g. in Haydon *et al*. 1994; Avise 2000; Grehan 2001).

Here, we review recent progress in the two streams of thinking associated with biogeography. Although we do not propose a new biogeographic method, we highlight the causes and consequences of the lack of a conceptual framework that would integrate ecology and history in biogeography, and how this required framework would allow biogeography to be fully useful in fields such as conservation.

L. A. S. Johnson published a paper (coauthored by Barbara Briggs) in 1975 on the evolution and classification of the plant family Proteaceae (Johnson and Briggs 1975). The biogeographic section of Johnson and Briggs paper is a clear example of an integrative approach to biogeography, discussing (with their legendary scientific rigour) the historical and ecological factors that explain the current distribution of the Proteaceae. It is not surprising that Lawrie Johnson pioneered an integrative approach to biogeography, since he was a botanist notable for the outstanding breadth of his interest and expertise. It has been almost 10 years since Lawrie passed away, but his work continues to influence every biologist in the southern hemisphere who is concerned with systematics, biogeography, ecology, and conservation. We are, in this paper, attempting to follow in his scientific footsteps in bridging ecology and

history in biogeography. We hope that Lawrie would have sympathised with our approach, as he surely would with our intent.

Spatial analysis in biogeography

Biogeography can be seen as a branch of spatial analysis (Crisci *et al*. 2000, 2003).

Spatial analysis deals with formal models of spatial organisation and provides a useful framework to discuss ecological and historical streams of thinking about biogeography. Therefore, it is important to place both approaches, historical and ecological biogeography, in the context of the spatial analysis.

Spatial analysis includes the study of four interrelated themes that can be applied to biogeography: spatial arrangement, inference of space–time processes, spatial prediction (future arrangements), and spatial postdiction (past arrangements) (Crisci 2001; Crisci *et al*. 2000, 2003). Each one of these themes is related either to historical biogeography and / or to ecological biogeography (Table 1), as explained below.

Spatial arrangement in biogeography

Spatial arrangement, which can be also labelled as spatial description, describes the distribution of species throughout geographic space and it also includes palaeobiogeography (description of fossil distributions). According to the historical and ecological biogeographic traditions, we have taxonomic and functional approaches to depict the spatial arrangement of species. These two approaches result in different divisions of the Earth's surface. The comparison between Takhtajan's (1986) and Bailey's (1998) regionalisation of the world help to illustrate such differences. Historical biogeography is mainly concerned with the taxonomic approach, and a classic example of this view is Takhtajan's biogeographic world map (Fig. 1). These biogeographic regions are circumscribed areas of the Earth's surface that share common, taxonomically distinctive biotas (Brown and Lomolino 1998). Takhtajan's regions are then based on the fact that these areas contain endemic and closely related taxa in many different groups of organisms. In contrast, ecological biogeography is mainly concerned with the

Table 1.   Spatial analysis in biogeography

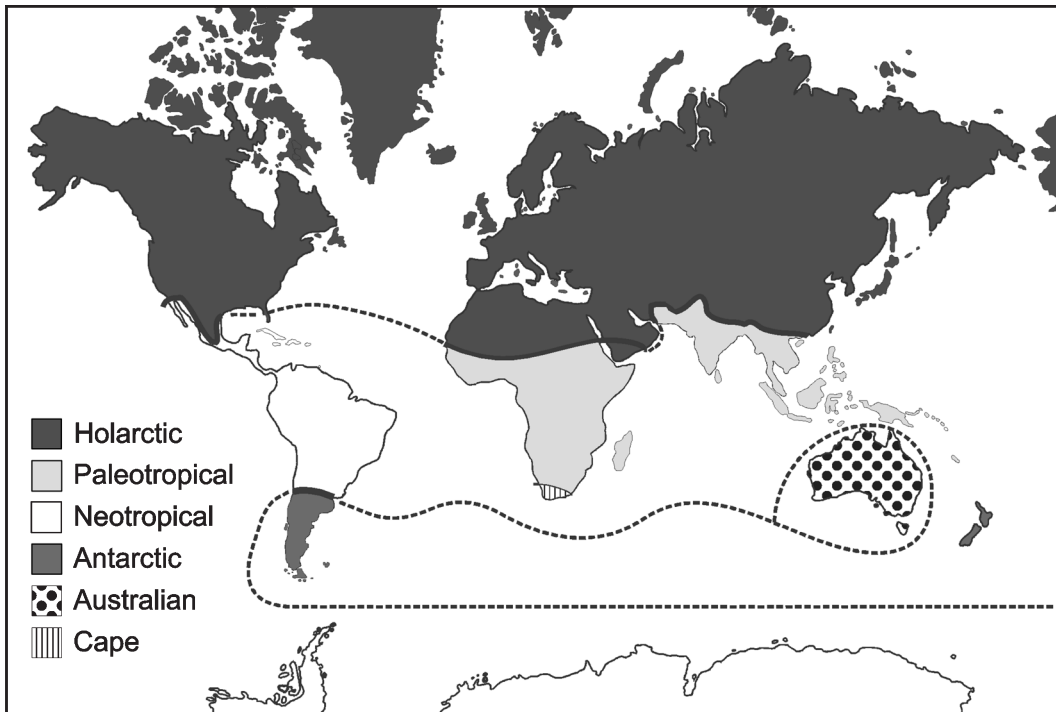|	Spatial arrangement	Inference of space–time processes	Spatial postdiction	Spatial prediction
Ecological biogeography	Ecoregions (e.g. Bailey's map)	Ecological constraints: e.g. soil composition, climate	–	Yes
Historical biogeography	Biogeographic regions (e.g. Takhtajan's map)	Historical events: dispersal, vicariance, extinction	Yes	–

