

Commentary Six

A Clade's-Eye View of Global Climate Change

Charles C. Davis, Erika J. Edwards, and Michael J. Donoghue

Recent climate change has had demonstrable effects on plant and animal communities around the world and will pose one of the most significant threats to biodiversity in the coming decades (Walther et al. 2002; Root et al. 2003; Parmesan 2006). Surprisingly, evolutionary biologists have had rather little impact on increasing the understanding of climate change and its consequences for biodiversity (though, there have been some studies of cases of rapid evolution (see Donoghue et al. 2009; Hendry et al. 2010), and phylogenetic approaches to this problem have been limited. But, as in numerous areas of biology (Futuyma 2004; see Hillis, Chapter 16), we see opportunities to use phylogenetic trees to make generalizations of practical importance and to predict responses to climate change. Here, our aim is to briefly highlight, by reference to several recently published examples, some of the ways in which phylogenies might be used to understand and cope with climate change. We focus on plant examples given our expertise, but there are several relevant animal examples that also support our points (e.g., Wiens et al. 2006).

Phylogeny, Historical Climate Change, and Climate Niche Evolution

Phylogenetic trees are commonly used to infer character evolution and historical biogeography and, in turn, to correlate changes with major climatic events in the past or with movements into novel environments. An emerging theme from such studies is that many lineages have persisted in particular biomes for much of their history, despite considerable opportunity (afforded by dispersal and shifting climates) to diversify into other zones (Donoghue 2008; Crisp et al. 2009). This form of phylogenetic niche conservatism is argued to be a major determinant of global biodiversity patterns, for example, the latitudinal species richness gradient (Ricklefs 2004;

Wiens and Donoghue 2004; Mittelbach et al. 2007). The apparent rarity of niche shifts from tropical to temperate biomes may reflect an underlying difficulty in making certain physiological adjustments, such as the evolution of frost tolerance (Donoghue 2008).

However, at the same time, many cases of niche evolution within biomes have been documented (Losos 2008). Plant examples include evening primroses in the arid regions of North America (Evans et al. 2009), honey-suckles in Mediterranean climates (Smith and Donoghue 2010), and subtropical laurel species from Europe and North Africa (Rodríguez-Sánchez and Arroyo 2008). Such studies integrate climate niche models and dated phylogenies to characterize a clade's biogeographic history and are useful in determining the abiotic factors that influence species' ranges. Thus, they can be valuable in assessing responses to future climate change. They are not without their limitations, however, and are unlikely to be particularly helpful in extracting predictions from more ancient evolutionary events for which adequate species occurrence data as well as precise information on paleoclimate and land configurations are often lacking. Examples of studies that have sought to make inferences about a clade's ancestral niche in deep time, independent of a particular geography, include the origin of water-use strategies in Cactaceae (Edwards and Donoghue 2006) and the age and persistence of tropical rain forest clades (Davis et al. 2005).

Interpreting such patterns in relation to current climate change provides some broad generalizations. For instance, based on historical patterns, it seems likely that if the Amazon basin dries (Cox et al. 2004), its newly formed arid community will likely be assembled via migration of pre-adapted desert lineages rather than via significant *in situ* evolution of rainforest species. Thus, the historical importance of habitat tracking in

response to climate change should motivate the maintenance of viable corridors for movement. In contrast, many climate shifts may fall within the range of a clade's adaptive potential; shifting precipitation patterns across the already arid American Southwest, for example, may promote rapid adaptive evolution in lineages that already inhabit this zone, as has apparently occurred over the past million years (Evans et al. 2009). Ultimately, by summing over such historical studies, it should be possible to make meaningful generalizations about the relative evolutionary lability of niche-related traits.

Such examples are perhaps the most obvious observations that a clade's-eye view of global climate change affords, but for several reasons, they may not always be very useful in confronting the practical realities of ongoing climate change. Modern landscapes have been so thoroughly modified by humans that it is no longer clear how species will respond. The resulting fragmentation reduces population sizes and impedes habitat tracking, which makes it difficult to draw comparisons with past events. Likewise, the human-induced movement of species around the globe makes it much more difficult to predict how these new, artificial communities will behave (Sax et al. 2007). Thus, although studies of responses to past climate changes provide useful history lessons and a deeper perspective on the relationship between the biosphere and climate, there may often be more powerful ways to incorporate phylogenetic thinking into decision-making and climate change mitigation efforts. These approaches all stem from the basic principle that phylogenies provide the ultimate framework for inferring how different attributes are distributed among organisms, which then can be used to make predictions about the traits of species that have not yet been studied in detail. As we emphasize in the following sections, simple clade-based approaches can help

researchers to identify potentially vulnerable lineages and can be used to produce refined global models relevant to understanding the biological impacts of climate change.

