UNSOLVED PROBLEMS IN ECOLOGY

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Preface

Andrew Dobson, Robert D. Holt, and David Tilman

The centenary of the Ecological Society of America inspired us to ask ecologists their thoughts about the next century, specifically on the broad question of "What are the Unsolved Problems in Ecology?" We imagined that they might identify two classes of problems: (1) Those people have wrestled with, but where solutions have remained elusive and (2) problems that someone may have just recognized as being potentially huge yet unexamined. The motivation for the book stems from a deep conviction that ecology will be a central defining science of the twenty-first century, just as physics defined the twentieth, and chemistry the nineteeth. Consequently, we put our authors in the position of defining what they think the key agenda for ecology will be within their area of research for the next decades to a full century. Sutherland et al. (2013) honored the centenary of the British Ecological Society by compiling a list of key unanswered questions—in effect, a series of bullet points aiming at future progress in the discipline. We, instead, asked authors to provide a more discursive reflection on open, important questions in the form of essays, providing a more expansive vista across possible future intellectual landscapes.

A strong motivation for the book was a previous volume of essays published in the 1970s that simply asked "What are the unsolved problems for the 20th Century" (Duncan and Weston-Smith 1977); there were only two biological chapters, including one by John Maynard Smith, who astutely pointed out that we did not know why sex had evolved. Curious as it seems, no one had explicitly realized that this was a problem prior to Maynard Smith's explication of the inherent "cost of sex" (1971, 1977; see Bell 1982); although Darwin as early as 1862 presciently remarked "we do not even in the least know why new beings should be produced by the union of two sexual elements, instead of by . . . parthenogenesis" (cited in Kirk 2006), and Bonner (1958) and others do adumbrate some aspects of the issue. This book chapter helped spark the genesis of a whole subdiscipline of studies within evolution, behavioral ecology, and epidemiology. We are ambitious enough to hope that at least one of our chapters in this volume can likewise unearth an intellectual goldmine that transforms thinking within ecology and the broader disciplines of evolution and environmental science. The other biological essay in the 1977 compilation was by Peter Grubb, who pointed out that our knowledge of leaf structure and function at the time was woefully inadequate. This chapter also led to multiple developments in plant physiology and ecology. We were delighted when Peter accepted our invitation to write a chapter for the current book, and doubly so, when he decided to write a chapter that describes how much we still need to know about leaf structure and function, some four decades after his initial distillation of this question.

Some unsolved questions that the authors in this volume bring up are radically new, but others are longstanding. Robert MacArthur towards the end of his life sketched an array of outstanding problems in ecology (MacArthur 1972), focused around the theme of species coexistence, many of which are still with us and touched on in the current volume, including for instance the need for network perspectives, and the importance of understanding "why are some species able to adjust niche widths rapidly when put in a new situation while others are rigid?"; the latter question foreshadowed current concerns with themes such as niche conservatism and evolutionary rescue. MacArthur argued for intellectual pluralism and suggested that ecologists needed to get beyond the biological sciences (including in particular, he notes, the earth sciences) to really come to grips with the issue of species coexistence. These insights resonate today.

We initially planned to obtain three temporal perspectives on the unsolved problems identified by the authors, corresponding roughly to different stages in the trajectories of careers. To this end, we split the set of authors we invited into three broad and overlapping categories: (1) We asked younger researchers whose careers are expanding rapidly as to what they see as the major conceptual challenges facing their research, (2) we asked midcareer scientists to describe what they plan to focus on as the major targets of opportunity in their own careers, and (3) we asked individuals who have helped to define the study of ecology over the last 30 to 50 years to describe the problems they have found intractable or continually challenging, given available techniques and methodology. The skeleton of this structure is faintly discernible within the chapters we received for the final volume, although we perceive two distortions, one of which can fairly readily be dealt with, the other of which presents a significant "unsolved problem in ecology." The first distortion is that we tended to ask people whom we knew personally to write chapters. Although we have all been active in the Ecological Society of America, the British Ecological Society, the American Society of Naturalists, and the Society for Conservation Biology (among others) for more than 30 years, we surely (if unconsciously) are biased in asking friends and colleagues, rather than a broader array of people we may have admired from a distance in these one involved for their patience, and hope that the final product matches our and your expectations. We have learned a lot and thoroughly enjoyed reading these contributions, and hope that you, and the broader readership of our community, may likewise profit from careful perusal of these essays.

References

Bell, G. 1982. The masterpiece of nature: The evolution and genetics of sexuality. University of California Press.
Bonner, J. M. 1958. The relation of spore formation to recombination. American Naturalist 92:193–200.
Duncan, R., and M. Weston-Smith, eds. 1977. The Encyclopaedia of Ignorance: Everything you ever wanted to know about the unknown. Oxford: Pergamon Press.
Kirk, D. L. 2006. Oogamy: Inventing the sexes. Current Biology 16:R1028–R1030.
MacArthur, R. 1972. Coexistence of species. In: J. A. Behnke, ed. Challenging biological problems: Directions toward their solutions. New York: Oxford University Press, 253–259.
Maynard Smith, J. 1971. What use is sex? Journal of Theoretical Biology 30:319–335.
Sutherland, W. J., et al. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

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PART I

POPULATIONS, VARIABILITY, AND SCALING

fluxes. A key topic raised by both Wiens and Levin also was addressed in a book published at nearly the same time (Ehleringer and Field 1993) in which many authors tackled the issue of scaling and cross-scale feedbacks from organismal physiology to global climate and back again.

In the decades since these papers were written, ecologists have continued to develop an understanding of long-term feedbacks, heterogeneity, and links across spatial scales. For example, the effects of forest warming over the short term have been demonstrated to stimulate soil respiration, whereas turnover in microbial composition can increase the carbon use efficiency of the community, leading to attenuation of soil respiration under continuous long-term warming (Melillo et al. 2002, Frey et al. 2013). The effects of diversity on productivity also function via long-term feedbacks. For example, long-term, chronic nutrient addition causes productivity to increase initially, but these effects attenuate over multiple decades because of ongoing loss of species diversity (Isbell et al. 2013). In a different subfield of ecology, research using metagenomic tools is highlighting the links and feedbacks among spatial scales that determine the resident microbial composition, or microbiome, of a host. For example, the identity and relative abundance of microbial species inhabiting an individual is determined at the regional scale by the composition and relative transmission ability of microbial species and at the local scale by the relative abundance of hosts and microbial competitive ability and fitness within individual host species (reviewed in Borer et al. 2013). Many factors, including the abiotic environment (Fenchel and Finlay 2004), host quality (Smith et al. 2005), and host behavior (Lombardo 2008), can play a role in these interactions and feedbacks across spatial scales.

In spite of the forward progress of this field, the fundamental issue of effectively using information about processes at one scale in predictions about outcomes at another scale remains unsolved. In 2011, the Macrosystems Biology program at the National Science Foundation (NSF) was launched to stimulate research and advance greater mechanistic understanding of processes spanning spatial scales (Dybas 2011). Although the availability of funding is certainly a key constraint on intellectual progress, identifying and collecting the types of data that will be useful for making predictions that span scales also represents a major challenge (Levin 1992, Ehleringer and Field 1993, Leibold et al. 2004, Elser et al. 2010, Nash et al. 2014). Perhaps most importantly, ecologists studying feedbacks and linkages across spatial scales are faced with tradeoffs in our capacity to gather data about the biosphere at any scale: the spatial extent versus the temporal extent of a study, the local replication versus the spatial extent of a study, or site-based experimental work versus large-scale observation (Soranno and Schimel 2014).

A New Tool Hiding in Plain Sight

Over the past several decades, a fairly continuous stream of publications has identified conceptual areas of spatial scaling where our ignorance remains vast (e.g., Wiens 1989, Levin 1992, Ehleringer and Field 1993, Peters et al. 2007, Borer et al. 2013). However, ecological science has changed a great deal during this time, giving us a range of new tools and more highly resolved data to study ecological scaling relationships. Meta-analysis has become an accepted tool for quantitative synthesis of the ecological literature and has been used, for example, to examine support for a range of hypotheses about the key determinants of species diversity across spatial scales (Field et al. 2009). Sequencing technology and metagenomics is rapidly extending the conceptual realm and spatial scales being actively considered by ecologists (Borer et al. 2013). Electronic technology also has changed our ability to tackle questions about scaling in myriad ways, including computerization of data acquisition and access, satellite imagery, remote sensing, drone technology, and interpolation of a wide array of environmental data (Campbell et al. 2013). One example of the exciting cutting-edge of technology to examine scaling in ecology is research that is advancing our ability to use remotely sensed spectral variation as a tool for estimating local and regional biodiversity, and concurrently documenting leaf-level traits and functional differences among taxa (Cavender-Bares et al. 2016).

However, the change in the past 30 years that is perhaps most underappreciated for its potential to advance this field is neither statistical nor technological; it is the shift in the culture of ecological science from a field dominated by single investigator projects to one of collaboration (Hampton and Parker 2011, Goring et al. 2014).

Distributed Experimental Networks

Most ecological research is conducted by one or a few scientists over relatively short time scales and small spatial scales (Heidorn 2008), and whereas large-scale, multi-investigator collaborations have become increasingly common in ecology over the past several decades (Nabout et al. 2015), the vast majority of these collaborations generate, share, and analyze observational data (e.g. Baldocchi et al. 2001, Weathers et al. 2013). Although observations of ecological systems represent an exceptionally important tool for characterizing and comparing among systems, manipulative experiments are a far more powerful tool for forecasting a system's behavior under novel environmental conditions. Given the pressing need to effectively forecast ecological responses in a changing global environment, multifactorial experiments measuring responses and feedbacks spanning spatial and temporal scales will be a key tool to complement meta-analyses, large-scale observations, and models.