Fig. 1. Floral regions of the world according to Takhtajan (1986).

functional approach and a classic example of this view is Bailey's (1998) map showing the ecoregions of the world (Fig. 2). Ecoregions are areas in which certain kinds of plants tend to occur together resulting in distinctive vegetation types (Brown and Lomolino 1998). It means that Bailey's map contains areas defined by major types of natural vegetation that occur wherever a particular set of climatic conditions prevail. These different views of
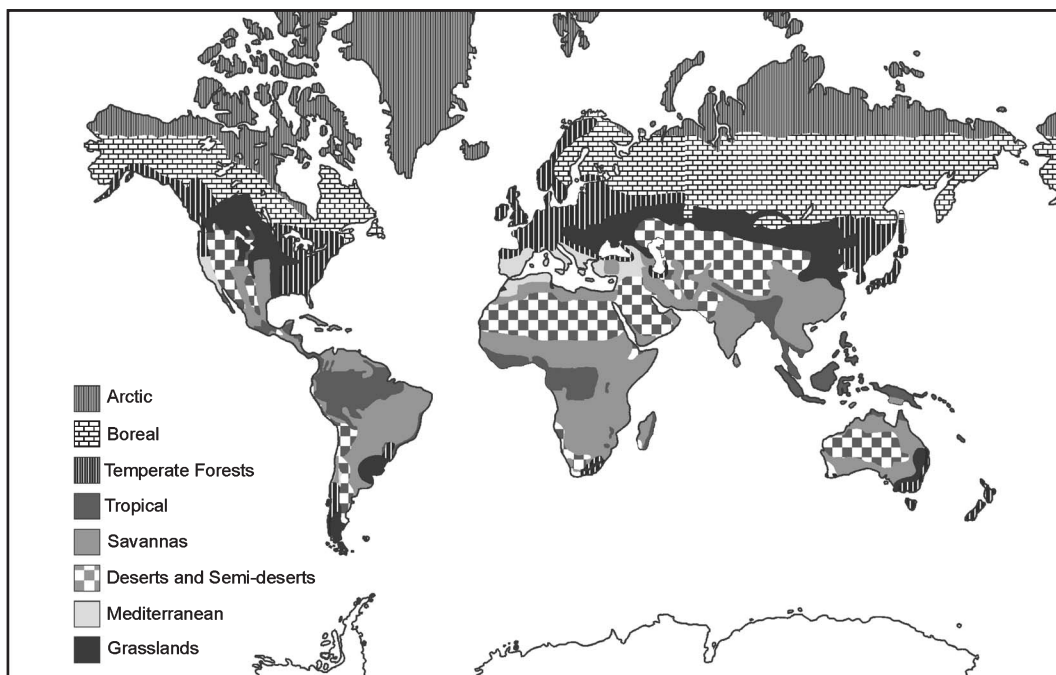

Fig. 2. Ecoregions of the world, summarised from Bailey (1998).

world mapping exemplify the question of different criteria to classify the world biota. These criteria in time refer to different processes occurring at different temporal scales (i.e. ecological and historical), which are used to explain such classifications.

Inference of space–time processes in biogeography

The study of space–time processes describes how movement or spatial interactions modify spatial arrangements. Space–time processes in biogeography include historical events and ecological constraints. The historical events, namely vicariance (i.e. the split of a taxon in two or more geographic subsets due to the appearance of a barrier), dispersal (i.e. the split of a taxon in two or more geographic subsets owing to expansion of a population across a pre-existing barrier), and extinction, can modify the geographic spatial arrangement of the species. The ecological constraints (including biotic, abiotic, evolutionary, and geologic factors) facilitate or constrain these events. For example, geologic factors acting in long time scales, such as plate tectonics, facilitate vicariance events. In contrast, the global patterns of major abiotic factors such as precipitation, temperature, or soil characteristics constrain the distribution in space of different groups of species. Several approaches to describe the climatic envelopes of plant functional types have been developed, ranging from very simple to detailed exercises (Holdridge 1947; Box 1981*a*, 1981*b*). Current generations of bioclimatic models relate patterns of climatic factors to current distribution of taxa by different approaches, from multiple regression to neural networks. GARP (Stockwell and Peters 1999) is one of the many examples of this approach. Another approach is the use of mechanistic models such as BIOME (Prentice *et al.* 1992) in which the distribution of species in space is based on plant physiological processes and biotic and abiotic constraints. For example, evergreen broad-leaf trees naturally occur in areas of the world that lie within certain precipitation and temperature ranges with grasslands replacing these forests when precipitation drops below a certain threshold, but this threshold varies depending on the average temperature.

