

commentary

A Darwinian approach to community ecology

In *A Darwinian approach to plant ecology* the late John Harper argued that evolution should be the conceptual basis for all plant ecology (Harper 1967). Quoting extensively from the *Origin of Species*, and taking examples from ecological restoration, interspecific competition and life-histories, his thesis was that evolution is central to understanding the diversity of adaptations and interactions in plants. Forty-odd years later this vision is playing out with the availability of information on the evolutionary history of species allowing ecologists to explore the links between evolution and ecology in ever more imaginative and detailed ways. In a new synthesis of our current understanding of the links between evolutionary theory and community ecology, Cavender-Bares and colleagues present a compelling case that community ecology has been revolutionised in the past 10 years through advances in phylogenetics and the application of evolutionary ideas. They argue that evolution is central to understanding interactions between species, the diversity of life histories and in deciding between competing hypotheses for species diversity.

Evolution and community assembly

Communities are vague entities at best (Ricklefs 2008) and the processes driving community composition are varied. On the one hand communities may be assembled primarily through migration, for example when habitat is cleared and a community is formed through immigration. On the other, if a community is allowed to develop and essentially left undisturbed for a long period, species will evolve *in situ*. This division is as old as ecology itself, reflecting the difference between Clements' and Gleason's theories on communities. The 'modern synthesis' for community ecology (e.g. for recent reviews see Ricklefs 2008, 2009, Vellend 2010) is that the species present within an area are determined by the relative balance of four processes: speciation, extinction, dispersal and ecological sorting. Traditional community ecology has put a great deal of emphasis on ecological sorting in a narrow sense, particularly focussing on the details of processes and interactions at the micro scale. However as Ricklefs (2009) succinctly puts it, "*The presence of shrub X*

might exclude herb Y from a 1-m² study plot, but much is left unexplained, including why X and Y are there is the first place". Historical factors must play a huge role in determining the composition of a community, through biogeography, speciation and adaptation. The imprint of these historical processes can be untangled if we know the phylogeny of the species present.

What can phylogeny tell us?

Phylogeny can tell us about the degree to which various historical factors shape the distribution of traits and diversity. It is straightforward to statistically test whether differences in species traits (specifically those which relate to niches) scale with phylogenetic distance or not. The expectation is that nearer to the tips of a phylogeny, species would be more divergent if niche processes are important, particularly character displacement. On the other hand, at larger scales phylogenetic niche conservatism should mean that larger clades are reasonably distinct.

Phylogeny will also be informative about the species that we might expect to co-occur. For example, competition at small scales will determine which species co-occur. Such processes may occur on scales of even a few metres. On the other hand at intermediate spatial scales we would expect to see phylogenetic clustering: as a consequence of its biogeographic history a group will be restricted to a given area.

Of course these predictions are only the expectation under one scenario: in practice other factors could operate. For instance, if species are highly mobile they would be expected to show less of an imprint of evolutionary history on their traits and phylogeography as they will show less spatial clustering and be adapted across a wider range of habitats. Modern phylogenetic comparative approaches allow a suite of patterns of diversity of traits and diversity to be modelled and tested.

When we look at small scales the composition of species within a community will reflect the interplay between the effects occurring at all of these scales as well as the outcome of ecological sorting. Biogeography and history determine the pool of species that can form a community. Then

interactions, the environment and micro-evolution combine to determine the traits of the species that are drawn from this pool in a given area.

The distribution of traits and species with respect to phylogeny exhibit a variety of patterns including clustering, randomness and overdispersion. Clustering of traits is where species from only those clades with specific adaptations can persist in the community; randomness is where species are drawn apparently at random with respect to their traits and phylogenetic position, most likely because the determinants of community composition are complex; and overdispersion occurs where traits leading to successful establishment are distributed throughout a phylogeny. By examining the phylogenetic distribution of traits and their dispersion it is possible to distinguish different types of processes driving species traits and community membership.

