

INTRODUCTION TO THE SPECIAL ISSUE

Evolutionary insights from studies of geographic variation: Contemporary variation and looking to the future

Julie R. Etterson^{2,6}, Heather E. Schneider³, Nicole L. Soper Gorden^{2,4}, and Jennifer J. Weber⁵

In an age of rapid global change, it is imperative that we continue to improve our understanding of factors that govern genetic differentiation in plants to inform biologically reasonable predictions for the future and enlighten conservation and restoration practices. In this special issue, we have assembled a set of original research and reviews that employ diverse approaches, both classic and contemporary, to illuminate patterns of phenotypic and genetic variation, probe the underlying evolutionary processes that have contributed to these patterns, build predictive models, and test evolutionary hypotheses. Our goal was to underscore the unique insights that can be obtained through the complementary and distinct studies of plant populations across species' geographic ranges.

KEY WORDS clinal variation; climate change; mating systems; evolutionary prediction; genetic differentiation; geographic variation; resurrection ecology

Understanding factors that govern genetic differentiation in plants across environmental gradients is just as relevant today as when the seminal research of Clausen, Keck, and Heisey (1948) was published more than half a century ago, and may be even more important given the rate of contemporary global change. In this special issue, we have collected new research on geographic patterns in plants that use a range of approaches from classic and contemporary, with the ultimate aim of enhancing our predictive capacity of plant evolution into the future. We recognize the importance of using contemporary geographic variation as a platform on which to build predictions about future patterns of variation in plant genotypes and phenotypes in a rapidly changing environment. The articles in this special issue highlight ongoing efforts to document spatial patterns of geographic variation in plants and probe the underlying mechanisms of differentiation across space and time with

the ultimate goal of enhancing our predictive capacity in the future.

A powerful approach to understanding genetic differentiation in the wild is to monitor it in action. In principle, the simplest way to achieve this goal is to measure population phenotype, genotype, and the environment over time (Fig. 1A). In practice, however, this type of study is logistically challenging and requires corresponding pedigree information to distinguish between the genetic and plastic bases for changes in phenotypic expression over time (Ghalambor et al., 2007; Merilä and Hendry, 2014). Pedigree information is especially difficult to obtain in plants that do not form recognizable family units and where biotic and abiotic pollen or seed dispersal can be extensive and therefore difficult to monitor over time.

Feasible experimental alternatives are based on space-for-time substitution (Pickett, 1989) where environmental gradients, for example, across latitude (Fig. 1B) or elevation (Fig. 1C), serve as proxies for temporal trends. Population studies conducted across spatial gradients can elucidate the genetic structure in general and the role of gene flow and drift in shaping geographic patterns of variation. Moreover, spatial variation in allele frequency for genes that underlie important traits, such as timing of flowering, provide a mechanistic understanding of adaptive differentiation.

Common garden experiments encompassing populations sampled across these gradients can also reveal genetically based trait differentiation (Fig. 1D). The inferential power of common garden

¹ Manuscript received 8 December 2015; revision accepted 16 December 2015.

² Department of Biology, University of Minnesota Duluth, 207A Swenson Science Building, Duluth, Minnesota 55812 USA;

³ Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, Santa Barbara, California 93106 USA;

⁴ Current address: Department of Natural Sciences (Biology), Mars Hill University, Mars Hill, North Carolina 28754 USA; and

⁵ Department of Biology, Fordham University, Bronx, New York 10458; current address: Southern Illinois University, Carbondale, Illinois 62901 USA

