

# The relationship between biogeography and ecology: envelopes, models, predictions

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This paper reviews ideas on the relationship between the ecology of clades and their distribution. Ecological biogeography represents a tradition that dates back to ancient times. It assumes that the distribution of organisms is explained by factors of present environment, especially climate. In contrast, modern systematics, following its origins in the Renaissance, concluded with Darwin that ‘neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions’. In many cases, species distribution models – ecological niche models – based on the current environment of a species (its environmental envelope) fail to predict the actual distribution of the species. In particular, they often over-predict distributions. In addition, a group’s niche often varies in space and time. These results provide valuable evidence that Darwin was correct, and many ecologists now recognise that there is a problem with the niche theory of distribution. Current ecological processes explain distribution at smaller scales than do biogeographical and evolutionary processes, but the latter can lead to patterns that are much more local than many ecologists have assumed. Biogeographical phenomena often occur at a much smaller scale than that of the Wallacean regions. In areas that have been subjected to marine inundation or intense tectonism, many centres of endemism are only tens of kilometres across. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, ••, ••–••.

**ADDITIONAL KEYWORDS:** California – centre of origin – climate – dispersal – Grinnell – niche – species distribution models.

## INTRODUCTION

Some of the most obvious patterns in biology are ecological. Examples include the bands of particular species observed at different elevations along a sea shore or a mountain range. This paper examines the question: How does a clade’s ecology relate to its geographical distribution?

Scheiner & Willig (2011) defined the domain of ecological theory as ‘the spatial and temporal patterns of the distribution and abundance of organisms’ and this would include biogeography. Yet in practice, ecologists in the strict sense (readers of the *Journal of Ecology*, *Ecology*, *Molecular Ecology* etc.) tend to discuss species distribution in terms of present environment, and focus on topics such as present abundance. In contrast, systematic or historical bio-

geographers (readers of the *Journal of Biogeography*, *Systematic Biology*, *Molecular Phylogenetics and Evolution* etc.) usually refer to deeper levels of space, time and phylogeny, and focus on topics such as distribution boundaries.

Chiarucci, Bacaro & Scheiner (2011) described this difference, with ecology concentrating on phenomena at smaller scales of space and time, and biogeography investigating larger scale patterns (Table 1). Both subjects investigate the same topic – biological differentiation – and the only real difference is the scale at which this is studied. Biogeographers study differentiation over large spatial and temporal scales, but use data that are less complete and accurate. Ecologists use more complete and accurate data, but study phenomena at smaller scales of space and time.

For example, a biogeographical region may comprise a centre of endemism 50 km across. *Within it*, distribution is determined by ecology, and species will occur in suitable habitats, for example, lowland

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**Table 1.** Scales of patterns investigated by ecology and biogeography (Chiarucci *et al.*, 2011)

	Typical realms of interest	
	Space	Time
Ecology	Local to regional	Up to decades (centuries)
Biogeography	Regional to global	Centuries to aeons

versus montane sites, or streamsides and swampy areas versus ridges. *At the smallest scales*, stochastic factors determine whether a tree is found at a certain spot or, say, a few centimetres to the left or right (Chase, 2014). Outside a biogeographical region, equivalent habitats may include different species, because of factors such as allopatry. Thus biogeography governs distribution at a ‘large’ scale, ecological factors operate at a ‘small’ scale. But where is the break and what, exactly is the relationship between ecology and biogeography?

### DOES ECOLOGY DETERMINE GEOGRAPHICAL DISTRIBUTION?

All naturalists know that unusual habitats in a region may harbour unusual species, and that many species are restricted, within their distribution region, to certain habitat types. But these observations do not mean that the habitat of a species determines its geographical distribution, as the species may not occur in another region even if suitable habitat is present. Ecology has a blind spot here and overlooks large-scale aspects of chronology and distribution. One of the main problems in addressing these sorts of questions has been the chasm between the work on distribution produced by ecologists and the biogeography produced by systematists and phylogeneticists. As Wiens (2011) pointed out, many ecological papers that aim to explain species diversity and distribution ignore evolutionary aspects of the patterns altogether.

### ECOLOGICAL BIOGEOGRAPHY

It has been known since ancient times that the distribution of plants and animals is related to climate. The broad vegetation types or biomes – forest, woodland, grassland and desert – reflect climate, and in colder or drier areas the community shifts towards the desert end of the spectrum. Plants with different physiognomy, or the gross structure, occur in different biomes. For example, large lianes and plants with large, membranous leaves are found in all rainforests,

but never in deserts or alpine localities. The ancient, ecological approach to the global distribution of biomes considered the physiognomy of organisms and vegetation types, but did not refer to systematic groupings. These required a more detailed study of morphology.

### TAXONOMIC BIOGEOGRAPHY SINCE ITS ORIGIN IN THE 16<sup>TH</sup> CENTURY

In contrast to ecological regions, known since ancient times, the biogeographical regions that have been proposed by taxonomists have focused not on physiognomic classes but on taxa, and the regions that these delimit show marked differences from ecological biomes. Modern taxonomy began in the Renaissance, with the first floras and faunas appearing in northern Italy in the 16<sup>th</sup> century. These works listed all the known species, not just the useful ones, as in earlier herbals. The new approach represents an important psychological break and the birth of modern systematics (Hheads, 2005). Work in systematics has studied all known aspects of an organism, and this has led to the recognition of more or less natural groups (clades or taxa).