Spatial prediction

Spatial prediction seeks to forecast future spatial arrangements. In biogeography, prediction is the forecasting of future species distributions and currently is of great interest in ecological biogeography. Scenarios of environmental change have created enormous interest in being able to predict the effects of climate change on the future distribution of species, plant functional types, or vegetation types. The earliest approaches used existent climatic envelopes with future climate, as predicted by global circulation models (GCMs), to generate future distributions of current vegetation types (Cramer and Leemans 1993). Climatic envelopes were replaced by the use of more mechanistic models, which include fully developed water balance subroutines, and used in conjunction with last generation climatic models to provide more realistic prediction of future vegetation patterns (Neilson 1995).

Spatial postdiction

Spatial postdiction seeks to establish, on the basis of present evidence, what the past spatial arrangements must have been like (postdiction or retrodiction). In a broad sense, palaeobiogeography could be included in spatial postdiction since fossil distributions as seen today could be used to infer distributions in the past. More often, in biogeography, postdiction is considered as the possibility of determining past biogeographic events in terms of the present evidence and it is the main objective of historical biogeography. The main sources of present evidence are taxon phylogenies and their distributional data. Reconstruction of past events in historical biogeography can be done from three different perspectives, each with a distinct objective (Crisci *et al.* 2003): (1) reconstruction of the distributional history of individual groups ('taxon biogeography'); (2) reconstruction of the history of areas of endemism (search for general area relationships, 'area biogeography'); and (3) reconstruction of the distributional history of biotas (all species inhabiting a specific region and sharing a geographical history). The latter two are the search for spatial homology—common spatial–temporal elements of shared biogeographic history.

An important question related to spatial postdiction is the concept of the distribution of species in time, or 'timing'. The importance of integrating time in historical biogeography is developed in a paper by Donoghue and Moore (2003). Also, in an interesting paper, Heads (2005) pointed out that 'correlating the age of taxa with that of associated paleogeographic events is probably the most promising method [for historical biogeography]'. Nevertheless, Heads remarked that these correlations have often been used in a simplistic way. Timing is one of the new insights in historical biogeography since data on the temporal distribution of taxa can provide important additional evidence in historical biogeographic analyses (Hunn and Upchurch 2001). The inclusion of such temporal information in biogeographic studies requires methodologies that allow assigning time values to taxa, meaning the time of origin and the time of each cladogenetic event in a phylogeny. Molecular clocks and fossil record are two main sources of time information. Temporal data may help to support or to reject hypotheses of phylogenetic-event causality that could be translated into biogeographic-event causality. Many papers in which timing is used to test biogeographic hypotheses are found in recent literature. In the following two examples, the vicariant origin of disjunct distributions among different plant taxa was analysed by molecular clock timing. The first example is

referred to the plant genus *Helleborus* L. (Ranunculaceae). It comprises 16 herbaceous perennial species distributed in Eurasia. The current distributional pattern of this genus shows a concentration of species in southern Europe and the Mediterranean regions and one disjunct species in eastern Asia (*H. thibetanus*). Sun *et al*. (2001) have hypothesised a possible vicariant origin for this disjunction. Two alternative hypotheses compete to explain this pattern: (1) a vicariant event of an earlier more continuous Tethyan distribution across Eurasia (Wu 1988), or (2) a long-distance dispersal event. Sun *et al*. (2001) agree with the hypothesis of a vicariant event originated by the uplifting of the Himalayas based on the evidence of a congruent disjunct pattern in other unrelated plant taxa. Molecular clock-calculated disjunction between *H. thibetanus* and its sister group (section *Helleborastrum*) was estimated by these authors in 22.96 million years ago (Middle Miocene). This disjunction time is about the period when the uplifting of Himalayas had started (Raven and Axelrod 1974). Therefore, in this first example the hypothesis of the authors was supported by molecular timing. In contrast, a second example shows how timing is used to reject a biogeographic hypothesis: The plant family Malpighiaceae includes trees, shrubs, and vines that are distributed widely in tropical and subtropical forests and savannas of the Old and New Worlds (Davis *et al*. 2002). According to Davis *et al*. (2002) several hypotheses have been proposed to explain the current distribution of Malpighiaceae. These hypotheses could be summarised as vicariant and dispersal hypotheses. Vogel (1990) has proposed the 'Gondwanian aborigine' hypothesis, a vicariant explanation in which the current distribution is due to the break-up of Western-Gondwana. According to Davis *et al*. (2002) the divergence estimates, based on molecular clocks and fossil evidence, indicate that Malpighiaceae originated well after the last known connection between Africa and South America (~105 million years ago) and the divergence estimates for the New World–Old World disjunctions are even younger, rendering the 'Gondwanian aborigine' hypothesis untenable. It is necessary to remark that some researchers might disagree with this interpretation since molecular clocks indicate only minimum ages for nodes and not absolute ages (for a detailed explanation see Heads 2005).

Ecology and history: a common challenge

Although ecological and historical biogeography are focused at different time scales in ecological and evolutionary time, respectively, they should be integrated in a common framework to understand distributional patterns (Fig. 3). For example, the genus *Nothofagus* Blumme contains many tree species, which dominate circum-Pacific temperate forests, and today exhibit a disjunct distribution, inhabiting areas currently isolated from each other as south-eastern Australia, Tasmania, New Guinea,

New Caledonia, New Zealand and southern South America. Many explanations have been proposed to understand the distributional patterns of *Nothofagus* species but it is only by integrating the biology, evolution, and environmental envelope of this plant genus that we can understand its current distribution. In order to show how historical and ecological approaches share a common challenge, we use the concept-map technique developed by Novak (1998).