Although most experiments in ecology are conceived of and performed by single investigators, large-scale, grassroots distributed experimental collaborations are rethinking ecological experimentation and are overcoming the historical tradeoffs in our capacity to gather long-term experimental data across multiple spatial scales (Borer et al. 2014a). By replicating the same experimental treatments and sampling protocols and openly sharing data with each other, ecologists collaborating in distributed experimental networks are able to replicate experiments and directly compare biological and abiotic responses across spatial scales ranging from centimeters to continents. Depending on the question, sampling can occur at multiple scales within sites (e.g., within individual, within plot, plot, block, site) to quantify a plethora of responses to experimental treatments that map onto future scenarios (e.g., multiple nutrients, herbivory, high-latitude warming, drought, and loss of biodiversity; see Arft et al. 1999, Borer et al. 2014b, Duffy et al. 2015, Fay et al. 2015).

This emerging approach to network science is requiring a rethinking of collaboration and a change in scientific culture (Guimerà et al. 2005, Hampton and Parker 2011, Borer et al. 2014a). By using common experimental treatment and sampling protocols and sharing data openly among collaborators, every site improves the dataset through contribution and each investigator benefits from the opportunity to contribute data and ideas as a result of their efforts (Borer et al. 2014a). As with any effective collaboration, careful fostering of a culture of trust and sharing means that contributors have confidence that their efforts will be included and rewarded (Hampton and Parker 2011). In this model, participation is voluntary, and for most distributed experiments organized as grassroots efforts, investigators at each site shoulder the cost of implementing the treatments and collecting the data rather than funding such efforts through a single centralized grant. This pay-to-play funding model means that participation, particularly by international collaborators in understudied regions of the world, is increased when costs are low. And, for a field that seems to perpetually struggle with physics envy, this model of egalitarian collaboration was once called “the dream” by the Director General of the European Center for Particle Research (CERN), Dr. Robert Aymar (Ford 2008).

To forecast future scenarios for ecological responses and feedbacks in nonanalog environmental conditions (Williams and Jackson 2007, Rockström et al. 2009), we need experiments that manipulate multiple global change factors over long periods of time, and we need to understand how novel conditions influence the resulting spatial patterns and processes across multiple scales. Without multifactorial experiments replicated across many sites, it remains difficult to effectively estimate interactions among factors and contingencies in responses associated with, for instance, climate, evolutionary, or geological history. Distributed experimental networks provide such an opportunity.

The benefits of a distributed experiment for tackling questions about processes spanning and feeding back across spatial scales are enormous. This widespread collaboration among scientists dramatically expands the spatial extent of observation while retaining resolution (grain) at the scale of individuals, but also generating data that can be aggregated to capture patterns at larger grain such as block or site. The spatial replication generated by a network with many collaborators allows clear quantification of responses that are shared among sites as well as responses that are contingent on site characteristics (e.g., climate, soils, or evolutionary history). The replication of experimental treatments across many sites and conditions also allows investigation into the patterns and feedbacks resulting from multiple interacting factors by breaking up the colinear and confounded variables that plague single-site studies. By working as a widespread collaborative team to establish multiple treatments and sample at locations spanning regions and continents, distributed experiments overcome the tradeoff between the spatial and temporal scales of sampling that has caused ecologists to rely so heavily on models and meta-analysis for which interactions among treatments and site variables are difficult (and usually impossible) to disentangle.

We provide a few case studies to develop how we envision that this type of approach, harnessing the intellectual and data collection power of scientists spanning regions and continents, could interlink with existing approaches (e.g., modeling, streaming data) to generate a predictive understanding of how biological processes will change and feed back across scales in response to changing environments on Earth.

Case Study 1: Plant Productivity

As we move across spatial and temporal scales of observation, the key controls on the processes and resulting patterns in primary productivity shift (Wiens 1989, Ehleringer and Field 1993, Polis 1999, Peters et al. 2007). For example, roots foraging for soil resources may occur at the scale of millimeters, inducing organismal constraints on productivity (Tian and Doerner 2013). At the scale of meters, intraspecific and interspecific interactions among organisms seeking the same resources may generate webs of direct and indirect interactions that may determine the net carbon fixation and annual productivity of a plant community. For example, concurrent changes and feedbacks in plant quality and composition in response to grazing (Zheng et al. 2012) or chronic nutrient addition (Isbell et al. 2013) can lead to long-term declines in productivity within fields. At regional scales, solar radiation, precipitation, nutrients, or other physical factors may impose the most important constraints on productivity (Polis 1999, Del Grosso et al. 2008). Although local, long-term patterns of evapotranspiration can predict the dominant flora, and thus biome, of a region, direct measurements of leaf-scale transpiration or small-scale measurements of local plant communities may fail to predict the larger-scale pattern (Wang and Dickinson 2012). Thus, we remain limited in our ability to use observed responses at the scale of roots and stomata to interpret satellite information or predict regional climate, although we believe that these changes are important pieces of the puzzle.

The use of meta-analysis has advanced our understanding of the role and interactions among climate, plant chemistry, and vegetation type on regional-scale patterns of plant productivity (Del Grosso et al. 2008). However, in spite of the important insights arising from synthesis across studies, such studies have relied on interpolation and derived metrics of production that may underestimate the role of local-scale processes and overestimate the role of regional climatic drivers (Shoo and Ramirez 2010). They also fail to provide a strong estimation of trajectories of productivity under future scenarios of climate and nutrient deposition. Thus, our ability to predict productivity responses to multiple interacting factors (e.g., concurrent changes in the supply rates of multiple nutrients or climate factors) and feedbacks from plant productivity to climate and nutrient cycles remains limited by the lack of simultaneous, direct manipulations of the environment and measurements of the rates of primary productivity within and among sites.

A coordinated, long-term experiment spanning a wide range of climate and nutrient supply could produce data to test the multiscale hypotheses generated with meta-analysis. By concurrently manipulating factors most likely to determine productivity within sites, regions, and across continents (e.g., climate, local nutrient supply, herbivory; Milchunas and Lauenroth 1993, Del Grosso et al. 2008, Fay et al. 2015), such a study could generate data to clarify the likely trajectories of change in productivity in future, nonanalog environments. These direct estimates of primary productivity, under a wide variety of natural and manipulated environments, produced through large-scale collaboration among scientists, would generate data to clarify the interactions among factors, spatial and temporal feedbacks, and spatial scales at which each factor most strongly constrains of host-associated microbes to multiple concurrent global change factors across a globally relevant range of conditions, a distributed experimental network could generate critical empirical data about the interactions and feedbacks among factors controlling the microbiome. By harnessing the capacity of the research community deeply invested in these questions, these data could effectively complement insights from metagenomic observations, single-site (or lab) studies, and models, providing insights about generality and contingencies determining a host's microbiome at an unprecedented range of spatial scales.

Conclusions

Perhaps this will simply be another essay pointing out our need for progress in understanding the mechanisms underlying ecological relationships spanning spatial and temporal scales. If so, it will be an essay in venerable company. However, as a discipline, we have an ever richer and more diverse set of young scientists spanning the globe. This growth and diversity of ecologists can become a direct asset that can position our field to rethink how we work as a society of scientists. We can harness the collective skills and knowledge of our amazing colleagues to create the newest tool in our own toolbox for generating previously unattainable experimental data documenting processes and feedbacks across scales. More generally, innovation and progress can come in many forms, including rethinking our approach to science. By rethinking how we study the world, redefining how we collect data, and pursuing avenues outside the range of conventional approaches, ecologists may be able to push this field further in the coming decades than we have in the preceding ones.

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References

Antony-Babu, S., J.E.M. Stach, and M. Goodfellow. 2008. Genetic and phenotypic evidence for *Streptomyces griseus* ecovars isolated from a beach and dune sand system. Antonie Van Leeuwenhoek International Journal of General and Molecular Microbiology 94:63–74.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, et al. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. Ecological Monographs 69:491–511.

Arrigo, K. R. 2005. Marine microorganisms and global nutrient cycles. Nature 437: 349–355.

Baas-Becking, L.G.M. 1934. Geobiologie of inleiding tot de milieukunde. The Hague: Van Stockum and Zoon.

Baldocchi, D., E. Falge, L. Gu, R. Olson, D. Hollinger, S. Running, et al. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem–scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society 82:2415–2434.

Borer, E. T., A.-L. Laine, and E. Seabloom. 2016. A multiscale approach to plant disease using the metacommunity concept. Annual Review of Phytopathology 54:397–418.

Borer, E. T., W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, and M. D. Smith. 2014a. Finding generality in ecology: A model for globally distributed experiments. Methods in Ecology and Evolution 5:65–73.

Borer, E. T., L. L. Kinkel, G. May, and E. W. Seabloom. 2013. The world within: Quantifying the determinants and outcomes of a host's microbiome. Basic and Applied Ecology 14:533–539.

Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, et al. 2014b. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520.

Borer, E. T., E. W. Seabloom, C. E. Mitchell, and A. G. Power. 2010. Local context drives infection of grasses by vector-borne generalist viruses. Ecology Letters 13:810–818.

Brüls, T., and J. Weissenbach. 2011. The human metagenome: our other genome? Human Molecular Genetics 20:R142–R148.

