

1 **Model systems in ecology, evolutionary biology, and behavior:**
2 **A call for diversity in our model systems and discipline**

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46
47 **Abstract**

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

62

63 **I. Introduction**

64 “*What is true for E. coli is true for the Elephant*” - J. Monod.

65 “*But not for Salmonella*” - E. Groisman

66 - Burton, Aisha, [Twitter post](#), 14 January 2021, 9:48 a.m.

67

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

76

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

84

85 The choice of study organism (or system), and its match to the question under study, is critical to
86 our science (Travis 2006). Researchers consider a myriad of factors when choosing a study
87 organism (Dietrich et al. 2020). The Krogh principle, popular in animal physiology, argues that a

88 study organism should be chosen because it displays a particular trait or physiological
89 mechanism of interest in a way that is distinctive and/or suitable to experimental study (Krogh
90 1929; Green et al. 2018). In addition to tractability, choice of study organism also reflects the
91 impact of access, resources, and economies (Burian 1993; Dietrich et al. 2020) — which means
92 there are biases in our current model systems, as we discuss more below. Study organisms are
93 also chosen because they might enable “horizontal” comparisons to other organisms, which can
94 allow for understanding general phenomena and processes (Burian 1993; Travis 2006; Dietrich
95 et al. 2020). The knowledge we collectively build reflects thousands of individual decisions
96 regarding which systems should be used to study which questions; in the end, “the principles and
97 facts that emerge will only be as reliable as our choices have been wise” (Travis 2006).

98
99 Ecologists and evolutionary biologists need a diversity of study systems in order to achieve our
100 goal of conceptual unification, and we must be thoughtful and creative about how we use and
101 develop those systems. This Special Feature highlights a variety of ways in which model systems
102 are currently being used to address timely and important questions in ecology and evolutionary
103 biology (Green n.d.; Penczykowski and Sieg n.d.; García-Robledo and Baer 2021; Gordon et al.
104 2021; Grant et al. 2021; Wale and Duffy 2021). In this introduction, we first seek to define what
105 we mean by the term “model system” (a surprisingly challenging task). Having done that, we
106 then ask where our model systems come from (both in terms of the skills required to develop
107 them or use them in new ways, and in terms of their history and geography), and also consider
108 where model systems research in ecology, evolution, and behavior (EEB) might be heading.

109
110 In a manuscript addressing the importance of diversity in ecology and evolutionary biology, it is

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

124 **II. What is a model system?**

125 “Model organism”, “model species”, and related terms have been criticized as some of the most
126 overused and under-defined words in life sciences (Katz 2016). It is therefore with some
127 trepidation that we seek to define “model system” for our purposes. As in one of the papers in
128 this special feature (Wale and Duffy 2021), we will first look to the subfield in which the
129 definition of “model systems” has received the most attention, biomolecular sciences (Dietrich et
130 al. 2014), before returning to consider its meaning in ecology, evolution, and behavior.

131

132 In biomolecular sciences, model organisms are experimental organisms that are studied in the
133 laboratory context as representatives of a broad range of organisms and processes (Jenner and

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

147

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

153

154 Here, we propose the following definition of “model system” for EEB: a species, taxon,
155 community, or ecosystem that has been studied from multiple angles with a goal of developing a
156 deep understanding of that organism (or taxon, community, or ecosystem) and in a manner that

157 enables comparisons with other systems to illuminate general ecological, evolutionary, and/or
158 behavioral principles. Prior discussions of model systems in EEB have contrasted work on
159 “model systems” vs. “natural populations” (Travis 2006). However, the terms “model system”
160 and “natural population” are not mutually exclusive. Rather, we propose that there are multiple
161 axes along which model systems fall (Figure 1). We are in full agreement with Travis (2006) that
162 “Robust inference requires horizontal comparisons and vertical integration” — the first half of
163 our definition is Travis’s “vertical integration”, and the second half is his “horizontal
164 comparisons”. In our definition, a model system need not necessarily be a single species (or
165 taxon) or a pair of closely interacting species. Moreover, it need not be experimentally
166 manipulable or amenable to laboratory study. Instead, in EEB, certain sites and ecosystems have
167 also emerged as model systems as a result of an extended history of study that has allowed us to
168 generate and test general ecological and evolutionary theory (Table S1, Figure 1). This includes
169 experimental species assemblages, such as the Cedar Creek biodiversity plots; natural tree plots,
170 such as the Forest Census Plot on Barro Colorado Island; and networks of such ecosystems, such
171 as the 72-site Forest Global Earth Observatory (ForestGEO). At a smaller scale, mesocosms and
172 microbial communities and ecosystems have emerged as model systems to study community
173 ecology (Datta et al. 2016; Goldford et al. 2018; Fugère et al. 2020), species interactions
174 (Mickalide and Kuehn 2019), ecosystem processes (de Jesús Astacio et al. 2020), and eco-
175 evolutionary dynamics (Lawrence et al. 2012; Matthews et al. 2016). These types of systems
176 allow us to incorporate ecological context and dynamics while still maintaining tractability
177 (Sanchez et al. 2021). While these types of systems are not part of the traditional definition of
178 “model systems”, they can be used to understand particular biomes and general principles at a
179 global scale, and allow us to avoid some of the biases that are associated with more traditional

180 model systems (Bolker 1995; Alfred and Baldwin 2015). Our definition of “model system” is
181 agnostic about the degree to which an organism (or community or ecosystem) is
182 “representative”. Any one system will be representative of some aspects of ecology and
183 evolutionary biology, and unusual in others. Research in natural and experimental contexts
184 provides insights into fundamental processes in EEB, as does work on organisms that are
185 representative and those that are unusual.

186
187 Even though variation is a key focus of research in EEB, model systems are generally chosen
188 and constructed in a way in which variation (or its drivers) are restricted or delimited. It is no
189 accident that the ecosystems that have emerged as model systems are often delimited places such
190 as islands or field plots; this isolation limits the contribution of “undesirable” variation or noise.
191 Similarly, when the model system is an organism rather than an ecosystem, we tend to select
192 organisms that we can standardize and isolate, such as by growing them in the lab (Table S1,
193 Figure 1) and/or whose environments can be easily simulated (e.g. ectotherms). For this reason,
194 model systems in EEB share some of the (biased) biological traits of model organisms in the
195 biomolecular sciences that make them intrinsically tractable, such as ease of husbandry in
196 laboratory conditions, fast generation times, and traits that are easily quantified (such as external
197 color variation).

198
199 As model systems become established, a positive feedback loop can kick in where research on
200 the system makes additional research more likely (Matthews and Vosshall 2020). The
201 development of standardized (and shared) knowledge about the system — protocols for rearing
202 them, an understanding of their natural history, techniques for quantifying variation, the

203 establishment of stock lines, mathematical models that describe their dynamics, etc. — makes
204 these systems more tractable for additional research and facilitates the expansion of work on the
205 system into new subdisciplines and new questions (Box 1). That is, over time, there is greater
206 vertical integration and more possibilities for horizontal comparison. The interconnection and
207 integration between subdisciplines that arises as a result is a major strength of working with
208 model systems.

209

210 At the same time, this expansion of research both through time and across subdisciplines can be
211 particularly susceptible to the propagation of unsupported assumptions and erroneous inferences
212 made early in the study of the system, potentially resulting in substantial bodies of work that rest
213 on shaky foundations. For especially long-studied model systems, some of these decades-old
214 assumptions may be ‘signs of the times,’ projections of entrenched sociocultural and political
215 values onto the study system that no one thought to question at the time (Haraway 1989, 1991).
216 Regardless of their source, these assumptions and inferences can become embedded into research
217 on the model system and become challenging to escape, even as their impact is magnified
218 throughout the field through horizontal and vertical integration. For example, Bateman’s (1948)
219 relatively early research on differences between male and female *Drosophila melanogaster* in the
220 relationship between mate number and reproductive success not only influenced further research
221 in *Drosophila* but also had profound consequences for the study of sexual selection, in a manner
222 that reinforced gender stereotypes (Hrdy 1986; Dewsbury 2005). Later efforts to replicate
223 Bateman’s (1948) experiments revealed its substantial errors and limitations (Snyder and
224 Gowaty 2007; Gowaty et al. 2012), and it remains a monumental task to fully evaluate the
225 impact of shortcomings in this early model system research on the field as a whole (Tang-

226 Martínez 2016; Hoquet 2020).

227

228 Taking an optimistic view of this challenge, large bodies of work on model systems present us
229 with unique opportunities to identify implicit assumptions and early errors, and to trace their
230 impact on scientific research. For example, *Anolis* lizards are a model system for studying
231 convergent evolution and adaptive radiation and have been the subject of research in behavioral
232 and evolutionary ecology for over a century (Losos 2009). This research includes over a hundred
233 papers published on territorial behavior in *Anolis*. Through a comprehensive close-reading to
234 evaluate evidence for territoriality in these papers, Kamath and Losos (2017) revealed that
235 territoriality was assumed rather than tested in the earliest research on anoles, and this early
236 assumption became entrenched in subsequent work in this system, implicitly and explicitly
237 shaping study design, data analysis, the interpretation of results, and publication. While similar
238 assumptions have likely been made in many other taxa described as territorial, their origins and
239 consequences were readily traceable in *Anolis* only because of the long history of research in this
240 model system.