⁶ Author for correspondence (e-mail: jetterson@d.umn.edu)

doi:10.3732/ajb.1500515

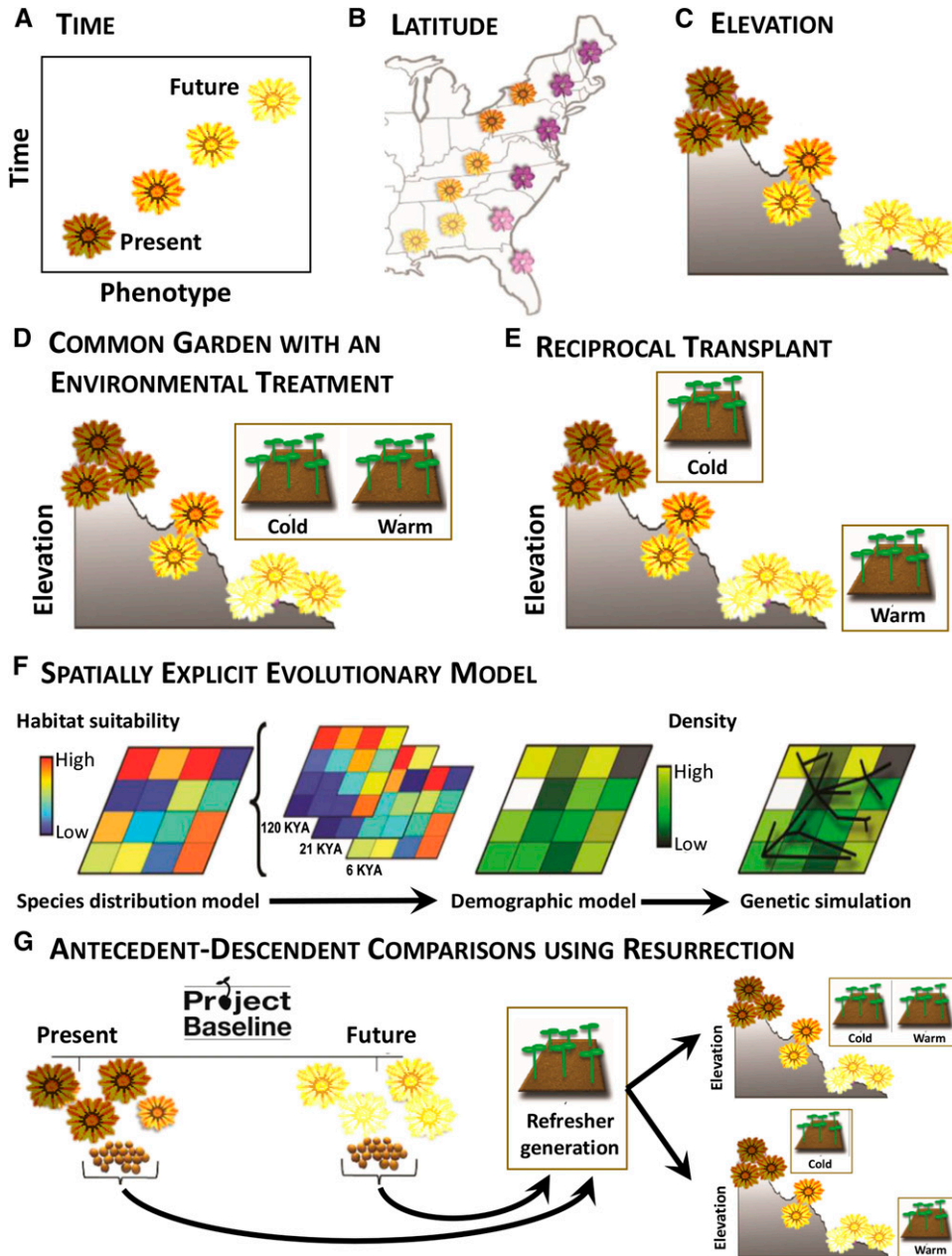


FIGURE 1 Major approaches for studying evolutionary response to environmental variation. (A) Temporal studies may demonstrate that plant phenotype has evolved over time as the environment has changed. Similar phenotypic clines may exist across (B) latitude or (C) elevation if temporal and spatial environmental gradients share fundamental drivers (e.g., temperature). (D) The genetic basis of phenotypic variation, such as spatial clines, can be studied in a simple common garden experiment where environmental variation is minimized or in a common garden with an experimental treatment that explicitly tests the adaptive value of traits in response to a specific environmental attribute (e.g., temperature). (E) Local adaptation in terms of overall fitness and the adaptive value of trait differentiation can be field-tested in reciprocal transplant experiments. For either of these experiments (D or E), population genetic parameters essential for evolutionary predictions, such as heritability and the correlation structure among traits, can be estimated if a pedigree structure is included in the design (e.g., half- or full-sib families). Molecular genetic techniques can also be used to dissect the genetic architecture of phenotypic patterns and associate these with environmental and geographical variation. (F) Spatially explicit evolutionary predictions can be made by coupling genetic information with species distribution and demographic models. (G) Evolutionary change over time and space can be directly observed by rearing offspring from antecedent and descendent populations that have been carried through a refresher generation to reduce environmental carryover effects and then tested in common garden or reciprocal transplant design.

