OPINION PAPER

Is it easy to move *and* easy to evolve? Evolutionary accessibility and adaptation

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Abstract

Recent phylogenetic studies have documented high levels of conservatism in ecological traits that seem at odds with the traditional view that organisms can readily adapt to different environments. We highlight the need for a new level of rigour in interpreting such patterns from both organismal and biogeographical perspectives. A handful of closely studied systems are revealing a greater number of ecological transitions than anticipated, but these are typically phylogenetically clustered, suggesting that the relative ease or difficulty of such adaptations is strongly context-dependent. We believe that this differential evolutionary 'accessibility' to certain adaptations is pervasive across the tree of life and we illustrate this with reference to several important ecological syndromes in plants. Differential accessibility derives in large part from the attributes of the organisms themselves – certain traits may act as 'enablers' that increase the likelihood of particular innovations. So far, we have made minimal progress in identifying precursor traits that underlie the evolution of ecological syndromes, but we are hopeful that improved phylogenetic resolution will allow for a surge of new insight. However, the accessibility of particular adaptations also derives from external factors, such as the relative location and extent of certain habitats and the competitive ability of the lineages that already occupy them. Better understanding of where particular lineages have existed in the past, and of the adjacency or connectivity of different environments through time, will also be necessary to explain how both dispersal and ecological diversification have jointly contributed to the assembly of the world's ecosystems.

Key words: Adaptation, climate change, historical biogeography, niche conservatism, phenotypic accessibility, precursor.

Introduction

There has been a pronounced shift in perspective in recent years concerning whether ecological attributes of organisms are evolutionary labile or relatively conserved. Historically, the ecological niche has been viewed as exceptionally labile and niche shifts were assumed to drive many speciation events. This perspective was derived from micro-evolutionary studies of divergent selection within populations (Antonovics and Bradshaw, 1970), the identification of ecotypes along environmental gradients (Clausen *et al.*, 1948), rapid adaptive radiations on islands (Baldwin and Sanderson, 1998; Losos *et al.*, 2003), and examples of extreme phenotypic plasticity in various plant functional traits (Dudley and Schmitt, 1996; Sultan, 2000). Based on such findings, it was widely assumed that niches would not be conserved at broader phylogenetic scales; instead, ecological traits were expected to be exceptionally labile within larger lineages.

Studies of ecological adaptation over the past decade have broadened to include phylogenetic analyses of niche evolution. Patterns of trait and environmental variation are now documented across many species—around the globe and through deep time—by combining ecological, geographical, and organismal trait data with phylogenetic knowledge. The

first wave of such studies documented unexpectedly high phylogenetic signals in niche-related traits, with related species (entire clades) sharing ecological attributes through considerable evolutionary time (Peterson *et al.*, 1999; Prinzing *et al.*, 2001; Wiens and Graham, 2005; Edwards and Donoghue, 2006). At the same time, it has been possible to trace the historical movements of various lineages across the landscape, thereby identifying important past corridors between disjunct yet similar climatic regions (Manos and Donoghue, 2001; Givnish and Renner, 2004). These discoveries have fuelled a new outlook on the relative roles of evolution versus dispersal in establishing the current global distribution of organisms: perhaps major ecological transitions are evolutionarily quite difficult and have happened rarely, but the few lineages that have succeeded in making such transitions have diversified across disjunct areas of new habitat. This emerging perspective was synthesized in an essay by Donoghue (2008), which he summarized with the phrase 'It is easier to move than to evolve.'

How can these differing views of ecological adaptation be reconciled? Are studies at micro- and macro-evolutionary scales truly at odds? We are inclined to think not. Perhaps lineages do continually explore novel environments but have higher rates of extinction in some environments than in others – this would be consistent with local niche shifts as a primary driver of speciation and niche conservatism as a deeper phylogenetic pattern. In this case, movement into a new environment might be relatively easy, but evolving a competitive, stable phenotype that will persist through deeper time might be harder. That is, local adaptation and ecotypic differentiation could be pervasive but relatively short-lived.