241

242 Long-studied model systems can be a compelling context in which to apply methods from the
243 humanities and social sciences to understand scientific practice (e.g., Haraway 1989; Kohler
244 1994; Rader 2004; Milam 2010). Such work makes explicit the ever-present feedbacks between
245 the questions we scientists ask and the identities, cultures, and sociopolitical contexts we bring to
246 our work. This kind of cross-disciplinary inquiry into model systems can seed ideas for novel
247 conceptual and empirical approaches to long-studied questions in EEB (Kamath and Losos 2018;
248 Kamath and Wesner 2020). Equally, because the assumptions and inferences made early in the

249 study of model systems can be deeply consequential, scientists working to establish new model
250 systems would do well to consider the value of insights from cross-disciplinary inquiry for their
251 work, including through formal collaborations with scholars in the social sciences and
252 humanities who study the human dimensions of scientific practice. In this way, model systems
253 can make room for disciplinary and methodological diversity in our study of the natural world.

254

255 **III. Our traditional model systems reflect historical biases**

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

265

266 Traditional model systems are generally highly constructed. At the beginning of the twentieth
267 century, model organisms for genetic studies were isolated from their environments to separate
268 environmental effects from the effects of the genes themselves; the main goals were to canalize
269 development, develop experimental tractability, and use biological knowledge in the production
270 of new technologies (Pauly 1987; Kohler 1994; Bowman and Rebolleda-Gómez 2020). Morgan
271 and his group, for example, developed standardized protocols to grow *Drosophila* (minimizing

272 variation in the expression of phenotypic traits), and made genetic lines enriched for differences
273 in Mendelian inherited traits (Kohler 1994). Similarly, the reference strain of *Saccharomyces*
274 *cerevisiae* that provided the foundation for early research in this system was generated via lab
275 crosses and selected because it was unusual in that it could be maintained as a haploid,
276 facilitating the study of mutations (Liti 2015). These goals of control and technological
277 development were closely linked to the increasing use of genetics for domestication, and the
278 eugenic desires to control the genetic makeup of domesticated animals, crops, and humans for
279 the “betterment of society” (Bowman and Rebolleda-Gómez 2020).

280

281 In addition, traditional model systems were often chosen for their convenience and proximity to
282 important Western scientific institutions. *Drosophila* for example was chosen as a model system
283 because it matched the academic calendar in the Northern United States; they were most
284 abundant in fruit orchards early in the fall and students could easily breed them indoors during
285 the winter (Kohler 1994). The common house mouse (*Mus musculus*) was common in Europe
286 and the industrialized cities in the U.S., and, in addition, mice were bred by mice fanciers for
287 their rare coat colors and odd behaviors. Thus, lines of mice bred for clear phenotypic
288 characteristics were commercially available. At the time when the mouse was becoming a model
289 for the study of genetics, there was a good market for “mouse fancy” in New England that
290 allowed Castle and Little to start their genetic studies in mice with lines from a farm in
291 Massachusetts (Rader 2004).

292

293 At the same time as these traditional biomolecular model systems became well-developed, the
294 establishment of modern academic ecology was accompanied by the extensive study and

295 establishment of particular ecological ecosystems as models (for example, Henry Cowles's work
296 on succession in the Indiana Dunes, Lindeman's research in Cedar Bog Lake (part of what is
297 now Cedar Creek Ecosystem Reserve), and Hutchinson's work on Linsley pond (Golley 1993)).
298 Over time, there was a growing awareness of the geographical biases in where ecological
299 research was being performed and a desire to do more systematic research in the tropics
300 (Richards 1963). One consequence of this was that the number of field stations rapidly increased
301 (Tydecks et al. 2016), but in a way that was uneven and that still reflected ease of access by
302 researchers from the United States. This contributed to the substantial overrepresentation (given
303 their size) of research done in Panama and Costa Rica (Stocks et al. 2008; Martin et al. 2012).
304 The uneven establishment of field stations in the tropics was strongly impacted by the
305 geopolitical context (Box 2). Despite efforts to expand the geographic range of research in EEB,
306 most of the research published in the major ecological journals is still based on sites in Europe
307 and in the United States (Martin et al. 2012).

308

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

318 emerging model systems (Matthews and Vosshall 2020; Box 1).

319

320 Overall, model systems emerge from the community, as a result of countless decisions made by
321 individual scientists (including early career scientists; Box 4), with a strong influence of our
322 institutional cultures. Therefore, in addition to focusing on diversity of our model systems, we
323 must focus on diversity and inclusion in our discipline.

324

325 **IV. EEB needs diverse scientists**

326 STEM disciplines were designed for one particular type of person, summarized by McGee
327 (2020) as “White men who are heterosexual, abled-bodied, Christian or atheist, middle-class or
328 above”. EEB as a discipline was also designed for this type of person, and, like STEM more
329 broadly (Valantine et al. 2016; McGee 2020; Montgomery 2020a) has been — and still is —
330 inhospitable to people who do not fit that mold (Graves 2019). This is especially true for
331 scientists who hold multiple minoritized identities (Ireland et al. 2018). It is important to note
332 that, despite these barriers, scientists from underrepresented groups have long made
333 contributions to EEB (Mackay et al. 2019; Jaffe et al. 2020; Lee 2020).

334

335 While we would benefit from more comprehensive data, it is clear that the demographics of EEB
336 still reflects these origins and this exclusion. To give some examples: of the US citizens and
337 permanent residents included in the US National Science Foundation’s Survey of Earned
338 Doctorates for 2019, 84% of earned doctorates in ecology and 77% in evolutionary biology went
339 to people who were White and not Hispanic or Latino; only eight PhD recipients in ecology and
340 evolutionary biology in 2019 were Black, and only one was Native American (National Center

341 for Science and Engineering Statistics (NCSES) 2019). In New Zealand, Māori and Pasifika are
342 severely underrepresented at the faculty level at universities and crown-research institutes, with
343 little progress over a decade (McAllister et al. 2020). Survey responses from attendees at the
344 Evolution 2019 meeting indicated that the representation of women drops with career stage, as
345 does representation of LGBTQ+ scientists (Rushworth et al. 2021); consistent with this, women
346 scientists tend to have shorter publishing careers (Huang et al. 2020). There is strong geographic
347 bias in the composition of editorial boards in ecology, evolutionary biology, and closely related
348 fields; an analysis of the editorial boards of 20 leading conservation biology journals revealed
349 that they had few or no editors from regions with the most biodiversity (Campos-Arceiz et al.
350 2018). Unfortunately, it is clear that our field is still far from being diverse, equitable, and
351 inclusive.

352

353 The lack of diversity in EEB holds back our science (Ireland et al. 2018). People with different
354 backgrounds and lived experiences will approach science differently, asking different questions
355 and pursuing different lines of research (Keller 1982; Stewart and Valian 2018). The science we
356 do — the questions we ask, and how we pursue answers — are influenced by our identities and
357 by the social and political context in which we were raised (Keller 1982; Harding 1986; Wall
358 Kimmerer 2013). Because gatekeepers often share many of the identities and backgrounds with
359 the traditional “model scientist”, many scientists who did not fit that mold were told that the
360 questions they asked were “not science” (Keller 1982; Haraway 1989; Wall Kimmerer 2013),
361 and surely many more who were told this were driven away from science. This is a problem from
362 a justice perspective, and it also means that science suffers. Students from underrepresented
363 groups are more innovative than majority students, though unfortunately their innovations and

364 contributions tend not to be recognized and appreciated (Hofstra et al. 2020). Moreover, for
365 teams working together on a project, diverse groups outperform homogeneous ones (Hong and
366 Page 2004) — a result that parallels findings in non-human communities (Tilman et al. 2001).

367
368 More importantly, the lack of diversity in EEB (and STEM more broadly) is a moral issue. While
369 there are clear arguments that science benefits from diversity (as discussed above), scientists
370 from underrepresented groups should have the same opportunities to do science and these
371 opportunities should not rest on appeals to exceptionalism or benefits to science. Everyone
372 should have an opportunity to do science.

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

375 *“If there is one loud and clear message from the research literature on workplace diversity,*
376 *it is that multiple, interacting, nested levels of context matter.”*
377 *— (Bond and Haynes 2014)*
378

379 Increasing diversity in EEB, and creating a discipline that is inclusive of people of all
380 backgrounds and identities, requires a focus on institutional structures and gatekeepers (McGee
381 2020). Many efforts to increase diversity in STEM disciplines focus on individual students,
382 especially on preparing these students (which often translates into attempts to “fix” or assimilate
383 students from underrepresented groups) (Bowman and Rebolleda-Gómez 2020; Halsey et al.
384 2020; McGee 2020; Schell et al. 2020). Alternatively, conversations focus on the changes that
385 will come as more diverse early career scholars to progress through the academic ranks, ignoring
386 that this is not a simple issue of demography (Holman et al. 2018). Instead of viewing the lack of
387 diversity through the problematic “pipeline” metaphor (Cannady et al. 2014; McGee 2020), we

388 must focus on changing structures, including focusing on how racism (and other “isms”) within a
389 department and institution underlie the lack of diversity (McGee 2020). If organisms that we
390 study fail to grow or thrive in an environment, we consider what aspects of the environment
391 might be causing that outcome (Montgomery 2020*a*, 2020*b*); it is essential that we do the same
392 with marginalized and minoritized scientists, and that we work to change our institutions
393 (including our departments and scientific societies) so that they are inclusive and enable
394 scientists who are outside the traditional “model scientist” mold to thrive (McGee 2020;
395 Montgomery 2020*a*, 2020*b*).