Campbell, J. L., L. E. Rustad, J. H. Porter, J. R. Taylor, E. W. Dereszynski, J. B. Shanley, et al. 2013. Quantity is nothing without quality: automated qa/qc for streaming environmental sensor data. Bioscience 63:574–585.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cavender-Bares, J., J. E. Meireles, J. J. Couture, M. A. Kaproth, C. C. Kingdon, A. Singh, et al. 2016. Associations of leaf spectra with genetic and phylogenetic variation in oaks: Prospects for remote detection of biodiversity. Remote Sensing 8:221.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences of the United States of America 104:17430–17434.

Cho, J. C., and J. M. Tiedje. 2000. Biogeography and degree of endemicity of fluorescent *Pseudomonas* strains in soil. Applied and Environmental Microbiology 66:5448–5456.

Clasen, J. L., and J. J. Elser. 2007. The effect of host *Chlorella NC64A* carbon: Phosphorus ratio on the production of *Paramecium bursaria Chlorella Virus-1*. Freshwater Biology 52:112–122.

Copeland, J. K., L. Yuan, M. Layeghifard, P. W. Wang, and D. S. Guttman. 2015. Seasonal community succession of the phyllosphere microbiome. Molecular Plant-Microbe Interactions 28:274–285.

Cottenie, K., E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: Regional vs. local processes in highly interconnected ponds. Ecology 84:991–1000.

Del Grosso, S., W. Parton, T. Stohlgren, D. L. Zheng, D. Bachelet, S. Prince, K. Hibbard, and R. Olson. 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89:2117–2126.

DiBaise, J. K., H. Zhang, M. D. Crowell, R. Krajmalnik-Brown, G. A. Decker, and B. E. Rittmann. 2008. Gut microbiota and its possible relationship with obesity. Mayo Clinic Proceedings 83:460–469.

Duffy, J. E., P. L. Reynolds, C. Boström, J. A. Coyer, M. Cusson, S. Donadi, et al. 2015. Biodiversity mediates top–down control in eelgrass ecosystems: A global comparative-experimental approach. Ecology Letters 18:696–705.

Dybas, C. 2011. NSF grants foster understanding of biological systems on regional to continental scales. National Science Foundation, Press Release 11-160. Washington, D.C.: National Science Foundation.

Ehleringer, J. R., and C. B. Field, eds. 1993. Scaling physiological processes: Leaf to globe. San Diego: Academic Press.

Ellis, E. C., K. K. Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606.

Elser, J. J., W. F. Fagan, A. J. Kerkhoff, N. G. Swenson, and B. J. Enquist. 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytologist 186:593–608.

Fay, P. A., S. M. Prober, W. S. Harpole, J.M.H. Knops, J. D. Bakker, E. T. Borer, et al. 2015. Grassland productivity limited by multiple nutrients. Nature Plants 1:15080.

Fenchel, T., and B. J. Finlay. 2004. The ubiquity of small species: Patterns of local and global diversity. Bioscience 54:777–784.

Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J.A.F. Diniz-Filho, et al. 2009. Spatial species-richness gradients across scales: A meta-analysis. Journal of Biogeography 36:132–147.

Ford, M. 2008. AAAS: Large-scale collaborations in physics. and https://arstechnica.com/science/2008/02/aaas-large-scale-collaborations-in-physics/.

Fraune, S., and T.C.G. Bosch. 2010. Why bacteria matter in animal development and evolution. Bioessays 32:571–580.

Frey, S. D., J. Lee, J. M. Melillo, and J. Six. 2013. The temperature response of soil microbial efficiency and its feedback to climate. Nature Climate Change 3:395–398.

Fukami, T. 2004. Community assembly along a species pool gradient: Implications for multiple-scale patterns of species diversity. Population Ecology 46:137–147.

Gill, S. R., M. Pop, R. T. DeBoy, P. B. Eckburg, P. J. Turnbaugh, B. S. Samuel, J. I. Gordon, D. A. Relman, C. M. Fraser-Liggett, and K. E. Nelson. 2006. Metagenomic analysis of the human distal gut microbiome. Science 312:1355–1359.

Goring, S. J., K. C. Weathers, W. K. Dodds, P. A. Soranno, L. C. Sweet, K. S. Cheruvelil, J. S. Kominoski, J. Rüegg, A. M. Thorn, and R. M. Utz. 2014. Improving the culture of interdisciplinary collaboration in ecology by expanding measures of success. Frontiers in Ecology and the Environment 12:39–47.

Guimerà, R., B. Uzzi, J. Spiro, and L.A.N. Amaral. 2005. Team assembly mechanisms determine collaboration network structure and team performance. Science 308: 697–702.

Hampton, S. E., and J. N. Parker. 2011. Collaboration and productivity in scientific synthesis. Bioscience 61:900–910.

Heidorn, P. B. 2008. Shedding light on the dark data in the long tail of science. Library Trends 57:280–299.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Isbell, F., P. B. Reich, D. Tilman, S. E. Hobbie, S. Polasky, and S. Binder. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proceedings of the National Academy of Sciences 110:11911–11916.

Kareiva, P. M. 2011. Natural capital: Theory and practice of mapping ecosystem services. New York: Oxford University Press.

Keesing, F., R. D. Holt, and R. S. Ostfeld. 2006. Effects of species diversity on disease risk. Ecology Letters 9:485–498.

Kiers, E. T., and R. F. Denison. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. Annual Review of Ecology Evolution and Systematics 39:215–236.

Lacroix, C., E. W. Seabloom, and E. T. Borer. 2014. Environmental nutrient supply alters prevalence and weakens competitive interactions among coinfecting viruses. New Phytologist 204:424–433.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Lombardo, M. P. 2008. Access to mutualistic endosymbiotic microbes: An underappreciated benefit of group living. Behavioral Ecology and Sociobiology 62:479–497.

Medina, M., and J. L. Sachs. 2010. Symbiont genomics, our new tangled bank. Genomics 95:129–137.

Melillo, J. M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, and S. Morrisseau. 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298:2173–2176.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Nabout, J. C., M. R. Parreira, F. B. Teresa, F. M. Carneiro, H. F. da Cunha, L. de Souza Ondei, S. S. Caramori, and T. N. Soares. 2015. Publish (in a group) or perish (alone): The trend from single- to multi-authorship in biological papers. Scientometrics 102:357–364.

Nash, K. L., C. R. Allen, D. G. Angeler, C. Barichievy, T. Eason, A. S. Garmestani, et al. 2014. Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology 95:654–667.

Nelson, K. E., G. M. Weinstock, S. K. Highlander, K. C. Worley, H. H. Creasy, J. R. Wortman, et al. 2010. A catalog of reference genomes from the human microbiome. Science 328:994–999.

Peay, K. G., M. I. Bidartondo, and A. E. Arnold. 2010. Not every fungus is everywhere: scaling to the biogeography of fungal-plant interactions across roots, shoots and ecosystems. New Phytologist 185:878–882.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern–process relationships: consequences for system dynamics. Ecosystems 10:790–796.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3–15.

Rockström, J., W. Steffen, K. Noone, A. Persson, F. S. Chapin, E. F. Lambin, et al. 2009. A safe operating space for humanity. Nature 461:472–475.

Rodriguez, R. J., J. F. White, A. E. Arnold, and R. S. Redman. 2009. Fungal endophytes: diversity and functional roles. New Phytologist 182:314–330.

Running, S. W. 2012. A measurable planetary boundary for the biosphere. Science 337:1458–1459.

Schimel, D. S., B. H. Braswell, and W. J. Parton. 1997. Equilibration of the terrestrial water, nitrogen, and carbon cycles. Proceedings of the National Academy of Sciences of the United States of America 94:8280–8283.

Shively, J. M., R. S. English, S. H. Baker, and G. C. Cannon. 2001. Carbon cycling: The prokaryotic contribution. Current Opinion in Microbiology 4:301–306.

Shoo, L. P., and V. V. Ramirez. 2010. Global potential net primary production predicted from vegetation class, precipitation, and temperature: Comment. Ecology 91:921–923.

Smith, V. H., T. P. Jones, and M. S. Smith. 2005. Host nutrition and infectious disease. An ecological view. Frontiers in Ecology and the Environment 3:268–274.

Soranno, P. A., and D. S. Schimel. 2014. Macrosystems ecology: Big data, big ecology. Frontiers in Ecology and the Environment 12:3–3.

Tian, X., and P. Doerner. 2013. Root resource foraging. Does it matter? Frontiers in Plant Science 4:303.

U'Ren, J. M., F. Lutzoni, J. Miadlikowska, and A. E. Arnold. 2010. Community analysis reveals close affinities between endophytic and endolichenic fungi in mosses and lichens. Microbial Ecology 60:340–353.

U'Ren, J. M., F. Lutzoni, J. Miadlikowska, A. Laetsch, and A. E. Arnold. 2012. Host and geographic structure of endophytic and endolichenic fungi at a continental scale. Am. J. Bot., in press.

van der Heijden, M.G.A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle. Sources and consequences. Ecological Applications 7:737–750.

Wang, K., and R. E. Dickinson. 2012. A review of global terrestrial evapotranspiration: Observation, modeling, climatology, and climatic variability. Reviews of Geophysics 50.

Weathers, K., P. Hanson, P. Arzberger, J. Brentrup, J. Brookes, C. Carey, et al. 2013. The Global Lake Ecological Observatory Network (GLEON): The evolution of grassroots network science. Limnology and Oceanography Bulletin 22:71–73.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

Williams, J. W., S. T. Jackson, and J. E. Kutzbacht. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738–5742.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Yatsunenko, T., F. E. Rey, M. J. Manary, I. Trehan, M. G. Dominguez-Bello, M. Contreras, et al. 2012. Human gut microbiome viewed across age and geography. Nature 486:222–227.