Figure 3 shows that the initial phase of historical biogeographic studies consists of the analysis of geographic distribution of individual species. This approach is based primarily on biogeographic processes or 'events'. Earth processes are dynamic, and changes in environmental factors are continually occurring at ecological and evolutionary temporal scales. The Earth surface has changed continually during the history of life. Seas have expanded and contracted, mountain ranges have risen and eroded, islands have appeared and disappeared, and also Earth's climate has experienced profound changes. This historical setting has enormously influenced the geographic distribution of species. The non-random distributional congruence of two or more species results in the areas of endemism. The definition of areas of endemism represents an old issue in biogeography. They were recognised as ontological units as long ago as the XIX century. de Candolle (1838), when writing about the distribution of Asteraceae plant family, postulated: 'these regions were not established *a priori*; I have only recognized as such those areas that are *naturally defined* and in which I have seen several endemic species' (our italics). Furthermore, Sclater (1858) wrote 'having the exact location and the geographical areas over which they extent (species)... to find the primary *ontological divisions* of the earth surface' (our italics). Therefore, areas of endemism are considered by most biogeographers as natural units (for more detailed discussion in defining and delimiting areas of endemism, see Crisci *et al*. 2003). Aggregation of areas of endemism, in turn, led to the establishment of biogeographic regions. These three categories of spatial geographic arrangements (individual areas, areas of endemism, and regions) are modified and shaped by space–time processes, namely dispersal, vicariance, and extinction that are the result of Earth history. The interaction between the different space–time processes and spatial arrangements suggest the historical causes that led to the current distributional patterns of species. It is interesting to note that scale problems have not received the same attention in historical biogeographic approaches that it has received in ecological biogeography. However, a discussion of how the scale of the analysis units could affect results in historical biogeography has been presented by Morrone and Escalante (2002) and Mast and Nyffeler (2003). These two papers illustrate how the search for similarity in biota among area units and the identification of areas of
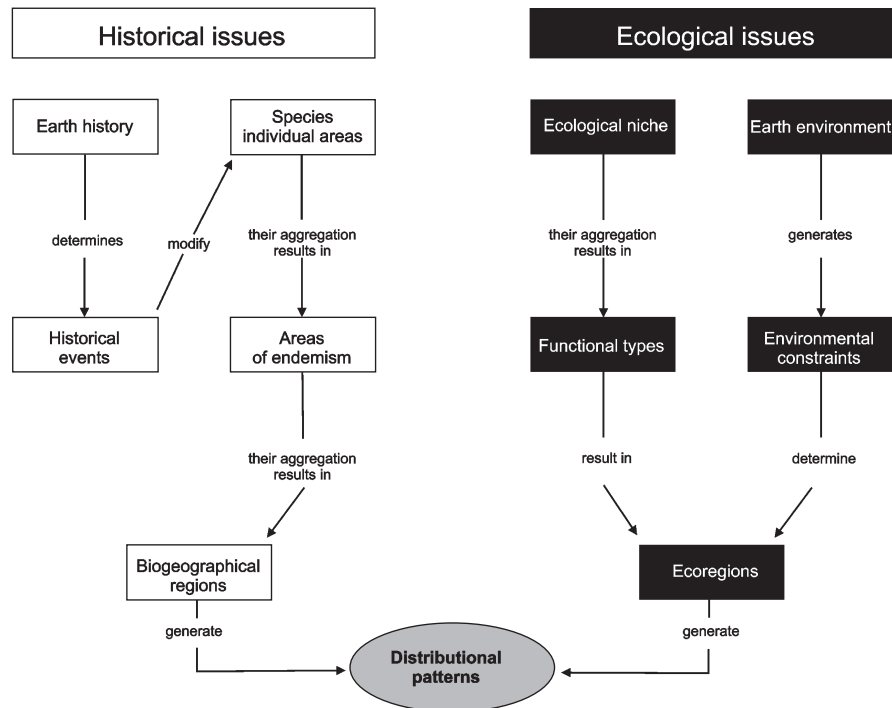
Fig. 3. Concept map showing the integration between historical and ecological biogeography. Historical issues are indicated in white boxes and ecological issues in black boxes. Their interaction is indicated in grey.

endemism, respectively, could be affected by the scale of area units considered.

Ecological biogeography also attempted to understand the geographic distribution of organisms. The ecological biogeographic approach was based primarily on abiotic constraints and secondarily in other ecological constraints. This approach first described global patterns of major climatic variables such as temperature and precipitation characteristics, including amount and seasonality, that resulted in global patterns of abiotic constraints. Independent of abiotic patterns, the existence of ecological niches that described the range of conditions within which a species grows and reproduces was recognised (Grinnell 1917). Clusters of species with similar niches yield the functional types or functional groups that are groups of species with similar morphological and physiological characteristics that share a common ecological role (Chapin 1993). Finally, the overlap of the geographic distribution of abiotic factors with the requirements of functional types yields the geographic distribution of vegetation types or ecological regions or ecoregions (Bailey 1998). The distribution of vegetation types results from the union of species, or groups of species, requirements or demands with the environmental matrix. Specific kinds of animals and microrganisms are associated with these vegetation types (Brown and Lomolino 1998). Individual vegetation types and animal functional groups

occur in regions of the world where environmental demands are met.