experiments is enhanced with the inclusion of an environmental treatment that permits tests of adaptive plasticity and the role of a specific environmental factor that is hypothesized to be an agent of natural selection (Fig. 1D). Reciprocal transplant experiments enrich our understanding of local adaptation in natural conditions (Fig. 1E). The inferential power of both of these approaches can be expanded by coupling these experiments with quantitative genetic methods that allow estimation of key parameters for predicting evolutionary change. Important quantitative genetic parameters include selection coefficients, heritability, and genetic correlations among traits that can inform correlated responses to selection that enhance or constrain evolutionary response.

Predictions of plant response to a changing environment can also be accomplished with species distribution modeling that typically estimates distributional shifts based on changes in habitat suitability. However, modeling methods continue to improve and methods that incorporate key demographic and genetic processes are likely to result in more biologically relevant predictions (Fig. 1F). Predictions obtained from each of these observational, experimental, and modeling approaches can be tested in the future using the resurrection approach (Franks et al., 2008). In this type of experiment, antecedent populations sampled at a known time and contemporary successor populations collected from the same site are raised side by side in a common environment, permitting the study of both phenotypic and genetic change that has occurred during the intervening time (Fig. 1G).

These methods (Fig. 1) complement each other and, when viewed together, provide a robust description of factors that govern patterns of geographical variation. Here we bring together a set

of studies and employ these diverse approaches for the purpose of advancing our understanding and improving our predictive capacity of geographic variation in plants as we head into a future that is fraught with uncertainty.

OVERVIEW OF SPECIAL ISSUE

We open with a series of articles that illustrate how phenotypic and genetic information obtained from a range of approaches, from classical to cutting edge, improve our understanding of how genetic, environmental, and interacting biotic and abiotic factors shape geographic variation and, in some instances, modify the temporal environment that plants experience. These articles are followed by interspecific studies that underscore the individualistic nature of species' responses, including a set of studies that focus on the important role of plant breeding systems in shaping genetic architecture. Finally, we look to the future with articles that grapple with the challenges of scaling up from local to regional scales, making evolutionary predictions based on standing genetic (co) variation, and implementing a new spatially explicit evolutionary modeling approach that incorporates climate, demographic, and genetic data. We conclude the issue with a description of a new research seed bank that was established as a resource for the broader scientific community that will vastly improve our ability to address these issues over the next five decades by providing baseline materials for antecedent–successor resurrection comparisons of plant populations, species, and communities across geographical ranges.

CONTEMPORARY GEOGRAPHIC VARIATION

In the first four articles in this special issue, diverse approaches were used to examine how geographical position and environmental attributes shape plant phenotypes and their underlying genetic basis. Each of these studies reports geographic patterns in plant phenotype, phenology, or major genes that contribute to these traits. Bontrager and Angert (2016) examined herbarium specimens from the Pacific Northwest to identify the effects of contrasting climate and isolation on mating-system related floral traits and reproductive output of *Clarkia pulchella*. They found that range-limiting factors differed spatially, with precipitation-limited reproductive output on the western (and perhaps southern) edges of the range, and increased selfing with high temperatures at the southern edge of the range, but with no apparent climate-driven limitations at the eastern or northern borders of the range. Erterson et al. (2016b) next report on a common garden study with a watering treatment that included 14 populations of *Solidago altissima* that were sampled across a major ecotone border between prairie and forest biomes and that encompass ploidy variation (diploid, tetraploid, and hexaploids). One of the major findings of this work is that diploids have diverged genetically to a greater extent than polyploids across latitudinal and longitudinal gradients and that clinal trends in phenology and phenotype are not simply a function of phenotypic plasticity in response to drought. Next, Sork et al. (2016) delved into the molecular genetic basis of phenotypic clines by examining gradients in allele frequency of candidate genes that are known to contribute to climate adaptation in the California endemic oak *Quercus lobata*. They found corresponding patterns between geographic and functional genes, providing evidence of the