396

397 Social science research demonstrates that organizational-level policies strongly influence the
398 degree to which minoritized groups are fully integrated into that organization and points to
399 changes that can be implemented to increase inclusion (Bond and Haynes 2014). These changes
400 include clearly communicating that behaviors that discriminate against individuals from certain
401 groups will not be tolerated, and clearly indicating that the organization views diversity as an
402 asset that is important to the (shared) mission of the organization and its employees (Bond and
403 Haynes 2014). Moreover, changes need to occur at multiple levels — a person’s trajectory in
404 science, and the environment they experience, are influenced by factors at multiple levels (Bond
405 and Haynes 2014; Valentine et al. 2016; Zea and Bowleg 2016). For example, scientists from the
406 Global South face major barriers even as immigrants in Europe, Canada, and the United States;
407 in addition to the influences of biased gatekeepers and departmental culture, institutional and
408 federal funding structures make it more expensive for departments to support these students and
409 further restricts access to key fellowships.

410

411 A variety of factors influence an early career scientist's transition to independence, including
412 structural factors (such as the ability to fund one's research, which continues to have striking
413 racial disparities: (Stevens et al. 2021)), institutional factors (including access to mentors,
414 research infrastructure and funds, and the teaching and service load), and individual factors (such
415 as persistence and self-efficacy) (Zea and Bowleg 2016). An important additional consideration
416 in EEB relates to field safety. Certain individuals are at greater risk of harm and conflict when
417 carrying out field work, and faculty, departments, and institutions must help people in their labs
418 evaluate these risks and consider strategies that can help mitigate them (Demery and Pipkin
419 2021).

420

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

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

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

443

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450

451 **Author contributions**

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

453

454 **Literature cited**

455 Alfred, J., and I. T. Baldwin. 2015. New opportunities at the wild frontier. *eLife* 4.
456 Altermatt, F., E. A. Fronhofer, A. Garnier, A. Giometto, F. Hammes, J. Klecka, D. Legrand, et

457 al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model
458 system in ecology and evolution. *Methods in Ecology and Evolution* 6:218–231.

459 Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-
460 Landau, S. J. Wright, K. Abu Salim, et al. 2015. CTFS-ForestGEO: a worldwide network
461 monitoring forests in an era of global change. *Global Change Biology* 21:528–549.

462 Ankeny, R. A. 2001. The natural history of *Caenorhabditis elegans* research. *Nature Reviews*
463 *Genetics*.

464 Ankeny, R. A., and S. Leonelli. 2011. What's so special about model organisms? *Studies in*
465 *History and Philosophy of Science. Part B. Studies in History and Philosophy of Modern*
466 *Physics*.

467 Ankeny, R., and S. Leonelli. 2020. *Model Organisms. Elements in the Philosophy of Biology.*
468 Cambridge University Press.

469 Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.

470 Bedford, N. L., and H. E. Hoekstra. 2015. *Peromyscus* mice as a model for studying natural
471 variation. *eLife* 4.

472 Bernal, X. E., B. Rojas, M. A. Pinto-E, Á. M. Mendoza-Henao, A. Herrera-Montes, M. I.
473 Herrera-Montes, A. Del Pilar Cáceres Franco, et al. 2019. Empowering Latina scientists.
474 *Science* 363:825–826.

475 Blount, Z. D. 2015. The unexhausted potential of *E. coli*. *eLife* 4.

476 Bolker, J. A. 1995. Model systems in developmental biology. *BioEssays* 17:451–455.

477 Bond, M. A., and M. C. Haynes. 2014. Workplace diversity: A social-ecological framework and
478 policy implications: Workplace diversity. *Social Issues and Policy Review* 8:167–201.

479 Bowman, M., and M. Rebolleda-Gómez. 2020. Uprooting Narratives: Legacies of Colonialism in
480 the Neoliberal University. *Hypatia* 35:18–40.

481 Burian, R. M. 1993. How the choice of experimental organism matters: epistemological
482 reflections on an aspect of biological practice. *Journal of the History of Biology* 26:351–
483 367.

484 Campos-Arceiz, A., R. B. Primack, A. J. Miller-Rushing, and M. Maron. 2018. Striking
485 underrepresentation of biodiversity-rich regions among editors of conservation journals.
486 *Biological Conservation* 220:330–333.

487 Cañizares-Esguerra, J. 2019. Screw Humboldt. *Medium*.

488 Cannady, M. A., E. Greenwald, and K. N. Harris. 2014. Problematizing the STEM pipeline
489 metaphor: Is the STEM pipeline metaphor serving our students and the STEM workforce?
490 *Science Education* 98:443–460.

491 Chaves-Campos, J. 2003. Localization of army-ant swarms by ant-following birds on the
492 Caribbean slope of Costa Rica: following the vocalization of antbirds to find the swarms.
493 *Ornitologia Neotropical* 14:289–294.

494 Clause, B. T. 1993. The Wistar Rat as a right choice: establishing mammalian standards and the
495 ideal of a standardized mammal. *Journal of the History of Biology* 26:329–349.

496 Datta, M. S., E. Sliwerska, J. Gore, M. F. Polz, and O. X. Cordero. 2016. Microbial interactions
497 lead to rapid micro-scale successions on model marine particles. *Nature Communications*.

498 de Jesús Astacio, L. M., K. H. Prabhakara, Z. Li, H. Mickalide, and S. Kuehn. 2020. Closed
499 microbial communities self-organize to persistently cycle carbon. *bioRxiv*.

500 Demery, A.-J. C., and M. A. Pipkin. 2021. Safe fieldwork strategies for at-risk individuals, their
501 supervisors and institutions. *Nature Ecology & Evolution* 5:5–9.

502 Denell, R. 2008. Establishment of *Tribolium* as a genetic model system and its early

503 contributions to evo-devo. *Genetics* 180:1779–1786.

504 Dewsbury, D. A. 2005. The Darwin-Bateman paradigm in historical context. *Integrative and*
505 *Comparative Biology* 45:831–837.

506 Dietrich, M. R., R. A. Ankeny, and P. M. Chen. 2014. Publication trends in model organism
507 research. *Genetics* 198:787–794.

508 Dietrich, M. R., R. A. Ankeny, N. Crowe, S. Green, and S. Leonelli. 2020. How to choose your
509 research organism. *Studies in History and Philosophy of Biological and Biomedical*
510 *Sciences* 80:101227.

511 Duan, S.-F., P.-J. Han, Q.-M. Wang, W.-Q. Liu, J.-Y. Shi, K. Li, X.-L. Zhang, et al. 2018. The
512 origin and adaptive evolution of domesticated populations of yeast from Far East Asia.
513 *Nature communications* 9:2690.

514 DuBay, S., D. H. Palmer, and N. Piland. 2020. Global inequity in scientific names and who they
515 honor. *bioRxiv*.

516 Ebert, D. 2011. A genome for the environment. *Science* 331:539–540.

517 Frézal, L., and M.-A. Félix. 2015. *C. elegans* outside the Petri dish. *eLife* 4.

518 Fugère, V., M.-P. Hébert, N. B. da Costa, C. C. Y. Xu, R. D. H. Barrett, B. E. Beisner, G. Bell, et
519 al. 2020. Community rescue in experimental phytoplankton communities facing severe
520 herbicide pollution. *Nature Ecology & Evolution* 4:578–588.

521 García-Robledo, C., and C. S. Baer. 2021. Demographic attritions, elevational refugia, and the
522 resilience of insect populations to projected global warming. *The American Naturalist*.

523 García-Robledo, C., E. K. Kuprewicz, C. L. Staines, T. L. Erwin, and W. J. Kress. 2016. Limited
524 tolerance by insects to high temperatures across tropical elevational gradients and the
525 implications of global warming for extinction. *Proceedings of the National Academy of*
526 *Sciences of the United States of America* 113:680–685.

527 Gewin, V. 2021. Respect and representation: Indigenous scientists seek inclusion for their
528 knowledge and for themselves. *Nature*.

529 Gilbert, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies.
530 *Proceedings of the National Academy of Sciences of the United States of America*
531 69:1403–1407.

532 Goldford, J. E., N. Lu, D. Bajić, S. Estrela, M. Tikhonov, A. Sanchez-Gorostiaga, D. Segrè, et al.
533 2018. Emergent simplicity in microbial community assembly. *Science* 361:469–474.