Phylogeny and Responses to Current Climate Change

The study by Willis et al. (2008) of rapid changes in species abundances in Thoreau's woods (Concord, Massachusetts, USA) provides a concrete example of the predictive power of phylogeny. They analyzed a data set initiated by the American conservationist Henry David Thoreau. Using statistical methods that incorporate phylogeny, they discovered that entire clades, which apparently have been less able to respond to climate change by adjusting their flowering phenology, have significantly declined in abundance. These results can help identify species and clades that likely face a greater risk of regional extinction as climate change proceeds. For example, we should be particularly concerned about the continued regional loss of species in the Liliaceae and Orchidaceae, but perhaps less so of species in the Brassicaceae and Fabaceae. The latter two clades contain species that are far better able to adjust their phenology to climate change and, thus, contain fewer species that have declined in abundance.

To what extent do these regional results relate to global patterns of decline? For example, should we be concerned about a potential worldwide decline of Orchidaceae due to climate change? If so, the outcome could be severe, and would have especially devastating impacts on regions with low community-wide phylogenetic diversity. For instance, the fynbos of the Cape Floristic Province of southern Africa contains about 9000 plant species, of which approximately 70% are endemic to an area of 90,000 km² (Linder and Hardy 2004). This richness is comparable to some Neotropical forests and is significantly greater

than other Mediterranean-type ecosystems (Kreft and Jetz 2007). Nevertheless, the fynbos flora is relatively clade-poor with respect to overall plant diversity (Linder and Hardy 2004; Forest et al. 2007). Thus, if the species belonging to any one of the small number of species-rich clades that compose the fynbos flora were negatively affected by climate change, it could disproportionately increase the magnitude of species loss in this system. Along these lines, the Asteraceae, Iridaceae, and Orchidaceae are three species-rich clades that have been shown to be relatively unable to adjust to climate change and are in significant decline in Concord. These three clades compose nearly 25% of the fynbos flora (Kruger and Taylor 1980). If the inability of these clades to respond to climate change extends across communities (i.e., from the temperate region of Concord to the fynbos of South Africa), then climate change-induced losses in the fynbos flora could be far greater than those sustained in phylogenetically more diverse communities. In the end, assessing the likelihood of such scenarios, will require more and better information on the geographic distribution of clades and phylogenetic diversity, a better understanding of the extent to which clade membership predicts climate change response, and knowledge of the regional abiotic factors that influence clade vulnerability across communities and biomes.

A Clade's-Eye View of Ecosystems

The Concord example highlights the utility of phylogenies in predicting how species and clades may respond to climate change. However, climate change research is charged with prediction making at many scales, and some of the most important problems are at the level of biosphere-atmosphere interactions and global biogeochemical cycles. Though less intuitive, a phylogenetic approach can pro-

vide important insights into these large-scale problems. Here, we highlight one study that outlined how integrating phylogenetic biology with ecosystem ecology could improve predictions of global carbon cycling under future climate change.

Edwards et al. (2007) explored a dataset of carbonic anhydrase (CA) levels in leaves. CA activity influences leaf oxygen isotope fractionation, which in turn, is used to estimate global primary production (GPP) and the role of terrestrial vegetation in the global carbon cycle (Gillon and Yakir 2001). Gillon and Yakir sampled a number of species for CA activity and found that grasses using the C_4 photosynthetic pathway as a whole had lower CA values than other functional types (e.g., trees, forbs). This result suggested that previous analyses may have grossly underestimated the role of C_4 grasses in GPP and that C_4 grasses may constitute the so-called missing carbon sink (Gillon and Yakir 2001). Reanalyzing these data within a phylogenetic framework, Edwards et al. (2007) found that CA levels were not significantly correlated with C_4 photosynthesis. Instead, one major subclade of grasses, which included a mix of C_3 and C_4 species, contained most of the species with low CA values. On this basis, they suggested the direct use of the low CA clade in calculating GPP. To do so, however, will require better information on the geographic distribution and relative abundance of this clade as well as the development of global carbon models that can take into account new, user-defined vegetation categories (as opposed to only traditional functional or taxonomic categories). More generally, these results nicely clarify the way in which taking phylogeny into consideration can help to refine models that are directly relevant to climate change.