Alternatively, perhaps the apparent discord between evolutionary timescales is simply because the term 'niche' has been used in very different ways. Studies at the micro-scale typically do not compare populations living in such disparate environments, such as a forest understory or a grassland, whereas macro-scale studies have often focused on such biome-level comparisons. An inherent assumption in this type of explanation is that there is something fundamentally different about evolutionary shifts within biomes and evolutionary shifts between them. However, there is little direct work to either support or refute this. It is clear that considerable physiological evolution can and does occur within individual biomes. Are shifts between biomes really more significant than within-biome ecological transitions? There is still a lack of general understanding of what physiological changes are necessary to shift biomes and which biome shifts might be more difficult than others.

The analysis by Crisp *et al.* (2009) of biome shifts in southern-hemisphere plant lineages highlights the difficulties faced with such studies. They conclude that there have been rather few speciation events that coincided with shifting from one biome to another; that is, closely related species tend to occupy the same biomes. But, what number of biome shifts would be surprising? In this case, and others like it, not enough is yet understood about the relative ease or difficulty of making the necessary physiological adjustments and how this varies among clades, nor is there any understanding of whether speciation events 'within a biome' actually indicate any sort of physiological or ecological stasis. Likewise, as we will emphasize below, it is difficult in such analyses to integrate the relative likelihood of moving to similar environments in different areas or, on the other hand, the spatial adjacencies and land areas of different biomes and how these have changed through time.

As the macro-scale approach to niche evolution matures, we imagine that the discord between these perspectives will blur. Here we highlight a second generation of phylogenetic studies that support a more nuanced view of niche conservatism and illustrate the key concept of differential evolutionary accessibility. The probability that a lineage will successfully diversify into a novel environment is dependent upon: (1) the relative evolutionary likelihood of realizing different ecologically significant phenotypes; and (2) the relative availability of novel habitats. Both of these factors will vary enormously from lineage to lineage, and throughout time and space, and together they provide a measure of the relative evolutionary accessibility of adaptation.

Major ecological transitions appear 'easy' in some lineages

As the sampling and resolution of phylogenetic studies improves, a new theme seems to be emerging – phylogenetic neighbourhoods that once were assumed to harbour one or several major ecological shifts are often 'hotbeds' of multiple transitions. To use a particularly well-studied example, C_4 photosynthesis is a complex ecological adaptation in plants that improves photosynthetic efficiency in hot, arid, and low CO_2 conditions (Pearcy and Ehleringer, 1984; Edwards and Ogburn, 2012; Sage *et al.*, 2012). Despite its complexity, it has evolved more than 62 times (Sage *et al.*, 2011), an estimate that will only grow in the coming years. The most well-known C_4 plants are the C_4 grasses, which dominate tropical and subtropical savannas and grasslands worldwide and are a critical element of these biomes. Grasses are ancestrally forest understory plants, and the evolution of C_4 photosynthesis was tightly correlated with movements out from the tropical forest understory and into hot, open biomes (Osborne and Freckleton, 2009; Edwards and Smith, 2010). This complex adaptation and biome shift did not happen once, or even a few times, but upwards of 24 times and mostly within the last 10 million years (Christin *et al.*, 2011; Grass Phylogeny Working Group II, 2012). In fact, roughly one-third of all known C_4 origins have occurred within one particular clade of grasses, the 'PACMAD' clade. C_4 photosynthesis may not be for everyone, but it seems to have been a relatively straightforward evolutionary stunt for PACMAD grasses.

