











ANNUAL MEETING

When the window is a mirror: how do dominant theories limit our understanding of nature? (ESA 2023 INS23)

Anita Simha^{1*} , Aubrie James^{2*} , Julia D. Monk³ , Heng-Xing Zou⁴ , Po-Ju Ke⁵ ,
Alexandra Wright⁶ , Malyon D. Bimler⁷, Christopher M. Moore⁸ , Suzanne Pierre⁹ ,
Lauren N. Carley¹⁰ , and Gaurav Kandlikar¹¹ 

¹Department of Biology, Duke University, 130 Science Dr, Durham, North Carolina 27710, USA

²Program in Art, Culture, and Technology, Massachusetts Institute of Technology, 77 Massachusetts Ave, Cambridge, Massachusetts 02139, USA

³Department of Environmental Science, Policy, and Management, University of California Berkeley, 130 Hilgard Way, Berkeley, California 94720, USA

⁴Department of BioSciences, Rice University, 6100 Main St, Houston, Texas 77005, USA

⁵Institute of Ecology and Evolutionary Biology, National Taiwan University, No.1, Sec. 4, Roosevelt Road, Taipei 106319 Taiwan

⁶Department of Biological Sciences, California State University Los Angeles, 5151 State University Dr, Los Angeles, California 90032, USA

⁷School of BioSciences, University of Melbourne, Parkville, Victoria 3052, Australia

⁸Department of Biology, Colby College, 4000 Mayflower Hill, Waterville, Maine 04901, USA

⁹Critical Ecology Lab c/o Inquiring Systems Inc, 887 Sonoma Ave #23, Santa Rosa, California 95404, USA

¹⁰Department of Plant and Microbial Biology, University of Minnesota Twin Cities, 1479 Gortner Ave, Minneapolis, Minnesota 55108, USA

¹¹Department of Biological Sciences, Louisiana State University, 202 Life Science Bldg, Baton Rouge, Louisiana 70803, USA

**These authors co-first authors. In our zealous desire for familiar models of explanation, we risk not noticing the discrepancies between our own predispositions and the range of possibilities inherent in natural phenomena. In short, we risk imposing on nature the very stories we like to hear. Evelyn Fox Keller, 1985 Reflections on Gender and Science*

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Why this session?

The narratives and metaphors that ecologists use to describe natural phenomena influence what we study and how we do it (Larson 2011, Craver and Darden 2013, Otto and Rosales 2020). Stories about ecological processes and patterns are told through particular frames and are laden with assumptions arising from their framing. For example, the tubercle bacillus became the cause of tuberculosis, rather than unregulated industrial capitalism, through storytelling: the framing of the story was biomedical, and as a result the assumption for how to treat tuberculosis was through individual medical intervention, rather than (for example) a social revolution (Levins and Lewontin 1985). More recently, a commonly cited solution to rising CO₂ emissions is to plant trees, which conveniently elides the social and economic roots of global warming.

The responsible use of particular frames, narratives, and analogies for understanding nature requires that we reflect on our choices: Which stories do we tell? How do we tell them? And how do they structure the way we study the natural world? To make room for this kind of reflection, we organized and participated in an Inspire session entitled “When the window is a mirror: how do dominant theories limit our understanding of nature?” at the ESA 2023 meeting. This session was an attempt to explore the limitations of current theory and their consequences for understanding what we observe in the natural world. In a set of case studies, we examined existing “mirrors”: examples in which ecological models are built on assumptions that constrain the research process, and in doing so reveal something about ourselves and the narratives we privilege.

Our speakers described the limits of theory on topics ranging from sexual behavior to plant–microbe interactions to genetic polymorphism. This allowed us to look for uniting themes across subdisciplines of ecology. In bringing these subdisciplines together, we attempted to highlight such limitations not as isolated exceptions, but rather as recurring consequences of singular, dominant ways of approaching ecological questions. Our session emphasized the importance of creativity and wonderment in scientific research and the power of pluralistic approaches for confronting theoretical limitations brought on by societal assumptions.