534 Golley, F. B. 1993. A history of the ecosystem concept in ecology: more than the sum of the
535 parts. Yale University Press.

536 Gordon, S. P., E. Burdfield-Steel, J. Kirvesoja, and J. Mappes. 2021. Safety in numbers: How
537 color morph frequency affects predation risk in an aposematic moth. *The American*
538 *Naturalist*.

539 Gowaty, P. A., Y.-K. Kim, and W. W. Anderson. 2012. No evidence of sexual selection in a
540 repetition of Bateman’s classic study of *Drosophila melanogaster*. *Proceedings of the*
541 *National Academy of Sciences of the United States of America* 109:11740–11745.

542 Grant, N. A., R. Maddamsetti, and R. E. Lenski. 2021. Maintenance of metabolic plasticity
543 despite relaxed selection in a long-term evolution experiment with *Escherichia coli*. *The*
544 *American Naturalist*.

545 Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin’s
546 finches. *Science* 296:707–711.

547 Grant, R. B. 2003. Evolution in Darwin’s Finches: a review of a study on Isla Daphne Major in
548 the Galápagos Archipelago. *Zoology* 106:255–259.

549 Graves, J. L. 2019. African Americans in evolutionary science: where we have been, and what's
550 next. *Evolution: Education and Outreach* 12:18.

551 Green, D. A. n.d. Monarch butterfly migration as an integrative model of complex trait
552 evolution. *The American Naturalist*.

553 Green, S., M. R. Dietrich, S. Leonelli, and R. A. Ankeny. 2018. "Extreme" organisms and the
554 problem of generalization: interpreting the Krogh principle. *History and Philosophy of the*
555 *Life Sciences* 40:65.

556 Griffiths, A. G., R. Moraga, M. Tausen, V. Gupta, T. P. Bilton, M. A. Campbell, R. Ashby, et al.
557 2019. Breaking Free: The Genomics of Allopolyploidy-Facilitated Niche Expansion in
558 White Clover. *The Plant cell* 31:1466–1487.

559 Halsey, S. J., L. R. Strickland, M. Scott-Richardson, T. Perrin-Stowe, and L. Massenburg. 2020.
560 Elevate, don't assimilate, to revolutionize the experience of scientists who are Black,
561 Indigenous and people of colour. *Nature Ecology & Evolution* 4:1291–1293.

562 Haraway, D. J. 1989. *Primate Visions: Gender, Race, and Nature in the World of Modern*
563 *Science*. Psychology Press.

564 Haraway, D. J. 1991. *Simians, cyborgs, and women: The reinvention of nature*. Routledge.

565 Harding, S. G. 1986. *The Science Question in Feminism*. Cornell University Press.

566 Hill, C., C. Corbett, and A. St Rose. 2010. *Why so few? Women in science, technology,*
567 *engineering, and mathematics*. American Association of University Women.

568 Hofstra, B., V. V. Kulkarni, S. Munoz-Najar Galvez, B. He, D. Jurafsky, and D. A. McFarland.
569 2020. The Diversity-Innovation Paradox in Science. *Proceedings of the National Academy*
570 *of Sciences of the United States of America* 117:9284–9291.

571 Holman, L., D. Stuart-Fox, and C. E. Hauser. 2018. The gender gap in science: How long until
572 women are equally represented? *PLoS Biology* 16:e2004956.

573 Hong, L., and S. E. Page. 2004. Groups of diverse problem solvers can outperform groups of
574 high-ability problem solvers. *Proceedings of the National Academy of Sciences of the*
575 *United States of America* 101:16385–16389.

576 Hoquet, T. 2020. Bateman's principles: why biology needs history and philosophy. *Animal*
577 *Behaviour* 168:e5–e9.

578 Hrdy, S. B. 1986. Empathy, polyandry, and the myth of the "coy" female. Pages 119–146 *in* R.
579 Bleier, ed. *Feminist approaches to science*. Pergamon Press.

580 Huang, J., A. J. Gates, R. Sinatra, and A.-L. Barabási. 2020. Historical comparison of gender
581 inequality in scientific careers across countries and disciplines. *Proceedings of the*
582 *National Academy of Sciences of the United States of America* 117:4609–4616.

583 Hutchinson, G. E. 1978. *An introduction to population ecology*. Yale University Press.

584 Ireland, D. T., K. E. Freeman, C. E. Winston-Proctor, K. D. DeLaine, S. McDonald Lowe, and
585 K. M. Woodson. 2018. (Un)Hidden Figures: A Synthesis of Research Examining the
586 Intersectional Experiences of Black Women and Girls in STEM Education. *Review of*
587 *Research in Education* 42:226–254.

588 Jaffe, K., J. C. Correa, and Z. Tang-Martínez. 2020. Ethology and animal behaviour in Latin
589 America. *Animal Behaviour* 164:281–291.

590 Jenner, R. A., and M. A. Wills. 2007. The choice of model organisms in evo-devo. *Nature*
591 *reviews. Genetics* 8:311–319.

592 Jones, F. C., M. G. Grabherr, Y. F. Chan, P. Russell, E. Mauceli, J. Johnson, R. Swofford, et al.
593 2012. The genomic basis of adaptive evolution in threespine sticklebacks. *Nature* 484:55–
594 61.

595 Kamath, A., and J. Losos. 2017. The erratic and contingent progression of research on
596 territoriality: a case study. *Behavioral Ecology and Sociobiology*.
597 ———. 2018. Reconsidering territoriality is necessary for understanding *Anolis* mating systems.
598 *Behavioral Ecology and Sociobiology*.
599 Kamath, A., and A. B. Wesner. 2020. Animal territoriality, property and access: a collaborative
600 exchange between animal behaviour and the social sciences. *Animal Behaviour*.
601 Katz, P. S. 2016. “Model organisms” in the light of evolution. *Current Biology* 26:R649–R650.
602 Keller, E. F. 1982. Feminism and Science. *Signs: Journal of Women in Culture and Society*
603 7:589–602.
604 Kohler, R. E. 1994. *Lords of the Fly: Drosophila Genetics and the Experimental Life*. University
605 of Chicago Press.
606 Krämer, U. 2015. Planting molecular functions in an ecological context with *Arabidopsis*
607 *thaliana*. *eLife* 4.
608 Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur, and E.
609 Bermingham. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest
610 dynamics plot in Panama. *Proceedings of the National Academy of Sciences of the United*
611 *States of America* 106:18621–18626.
612 Krogh, A. 1929. The progress of physiology. *Science* 70:200–204.
613 Lampert, W. 2011. *Daphnia: Development of a model organism in ecology and evolution*.
614 International Ecology Institute.
615 Lawrence, D., F. Fiegna, V. Behrends, J. G. Bundy, A. B. Phillimore, T. Bell, and T. G.
616 Barraclough. 2012. Species interactions alter evolutionary responses to a novel
617 environment. *PLoS Biology* 10:e1001330.
618 Lee, B.-Y., B.-S. Choi, M.-S. Kim, J. C. Park, C.-B. Jeong, J. Han, and J.-S. Lee. 2019. The
619 genome of the freshwater water flea *Daphnia magna*: A potential use for freshwater
620 molecular ecotoxicology. *Aquatic toxicology* 210:69–84.
621 Lee, D. N. 2020. Diversity and inclusion activisms in animal behaviour and the ABS: a historical
622 view from the U.S.A. *Animal Behaviour* 164:273–280.
623 Leonelli, S. 2007. Growing weed, producing knowledge: an epistemic history of *Arabidopsis*
624 *thaliana*. *History and Philosophy of the Life Sciences* 29:193–223.
625 Leonelli, S., and R. A. Ankeny. 2013. What makes a model organism? *Endeavour* 37:209–212.
626 Lewontin, R. C. 2001. *The Triple Helix: Gene, Organism, and Environment*. Harvard University
627 Press.
628 Liti, G. 2015. The fascinating and secret wild life of the budding yeast *S. cerevisiae*. *eLife* 4.
629 Losos, J. B. 2009. *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*.
630 University of California Press.
631 Lowry, D. B., J. M. Sobel, A. L. Angert, T. Ashman, R. L. Baker, B. K. Blackman, Y.
632 Brandvain, et al. 2019. The case for the continued use of the genus name *Mimulus* for all
633 monkeyflowers. *Taxon* 68:617–623.
634 Mackay, A. W., D. Adger, A. L. Bond, S. Giles, and E. Ochu. 2019. Straight-washing ecological
635 legacies. *Nature Ecology & Evolution* 3:1611.
636 Magurran, A. E. 2005. *Evolutionary Ecology: The Trinidadian Guppy*. Oxford University Press.
637 Malik, A. H., J. M. Ziermann, and R. Diogo. 2018. An untold story in biology: the historical
638 continuity of evolutionary ideas of Muslim scholars from the 8th century to Darwin’s
639 time. *Journal of biological education* 52:3–17.
640 Markow, T. A. 2015. The secret lives of *Drosophila* flies. *eLife* 4.

641 Marquis, R. J. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* 226:537–539.

642 Martin, L. J., B. Blossey, and E. Ellis. 2012. Mapping where ecologists work: biases in the
643 global distribution of terrestrial ecological observations. *Frontiers in Ecology and the*
644 *Environment* 10:195–201.

