Model systems in ecology, evolution, and behavior: A call for diversity in our model systems and discipline

Sistemas modelo en ecología, evolución y comportamiento: un llamado a la diversificación de los sistemas modelo, y nuestras disciplinas

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Running head: EEB needs diverse systems and scientists

Keywords: model organisms; biodiversity; diversity in STEM; equity; inclusion; model system

The authors wish to be identified to the reviewers.
This manuscript is submitted as part of the Vice Presidential Symposium.

Manuscript elements: main text, Figure 1 (color), Boxes 1-4, Table S1 (proposed as a supplemental table due to size)

Abstract

Ecologists and evolutionary biologists are fascinated by life's variation, but also seek to understand phenomena and mechanisms that apply broadly across taxa. Model systems can help us extract generalities from amidst all the wondrous diversity, but only if we choose and develop them carefully, use them wisely, and have a range of model systems from which to choose. In this introduction to the Special Feature on Model Systems in Ecology, Evolution, and Behavior, we begin by grappling with the question, "what *is* a model system?" We then explore where our model systems come from, in terms of the skills and other attributes required to develop them, and the historical biases that influence traditional model systems in EEB. We emphasize the importance of communities of scientists in the success of model systems — narrow scientific communities can restrict the model organisms themselves. We also consider how our discipline was built around one type of "model scientist" — a history still reflected in the field. This lack of diversity in EEB is unjust, and also narrows the field's perspective, including by restricting the questions asked and talents used to answer them. Increasing diversity, equity, and inclusion will require acting at many levels, including structural changes. Diversity in EEB, both in model systems and the scientists who use them, strengthens our discipline.

Resumen

Ecólogos y biólogos evolutivos han mostrado una profunda fascinación por la gran variación en formas de vida, y al mismo tiempo se han esforzado en entender fenómenos y mecanismos generalizables a todos los organismos. El uso de organismos modelo ayuda a abstraer generalidades de esta diversidad compleja y maravillosa. Estas generalizaciones serán posibles solamente si seleccionamos un rango amplio de sistemas modelos, y los desarrollamos cuidadosa y sabiamente. En la introducción de esta edición especial sobre *Sistemas Modelo en Ecología, Evolución y Comportamiento* (EEC), primero nos preguntamos, *¿qué es un sistema modelo?* Luego exploramos el origen de estos sistemas, las técnicas, atributos y recursos requeridos para su desarrollo, y los sesgos históricos que han influenciado el uso de un número limitado de sistemas modelo en EEC. Enfatizamos la importancia de las comunidades científicas para el

éxito de los organismos modelo — comunidades restringidas pueden limitar las posibilidades de los organismos modelo. También discutimos cómo la investigación usando estos modelos se ha construido alrededor de arquetipos sociales, que han definido quien es (o no) el "modelo de un científico" – un sesgo histórico que aún se refleja en nuestras disciplinas e instituciones. Esta carencia de diversidad en EEC es injusta, y promueve una perspectiva miopica, que limita las preguntas y el talento en la comunidad científica. Aumentar la diversidad, igualdad e inclusión requiere acciones a muchos niveles, incluyendo cambios estructurales en nuestras instituciones. Este es un llamado a incrementar la diversidad en ecología, evolución y comportamiento. Tanto con el establecimiento de nuevos sistemas modelo, como con la inclusión y participación de grupos diversos de científicos. Solo así podremos fortalecer nuestras disciplinas.

I. Introduction

"What is true for E. coli *is true for the Elephant"* - *J. Monod.*
"But not for Salmonella*"* - *E. Groisman*
- Burton, Aisha, Twitter post, 14 January 2021, 9:48 a.m.

As scientists studying ecology, evolutionary biology, and behavior, we love, celebrate, and are captivated by life's diversity — those "endless forms most beautiful", as Charles Darwin famously framed it. At the same time, we seek to understand how the natural world works — to identify general phenomena and the mechanisms driving them. Indeed, the American Society of Naturalists has identified "conceptual unification of the biological sciences" as its purpose. Thus, ecologists and evolutionary biologists face a challenge: extracting general principles and mechanisms from amidst all the wonderful diversity surrounding us (Kokko 2020). We aim to see the forest *and* the trees.

Model systems can help us meet this conceptual-unification-despite-abundant-diversity challenge (Kokko 2020), but only if we choose (and develop) our model systems carefully, use them wisely, and have a range of model systems from which to choose. Despite what Jacques Monod claimed, what is true for *Escherichia coli* is *not* necessarily true for the elephant. Indeed, even if we consider things at a narrower scale, mice, zebra fish, *C. elegans*, and fruit flies can't represent all animals, *Arabidopsis* can't represent all plants, and *E. coli* and *Saccharomyces cerevisiae* can't represent all microbes.

The choice of study organism (or system), and its match to the question under study, is critical to our science (Travis 2006). Researchers consider a myriad of factors when choosing a study organism (Dietrich et al. 2020). Choice of study organism is often influenced by tractability (Krogh 1929; Green et al. 2018), and also reflects the impact of access, resources, and economies (Burian 1993; Dietrich et al. 2020) — which means there are biases in our current model systems, as we discuss more below. Study organisms are also chosen because they might enable comparisons to other organisms, which can reveal general phenomena and processes (Burian

1993; Travis 2006; Dietrich et al. 2020). The knowledge we collectively build reflects thousands of individual decisions regarding which systems should be used to study which questions (Travis 2006); however, these decisions are not fully independent but, rather, influenced by social networks, prior research, mentoring relationships, and other factors. In the end, "the principles and facts that emerge will only be as reliable as our choices have been wise" (Travis 2006).

Ecologists and evolutionary biologists need a diversity of study systems to achieve our goal of conceptual unification, and we must be thoughtful and creative about how we use and develop those systems. This Special Feature highlights a variety of ways in which model systems are currently being used to address timely and important questions in ecology and evolutionary biology (García-Robledo and Baer 2021; Gordon et al. 2021; Grant et al. 2021; Green 2021; Penczykowski and Sieg 2021; Wale and Duffy 2021). In this introduction, we first seek to define what we mean by the term "model system" (a surprisingly challenging task). Having done that, we then ask where our model systems come from (both in terms of the skills required to develop them or use them in new ways, and in terms of their history and geography), and also consider where model systems research in ecology, evolution, and behavior (EEB) might be heading.

In a manuscript addressing the importance of diversity in ecology and evolutionary biology, it is essential to emphasize that EEB needs diversity not just in terms of what organisms we study, but also in terms of who does those studies. EEB as a field was built around one type of "model scientist" — someone who is white, male, cis-gendered, affluent, not disabled, and without major caregiving responsibilities (to list only a few salient features). Unfortunately, the demographics of our field still reflect those origins (Rushworth et al. 2021), as do science, technology, engineering, and mathematics (STEM) more broadly (McGee 2020). This lack of representation in EEB is a clear moral and ethical issue, which on its own makes this important to address. In addition, as we discuss more below, this lack of diversity narrows the field's perspective and holds back our science. Thus, we also discuss some of the impacts of the lack of diversity in EEB, and cover strategies for achieving a more diverse, equitable, and inclusive discipline. Diverse scientists will yield the diverse model systems and diverse perspectives that EEB needs if we are to meet the challenge of identifying the general principles and mechanisms that generate endless forms most beautiful.

II. What *is* a model system?

"Model organism", "model species", and related terms have been criticized as some of the most overused and under-defined words in life sciences (Katz 2016). It is therefore with some trepidation that we seek to define "model system" for our purposes.

