

Phylogeny in the Service of Ecological Restoration¹

More than 20 years ago, Vane-Wright, Humphries, and Williams (1991) first proposed that phylogeny—the evolutionary history of organisms—should inform biodiversity conservation priorities. Since then, the use of phylogenetic diversity or distinctiveness as a conservation criterion has been hypothesized to help maintain biodiversity (Rosauer and Mooers, 2013), preserve evolutionary potential and future economic benefits in biodiversity hotspots (Forest et al., 2007), and conserve communities with greater functional diversity (Mouquet et al., 2012) and greater net ecosystem function (Srivastava et al., 2012). Phylogeny is an active part of the conservation dialogue, even if phylogenetic perspectives have not been broadly integrated into conservation planning (Winter et al., 2013).

In contrast, phylogeny has yet to be embraced as a tool in the field of restoration ecology. A recent review found that 88% of restoration ecology studies assessed biodiversity in some way. Of those, the vast majority focused on species-level diversity, 11% investigated functional diversity, and only one assessed genetic diversity. None assessed phylogenetic diversity (Brudvig, 2011 and personal communication). Moreover, very few researchers have even discussed the potential for phylogeny to influence restoration outcomes (Cavender-Bares and Cavender, 2011; Montoya et al., 2012; Verdú et al., 2012). We believe that this is a missed opportunity. Phylogenetic diversity is not expected to have a uniform effect on community structure in all situations (Cavender-Bares et al., 2009; Mayfield and Levine, 2010). However, phylogeny integrates over the evolutionary history of functional traits and provides a useful predictor of ecological dynamics that often outperforms trait-based predictors (Cadotte et al., 2009). Moreover, the few studies that have investigated the effects of phylogenetic distance on restoration outcomes have found that beneficial processes such as facilitation increase with evolutionary distance between co-occurring species (Verdú et al., 2012). More work is needed to realize the potential of phylogeny to predict restoration outcomes.

There is equally good reason to expect phylogenetic diversity to be a useful metric of restoration progress. Processes such as fire or herbivory, which influence competitive interactions and select for particular traits, have been shown to modify phylogenetic structure, the shape of the phylogenetic tree for those organisms in a community (Verdú and Pausas, 2007; Begley-Miller et al., 2014; D. J. Larkin et al., unpublished manuscript). Moreover, changes in phylogenetic structure have been shown to have important consequences for ecosystem processes and functions that are relevant to restoration. For example, productivity, stability, support for higher trophic levels, and resistance to invasion and herbivory are all positively correlated with phylogenetic diversity (e.g., Cadotte et al., 2009; Srivastava et al., 2012). Because restoration involves

guiding the community assembly process, we would expect restoration outcomes to be measurable through their effects on community structure and phylogenetic diversity.

Why, then, has phylogeny not been used as a tool to predict restoration outcomes (Verdú et al., 2012)? Why is it considered so little, if at all, by practitioners? As the previous paragraphs argue, the scientific rationale for investigating the effects of phylogeny on restoration is strong. Furthermore, restoration practitioners with whom we have discussed the idea of phylogenetically informed restoration are genuinely intrigued. We believe that the limiting factors are largely related to methodological gaps and inadequate communication across disciplines. Until recently, phylogenetic study required substantial laboratory technology, financial support, and time. Even now, despite recent innovations in phylogenetic synthesis (Beaulieu et al., 2012; Pearse and Purvis, 2013) and community phylogenetic analysis (Pearse et al., 2015), phylogenetic tools are unfamiliar and largely inaccessible to most restoration practitioners. Until tools of phylogenetic analysis approach the accessibility of metrics such as species diversity or floristic quality (Swink and Wilhelm, 1994), progress in the application of phylogenetic research to the practice of ecological restoration will be limited (Cook et al., 2013). Wider dissemination of phylogenetic ideas, development of simpler tools for phylogenetic analysis, and training opportunities geared toward practitioners rather than researchers would enable broader use of phylogeny in restoration.