The new ‘systematic’ approach in biology showed that the distributions of the component clades that make up a biota are *not* simply related to climate. In practice, most clades have distributions that show strange, intriguing configurations that are repeated in many groups, but do not coincide with climatic zones. Tropical rainforests in America, Africa and Asia share similar climate and have a similar structure, but their respective floras and faunas are very different. No species or any clade, apart from anthropogenic weeds, is found in all tropical rainforest zones and only there, and the same applies to desert and the other biomes.

As their research developed, systematists discovered that underlying the biomes is a global pattern of differentiation in the clades, as summarized in schemes of biogeographical boundaries and regions. This work culminated in the recognition of global boundaries that affect many groups, but show no obvious correlation with climate, soil type or any other feature of the physical environment. Wallace’s line is the best known, but there are many similar cases (Hheads, 2012). Thus the age of exploration led to the discovery that many different areas of the Earth had different creatures, even though they had similar climates. After 3 centuries of collecting on a global scale by systematists, Darwin (1859: 346) was able to conclude:

In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that

*neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions.* [Italics added]

This conclusion contrasts with the usual ecological view, but provides the main theme of this paper; the distribution of groups is *not* caused simply by present climate and environmental conditions; the ‘historical’ factor is also implicated.

Darwin (1859) was well aware of the ecological niche (he referred to it as a group’s ‘place in the economy of nature’), but he understood that a group’s niche does not explain its geographical distribution. There may well be a correlation between niche breadth and geographical range size (Slatyer, Hirst & Sexton, 2013), but which causes which? Slatyer *et al.* assumed that greater niche breadth causes greater range size, and described this as ‘intuitively appealing’. Yet greater range size in itself can cause greater niche breadth. For example, in a group with a greater range size it is more likely that some populations will be caught up in an orogeny, say, and be converted into alpiners, or caught in a subsidence and be converted into lowland or coastal populations.

Following Darwin, most taxonomic plant geographers viewed distribution in systematic and historical terms (Hagen, 1986). This is seen in the detailed geographical syntheses for large, global groups that were produced in the 19<sup>th</sup> century (for example, Bentham, 1873). Using primitive but workable classifications, these accounts described the main centres of endemism, absence, diversity, disjunction and taxonomic incongruence in vast groups, from global to local scales.

#### MODERN ECOLOGY

Modern ecology has more or less ignored the work on systematic biogeography. Instead, it has concentrated on large-scale biomes and small-scale plots, and has assumed that the same factors governing biome distributions also determine clade distribution. For example, Pearson & Dawson (2003) wrote: ‘It is a central premise of biogeography that climate exerts a dominant control over the natural distribution of species’. But, again, there are very few pantropical or pantemperate species other than introduced weeds. Thus orthodox ecology often admits that climate determines distribution *only within a single biogeographical region*. But the delimitation of regions is controversial and arbitrary. Wallace’s regions are often cited, but in Africa (Wallace’s ‘Ethiopian Region’), for example, the biota in the drier areas south of the rainforest is very different from that in the drier areas north of the rainforest, despite their similar environments and location within what is supposed to be a single region.

In contrast to the systematists, ecologists have tended to ignore biogeographical problems, such as why the species and genera of tropical America, Africa, and Asia are so different. As Hagen (1986) wrote, ‘Most [early] ecologists were skeptical of historical explanations, emphasizing instead the proximate, environmental causes of distribution’. This environmental determinism or ‘niche theory’ continued until modern times.

Ricklefs & Jenkins (2011) wrote that ecology and biogeography had diverged by the early 20<sup>th</sup> century, with the British Ecological Society forming in 1913 and the Ecological Society of America in 1915. The main focus of ecology narrowed to local scales of space, time and phylogeny, and concerned itself with species and local communities rather than genera and families at regional and global scales. While ecology focused on the present, local environment, systematists continued to investigate taxonomy, biogeography and history at all scales. The biogeographical regions they recognised implied that significant boundaries underlie apparent ecological entities, such as ‘tropical American rainforest’ or ‘African savanna’.

Ricklefs & Jenkins (2011) considered that:

The schism between ecology and biogeography possibly peaked during the 1970s, soon after Robert MacArthur (1965, 1972) explicitly excluded history from the purview of ecology . . . one could argue that ecologists further weakened the study of biogeography through the development of the equilibrium theory of island biogeography, which was essentially nonhistorical.

Some recent authors have continued with the ecological tradition: ‘A central tenet of biogeography is that the broad outlines of species ranges are determined by climate’ (Araújo, 2012). Others have agreed instead with Darwin. For example, Peterson (2006) wrote: ‘Certainly, an appreciation of the basic tenets of historical biogeography would suggest that species will *not* inhabit all areas that meet their niche requirements . . .’. [Italics added]. Thus a profound disagreement persists.

#### GRINNELL AND MATTHEW: CLIMATE DETERMINES BIOGEOGRAPHY AND EVOLUTION

Grinnell (1914, 1917) was one of the most influential modern ecologists and accepted that the climatic niche of a species determined its geographical distribution. In a similar way, W.D. Matthew was perhaps the most influential modern biogeographer, and regarded climate as the main determinant of evolution (Matthew, 1915). (This was in opposition to the ‘internalist’ views prevailing in paleontology at the time; Griesemer, 1990). Grinnell and Matthew’s studies on climate and evolution provided the

biogeographical principles that were adopted by the Modern Synthesis (Heads, 2005). The two authors established, over Darwin's view, the idea that the distribution of a group was determined by the climate.