In biomolecular sciences, model organisms are experimental organisms that are studied in the laboratory context as representatives of a broad range of organisms and processes (Jenner and Wills 2007; Ankeny and Leonelli 2011; Leonelli and Ankeny 2013); in biomedical sciences, model organisms are often chosen (and developed) based on similarity to humans. Classical model organisms often exhibit a number of characteristics that make them amenable to laboratory life, including short generation times, small size, and ease of manipulation and measurement, which is why Bolker (1995) argued that “model systems are likely to be peculiar with respect to their own taxa, but relatively consistent with respect to each other.” Biomolecular researchers who work on model organisms tend to share the rationale that despite the (unusual) biological characteristics that make model organisms models, the conclusions one makes from them are generalizable because traits are evolutionarily conserved (Ankeny and Leonelli 2011, 2020), and that understanding core biomolecular phenomena is best achieved by divorcing organisms from their ecological context (Ankeny and Leonelli 2020). The processes used to construct these ‘traditional’ model organisms (including standardization and modes of manipulation), and the scientific culture that surrounds their study, are as much a part of what makes an organism a ‘model’ as are their inherent biological traits (Ankeny and Leonelli 2020).

There are challenges to adopting the biomolecular definition of a “model system” for EEB because our fundamental goal is different. We seek to understand genetic and phenotypic *variation* and how the context in which organisms live modulates this variation. As such, the organism’s environment is a feature of the system that must also be studied (Bartholomew 1966) — some of us would even argue that there is no meaningful organism without its environment (*e.g.*, Lewontin 2001).

Here, we propose the following definition of “model system” for EEB: a species, taxon, community, or ecosystem that has been studied from multiple angles with a goal of developing a deep understanding of that organism (or taxon, community, or ecosystem), in a manner that enables comparisons with other systems to illuminate general ecological, evolutionary, and/or behavioral principles; achieving this will require that the system has been studied long enough for a substantive body of knowledge to have been generated. Model systems are designated as such by the community — a single person cannot decide on their own that something is a model system; crucially, this can lead to gatekeeping and adds to the importance of having diversity in our discipline, as we discuss more in the second half of this paper. Prior discussions of model systems in EEB have contrasted work on “model systems” vs. “natural populations” (Travis 2006). However, the terms “model system” and “natural population” are not mutually exclusive. Rather, we propose that there are multiple axes along which model systems fall (Figure 1). We are in full agreement with Travis (2006) that “Robust inference requires horizontal comparisons and vertical integration” — the first part of our definition is Travis’s “vertical integration” (*i.e.*, the study within a single system of processes at a number of levels of biological organization), and the second part is his “horizontal comparisons” (*i.e.*, when a single question is studied at the same level of biological organization in multiple systems). In our definition, a model system need not necessarily be a single species (or taxon) or a pair of closely interacting species. Moreover, it need not be amenable to laboratory study. Instead, in EEB, certain sites and ecosystems have also emerged as model systems as a result of an extended history of study that has allowed us to generate and test general ecological and evolutionary theory (Table S1, Figure 1). This includes experimental species assemblages, such as the Cedar Creek biodiversity plots; natural tree plots, such as the Forest Census Plot on Barro Colorado Island; and networks of such ecosystems, such as the 72-site Forest Global Earth Observatory (ForestGEO). At a smaller scale, mesocosms and microbial communities and ecosystems have emerged as model systems to study community ecology (Datta et al. 2016; Goldford et al. 2018; Fugère et al. 2020), species interactions (Mickalide and Kuehn 2019), ecosystem processes (de Jesús Astacio et al. 2020), and eco-evolutionary dynamics (Lawrence et al. 2012; Matthews et al. 2016). These types of systems allow us to incorporate ecological context and dynamics while still maintaining tractability (Sanchez et al. 2021). While these types of systems are not part of the traditional definition of "model systems", they can be used to understand particular biomes and general principles at a global scale, and allow us to avoid some of the biases that are associated with more traditional model systems (Bolker 1995; Alfred and Baldwin 2015). Our definition of "model system" is agnostic about the degree to which an organism (or community or ecosystem) is "representative". Any one system will be representative of some aspects of ecology and evolutionary biology, and unusual in others. Research in natural and experimental contexts provides insights into fundamental processes in EEB (Bartholomew 1966), as does work on organisms that are representative and those that are unusual; there can be as much to learn from a system that is an exception to a rule as from one that adheres to it.

Even though variation is a key focus of research in EEB, model systems are generally chosen and constructed in a way in which variation (or its drivers) are restricted or delimited. It is no accident that the ecosystems that have emerged as model systems are often delimited places such as islands or field plots; this isolation limits the contribution of "undesirable" variation or noise. Similarly, when the model system is an organism rather than an ecosystem, we tend to select organisms that we can standardize and isolate, such as by growing them in the lab (Table S1, Figure 1). For this reason, model systems in EEB share some of the (biased) biological traits of model organisms in the biomolecular sciences that make them intrinsically tractable, such as ease of husbandry in laboratory conditions, fast generation times, and traits that are easily quantified (such as external color variation).

After defining what is a model system, it's worth considering what is *not* a model system. Systems that do not yet have the technology and knowledge base to allow for horizontal and vertical integration are not model systems. Sometimes, this is due to a lack of research on a particular system. Other times, this is because aspects of the system (*e.g.*, life history traits) pose challenges, especially given current institutional structures. While people have sometimes found creative solutions to working on such systems (*e.g.*, with periodical cicadas (Yang 2004)), current tenure review processes and models for funding graduate students can make it challenging to work on longer lived organisms or on longer term phenomena (Box 1).

Importantly, something that is a model system for one subarea of EEB is not necessarily a model system for all model areas (though certainly particular systems can be models for multiple areas). By our definition, systems can move from non-model to model status once a sufficient knowledge base has been developed and recognized by the community; systems cannot move from model to non-model status, though certain model systems may fall out of favor or stop being the subject of study due to other concerns (*e.g.*, biosecurity; Wale and Duffy 2021).

As model systems become established, a positive feedback loop can kick in where research on the system makes additional research more likely (Matthews and Vosshall 2020). The development of standardized (and shared) knowledge about the system — protocols, natural history knowledge, techniques for quantifying variation, stock lines, mathematical models, etc. — makes these systems more tractable for additional research and facilitates the expansion of work on the system into new subdisciplines and new questions (Box 1). Over time, there is greater vertical integration and more possibilities for horizontal comparison. The interconnection and integration between subdisciplines that arises as a result is a major strength of working with model systems.

At the same time, this expansion of research both through time and across subdisciplines can be particularly susceptible to the propagation of unsupported assumptions and erroneous inferences made early in the study of the system, potentially resulting in substantial bodies of work that rest on shaky foundations. For especially long-studied model systems, some of these decades-old assumptions may be 'signs of the times,' projections of entrenched sociocultural and political values onto the study system that no one thought to question at the time (Haraway 1989, 1991). Regardless of their source, these assumptions and inferences can become embedded into research on the model system and become challenging to escape, even as their impact is magnified throughout the field through horizontal and vertical integration. For example, *Anolis* lizards are a model system for studying convergent evolution and adaptive radiation and have been the subject of research in behavioral and evolutionary ecology for over a century (Losos 2009). This research includes over a hundred papers published on territorial behavior in *Anolis*. Through a comprehensive close-reading to evaluate evidence for territoriality in these papers, Kamath and Losos (2017) revealed that territoriality was assumed rather than tested in the earliest research on anoles, and this early assumption became entrenched in subsequent work in this system, implicitly and explicitly shaping study design, data analysis, the interpretation of results, and publication. While similar assumptions have likely been made in many other taxa described as territorial, their origins and consequences were readily traceable in *Anolis* only because of the long history of research in this model system.