In a similar vein, adaptation to seasonally cold temperate biomes has been heralded as an especially difficult ecological transition (Wiens and Donoghue, 2004), requiring a host of adaptations to freezing temperatures and a shortened growing season. Because a large number of taxonomically recognized plant lineages lack a significant temperate element, it has been suggested that shifts into the temperate zone have

been relatively rare (Donoghue, 2008). Here again, as phylogenies have become increasingly well resolved, there is a subtle wrinkle, which we illustrate with our own work on the plant lineage *Viburnum*. *Viburnum* is a mostly northern hemisphere temperate plant clade of roughly 170 species, with a handful of species in tropical southeast Asia and a recent radiation into cloud forests in the mountains of Latin America (Clement and Donoghue, 2011). Although it has long been viewed as a temperate lineage, *Viburnum* is more likely an ancestrally tropical clade that includes a number of separate temperate lineages – phylogenetic analyses have revealed multiple transitions (perhaps seven or eight) between wet tropical and temperate forest biomes (Schmerler *et al.*, 2012). Like the C$_4$ syndrome within PACMAD grasses, the temperate zone appears to have been readily accessible to *Viburnum*. Repeated 'biome-hopping' has been demonstrated in other lineages and in other contexts as well. For example, many plant groups spanning the fynbos and karoo biomes of South Africa actually transitioned between these multiple times (e.g. *Pelargonium*, *Moraea*; Verboom *et al.*, 2009), and the evolutionary assembly of the Cerrado tree community occurred via repeated movements from nearby wet and dry tropical forests in just a subset of lineages (e.g. a minimum of 11 movements in *Mimosa* alone; Simon *et al.*, 2009).

We imagine that most organismal evolution will conform to this general pattern of heightened accessibility of certain adaptations within certain lineages, and we expect improved sampling in phylogenetic studies to reveal many more such hotbeds of evolution. Typical models of trait evolution used in phylogenetic analyses do not accommodate such evolutionary heterogeneity, but there have been several recent attempts to statistically identify the clustering of evolutionary events. For example, the 'precursor model' of Marazzi *et al.* (2012) identified a major legume lineage with an increased propensity to evolve extrafloral nectaries and also pinpointed the PACMAD clade as a C$_4$ evolutionary hotspot (Christin *et al.*, 2013). Likewise, the 'hidden rates model' of Beaulieu *et al.* (2013) highlighted significant shifts in the transition rate between herbaceous and woody plants within campanulid angiosperms. These are encouraging results, though identifying phylogenetic hotspots will not, in itself, answer the 'easier to move or evolve' question. For this, the mechanisms contributing to elevated accessibility need to be disentangled.

Evolutionary accessibility—location, location, location!

It has long been appreciated that certain traits may act as 'developmental enablers' (*sensu* Donoghue, 2005) of major evolutionary innovation. There is nothing mysterious about this. If certain underlying traits are already in place in a particular lineage, it may make it easier to originate certain other traits. In the case of PACMAD grasses, for example, it appears that the entire lineage is characterized by having large bundle sheath cells and that this increases the functionality of intermediate phenotypes along the C$_4$ evolutionary trajectory (Christin *et al.*, 2013; Griffiths *et al.*, 2013). We think this

goes a long way towards explaining the clustered C$_4$ origins in grasses, but it does not take into consideration another extremely important variable, namely whether all grasses have had equal exposure to environments that would select for C$_4$ evolution. The Pooideae are another large lineage of grasses (~3000 species) and are exclusively C$_3$ plants. They have small bundle sheath cells, but they also live in colder environments where the C$_4$ pathway is not adaptive. Are there no C$_4$ Pooids because they are anatomically disadvantaged to evolve the pathway, because they have not had much opportunity to colonize tropical, open environments, or more likely, because of some combination of these reasons?

The point is that there is an important connection between ecological opportunity and character evolution. It is hard to evaluate whether a tropical lineage of plants, confined, for example, to a small region of the Amazon basin, has the capability of evolving adaptations to the seasonally freezing climates of high northern latitudes. These plants may well have the capability, but have simply never been tested owing to the physical disconnection between these environmental conditions. Just as too little is known about the accessibility of different morphological/physiological states, in general how easy or hard it has been for different groups of organisms to track particular environments around the globe through time is not understood: that is, there is a lack of detailed understanding of which climate conditions have existed when and where. And, just as spatial continuity facilitates environmental tracking, the spatial adjacency of different environments over time will influence the relative likelihood of transitions between them. For example, transitions between tropical and temperate forests might have been more likely in Asia owing to the continuity of these two environments throughout the Cenozoic (Latham and Ricklefs, 1993). By comparison, it presumably would have been harder to make such shifts in the Americas where these environments have not continuously been in contact.