Finally, as shown in Fig. 3, distributional patterns of organisms are the result of ecology and history and represent the ultimate and common objective of historical and ecological biogeographic approaches. Consequently, distributional patterns cannot be fully understood without an integration of both subdisciplines.

Once the common challenge and scale and epistemological differences of ecological and historical biogeography (Fig. 3) has been established, it is necessary to consider how both approaches are required to deal with pressing environmental issues. Figure 4 shows the way in which historical events and environmental constraints are the drivers that determine distributional patterns, and how the changes of such distributional patterns could influence human activities. Human activities, in turn, may affect these drivers, resulting in changes in distributional patterns of organisms. This situation highlights why it is necessary to find an integrating conceptual framework that will allow biogeography to play a central role in conservation efforts. Thus, the environmental factors and historical events, jointly determine the current distributional patterns of species, vegetation types, ecoregions, and ultimately ecosystems. The characteristics of these ecosystems determine the provision of goods and services to humans (Daily 1997). Human
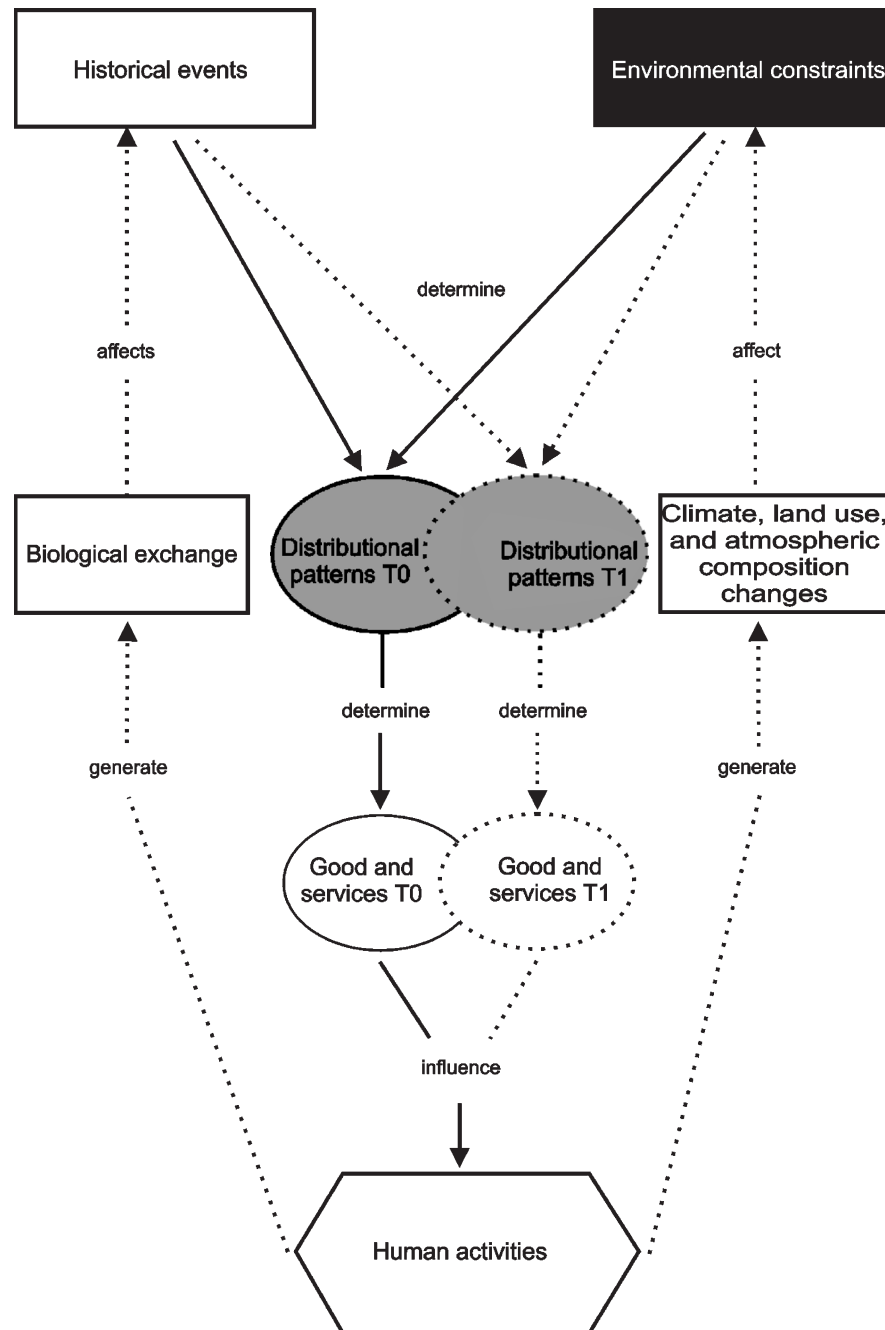
Fig. 4. Concept map showing how human activities influence and are influenced by distributional patterns of species through the changes in historical events and environmental constraints. Dotted lines indicate human-mediated changes on distributional patterns.

well-being depends on the flow of traditional goods and services such as food, fibre and shelter. However, ecosystems provide many more types of goods and services, which are essential for human well-being, although currently they may not have a market value. For example, these goods and services include the provision of clean water and clean air, the maintenance of biodiversity, soil fertility, and the stable chemical composition of the atmosphere (Daily 1997).