Long-studied model systems can be a compelling context in which to apply methods from the humanities and social sciences to understand scientific practice (*e.g.*, Haraway 1989; Kohler 1994; Rader 2004; Milam 2010). Such work makes explicit the ever-present feedbacks between the questions we scientists ask and the identities, cultures, and sociopolitical contexts we bring to our work. This kind of cross-disciplinary inquiry into model systems can seed ideas for novel conceptual and empirical approaches to long-studied questions in EEB (Kamath and Losos 2018; Kamath and Wesner 2020). Equally, because the assumptions and inferences made early in the study of model systems can be deeply consequential, scientists working to establish new model systems would do well to consider the value of insights from cross-disciplinary inquiry for their work, including through formal collaborations with scholars in the social sciences and humanities who study the human dimensions of scientific practice. In this way, model systems can make room for disciplinary and methodological diversity in our study of the natural world.

III. Our traditional model systems reflect historical biases

Model systems not only allow us to answer scientific questions, but also play an important role in shaping the questions asked (Ankeny 2001; Leonelli 2007). This means that the history that shaped the establishment of our model systems has real effects on our science today and makes it important to consider the biases and historical contingencies associated with their establishment. Particular organisms become model systems not only because of their biology, but also because of a variety of other factors, including the institutional structures that support them. Indeed, whole institutions have been created for the development, domestication, and standardization of traditional model systems and their associated protocols (Burian 1993; Clause 1993; Kohler 1994; Leonelli 2007).

Traditional model systems are generally highly constructed (*e.g.*, genetic lines are carefully bred, standard breeding conditions carefully designed, and unwanted variation selected out). Thomas Hunt Morgan (1866-1945) and his group, for example, developed standardized protocols to grow *Drosophila* (minimizing variation in the expression of phenotypic traits), and made genetic lines enriched for differences in Mendelian inherited traits (Kohler 1994). Similarly, the reference strain of *Saccharomyces cerevisiae* that provided the foundation for early research in this system was generated via lab crosses and selected because it was unusual in that it could be maintained as a haploid, facilitating the study of mutations (Liti 2015). These goals of control and technological development were closely linked to the increasing use of genetics for domestication, and the eugenic desires to control the genetic makeup of domesticated animals, crops, and humans for the “betterment of society” (Bowman and Rebolleda-Gómez 2020).

In addition, because science was dominated by Western scientific institutions, traditional model systems were often chosen because they were easy to access and amenable to study by scientists working at those institutions. *Drosophila*, for example, was chosen as a model system because its phenology made work on it convenient given the academic calendar in the Northern United States; they were most abundant in fruit orchards early in the fall and students could easily breed them indoors during the winter (Kohler 1994). The common house mouse (*Mus musculus*) was common in Europe and the industrialized cities in the U.S., and, in addition, mice were bred by mice fanciers for their rare coat colors and odd behaviors; thus, lines of mice bred for clear phenotypic characteristics were commercially available. At the time when the mouse was becoming a model for the study of genetics, there was a good market for "mouse fancy" in New England that allowed Castle and Little to start their genetic studies in mice with lines from a farm in Massachusetts (Rader 2004).

At the same time as these traditional biomolecular model systems became well-developed, the establishment of modern academic ecology was accompanied by the extensive study and establishment of particular ecological ecosystems as models (for example, work by Henry Cowles (1869-1939) on succession in the Indiana Dunes, research by Raymond Lindeman (1915-1942) in Cedar Bog Lake (part of what is now Cedar Creek Ecosystem Reserve), and work by G. Evelyn Hutchinson (1903-1991) on Linsley pond (Golley 1993)). Over time, there was a growing awareness of the geographical biases in where ecological research was being performed and a desire to do more systematic research in the tropics (Richards 1963). One consequence of this was that the number of field stations rapidly increased (Tydecks et al. 2016), but in a way that was uneven and that still reflected ease of access by researchers from the United States. This contributed to the substantial overrepresentation (given their size) of research done in Panama and Costa Rica (Stocks et al. 2008; Martin et al. 2012). The uneven establishment of field stations in the tropics was strongly impacted by the geopolitical context (Box 2). Despite efforts to expand the geographic range of research in EEB, most of the research published in the major ecological journals is still based on sites in Europe and in the United States (Martin et al. 2012).

It is clear that there are strong historical and systemic biases impacting the classic model systems in EEB, as well as clear gaps in our existing model systems (Box 3, Table S1). Recently, there has been a push to expand and diversify the use of models, by including more female animals in biomedical studies (Shansky 2019), including more phylogenetic diversity around well studied model organisms and traits of interest (Jenner and Wills 2007), and adding more ecological complexity in our systems (Rillig and Antonovics 2019; Sanchez et al. 2021). Filling the gaps in existing model systems will also require a concerted effort by researchers and funding agencies to invest in the resources (including establishing strain databases, molecular toolkits, computational software) and studies of natural history that facilitate research using emerging model systems (Matthews and Vosshall 2020; Box 1).

Overall, model systems emerge from the community, as a result of countless decisions made by individual scientists (including early career scientists; Box 4), with a strong influence of our institutional cultures. Increasing buy-in from the community is often beneficial for the model system (and the scientists whose careers are tied to these models), but these communities can also serve as gate-keepers. Therefore, in addition to focusing on diversity of our model systems, we must focus on diversity and inclusion in our discipline. Indeed, when new model systems are built with intention, this can be a mechanism for increasing diversity and inclusion in EEB (Box 4).

IV. EEB needs diverse scientists

STEM disciplines were designed for one particular type of person — white men who are cis-gendered, heterosexual, not disabled, and from relatively affluent backgrounds (McGee 2020). EEB as a discipline was also designed for this type of person and, like STEM more broadly has been — and still is — inhospitable to people who do not fit that mold (Valantine et al. 2016; Graves 2019; Kaishian and Djoulakian 2020; McGee 2020; Montgomery 2020*a*; Wanelik et al. 2020). This is especially true for scientists who hold multiple minoritized identities (Ireland et al. 2018). It is important to note that, despite these barriers, scientists from underrepresented groups have long made contributions to EEB (Bronstein and Bolnick 2018; Mackay et al. 2019; Jaffe et al. 2020; Lee 2020).

While we would benefit from more comprehensive data, it is clear that the demographics of EEB still reflects these origins and this exclusion. To give some examples: according to the US National Science Foundation's Survey of Earned Doctorates, 387 US citizens and permanent residents earned PhDs in ecology in 2019; 192 earned PhDs in evolutionary biology (National Center for Science and Engineering Statistics (NCSES) 2019). 322 of those who earned PhDs in ecology were White and not Hispanic or Latino (~83% of the total); the comparable number for evolutionary biology was 146 (~76% of the total). Only eight (1.4%) PhD recipients in ecology and evolutionary biology in 2019 were Black, and only one (0.2%) was Native American (NCSES 2019). In New Zealand, Māori and Pasifika are severely underrepresented at the faculty level at universities and crown-research institutes, with little progress over a decade (McAllister et al. 2020). Survey responses from attendees at the Evolution 2019 meeting indicated that the representation of women drops with career stage, as does representation of LGBTQ+ scientists (Rushworth et al. 2021); consistent with this, women scientists tend to have shorter publishing careers (Huang et al. 2020). An analysis of top-publishing authors in ecology, evolution, and conservation found that only 11% are women, and that ten countries from the Global North (inclusive of Australia) account for 86% of top-publishing authors (Maas et al. 2021). There is also strong geographic bias in the composition of editorial boards in ecology, evolutionary biology, and closely related fields; an analysis of the editorial boards of 20 leading conservation biology journals revealed that they had few or no editors from regions with the most biodiversity (Campos-Arceiz et al. 2018). Unfortunately, it is clear that our field is still far from being diverse, equitable, and inclusive.