Zheng, S., H. Ren, W. Li, and Z. Lan. 2012. Scale-dependent effects of grazing on plant C: N: P stoichiometry and linkages to ecosystem functioning in the Inner Mongolia grassland. PLOS One 7:14.

been exposed (Szybalski and Bryson 1952). Cross-resistance is also discussed in the insecticide resistance literature, where arthropods that have coevolved with certain plant defensive chemicals are usually the first to evolve resistance to novel pesticides (Dawkar et al. 2013). For instance, in a common crop pest, the spider mite *Tetranychus urticae*, similar suites of genes are important for coping with natural chemical defenses in tomato plants and for resistance to pesticides (Dermauw et al. 2013). In the ecological and ecotoxicology literature, the concept of multipurpose traits has been termed *cotolerance,* first used when it was observed that grass species adapted to one heavy-metal pollutant were often also tolerant of elevated levels of other metallic elements (Cox and Hutchinson 1979). Most intriguing for multidimensional anthropogenic change, cotolerance may also occur between seemingly disparate types of stressors, but those that share similar mechanisms of damage to organisms. For example, frogs locally adapted to the genotoxic effects of increased ultraviolet type B radiation at higher elevations exhibit increased resistance to polycyclic aromatic hydrocarbons, pollutants that also have genotoxic effects (Marquis et al. 2009). We argue that considering the natural stressors to which organisms are currently adapted may help us predict which species may tolerate novel, anthropogenic stressors in a way that current models may not.

Ramping up existing plastic responses and multipurpose traits represent two areas where extending reaction norms into novel space may result in an adaptive response. However, it is unclear to what extent these responses would result in adaptive plastic responses when considering complex, multidimensional environmental change. Ramping up heat-shock protein response may be adaptive given a simple linear change in temperature. But even for climate change, there are changes in extreme weather events, temperature variability, precipitation, and humidity. At the same time, there are changes on many axes that can be challenging to align in a linear fashion. Organisms are presented with novel toxins, predators, resources, habitat structure, and levels of available nutrients. For such complex landscapes of environmental change, we argue that "developmental selection" forms of plasticity are the most likely to produce adaptive, novel phenotypes.

Developmental Selection and Adaptive Plastic Responses to Novel Environments

A reaction norm approach can be useful for some applications, but it alone fails to capture the underlying developmental mechanism of plasticity, which can have major implications for the likelihood that an adaptive trait develops in a novel environment. Developmental selection is a mechanism of plasticity that involves both variability and refinement within an individual over developmental time (Snell-Rood 2012). In the case of learning and neural development, variability stems from different motor patterns produced in response to various environmental stimuli or on the basis of broad neural projections early in development; reinforcement stems from strengthening or weakening of neural connections that lead to positive or negative consequences, respectively. Similar processes occur in the development of adaptive immunity, from initial variability of B-cell antibodies to reinforcement based on interaction with antigens (Frank 1996). Although developmental selection is best characterized with respect to behavior and immunity, the basic components of the process are present throughout other levels of development (Snell-Rood et al. 2019, Snell-Rood 2012). The development of muscle and bone structure is responsive to mechanical load—in this case, there is spatial selection on cells that tend to experience more force, which may vary depending on the foraging or locomotor behavior of an individual (Adams et al. 2003, Menegaz 2010). Stochasticity in gene expression, coupled with epigenetic mechanisms that are responsive to environmental inputs suggests such mechanisms may even play out at the level of gene expression (Feinberg and Irizarry 2010). Finally, diversity in the microbiome may be selectable within an individual depending on their diet or environmental conditions (Gilbert 2010). It is possible that organisms that rely more on developmental selection at some levels (e.g., morphology), also rely on it at other levels (e.g., behavior, physiology), either because plasticity in one developmental system requires complementary plasticity in other systems, or due to common selective pressures (West-Eberhard 2003).

Forms of plasticity that rely on developmental selection are likely to result in an adaptive response to a novel environment because they involve sampling and selection within an individual. One can think of an individual exploring phenotypic space over developmental time, adopting traits that work particularly well in the local environment. However, the benefits of developmental selection scale directly with the costs, which stem from the sampling process (Frank 1996). Gathering information takes time, energy, and investment in structures to process such information, such as large, energetically expensive brains in the case of learning, or the production of many B cells in the case of acquired immunity. This "cost of being naïve" means that reliance on developmental selection should lead to lengthened developmental time, delays in reproduction, and dependence on greater parental investment to survive this sampling period, thus resulting in lower fecundity. In other words, developmental selection forms of plasticity should shift life histories from fast to slow life histories (Snell-Rood 2012). It is possible that quantifying aspects of an organism's life history might hint at their developmental selection potential, but this is an area in need of more research.

Developmental selection forms of plasticity should be particularly important in considering responses of organisms to novel environments that differ from ancestral environments in a range of different ways. Many of the classic examples of plasticity, such as social insect castes or seasonal polyphenisms, fall into a different category—that of evolved developmental programs, or plastic developmental switches (West-Eberhard 2003). However, these forms of plasticity tend to be specific to the environmental range in which they have evolved. Furthermore, switch mechanisms of plasticity are not conducive to complex landscapes of environmental variation because developmental programs specific to a wide range of environments are vulnerable to relaxed selection (Snell-Rood et al. 2010).

These ideas suggest that different mechanisms of plasticity should have different population-level consequences in the face of environmental change. Developmental selection forms of plasticity should be more likely to result in adaptive responses to novel environments for a significant portion of a population. Other forms of plasticity may be more likely to result in nonadaptive plastic responses in variable directions across a population (Ghalambor et al. 2007). These population-level consequences may generate interactions between different types of plasticity and evolutionary responses to new environments. Developmental selection forms of plasticity should be likely to shift an entire population to a novel selective peak. Models suggest such a shift will reduce selection intensity (Lande 2015), referred to as *behavioral inertia* with respect to plasticity in behavior (Huey et al. 2003). However, these forms of plasticity are extremely costly, which should select for loss of plasticity and the genetic assimilation of the novel phenotype if the novel environment is somewhat stable or can be stabilized through behavioral choices such as habitat preferences (Snell-Rood 2013, Stamps 1995). Because the entire population persists, underlying genetic variation may be maintained, facilitating evolutionary responses. At the same time, because developmental selection forms of plasticity are associated with life-history tradeoffs associated with a slower life history, it is possible that population growth rate may be slower, dampening the evolutionary response to rapid environmental change (Reznick and Ghalambor 2001). For nonadaptive forms of plasticity, where population-level responses are uncorrelated, it is more likely the population will go through a bottleneck, and the exact direction of phenotypic change may be less likely to predict. Regardless, it is clear there are multiple interesting and open questions about how plastic responses will interact with evolutionary responses to novel environments, paving the way for both theoretical and empirical work in the decades to come. Recent models of evolutionary rescue in novel environments have begun to incorporate plasticity, but we suggest that considering the mechanism of plasticity will substantially change the outcome (Ashander et al. 2016, Chevin et al. 2013).

Open Questions

We have suggested that certain forms of plasticity may be more likely to produce adaptive responses to novel environments. However, this is a wide-open area of inquiry. In considering reactions to environmental change along multiple axes, it is clear that adaptive responses will include plasticity in a range of traits (e.g., behavior, physiology), often coupled with traits that work well in a range of environments (multipurpose traits or generalized responses to stress). Can we predict which species are capable of enhanced developmental selection or generalized responses to stress? The costs associated with developmental selection forms of plasticity suggest that species with slower, K-selected life-history traits may be more likely to invest in such plasticity. Interestingly, it has also been suggested that long-lived species would be more likely to have multipurpose traits to cope with changing conditions over their lifetime, such as higher levels of enzymes to cope with oxidative stress (Beckman and Ames 1998). Future work is needed to clarify whether life-history traits would be enough to predict adaptive responses to novel conditions, or whether other traits, such as degree of specialization, might be more accurate.

In considering the costs and tradeoffs associated with plasticity, it's important to note that humans are drastically altering nutrient and resource availability. To what extent does anthropogenic change in nutrient availability interact with plasticity in responses to novel conditions? It is possible that increases in resource availability ameliorate tradeoffs between costly forms of plasticity and life history traits (Snell-Rood et al. 2015), which could explain patterns of plasticity in invasive species relative to non-invaders (Davidson et al. 2001). In this case, regions or species that see greater increases in resource availability may have not only adaptive plastic responses to novel environments, but also population-level evolutionary responses as tradeoffs with fecundity are minimized.

If plasticity plays an important role in survival in novel environments, to what extent will diversification in such environments be biased by existing developmental programs? Will the mechanisms of plasticity provide the axes upon which genetic divergence proceeds? Although some evidence suggests that diversification may be biased along axes of adaptive plasticity (Pfennig 2010, Parsons et al. 2016), other recent research calls into question the directionality of this change (Ghalambor et al. 2015). This underscores the importance of considering both adaptive and nonadaptive plasticity when evaluating the potential drivers of genetic change in novel environments.

There has been increasing interest over the last decade in understanding the role of plasticity in responses to rapid environmental change. However, the complexity of such environmental change demands a consideration of the types of plasticity that are likely to produce adaptive responses to novel environments. In the coming decades, advances in techniques that can be used to quantify and manipulate developmental mechanisms will no doubt help clarify the extent to which developmental selection, and associated life-history tradeoffs, are indeed important players in this equation.

References

Adams, C. E., C. Woltering, and G. Alexander. 2003. Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus*. Biological Journal of the Linnean Society 78(1):43–49.

Araujo, M. B., A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93(7):1527–1539.

Ashander, J., L. M. Chevin, and M. L. Baskett. 2016. Predicting evolutionary rescue via evolving plasticity in stochastic environments. Proceedings of the Royal Society B: Biological Sciences 283(1839):20161690.