Case studies

Julia D. Monk. Reframing the lenses through which we study same-sex sexual behavior

Same-sex sexual behavior (SSB) is widespread throughout the animal kingdom. For years, Western scientists ignored, downplayed, or discounted this behavior as a costly aberration. More recent work, including our own, has recognized that SSB is not only common but may have a long evolutionary history and need not incur fitness costs (Monk et al. 2019, Lerch and Servedio 2021, Richardson and Zuk 2023). As recognition of the scope of SSB among animals has grown in both scientific understanding and popular culture, many have questioned what these insights mean for our understanding of human sexuality; does the fact that animals engage in SSB make it “natural”? Demonstrating the diversity of sexual systems and sexual behaviors found in nature is undoubtedly vital for increasing feelings of belonging among queer students and researchers in the sciences (Casper et al. 2022). However, our reframing of the study of SSB in animals shows us how what we understand to be “natural” in the first place is inevitably shaped by the cultures, norms, and values

that scientists ourselves hold. We argue that there is great danger in positioning what is deemed “objectively natural” as the arbiter of what is culturally normative, moral, or appropriate. Instead, as scientists we should aim to interrogate and articulate our values and politics, and think critically about how they inform our decisions; what questions we ask, hypotheses we make, methods we use, results and voices we uplift, and interpretations we favor. It is important to study and share the extraordinary sexual diversity found among nonhuman species, and indeed to combat narratives that aim to simplify the public’s understanding of biological sex and sexual behavior. However, we should be clear that queer and trans identities are valid no matter the science on animal behavior and sexual evolution, and that acceptance of human diversity should not be predicated on our constantly shifting understanding of the “natural” world.

Heng-Xing Zou. It's about time: Bridging theory and practice of priority effects

The temporal order and interval of community assembly can often affect how species interact. Generally defined as “priority effect,” this phenomenon interested both empiricists and theoreticians (Fukami 2015). However, our theories are often limited in their ability to characterize priority effects in nature because they do not incorporate two principles about time. First, ecological communities operate on a range of time scales. Priority effects influence communities of organisms ranging from bacteria and yeast to plant and amphibian communities. The vast differences in life history among these communities may imply distinctive underlying biological mechanisms for priority effects in each community. Second, all ecological processes take time; therefore, changes in species interactions should depend on the length of the difference in arrival times, which can determine their relative sizes or the degree of habitat modification (Rudolf 2019). These features are not well incorporated into theoretical explanations of priority effects, which are often based on positive frequency dependence: if both species limit the other more than themselves, the more abundant species wins (Ke and Letten 2018). This conception is detached from the two principles about time because the early species is not necessarily more abundant in communities with slow-reproducing species, and this theory does not allow for temporal changes in species interactions. To bridge theory and experiments of priority effects, we define those arising from positive frequency dependence as “frequency-dependent” priority effects, and those arising from temporal changes in species interactions as “trait-dependent” priority effects, because they are usually caused by changes in traits over arrival times, such as size, age, or behavior (Zou and Rudolf 2023). This categorization accommodates diverse biological mechanisms in nature, including interactions beyond competition that change with time. Models of priority effects should be designed with the two principles about time in mind to capture different ecosystems more accurately.

Po-Ju Ke. Exploring the temporal dimensions of plant–soil microbe interactions

Plant communities are shaped by their bidirectional interactions with beneficial and detrimental soil microbes (van der Putten et al. 2013). To predict the long-term consequences of plant–soil microbe interactions, ecologists often employ a two-phased experiment inspired by the theory of plant–soil feedback (Bever et al. 1997). The classic experimental design consists of a conditioning phase, during which plants modify the soil community, and a subsequent response phase, during which plants respond to the modification. However, like theoretical models, experiments are also an abstraction of nature. Specifically, by immediately transplanting the responding seedling after soil conditioning, experiments

implicitly assume that new plants immediately arrive or that the conditioned microbial legacies are long-lasting after the death of the host plant. Nevertheless, recent research has shown that this assumption may not hold in various systems, such as those characterized by distinct seasonality or frequent disturbance (Nagendra and Peterson 2016, Esch and Kobe 2021). Neglecting the temporal decay of microbial legacies in these systems can lead to incorrect predictions of plant competitive outcomes or an overestimation of microbial impact (Ke et al. 2021). Therefore, while the common two-phased design aims for generality, it is crucial to consider the natural history of different systems when extrapolating experimental results to a natural context (Travis 2020).

