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Meeting report

Integrating ecology into macroevolutionary research

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On 9 March, over 150 biologists gathered in London for the Centre for Ecology and Evolution spring symposium, 'Integrating Ecology into Macroevolutionary Research'. The event brought together researchers from London-based institutions alongside others from across the UK, Europe and North America for a day of talks. The meeting highlighted methodological advances and recent analyses of exemplar datasets focusing on the exploration of the role of ecological processes in shaping macroevolutionary patterns.

Keywords: diversification; fossil record; trait evolution; molecular phylogenetics

1. INTRODUCTION

Quantitative macroevolutionary research has typically relied on models that, in their simplest incarnations, assume neutrality among traits, individuals or lineages, such as the birth–death model of lineage diversification [1,2] and the Brownian motion model of trait evolution [3]. It has only been in recent years that robust molecular phylogenies have become large and sufficiently well sampled to offer the statistical power necessary to make parameter estimation worthwhile for complex models. Similarly, advances in palaeontological analytical protocols have also permitted more robust analyses of diversity dynamics in the fossil record (e.g. [4]). Excitingly, as the insights from phylogenies and fossils converge, there have been efforts to explore routes to mutual illumination (e.g. [5]). Our

meeting brought together researchers working on a broad variety of taxa, approaches and timescales. The breadth of research on display was impressive and we appear to be on the cusp of a much greater understanding of how and to what extent ecological processes affect macroevolutionary dynamics. Below, we summarize the four dominant themes that recurred throughout the day.

2. ECOLOGY AND DIVERSIFICATION THROUGH TIME

It is now clear from both phylogenies and fossils that macroevolutionary patterns often depart strongly from those that arise under constant rate birth–death and Brownian motion modes and that ecology is a strong candidate for the missing component [4,6,7]. H el ene Morlon ( cole Polytechnique, Paris), in a meta-analysis of 289 molecular phylogenies, demonstrated widespread evidence for speciation rates declining through time, consistent with diversification being diversity dependent and subject to constraints [8]. Lynsey McInnes (Imperial College London) also stressed that diversity differences among mammalian clades could be explained by considering how area influences both diversification rates and diversity limits [9]. Tim Barraclough (Imperial College London) took a thought-provoking further step and outlined how selection and drift could conceivably produce evolutionarily independent units above the species level [10].

3. FOSSILS AND MOLECULES

A common theme across the day's talks was how fossil information can be incorporated into models of diversification to underpin the patterns seen in molecular phylogenies. The fossil record tells us that extinction has been common [11]. Molecular phylogenies usually include only extant taxa and high levels of extinction can remove information from which we can infer past processes. Indeed, McInnes presented the results from a simulation study to show that changes in a clade's carrying capacity (or diversity limits) can sometimes be detected from reconstructed phylogenies alone, but that extinction may erode the signal of past diversity dynamics [12]. While extinction can be estimated from phylogenies under a constant rate birth–death process [2], typical estimates are very low with wide confidence limits [13], leading to concerns about the interpretation of the diversification parameters estimated from molecular phylogenies [5]. The conflict between fossils and phylogenies was a challenge identified by contributors at the 2009 Society of Systematic Biology's 'Evolutionary Bangs and Whimpers' symposium [14]. Encouragingly, it was apparent from several talks at our meeting that this baton has since been picked up and run with. Luke Harmon (University of Idaho) presented a new statistical approach designed to incorporate data on fossil richness in the past to derive more accurate inferences of diversification shifts through time from reconstructed phylogenies and more realistic (non-zero) estimates of extinction rates (an extension of the MEDUSA approach, [15]), while Morlon outlined promising new work on a likelihood-based

method that can accommodate diversity declines in reconstructed phylogenies and so reconcile fossil and molecular data on cetaceans without incorporating fossil data *per se*.

Samuel Turvey (Zoological Society of London) demonstrated that human-caused biodiversity loss throughout recent millennia has biased the faunal composition and structure of today's ecosystems, complicating the interpretation of macroevolutionary processes using modern ecological data alone; incorporating data on recently extinct taxa can aid our understanding of how the processes driving extinction have changed over historical time [16]. Finally, Andy Purvis (Imperial College London) presented a species-level phylogeny of extinct and extant Cenozoic planktonic foraminifera [17], which is perhaps unique in its completeness and promises to be of great value as a model system for macroevolution, offering the opportunity to directly compare inferences made from fossil taxa with those from extant taxa.