Beyond the mechanics of making and analyzing phylogenies, traditional disciplinary distinctions have likely limited the integration of phylogenetic ideas into applied ecology. Throughout the 20th century, ecological and evolutionary perspectives in biology became more disparate, but evolutionary approaches are increasingly being incorporated into community ecology in recent years (Cavender-Bares et al., 2009). As the goal of restoration has shifted from replicating historic assemblages to using those assemblages as a guide (Higgs et al., 2014), a space has opened for phylogenetic diversity and distinctiveness as restoration criteria. Distributions of phylogenetic community structure of past assemblages might, for example, serve as a baseline for restorations. Where does the phylogenetic structure of our seed mixes, planting lists, and existing restorations fall relative to reference communities? There has been no real argument against the use of phylogeny in restoration (though see discussion between Rosauer and Mooers, 2013; Winter et al., 2013). Rather, we believe the pressing need is for more exchange between restorationists, who tend to take an ecological view, and phylogeneticists, who tend to think in evolutionary terms.

Research on integrating phylogeny into ecological restoration research will need to address three main questions:

1. *What are typical patterns of community phylogenetic structure in restored plant communities relative to reference systems?* The restoration literature is filled with examples of restorations

¹Manuscript received 23 March 2015; revision accepted 24 April 2015.
doi:10.3732/ajb.1500119

failing to live up to reference systems in terms of taxonomic diversity. Do the same patterns hold true for phylogenetic diversity? Is phylogenetic structure a good predictor of the functional trait space occupied by restored plant assemblages? Phylogenetic diversity appears to be lower in restored tallgrass prairie than in remnants, in association with the functional trait composition of the remnant and restored communities (D. J. Larkin et al., unpublished manuscript; W. Sluis, [Trine University], M. Bowles, M. Jones [Christopher Burke Engineering], and R. Barak, unpublished data), but more research is needed to determine whether this is a general pattern across systems and sites.

2. *How do phylogenetic diversity, measured trait diversity, and trait selection shape restoration outcomes?* Restoration practitioners have decades of experience establishing species assemblages. How much and in what ways can phylogeny enhance this rich body of experience and knowledge? Experiments are needed to evaluate the partial effects of phylogenetic diversity, trait diversity, and enrichment of species mixes for particular traits on restoration outcomes (e.g., productivity, maintenance of species assemblages over time, resistance to invasion, and resilience to climatic variation). Where possible, such research should be undertaken in direct collaboration with restoration practitioners and projects, to maximize the applicability of research outcomes to restoration practice.

3. *How can we build phylogenetic tools that restorationists can use to plan and monitor restorations?* Without a toolkit and a frame of reference for analysis, it will be difficult for restorationists to avail themselves of phylogenetic research. An integrated toolkit for phylogenetic analysis and interpretation of survey data, seed mixes, and restoration plans would allow ecological restorationists to evaluate key questions about whether and how well phylogeny works as a tool for restoration planning and monitoring. What are appropriate targets for phylogenetic diversity in restoration? How can phylogenetic considerations be reconciled with other restoration criteria related to taxonomic diversity, target species, or ecosystem services? Does phylogenetic diversity influence the long-term sustainability and resilience of restored assemblages? We will find answers to such questions only by incorporating phylogenetic tools into ecological restoration and evaluating the results.

We suspect that phylogeny will turn out to be a powerful and practical tool for applied ecology. The only way we can rigorously test the utility of applying phylogenetic knowledge to ecological restoration is by undertaking an ambitious program of phylogenetic research in a restoration context and bringing practitioners and researchers together to develop tools that address management needs. We need both the research and a more active conversation across disciplines.

ACKNOWLEDGEMENTS

The authors thank Lars Brudvig, Nicole Cavender, Pamela Diggle, Eric Higgs, Molly Fifield Murray, Joy Zedler, and an anonymous reviewer for comments on an early draft of this manuscript. This article is based in part upon work supported by the National Science Foundation under grant numbers NSF-DEB 1354551 and 1354426.