The lack of diversity in EEB holds back our science (Ireland et al. 2018; Duc Bo Massey et al. 2021). People with different backgrounds and lived experiences will approach science differently, asking different questions and pursuing different lines of research (Keller 1982; Stewart and Valian 2018; Duc Bo Massey et al. 2021). The science we do — the questions we ask and how we pursue answers — are influenced by our identities and by the social and political context in which we were raised (Keller 1982; Harding 1986; Wall Kimmerer 2013; Duc Bo Massey et al. 2021). Because gatekeepers often share many of the identities and backgrounds with the traditional “model scientist”, many scientists who did not fit that mold were told that the questions they asked were “not science” (Keller 1982; Haraway 1989; Wall Kimmerer 2013), and surely many more who were told this were driven away from science. This is a problem from a justice perspective, and it also means that science suffers. Students from underrepresented groups are more innovative than majority students, though unfortunately their innovations and contributions tend not to be recognized and appreciated (Hofstra et al. 2020). Moreover, for teams working together on a project, diverse groups outperform homogeneous ones (Hong and Page 2004) — a result that parallels findings in non-human communities (Tilman et al. 2001). Model systems research will benefit greatly from a more diverse community of researchers.

More importantly, the lack of diversity in EEB (and STEM more broadly) is a moral and ethical issue. While there are clear arguments that science benefits from diversity (as discussed above), scientists from underrepresented groups should have the same opportunities to do science and these opportunities should not rest on appeals to exceptionalism or benefits to science. Everyone should have an opportunity to do science.

V. Increasing diversity, equity, and inclusion in EEB will require acting at many levels, including making structural and institutional changes

“If there is one loud and clear message from the research literature on workplace diversity, it is that multiple, interacting, nested levels of context matter.”

— (Bond and Haynes 2014)

Increasing diversity in EEB, and creating a discipline that is inclusive of people of all backgrounds and identities, requires a focus on institutional structures and gatekeepers (McGee 2020). Many efforts to increase diversity in STEM disciplines focus on individual students, especially on preparing these students (which often translates into attempts to “fix” or assimilate students from underrepresented groups; Bowman and Rebolleda-Gómez 2020; Halsey et al. 2020; McGee 2020; Schell et al. 2020). Alternatively, conversations focus on the changes that will come as more diverse early career scholars to progress through the academic ranks, ignoring that this is not a simple issue of demography (Holman et al. 2018). Instead of viewing the lack of diversity through the problematic “pipeline” metaphor (Cannady et al. 2014; McGee 2020), we must focus on changing structures, including focusing on how racism (and other “isms”) within a department and institution underlie the lack of diversity (McGee 2020). If organisms that we study fail to grow or thrive in an environment, we consider what aspects of the environment might be causing that outcome (Montgomery 2020*a*, 2020*b*); it is essential that we do the same with marginalized and minoritized scientists, and that we work to change our institutions (including our departments and scientific societies) so that they are inclusive and enable scientists who are outside the traditional "model scientist" mold to thrive (McGee 2020; Montgomery 2020*a*, 2020*b*).

One major challenge in EEB relates to who has access to research opportunities; at present, such opportunities are often inaccessible to individuals who come from socioeconomically disadvantaged backgrounds. A lack of accessibility to field courses and fieldwork can prevent people from entering the field (Beltran et al. 2020; McGill et al. 2021). Moreover, positions where early career scientists, including field and laboratory technicians, are expected to work *pro bono*, or even pay for the experience, excludes research participation by individuals unable to self-fund or work for free, which disproportionately cuts off research opportunities for individuals from underrepresented groups (Fournier and Bond 2015; Emery et al. 2019). Additional challenges include working towards developing an understanding (and respect) for the social, cultural, and environmental experiences shared among individuals belonging to underrepresented groups. Doing so will increase the absent sense of "belonging" for these individuals within EEB and academia and nurture a field wherein one doesn't feel they need to conform to the cultural norms instituted by gatekeepers to ensure successful careers (Duc Bo Massey et al. 2021; McGill et al. 2021).

Social science research demonstrates that organizational-level policies strongly influence the degree to which minoritized groups are fully integrated into that organization and points to changes that can be implemented to increase inclusion (Bond and Haynes 2014). These changes include clearly communicating that behaviors that discriminate against individuals from certain groups will not be tolerated, and clearly indicating that the organization views diversity as an asset that is important to the (shared) mission of the organization and its employees (Bond and Haynes 2014). Moreover, changes need to occur at multiple levels — a person's trajectory in science, and the environment they experience, are influenced by factors at multiple levels (Bond and Haynes 2014; Valantine et al. 2016; Zea and Bowleg 2016). For example, scientists from the Global South face major barriers even as immigrants in Europe, Canada, and the United States. Immigrant scientists and international students from non-privileged backgrounds start their careers abroad at economic disadvantage, as a substantial portion of their income must be invested in fees associated with immigration. In addition to the influences of biased gatekeepers and departmental culture, institutional and federal funding structures make it more expensive for departments to support these students and further restricts access to key fellowships. An important additional consideration in EEB relates to field safety. Certain individuals are at greater risk of harm and conflict when carrying out field work, and faculty, departments, and institutions must help people in their labs evaluate these risks and consider strategies that can help mitigate them (Demery and Pipkin 2021).

Several recent articles highlight specific changes that can be made to promote diversity and inclusion in academia, STEM, and EEB. Some of these are aimed at people in majority groups, and especially at White faculty (Sensoy and DiAngelo 2017; Platt 2020; Schell et al. 2020; Stevens et al. 2021)), while others are aimed at scientists from underrepresented groups (Halsey et al. 2020; Tseng et al. 2020). One common theme is the importance of welcoming scholars from underrepresented groups to bring their authentic selves to their research, rather than expecting them to assimilate to majority cultural norms; as Schell et al. (2020) note, we appreciate and recognize the value of diversity in the ecosystems we study, yet expect homogeneity and assimilation of those carrying out the work. In order for EEB to be truly inclusive — and for our science to benefit from diversity — marginalized voices need to be heard, centered, and amplified.

VI. Diverse scientists will yield diverse model systems and diverse perspectives, improving our understanding of ecology and evolutionary biology

Our understanding of ecology and evolutionary biology is the product of thousands of individual decisions regarding what questions to ask and which systems to study. When those decisions are made by relatively homogenous groups, and when our work focuses on relatively few taxa, the conclusions we draw will be limited, and our understanding constrained. If we wish to uncover general phenomena and processes in ecology and evolutionary biology, we must support and nurture work on many different model systems, and we must invite and welcome contributions from scientists of all backgrounds and identities. Diverse model systems and diverse scientists will provide diverse perspectives which, in turn, will allow us to understand endless forms most beautiful.

