

## PHYLOGENETIC ECOLOGY AT WORLD SCALE, A NEW FUSION BETWEEN ECOLOGY AND EVOLUTION

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**Abstract.** One fusion between ecology and evolution is well established, under the title of population biology. The years 2006–2020 will see a new fusion, likely to prove equally creative. Inputs from ecology to this second fusion will be worldwide data sets for ecological traits across many species. Inputs from evolution will be phylogenetic trees with well-resolved topology and with increasingly tight geological dates for each branch point. There will be unification of two aims: first to explain the spread of different ways of making a living, across the range of present-day species; and second, to narrate the evolutionary history that has led up to present-day ecology.

*Key words:* ecological traits of species; evolution; fusion; historical ecology; phylogeny; world data sets.

### INTRODUCTION

A new fusion has begun between world-scale ecology and geological-scale evolution. This is a brief sketch of where this fusion may carry us in 10–15 years. Examples are drawn from terrestrial plant ecology, but the general points apply to most taxa and habitats.

### SOME HISTORY

Since the 1960s, population biology has embodied the merger between ecology and evolution. Its foundation is that core quantities of population ecology are the same as some core quantities of population genetics. For projecting population numbers and for measuring fitness, the nuts and bolts are the same: numbers of offspring, and chances of surviving to the next age or stage. The birth of population biology was marked by an important collection of papers on “genetics of colonizing species” (Baker and Stebbins 1965) and by the high impact of the first two volumes of Princeton Monographs in Population Biology (MacArthur and Wilson 1967, Levins 1968). For many researchers who graduated during the 1960s and 1970s, population biology has represented both a personal research program and an aspiration toward unifying the biological sciences.

From the 1960s, field manipulative experiments have been the favored research style in ecology. Stronger evidence, and much more of it, has accumulated about many topics. Reviews and meta-analyses in ecology often report hundreds of field experiments (Connell 1983, Crawley 1983, Schoener 1983, Goldberg and Barton 1992, Gurevitch et al. 1992, Wilson and Agnew 1992, Cappuccino and Harrison 1996). We are coming

to a point of diminishing returns, where, if satisfying generalizations have not yet crystallized, then it is unlikely that a couple more experiments will solve the problem. We need better tools for putting species and situations in context, as much as we need more experimental evidence.

The tools for putting things in context will need to compare traits, and their costs and benefits, across species and situations. Population biology has been at its most effective in tackling microevolutionary demography and genetics within species, and has had less to say about similarities and differences across species. By fusing phylogeny with ecological trait data sets at the world scale, we can provide a context where experimental and physiological knowledge can be organized.

### UNIFICATION BETWEEN ECOLOGICAL AND EVOLUTIONARY QUESTIONS, AND THE NEW ELEMENTS MAKING IT POSSIBLE

The central activity of the new fusion is mapping ecologically meaningful quantitative traits of species onto phylogenetic trees. The idea of taking ecological traits of present-day species and recasting them as phylogenetic divergence events is not new (Felsenstein 1985), but its usage is changing direction. Through the past 20 years, common ancestry has often been seen as just a statistical hazard; that is, a lack of independence (Harvey et al. 1995, Westoby et al. 1995). Phylogenetic comparative methods have often been presented as protection against the risk that patterns across species might falsely be attributed to ongoing natural selection. Anxiety about this supposed error (the “adaptationist program”; Gould and Lewontin 1979) has been widespread in evolutionary biology, but is subsiding now. Evolutionary history and present-day ecological competence are not alternative hypotheses (Westoby et al. 1995). Rather, they should be interlocking parts of a unified account of trait variation across species.

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One reason for the shift to a more constructive direction is that data sets for some quantitative species traits are reaching substantial global coverage. For seed mass coverage is now  $>10^4$  species (Moles et al. 2005), and for several other plant ecological traits,  $>10^3$  species (e.g., Reich and Oleksyn 2004, Wright et al. 2004; see also the wood anatomy database “InsideWood,” *available online*).<sup>2</sup> These large numbers of species give a picture of the whole of the seed plants worldwide, not just of particular clades that might or might not be representative. Also they populate the phylogenetic tree at sufficient density that wide divergences in a trait can be located fairly closely to particular branch points in the tree. Trait data sets will continue to grow rapidly (Cornelissen et al. 2003) through informal collaboration to merge data and through further data collection. The shift in direction is also becoming possible because phylogenetic topologies are being clarified, mainly through molecular information. For plants, networks of systematists have taken collective responsibility (see P. F. Stevens’s Angiosperm Phylogeny web site).<sup>3</sup> This has been one of the great collaborative achievements in science.

These circumstances are making possible a shift in mental frame. The traditional question has been whether evolutionary divergence in trait A has been consistently correlated with divergence in trait B, in some subset of clades. But increasingly we can ask what are the historical sources of the range of ecologies, across the whole spread of present-day species and environments. Moles et al. (2005), for example, identified the 20 evolutionary divergences in seed mass that made the largest contribution to the sum-of-squares for seed mass across present-day species. From this arise more detailed questions. Has the total spread of the ecological trait in the present day arisen mainly through a few strong divergence events, or did it arise diffusely through evolutionary history? Was the present-day spread of the ecological trait generated at particular geological times and under particular evolutionary-history circumstances? For seed plants, dates for evolutionary divergences are still decidedly loose (Wikström et al. 2001, Davies et al. 2004, Sanderson et al. 2004). But estimates are tightening up, as molecular clocks improve and as fossil information is integrated better with the genetic phylogenies. Given tighter geological dates, particular divergences can be interpreted in the context of all kinds of geoscience information, about the locations of continents and about temperatures and seasonality and atmospheric CO<sub>2</sub> and geomorphology at the time.