Human beings perceive nature mostly through the flow of goods and services that directly or indirectly shape their behaviour and determine their activity patterns. Human activity in its pursuit of improving human well-being has inadvertently resulted in dramatic changes in the environment. Anthropogenic global change, which includes alterations of the composition of the atmosphere, the climate, and land use, has modified the global patterns

of environmental constraints. Similarly, human activities that increased biological exchange, such as trade or the deliberate introduction of species into new areas, have created new historical events. New sets of environmental constraints and historical events, which derived from human activity, result in new distribution patterns of species and new patterns of the provision of goods and services. Observed differences between current distribution of species and the potential distribution of species highlight the human effects on modifying both environmental constraints (e.g. climate change, changes in land use) and creating new historical events (e.g. human-mediated dispersal events as biological invasions). Scenarios of changes in biodiversity in this century indicate that changes will affect most biomes and ecosystems, and that they will mostly result from changes in land use, climate, nitrogen deposition, biotic exchange, and CO_2 concentration in the atmosphere (Sala *et al*. 2000). A synthetic biogeographical approach may aid in tackling the most dramatic and current conservation problems.

Implications for conservation and other pressing environmental issues

Conservation strategies, such as selection of protected areas, need to take into consideration changes in environmental factors and human-driven events. For example, rapid climate change may shift the environmental conditions of a protected area in a way that may not be able to support the species or ecosystems that it attempted to protect. The following example may highlight the advantages of the integration between ecology and history in order to assure the efficacy of conservation efforts. In the last two decades, many scientists have focused on the selection of 'hotspots' as conservation targets (Myers 1990; Pressey *et al*. 1993; Prendergast *et al*. 1999; Myers *et al*. 2000). Hotspots are defined as areas with exceptional concentrations of endemic species and experiencing exceptional loss of habitat (Myers *et al*. 2000). These two requirements are clearly historical and ecological ones. Myers *et al*. (2000) argued that the second criterion of hotspots status (exceptional loss of habitat) only applies if the first one is accomplished (endemic concentrations). According to such criteria, Myers *et al*. have established 25 hotspot areas at the global scale, each one containing at least 1500 endemic plant species (i.e. 0.5% of all plants species around the world). Hotspots are the result of the overlapping of non-random distributional patterns of species and are especially rich areas of endemism. So, the entire hotspots argument is primarily based on a historical biogeographic concept: the areas of endemism. However, in order to define 'threat areas' it became necessary to identify patterns of drivers of global change that may affect these areas. That is, ecological criteria are needed to assure the optimisation of resources invested in conservation efforts. Estimates of climate change may assist in the prioritisation

of conservation resources. In this way, areas where climate may change and in the near future may not support the same vegetation type and may have lower priority for conservation than those areas only threatened by land-use change and more likely to be successfully preserved with current conservation tools. This example shows how an integrated approach from history and ecology could help address conservation challenges. That is, a historical-based approach serves as a primary source of information to identify target areas for conservation (identifying distributional patterns at present or T0 in Fig. 4). In a second step, an ecological based approach determines whether or not to invest conservation efforts according to future scenarios of global change (distribution patterns in the future or T1 in Fig. 4).

An example of how, in the past, failures to integrate historical and ecological approaches have led to erroneous conclusions in the conservation field is represented by the unsuccessful Life Projects to protect two flagship species for conservation in Europe: the Spanish imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*). According to Ferrer and Negro (2004) the critical conservation status of these species has been attributed to human persecution and habitat loss. Today, a significant proportion of their populations are within natural reserves and in the last 30 years both species have been protected by laws. Despite these efforts both the Spanish imperial eagle and Iberian lynx have lost a significant proportion of their geographic ranges and are represented by less than 500 individuals each (Delibes *et al*. 2000; Ferrer 2001). Conversely, their sister species (eastern imperial eagle = *A. heliaca* and Eurasian lynx = *L. lynx*, respectively) exhibit relatively healthy populations. In view of these facts a natural question arose: why two non-related species inhabiting the same area—southern Iberian peninsula—are not responding to the conservation efforts in the same way as their sister species that inhabit similar areas in eastern Europe and Asia? As an answer to this question Ferrer and Negro (2004) explored an historical biogeographic explanation. Knowing that both pairs of sister species diverged ~835 000 and 1 130 000 years ago in the light of molecular evidence, these authors yield to the conclusion that these divergences in two unrelated taxa (*Aquila* and *Lynx*) were due to a vicariant event originated by Pleistocene glaciations. Furthermore, they postulated that the existence in Central Europe of temperate forests during interglacial periods (Tallis 1990) possibly prevented the western and eastern eagles and lynx regaining contact after their initial separation about one million years ago. In this way, the western eagle and lynx have become relict species living in isolated and small areas and therefore they are naturally extinction-prone. Their biogeographical origin accounted for the current difficulties experienced by local conservation efforts. Finally, Ferrer and Negro (2004), recognising the historical similarities between these Iberian species, proposed