Acknowledgments

We thank Dr. Aisha Burton for permission to use her tweet as the epigraph. We also thank two anonymous reviewers for their feedback on an earlier version of this manuscript, and Robert Arlinghaus, Jeremy Fox, Sarah Knutie, Anna-Liisa Laine, Jonathan Losos, David Lowry, Levi Morran, Amy Pedersen, Ken Olsen, Tamal Roy, and Trisha Wittkopp for their feedback on Table S1. MAD acknowledges support from the Moore Foundation (GBMF9202; DOI: https://doi.org/10.37807/GBMF9202). CGR acknowledges support from the National Science Foundation (Dimensions of Biodiversity Grant #1737778).

Author contributions

All authors contributed to the framing, writing, and editing of this paper.

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FIGURE LEGEND

Figure 1. Model systems in EEB vary along a number of axes, including their tractability for field studies and for lab studies, and the biological scales at which they are typically studied. This multidimensional view of space that model systems occupy harkens back to Hutchinson's concept of the niche and his classic depiction of squirrels in an *n-dimensional hypervolume* (1978). A model system's position in this space influences the questions it is best suited to address. Further extending the Hutchinsonian metaphor, the *realized* space of a model system depends on both the biological features (*i.e., fundamental* aspects) and on the history of accumulated knowledge and techniques related to a particular system. In this figure, we represent approximately where a subset of common model systems in EEB fall along these three axes (c.f., Table S1). Organism silhouettes are from PhyloPic and 4vector.

Box 1. Skills and other attributes associated with developing new model systems, nurturing nascent model systems, and using existing systems in new ways.

While people sometimes take the existence of model systems for granted, developing new model systems, nurturing nascent model systems, and using existing systems in new ways requires skills on the part of individual researchers, and is facilitated by certain attributes of institutions and of the study system. We describe some particularly important attributes in this Box.

Individual attributes

Developing a new model system requires insight — what are the major gaps in our knowledge? What are major outstanding questions? What tools and methodologies can be leveraged to address those questions? What is the potential of a particular organism or system? And, just as importantly, what are its limitations? It also requires foresight — where is the field headed? Are there new technologies on the horizon that will open up major new research opportunities?

Developing a new model system also requires strong natural history skills, including excellent observational skills and record keeping. It requires an ability to tinker — having the curiosity, ingenuity, resourcefulness, and instincts to modify aspects of the environment or setup in a way that facilitates studies within a particular system. And, unquestionably, it requires an ability to persevere through setbacks — something that can be greatly facilitated by particular institutional structures, as we discuss more below.

Developing model systems also requires being a good collaborator, mentor, and communicator. Collaboration will promote studies on the same system by multiple researchers, which is required for building the depth of knowledge needed in order to achieve the "model system" designation. These collaborations are facilitated by a culture of openly sharing data, protocols, and other materials (Ankeny and Leonelli 2020; Matthews and Vosshall 2020) and by strong communication skills. A scientist who has an amazing vision but is unable to communicate that with others (including potential funders, collaborators, students, and others) will have limited impact. Networking skills are also useful, as they can help develop connections that allow for new lines of study on a particular system and that recruit more people to work on the system.

Institutional and structural attributes

Model systems are extensively studied from a variety of angles, yielding deep knowledge of that system. Thus, developing a model system is supported by having a diversity of researchers who work on the same system, but approach it from different angles (or subdisciplines), using different techniques and approaches and with different perspectives. Crucially, EEB will only benefit from those diverse perspectives if our departments, field stations, meetings, and all of the other places where we do our work are inclusive spaces.

Funding is also a crucial component of developing new model systems. Building deep knowledge of a system requires many years of study by many people — something that can only be achieved with financial support. A major challenge in today's funding climate is supporting work on the natural history of a system, and funding that supports high risk/high reward projects.

A related factor is that there need to be structures in place that protect an individual researcher from the impacts of failures, such as job stability, supportive mentors, and other systems (*e.g.*, evaluating candidates based on a few publications of their choosing rather than their total number of publications). It is not clear whether there is a particular time in one's career where it is "best" to develop a new model system; some researchers begin developing them relatively early in their careers, while others wait until they have already established themselves. As with so many things, a wide range of circumstances (not to mention serendipity) will play an important role in the timing.

Organism or study system attributes

Some organisms (or communities or ecosystems) are more readily established as model systems, based on factors such as ease of working with them in the field and/or lab, generation time, organism size, and population abundances. An organism that is small, abundant, reproduces quickly, and grows well in the field and the lab is more likely to become established as a model system than an organism that is large, rare, or difficult to grow. However, while there are challenges with organisms with more complex life histories (*e.g.,* parasites that must pass through multiple hosts, organisms with biennial or multiannual life cycles), model systems that capture these diverse realities are essential for addressing fundamental questions in ecology and evolution. One possibility is to assemble longer term datasets over time, with new members of a lab analyzing data collected by prior lab members, and "paying it forward" by collecting additional data.

Using existing systems in novel ways

There is strong overlap between the skills needed to develop a model system and those needed to take an existing system and use it in a novel way, including insightfulness, a sense of where the field is heading, and good communication skills. Two additional attributes that are particularly important for using model systems in innovative ways are creativity and big picture thinking, both of which enable a scientist to see beyond the scope of how a system has been used in the past. Without these, it is easy to remain within the confines of what has already been done, rather than to use those as a foundation for a leap off in a new and exciting direction. Some useful questions to ask in the context of taking existing systems in new directions include: Are there modes of inquiry from other disciplines or modes of thought that could be newly applied to this system? How could our knowledge of an existing system change as a result of these new perspectives?

Finally, we note that serendipity can definitely play a role. Sometimes, model systems begin to be used in a new way because of a chance observation that occurs during a study of an entirely different question. However, these serendipitous occurrences will only lead to new directions if the attributes listed above are present. As Louis Pasteur put it: chance favors only the prepared mind.

Developing new systems

As discussed elsewhere in this manuscript, many traditional model systems were developed by people in positions of power (*e.g.*, at traditionally powerful and wealthy institutions), and work on those systems is sometimes deemed important or worthy simply by virtue of being done in an established model system. We call on our community to use more of a bottom-up or community organizing approach as novel model systems are developed, getting buy-in from diverse members of our community.

Box 2. Model systems in the tropics

The establishment of model systems in the tropics was strongly influenced by sociopolitical context and ease of access to researchers from the United States. As a result of the Spanish-American war, the U.S colonized not only Cuba, but also Puerto Rico, Guam, and the Philippines. In 1904, the U.S. took formal control of the Panama Canal after actively supporting the separation of Panama from Colombia. Aided by the increased influence and control in the region, U.S. institutions established different research sites in Central America and the Caribbean (*e.g.*, Cinchona in Jamaica, the Harvard Botanical Garden in Cuba, and Barro Colorado Island in the Panama Canal region) (Raby 2017).

After the Cuban revolution in 1959, Atkins Garden — at the time a main research center in the Neotropics — was forced to close its doors (Raby 2017). The National Science Foundation, together with the Organization of American States, sponsored three meetings to create a strategy to facilitate research of US scientists in tropical research (Stone 1988). The result of these meetings was the formation of the Organization for Tropical Studies (OTS), a consortium of universities and research centers in Latin America and the United States, with field stations in Costa Rica and South Africa (Rocha and Braker 2021).