Other incremental advances are coming together to make the new fusion possible. Progressively, more herbarium and museum records are becoming available as point locations, rather than as presence in a grid cell. This is a precondition for relating them to fine-scale

environment. Given accurate latitude, longitude, and elevation above sea level, climate properties can be estimated at a location. Soil geography is still very difficult though, and much more work lies ahead to get its informatics in order.

Obviously, data sets across many species have most value when the ecological meaning of a trait is firmly understood. This means when mechanism and physiology mesh together with coordination with other traits and with field experiments about costs and benefits and with observed environmental distribution. So far, comparative plant ecology has worked with physical and chemical traits, or with assays like potential relative growth rates (Cornelissen et al. 2003). It is now becoming feasible to compare selected proteins and their function across large numbers of species (Driskell et al. 2004, Jobson et al. 2004). This is opening up metabolic and developmental traits that would be impractical to bioassay across thousands of species. Benner et al. (2002) coined the rousing phrase “planetary proteomics.” They wrote, “Imagine a comprehensive model of life on Earth . . . that captures history and function from the molecule to the planet.” Integrating proteomics and functional genomics into comparative ecology is an exciting prospect.

Accumulation of data is not enough by itself. Software for interconversion and for asking intelligent questions will be needed, as will social incentives for data sharing. Over the next 15 years software tools will develop for connecting fluently between phylogenetic tree structures, ecological traits across many species, physical geography, geoscience mapping of past environments, and genomics and proteomics. This will be an informatics challenge on a much larger scale than existing bioinformatics.

#### LOOKING FORWARD

Consider this thought experiment. When new-generation textbooks are written 10–20 years from now, might they be structured differently from at present? I think they will. They will unify topics that are taught separately at present:

- traditional botany: survey of leading clades such as the prominent angiosperm families, their features, and biogeography;
- quantitative functional ecology: traits that define the spread of present-day ecologies across species, like leaf mass per area, seed size, stem conductance, and defensive chemistry; and the manner in which climate and soils can adjust what might be the best compromise on these trade-offs;
- paleobotany: the timeline of key evolutionary divergences and the historical circumstances of environment and biology that surrounded them.

Textbooks fusing these three strands will teach a sort of ecological systematics. They will hark back to the tradition in which well-trained students knew the natural

<sup>2</sup> <http://insidewood.lib.ncsu.edu/search>

<sup>3</sup> <http://www.mobot.org/MOBOT/research/APweb>

history of families. But in the new fusion, clades will be embedded in tree thinking, rather than seen as natural categories. The paleohistory leading up to them will be explicit and dated and informed by modern geoscience. The natural history will be enriched by quantitative cost–benefit analyses of the strategies of leaves, stems, roots, flowers, and seeds. Everything old will be new again.

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#### LITERATURE CITED

- Baker, H. G., and G. L. Stebbins, editors. 1965. *Genetics of colonizing species*. Academic Press, New York, New York, USA.
- Benner, S. A., M. D. Caraco, J. M. Thomson, and E. A. Gaucher. 2002. Paleontological, geological, and molecular histories of life. *Science* **296**:864–868.
- Cappuccino, N., and S. Harrison. 1996. Density-perturbation experiments for understanding population regulation. Pages 53–64 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors. *Frontiers of population ecology*. CSIRO Australia, Melbourne, Australia.
- Connell, J. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661–696.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**:335–380.
- Crawley, M. 1983. *Herbivory*. Blackwell Scientific, Oxford, UK.
- Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences (USA)* **101**:1904–1909.
- Driskell, A. C., C. Ane, J. G. Burleigh, M. M. McMahon, B. C. O'Meara, and M. J. Sanderson. 2004. Prospects for building the tree of life from large sequence databases. *Science* **306**:1172–1174.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1–15.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**:771–801.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. *Proceedings of the Royal Society of London B* **205**:581–598.
- Gurevitch, J., L. Morrow, A. Wallace, and J. Walsh. 1992. A meta-analysis of field experiments on competition. *American Naturalist* **140**:539–372.
- Harvey, P. H., A. F. Read, and S. Nee. 1995. Why ecologists need to be phylogenetically challenged. *Journal of Ecology* **83**:535–536.
- Jobson, R. W., R. Nielsen, L. Laakkonen, M. Wikstrom, and V. A. Albert. 2004. Adaptive evolution of cytochrome c oxidase: infrastructure for a carnivorous plant radiation. *Proceedings of the National Academy of Sciences (USA)* **101**:18064–18068.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. *Science* **307**:576–580.
- Reich, P. B., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences (USA)* **101**:11001–11006.
- Sanderson, M. J., J. L. Thorne, N. Wikstrom, and K. Bremer. 2004. Molecular evidence on plant divergence times. *American Journal of Botany* **91**:1656–1665.
- Schoener, T. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240–285.
- Westoby, M., M. R. Leishman, and J. M. Lord. 1995. On misinterpreting the “phylogenetic correction.” *Journal of Ecology* **83**:531–534.
- Wikström, N., V. Savolainen, and M. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London B* **268**:2211–2220.
- Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**:263–336.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* **428**:821–827.