Modern ecologists have accepted the model. For example, Beever *et al.* (2010) wrote that: 'Within mountainous terrain in particular, the distributional limits of biotas have long been known to be strongly controlled by climate . . .'. In this approach, 'Species range limits are essentially the expression of a species' ecological niche in space.' (Sexton *et al.*, 2009). Nevertheless, other authors have concluded that two adjacent (allopatric) sister-clades can occur in different areas with similar climate. This is seen in Mexican jays, for example (McCormack, Zellmer & Knowles, 2009), and other cases discussed below.

#### GRINNELL AND NICHE THEORY: THE ECOLOGICAL MODEL OF DISTRIBUTION AND THE CALIFORNIAN BIOTA

Grinnell (1904) studied the chickadee *Parus rufescens* (Paridae), a bird that inhabits a narrow strip along the western seaboard of North America from Alaska to southern California (Santa Barbara County), and also occurs inland around the US/Canada border east to Montana. It is more or less allopatric with the related *P. hudsonicus* to the north and east, and with *P. sclateri* in Mexico. Grinnell wrote that the influences determining the distribution area of *P. rufescens* 'may be safely assumed to be atmospheric humidity, with associated floral conditions. For this habitat coincides quite accurately with the narrow coastal belt of excessive cloudy weather and rainfall'. But the southern California coast is much sunnier, drier and warmer than Washington, let alone Alaska.

Grinnell (1904) proposed a model for the evolution and distribution of *P. rufescens* with a centre of origin (in the northeast), dispersal to the west, and adaptation to the conditions there. Yet the simple allopatry between *P. rufescens* and its allies indicates that neither centre of origin nor dispersal are necessary, as evolution by simple vicariance would produce the pattern. Grinnell's (1904) study was an early and influential application of what became the standard approach for 20<sup>th</sup> century ecologists, one that is based on a centre of origin, dispersal, and adaptation (the CODA model; Lomolino & Brown, 2009).

In another influential account, Grinnell (1917) studied the California thrasher *Toxostoma redivivum* (Mimidae) that extends from the California/Oregon border south to the much warmer northern Baja California. Yet Grinnell wrote that *T. redivivum* is: 'unquestionably delimited in its range in ultimate analysis by temperature conditions (p. 430) and referred to this ecological setting as the 'niche' of the

species. Nevertheless, belts of similar temperature extend from the west to the east coast of the southern USA.

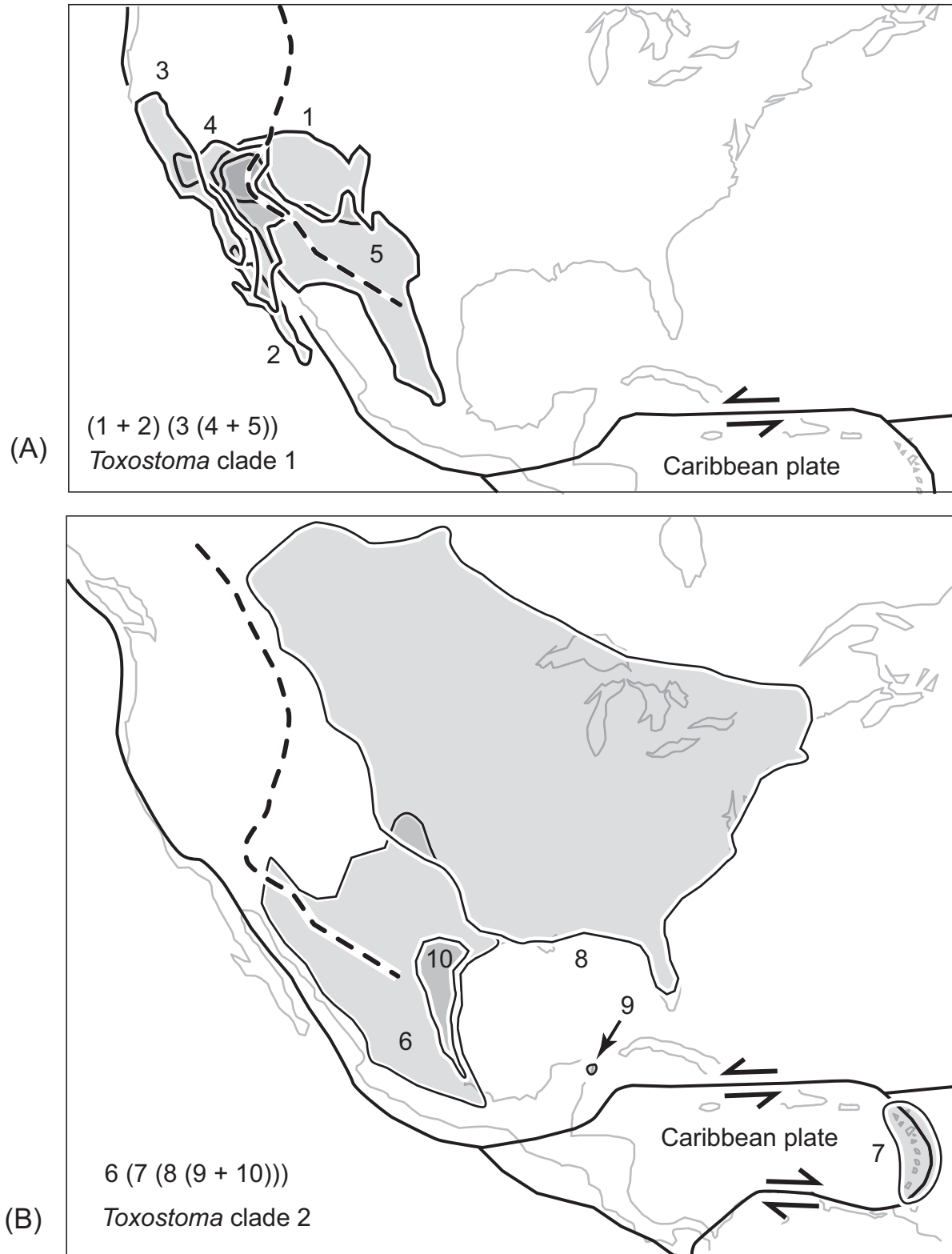
The distribution of a species can be examined in terms of its present ecology and environment, but also in its phylogenetic context. *Toxostoma*, including the California thrasher, has a widespread distribution with two main clades (Fig. 1; Lovette *et al.*, 2012). The first main clade (species 1–5) has an obvious centre of diversity in California/Baja California, with all five species present there (two endemic). In contrast, the second main clade (species 6–10) is completely absent there, despite having an extensive range from the Lesser Antilles and Mexico through the USA (west to Arizona) and north to Canada. Thus although there is extensive overlap between the two main clades in northern Mexico (mainly involving species 5 and species 6), overall they show basic allopatry. For *Toxostoma* as a whole, the first question is: what is the reason for this high level of allopatry? The main break in the genus underlies the endemism of the California thrasher, *T. redivivum*, in phylogeny and in geography. Does the endemism reflect current ecological conditions or does it have a broader evolutionary context and date back to earlier geography and climate?