Sasha Wright. Interdependence is common: Living plants affect microclimates

Plants have the capacity to change the climate around them (Lembrechts 2023, Novick and Barnes 2023). In particular, plants open their stomata to photosynthesize and consequently move water out of the soil and into the air around their leaves. This cools and humidifies microclimates and macroclimates. Grasses can do this at small scales (Wright et al. 2021), while tropical forest trees can drive climatic changes at the scale of entire regions (Wright et al. 2017). Initial attempts to quantify the effect of vegetation on climate have focused on understory temperatures (e.g. Lembrechts 2023), which are locally correlated with relative humidity and vapor pressure deficit. These attempts have shown that every type of vegetation on earth can either cool or warm the microclimate (warming is most common in cold biomes where vegetation can insulate and create areas of warmer air). These changes in microclimate conditions affect performance of plants (Aguirre et al. 2021), plant trait expression (Watson et al. 2023), plant–plant interaction strengths (Wright et al. 2014), and productivity (Aguirre et al. 2021). Because vegetation-induced temperature, humidity, and vapor pressure deficit changes are ubiquitous and inevitable, I think it is important to reimagine a world where all other types of interactions (including competition) are nested within these constructed microclimates.

Malyon Bimler. Must all plants compete? Evidence of self-facilitation challenges our understanding of how plant diversity is maintained in complex systems

Plants compete for resources, and in a purely competitive world diversity is maintained by intraspecific competition: a plant species must compete with itself more strongly than with other species to ensure coexistence. Intraspecific competition has become so central to our understanding of plant diversity that it is standard procedure to set all plant interactions as competitive when simulating plant communities or parameterizing population and species distribution models. While we know that plants are also capable of intraspecific facilitation, these beneficial interactions are rarely accounted for in frameworks of diversity maintenance, and certainly not in predictions of coexistence. In this talk, I present extensive evidence of intraspecific facilitation in a diverse, natural plant system when relaxing the above restrictions on models and parameterizations. We found that intraspecific facilitation varied idiosyncratically across species and environmental conditions, indicating it is not simply an isolated exception, but rather a pervasive force shaping community diversity. Current theoretical frameworks do not allow coexistence when intraspecific facilitation is operating, despite empirical evidence to the contrary. Competitive theories of diversity maintenance can therefore describe certain conditions under which coexistence should arise but clearly do not capture the full spectrum of conditions under which coexistence can arise. Current theory is thus

neither exhaustive nor should it be limiting. Creating novel theory which better reflects what we observe in nature requires us to be inspired by the unexpected rather than blinded to it.

Christopher Moore. The need to re-source the way we think about resources in mutualism