that any conservation effort would jointly manage both species, an obvious step that only could be reached through the search of the geographic history of both taxa. After many years and many conservation plans the two species are still endangered. Most of the attempted conservation efforts were based on ecological studies [e.g. habitat selection (Palomares *et al*. 2000), human-related mortality, and population size (Ferreras *et al*. 2001), population fecundity (Ferrer and Bisson 2003)]. However, Ferrer and Negro (2004) showed the fact that the biogeographical history of these endangered taxa is the main cause of their actual status. The ecological approach alone was insufficient to fully understand the causes of the populations extinction of these two species. The addition of an historical component to this problem showed a complete picture. This case clearly shows that ecology without history, or history without ecology, are insufficient to design a successful plan of conservation management.

Other cases in which integrated frameworks are required are the deliberate or accidental introduction of species that may jeopardise many local conservation efforts. In order to understand invasion processes and to develop scenarios of future invasions we need to take into account human-induced changes in both environmental constraints and historical events. Current understanding of how these two factors interacted in the past in combination with scenarios of how they will change in the future will yield scenarios of biotic invasions. Also, knowledge of the distributional patterns of disease vectors (postdiction) together with the projection on how distributional patterns may change (prediction) constitutes the basis for controlling the spread of current or newly appearing diseases (Pascual *et al*. 2000).

As shown above, biogeography can be used to set priorities for conservation of biological diversity, but also to design strategies to control biological invasions and vectors of human diseases, to provide information about the former distribution of species, and to guide development of ecological restoration initiatives, among other applications.

In order to ameliorate the effects of the profound changes in biodiversity, which occur globally and pose serious threats to human well-being, we suggest that it is urgent that the different environmental disciplines join efforts under a common framework. Biogeography has much to contribute to these efforts.

Acknowledgments

References

Avise JC (2000) 'Phylogeography: the history and formation of species.' (Harvard University Press: Boston)

Bailey RG (1998) 'Ecoregions: the ecosystem geography of the oceans and continents.' (Springer-Verlag: New York)

Box EO (1981*a*) 'Macroclimate and plant forms: an introduction to predictive modelling in phytogeography.' (Dr Junk Publisher: The Hague)

Box EO (1981*b*) Predicting physiognomic vegetation types with climate variables. *Vegetatio* **45**, 127–139. doi: 10.1007/BF00119222

Brown JH, Lomolino MV (1998) 'Biogeography. 2nd edn.' (Sinauer: Sunderland)

de Candolle AP (1838) 'Statistique de la Familie des Composées.' (Treutel & Würtz: Paris)

Chapin FS (1993) Functional role of growth forms in ecosystem and global processes. In 'Functional role of growth forms in scaling physiological processes: leaf to globe'. (Eds JR Ehleringer, CB Field) pp. 287–312. (Academic Press: San Diego)

Cramer WP, Leemans R (1993) Assessing impacts of climate change on vegetation using climate classification systems. In 'Vegetation dynamics and global change'. (Eds AM Solomon, HH Shugart) pp. 190–217. (Chapman and Hall: New York)

Craw RC, Grehan JR, Heads MJ (1999) 'Panbiogeography: tracking the history of life.' (Oxford University Press: Oxford)

Crisci JV (2001) The voice of historical biogeography. *Journal of Biogeography* **28**, 157–168.
doi: 10.1046/j.1365-2699.2001.00523.x

Crisci JV, Katinas L, Posadas P (2000) 'Introducción a la teoría y práctica de la biogeografía histórica.' (Sociedad Argentina de Botánica: Buenos Aires)

Crisci JV, Katinas L, Posadas P (2003) 'Historical biogeography: an introduction.' (Harvard University Press: Boston)

Daily GC Ed (1997) 'Nature's services. Societal dependence on natural ecosystems.' (Island Press: Washington DC)

Davis CC, Bell CD, Mathews S, Donoghue M (2002) Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences USA* **99**, 6833–6837. doi: 10.1073/pnas.102175899

Delibes M, Rodríguez A, Ferreras P (2000) 'Action plan for the conservation of the Iberian lynx (*Lynx pardinus*) in Europe. No. 111.' (Council of Europe Publishing, Nature and Environment: Strasbourg)

Donoghue MJ, Moore BR (2003) Toward an integrative historical biogeography. *Integrative and Comparative Biology* **43**, 261–270.

Ferrer M (2001) 'The Spanish imperial eagle.' (Lynx Editions: Barcelona)

Ferrer M, Bisson I (2003) Age and territory-quality effects on fecundity in the Spanish imperial eagle (*Aquila adalberti*). *The Auk* **120**, 180–186.

Ferrer M, Negro JJ (2004) The near extinction of two large European predators: super specialists pay a price. *Conservation Biology* **18**, 344–349. doi: 10.1111/j.1523-1739.2004.00096.x

Ferreras P, Gaona P, Palomares F, Delibes M (2001) Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. *Animal Conservation* **4**, 265–274. doi: 10.1017/S1367943001001317

Grehan JR (2001) Panbiogeography from tracks to ocean basins: evolving perspectives. *Journal of Biogeography* **28**, 413–429. doi: 10.1046/j.1365-2699.2001.00539.x

Grinnell J (1917) The niche-relationships of the California Thrasher. *The Auk* **34**, 427–433.

