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commonly observed between closely related species. Qualitatively different changes in less peripheral parts of GRNs will result in larger phenotypic effects, such as those that roughly separate different families, orders, or classes. Such changes tend to occur less frequently because of the greater likelihood of downstream pleiotropic effects that can disrupt development. These claims put up for discussion a lot of fundamental issues that have already started to be debated (once again in most cases) in the recent literature. Is macroevolution just microevolution writ large, or are they underpinned by qualitatively different kinds of genetic change? Are there marked discontinuities in evolutionary step sizes based on where the regulatory genome is changed by a mutation, and might these correlate with observed differences in the amount of intraspecific phenotypic variation and the step size of morphological transformations at different times in a clade’s history? Is, in contrast to what all good neo-Darwinians should assert, homology perhaps more than just historical residue? What are the relative contributions of external selection pressures and internal constraints in determining the direction of evolutionary change? Have there been, as Davidson & Erwin (2006) claim, no new origins of phylum-level body parts since the Cambrian because of the constraints imposed by GRN kernels? These fundamental issues are always worth discussing, and they deserve our dedicated attention. However, as Davidson himself candidly admits, there is now a more pressing need for more empirical data. History shows that personal conviction and intuition are insufficient to resolve these issues. Let us hope that the next decade will shed new empirical light on these fascinating fundamentals of systematics.

References


Biogeography in a Changing World


The book ‘Biogeography in a Changing World’ is in large part based on the papers presented at a symposium titled ‘What is Biogeography?’ held in Cardiff in August 2005 as part of the Fifth Biennial Meeting of the Systematics Association. According to the editors of the book, biogeography is suffering from something like an identity crisis, being closely connected to and partly dependent on other biological disciplines (such as ecology, evolution, taxonomy or molecular systematics) but also struggling to maintain a position as an independent discipline with a core of accepted knowledge and methodological principles that guide research. Contributors to the book are current leading proponents of differing methods in biogeography and the aim of the book was to produce a broad-based perspective on the nature of biogeography offering both historical perspectives and methodological advances as well as a foresight as to what the future might hold for the discipline. Rather worryingly, Adams’ foreword and his animation of an expanding
earth featured uncompromisingly on the cover and McCarthy’s final chapter, seem at odds with the declared pluralistic approach of the book, and leave the reader with the feeling that perhaps here current geological understanding is being unhinged with the wrong tools.

Given the many definitions in the book for subdisciplines of biogeography, e.g. historical, cladistic, or phylogenetic biogeography, it is obvious that there is no easy answer to the question ‘what is biogeography?’. It is also obvious that biogeography as a discipline is severely divided with authors stressing the importance of finding shared patterns of distribution and others focussing on identifying causes of patterns, some stressing the importance of vicariance, and others of dispersal. We find it a pity that Ebach’s introductory pages put more effort in carving a deep fracture between disciplines – ultimately pinpointing at the alleged ‘faults’ of phylogenetics – rather than preparing a constructive framework for a subsequent synthesis. We could not help but sometimes feeling ‘attacked’ by some authors for being phylogeographers and failing to use terms, concepts, methods and philosophies that are central to biogeography.

However, if such concepts are not without controversy even amongst biogeographers themselves, that should come as no surprise! In our opinion – as fortunately Riddle & Hafner manage to convey in Chapter 7 – genetic tools have the potential to ‘solve’ or at least circumvent many controversies in biogeography, by discovering patterns (e.g. revealing cryptic species) and at the same time uncovering processes (e.g. direction of gene flow) or to provide a historical biogeography for one (or several species) that may include episodes of vicariance followed by range expansion and dispersal.

The first chapter by Williams is aimed at providing an historical grounding for the book, by focusing on the ‘thefold parallelism’ between ontogeny, phylogeny and paleontology – championed in particular by Ernst Haeckel at the end of the 19th century – and discussing its importance in the development of modern biogeographical thinking. Whilst we believe that an historical perspective is crucial to understand the rise (and fall) of scientific ideas, we also felt that if this chapter had been 60% shorter, it would have provided a much more focused ‘rooting’ for the subsequent essays. Instead, it offers a huge amount of interesting, yet largely irrelevant, information about the ‘conflicts of intellect’ between Haeckel and Agassiz.

The conclusion of the chapter, well in line with Ebach’s opening, again seems to call for the need for biogeographers to ‘stick’ to classification of areas, and refrain from using methods aimed at ‘discovering ancestry’, which – more than three decades after Dobzhansky’s famous statement – sounds puzzling to say the least.

In the second chapter, Parenti warns against the philosophy that one aim of historical biogeography is to generate an explanation as well as to discover a pattern. She also warns against a rejection of biogeographic patterns using estimates of divergence times based on molecular data (because calibrations rely for a large part on fossils). She unjustly blames the application of molecular tools to biogeography for reviving untestable hypotheses of center of origin, recognition of ancestors, and dismissal of the importance of Earth history at all levels. However, she admits that molecular data also have great potential to unravel fine scale patterns of relationships among endemic areas, especially throughout the marine realm where they have not been expected. She also calls for a reclassification of global biogeographic regions, which should include
both terrestrial and marine components.