genetic architecture of adaptation. The final paper in this section highlights the importance of phenotypic plasticity for seed dormancy. Burghardt et al. (2016) used empirical data from a latitudinal gradient in wild populations of *Arabidopsis thaliana* to model the effect of phenotypic adjustment in the duration of dormancy that ultimately results in consistent exposure to climate over space and time. In summary, each of these studies identified strong geographical patterns that would not have been detected with examination of only one or a few populations, highlighting the importance of using studies of geographic variation to understand spatial drivers of population traits.

Two studies follow that focus on contrasting effects of environmental gradients on different species. In a comparative study of seed mass and dispersal traits across the ranges of seven species, Soper Gorden et al. (2016) found inconsistent patterns of covariance between geographic and climatic factors among all species, with the exception that annual species' seed traits corresponded more closely to collection-year weather as opposed to perennial species that covaried more strongly with long-term climate means. Overall, this study suggests that the scale of climate variation that molds seed traits is highly species-specific and is fundamentally different within and between species ranges. Similarly, in a study of three California oak species, Riordan et al. (2016) found that genetic variation was significantly associated with climate and geography for two species but not the third and that phenotypic variation was associated with climate in only one species. Their data suggest that these species-specific patterns are likely to disrupt sympatric distributions of these species in the future as climate changes.

The next three papers in this issue focus on the extent to which mating systems influence patterns of differentiation across geographic ranges and include studies of an asexual fern, selfing and outcrossing subspecies, and a meta-analysis of data from 98 selfing and outcrossing sister taxa. In a transplant experiment of multiple populations of *Vittaria appalachiana*, a patchily distributed asexual fern with limited dispersal, Chambers and Emery (2016) found highly variable population responses to contrasting environments, including countergradient selection for more robust genotypes in the northern range and limited local adaptation. Pettengill et al. (2016) compared how mating systems affect molecular variation for two subspecies of *Clarkia xantiana*, one outcrossing and one selfing. Mating systems strongly influenced geographic variation; population genetic structure was evident for the selfer but not the outcrosser, whereas the outcrosser showed an effect of isolation by distance that was lacking in the selfer. In contrast, Grossenbacher et al. (2016) found no effect of mating system on the extent of geographic overlap among numerous pairs of sister taxa. Because selfing limits gene flow, it was expected that selfing taxa would have ranges that overlapped with their closest relatives more often than outcrossing taxa. However, this study showed that although recently diverged sister pairs had greater range overlap than pairs that diverged in the more distant past, this pattern did not depend on mating system. Taken together, this collection of new research highlights the variability in species responses to geographic or climate variability, including the often large differences among even closely related species.

LOOKING TO THE FUTURE

An important goal of geographic studies is to improve our understanding of factors that govern persistence of species and critical