645 Matthews, B., T. Aebischer, K. E. Sullam, B. Lundsgaard-Hansen, and O. Seehausen. 2016.
646 Experimental evidence of an eco-evolutionary feedback during adaptive divergence.
647 *Current Biology* 26:483–489.

648 Matthews, B. J., and L. B. Vosshall. 2020. How to turn an organism into a model organism in 10
649 “easy” steps. *The Journal of Experimental Biology* 223.

650 Mavárez, J., C. A. Salazar, E. Bermingham, C. Salcedo, C. D. Jiggins, and M. Linares. 2006.
651 Speciation by hybridization in *Heliconius* butterflies. *Nature* 441:868–871.

652 McAllister, T. G., S. Naepi, E. Wilson, D. Hikuroa, and L. A. Walker. 2020. Under-represented
653 and overlooked: Māori and Pasifika scientists in Aotearoa New Zealand’s universities and
654 crown-research institutes. *Journal of the Royal Society of New Zealand* 1–16.

655 McGee, E. O. 2020. Interrogating Structural Racism in STEM Higher Education. *Educational*
656 *Researcher* 49:633–644.

657 McKenna, D. D., and B. D. Farrell. 2006. Tropical forests are both evolutionary cradles and
658 museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the*
659 *United States of America* 103:10947–10951.

660 McKinnon, J. S., and H. D. Rundle. 2002. Speciation in nature: the threespine stickleback model
661 systems. *Trends in ecology & evolution* 17:480–488.

662 Mickalide, H., and S. Kuehn. 2019. Higher-Order Interaction between Species Inhibits Bacterial
663 Invasion of a Phototroph-Predator Microbial Community. *Cell Systems*.

664 Milam, E. L. 2010. Looking for a Few Good Males: Female Choice in Evolutionary Biology.
665 JHU Press.

666 Montgomery, B. L. 2020a. Lessons from Microbes: What Can We Learn about Equity from
667 Unculturable Bacteria? *mSphere* 5.

668 ———. 2020b. Planting Equity: Using What We Know to Cultivate Growth as a Plant Biology
669 Community. *The Plant Cell* 32:3372–3375.

670 Muschiol, D., F. Schroeder, and W. Traunspurger. 2009. Life cycle and population growth rate
671 of *Caenorhabditis elegans* studied by a new method. *BMC Ecology* 9:14.

672 National Center for Science and Engineering Statistics (NCSES). 2019. *Doctorate Recipients*
673 *from U.S. Universities: 2019* (No. NSF 21-308).

674 Neff, E. P. 2020. Where the wild zebrafish are. *Lab animal* 49:305–309.

675 Parichy, D. M. 2015. Advancing biology through a deeper understanding of zebrafish ecology
676 and evolution. *eLife* 4.

677 Park, T. 1948. Experimental studies of interspecies competition. I. Competition between
678 populations of the flour beetles, *Tribolium confusum* Duvall and *Tribolium castaneum*
679 Herbst. *Ecological Monographs* 18:267–307.

680 Pauly, P. J. 1987. *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*. Oxford
681 University Press.

682 Penczykowski, R. M., and R. D. Sieg. n.d. *Plantago spp.* as models for studying the ecology and
683 evolution of species interactions across environmental gradients. *The American Naturalist*.

684 Phifer-Rixey, M., and M. W. Nachman. 2015. Insights into mammalian biology from the wild
685 house mouse *Mus musculus*. *eLife* 4.

686 Pinto-Tomás, A. A., M. A. Anderson, G. Suen, D. M. Stevenson, F. S. T. Chu, W. W. Cleland, P.

687 J. Weimer, et al. 2009. Symbiotic nitrogen fixation in the fungus gardens of leaf-cutter
688 ants. *Science* 326:1120–1123.

689 Platt, M. O. 2020. We exist. We are your peers. *Nature Reviews Materials* 5:783–784.

690 Raby, M. 2017. *American Tropics: The Caribbean Roots of Biodiversity Science*. UNC Press
691 Books.

692 Rader, K. 2004. *Making Mice: Standardizing Animals for American Biomedical Research, 1900-
693 1955*. Princeton University Press.

694 Replansky, T., V. Koufopanou, D. Greig, and G. Bell. 2008. *Saccharomyces sensu stricto* as a
695 model system for evolution and ecology. *Trends in Ecology & Evolution* 23:494–501.

696 Rettenmeyer, C. W. 1963. Behavioral studies of army ants. *University of Kansas Science
697 Bulletin* 44:281–465.

698 Richards, P. W. 1963. What the Tropics Can Contribute to Ecology. *The Journal of Ecology*.

699 Rillig, M. C., and J. Antonovics. 2019. Microbial biospherics: The experimental study of
700 ecosystem function and evolution. *Proceedings of the National Academy of Sciences of
701 the United States of America* 116:11093–11098.

702 Rocha, O. J., and E. Braker. 2021. The Organization for Tropical Studies: History,
703 accomplishments, future directions in education and research, with an emphasis in the
704 contributions to the study of plant reproductive ecology and genetics in tropical
705 ecosystems. *Biological Conservation* 253:108890.

706 Rojas, B., E. Burdfield-Steel, C. De Pasqual, S. Gordon, L. Hernández, J. Mappes, O.
707 Nokelainen, et al. 2018. Multimodal aposematic signals and their emerging role in mate
708 attraction. *Frontiers in Ecology and Evolution* 6.

709 Rushworth, C. A., R. S. Baucom, B. K. Blackman, M. Neiman, M. E. Orive, A. Sethuraman, J.
710 Ware, et al. 2021. Who are we now? A demographic assessment of three evolution
711 societies. *Evolution*.

712 Sanchez, A., S. Estrela, and M. Rebolleda-Gomez. 2021. Multi-replicated enrichment
713 communities as a model system in microbial ecology.

714 Schell, C. J., C. Guy, D. S. Shelton, S. C. Campbell-Staton, B. A. Sealey, D. N. Lee, and N. C.
715 Harris. 2020. Recreating Wakanda by promoting Black excellence in ecology and
716 evolution. *Nature Ecology & Evolution* 4:1285–1287.

717 Sensoy, Ö., and R. DiAngelo. 2017. “We Are All for Diversity, but . . .”: How Faculty Hiring
718 Committees Reproduce Whiteness and Practical Suggestions for How They Can Change.
719 *Harvard Educational Review* 87:557–580.

720 Shansky, R. M. 2019. Are hormones a “female problem” for animal research? *Science* 364:825–
721 826.

722 Snyder, B. F., and P. A. Gowaty. 2007. A reappraisal of Bateman’s classic study of intrasexual
723 selection. *Evolution* 61:2457–2468.

724 Stevens, K. R., K. S. Masters, P. I. Imoukhuede, K. A. Haynes, L. A. Setton, E. Cosgriff-
725 Hernandez, M. A. Lediju Bell, et al. 2021. Fund Black scientists. *Cell*.

726 Stewart, A. J., and V. Valian. 2018. *An Inclusive Academy*. MIT Press.

727 Stocks, G., L. Seales, F. Paniagua, E. Maehr, and E. M. Bruna. 2008. The geographical and
728 institutional distribution of ecological research in the tropics: The geography of tropical
729 ecology. *Biotropica* 40:397–404.

730 Stone, D. E. 1988. The Organization for Tropical Studies (OTS): a success story in graduate
731 training and research. Pages 143–187 in F. Aldemeda and C. M. Pringle, eds. *Tropical
732 Rainforest Diversity and Conservation*. California Academy of Sciences and Pacific

733 Division, AAAS, San Francisco.

734 Strong, D. R. 1977. Insect Species Richness: Hispine beetles of *Heliconia latispatha*. *Ecology*

735 58:573–582.

736 Tang-Martínez, Z. 2016. Rethinking Bateman’s Principles: Challenging Persistent Myths of

737 Sexually Reluctant Females and Promiscuous Males. *Journal of Sex Research* 53:532–

738 559.

739 Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and

740 productivity in a long-term grassland experiment. *Science* 294:843–845.

741 Travis, J. 2006. Is it what we know or who we know? Choice of organism and robustness of

742 inference in ecology and evolutionary biology. *The American Naturalist* 167:303–314.

743 Tribolium Genome Sequencing Consortium, S. Richards, R. A. Gibbs, G. M. Weinstock, S. J.

744 Brown, R. Denell, R. W. Beeman, et al. 2008. The genome of the model beetle and pest

745 *Tribolium castaneum*. *Nature* 452:949–955.

746 Tseng, M., R. W. El-Sabaawi, M. B. Kantar, J. H. Pantel, D. S. Srivastava, and J. L. Ware. 2020.

747 Strategies and support for Black, Indigenous, and people of colour in ecology and

748 evolutionary biology. *Nature Ecology & Evolution* 4:1288–1290.

749 Tydecks, L., V. Bremerich, I. Jentschke, G. E. Likens, and K. Tockner. 2016. Biological Field

750 Stations: A Global Infrastructure for Research, Education, and Public Engagement.

751 *Bioscience* 66:164–171.