Species 8 in *Toxostoma*, *T. rufum*, occurs in the eastern USA and Canada. Grinnell's (1917) model of ecological determinism would assume that its distribution was caused by environmental factors. Yet a distribution model for this bird based on the climate, vegetation and soil types of its known localities predicted – incorrectly – that it would also occur in California, Mexico, and the Caribbean, where other *Toxostoma* species are present (Peterson, 2001). This provides excellent evidence that the absence of *T. rufum* from California is *not* caused by climate, vegetation or soil type, and contradicts Grinnell's (1917) model.

In a similar way, the second main *Toxostoma* clade as a whole is very widespread – from the Caribbean to Canada – and so its absence from California is probably not the result of climatic limitations. Instead, the absence reflects historical vicariance with its sister-group, which has its centre of diversity in California.

*Toxostoma redivivum* (Grinnell, 1917) and *T. rufum* (Peterson, 2001) both occur in areas (northern California and the eastern USA/Canada, respectively) where they are the only members of the genus present. This is consistent with the idea that they originated at their present sites, by simple allopatric differentiation within the California clade and the widespread clade, respectively. A critical question for this speciation is its timing, and other aspects of distribution in *Toxostoma* shed light on this.





**Figure 1.** Distribution of *Toxostoma* (Mimidae). (a). Clade 1. 1 = *T. bendirei*, 2 = *T. cinereum*, 3 = *T. redivivum*, 4 = *T. lecontei*, 5 = *T. crissale*. (b). Clade 2. 6 = *T. curvirostre*, 7 = *T. ocellatum*, 8 = *T. rufum*, 9 = *T. guttatum*, 10 = *T. longirostre* (phylogeny from Lovette *et al.*, 2012; distributions from IUCN, 2014). Continuous line = plate margin; dashed line = Sevier fold-and-thrust belt.

*Toxostoma* as a whole ranges from the Lesser Antilles and southern Mexico throughout the USA and parts of Canada, but is absent from the Greater Antilles where it is represented by diverse other Mimidae. The Lesser Antilles endemic *T. ocellatum* is of special interest as it is not nested in, or sister to, a mainland species, but is instead sister to a diverse clade with a wide distribution in Cozumel Island, north-eastern Mexico, and much of eastern North America. This implies an old break between *T. ocellatum* and its sister, and the location of the break suggests that it was mediated by the formation and history of the Caribbean plate. Strike-slip (horizontal) fault movements along the northern and southern margins of the Caribbean plate (Fig. 1) have translated the eastern margin of the plate – an active subduction zone producing the Lesser Antilles – to the east. (The Lesser Antilles species is likely to be much older than the current islands themselves, and have survived as a metapopulation at the subduction zone). Before this displacement, the Lesser Antilles species would have been adjacent to the Cozumel Island and Mexican species. This is of direct relevance for dating the California-centred clade of *Toxostoma* (species 1–4), as the phylogeny indicates that the Lesser Antilles species originated after the California-centred clade.

From the mid-Cretaceous to the Eocene, the tectonic development of western America was dominated by the subduction in the west, and this caused large-scale folding and thrusting in the trans-continental Sevier belt (Fig. 1). The location of the fold-and-thrust belt suggests it could have caused the main break in *Toxostoma*, with subsequent dispersal of species 1, 5 and 6 across the belt. The chronology would be consistent with eastward tectonic displacement of the Lesser Antilles species through the Cenozoic, and coeval differentiation of *Toxostoma* species within California.

In this model, it is not the diversity of habitats, including the mountains, that caused the California speciation; instead, common factors brought about both, together. The current habitat preserves the diversity, but did not cause it; instead, the *changes* that created the habitat diversity (such as terrane accretion, orogeny, strike-slip displacement and volcanism) also caused the speciation. After evolving within their respective ranges, species may have evolved a degree of local adaptation to current conditions, but their ecology to begin with is largely inherited.