Aside from adjacency and continuity, several other geographical factors influence the likelihood of making successful transitions into particular environments. First, the area available for occupancy can be a significant factor; for instance, some have proposed that the Old World tropics harbour many more origins of mangroves than the New World because there is more available coastline (Ricklefs *et al.*, 2006). Second, certain environments have simply been around much longer than others. For example, tropical rainforest habitats have been available at least throughout the Cenozoic, whereas deserts and Mediterranean climates have originated and become widespread much more recently. It may be easier for lineages to move into such new habitats early in their existence if there has been less time to permit the evolution of adapted competitors. This concept is illustrated in the extreme by the relative ease of niche filling by colonizing lineages of newly formed oceanic islands (Carlquist, 1974).

This interaction between organismal and environmental accessibility confounds our ability to discern whether moving or evolving is 'easier' based simply on phylogenetic patterns. Multiple shifts within a lineage might be attributed to the relative evolutionary ease of making such transitions, but this number will at least in part reflect the adjacency or disjunction

of the relevant environments through time. In the end, accessibility is what we need to know to develop an understanding of the relative ease of both trait evolution and lineage movements through time. And, as we have just highlighted, understanding the interaction between these two – trait evolution and environmental connections – is ultimately what is needed to develop worthy predictive models. In the absence of such knowledge, phrases such as 'it's easier to move than to evolve' may serve to highlight our ignorance more than to guide productive research.

Many of the points being made in this paper are illustrated in Fig. 1. At one extreme, shown in scenario 1, movements among areas are relatively easy, while character evolution is less so. Here, we see one shift in lineage A from the ancestral 'green' environment into a geographically adjacent patch of a novel 'blue' environment, followed by the spread of that lineage to several other disjunct areas of the novel blue environment. This represents the 'easier to move than to evolve' scenario. At the other end of the spectrum, shown in scenario 2, ecological shifts are relatively easy and each of the three areas with the disjunct patches is readily occupied by multiple lineages (A, B, and C) living in adjacent areas within the ancestral environment. In this case, there has been no subsequent movement between disjunct areas of the novel environment. This might be called the 'easier to evolve than to move' scenario. Scenario 3 shows a situation where it is 'easy to move and easy to evolve.' The several lineages present in the ancestral environment can adapt to the novel environment, and have done so multiple times, and there is also considerable dispersal between the disjunct patches of the novel environment. There are, of course, a variety of other possibilities distributed around the margins of the movement–evolution space shown in Fig. 1. We might have shown a 'hard to evolve and hard to move' scenario in the upper right hand corner, which would leave some disjunct patches of the novel environment essentially uncolonized. A scenario situated in between scenarios 1 and 3 on the evolution axis might show multiple evolutionary origins of the ability to occupy the disjunct patches, but with even more movement among the blue areas. 'Easier to move than to evolve' can be viewed as a relative statement, which places no upper bound on the absolute number of evolutionary changes or movements.

Finally, of greater interest and – we think – realism, scenario 4 illustrates the relative accessibility concepts highlighted above. In this case, lineage A has an elevated phenotypic accessibility to the novel environment and these ecological transitions happen a number of times. Thus evolution is hard for some lineages (B, C) but easy for others (A). There is also a geographical bias in accessibility to the disjunct patches, with only one adjacent region providing a ready opportunity for lineage A to adapt. The opportunity for subsequent movement between disjunct areas of environment 2 is also variable and may change due to the emergence and loss of corridors or even the global expansion or retraction of environment 2 through time. Importantly, without detailed phylogenetic knowledge of lineage A, scenario 4 is indistinguishable from scenario 1, though the underlying biology is quite different. In both of the empirical cases highlighted here – C_4 evolution