Beckman, K. B., and B. N. Ames. 1998. The free radical theory of aging matures. Physiological Reviews 78(2):547–581.

Chevin, L. M., R. Gallet, R Gomulkiewicz, R. D. Holt, and S. Fellous. 2013. Phenotypic plasticity in evolutionary rescue experiments. Philosophical Transactions of the Royal Society B: Biological Sciences 368(1610):20120089.

Chevin, L. M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. Plos Biology 8(4):8.

Cox, R. M., and T. C. Hutchinson. 1979. Metal co-tolerances in the grass *Deschampsia cespitosa*. Nature 279(5710):231–233.

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14(4):419–431.

Dawkar, V. V., Y. R. Chikate, P. R. Lomate, B. B. Dholakia, V. S. Gupta, and A. P. Giri. 2013. Molecular insights into resistance mechanisms of lepidopteran insect pests against toxicants. Journal of Proteome Research 12(11):4727–4737.

Dermauw, W., N. Wybouw, S. Rombauts, B. Menten, J. Vontas, M. Grbic, R. M. Clark, R. Feyereisen, and T. Van Leeuwen. 2013. A link between host plant adaptation and pesticide resistance in the polyphagous spider mite *Tetranychus urticae*. Proceedings of the National Academy of Sciences of the United States of America. 110(2):E113–E122.

Feder, M. E., and G. E. Hoffmann. 1999. Heat-shock proteins, molecular chaperones, and the stress response: Evolutionary and ecological physiology. Annual Review of Physiology 61:243–282.

Feinberg, A., and R. A. Irizarry. 2010. Stochastic epigenetic variation as a driving force of development, evolutionary adaptation, and disease. Proceedings of the National Academy of Sciences of the United States of America 107:1757–1764.

Foden, W. B., S. H. M. Butchart, S. N. Stuart, J.-C. Vie, H. R. Akcakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, L. Cao, et al. 2013. Identifying the world's most cli-

Variance-Explicit Ecology

A Call for Holistic Study of the Consequences of Variability at Multiple Scales

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Variability or heterogeneity is everywhere in ecology and evolution. For instance, Levins (1968) introduces his classic work “Evolution in Changing Environments: Some Theoretical Explorations” as “a series of explorations . . . around the common theme of the consequences of environmental heterogeneity.” We have many reasons for studying variability at different levels, including within-individual variation through time or in modular organisms (e.g., tree branches); among or across individual variation in genetics or traits (including behaviors) within a population, guild, community, or ecosystem; or as environmental (e.g., meteorological, hydrological, limnological, oceanographic) drivers of processes of interest. Yet, ecologists most frequently manipulate the mean value of a driving variable of interest and look at its ecological effects and ignore variation in that driving variable or process of interest. For instance, we might rear an insect or plant at three average temperatures and then use analysis of variance to compare individual growth rates at these temperatures but overlook variation in temperature over time and its effects on growth rate. Most frequently, patterns of spatial or temporal variation in either biotic or abiotic factors are used to make inferences about underlying mechanisms (e.g., using geostatistical techniques, Rossi et al. 1992 or using power law plots, Taylor 1961). Variation may even be treated as an annoyance, requiring larger sample sizes to achieve statistical power or as unexplained variation for things that are stochastic or where mechanisms are not understood. As we aim to illustrate, although we have frameworks and sometimes good knowledge about direct effects of single forms of variation, we frequently miss important questions and opportunities about the mechanisms involved, how multiple forms and scales of variation combine, and effects across organizational levels.

A major unsolved problem in ecology is resolving the relative importance between different types and scales of variability to ecological processes.

Organisms experience and respond to variation at many different biological and ecological levels, ranging from physiological to behavioral to populations and communities, and eventually to metapopulations, metacommunities, and geographic ranges. We will argue that certain forms of variation have been quite well studied, but that we lack research programs that might provide information about the relative importance of different mechanisms and interactions among them. Investigating these gaps might provide a mechanistic framework for how to understand how different forms of variation combine to affect ecological problems. A variety of general questions follow from our line of reasoning. What is the relative importance of different mechanisms by which variability influences ecology and what is the relative importance of variability at different scales? At what scales is variability averaged over so that it does not matter? At what scales does variability most influence ecology and how does it do so?

There have been several calls for more explicit consideration of the consequences of variability in ecology, either limited to particular mechanisms by which variation acts (e.g., through nonlinear averaging, Ruel and Ayres 1999), or effects on particular levels of ecological organization (e.g., Bolnick et al. 2011). There are a growing number of studies that do just that, but most are restricted to one scale and type of variability. Moreover, most studies either focus solely on one mechanism or ignore mechanisms altogether and instead just measure the net effect of variation. An example of a kind of problem that ecologists have worked extensively on and for which we have a relatively good understanding of the role of variation is the literature linking plant diversity with plant yield (biomass production). Most of this literature indicates that increasing functional trait diversity (variability) in plant communities leads to increased plant biomass and greater overall resource utilization (e.g., Cardinale et al. 2006). This positive effect on biomass comes partly from a sampling effect and more substantially through niche complementarity and/or positive interspecific interactions (van Ruijven and Berendse 2005). Moving beyond plants, there is less understanding of the effects of plant trait diversity on higher trophic levels (e.g., Ruel and Ayres 1999, Benedetti-Cecchi 2000). A recent meta-analysis that we took part in suggests there could be relatively consistent negative effects of (within-species) variation in plant nutritional quality traits on average herbivore performance through Jensen's Inequality (Wetzel et al. 2016). Considering predators and herbivores, Mason et al. (2014) suggested that some generalist herbivores perform better feeding on a diversity of resources and that this may affect higher trophic levels; Arctiid caterpillars (*Grammia incorrupta*) were well defended against predators when they sequestered secondary metabolites from several different plant species but poorly defended when they sequestered compounds from only one plant species. Overall, such studies show that for certain problems we understand some mechanisms by which a particular form of variation acts on processes of interest. Equally well, the effects of certain forms of individual variation in altering population dynamics have been widely studied (e.g., Grimm 1999), as have several other problems relating variation to processes within a single species or trophic level in ecology and evolution. There has been less work exploring how variation among multiple trophic levels combines to affect herbivore performance. For instance, how does variation in herbivore traits relate to variation in plant traits to affect herbivore performance (Moreira et al. 2016)?

To describe the background and elements required to proceed towards an integration of scales and types of variation and mechanisms by which variation acts, we present the following: (1) An overview of scales and types of biotic and abiotic variation by describing three frameworks for classifying them. (2) A summary of common mechanisms by which variation influences ecological dynamics. (3) A description of what might be gained by integrating different types and scales of variation. (4) We conclude by highlighting some next steps that could move us towards a conceptual framework for how organisms integrate multiple types and scales of variation.

Ways of Classifying Scales and Types of Variation

The literature describes a range of ways of classifying variation or that can be borrowed from classifications of other ecological patterns. We present three such classifications, one based on the structure of environmental variation, a second recognizing the hierarchical nature of biological or ecological organization, and a general scheme that might be applied to any type of variation.

Environmental Variation

Environmental variation is most commonly viewed as the physical, chemical, and geological factors that are largely independent of biotic factors at least over the time scales of most concern to ecologists; such factors were termed *scenopoetic* in an ecological niche context by Soberón and Arroyo-Peña (2017). Such environmental variation merits separate consideration from biotic variation because it has its own scaling and structure, occurring continuously from microscopic to global scales. For example, temperature varies temporally at a scale of minutes as clouds pass in front of the sun, at a scale of hours as the sun rises, peaks, and sets; at a scale of months as the seasons progress; at scales of years to decades (sunspot cycles, el Niño cycles etc.); and at geologic timescales through glacial cycles. Environmental variation may have stochastic and predictable components. Some work also separates recurrent stochastic components from extreme events, including hurricanes, floods, and fires (e.g., Shaffer 1981, Yang et al. 2008, Yang et al. 2010). Temporal environmental variation is often somewhat cyclical and predictable, as exemplified by daily temperature cycles, seasonal variation, and sunspot cycles. Spatial variation often increases with distance. For instance, Bell et al. (1993) studied variation in physical variables in lakes or soil nutrients from a variety of geographic areas and found that, in general, environmental variation continued to increase with spatial scale of study (distance). The scaling of different environmental factors with distance or with time has been used to identify relevant processes in studies of scaling (Levin 1992, Storch et al. 2007). Denny (2015) describes how to use principles from engineering and physics to understand both physical environment interactions and subsequent species interactions through what he terms “ecological mechanics.”

The extent to which environmental (and biotic) variation is encountered by an organism depends on its scale of movement, longevity, and life cycle. Within life cycles, periods of dormancy versus intense resource use are particularly relevant. Spatial and temporal variation are both potentially relevant in several ways. McPeek and Kalisz (1998) modeled the effect of spatial, temporal, and spatiotemporal variation on the evolution of dormancy versus dispersal, finding that pure temporal variation promotes dormancy and that spatial and spatiotemporal variation promote dispersal. Cyclical seasonal migration of North American and European passerine birds is known to be a response to extreme temperatures (Newton and Dale 1996a, 1996b), whereas Australian butterflies respond to extreme dry conditions (Dingle et al. 2001).

In some cases, biotic factors may interact with abiotic factors, and even then, it may be a valid simplification to separately consider abiotic environmental factors if we are studying processes that operate at very different timescales relative to the rate of change of environmental factors through biotic–abiotic coupling (e.g., many ecosystem processes). However, if we were studying long-term tree growth, then a feedback between habitat fragmentation and microclimate might be relevant (e.g., Laurance and Williamson 2001); for long-lived perennial grasses mineral nutrients in soils may depend on grazing history (e.g., McNaughton et al. 1997). For such processes it would make sense to instead think about how to combine different forms of biotic and abiotic variation into analyses.