4. TRAITS

Recent insights into trait evolution have mirrored those of studies of lineage diversification by showing a move away from simple null models and the incorporation of more ecology (e.g. [18,19]). Both Gavin Thomas (University of Bristol) and Harmon presented methods for exploring departures from a single constant rate Brownian model of trait evolution. Harmon discussed AUTEUR (Accommodating Uncertainty in Trait Evolution Using R) a model that allows fitting different rates of trait diversification in different parts of the tree using reversible-jump Markov Chain Monte Carlo methods. He also outlined MECCA (Modelling the Evolution of Continuous Characters using Approximate Bayesian Computation), a flexible method for jointly modelling lineage and character evolution on incomplete trees under the assumption that traits will influence clade diversification. Thomas introduced a new model combining bounded Brownian motion (borrowed from the economic literature: [20]) and character displacement via interspecific competition.

Three more data-oriented presentations also demonstrated how trait-based analyses can lend insight into the diversification of clades. Using comparisons of taxonomic diversity and morphological disparity in both living and fossil carnivorous mammals, Anjali Goswami (University College London) demonstrated that disparity in cranial morphology is much greater in metatherian carnivores than the more species-rich eutherian carnivore radiations, refuting the hypothesis that developmental constraints have limited the morphological evolution of the marsupial cranium [21]. Using coalescent-based estimates of split times between 22 pairs of ithomiine and heliconiine butterfly taxa across an Amazonian suture zone, Kanchon Dasmahapatra (University College London) demonstrated how a careful study incorporating lineage-specific traits can topple long-standing hypotheses of lineage diversification [22]. Finally, Purvis also demonstrated how dividing foraminifera into broad ecological subtypes based on morphology can expose previously hidden patterns in the diversification of a clade [23].

5. NEW METHODS, NEW DATA

The speakers presented an inspiring variety of new methods. Harmon focused pragmatically on what we want to know from the—often patchy—data that we have to hand. Both Harmon and Thomas emphasized the potential of approximate Bayesian computation (ABC) as a means of exploring more complex ecological hypotheses in the absence of likelihood formulae [24], as long as the process can be simulated. While the prospects for applying this approach to macroevolutionary questions are undoubtedly exciting, the potential of ABC as a panacea for macroevolutionary research requires further investigation given ongoing discussions regarding the specification of appropriate priors and choice of summary statistics [24]. A perhaps surprising methods-related theme of the day was the co-opting of coalescent theory from population genetics to explore macroecological and macroevolutionary patterns by James Rosindell (University of Leeds), Barraclough [10], Morlon *et al.* [8] and Dasmahapatra *et al.* [22].

In a fascinating counterpoint to the other talks of the day, Rosindell explored the macroevolutionary patterns predicted by neutral models where all individuals have equal prospects of death and reproduction [25]. He argued that incorporating more realistic modes of 'protracted speciation', where speciation is a gradual process, dramatically improves neutral predictions of macroevolutionary patterns such as mean species lifetimes [26]. Phylogenetic trees and several patterns of island endemism can be predicted by neutral models with results in accord with the existing data and verbal models [27]. Rosindell remarked that although the real world is not neutral, neutral theory has great potential to provide null models that simultaneously predict macroecological and macroevolutionary patterns.

The wealth of new methods on show was complemented by the presentation of recently compiled and impressively sampled datasets. Beyond those already mentioned above, Bill Baker (Royal Botanic Gardens, Kew) presented a complete genus-level phylogeny of the palms [28], which he used to shed light on the clade's tempo and mode of diversification in tropical rainforests and make inferences on the origin and evolution of diversity in this habitat type as a whole.

6. WHERE TO?

One participant commented, that while he enjoyed the diversity of research presented at the symposium, he was surprised by the lack of integration of ecology into the analyses. This is perhaps a fair reflection on the state of the art and highlights that much more remains to be done. Our task now is to continue to generate robust hypotheses and gather the pertinent data in order to advance our appreciation of the role of ecology on macroevolution. On the evidence of this one day symposium these are exciting times for macroevolutionary research, with advances occurring on multiple fronts, meaning that we should expect to see substantial insights in the coming years.

Videos of most of the day's talks are available to view at: www.vimeo.com/cee2011. We thank the Centre for Ecology and Evolution, the Grantham Institute for Climate Change and Wiley-Blackwell Methods in Ecology and Evolution for

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