The broader affinities of the California fauna and its components suggest that their distribution is not caused by sea mist or any other aspect of the present environment. Instead, their origin and distribution are related to the origin of neighbouring regions of

endemism in parts of western America and the Caribbean that were caused by plate tectonics. If the origin of the modern California biota, including the clade of *Toxostoma* comprising species 1–5, was mediated by tectonics, this would also explain the state's great diversity compared with most parts of the USA.

As with the fauna, the evolution of the Californian flora is often related to the current, Mediterranean-type climate and its development at 2 to 5 Ma. Yet molecular clock studies provide minimum estimates of clade age, and have found that the climatic change was not a major cause of diversification in the Californian flora; instead, Lancaster & Kay (2013) concluded that 'the role of the current Mediterranean climate in promoting diversification has been overemphasized . . .'. These authors found that the high species richness in Mediterranean-type regions 'may generally predate the onset of the Mediterranean climate . . .'. Recent work suggests that many plant adaptations commonly found in Mediterranean [climate] regions, such as sclerophylly and the ability to resprout following fire, also predate the Mediterranean climate . . .'. Lancaster & Kay (2013) also concluded that the diversity in California is not the result of immigration. Thus they found that neither current climate nor immigration explain the California biota, and this contradicts the traditional CODA model. Instead, it is consistent with old, in-situ evolution mediated by plate tectonics.

#### MODERN RESPONSES TO GRINNELL'S NICHE THEORY OF DISTRIBUTION

If a group's niche does not determine its geographical distribution, what is the relationship between the two? Drake (2013) wrote that this question is 'one of the most fraught in ecology', and suggested that 'The root of this controversy is the lack of truly clear concepts . . .'. Critical examination of the basic concepts in the field have been neglected, and Peterson *et al.* (2011) wrote that in previous work on niches and distributions, '*conceptual and methodological rigour* took back seat to rapid development of *software and data* resources . . .'. [Italics added]. The inevitable result is that ecology-biogeography is now a field 'rife with ill-defined jargon and loosely defined terms'.

The modern approach of macroecology was developed by ecologists searching for generalized patterns at large spatial and temporal scales, who realised that 'small-scale local processes alone were not able to fully explain the abundance and distribution of species' (Keith *et al.*, 2012). Yet this approach retained many of the traditional ecological concepts. For example, the book by Peterson *et al.* (2011) focused 'on the complex relationships between ecological niches and geographic distributions of species', but while

‘climate’ or ‘climatic’ were cited 96 times and ‘Pleistocene’ seven times, neither ‘Pliocene’, ‘Miocene’, ‘Cretaceous’ nor ‘tectonics’ were mentioned at all. This sort of emphasis is typical for ecological work and contrasts with studies on evolutionary biogeography.

## CLIMATE AND DISTRIBUTION

Modern applications of Grinnell’s theory include species distribution models (SDMs) or ‘niche models’. These aim to reconstruct the ecological requirements of species and thus predict their geographical distributions. If the known localities of a species experience rainfall of  $x$ , temperature of  $y$ , and so on, it is assumed that the total range of the species is made up of all the areas with those conditions. As Higgins, O’Hara & Römermann (2012) wrote: ‘Species distribution modelling is the process of discovering the *conditions* under which a species can [or, rather, does] survive, and thus delimiting the areas in space where we might expect to find a species’ [*italics added*]. In this way the predictions that the models make incorporate Grinnell’s (1917) idea that species distributions are determined by the current environment, rather than historical factors.

The simplest distribution models are climate envelope models (the ‘climate envelope’ describes the climatic conditions in which a clade is currently found) or more general habitat suitability models. Overall, the approach correlates species locality records with environmental data to explain and predict species distributions. The vast majority of SDM studies to date have been correlative (Robinson *et al.*, 2011). Correlative SDMs identify places that are suitable for the survival of a species by identifying its environmental requirements (based on its realised niche), usually aspects of the physical environment. Aspects of the biotic environment and biotic interactions are much more difficult to model, although this is being attempted now. Historical aspects are even more difficult to incorporate and are usually overlooked.

SDMs are often described as predicting species distributions (Elith & Leathwick, 2009), but really they only identify regions where environmental conditions are similar to areas where a species is known to occur (Pearson *et al.*, 2007). Climate-based models assume that macro-climate acts as the primary determinant of the distributions of species (Grinnell, 1917), but many studies have shown that there can be a great difference between a species’ actual distribution and areas of suitable climate. Some examples are discussed next.

### CLIMATE-BASED SDMS OFTEN DO NOT WORK

Species distribution modelling for narrow-ranging species is often not carried out because of statistical

constraints (Platts *et al.*, 2014). Yet there are also problems in modelling distributions of wider-ranging species. Beale & Lennon (2012) wrote that uncertainty in SDMs has often been underestimated and a false precision assigned to predictions of geographical distribution. As Elith & Leathwick (2009) suggested, ‘SDMs are used to gain evolutionary and ecological insight’, and one of the most interesting aspects of the climate-based models is that they predict many aspects of species distribution so poorly. In the example mentioned above, an SDM for *Toxostoma rufum* based on climate and vegetation predicted, incorrectly, that it would occur in California (Peterson, 2001). This sort of result suggests there are problems with the whole idea of ecological determinism; despite the widespread use of SDMs, Soberón & Nakamura (2009) concluded that ‘important conceptual issues in this field remain confused’ (cf. Araújo & Guisan, 2006). Hof, Jansson & Nilsson (2012) proposed that the main limitation of SDMs ‘lies in their assumption that species’ ranges are determined mostly by climate, which is arguable’. Thus the question as to whether climate by itself is sufficient or even the most important factor for explaining species distributions has become controversial in ecology (Dormann, 2007), and ecologists are beginning to appreciate the insight gained by the 19<sup>th</sup> century systematists – distribution is not caused simply by climate.