Haydon DT, Crother BI, Pianka ER (1994) New directions in biogeography? *Trends in Ecology & Evolution* **9**, 403–406. doi: 10.1016/0169-5347(94)90067-1

Hengeveld R (1990) 'Dynamic biogeography.' (Cambridge University Press: Cambridge)

Heads M (2005) Dating nodes on molecular phylogenies: a critique of molecular biogeography. *Cladistics* **21**, 62–78.

Holdridge LR (1947) Determination of the world formations from simple climatic data. *Science* **105**, 367–368.

Humphries CJ, Parenti L (1999) 'Cladistic biogeography: interpreting patterns of plant and animal distributions.' (Oxford University Press: New York)

Hunn CA, Upchurch P (2001) The importance of time / space in diagnosing the causality of phylogenetic events: towards a "chronobiogeographical" paradigm? *Systematic Biology* **50**, 391–407. doi: 10.1080/106351501300317996

Johnson LAS, Briggs BG (1975) On the Proteaceae—the evolution and classification of a southern family. *Botanical Journal of the Linnean Society* **70**, 83–182.

MacArthur RH, Wilson EO (2001) 'The theory of island biogeography.' (Princeton University Press: Princeton)

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hooved mammals. *American Naturalist* **119**, 757–773. doi: 10.1086/283953

Marshall LG, Sempere T (1993) Evolution of the Neotropical Cenozoic land mammal fauna in its geochronologic, stratigraphic and tectonic context. In 'Biological relationships between Africa and South America'. (Ed. P Goldblatt) pp. 329–392. (Yale University Press: New Haven)

Mast AR, Nyffeler R (2003) Using a null model to recognize significant co-ocurrence prior to identifying candidate areas of endemism. *Systematic Biology* **52**, 271–280.

Morain SA (1984) 'Systematic and regional biogeography.' (Van Nostrand and Reinhold: New York)

Morrone JJ, Escalante T (2002) Parsimony analysis of endemicity (PAE) of Mexican terrestrial mammals at different area units: when size matters. *Journal of Biogeography* **29**, 1095–1104. doi: 10.1046/j.1365-2699.2002.00753.x

Myers AA, Giller PS (eds) (1988) 'Analytical biogeography: an integrated approach to the study of animal and plant distributions.' (Chapman and Hall: New York)

Myers N (1990) The biodiversity challenge: expanded hotspots analysis. *Environmentalists* **10**, 243–256.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. doi: 10.1038/35002501

Neilson RP (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications* **5**, 362–385.

Nelson G (1978) From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology* **11**, 269–305. doi: 10.1007/BF00389302

Nelson G, Platnick NI (1981) 'Systematics and biogeography: cladistics and vicariance.' (Columbia University Press: New York)

Novak JD (1998) 'Learning, creating, and using knowledge: Concepts Maps^{TM} as facilitative tools in schools and corporations.' (Laurence Erlbaum Associates Publishers: Mahwah, NJ)

Palomares S, Delibes M, Ferreras P, Fedriani JM, Calzada J, Revilla E (2000) Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Conservation Biology* **14**, 809–818. doi: 10.1046/j.1523-1739.2000.98539.x

Paruelo JM, Lauenroth WK, Epstein HE, Burke IC, Aguiar MR, Sala OE (1995) Regional climatic similarities in the temperate zones of North and South America. *Journal of Biogeography* **22**, 2689–2699.

Pascual M, Rodó X, Ellner SP, Colwell R, Bouma MJ (2000) Cholera dynamics and the El Niño southern oscillation. *Science* **289**, 1766–1769. doi: 10.1126/science.289.5485.1766

Prendergast JR, Quinn RM, Lawton JH (1999) The gaps between theory and practice in selecting nature reserves. *Conservation Biology* **13**, 484–492. doi: 10.1046/j.1523-1739.1999.97428.x

Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH (1993) Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology & Evolution* **8**, 124–128. doi: 10.1016/0169-5347(93)90023-I

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**, 117–134.

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* **61**, 539–673.

Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. doi: 10.1126/science.287.5459.1770

Sclater PL (1858) On the general geographic distribution of the members of the class Aves. *Journal of the Linnean Society, Zoology* **2**, 130–145.

Sun H, McLewin W, Fay MF (2001) Molecular phylogeny of *Helleborus* (Ranunculaceae), with an emphasis on the East Asian–Mediterranean disjunction. *Taxon* **50**, 1001–1018.

Stockwell D, Peters D (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* **13**, 143–158. doi: 10.1080/136588199241391

Takhtajan AH (1986) 'Floristic regions of the world.' (University of California Press: Berkeley)

Tallis J (1990) 'Climate change and plant communities.' (Academic Press: London)

Vogel S (1990) History of the Malpighiaceae in the light of pollination ecology. *Memoirs of the New York Botanical Garden* **55**, 130–142.

Whittaker RJ (1998) 'Island biogeography: ecology, evolution and conservation.' (Oxford University Press: Oxford)

Wu CY (1988) Hengduan mountain flora and its significance. *Journal of Japanese Botany* **63**, 297–311.