752 US Fish & Wildlife Service,. 2018. *Zebra Danio (Danio rerio) Ecological risk screening*

753 *summary*.

754 Valantine, H. A., P. K. Lund, and A. E. Gammie. 2016. From the NIH: A Systems Approach to

755 Increasing the Diversity of the Biomedical Research Workforce. *CBE Life Sciences*

756 *Education* 15.

757 Wale, N., and M. A. Duffy. 2021. The use and underuse of model systems in infectious disease

758 ecology & evolutionary biology. *The American Naturalist*.

759 Wall Kimmerer, R. 2013. Braiding Sweetgrass. Milkweed Editions.

760 Wilf, P., C. C. Labandeira, W. J. Kress, C. L. Staines, D. M. Windsor, A. L. Allen, and K. R.

761 Johnson. 2000. Timing the radiations of leaf beetles: hispines on gingers from latest

762 cretaceous to recent. *Science* 289:291–294.

763 Wu, C. A., D. B. Lowry, A. M. Cooley, K. M. Wright, Y. W. Lee, and J. H. Willis. 2008.

764 *Mimulus* is an emerging model system for the integration of ecological and genomic

765 studies. *Heredity* 100:220–230.

766 Yen, E. C., S. A. McCarthy, J. A. Galarza, T. N. Generalovic, S. Pelan, P. Nguyen, J. I. Meier, et

767 al. 2020. A haplotype-resolved, de novo genome assembly for the wood tiger moth (*Arctia*

768 *plantaginis*) through trio binning. *GigaScience* 9.

769 Zakhartsev, M., and M. Reuss. 2018. Cell size and morphological properties of yeast

770 *Saccharomyces cerevisiae* in relation to growth temperature. *FEMS Yeast Research* 18.

771 Zalucki, M. P., and A. R. Clarke. 2004. Monarchs across the Pacific: the Columbus hypothesis

772 revisited. *Biological Journal of the Linnean Society* 82:111–121.

773 Zea, M. C., and L. Bowleg. 2016. The Final Frontier-Transitions and Sustainability: From

774 Mentored to Independent Research. *AIDS and Behavior* 20 Suppl 2:311–317.

775 Zhan, S., W. Zhang, K. Niitepöld, J. Hsu, J. F. Haeger, M. P. Zalucki, S. Altizer, et al. 2014. The

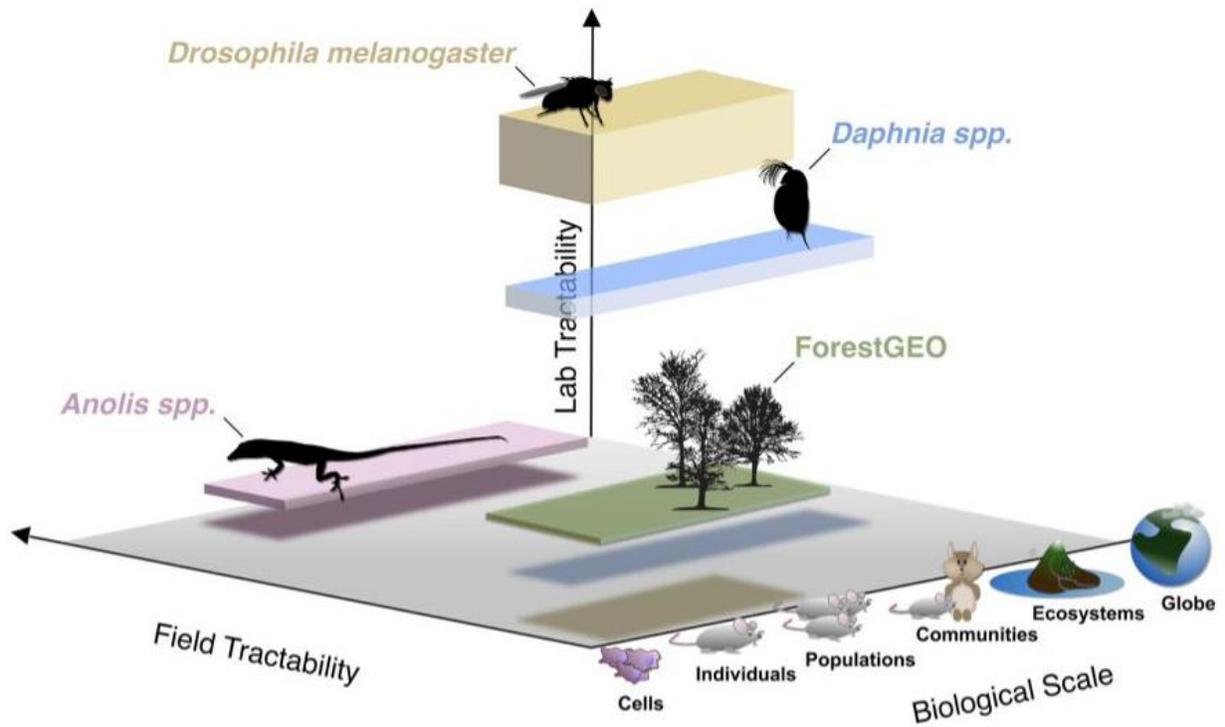
776 genetics of monarch butterfly migration and warning colouration. *Nature* 514:317–321.

777 Zhan, S., W. Zhang, K. Niitepöld, J. Hsu, J. F. Haeger, M. P. Zalucki, S. Altizer, et al. 2014. The

778 genetics of monarch butterfly migration and warning colouration. *Nature* 514(7522):317-

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782
 783 **Figure 1. Model systems in EEB vary along a number of axes, including their tractability**
 784 **for field studies and for lab studies, and the biological scales at which they are typically**
 785 **studied.** This multidimensional view of space that model systems occupy harkens back to
 786 Hutchinson’s concept of the niche and his classic depiction of squirrels in an *n-dimensional*
 787 *hypervolume* (1978). A model system's position in this space influences the questions it is best
 788 suited to address. Further extending the Hutchinsonian metaphor, the *realized* space of a model
 789 system depends on both the biological features (i.e., *fundamental* aspects) and on the history of
 790 accumulated knowledge and techniques related to a particular system. In this figure, we represent
 791 approximately where a subset of common model systems in EEB fall along these three axes (c.f.,
 792 Table S1). Organism silhouettes are from PhyloPic and 4vector.
 793

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

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

800

801 *Individual attributes*

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

807

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

814

815 Developing model systems also requires being a good collaborator, mentor, and communicator.

816 Collaboration will promote studies on the same system by multiple researchers, which is required

817 for building the depth of knowledge needed in order to achieve the “model system” designation.
818 These collaborations are facilitated by a culture of openly sharing data, protocols, and other
819 materials (Ankeny and Leonelli 2020; Matthews and Vosshall 2020) and by strong
820 communication skills. A scientist who has an amazing vision but is unable to communicate that
821 with others (including potential funders, collaborators, students, and others) will have limited
822 impact. Networking skills are also useful, as they can help develop connections that allow for
823 new lines of study on a particular system and that recruit more people to work on the system.

824

825 *Institutional and structural attributes*

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

832

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

837

838 A related factor is that there need to be structures in place that protect an individual researcher
839 from the impacts of failures, such as job stability, supportive mentors, and other systems (e.g.,

840 evaluating candidates based on a few publications of their choosing rather than their total number
841 of publications). It is not clear whether there is a particular time in one's career where it is "best"
842 to develop a new model system; some researchers begin developing them relatively early in their
843 careers, while others wait until they have already established themselves. As with so many
844 things, a wide range of circumstances (not to mention serendipity) will play an important role in
845 the timing.

846

847 *Organism or study system attributes*

848 Some organisms (or communities or ecosystems) are more readily established as model systems,
849 based on factors such as ease of working with them in the field and/or lab, generation time,
850 organism size, and population abundances. An organism that is small, abundant, reproduces
851 quickly, and grows well in the field and the lab will be much easier to establish as a model
852 system than an organism that is large, rare, difficult to grow, and with long generation times.
853 Crucially, this leads to significant gaps in our existing model systems (and knowledge), as we
854 discuss more in the main text.

855

856 *Using existing systems in novel ways*

857 There is strong overlap between the skills needed to develop a model system and those needed to
858 take an existing system and use it in a novel way, including insightfulness, a sense of where the
859 field is heading, and good communication skills. Two additional attributes that are particularly
860 important for using model systems in innovative ways are creativity and big picture thinking,
861 both of which enable a scientist to see beyond the scope of how a system has been used in the
862 past. Without these, it is easy to remain within the confines of what has already been done, rather

863 than to use those as a foundation for a leap off in a new and exciting direction. Some useful
864 questions to ask in the context of taking existing systems in new directions include: Are there
865 modes of inquiry from other disciplines or modes of thought that could be newly applied to this
866 system? How could our knowledge of an existing system change as a result of these new
867 perspectives?