Biotic Variation

Biotic variation in traits relevant to ecological interactions occurs from subindividual to between individuals within a species or across species. Raw genetic and somatic variation within individuals (or part of them), expressed as traits including behaviors that vary in timing and sequence, may relate to subspecific (e.g., races, morphs) variation, other taxonomic levels, and to higher organizational levels within ecology, paleobiology, biogeography, and other biological sciences. A brief tour of relevant levels of biotic organization helps to identify some of the things that each level contributes or emphasizes. Of course, lower-level variation is included in higher organizational levels but may or may not have effects on higher-level processes. For instance, there is a growing literature on community and ecosystem genetics that investigates the effects of genotype on processes from communities to ecosystems (Whitham et al. 2003).

At the level of within-individual variation, individual organisms frequently respond in plastic ways to ambient environmental and biotic conditions, including behaviors, physiological acclimation, developmental flexibility, life-historical changes in timing, and as ecological engineers (Jones et al. 1997). Critically, such plasticity changes both variability encountered and the relationship between this variability and emergent or higher-level processes performed by the organism. Although there is a great deal of literature on behavioral plasticity, developmental plasticity, life histories, and related subjects, it is unusual for studies to make links to emergent higher-level processes of interest. Beyond plasticity, individual history may produce changes in organisms. A plant phenotype might vary through time depending on the history of herbivory and plant responses to herbivory through inducible defenses (Adler and Karban 1994, Karban and Baldwin 1997). Individual history of infection may alter the susceptibility to the same or new diseases in the future in ways that are either positive or negative. Carryover effects from one habitat to another may produce a relevance of spatial history (e.g., Talley et al. 2006), and there are several named temporal carryover effects (e.g., maternal effects) that produce time-lagged responses (e.g., Ratikainen et al. 2008). Organisms with repeating structures, such as plants with multiple leaves and reproductive organs, may produce especially high variation among organs within individuals (Herrera 2009).

Variability among individuals within a population is recognized as intraspecific trait variation (e.g., Bolnick et al. 2011), arising through phenotypic plasticity, genetic diversity (Hughes et al. 2008), and ontogeny, including life histories and history more generally. Just as species may have different population dynamics, or serve different roles in communities or ecosystems, the same is true of individuals with different traits within a species. Intraspecific variation has been a recent focus of study in ecology (e.g., reviews by Hughes et al. 2008, Bolnick et al. 2011), yet as far back as the 1970s Lomnicki (1978) pointed out that population regulation could not occur if all individuals within a population were identical. Recent synthetic analyses indicate that approximately 30% to 50% of additively, synergistically, or antagonistically. Ideas about resonance emphasize that processes acting at different temporal or spatial frequencies may amplify or cancel out variation (e.g., Blarer and Doebeli 1999). Such ideas are interesting and poorly explored given that both individual growth and population growth have associated timescales, and that density-dependent functions produce characteristic return times for populations returning to an equilibrium (e.g., Luckinbill and Fenton 1978). Nonlinear equations have the ability to amplify variation, as is emphasized in the literature on chaotic dynamics (e.g., Hastings et al. 1993); viz., small amounts of variation in initial conditions can lead to large differences in the emergent (population) dynamics. The approach led Hastings et al. (1993) to ask questions about nonlinear dynamics, such as what are the respective roles of endogenous and exogenous factors, and do they interact? More generally, determining the role of variation in an input variable on a process of interest requires us to determine if the dynamics are nonlinear or not.

Another important effect of nonlinearity of functions is how variation in an input variable affects the average value of the output variable, our process of interest. Jensen's Inequality describes the role of nonlinearity in altering the output from a mathematical function (reviewed by Ruel and Ayres 1999). Variation in an input variable to a function that is concave down will reduce the average value that is given by the function relative to a linear function, and a convex function does the opposite. Sibly et al. (2005) found that most population time series produced nonlinear and concave curves for per-capita growth as a function of population size (or density); consequently, variation in population density reduces average population size below the equilibrium abundance (carrying capacity). (The statistics of Sibly et al. were criticized in several published comments but the general point about the shape of functions and effect of variation is well illustrated by the example.) Nonlinear or nonmonotonic functions are common in ecology and arise through a variety of mechanisms, as reviewed by Zhang et al. (2015). Mechanisms leading to nonlinearity include the law of tolerance, whereby species underperform with either too little or too much of a required ecological factor (Shelford 1931), through the action of adaptive behaviors or physiological adaptation altering relationships between environmental factors and organismal responses, or by sequentially combining multiple synergistic (or antagonistic) factors so as to produce nonlinear outcomes (Zhang et al. 2015). The strong role of nonlinearity leads us to question whether we should be using general mechanistic functional forms for particular problems (e.g., functional responses of predators to prey, or allometric equations), or whether we should use more flexible functional forms to represent arbitrary forms of nonlinearity (e.g., cubic splines (Schluter 1988), or response surface methodologies (Inouye 2005)). Nonmechanistic statistical equations can still be used to infer things like the size of a Jensen effect or whether environmental variation as an input is amplified or damped down in the output from the mathematical function of interest. In some cases, nonlinear averaging may serve as a null model to predict the expected effect (Koussoroplis et al. 2017). For instance, Pearse et al. (2018) looked at how experimental variance in the concentration of a plant toxin in artificial diet altered herbivore performance and found that nonlinear averaging predicted toxin variance would enhance performance, whereas the observed effect was negative. The authors hypothesized that the costs of physiological acclimation in the face of trait variance (Wetzel and Thaler 2016) explained the difference between the predicted and observed results.

Mechanisms Involving Biology and Ecology

Physiological Responses and Consequences

When individuals directly encounter biotic or abiotic variability within their lifetime and are unable to use behavioral mechanisms to avoid it, it is likely to have important physiological consequences. Variability is especially important for organismal physiology because when it is high it encompasses extreme values, which is when physiological stress is expected to be greatest and the consequences of not dealing with conditions may be most harmful. This occurs because relationships between environmental variables and organismal performance tend to be concave-down over large environmental ranges as expressed by Shelford's law of tolerance (1932); the general mechanism behind this is Jensen's Inequality (or nonlinear averaging), discussed previously.

The physiological responses of consumers to diet species diversity–trait diversity at the guild or community level—are especially well studied. It was long believed that diverse diets helped consumers achieve balanced nutrient intake and diluted the effects of toxic defenses associated with any one prey species (Bernays et al. 1994). A recent meta-analysis, however, indicates that mixed-species diets tend to be no better for consumers than the best single-species diet, and they are typically worse than the best single-species diet when diet species possess chemical defenses (Lefcheck et al. 2013). This suggests that consumers facing greater diet variability may experience reduced physiological performance (Wetzel and Thaler 2018). It is often not clear how to view heterogeneity within diets. For instance, Marzetz et al. (2017) show that the chemical composition of algal species as food are more important to growth rates of *Daphnia* than are the algal species' identities or diversity. One general way forward may be to use colimitation theory to integrate several physical and/or biotic factors into a single unified conceptual framework that incorporates potential nonlinearities that arise in a multivariate context, but which are not apparent when factors are considered unidimensionally (Koussoroplis et al. 2017).

Organisms can have important physiological adaptations that help them cope with variability. These take the form of physiological plasticity, which allows organisms to change their physiology to maximize performance under current conditions, or fixed phenotypes that are useful for coping with variable environments. Examples of plastic responses to variability include insect herbivores that reshape their digestive chemistry in response to changing plant conditions (e.g., Bolter and Jongsma 1995), and tadpoles, which change gut size in response to predation risk and food availability (Relyea and Auld 2004). If phenotypic alterations of this nature are costly, which they certainly are for insect herbivores acclimating to plant conditions, then high variability could lead to costly repeated acclimation (Wetzel and Thaler 2016). Rather than changing physiology to match current biotic and abiotic conditions, some organisms pay a permanent cost to be constantly ready for changing conditions. For example, 38 predatory fish species maintained gut sizes two- to three-fold larger than necessary for the average amount of prey they encountered; this allowed them to be ready to process rare pulses of high food abundance (Armstrong and Schindler 2011).

Behavioral Responses and Consequences

Movement, activity patterns and resource selection are major ways that organisms modulate the amount and type of abiotic and biotic variability that they experience. We often think about resource selection as having the goal of getting an organism to resources of a certain quality or quantity, but resource selection is likely to be vital for coping with variability in resource quality and quantity. Optimality theory suggests a wide range of ways organisms reduce costs, such as decisions when to leave patches in response to declining food quality (from the marginal value theorem) (MacArthur and Pianka 1966; Charnov 1976), or when to consume less-profitable food items (from optimal diet theory) (e.g. Emlen 1966). Game theory shows how such decisions can be contingent on other individuals if an organism is maximizing resource intake (or some other currency). Similarly, habitat selection behavior modifies the environmental variation that an organism experiences (e.g., Morris 2003). These central ideas in behavioral ecology alter the relationship between variability encountered and a fitness-related output. Of course, for real organisms the ability of such behaviors to reduce variability between input and output has its limits. For instance, Sih and Christensen (2003) identified conditions such as prey mobility that prevented predators from foraging optimally, and which may therefore lead to a more direct relationship between prey variation and variation in food intake.