OTS has offered the field course "Fundamentals of Tropical Biology" since 1961. The origin and popularization of many tropical model systems can be traced to research performed in OTS field stations and OTS field courses. Examples of classic model systems developed in OTS stations include *Heliconius* butterflies, *Piper* shrubs, army ants, interactions between leafcutter ants and associated microorganisms, and interactions between Zingiberales "banana-like plants" and rolled-leaf beetles (Rettenmeyer 1963; Gilbert 1972; Strong 1977; Marquis 1984). This history helps explain why studies in Costa Rica are highly overrepresented given its size (Stocks et al. 2008; Martin et al. 2012).

Many tropical model systems, including those still in use today, were developed by researchers from the Global North. While there is still a problem of underrepresentation of people from tropical countries as active participants in the science conducted there (Stocks et al. 2008), the efforts of OTS to promote inclusion of tropical scientists for over 50 years has led to a growing number of researchers from the Global South working on these classical tropical systems (Chaves-Campos 2003; Mavárez et al. 2006; Pinto-Tomás et al. 2009; García-Robledo et al. 2016). Although many scientists in the Global South are playing central roles in research involving classic tropical model systems, men continue to outnumber women (Hill et al. 2010). In addition to the stereotypes and implicit biases that reduce participation of minorities in STEM, Latina scientists have to face the challenges associated with culturally ingrained concepts of masculinity ("machismo"; Bernal et al. 2019).

Box 3. How to assess whether there are gaps in existing model systems

We propose that the general approach used by Wale and Duffy (2021) can provide a framework for evaluating whether existing model systems in use in a given subdiscipline are sufficient, or whether the subdiscipline would benefit from additional systems.

Evaluating currently used systems

Step 1: Identify the key processes and phenomena of interest to a subdiscipline. For example, existing theory on the ecology and evolution of infectious diseases points to three processes — transmission, disease, and recovery — as fundamental. Making these key processes and phenomena explicit also allows for researchers to add or modify them, which can be an important way in which research in a subdiscipline progresses.

Step 2: Review the current model systems that are in use in that subdiscipline. This review should focus on assessing whether each individual study on a given system explores the fundamental processes identified in step 1. While carrying out the review, it is likely that additional important features and differences will emerge (*e.g.*, related to the scale at which particular processes are studied in particular systems).

Step 3: Using the results from step 2, evaluate whether the systems currently in use in that subdiscipline are capturing a wide range of parameter space for the processes of interest. Can the systems currently in use illuminate core themes and processes for that subdiscipline (Jenner and Wills 2007)?

Step 4: What are the underlying assumptions about existing model systems? Have those assumptions been tested?

Step 5: Consider whether, in addition to the key processes identified, there are other notable gaps in the model systems currently in use. One that is likely to be true in many subdisciplines is that existing model systems might come from a relatively restricted geographical area, or may represent only certain life history traits (Table S1). We propose considering how broadly you can apply knowledge using current systems. Does it only tell you about a certain type of organism or ones that live in certain locales? How well is the parameter space in Figure 1 covered? Similar to what is often done with mathematical models, it is important to be explicit about what our model systems represent and, even more importantly, what they do not represent.

Steps to take if (or, more likely, when) gaps are identified

Some questions to ask when trying to identify systems that might be developed and used to fill existing gaps:

1. Are there model systems in use in other areas of ecology, evolutionary biology, and behavior (or, if not, other areas of biology) that can help fill those gaps?
2. Are there nascent study systems that are promising — for example, ones that have been studied in nature for a long time but that would benefit from development of novel molecular tools?
3. Can the model systems under consideration be manipulated and studied on the time scales of a PhD program or while an assistant professor? If not, how have others who work on organisms or processes with longer time scales approached those questions?
4. Can museum collections be of use, including to extend temporal and/or spatial scales? Consider, however, the likelihood of biased representation within museum collections (Loiselle et al. 2007; Wehi et al. 2012; Gower et al. 2019; Thompson and Birkhead 2020).
5. What sources of information might exist outside those typically considered by Western scientists? Are there other historical records (*e.g.*, phenological data collected by community scientists, or existing photo or video collections) that can be used to address the question? What do local communities already know about the system? What work has been done on the topic by non-Western scholars (including work published in languages other than English)?

Checkpoint: When considering the development of a new potential model system, it is essential to ask whether it will be done in a way that increases or decreases inequity? Unfortunately, there is a long history of extractive practices that reinforce colonialism and imperialism (DuBay et al. 2020; Gewin 2021), of research that “discovers” things that were already well known in local communities (*e.g.,* Cañizares-Esguerra 2019), and of research that ignores the contribution of non-Western scientists (*e.g.,* Malik et al. 2018).

Researchers should also consider whether their work would benefit from establishing multiple taxa at the same time (depending on the study topic, these might be chosen because they are closely related, or, alternatively, because they encompass phylogenetic breadth).

Box 4. Additional considerations for early career researchers

As early career scientists establish their careers, they must make decisions about what systems to study. Making these decisions often involves considerations beyond just the scientific questions they are interested in tackling. Will they have access to the necessary resources? Will the field be welcoming? Will they be able to carve out a niche of their own?

A key challenge for early career scientists is how to differentiate from previous mentors and other established groups. How does a seedling lab carve out their space in a crowded forest? Even in cases where the community working on a particular model system is welcoming and eager to share resources, early career researchers face challenges in establishing their independent groups. The reality is likely to be that seedling labs will have relatively few resources (in terms of both people and funding), while the research forest might have some large trees that cast a very long shadow. And, unfortunately, the research environment for particular model systems is not always welcoming, especially for early career scientists who do not fit the traditional "model scientist" mold. A key aspect of working on model systems is the community associated with it, which provides a variety of perspectives (*e.g.*, from different subfields of EEB), that can share protocols and help someone learn new techniques, and that can help an early career researcher negotiate a distinct intellectual niche within that research community; whether scientists from underrepresented groups are less (or more) likely to work on model systems would be an interesting topic for further investigation.

As a result, in some cases, early career scientists will decide that the best path forward is to establish a new model system, or to take an existing model system and use it in a very different way. This has the advantage of avoiding competition. Establishing a new system (or using an existing one in a very different way) also can mean that work on a particular system (or in a particular subdiscipline) is done by diverse scientists from the start, with the potential to establish a healthy, equitable, and inclusive culture right from the beginning.

However, as always in ecology and evolution and in life, there are tradeoffs. While there are advantages to establishing new systems, there are also important drawbacks. First, there is a larger-than-average chance of failure when trying to do something completely new; deciding whether to take on this risk at a particularly vulnerable career stage will require careful thought. Second, establishing new systems will require funding, including for natural history work and for work that is high risk/high reward, neither of which are well-supported in current funding climates (as also mentioned in Box 1). Third, moving into a new model system from an established model system may lead to a loss of research connections and community, including potentially an impact on the rate at which papers are cited.