868

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

874

875 **Box 2. Model systems in the tropics**

876 The establishment of model systems in the tropics was strongly influenced by sociopolitical
877 context and ease of access to researchers from the United States. As a result of the Spanish-
878 American war the U.S colonized not only Cuba, but Puerto Rico, Guam, and the Philippines. In
879 1904, the U.S. took formal control of the Panama Canal after actively supporting the separation
880 of Panama from Colombia. Aided by the increased influence and control in the region, U.S.
881 institutions established different research sites in Central America and the Caribbean (e.g.
882 Cinchona in Jamaica, the Harvard Botanical Garden in Cuba, and Barro Colorado Island in the
883 Panama Canal region) (Raby 2017).

884

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

892

893 OTS has offered the field course “Fundamentals of Tropical Biology” since 1961. The origin and
894 popularization of many tropical model systems can be traced to research performed in OTS field
895 stations and OTS field courses. Examples of classic model systems developed in OTS stations
896 include *Heliconius* butterflies, *Piper* shrubs, army ants, interactions between leafcutter ants and
897 associated microorganisms, and interactions between Zingiberales “banana-like plants” and
898 rolled-leaf beetles (Rettenmeyer 1963; Gilbert 1972; Strong 1977; Marquis 1984). This history
899 helps explain why studies in Costa Rica are highly overrepresented given its size (Stocks et al.
900 2008; Martin et al. 2012).

901

902 Many tropical model systems, including those still in use today, were developed by researchers
903 from the Global North. While there is still a problem of underrepresentation of people from
904 tropical countries as active participants in the science conducted there (Stocks et al. 2008), the
905 efforts of OTS to promote inclusion of tropical scientists for over 50 years has led to a growing
906 number of researchers from the Global South working on these classical tropical systems
907 (Chaves-Campos 2003; Mavárez et al. 2006; Pinto-Tomás et al. 2009; García-Robledo et al.

908 2016). Although many scientists in the Global South are playing central roles in research
909 involving classic tropical model systems, men continue to outnumber women (Hill et al. 2010).
910 In addition to the stereotypes and implicit biases that reduce participation of minorities in STEM,
911 Latina scientists have to face the challenges associated with culturally ingrained masculine pride
912 (“machismo”) (Bernal et al. 2019).

913

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

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

918

919 *Evaluating currently used systems*

920 Step 1: Identify the key processes and phenomena of interest to a subdiscipline. For example,
921 existing theory on the ecology and evolution of infectious diseases (e.g., early work by Anderson
922 & May) points to three processes — transmission, disease, and recovery — as fundamental.
923 Making these key processes and phenomena explicit also allows for researchers to add or modify
924 them, which can be an important way in which research in a subdiscipline progresses.

925

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

931
932 Step 3: Using the results from step 2, evaluate whether the systems currently in use in that
933 subdiscipline are capturing a wide range of parameter space for the processes of interest. Can the
934 systems currently in use illuminate core themes and processes for that subdiscipline (Jenner and
935 Wills 2007)?

936
937 Step 4: What are the underlying assumptions about existing model systems? Have those
938 assumptions been tested?

939
940 Step 5: Consider whether, in addition to the key processes identified, there are other notable gaps
941 in the model systems currently in use. One that is likely to be true in many subdisciplines is that
942 existing model systems might come from a relatively restricted geographical area, or may
943 represent only certain life history traits (Table S1). We propose considering how broadly you can
944 apply knowledge using current systems. Does it only tell you about a certain type of organism or
945 ones that live in certain locales? How well is the parameter space in Figure 1 covered? Similar to
946 what is often done with mathematical models, it is important to be explicit about what our model
947 systems represent and, even more importantly, what they do not represent.

948
949 *Steps to take if (or, more likely, when) gaps are identified*

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

- 952 1. Are there model systems in use in other areas of ecology, evolutionary biology, and
953 behavior (or, if not, other areas of biology) that can help fill those gaps?

- 954 2. Are there nascent study systems that are promising — for example, ones that have been
955 studied in nature for a long time but that would benefit from development of novel
956 molecular tools?
- 957 3. Can the model systems under consideration be manipulated and studied on the time
958 scales of a PhD program or while an assistant professor? If not, how have others who
959 work on organisms or processes with longer time scales approached those questions?
- 960 4. Can museum collections be of use, including to extend temporal and/or spatial scales?
- 961 5. What sources of information might exist outside that typically considered by Western
962 scientists? Are there other historical records (e.g., phenological data collected by
963 community scientists, or existing photo or video collections) that can be used to address
964 the question? What do local communities already know about the system? What work has
965 been done on the topic by non-Western scholars (including work published in languages
966 other than English)?

967

968 *Checkpoint:* When considering the development of a new potential model system, it is essential
969 to ask whether it will be done in a way that increases or decreases inequity? Unfortunately, there
970 is a long history of extractive practices that reinforce colonialism and imperialism (DuBay et al.
971 2020; Gewin 2021), of research that “discovers” things that were already well known in local
972 communities (e.g., Cañizares-Esguerra 2019), and of research that ignores the contribution of
973 non-Western scientists (e.g., Malik et al. 2018).

974

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

978

979 **Box 4. Additional considerations for early career researchers**

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

984

985 A key challenge for early career scientists is how to differentiate from previous mentors and
986 other established groups. How does a seedling lab carve out their space in a crowded forest?
987 Even in cases where the community working on a particular model system is welcoming and
988 eager to share resources, early career researchers face challenges in establishing their
989 independent groups. The reality is likely to be that seedling labs will have relatively few
990 resources (in terms of both people and funding), while the research forest might have some large
991 trees that cast a very broad shadow. And, unfortunately, the research environment for particular
992 model systems is not always welcoming, especially for early career scientists who do not fit the
993 traditional “model scientist” mold.

994

995 As a result, in some cases, early career scientists will decide that the best path forward is to
996 establish a new model system, or to take an existing model system and use it in a very different
997 way. This has the advantage of avoiding competition. Establishing a new system (or using an

998 existing one in a very different way) also can mean that work on a particular system (or in a
999 particular subdiscipline) is done by diverse scientists from the start, with the potential to
1000 establish a healthy, equitable, and inclusive culture right from the beginning.
1001
1002 However, as always in ecology and evolution and in life, there are tradeoffs. While there are
1003 advantages to establishing new systems, there are also important drawbacks. First, there is a
1004 larger-than-average chance of failure when trying to do something completely new; deciding
1005 whether to take on this risk at a particularly vulnerable career stage will require careful thought.
1006 Second, establishing new systems will require funding, including for natural history work and for
1007 work that is high risk/high reward, neither of which are well-supported in current funding
1008 climates (as also mentioned in Box 1).

1009
1010

1011 **References associated with Table S1:**

1012 *E. coli*: (Blount 2015)
1013 *S. cerevisiae*: (Replansky et al. 2008; Liti 2015; Duan et al. 2018; Zakhartsev and Reuss 2018)
1014 Microbial self-assembled communities: (Sanchez et al. 2021)
1015 Protist microcosms: (Altermatt et al. 2015)
1016 *C. elegans*: (Muschiol et al. 2009; Frézal and Félix 2015)
1017 *D. melanogaster*: (Markow 2015)
1018 *Daphnia spp.*: (Ebert 2011; Lampert 2011; Lee et al. 2019)
1019 *Cephaloleia spp.* (rolled leaf beetles): (Wilf et al. 2000; McKenna and Farrell 2006; García-
1020 Robledo et al. 2016)
1021 *D. rerio* (zebrafish): (Parichy 2015; US Fish & Wildlife Service, 2018; Neff 2020)
1022 *P. reticulata* (guppy): (Magurran 2005)
1023 *G. aculeatus* (three-spined stickleback): (McKinnon and Rundle 2002; Jones et al. 2012)
1024 *A. plantaginis* (wood tiger moth): (Rojas et al. 2018; Yen et al. 2020; Gordon et al. 2021)
1025 *Tribolium*: (Park 1948; Denell 2008; Tribolium Genome Sequencing Consortium et al. 2008)
1026 *D. plexippus* (monarch butterfly): (Green n.d.; Zalucki and Clarke 2004; Zhan et al. 2014)
1027 *Anolis* lizards: (Losos 2009)
1028 *Mimulus*: (Wu et al. 2008; Lowry et al. 2019)
1029 *Arabidopsis*: (Krämer 2015)

- 1030 *Trifolium*: (Griffiths et al. 2019)
- 1031 Cedar Creek: (Tilman et al. 2001)
- 1032 Galápagos finches: (Grant and Grant 2002; Grant 2003)
- 1033 *Plantago*: (Penczykowski and Sieg n.d.)
- 1034 *Mus musculus*: (Phifer-Rixey and Nachman 2015)
- 1035 *Peromyscus*: (Bedford and Hoekstra 2015)
- 1036 Barro Colorado Island: (Kress et al. 2009)
- 1037 ForestGEO: (Anderson-Teixeira et al. 2015)
- 1038