Dominant theories of population ecology limit our understanding of the population ecology of mutualism. For nearly a half century we have seen marginalization of the theoretical study of mutualism through explicit dismissal (“... unlike trophic interactions, mutualisms do not seem to be of universal importance,” Turchin (2013)) and self-admonishing “laziness” (May 1981). But this systemic underrepresentation of mutualism relative to other interspecific interactions like competition and predation is most clearly observed through quantitative analysis of books Simha et al. (2022) and primary literature (Bronstein 1994, Raerinne 2020). Recently, however, mutualism has been viewed and modeled as a consumer–resource interaction (e.g., Holland et al. 2005), which has been incredibly important and useful theoretically (e.g., De Mazancourt and Schwartz 2010, Holland and DeAngelis 2010) and empirically (e.g., Lim et al. 2018). Although framing mutualism as a consumer–resource interaction helps it fit within the dominant theoretical framework, and provides some mathematical conveniences (i.e., to “put a curve on it” in order to prevent unbounded growth, and because a Type I functional response can be recovered by a Type II response by setting a parameter to 0), I wanted to draw attention to the idea that not all mutualisms can or should be described by this framework. Conceptually there are some issues for the most common and ecologically important mutualisms like pollination, seed dispersal, and defense where half of the entire interaction is not a consumer–resource interaction. For example, Revilla (2015) asked, “... what is the handling time of a plant that uses a pollinator or seed disperser? Or at which rate does a plant attack a service?” I also presented unpublished data showing that the Holling type II numerical and functional responses do not seem to be common across empirical studies of mutualism: most seem to be unimodal. Mutualistic interactions are wonderfully diverse and essential parts of communities and ecosystems. Although many mutualisms fit within the dominant consumer–resource theory, I ask that we continue to better understand mutualisms by not assuming they are fully explained as a consumer–resource interaction and embracing and marveling in their diversity and complexity.

Suzanne Pierre. Geology and greed: Long- and short-term drivers of plant community assemblage

The distributions of parent materials, topography, and latitude, as well as disturbance history and the presence of nearby islands, are important drivers of island biodiversity dynamics (Brandeis et al. 2009, Carstensen et al. 2012, Whittaker et al. 2017). These conditions have also been influential in the process of European colonization of Caribbean islands due to their influence on island suitability for colonial extraction (Parsons 1975, Watts 1990, Mahony and Endfield 2018). Suitability for plantation colonialism may include potential landscape productivity (e.g. latitude, mean annual temperature, mean annual precipitation, and altitude), resources to support long-term intensive monocropping (e.g., groundwater availability), and sufficient resources to manage large enslaved populations (Ross 2017). The biogeographical determinants of European plantation colonization and consequences for island biogeography following sustained plantation disturbances remain largely unaddressed in terrestrial ecology. Through a field study on the former Danish colony of St. Croix (U.S. Virgin Islands), my colleagues and I aim to test whether the aforementioned state factors predict the intensity of colonial ecosystem disturbance (proxied by duration of colonization, cultivated

area, primary crops, and cumulative enslaved populations from Danish archival records). Our work uses interdisciplinary methods to describe how the relationship between state factors and degree of colonization may be predictive of the reassembly of forest vegetation communities following the abandonment of sugarcane plantation fields. We hypothesize that post-plantation soil environments are physically disturbed and nutrient-limited due to long-term agricultural degradation. On post-plantation islands like St. Croix, the relative abundance taxa with functional traits that can alleviate resource limitations (e.g., leguminous, C4 photosynthetic, and arbuscular mycorrhizal taxa (Dovrat et al. 2020)) may vary along axes of former plantation intensity and state factors which are known to present the greatest utility for colonial exploitation (i.e., greatest contiguous area of alluvial soils, highest annual precipitation, dominant calcareous parent material, etc.). As we scale our field-based, island-specific work up to larger spatial scales, we ultimately aim to interrogate ahistorical notions of the biogeographic drivers of twentieth-century and present-day forest vegetation community structure and function within the footprint of European plantation colonialism.

Lauren Carley. The “puzzle” of polymorphism: An evolutionary ecologist’s perspective

In Simha et al. (2022), we describe a “diversity paradox” in community ecology: multispecies communities are ubiquitous in nature, although many classical approaches to ecological modeling suggest that species “should” not coexist except under special conditions. I argue that a parallel framework exists in evolutionary biology and population genetics, framing the persistence of polymorphism despite the action of natural selection as a surprising occurrence that warrants special explanation.

While classical theory expects commonly studied forms of natural selection like directional and stabilizing selection to reduce genetic variation over time (Falconer 1996), many biological processes can complicate these predictions. For example, pleiotropy, plasticity, epistasis, and demographic compensation can all complicate the mapping of genetic variation onto fitness. Similarly, geographic variation in drivers of natural selection and interactions between multiple drivers can complicate inference about responses to selection made using static estimates of selection coefficients. Finally, balancing selection can also maintain rather than deplete natural variation (Hedrick 2006, Mitchell-Olds et al. 2007). Nevertheless, predictions concerning diversifying forms of natural selection are less commonly made, and tested, when framing research about genetic polymorphism.