References associated with Table S1:

E. coli: (Blount 2015)
S. cerevisiae: (Replansky et al. 2008; Liti 2015; Duan et al. 2018; Zakhartsev and Reuss 2018)
Microbial self-assembled communities: (Sanchez et al. 2021)
Protist microcosms: (Altermatt et al. 2015)
C. elegans: (Muschiol et al. 2009; Frézal and Félix 2015)
D. melanogaster: (Markow 2015)
Daphnia spp.: (Ebert 2011; Lampert 2011; Lee et al. 2019)
Cephaloleia spp. (rolled leaf beetles): (Wilf et al. 2000; McKenna and Farrell 2006; García-Robledo et al. 2016)
D. rerio (zebrafish): (Parichy 2015; US Fish & Wildlife Service, 2018; Neff 2020)
P. reticulata (guppy): (Magurran 2005)
G. aculeatus (three-spined stickleback): (McKinnon and Rundle 2002; Jones et al. 2012)
A. plantaginis (wood tiger moth): (Rojas et al. 2018; Yen et al. 2020; Gordon et al. 2021)
Tribolium: (Park 1948; Denell 2008; Tribolium Genome Sequencing Consortium et al. 2008)
D. plexippus (monarch butterfly): (Zalucki and Clarke 2004; Zhan et al. 2014; Green 2021)
Anolis lizards: (Losos 2009)
Mimulus: (Wu et al. 2008; Lowry et al. 2019)
Arabidopsis: (Krämer 2015)
Trifolium: (Griffiths et al. 2019)
Cedar Creek: (Tilman et al. 2001)
Galápagos finches: (Grant and Grant 2002; Grant 2003)
Plantago: (Penczykowski and Sieg 2021)
Mus musculus: (Phifer-Rixey and Nachman 2015)
Peromyscus: (Bedford and Hoekstra 2015)
Barro Colorado Island: (Kress et al. 2009)
ForestGEO: (Anderson-Teixeira et al. 2015)

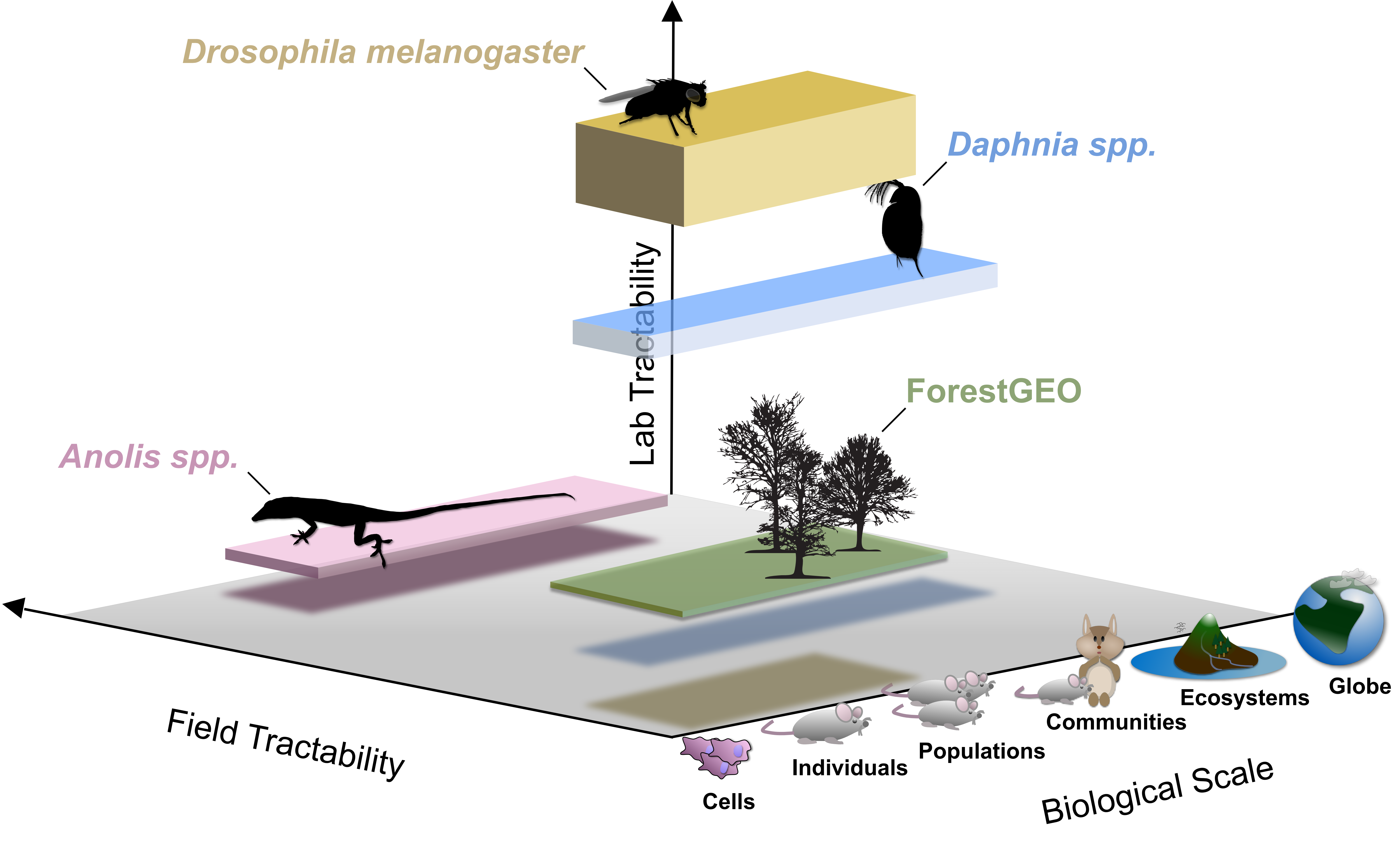
Drosophila melanogaster
Daphnia spp.
Lab Tractability
ForestGEO
Anolis spp.
Field Tractability
Cells
Individuals
Populations
Communities
Ecosystems
Globe
Biological Scale

Table S1. Twenty five model systems in ecology, evolutionary biology, and behavior. This is not an exhaustive list of model systems, but, rather, reflects an attempt to demonstrate some of the variation that exists along multiple axes in model systems used in EEB, including the axes covered in Figure 1. We stress that there are additional model systems, some of which have been the subject of important work in EEB, that are not included in this table. Notably, as discussed in the main text, model systems in EEB include not only organisms, but whole communities and ecosystems. In many cases, tractability arises from extensive knowledge of the natural history of these systems, rather than due to inherent characteristics of the system. "NA" indicates when a particular cell is not applicable to a particular system.

Model system	**Taxonomic group**	**Ecosystem or biome**	**Pre-Columbian geographic distribution**	**Current geographic distribution**	**Generation time**	**Organism size (approximate length, meters)**	**Published genome?**	**Lab tractability**	**Ability to track individuals in the field**	**Ability to do field experiments & manip-ulations**	**Degree to which system is studied in the context of its natural history**	**Major biological scale(s) of study**	**Key references**
Escherichia coli	Bacteria	Aquatic & terrestrial (often within other organisms but also free-living)	Global	Global	Minutes to hours	10^{-6}	Yes	High	Low	Low	Limited	Cellular, individual, population	(Blount 2015)
Saccharomyces cerevisiae	Yeast	Terrestrial (natural habitat is decaying fruit)	Originated and domesticated in Far East Asia	Global	Minutes	10^{-6}-10^{-5}	Yes	High	Low	Low	Limited	Cellular	(Replansky et al. 2008; Liti 2015; Duan et al. 2018; Zakhartsev and Reuss 2018)
Microbial self-assembled communities	Mostly bacteria	Aquatic & terrestrial	Global	Global	Minutes to hours	10^{-6}-10^{-5}	Some	High	NA	NA	Limited	Individual, population, community, ecosystem	(Sanchez et al. 2021)
Protist microcosms	Non-monophyletic eukaryotic group	Aquatic	Global	Global	Hours to days	10^{-5}-10^{-3}	Some	High	NA	NA	Mixed	Population, community, ecosystem	(Altermatt et al. 2015)
Caenorhabditis elegans	Nematode	Terrestrial (in rotting fruit & vegetation)	Unknown	All continents except Antarctica	Days	10^{-3}	Yes	High	Low	Low	Limited	Cellular, individual, population	(Muschiol et al. 2009; Frézal and Félix 2015)
Drosophila melanogaster (fruit fly)	Insect	Terrestrial	Africa, Asia, Europe	All continents except Antarctica	Days to weeks	10^{-3}	Yes	High	Low	Low	Limited	Cellular, individual, population	(Markow 2015)
Daphnia spp. (water flea)	Crustacean	Aquatic (freshwater)	All continents except Antarctica	All continents except Antarctica	Days	10^{-3}	Yes (*D. pulex & D. magna*)	High	Low	Moderate	Mixed	Cellular, individual, population, community, ecosystem	(Ebert 2011; Lampert 2011; Lee et al. 2019)
Cephaloleia spp. (rolled-leaf beetles)	Insect	Terrestrial	Neotropics	Neotropics	Months	10^{-3}-10^{-2}	No	High	High	Low	High	Individual, population, community	(Wilf et al. 2000; McKenna and Farrell 2006;