in grasses and tropical/temperate transitions in *Viburnum* – earlier perspectives resembled scenario 1, but we now know that scenario 4 is more realistic. The C_4 story is particularly remarkable; estimates of the number of C_4 origins have consistently increased as phylogenetic sampling has improved (Giussani *et al.*, 2001; Grass Phylogeny Working Group, 2001; Kellogg, 2001; Aliscioni *et al.*, 2003; Christin *et al.*, 2009; Grass Phylogeny Working Group II, 2012). The sheer number of transitions we now recognize has fundamentally altered how we view the relative 'difficulty' of evolving this fairly complicated syndrome—provided, of course, with a particular underlying organismal structure and an ecological opportunity.
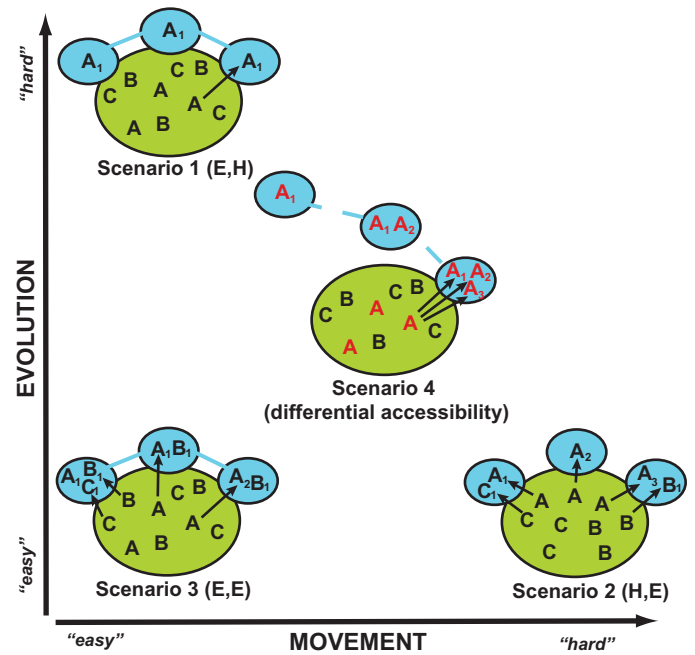
Fig 1. Alternative scenarios of how new environments are colonized, depending on the relative ease of movement versus adaptation. Green circles represent an ancestral environment type and blue circles represent three geographically disjunct patches of a novel environment. In scenarios 1–3, these disjunct patches lie adjacent to the ancestral environment, indicating a high geographical accessibility. In scenario 4, only one disjunct patch is directly geographically accessible to the ancestral environment. Blue lines indicate viable dispersal corridors connecting one disjunct patch to another and dotted lines in scenario 4 indicate that these corridors are only available during certain periods of geological time. Each individual letter could represent a population, a species, or an entire clade, as this conceptual framework is independent of scale. The numbered letters in disjunct patches denote each ecological transition event from green to blue: for example, in scenario 1, A1 represents a single transition from the ancestral environment to a disjunct patch, and A1 subsequently dispersed to other available disjunct patches via dispersal corridors. This represents the 'easier to move than evolve' scenario, where ecological transitions are infrequent and movement of preadapted lineages is more common. See text for full discussion of all scenarios. E, Easy; H, hard.

Conclusion

So how can progress be made in this area? First, we need to take seriously the idea of understanding (ultimately in quantitative terms) the mechanistic underpinnings of various morphological and physiological transitions and get to the point that predictions can be made about the relative ease or difficulty of evolving traits in organisms with different underlying structures in place. Here we believe that well-sampled, detailed phylogenies of smaller groups are more likely to yield relevant insights than the sparsely sampled 'big tree' approaches that have recently become so popular. The identification and careful analysis of phylogenetic 'hotspots' of adaptive evolution will greatly improve understanding of the genetic and developmental mechanisms that bear on increased accessibility. Second, we need to pay more attention to the continuity and disjunction of environments (similar and different) over evolutionary time. Ultimately, we must quantify the historical opportunities for ecological transitions independently, with or without major physiological changes. In this endeavour, we need to pay special attention to inputs from paleontologists, climatologists, and historical biogeographers (Graham, 2011) and find new ways to incorporate this information more directly into our analyses.

Acknowledgements

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