species interactions into the future. Given this, the second section of this special issue focuses on making and testing predictive hypotheses. This section opens with a review by Burkle et al. (2016) that addresses the challenges of scaling up inferences from regional to larger geographic scales using plant–pollinator interactions as an example. Next, Sexton and Dickman (2016) review biotic and abiotic factors that could inhibit population expansion at contrasting scales and then report on experiments conducted in the California Sierra Nevada that test limiting factors at a local scale in *Mimulus leptaleus* (meters) and a broader scale in *Mimulus laciniatus* (kilometers). This work underscores the importance of habitat limitations at both spatial scales. Schneider and Mazer (2016) follow with a common garden study of elevational samples of two *Clarkia* sister species where the among-trait genetic correlations form the basis of evolutionary predictions for reproductive traits. The authors suggest that selection for earlier flowering with climate change may promote correlated responses in herkogamy and selfing, which may be a genetically risky and unanticipated outcome of climate change. Next, Brown et al. (2016) present a new spatially and genetically explicit approach to modeling population response to climate change. The authors illustrate their model using spatial, genetic, and demographic data on *Penstemon deustus* and predict a decrease in allelic diversity across the landscape, but importantly, also identify regional pockets of allelic diversity that are predicted to be less suitable for this species in the future. Finally, we introduce a unique national resource, called Project Baseline, which has recently been established for the purpose of testing evolutionary predictions across time and space (Etterson et al., 2016a). This research seed bank, which includes multiple populations of more than 50 wild plant species sampled across their ranges, was developed for the express purpose of characterizing the spatial and temporal dimensions of microevolution during what is expected to be an unprecedented period of rapid environmental change. Over the next 50 years, biologists will be able to withdraw seeds representing “ancestral” populations and directly compare them with their contemporary counterparts in the future using the resurrection approach. As technology changes throughout the 50-year life of the collection, biologists will have improved ability to dissect the genetic architecture of evolution and test the predictions represented in this special issue.

CONCLUDING REMARKS

Ecosystems are not static; conditions frequently change annually, and populations are constantly adapting to the resulting shifts in selective pressures. Overlaying this constant background of environmental fluctuation is the unprecedented, rapid shift in abiotic conditions due to global climate change that has given rise to the concern that plant populations may not be able to adapt quickly enough to survive, especially in a degraded habitat (Etterson and Shaw, 2001; Visser, 2008; Sexton et al., 2009; Springate et al., 2011; Quintero and Wiens, 2013). Thus, it is becoming increasingly important that we understand how plants respond to their environment across spatial and temporal gradients to better predict how wild plant species will respond in the future. To this end, we have given careful consideration to information that can be derived from traditional and contemporary approaches that illuminate patterns and provide direction on how best to build and test predictive models.

Continued research in this field is critical for predicting potential outcomes of climate change at the population, community, and ecosystem levels and can be used to inform management, conservation, and restoration plans. Moving forward, we hope that the innovative and thought-provoking articles in this special issue will inspire increased interest in the study of evolution utilizing geographic variation to examine spatial and temporal patterns in plants.

ACKNOWLEDGEMENTS

This special issue emanated from a symposium entitled “Evolutionary insights from studies of geographic variation: Establishing a baseline and looking to the future” held at the 2014 Annual Meeting of the Botanical Society of America in Boise, Idaho. This symposium was organized by three postdoctoral researchers, N. Soper Gorden, H. Schneider, and J. Weber, who were instrumental in establishing a research seed bank to study geographic variation in plant evolution called Project Baseline (NSF DEB 1142784 to J. Etterson, S. Franks, and S. Mazer). The authors thank the speakers at the symposium, who stimulated conversations about the special importance of plant studies that span geographic ranges as we head into an uncertain future. They also thank the rest of this special issue’s Associate Editors, Jesse Bellemare, Steve Franks, Chris Herlihy, and Jason Sexton, and the reviewers who provided valuable comments on the manuscripts, as well as Amy McPherson, Richard Hund, and other support staff at the *American Journal of Botany* for their editorial assistance.