Extreme variation may also be coupled with unusual and interesting behaviors. Nomadism is thought to arise in response to extremes of spatiotemporal variation in resource availability or environmental conditions. For instance, desert locust outbreaks track spatiotemporally variable rainfall and subsequent periods of plant germination and growth (Jonzén et al. 2011). Environmental variation that is novel to an organism may also produce different ecological effects to that which is routinely encountered. Hence, Sih and colleagues coined the term human-induced rapid environmental change (HIREC) to draw attention to anthropogenic changes that place organisms under conditions (e.g., population) the species has not experienced before and may produce either individual- or population-level responses (Robertson et al. 2013).

Population and Community Responses and Consequences

Population and community responses to variation are numerous. Various mechanisms for the consequences of and responses to trait variation were reviewed by Bolnick et al. (2011) and serve as a starting point: (1) diversification of species interactions, such as increased generalism, through traits affecting the kinds of interactions and with which other individuals or species focal individuals interact; (2) a portfolio effect produced by covariation among individuals with different traits; (3) phenotypic subsidy whereby genetic variation or plasticity decouple phenotype and fitness; (4) trait variation as a source of adaptive variation in rapid evolution; and (5) sampling effects whereby small populations contain only a small number of traits. Population ecologists often relate variation to extinction risk through population viability analyses and decompose mechanisms into those involving demographic and environmental stochasticity, or more extreme catastrophes (Shaffer 1981). At a multispecies level there is a large body of research on indirect interactions that are trait- or density-mediated (e.g. Bolker et al. 2003), indirect effects (e.g., Menge 1995), and positive versus negative species interactions (e.g., Tylianakis et al. 2008). All the above serve as potential mechanisms for how interspecific variation modifies processes of interest. Surprisingly little empirical work has evaluated the mechanisms described by Bolker et al. (2003) and their relative importance.

Metapopulation and Metacommunity Responses and Consequences

Source–sink dynamics (Pulliam 1988) and habitat-specific demography recognize that habitat areas have heterogeneous effects on population dynamics. Similarly, species sorting and mass effects ideas from metacommunity theory do the same for whole communities (Leibold et al. 2004). Rescue and mass effects across space alter the ability of species to cope with low-quality habitats (Pulliam 1988; Leibold et al. 2004). Most frequently, such ideas are applied to constant habitat heterogeneity, but we can also view habitats as changing, as captured by ideas about source–sink inversions (e.g., Boughton 1999) or temporally autocorrelated environmental conditions (Gonzalez and Holt 2002). Local adaptation may drive whether populations are sources or sinks and modify source–sink dynamics (e.g. Dias 1999), or metacommunity dynamics (Urban et al. 2008).

The Motivation for Integrating Different Forms of Variation and Processes of Interest

As outlined in the introduction, although the effects of variation in some processes have been quite well studied, three related problems have been poorly explored: (1) consideration of multiple forms of variation, (2) consideration of variation at multiple scales, and (3) the relative importance of different mechanisms by which variation influences ecology. Nor are interactions among types of variability usually a subject of study. Consider a focal herbivore species feeding on a single species of plant and which is fed on by a specialist predator. This scenario includes variation in the physical environment and that which arises from variation within, and emergence of, variation across three interacting species or trophic levels. Variation in the physical environment might (for example) include spatial variation in mineral nutrients, water availability, and climatic variation at multiple space and time scales that can act on any species. A natural question is what forms of physical variation affect each species? To what extent does plasticity of any kind reduce the relationship between variation in a physical variable and processes of interest in each species? Or conversely do some forms of physical variation actually lead to increased variation in the process of interest? Does individual variation produce different outcomes of the process of interest, and is the net effect to dampen or enhance variation in the process of interest? The answers to such questions mean that we should also be interested in what the biological and ecological mechanisms are, and what kinds of mathematical functions can be used to represent them. Species interactions could also dampen (filter) or amplify variation in traits of one species in their population dynamics or other processes in which the species participates. Again the ecological and biological mechanisms and functional forms are of interest.

Individuals experience variance in abiotic and biotic conditions within their lifetime, and simultaneously the population encompassing those individuals' experiences interindividual variability, and again simultaneously populations within a metapopulation experience landscape-level variability. It is well established that variability on one scale matters for adjacent scales. An unresolved question is if variability matters for more

Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A multitrait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology 24:1192–1201.

Armstrong, J. B., and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature 476:84–87.

Bell, G., M. J. Lechowicz, A. Appenzeller, M. Chandler, E. DeBlois, L. Jackson, B. Mackenzie, R. Perziosi, M. Schallenberg, and N. Tinker. 1993. The spatial structure of the physical environment. Oecologia 96:114–121.

Benedetti-Cecchi, L. 2000. Variance in ecological consumer–resource interactions. Nature 407:370–374.

Bernays, E. A., K. L. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: Tests of two hypotheses. Ecology 75:1997–2006.

Blair, G. R., D. E. Rogers, and T. P. Quinn. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Transactions of the American Fisheries Society 122:550–559.

Blarer, A., and M. Doebeli. 1999. Resonance effects and outbreaks in ecological time series. Ecology Letters 2:167–177.

Bolker, B., M. Holyoak, V. Krivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V.H.W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Bolter, C. J., and M. A. Jongsma. 1995. Colorado potato beetles (*Leptinotarsa decemlineata*) adapt to proteinase inhibitors induced in potato leaves by methyl jasmonate. Journal of Insect Physiology 41:1071–1078.

Cardinale, B. J., D. S. Srivastava, J. Emmett Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Chesson, P. 2012. Scale transition theory: Its aims, motivations and predictions. Ecological Complexity 10:52–68.

Cook-Patton, S.C., S. H. McArt, A. L. Parachnowitsch, J. S. Thaler, and A. A. Agrawal. 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. Ecology 92:915–923.

Crutsinger, G. M. 2015. A community genetics perspective: Opportunities for the coming decade. New Phytologist 210:65–70.

Denny, M. 2015. Ecological mechanics: Principles of life's physical interactions. Princeton, N.J.: Princeton University Press.

Denny, M., L. Benedetti-Cecchi. 2012. Scaling up in ecology: mechanistic approaches. Annual Review of Ecology, Evolution, and Systematics 43:1–22.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326–330.

Dingle, H., W. A. Rochester, and M. P. Zalucki. 2000. Relationships among climate, latitude and migration: Australian butterflies are not temperate-zone birds. Oecologia 124:196–207.

Emlen, J. M. 1966. The role of time and energy in food preferences. American Naturalist, 100:611–617.

Gonzalez, A., and R. D. Holt. 2002. The inflationary effects of environmental fluctuations in source-sink systems. Proceedings of the National Academy of Sciences of the United States of America 99:14872.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? Ecological Modelling 115:129–148.

Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H.C.J. Godfray. 1993. Chaos in ecology: Is Mother Nature a strange attractor? In: D. G. Fautin, eds. Annual Review of Ecology and Systematics, Vol. 24. Palo Alto: Annual Reviews, 1–33.

Herrera, C. M. 2009. Multiplicity in unity: Plant subindividual variation & interactions with animals. Chicago: University of Chicago Press.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Inouye, B. D. 2005. The importance of the variance around the mean effect size of ecological processes: comment. Ecology 86:262–265.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Jonzén, N., E. Knudsen, R. D. Holt, and B. E. Sæther. 2011. Uncertainty and predictability: The niches of migrants and nomads. In: E. J. Milner-Gulland, J. M. Fryxell, A. and R. E. Sinclair, eds. Animal migration: A synthesis. Oxford: Oxford University Press.

Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. Chicago: University of Chicago Press.

Kendall, B. E., C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet, and S. N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. Ecology 80:1789–1805.

Koussoroplis, A.-M., S. Pincebourde, and A. Wacker. 2017. Understanding and predicting physiological performance of organisms in fluctuating and multifactorial environments. Ecological Monographs 87:178–197.

Laurance, W. F., and G. B. Williamson. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the amazon. Conservation Biology 15:1529–1535.

Lefcheck, J. S., M. A. Whalen, T. M. Davenport, J. P. Stone, and J. E. Duffy. 2013. Physiological effects of diet mixing on consumer fitness: A meta-analysis. Ecology 94:565–572.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The MacArthur award lecture. Ecology 73:1943–1967.

Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton, N.J.: Princeton University Press.

Lomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. Journal of Animal Ecology 47:461–475.

Luckinbill, L. S., and M. M. Fenton. 1978. Regulation and environmental variability in experimental populations of protozoa. Ecology 59:1271–1276.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603–609.

Marzetz, V., A.-M. Koussoroplis, D. Martin-Creuzburg, M. Striebel, and A. Wacker. 2017. Linking primary producer diversity and food quality effects on herbivores: A biochemical perspective. Scientific Reports 7:11035. http://doi.org/10.1038/s41598-017-11183-3.

Mason, P., M. Bernardo, and M. Singer. 2014. A mixed diet of toxic plants enables increased feeding and anti-predator defense by an insect herbivore. Oecologia 176:477–486.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–1800.

McPeek, M. A., and S. Kalisz. 1998. On the joint evolution of dispersal and dormancy in metapopulations. Advances in Limnology 52:33–51.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

Messier, J., B. J. McGill, M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters 13:838–848.

Moreira, X., L. Abdala-Roberts, B. Castagneyrol, K. A. Mooney. 2016. Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. Current Opinion in Insect Science 14:1–7.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.

Newton, I., and L. C. Dale. 1996a. Bird migration at different latitudes in eastern North America. Auk 113:626–635.

Newton, I., and L. Dale. 1996b. Relationship between migration and latitude among west European Birds. Journal of Animal Ecology 65:137–146.

Orland, M. C. 2003. Scale-dependent interactions between intrinsic and extrinsic processes reduce variability in protist populations. Ecology Letters 6:716–720.