Concluding Thoughts

In all of the cases highlighted here, phylogenetic trees allow investigators to make generalizations that can help in making practical decisions and setting priorities when there is incomplete information. In the end, it is the predictive power of phylogenies that makes them useful in such a wide variety of applications, including understanding and dealing with climate change. Although there have been few concrete practical applications to this problem so far, we see great potential in such approaches and an urgent need for more rapid integration of phylogenetic biology and climate change research.

Literature Cited

- Cox, P. M., R. A. Betts, M. Collins, and 3 others. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theor. Appl. Climatol.* 78: 137–156.
- Crisp, M. D., M. T. K. Arroyo, L. G. Cook, and 7 others. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458: 754–756.
- Davis, C. C., C. O. Webb, K. J. Wurdack, and 2 others. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of tropical rain forests. *Am. Nat.* 165: E36–E65.
- Donoghue, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl. Acad. Sci. USA* 105: 11549–11555.
- Donoghue, M. J., T. Yahara, E. Conti, and 15 others. 2009. bioGENESIS: Providing an evolutionary framework for biodiversity science. *DIVERSITAS Report* 6: 1–52.
- Edwards, E. J. and M. J. Donoghue. 2006. *Pereskia* and the origin of the cactus life-form. *Am. Nat.* 167: 777–793.
- Edwards, E. J., C. J. Still, and M. J. Donoghue. 2007. The relevance of phylogeny to studies of global change. *Trends Ecol. Evol.* 22: 243–249.
- Evans, M. E. K., S. A. Smith, R. S. Flynn, and 1 other. 2009. Climate, niche evolution, and

- diversification of the "bird-cage" evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *Am. Nat.* 173: 225–240.
- Forest, F., R. Grenyer, M. Rouget, and 10 others. 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445: 757–760.
- Futuyma, D. J. 2004. The fruit of the tree of life: Insights into evolution and ecology. In J. Craft and M. J. Donoghue (eds.), *Assembling the Tree of Life*, pp. 25–39. Oxford University Press, New York.
- Gillon, J. and D. Yakir. 2001. Influence of carbonic anhydrase activity in terrestrial vegetation on the ^{18}O content of atmospheric CO_2 . *Science* 291: 2584–2587.
- Hendry, A. P., L. G. Lohmann, E. Conti, and 15 others. 2010. Evolutionary biology in biodiversity science, conservation, and policy: A call to action. *Evolution* 64: 1527–1528.
- Kreft, H. and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci. USA* 104: 5925–5930.
- Kruger, F. J. and H. C. Taylor. 1980. Plant species diversity in Cape fynbos: Gamma and delta diversity. *Plant Ecol.* 41: 85–93.
- Linder, H. P. and C. R. Hardy. 2004. Evolution of the species-rich Cape flora. *Phil. Trans. Roy. Soc. Lond. B* 359: 1623–1632.
- Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11: 995–1003.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, and 19 others. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol. Lett.* 10: 315–331.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Evol. Syst.* 37: 637–669.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7: 1–15.
- Rodríguez-Sánchez, F. and J. Arroyo. 2008. Reconstructing the demise of Tethyan plants: Climate-driven range dynamics of *Laurus* since the Pliocene. *Global Ecol. Biogeogr.* 17: 685–695.
- Root, T. L., J. T. Price, K. R. Hall, and 3 others. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- Sax, D. F., J. J. Stachowicz, J. H. Brown, and 9 others. 2007. Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* 22: 465–471.
- Smith, S. A. and M. J. Donoghue. 2010. Combining historical biogeography with niche modeling in the *Caprifolium* clade of *Lonicera* (Caprifoliaceae, Dipsacales). *Syst. Biol.* 59: 322–341.
- Walther, G. R., E. Post, P. Convey, and 6 others. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- Wiens, J. J. and M. J. Donoghue. 2004. Historical biogeography, ecology, and species richness. *Trends Ecol. Evol.* 19: 639–644.
- Wiens, J. J., C. H. Graham, D. S. Moen, and 2 others. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168: 579–596.
- Willis, C. G., B. Ruhfel, R. B. Primack, and 2 others. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl. Acad. Sci. USA* 105: 17029–17033.