Our work illustrates how complicating phenomena influence the evolution of genetic and phenotypic variation across the landscape. Focusing on just one polymorphism in one study species, we found that the genes controlling variation in plant secondary chemistry have pleiotropic effects on drought tolerance and anti-herbivore defense. We also found that there is plasticity in the mapping of variation in chemical biosynthesis genes onto fitness, that the magnitude and direction of selection exerted by herbivory and drought vary across fitness components, and that the net effects of these selective drivers are interactive, varying in complex ways at small spatial scales (Carley and Morris, unpublished data). Ultimately, secondary metabolites experience balancing selection that maintains variation; there is no single optimum genotype or phenotype that is consistently favored (Carley and Mitchell-Olds 2021). This work demonstrates that real-world conditions driving selection and adaptation may frequently violate simple model assumptions, and that explicit study of “complicating factors” may often be necessary for understanding intraspecific genetic and phenotypic variation.

Gaurav Kandlikar. *What we talk about when we teach about models*

If we are to move our discipline to confront the limitations of our conceptual frameworks, we should rethink the way we teach ecology. I advanced this thesis with a reading of Jorge Luis Borges' short story "Del Rigor en la Ciencia" ("On Exactitude in Science"; Borges 1960). This story tells of a time when cartographers were so obsessed with detail that they "struck a Map of the Empire whose size was that of the Empire, and which coincided point for point with it." In the generations that followed, this obsession with detail vanished, and the unruly map was abandoned to the "Inclemencies of the Sun and Winter." I use this short story to offer three lessons:

1. *Models reflect the cultural zeitgeist.* While we often teach models as objective efforts to make sense of nature, our model frameworks are often influenced by arbitrary and subjective constraints like what tools we have at our disposal, what approaches we find to be "elegant," and what details one generation happens to become obsessed with.
2. *The value of a model lies in its ability to help us navigate complexity.* Ecologists often engage in elaborate mental gymnastics when dominant models don't match what we observe. The story reminds us that when a model has too much detail, too little detail, or any number of other flaws that lead us astray, we shouldn't be afraid to abandon it and move on.
3. *We should embrace diverse source material in our classrooms.* By diverse, I mean that we should look beyond the confines of ecology textbooks and journals to help prepare students to wrestle with conceptual problems. Short stories, poetry, and other media can draw attention to the intentions and impacts of our models in a way that material within the traditional confines of "ecology" does not. By "source material," I mean that we should encourage attempts to engage with material in its original form rather than only in summaries or translations, because often, the source material expresses a degree of nuance and care that gets lost in subsequent versions.

Summary and future directions

Summary of discussion

What we think models capture or portray, an image of what is outside (window) vs some version of ourselves (mirror), is an important aspect of the future of modeling in ecology. During the panel discussion, one question was about the role of mathematical modeling in theory as computational power becomes less limiting. As computational limitations that necessitated simpler mathematical models are dissolved, do general models become obsolete? The example the audience member provided was individual-based models (IBMs), which model individuals to understand the dynamics of populations, as opposed to modeling populations themselves. The implication of this question was that an increasing ability to compute population changes at finer-and-finer resolution is the main goal of modeling, but it's worth asking if this is truly the case. One speaker raised this issue by bringing up the short story "On Exactitude in Science," which warns against the limitations of higher and higher model precision while highlighting the importance of generality in models for making sense of the world around us (Kandlikar). On the other hand, all of the speakers demonstrated how overly general theory has led us astray in making sense of the world around us by collapsing or ignoring important axes of variation. The easy take-home message from our session would be that perhaps we should sacrifice model generality in favor of precision and realism (Levins 1966).