In practice, SDMs often provide inaccurate predictions, as in *Toxostoma rufum*, and the idea that climate on its own determines distribution is also contradicted by many other observations. For example, some alpine plants show luxuriant growth if cultivated in the lowlands, and so are probably absent there because of competition or predation, not climate *per se*. Feeley & Silman (2011) suggested that many SDMs under-predict the extent of species ranges simply because of sampling (collection) deficiencies, and they advocated ‘more collecting’. The problems with the approach are likely to involve additional factors though, as there are also many cases of drastic over-prediction, and a few examples are cited next to illustrate this.

### OVER-PREDICTION OF DISTRIBUTIONS BY SDMS

Fifty five tree species in Europe were shown to have an observed distribution that filled, on average, only 38% of their potential distribution, as predicted by climate (Svenning & Skov, 2004). For mammals in Mexico, the figure was 50% (Munguía, Peterson & Sánchez-Cordero, 2008). Munguía *et al.* (2012) fitted bioclimatic envelopes for all amphibian species worldwide (5544 species) and found that, on average, species only occupied 30% of their potential distribu-

tions. Even within the global biogeographical regions of Wallace, more or less equivalent to the continents, the amphibian species filled, on average, only 57% of their potential habitat.

SDMs for 12 chameleon species in Madagascar predicted the eastern Madagascar parts of the ranges correctly, but also predicted, incorrectly, that six of the species would also occur in central-western Madagascar and three in south-eastern Madagascar (for modelled distributions, see Raxworthy *et al.*, 2003; for actual distributions see IUCN, 2014).

The *Anopheles dirus* complex is a clade of mosquitoes that ranges from India to Taiwan, and is the most efficient malaria vector there. The distribution of the *A. dirus* complex was predicted in an SDM, but this made significant over-predictions in Sri Lanka, the Philippines and Indonesia where the complex is replaced by related clades (Obsomer, Defourny & Coosemans, 2012), and the model suggests that the allopatry is not caused by climate.

These results from climate-based distribution models undermine the idea of ecological determinism, even within a group's own continent. Instead, they suggest that distribution boundaries and patterns of allopatry are determined by historical and phylogenetic effects.

#### OTHER CRITICISM OF CLIMATE-BASED DISTRIBUTION MODELS

Beale, Lennon & Gimona (2008) sampled 100 European bird species, and in 68 of these they found no macroscale associations with climate; species–climate associations found by climate envelope methods were no better than chance. They wrote:

... there are many reasons why species distributions may not match climate, including biotic interactions ... , adaptive evolution ... , dispersal limitation ... , and historical chance. ... the degree to which species really are constrained by climate remains unresolved ... [p. 14908]. Most climate models are no better than chance associations ... By using the best available datasets and one of the best known taxonomic groups we are currently unable to build useful distribution models for many species. ... Because birds are perceived to be equally strongly associated with climate as other species groups and trophic levels [...] our results cast doubt on the predictions of climate envelope models for all taxa, ... [p. 14910].

(See also Beale, Lennon & Gimona, 2009). Although these results are controversial they appear to be robust (Chapman, 2010). A study of plant distributions in Britain likewise found 'Weak climatic associations' and concluded: 'Climatic limitation of species

distributions may have been overstated' (Chapman, 2010). Sinclair, White & Newell (2010: 7) wrote in the same vein:

We question whether current modelling approaches and outputs are practically useful ... Until [SDMs] offer insights that are more precise than what we can derive from basic ecological theory, we question their utility in deciding how to allocate scarce funds to large-scale conservation projects.

These authors also highlighted the fundamental conceptual problem: 'It is often assumed that organisms are found in the environmental space that best suits their requirements ...'.

In a paper on SDMs titled 'Not as good as they seem', Jiménez-Valverde, Lobo & Hortal (2008) referred to '... the general inaccuracy of the predictions of the realised distribution provided by species distribution modelling methods.' Cayuela *et al.* (2009: 320) described case studies in tropical America and concluded that:

Those species that are most in need of conservation actions, namely those that are the rarest or most threatened, are those for which SDM is least likely to be useful. We found that only 15% of the tree species of conservation concern in Central America could be reliably modelled using data from a substantial source. [In a study of distributions in the Andes] a large proportion of the target species could not be effectively modelled with Maxent ... We also suggest that researchers using SDMs should become more open regarding the limitations of SDMs ... Reviewers and editors should also be prepared to accept studies that rigorously document model failures as well as successes ...

The conclusions of all the authors cited here contradict the standard paradigm, ecological determinism (Grinnell, 1914, 1924), and instead support Darwin's (1859) view that species distributions are not caused by 'climatal and other physical conditions'.

#### NICHE MODELS IN MARINE SYSTEMS

Keith *et al.* (2013) concluded that Indo-Pacific corals are assembled within 11 distinct faunal provinces, with province limits characterized by co-occurrence of multiple species range boundaries. They found that: 'Unexpectedly, these faunal breaks are poorly predicted by contemporary environmental conditions and the present-day distribution of habitat. Instead, faunal breaks show striking concordance with geological features (tectonic plates and mantle plume tracks)'. This conclusion matches the results seen in many terrestrial groups: historical processes account for more of the present-day biogeographical patterns than explanations based on current environmental conditions.