In chapter three, Grehan starts with yet another stern attack of molecular methods (a section entitled ‘Molecular Mythology’!) and the defence of systematic ‘biogeographic maps’, fully independent from a Darwinian approach, as fundamental units of biogeography. He then goes on in the attempt to deconstruct a long-distance dispersal model developed for a genus of daisies. Data from other taxa with similar disjunct distributions are invoked to support a ‘fit-for-all’ vicariance model possibly consistent with an expanding Earth. Despite the lack of details provided, a number of aspects remain unclarified, and a great extent of the evidence provided could be interpreted in more that one way.

The fourth chapter by Hausdorf & Hennig deals with biotic element analysis and vicariance biogeography. These authors provide a clear argument that it should be tested first whether the clustering of ranges is stronger than expected by chance (thus vicariance should not be predisposed) and describe how this should be done with some clear examples. The appropriate units for this are biotic elements, i.e. groups of taxa with similar ranges, and not areas of endemism because they cannot be delimited if dispersal occurred. Secondly, another prediction of the vicariance model is tested, namely that closely related species originate on different sides of an emerging barrier. Their case studies indicated that speciation modes other than vicariance were frequent or that the imprint of vicariance on the ranges was often obscured by extensive postspeciational dispersal, regional extinction or sympatric speciation. The methods described in this chapter can help to identify those taxa and areas that are most promising for further analysis of vicariance events.

Chapter 5, by Stuessy, is a clear and useful synopsis on the different processes affecting species and genetic diversity during the four successive phases in the ontogeny of island biogeography. Shifting from the classical McArthur & Wilson’s model, the author stresses that diversity never really reaches an equilibrium, and that island-island and/or island-continent comparisons of biological diversity should always take into account the ‘ontogenetic phase’ of the biotas considered.

According to Sanmartín in chapter 6 historical biogeography aims to infer the distribution history of biotas and to identify the causal factors or processes that have shaped those distributions over time. She reviews recent methodological developments that are event-based and have led to an extraordinary revolution in biogeographic studies. She convincingly shows that including all biogeographic processes into the analysis is the way forward for biogeography. She clearly explains and compares two event-based methods, dispersal-vicariance analysis and parsimony-based tree fitting, and offers practical tips as to when to use which method. She dismisses a common critique against event-based methods (that if the models are wrong, the biogeographic inference would be wrong) by citing Ronquist’s (2003) argument in favour of model-based methods in phylogenetic analysis (such as Maximum Likelihood and Bayesian inference) ‘ignoring process in the formulation of a method does not make it more objective; the method’s performance is still determined by the nature of the evolutionary processes being studied’.

The excellent chapter 7, by Riddle & Hafner, is the only chapter that attempts to bring historical biogeography and phylogeography closer together. The authors identify two promising areas of growth likely to bridge the gap between phylogeographic and area-based biogeography:
statistical phylogeography and comparative phylogeography. Indeed, as neatly synthesized in Figure 7.4, the latter (defined as the geographical comparison of evolutionary subdivision across multiple co-distributed species or species complexes; Arbogast & Kenagy 2001) can generate the hypothesis than can be subsequently tested by the former. The authors also present a case study illustrating the application of a five-step approach to interactively and successfully employ phylogeographic and biogeographic analyses in the study of the warm desert biota of western North America.

As much as chapter 7 seemed to finally come to a fruitful synthesis, we were left bemused by McCarthy’s closing contribution. As early as in the abstract, and all the way to the final summary, the author seems to follow a personal agenda to use some selected biogeographic evidence that would uphold the expanding Earth theory. McCarthy argues that for a number of relatively closely related taxa found on both sides of the Pacific Ocean, dispersal interpretations do not fit, whilst a vicariance interpretation of an expanding Earth, featuring a spectacular opening and expansion of the Pacific beginning in the Triassic, would explain all disjunct distributions. Unfortunately, McCarthy does not adopt a rigorous scientific approach for his paper, especially for scientists that are unfamiliar with the expanding Earth theory. He lists his arguments leaving little room for the consideration of alternative possibilities, even though the explanation provided (the expanding Earth) is by far the least parsimonious. Not only – as noted by Briggs (2004) – can the expanding Earth theory not explain the Precambrian to Paleozoic fossil record of marine life, which provides evidence of extensive oceans, but more importantly, the very geological and physical disciplines that he invokes as support for the theory have long dismissed the expanding Earth as pseudoscience, on the grounds of its disagreement with paleomagnetic estimates of the Earth radius (McElhinney et al., 1978) and its moment of inertia (Williams, 2000). Perhaps even more gravely, expanding Earth assumptions are in contrast with overwhelming evidence of subduction and the basic principles of Einstein’s theory of General Relativity, and the Standard Model of particle physics.

McCarthy’s final summary should have probably included a fourth point, stating: ‘no researcher supporting the expanding Earth theory has hitherto provided any scientifically sound framework to uphold what essentially are plain speculations and grave assumptions’.

In our opinion, biogeography cannot survive without embracing genetic tools, a bit like systematics has done before. This book was certainly an unconventional read to us and sparked some ideas about focussing more on species with shared distribution patterns in a comparative framework. Yet, we are still unsure as to the real purpose of the book: if its main intent was to bridge different approaches and philosophies currently contributing to biogeographic analysis, and to pave the way for their synthesis and integration, we believe the objectives have not been met, as only one chapter (7) seems to possess such synthetic characteristics. If the goal was instead to simply showcase the current methods in biogeography and forecast its potential future developments, the picture obtained is still that of a field characterised by a deep fracture, across which the ‘dispersal’ of novel ideas for scientific integration appears strongly hindered.

References

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