What we propose instead aligns more closely with Levins (1966)'s call for understanding nature through a multiplicity of approaches (see also Odenbaugh 2005). By “embracing and marveling in ... diversity and complexity” (Moore), perhaps we can reframe modeling not as an effort to capture singular, generalizable truths about the natural world, nor to precisely recapitulate the complexity of nature. Instead, we might take advantage of and accept that “all models are wrong” in that each captures both an image of what is outside and some version of ourselves. If all models are simultaneously windows and mirrors, we can become interested in what model diversity reveals about nature (and our relation to it) rather than the pursuit of the grails of generality, precision, and realism.

Another theme that emerged was a discussion about how we can better incorporate the ideas from this session into the way we teach ecology. Do we simply stop teaching ideas and models that have so deeply shaped the discipline, but that seem to reflect assumptions informed by social biases more than nature? Or, if we are not to simply abandon such ideas in the classroom, how can we better convey the sense of uncertainty and contemplation conveyed by the talks in this session? Given the outsized roles that dominant ideas (by definition) play in the historical and contemporary structure of the field, excluding them outright seems unsatisfactory. A more fruitful path forward will be to make space for discussions about the social–historical origins of ideas, their impacts on the field, and their limitations. For example, to help students better understand the history of ideas shaping community ecology, one of the speakers (Wright) introduces students to the terrestrial and theoretical ecology academic family trees (<https://academicfamilytree.org>) to highlight their origins. This helps foster conversations about the cultural forces that determine the path of “foundational” papers, and the privilege that some authors enjoy in their efforts to disseminate their ideas. More generally, incorporating lessons from the history and philosophy of ecology, and from fields like Science & Technology Studies, in traditional “ecology” classrooms will help train ecologists to assess how “mirrors” and “windows” interact to shape our understanding of, and relationship with, nature.

Teaching a wider range of ideas than are emphasized in most ecology texts is also essential. Several speakers highlighted the often-overlooked role of positive interactions within and between species (Wright, Bimler, Moore); more thoroughly introducing students to the diversity and importance of these interactions may ultimately help the field incorporate such interactions into our understanding of ecological communities. The last speaker (Kandlikar) advocated for more fearless experimentation in the classroom. Students' introduction to ecology in the classroom shapes the way they will approach ecological ideas throughout their lives. Embracing uncertainty and intentionally breaking dubious conventions, and sharing with students the rationale for doing so, will be an important step in developing future generations of scientists and thinkers.

Future directions

A unifying takeaway from our session was the importance of historicizing and interrogating assumptions and the narratives that go along with them. For example, the assumption that same-sex sexual behavior in animals incurs a fitness cost and should therefore be rare (discussed by Monk) may stem from Western, Victorian-era values of sexuality. Similarly, early modern sexual values have “haunted” plant biology since Linnaeus (Subramaniam and Bartlett 2023). Even in the current day, narratives of Asian plants' invasion in the United States mirror anti-Asian xenophobia, even when such characterizations belie ecological reality (Cardozo and Subramaniam 2013). We believe that putting assumptions into their historical contexts (for example by using methods suggested by Wright, Taylor (2010)) can empower ecologists to spot potential cases of “double transference” such

as these, when social values are transposed onto nature, deemed natural, and then used to justify existing social orders (Foster et al. 2011).

Drawing from allied disciplines and subdisciplines such as Black ecologies (Hare 1970, Hosbey et al. 2022), queer ecology (Mortimer-Sandilands and Erickson 2010), and Indigenous ecology (Reo and Ogden 2018, Hart-Fredeluces et al. 2021), in addition to cross-disciplinary work with art, history, and philosophy, can inspire new frames and conceptualizations through which to understand nature. Whether simplifying assumptions are maintained by colonial ideologies, historical convention, or sheer convenience, leaving our assumptions unexamined limits our understanding of nature in its expansive possibilities. We believe that ecological inquiry will be strengthened by explicit consideration of our simplifying assumptions, and their roots and consequences, as ecological theory unfolds.

Data availability statement

No data were collected for this study.

Reading Recommendations from Participants

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