## NICHE VARIATION IN TIME AND SPACE

Species niches can change through time. For example, in Australia, SDMs failed to predict survival of tree species in glacial refugia that were identified from genetic evidence, indicating that the realized niches of the species may have changed since the last glacial maximum (Worth *et al.*, 2014).

Species can also occupy different niches in different areas. This regional niche variation has often been observed, and it means that SDMs are not necessarily transferable among regions. For example, SDMs for alpine species shared between Switzerland and Austria, based on climate and topography, showed weak transferability between the two countries, even when the abiotic conditions remained constant (Randin *et al.*, 2006). The study noted that this could be caused by biotic factors, as regional species pools usually differ in distinct parts of a species' range as the result of historical influences. As Bahn & McGill (2012) concluded, 'current opinion about how well distribution models perform may be overly optimistic when extrapolating into new areas or new climate regimes for either prediction or understanding ...'.

In Australia, McAlpine *et al.* (2008) found that 'Regional variation in habitat relationships within such broad geographical ranges is an emerging issue in ecology ...'. Duncan, Cassey & Blackburn (2009) found similar results for SDMs of African dung beetles introduced to Australia. Most Australian climate envelope models provided a good fit to the Australian data, but models developed in the native range performed poorly, implying that non-climatic factors limit the native distribution of these species. Duncan *et al.* concluded (p. 1455): 'Our results suggest that climate may not be the major factor limiting native distributions in some, if not most, cases'.

Zanini, Pellet & Schmidt (2009) observed that SDMs are usually established for only one region and generally show low transferability across regions. They wrote that habitat characteristics alone cannot explain patterns of distribution, and that 'This is a central but poorly understood issue ...'. Instead of rejecting the primary significance of habitat, Zanini *et al.* suggested that further information on habitat parameters might explain the problem. Nevertheless, a solution may require a review of basic concepts, not just more data.

Dormann *et al.* (2012) wrote that predictions based on correlative models:

...are usually limited in their biological realism and their transferability to novel environments ... [p. 2120]. Several studies have explored the transferability of a model to other species ..., other sites ... and other times ... Overall, generality was found to be very low ... [p. 2124].

The authors also made the crucial point that 'In very few cases can we claim to understand distributional constraints, and SDMs are thus valuable for *generating hypotheses* ...' [p. 2121; italics in original]. One hypothesis suggested by the models is the idea that current ecology does not explain distribution. The results from the SDM literature are valuable as they constitute a large-scale test of Darwin's (1859) and Grinnell's (1917, 1924) conflicting ideas on the significance of climate for distribution. The studies support Darwin's conclusion and indicate that climate is not the determining factor that has been assumed in much ecological work.

The habitat or niche of a species may show regional variation because of genetic differentiation within the species. This is often the case in species with strong phylogeographic structure, with different genotypes inhabiting different areas (D'Amen, Zimmermann & Pearman, 2013). Yet niche variation can also occur in populations of a species *without* any evident structure. The niche may also vary across a geographical range simply because of long-term changes in the landscape. Murphy & Lovett-Doust (2007) found that 'the niche space occupied by the wide-ranging North American tree *Gleditsia triacanthos* (Fabaceae) varies regionally, and between some regions there may be a complete absence of niche overlap ... This lack of overlap appears to be driven primarily by regional differences in abiotic conditions, rather than regional adaptation *per se*'. In a similar way, if a mountain range is uplifted beneath one area of a lowland community, the species in this part (minus some extinctions) will become montane, and will occupy different niches. This sort of process means that niche variation within a species can also occur over time.

Even at the global scale, many species may grow better in regions where they have never occurred. Many local endemics become weeds when introduced elsewhere; for example, two of the three stick insect species present in Britain are New Zealand endemics that have become weedy in Britain (Lee, 1999). Thus there is no real reason to assume that species are best adapted to their own region.

## BIOTIC FACTORS AND DISTRIBUTION

As discussed in the last section, most SDMs (niche models) are based on abiotic factors, and in many cases they do not perform well. Authors are now acknowledging this, and are looking at the significance of biotic factors in structuring distribution.

## SDMS THAT INCLUDE BIOTIC FACTORS (DISPERSAL, BIOTIC INTERACTIONS ETC.)

Godsoe & Harmon (2012) concluded that: 'Despite their promise, the interpretation of SDMs is fraught

with conceptual ambiguity'. They also observed that SDMs as currently implemented model only 'a tiny subset' of the factors moulding distribution. Given the acknowledged failure of SDMs based on abiotic factors, some ecologists are now attempting to integrate biotic factors and processes (competition, predation, parasitism, dispersal ability etc.) into the models (Dormann *et al.*, 2012; Wisz *et al.*, 2012). As yet there have been few process-based SDMs (Dormann *et al.*, 2012), and there are many problems in this approach.

For example, processes such as longer term colonization rates are difficult to quantify 'because they critically depend on the frequency of long-distance dispersal events, which is hard to measure' (Schurr *et al.*, 2007). Thus, dispersal data are seldom sufficient for detecting a relationship between dispersal ability and range size (Gaston & Blackburn, 2003). Birand, Vose & Gavrillets (2012) found that: 'high dispersal abilities and broad niche widths may not always promote large ranges ...'. In marine species, Lester *et al.* (2007) showed that in most cases dispersal abilities do not correlate with range sizes; 'Our results suggest dispersal is not a general determinant of range size'. This idea has also been proposed for plants in tropical floras (see references in Heads, 2003: 390).