LITERATURE CITED

- Bontrager, M., and A. L. Angert. 2016. Effects of range-wide variation in climate and isolation on floral traits and reproductive output of *Clarkia pulchella*. *American Journal of Botany* 103: 10–21.
- Brown, J. L., J. J. Weber, D. F. Alvarado-Serrano, M. J. Hickerson, S. J. Franks, and A. C. Carnaval. 2016. Predicting the genetic consequences of future climate change: The power of coupling spatial demography, the coalescent, and historical landscape changes. *American Journal of Botany* 103: 153–163.
- Burghardt, L. T., C. J. E. Metcalf, and K. Donohue. 2016. A cline in seed dormancy helps conserve the environment experienced during reproduction across the range of *Arabidopsis thaliana*. *American Journal of Botany* 103: 47–59.
- Burkle, L. A., J. A. Myers, and R. T. Belote. 2016. The beta-diversity of species interactions: Untangling the drivers of geographic variation in plant–pollinator diversity and function across scales. *American Journal of Botany* 103: 118–128.
- Chambers, S. M., and N. C. Emery. 2016. Population differentiation and counter-gradient variation throughout the geographic range in the fern gametophyte *Vittaria appalachiana*. *American Journal of Botany* 103: 86–98.
- Clausen, J., D. Keck, and W. Heisey. 1948. Experimental studies on the nature of species III: Environmental responses of climatic races of *Achillea*. Carnegie Institution of Washington, Washington, D.C., USA.
- Etterson, J. R., S. J. Franks, S. J. Mazer, R. G. Shaw, N. L. Soper Gorden, H. E. Schneider, J. J. Weber, K. J. Winkler, and A. E. Weis. 2016a. Project Baseline: An unprecedented resource to study plant evolution across space and time. *American Journal of Botany* 103: 164–173.
- Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294: 151–154.
- Etterson, J. R., R. H. Toczydlowski, K. J. Winkler, J. A. Kirschbaum, and T. McAulay. 2016b. *Solidago altissima* differs with respect to ploidy frequency and clinal variation across the prairie–forest biome border in Minnesota. *American Journal of Botany* 103: 22–32.
- Franks, S. J., J. C. Avise, W. E. Bradshaw, J. K. Conner, J. R. Etterson, S. J. Mazer, R. G. Shaw, and A. E. Weis. 2008. The resurrection initiative: Storing ancestral genotypes to capture evolution in action. *BioScience* 58: 870–873.

- Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* 21: 394–407.
- Grossenbacher, D., R. D. B. Runquist, E. E. Goldberg, and Y. Brandvain. 2016. No association between plant mating system and geographic range overlap. *American Journal of Botany* 103: 110–117.
- Merilä, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications* 7: 1–14.
- Pettengill, J. B., R. D. B. Runquist, and D. A. Moeller. 2016. Mating system divergence affects the distribution of sequence diversity within and among populations of recently diverged subspecies of *Clarkia xantiana* (Onagraceae). *American Journal of Botany* 103: 99–109.
- Pickett, S. T. 1989. Space-for-time substitution as an alternative to long-term studies. In G. E. Likens [ed.], *Long-term studies in ecology: Approaches and alternatives*, 110–135. Springer-Verlag, New York, New York, USA.
- Quintero, I., and J. J. Wiens. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters* 16: 1095–1103.
- Riordan, E. C., P. F. Gugger, J. Ortego, C. Smith, K. Gaddis, P. Thompson, and V. L. Sork. 2016. Association of genetic and phenotypic variability with geography and climate in three southern California oaks. *American Journal of Botany* 103: 73–85.
- Schneider, H. E., and S. J. Mazer. 2016. Geographic variation in climate as a proxy for climate change: Forecasting evolutionary trajectories from species differentiation and genetic correlations. *American Journal of Botany* 103: 140–152.
- Sexton, J. P., and E. E. Dickman. 2016. What can local and geographic population limits tell us about distributions? *American Journal of Botany* 103: 129–139.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics* 40: 415–436.
- Soper Gorden, N. L., K. J. Winkler, M. R. Jahnke, E. Marshall, J. Horky, C. Huddelson, and J. R. Etterson. 2016. Geographic patterns of seed mass are associated with climate factors, but relationships vary between species. *American Journal of Botany* 103: 60–72.
- Sork, V. L., K. Squire, P. F. Gugger, S. E. Steele, E. D. Levy, and A. J. Eckert. 2016. Landscape genomic analysis of candidate genes for climate adaptation in a California endemic oak, *Quercus lobata*. *American Journal of Botany* 103: 33–46.
- Springate, D. A., N. Scarcelli, J. Rowntree, and P. X. Kover. 2011. Correlated response in plasticity to selection for early flowering in *Arabidopsis thaliana*. *Journal of Evolutionary Biology* 24: 2280–2288.
- Visser, M. E. 2008. Keeping up with a warming world: Assessing the rate of adaptation to climate change. *Proceedings of the Royal Society, B, Biological Sciences* 275: 649–659.