Pearse, I. S., R. Paul, P. J. Ode. 2018. Variation in plant defense suppresses herbivore performance. Current Biology 28:1981–1986.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ratikainen, I. I., J. A. Gill, T. G. Gunnarsson, W. J. Sutherland, H. Kokko. 2008. When density dependence is not instantaneous: theoretical developments and management implications. Ecology Letters 11:184–198.

Relyea, R. A., and J. R. Auld. 2004. Having the guts to compete: how intestinal plasticity explains costs of inducible defences. Ecology Letters 7:869–875.

Robertson, B. A., J. S. Rehage, and A. Sih. 2013. Ecological novelty and the emergence of evolutionary traps. Trends in Ecology and Evolution 28:552–560.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependences. Ecological Monographs 62:277–314.

Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology and Evolution 14:361–366.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience 31:131–134.

Shelford, V. E. 1931. Some concepts of bioecology. Ecology 12:455–467.

Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. Science 309:607–610.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Sih, A., and B. Christensen. 2001. Optimal diet theory: When does it work, and when and why does it fail? Animal Behaviour 61:379–390.

Soberón, J., and B. Arroyo-Peña, B. 2017. Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. PLOS One 12:e0175138. doi: https://doi.org/10.1371/journal.pone.0175138.

Storch, D., P. A. Marquet, and J. H. Brown. 2007. Introduction: Scaling biodiversity—what is the problem? In: D. Storch, P. A. Marquet, and J. H. Brown, eds. Scaling biodiversity. Cambridge: Cambridge University Press.

Talley, T. S. 2007. Which spatial heterogeneity framework? Consequences for conclusions about patchy population distributions. Ecology 88:1476–1489.

Talley, D. M., G. R. Huxel, and M. Holyoak. 2006. Connectivity at the land-water interface. In: K. Crooks and M. Sanjayan, eds. Connectivity conservation. Cambridge: Cambridge University Press.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732–735.

Tobler, W. R. 1970. A computer movie simulating urban growth in the Detroit region. Economic Geography 46:234–240.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Underwood, N. 2004. Variance and skew of the distribution of plant quality influence herbivore population dynamics. Ecology 85:686–693.

Underwood, N. 2009. Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect. Journal of Animal Ecology 78:839–847.

Urban, M. C., M. A. Leibold, P. Amarasekare, L. De Meester, R. Gomulkiewicz, M. E. Hochberg, et al. 2008. The evolutionary ecology of metacommunities. Trends in Ecology & Evolution 23:311–317.

van Ruijven, J., and F. Berendse. 2005. Diversity–productivity relationships: initial effects, long-term patterns, and underlying mechanisms. Proceedings of the National Academy of Sciences of the United States of America 102:695–700.

Wetzel, W.C., H. M. Kharouba, M. Robinson, M. Holyoak, and R. Karban. 2016. Variability in plant nutrients reduces insect herbivore performance. Nature 539:425–427.

Wetzel, W. C., and J. S. Thaler. 2016. Does plant trait diversity reduce the ability of herbivores to defend against predators? The plant variability-gut acclimation hypothesis. Current Opinion in Insect Science 14:25–31.

Wetzel, W. C., and J. S. Thaler. 2018. Host-choice reduces, but does not eliminate, the negative effects of a multi-species diet for an herbivorous beetle. Oecologia 186: 483–493.

Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, et al. 2015. Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84:559–573.

Whittle, P. 1956. On the variation of yield variance with plot size. Biometrika 43:337–343.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. Ecological Monographs 80:125–151.

Zhang, Z., C. Yan, C. J. Krebs, and N. C. Stenseth. 2015. Ecological non-monotonicity and its effects on complexity and stability of populations, communities and ecosystems. Ecological Modelling 312:374–384.

Why Does Intragenotypic Variance Persist?

C. Jessica E. Metcalf and Julien F. Ayroles

Evidence for Intragenotypic Variability

Phenotypes vary across traits and species, and it has long been understood that such differences emerge from genetic and environmental variation. However, striking phenotypic differences are also observed among individuals with identical genotypes and that experience identical and constant environments. Such variation is known as intragenotypic variability (*Bradshaw 1965*) and refers to the nongenetic component of phenotypic variance. Note that our focus is specifically on variation evident even in organisms reared in nominally identical environments, and therefore we are explicitly not considering phenotypic plasticity.

Evidence for intragenotypic variability is fairly ubiquitous. In plants, variability in flowering time and germination provide well-studied examples (Bradford 2002). In insects, the fruit fly Drosophila spp. has been a useful model system for titrating the magnitude of intragenotypic variance. For example, by inbred lines, a suite of phenotypic traits can be measured for a large number of individuals within a single genotype in rigorously controlled environmental conditions (Kain et al. 2015). With these techniques, intragenotypic variability has been characterized in bristle number (Mackay and Lyman 2005), sleep (Harbison et al. 2013), thermal or phototactic preference (Kain et al. 2015), and locomotor behavior (Ayroles 2015), to list only a few. One of the key advances that has allowed this progress in characterizing variability is the development of automated instruments that can capture large numbers of phenotypes with high precision and low statistical error (Kain et al. 2015, Ayroles 2015). Using similar techniques, studies of wild isolates of the worm model organism *Caenorhabditis elegans* have, for example, uncovered high intragenotypic variability in lifetime fecundity (Diaz and Viney 2014). Interestingly, this variance is negatively correlated with the mean lifetime fecundity, suggesting a trade-off between these two levels of variation (mean and variance). Beyond model organisms and academic investigations, a large body of work on this topic has been driven by agricultural breeding

Determining that diversifying bet-hedging is occurring may be nontrivial (Simons 2011). Variance in fitness is highly likely to increase within a generation as a result of intragenotypic variability—rather than the reduction expected under bet-hedging. Consequently, multigenerational tests of the effects of phenotypic variation on fitness variance will be necessary to establish that bet-hedging is the driving selective force, as the key point is reduction in the variance *across* generations (Simons 2011). Combining empirical data with mathematical models and simulation has been a core feature of grappling with this challenge (Kain et al. 2015, Gremer and Venable 2014, Metcalf et al. 2008, Rees et al. 2006).

Facing Competitors: Game Theory, Adaptive Dynamics

A key feature of the environment of most individuals is the presence of other individuals in the population, their phenotypes, and their absolute or relative abundances. Where frequency or density dependence is operating, the success of a phenotype will be predicated on what other individuals are doing. If similarity of phenotypes results in increased competition, and thus reduced fitness, this can result in selection for intragenotypic variability among offspring (Metcalf et al. 2015), an effect that might be further amplified by variation in the environment. In this case, variable phenotypes represent unexploited strategies (von Neumann and Morgenstern 1944). An example might be phenological traits, such as timing of germination within the year. If all individuals germinate at once, this will maximize competition, and selection is expected to favor individuals who produce offspring with a distribution of germination times. Although some of the offspring will be germinating in suboptimal conditions in terms of the abiotic environment (e.g., too dry or too wet), these will also be conditions that feature fewer competitors, and thus might be associated with higher fitness. Under a simple model of phenology in an annual plant under competition for recruitment microsites, the convergent stable strategy (i.e., one that can invade all other strategies and cannot be invaded by any strategy) can be shown to reflect a degree of variance under a range of different contexts (Metcalf et al. 2015), indicative of selection for intragenotypic variance.

Understanding the fitness consequences of phenotypic variability is generally challenging. In a comprehensive set of simulations, Bruijning et al. (2020) investigated such consequences under a range of commonly encountered relationships between traits, fitness, and environmental conditions and showed that, especially under fluctuating environments, there can be clear fitness advantages of maintaining intragenotypic variability.

As for bet-hedging, theoretical approaches are key to characterizing the conditions in which competition may lead to the expression of alternative phenotypes, in this case building on evolutionary game theory. However, unlike bet-hedging, generation of hypotheses about the role of competition in maintaining phenotypic variability linked to specific systems, and formal tests with empirical data, remain rare.

Probing the Adaptive Basis of Intragenotypic Variance

Tests Using Experimental Evolution

A major barrier to investigation into the fitness consequences of intragenotypic variability has long been the necessity of characterizing the phenotypes of many individuals across a population, to appropriately characterize variance, often a nontrivial task. Further, for bet-hedging scenarios, experiments must feature multiple generations under different scales of environmental fluctuations. Given these challenges, experimental evolution (Fuller et al. 2005) can be a powerful approach to testing hypotheses about the nature of the forces maintaining variable levels of phenotypic variability, offering both experimental flexibility and the opportunity to pair experiments with modeling. Although measuring the ultimate phenotype of interest (i.e., fitness) remains challenging, as it requires characterizing both survival and fertility of each individual, a number of life-history traits known to be highly correlated with fitness can be measured and manipulated. Examples of such experiments aimed at testing bet-hedging strategies remain rare, but the emergence of novel technologies (Ayroles 2015) allowing automation of phenotype characterization opens the way to a series of experimental tests of the adaptive basis of intragenotypic variation. This has been particularly true for microbial systems (Kawecki et al. 2012), where, for example, *de novo* evolution of bet-hedging traits has been demonstrated in bacteria, and the nuances of the context specificity of this evolution has been described (Beaumont et al. 2009).

An experimental evolutionary assay of the role of competition in selecting for intragenotypic variance will necessarily feature some form of resource limitation. For example, the outcome of competition between individuals and populations featuring differential levels of heritable variance could be characterized. If intragenotypic variability increases fitness in competitive settings, we expect that genotypes encoding higher variability will spread within experimental populations. More complex outcomes, including evolutionary branching, are also possible, and, as noted previously, experiments paired with theoretical models are likely to be an important driver of progress in understanding the underlying selec-