Apart from dispersal, other aspects of ecology also fail to predict distribution well. Hobbs, Jones & Munday (2010) studied angelfishes (Pomacanthidae) on reefs around Indian Ocean islands. They found that endemic species used similar resources to many widespread species. Other studies have also demonstrated that overall niche widths do not correlate with range sizes (Gregory & Gaston, 2000; Lehman, 2004).

Cassini (2011) gave an accurate summary: 'The design of models that incorporate biological processes is very difficult, because they require the estimation of many parameters and thus inevitably make many assumptions ... Currently, such models are more useful for the theoretical analysis ... than for providing practical tools ...'. The new SDMs integrating biological processes are much more difficult to produce and do not appear to solve problems any better than previous models. Abiotic and biotic aspects of the environment can determine local distribution and some structural aspects of the vegetation in an area, but not the plant and animal clades that are present, or their boundaries. With clades, 'historical factors' come into play.

## HISTORY AND DISTRIBUTION

The studies cited above indicate that in many cases neither the climate-based distribution models nor the models that incorporate biotic factors actually work in

practice. These results are not widely acknowledged, and most ecologists still agree that: 'The distributions of species are determined by the distributions of the environmental conditions where they can persist' (Higgins *et al.*, 2012). Nevertheless, a growing number of ecologists recognises that the models need to move beyond present 'conditions', both abiotic and biotic, and to incorporate history over geological time. Wiens (2011) wrote: 'At present, I am unaware of any large-scale biogeographic patterns that are created by competitive interactions or by biotic interactions in general'. Large-scale biogeographical boundaries such as Wallace's line may be maintained by local ecological interactions, but these are unlikely to have caused the boundaries to begin with. Instead, the breaks have been formed by historical, phylogenetic events associated with geological processes, not current conditions (Heads, 2014). Even at small scales, a biogeographical region such as a centre of endemism may only be a few kilometres across. These are especially common in areas that have been subjected to major geological disturbance, such as marine inundation or tectonism.

## CONCLUSIONS

Two of the most obvious attributes of a species are its present habitat and biology, including its means of dispersal. Making observations on these is often straightforward, and it is not surprising they have been assumed to cause distribution. Nevertheless, models based on these factors often do not work in practice and fail to explain many concrete examples of distribution. One review concluded: 'It has often proven frustratingly difficult to explain what determines the limits of a particular species at a given place and time' (Gaston, 2009).

Accepting the idea that historical factors can be at least as significant as current conditions in determining distribution would require a new synthesis of ecology and biogeography. Despite the long-term schism between ecology and biogeography, Ricklefs & Jenkins (2011) noted a recent trend towards unification.

Different groups have different habitats, and this is a useful guide to their location within their region. Nevertheless, many groups include a small number of anomalous populations found in atypical environments, such as coastal populations in a group that is generally montane. These can indicate historical effects, such as subsidence followed by ecological lag, and many populations may have a relictual ecology, surviving in sub-optimal habitat. Populations with anomalous ecology are often located in particular geographical areas, and these

often coincide with tectonic features. This suggests that ecological patterns can reflect events in geological time.

The conclusion reached here is that current ecology prevents species from establishing in some areas, but does not explain why they occur where they do to begin with. A species is present at a site because it is in the species pool of the region, and the different habitats in a region draw their species from this pool. A group may be eliminated from a site by local ecological conditions, but these do not determine the regional pool. Within a geographical region, a species may occur only on mountains, for example, but its montane ecology does not explain why it occurs on those particular mountains and not others. The same is true for the distribution of 'rainforest species', 'volcanic island species' or species of any other habitat. A group's biogeography – its geographical distribution – determines the particular range of habitats and niches that are available to it, and if it is viable in at least one of these it will survive.

One of the main factors determining the distribution of a group is the distribution of its immediate ancestor. For example, if a global group splits into northern and southern hemisphere groups, each of these groups already has a very large range at the time of its origin. If a group in ancestral North America splits into western and eastern descendants, these begin life with much smaller range sizes. A group's original ecology and distribution are inherited from its ancestor. The original range can undergo subsequent expansion or contraction, but in many cases a group's original distribution and its allopatry with relatives can persist for millions of years. Thus distribution often represents inherited information, and many studies in molecular phylogenetics now provide maps of distributions, as the clades show such clear spatial structure. In its move towards biogeography, this work in genetics is now producing more interesting distribution maps than ecology, which has not yet digested the great progress made in molecular biogeography.

Reductionist 'population thinking' became popular in the field of evolution and systematics through the 20<sup>th</sup> century, but biologists interested in gaining a broader perspective on species can also look up to phenomena at the genus and family level. As Wiens *et al.* (2010) stressed, ecologists and conservation biologists need to be aware that 'many of the traits and patterns they study may have ancient roots that go far deeper than the species and ecological conditions seen today'. Processes such as hybridism and the inheritance of ancestral polymorphism mean that evolution often proceeds by the recombination of ancestral characters, and so these characters and their distributions can be much older than the

modern species that carry them. Likewise, an ancestor that was widespread and had a wide range of ecology may leave descendants that inherit different habitat types during differentiation. For example, a genus comprising one species in well-drained forest and one in swamp forest may be derived from an ancestor that lived in both types of habitat. In this case each modern species has inherited, not invaded, its habitat type.

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