LITERATURE CITED

- BEAULIEU, J. M., R. H. REE, J. CAVENDER-BARES, G. D. WEIBLEN, AND M. J. DONOGHUE. 2012. Synthesizing phylogenetic knowledge for ecological research. *Ecology* 93: S4–S13.
- BEGLEY-MILLER, D. R., A. L. HIPPI, B. H. BROWN, M. HAHN, AND T. P. ROONEY. 2014. White-tailed deer are a biotic filter during community assembly, reducing species and phylogenetic diversity. *AOB Plants* 6: plu030.
- BRUDVIG, L. A. 2011. The restoration of biodiversity: Where has research been and where does it need to go? *American Journal of Botany* 98: 549–558.
- CADOTTE, M. W., J. CAVENDER-BARES, D. TILMAN, AND T. H. OAKLEY. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4: e5695.
- CAVENDER-BARES, J., AND N. CAVENDER. 2011. Phylogenetic structure of plant communities provides guidelines for restoration. In S. Greipsson [ed.], *Restoration ecology*, 119–129. Jones & Bartlett Learning, Sudbury, Massachusetts, USA.
- CAVENDER-BARES, J., K. H. KOZAK, P. V. A. FINE, AND S. W. KEMBEL. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- COOK, C. N., M. B. MASCIA, M. W. SCHWARTZ, H. P. POSSINGHAM, AND R. A. FULLER. 2013. Achieving conservation science that bridges the knowledge–action boundary. *Conservation Biology* 27: 669–678.
- FOREST, F., R. GRENYER, M. ROUGET, T. DAVIES, R. COWLING, D. FAITH, A. BALMFORD, ET AL. 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445: 757–760.
- HIGGS, E., D. A. FALK, A. GUERRINI, M. HALL, J. HARRIS, R. J. HOBBS, S. T. JACKSON, ET AL. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12: 499–506.
- MAYFIELD, M. M., AND J. M. LEVINE. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- MONTOYA, D., L. ROGERS, AND J. MEMMOTT. 2012. Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends in Ecology & Evolution* 27: 666–672.
- MOUQUET, N., V. DEVICTOR, C. N. MEYNARD, F. MUNOZ, L.-F. BERSIER, J. CHAVE, P. COUTERON, ET AL. 2012. Ecophylogenetics: Advances and perspectives. *Biological Reviews of the Cambridge Philosophical Society* 87: 769–785.
- PEARSE, W. D., M. W. CADOTTE, J. CAVENDER-BARES, A. R. IVES, C. M. TUCKER, S. C. WALKER, AND M. R. HELMUS. 2015. *pez*: Phylogenetics for the Environmental Sciences. *Bioinformatics*. doi: 10.1093/bioinformatics/btv277
- PEARSE, W. D., AND A. PURVIS. 2013. phyloGenerator: An automated phylogeny generation tool for ecologists. *Methods in Ecology and Evolution* 4: 692–698.
- ROSAUER, D. F., AND A. O. MOOERS. 2013. Nurturing the use of evolutionary diversity in nature conservation. *Trends in Ecology & Evolution* 28: 322–323.
- SRIVASTAVA, D. S., M. W. CADOTTE, A. A. M. MACDONALD, R. G. MARUSHIA, AND N. MIROTCHEV. 2012. Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 15: 637–648.
- SWINK, F., AND G. WILHELM. 1994. *Plants of the Chicago region*, 2nd ed. The Morton Arboretum, Lisle, Illinois, USA.
- VANE-WRIGHT, R. I., C. J. HUMPHRIES, AND P. H. WILLIAMS. 1991. What to protect?—Systematics and the agony of choice. *Biological Conservation* 55: 235–254.
- VERDÚ, M., L. GÓMEZ-APARICIO, AND A. VALIENTE-BANUET. 2012. Phylogenetic relatedness as a tool in restoration ecology: A meta-analysis. *Proceedings. Biological Sciences* 279: 1761–1767.
- VERDÚ, M., AND J. G. PAUSAS. 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology* 95: 1316–1323.
- WINTER, M., V. DEVICTOR, AND O. SCHWEIGER. 2013. Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution* 28: 199–204.

Andrew L. Hipp^{2,8}, Daniel J. Larkin^{3,8}, Rebecca S. Barak^{3,4}, Marlin L. Bowles², Marc W. Cadotte⁵, Sarah K. Jacobi³, Eric Lonsdorf³, Bryant C. Scharenbroch^{2,6}, Evelyn Williams³, AND Evan Weiher⁷

²The Morton Arboretum, Lisle, Illinois 60532 USA; ³Chicago Botanic Garden, Glencoe, Illinois 60222 USA; ⁴Plant Biology and Conservation, Northwestern University, Evanston, Illinois 60208 USA; ⁵Department of Biological Sciences, University of Toronto-Scarborough, Toronto ON M1C 1A4 Canada; ⁶College of Natural Resources, University of Wisconsin Stevens Point, Stevens Point, Wisconsin 54481 USA; and ⁷Department of Biology, University of Wisconsin-Eau Claire, Eau Claire, Wisconsin 54702 USA

⁸Authors for correspondence (ahipp@mortonarb.org; dlarkin@chicagobotanic.org)

KEY WORDS: biodiversity; phylogenetic diversity; phylogenetic structure; restoration outcomes.