													García-Robledo et al. 2016)
Danio rerio (zebrafish)	Ray-finned fish	Aquatic (freshwater)	South Asia	Indian subcontinent, small introduced populations in North & South America	~1 year	10^{-2}	Yes	High	Low	Low	Mixed	Cellular, individual, population	(Parichy 2015; US Fish & Wildlife Service, 2018; Neff 2020)
Poecilia reticulata (guppy)	Ray-finned fish	Aquatic (freshwater)	Neotropics	All continents except Antarctica	Months	10^{-2}	Yes	High	High	High	High	Cellular, individual, population, community, ecosystem	(Magurran 2005)
Gasterosteus aculeatus (three-spined stickleback)	Ray-finned fish	Aquatic (marine & freshwater)	Asia, Europe, North America	Asia, Europe, North America	1-3 years	10^{-2}	Yes	High	Low	High	High	Cellular, individual, population	(McKinnon and Rundle 2002; Jones et al. 2012)
Arctia plantaginis (wood tiger moth)	Insect	Terrestrial	Europe	Holarctic realm	~1 year (but can be less in the lab)	10^{-2}	Yes	High	Low	High	Limited	Individual, population, community	(Rojas et al. 2018; Yen et al. 2020; Gordon et al. 2021)
Tribolium castaneum & T. confusum (flour beetles)	Insect	Terrestrial	Africa, Asia, Oceania	Global	~1 month	10^{-2}	Yes for *T. castaneum*	Moderate	Moderate	Moderate	High	Individual, population, and community	(Park 1948; Denell 2008; Tribolium Genome Sequencing Consortium et al. 2008)
Danaus plexippus (monarch butterfly)	Insect	Terrestrial (grassland)	North America but disputed; see footnote 1	All continents except Antarctica and Asia	Weeks	10^{-2}-10^{-1}	Yes	Moderate	Low	Moderate	Mixed	Cellular, individual, population, community	(Green n.d.; Zalucki and Clarke 2004; Zhan et al. 2014)
Anolis spp. (anole lizards)	Lizard	Terrestrial (ground dwelling and arboreal)	North, Central, and South America	North, Central, and South America, Asia, Western Pacific Islands (Micronesia)	Months to years	10^{-2}-10^{-1}	Yes	Low-Moderate	Low to moderate	Moderate to high	High	Individual, population, community	(Losos 2009)
Mimulus guttatus/ Erythranthe guttata (monkeyflower); see footnote 2	Phrymaceae (lopseed)	Terrestrial (sea level to alpine habitats)	North America	Mostly North America, invasive in Europe and New Zealand	Months	10^{-2}-10^{-1}	Yes	High	High	High	High	Population, community	(Wu et al. 2008; Lowry et al. 2019)

Arabidopsis thaliana (thale cress)	Brassicaceae (mustard)	Terrestrial (gravelly soil, including disturbed areas)	Asia and Europe	All continents except Antarctica, predominantly in Asia, Europe, and North America	Weeks	10^{-2}-10^{-1}	Yes	High	High	High	Limited	Cellular, individual & population	(Krämer 2015)
Trifolium repens (white clover)	Fabaceae (legume)		Europe, Asia, North Africa	All continents except Antarctica	Months	10^{-2}-10^{-1}	Yes; see footnote 3	High	High	High	High	Cellular, individual, population, community	(Griffiths et al. 2019)
Cedar Creek	All domains, with a particular focus on flowering plants	Terrestrial (grassland)	NA	North America	Variable	10^{-2}-10^{0}	NA	Not lab tractable	High	High	Mixed	Individual, population, community, ecosystem	(Tilman et al. 2001)
Galápagos ground finches	Bird	Terrestrial	Galápagos Islands	Galápagos Islands	~1 year	10^{-1}	Yes	Not lab tractable	Moderate to high	Low to moderate	High	Individual and population	(Grant and Grant 2002; Grant 2003)
Plantago lanceolata and *P. major* (ribwort and broadleaf plantain)	Plantaginaceae (plantain)	Terrestrial (grasslands, pastures, disturbed habitats)	Asia and Europe	All continents except Antarctica	Months	10^{-1}	No	High	High	High	High	Individual, population, community	(Penczykowski and Sieg n.d.)
Mus musculus (house mouse)	Mammal	Terrestrial	Asia and Europe	All continents except Antarctica	Weeks	10^{-1}	Yes	High	Moderate	Moderate	Limited	Cellular, individual	(Phifer-Rixey and Nachman 2015)
Peromyscus spp. (deer mouse)	Mammal	Terrestrial	North and Central America	North and Central America	Weeks	10^{-1}	Yes	Moderate	Moderate to high	Moderate	High	Individual, population	(Bedford and Hoekstra 2015)
Barro Colorado Island Forest Census Plot	All domains, with a particular focus on flowering plants	Terrestrial (forest)	NA, but see footnote 4	Central America	Variable	Variable, up to 10^{2}	NA	Mixed	High	Moderate	High	Individual, population, community, ecosystem, global	(Kress et al. 2009)
ForestGEO	All domains, with a particular focus on flowering plants	Terrestrial (forest)	NA	All continents except Antarctica	Variable	Variable, up to 10^{2}	NA	Not lab tractable	High	Moderate	High	Individual, population, community, ecosystem, global	(Anderson-Teixeira et al. 2015)

Footnotes:

1. The earliest written reports of monarchs outside the Americas appear in the 1830s from records of European colonialists. Monarchs' current host plant association (non-native species, likely recent introductions) support the idea of their recent establishment across the Pacific Islands. On the other hand, the Mãori of New Zealand have a traditional name for the monarch butterfly ("kãkâhû") (Zalucki and Clarke 2004). Consistent with the suggestion of a much older range expansion, demographic analyses of genomic sequencing data suggest Pacific and Atlantic dispersal events occurred as early as 2,000-3,000 years ago (Zhan et al. 2014).
2. The genus *Mimulus* was split into multiple genera in 2012, with *Mimulus guttatus* being moved into the genus *Erythranthe* (Barker et al. 2012). However, there is strong disagreement about this taxonomic revision, and calls to retain *Mimulus guttatus* as the name for this group, including because of its prominence as a result of it being a well-established model system (Lowry et al. 2019).
3. The published reference genome for white clover is a draft shotgun assembly (Griffiths et al. 2019).
4. Barro Colorado Island is located in the middle of Gatun Lake, which was created during the formation of the Panama Canal. Thus, this habitat existed prior to colonial influences in the region, but it only became an

island in the early 1900s.

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