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 & manipulations	Degree to which system is studied in the context of its natural history	Major biological scale(s) of study	Key references
<i>Escherichia coli</i>	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)
<i>Saccharomyces cerevisiae</i>	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)
<i>Caenorhabditis elegans</i>	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)
<i>Drosophila melanogaster</i> (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)
<i>Daphnia spp.</i> (water flea)	Crustacean	Aquatic (freshwater)	All continents except Antarctica	All continents except Antarctica	Days	10 ⁻³	Yes (<i>D. pulex</i> & <i>D. magna</i>)	High	Low	Moderate	Mixed	Cellular, individual, population, community, ecosystem	(Ebert 2011; Lampert 2011; Lee et al. 2019)
<i>Cephaloleia spp.</i> (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)
<i>Danio rerio</i> (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)
<i>Poecilia reticulata</i> (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)
<i>Gasterosteus aculeatus</i> (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)
<i>Arctia plantaginis</i> (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)
<i>Tribolium castaneum</i> & <i>T. confusum</i> (flour beetles)	Insect	Terrestrial	Africa, Asia, Oceania	Global	~1 month	10 ⁻²	Yes for <i>T. castaneum</i>	Moderate	Moderate	Moderate	High	Individual, population, and community	(Park 1948; Denell 2008; Tribolium Genome Sequencing Consortium et al. 2008)
<i>Danaus plexippus</i> (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)
<i>Anolis</i> 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)
<i>Mimulus guttatus</i> / <i>Erythranthe guttata</i> (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)

<i>Arabidopsis thaliana</i> (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)
<i>Trifolium repens</i> (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)
<i>Plantago lanceolata</i> and <i>P. major</i> (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.)
<i>Mus musculus</i> (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)
<i>Peromyscus</i> 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 Māori of New Zealand have a traditional name for the monarch butterfly ("kākāhū") (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.

Table References:

- Altermatt, F., E. A. Fronhofer, A. Garnier, A. Giometto, F. Hammes, J. Klecka, D. Legrand, et al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution* 6:218–231.
- Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. J. Wright, K. Abu Salim, et al. 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* 21:528–549.
- Barker, W. R., Nesom, G.L., Beardsley, P.M., and N. S. Fraga. 2012. A taxonomic conspectus of *Phrymaceae*: A narrowed circumscription for *Mimulus*, new and resurrected genera, and new names and combinations. *Phytoneuron* 39:1–60.
- Bedford, N. L., and H. E. Hoekstra. 2015. *Peromyscus* mice as a model for studying natural variation. *eLife* 4.
- Blount, Z. D. 2015. The unexhausted potential of *E. coli*. *eLife* 4.
- Denell, R. 2008. Establishment of *Tribolium* as a genetic model system and its early contributions to evo-devo. *Genetics* 180:1779–1786.
- Duan, S.-F., P.-J. Han, Q.-M. Wang, W.-Q. Liu, J.-Y. Shi, K. Li, X.-L. Zhang, et al. 2018. The origin and adaptive evolution of domesticated populations of yeast from Far East Asia. *Nature communications* 9:2690.
- Ebert, D. 2011. A genome for the environment. *Science* 331:539–540.
- Frézal, L., and M.-A. Félix. 2015. *C. elegans* outside the Petri dish. *eLife* 4.
- García-Robledo, C., E. K. Kuprewicz, C. L. Staines, T. L. Erwin, and W. J. Kress. 2016. Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proceedings of the National Academy of Sciences of the United States of America* 113:680–685.
- Gordon, S. P., E. Burdfield-Steel, J. Kirvesoja, and J. Mappes. 2021. Safety in numbers: How color morph frequency affects predation risk in an aposematic moth. *The American Naturalist*.
- Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- Grant, R. B. 2003. Evolution in Darwin's Finches: a review of a study on Isla Daphne Major in the Galápagos Archipelago. *Zoology* 106:255–259.
- Green, D. A. n.d. Monarch butterfly migration as an integrative model of complex trait evolution. *The American Naturalist*.
- Griffiths, A. G., R. Moraga, M. Tausen, V. Gupta, T. P. Bilton, M. A. Campbell, R. Ashby, et al. 2019. Breaking Free: The Genomics of Allopolyploidy-Facilitated Niche Expansion in White Clover. *The Plant cell* 31:1466–1487.
- Jones, F. C., M. G. Grabherr, Y. F. Chan, P. Russell, E. Mauceli, J. Johnson, R. Swofford, et al. 2012. The genomic basis of adaptive evolution in threespine sticklebacks. *Nature* 484:55–61.
- Krämer, U. 2015. Planting molecular functions in an ecological context with *Arabidopsis thaliana*. *eLife* 4.
- Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur, and E. Bermingham. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proceedings of the National Academy of Sciences of the United States of America* 106:18621–18626.
- Lampert, W. 2011. *Daphnia*: Development of a model organism in ecology and evolution. International Ecology Institute.
- Lee, B.-Y., B.-S. Choi, M.-S. Kim, J. C. Park, C.-B. Jeong, J. Han, and J.-S. Lee. 2019. The genome of the freshwater water flea *Daphnia magna*: A potential use for freshwater molecular ecotoxicology. *Aquatic toxicology* 210:69–84.
- Liti, G. 2015. The fascinating and secret wild life of the budding yeast *S. cerevisiae*. *eLife* 4.
- Losos, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press.
- Lowry, D. B., J. M. Sobel, A. L. Angert, T. Ashman, R. L. Baker, B. K. Blackman, Y. Brandvain, et al. 2019. The case for the continued use of the genus name *Mimulus* for all monkeyflowers. *Taxon* 68:617–623.
- Magurran, A. E. 2005. *Evolutionary Ecology: The Trinidadian Guppy*. Oxford University Press.
- Markow, T. A. 2015. The secret lives of *Drosophila* flies. *eLife* 4.
- McKenna, D. D., and B. D. Farrell. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America* 103:10947–10951.
- McKinnon, J. S., and H. D. Rundle. 2002. Speciation in nature: the threespine stickleback model systems. *Trends in ecology & evolution* 17:480–488.
- Muschiol, D., F. Schroeder, and W. Traunspurger. 2009. Life cycle and population growth rate of *Caenorhabditis elegans* studied by a new method. *BMC Ecology* 9:14.
- Neff, E. P. 2020. Where the wild zebrafish are. *Lab animal* 49:305–309.
- Parichy, D. M. 2015. Advancing biology through a deeper understanding of zebrafish ecology and evolution. *eLife* 4.
- Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duvall and *Tribolium castaneum* Herbst. *Ecological Monographs* 18:267–307.
- Penczykowski, R. M., and R. D. Sieg. n.d. *Plantago* spp. as models for studying the ecology and evolution of species interactions across environmental gradients. *The American Naturalist*.
- Phifer-Rixey, M., and M. W. Nachman. 2015. Insights into mammalian biology from the wild house mouse *Mus musculus*. *eLife* 4.
- Replansky, T., V. Koufopanou, D. Greig, and G. Bell. 2008. *Saccharomyces sensu stricto* as a model system for evolution and ecology. *Trends in Ecology & Evolution* 23:494–501.
- Rojas, B., E. Burdfield-Steel, C. De Pasqual, S. Gordon, L. Hernández, J. Mappes, O. Nokelainen, et al. 2018. Multimodal aposematic signals and their emerging role in mate attraction. *Frontiers in Ecology and Evolution* 6.
- Sanchez, A., S. Estrela, and M. Rebolledo-Gomez. 2021. Multi-replicated enrichment communities as a model system in microbial ecology.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Tribolium Genome Sequencing Consortium, R. A. Gibbs, G. M. Weinstock, S. J. Brown, R. Denell, R. W. Beeman, et al. 2008. The genome of the model beetle and pest *Tribolium castaneum*. *Nature* 452:949–955.
- US Fish & Wildlife Service,. 2018. *Zebra Danio (Danio rerio) Ecological risk screening summary*.
- Wilf, P., C. C. Labandeira, W. J. Kress, C. L. Staines, D. M. Windsor, A. L. Allen, and K. R. Johnson. 2000. Timing the radiations of leaf beetles: hispines on gingers from latest cretaceous to recent. *Science* 289:291–294.
- Wu, C. A., D. B. Lowry, A. M. Cooley, K. M. Wright, Y. W. Lee, and J. H. Willis. 2008. *Mimulus* is an emerging model system for the integration of ecological and genomic studies. *Heredity* 100:220–230.
- Yen, E. C., S. A. McCarthy, J. A. Galarza, T. N. Generalovic, S. Pelan, P. Nguyen, J. I. Meier, et al. 2020. A haplotype-resolved, de novo genome assembly for the wood tiger moth (*Arctia plantaginis*) through trio binning. *GigaScience* 9.
- Zakhartsev, M., and M. Reuss. 2018. Cell size and morphological properties of yeast *Saccharomyces cerevisiae* in relation to growth temperature. *FEMS Yeast Research* 18.
- Zalucki, M. P., and A. R. Clarke. 2004. Monarchs across the Pacific: the Columbus hypothesis revisited. *Biological Journal of the Linnean Society* 82:111–121.
- Zhan, S., W. Zhang, K. Niitepöld, J. Hsu, J. F. Haeger, M. P. Zalucki, S. Altizer, et al. 2014. The genetics of monarch butterfly migration and warning colouration. *Nature* 514:317–321.