A key assumption is that phylogeny is a good reflection of evolutionary history: this includes the relationship between species (the topology of the phylogeny) and evolutionary distances (branch lengths). There are a number of reasons why the phylogeny might not accurately reflect history, or it is frequently the case that there is uncertainty such that different phylogenies are equally as well supported. Moreover, it is important not to regard the incorporation of phylogeny as an end in itself: phylogenies need to be used along with an explicit hypothesis-testing framework. This is a strong point made by Cavender-Bares et al. (e.g. see their figure 4 for an example of how this can be done).

Challenges and opportunities

The revolution in the availability of phylogenetic information has had enormous impacts in evolution and ecology, and the review by Cavender-Bares et al. shows how this has impacted on community ecology. Indeed, major advances continue to happen: for example, recent weeks have seen the first publication of a phylogeny for an entire tropical tree community (the famous Barro Colo-

rado Island study site) assembled from DNA barcodes (Kress et al. 2009). The ease with which we can now assemble evolutionary histories of groups of species is quite remarkable.

The challenges lie in exploiting this information and Cavender-Bares and colleagues point out that there are several areas where much remains to be done. For example, there are increasingly sophisticated models linking traits to community assembly (e.g. Purves et al. 2008) but there are challenges in linking these models to evolution and predicting how traits will evolve and relate to phylogeny. Simple niche-filling models have been developed for adaptive radiations (Price 1997, Freckleton and Harvey 2006), however this area is in its infancy.

Importantly this work is starting to tell us about the degree to which traits predicting community assembly are phylogenetically constrained, that is the degree to which historical factors drive community composition or, equivalently, the degree to which species within communities are ecologically labile. In the face of climate and environmental change this will inform us about which systems and which species are likely to respond – or not – to these changes, and the potential for evolutionary compensation.

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symposium summary

The importance of being small: does size matter in biogeography?

One-day symposium at Systematics, the First BioSyst conference – Leiden, The Netherlands, 13th August 2009

Since the 18th century, scientific expeditions in remote places have discovered new species and even new orders and new classes of macro-organisms with limited distribution. In contrast, scientists have discovered that microscopic organisms found in remote places could be mostly ascribed to taxa already known in their home countries. This idea was encapsulated by Beijerinck (1913) and Baas-Becking (1934), and became known as the 'everything is everywhere' (EisE) hypothesis: micro-organisms are globally distributed due to their potential for long-range dispersal (Kellogg and Griffin 2006) and large abundances (Finlay 2002). The assumption that organisms smaller than 2 mm are cosmopolitan in their distribution is best supported when species are defined using traditional taxonomy based on morphological characters. However, the EisE hypothesis has been challenged recently as molecular evidence has revealed a high degree of cryptic diversity, restricted dispersal and phylogeographic patterns in a variety of microscopic organisms, including both prokaryotes and eukaryotes (e.g. Martiny et al. 2006, Green et al. 2008).

The recent debate on the EisE hypothesis began after the contributions by Finlay and Fenchel (e.g. Finlay and Clarke 1999, Finlay 2002, Fenchel and Finlay 2004), and different research groups are currently trying to test its reliability on different model organisms. Thus, it was considered timely to organize a full-day symposium on this topic, and that was held during the BioSyst meeting in Leiden, a joint conference of all the

European systematics associations.

The current debate on the EisE hypothesis divides scientists in two major groups (Whitfield 2005). One group follows the EisE hypothesis in its original form, assuming that species differences in samples from different areas occur because of environmental differences, and not because of restricted dispersal. Thus, 'everything is everywhere, but the environment selects' is considered the rule for micro-organisms. The other group proposes that traditional taxonomy of microscopic organisms based only on morphological characters is not able to resolve their actual diversity, and cosmopolitan ranges therefore result from misidentification and lumping of spatially isolated lineages. Thus, cosmopolitanism is considered an exception in micro-organisms, as it is in macro-organisms.

It has been suggested that the EisE hypothesis incorporating environmental selection may be difficult to falsify because of unmeasured aspects of the environment that differ consistently among regions (Foissner 2006). However, if we assume a dense sample of equivalent habitats across sampling regions, the hypothesis makes clear predictions about genotype distributions. If EisE is the rule, the degree of genetic relatedness between two individuals should be independent of the geographical distance between them. Conversely, if EisE does not hold true, spatially explicit models should work in the same way as they do for macro-organisms, and genetic diversity should be related to geographical distances by a classical