

Manuscript intended as a *Viewpoint* for the special issue “Exploring the border between ecology and evolution” in *Ecology Letters*

Beyond adaptation: Incorporating other evolutionary processes and concepts into eco-evolutionary dynamics

Last revision: September 28, 2022

Authors

Masato Yamamichi^{1,2,*}, Stephen P. Ellner^{3,§}, Nelson G. Hairston Jr.^{3,¶}

¹School of Biological Sciences, The University of Queensland, St. Lucia, Brisbane, QLD 4072, Australia

²Department of International Health and Medical Anthropology, Institute of Tropical Medicine, Nagasaki University, 1-12-4 Sakamoto, Nagasaki 852-8523, Japan

³Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

*Email: m.yamamichi@uq.edu.au, Tel: +61-7-3365-1864, ORCID: 0000-0003-2136-3399

§ORCID: 0000-0002-8351-9734, ¶ORCID: 0000-0002-0615-9843

Running title | Eco-evolutionary dynamics with various evolutionary concepts

Keywords | evolutionary branching, evolutionary rescue and suicide, extinction vortex, genetic drift, hard and soft selection, mutation, rapid evolution, relative and absolute fitness, sexual selection and conflict, speciation reversal

Type of Article | Viewpoint

Abstract word count | 150, **Main text word count** | 2022

No. of figures, tables, and boxes | 0, **Number of citations** | 71

Authorship | MY conceived the study and wrote the first draft of the manuscript. All authors contributed substantially to writing.

Abstract

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes at multiple scales (populations, communities, and ecosystems) and with multiple interspecific interactions (antagonistic, mutualistic, and competitive). However, evolution has often been conceptualized as a single process: short-term adaptive genetic change driven by natural selection. Here we argue that other diverse evolutionary processes should also be considered, to explore the full spectrum of feedbacks between ecological and evolutionary processes. Relevant but underappreciated processes include (1) drift and mutation, (2) disruptive selection causing lineage diversification or speciation reversal, (3) evolution driven by relative fitness differences that may decrease population growth, and (4) topics including multilevel selection, sexual selection and conflict, hard and soft selection, and genetic/genomic architectures/signatures. Because natural selection is not the sole mechanism of rapid evolution, it will be important to integrate a variety of concepts in evolutionary biology and ecology to better understand and predict eco-evolutionary dynamics in nature.

Main text

Ecologists have revealed that microevolution (i.e., allele frequency changes over a few generations) can be rapid enough to affect contemporary ecological processes (e.g., Pimentel 1961; Thompson 1998; Yoshida *et al.* 2003; Hairston *et al.* 2005; Fussmann *et al.* 2007; Schoener 2011; Hendry 2016; Bassar *et al.* 2021; Rudman *et al.* 2022). Although ecology and evolutionary biology have been neighboring research areas from the age of Darwin, the prevailing assumption had long been that ecological processes occur much faster than evolutionary processes (Darwin 1859; Slobodkin 1961). Thus, the idea of concurrent ecological and evolutionary dynamics and the feedbacks between them is exciting not only for synthesizing the two basic scientific disciplines, but also for its applied aspects, such as the need to predict future eco-evolutionary responses to ongoing environmental change (Gomulkiewicz & Holt 1995; Kinnison & Hairston 2007; Hoffmann & Sgrò 2011).

Studies of eco-evolutionary dynamics have integrated evolution with ecological processes operating at the population (Yoshida *et al.* 2003; Coulson *et al.* 2017), community (Johnson & Stinchcombe 2007), and ecosystem scales (Matthews *et al.* 2011). Researchers have also considered the interplay of eco-evolutionary dynamics in the context of multiple types of interspecific interactions including antagonistic (Post & Palkovacs 2009), mutualistic (Jones *et al.* 2009; Northfield & Ives 2013), and competitive (Hart *et al.* 2019; Pastore *et al.* 2021) interactions.

However, evolution in this framework has typically been reduced conceptually to a single process: short-term adaptive evolution driven by natural selection (Bassar *et al.* 2021), with an emphasis (at least initially) on situations where rapid adaptation to a detrimental change in the biotic or abiotic environment prevents population decline and possible extinction (Bell 2017). This may be a historical legacy from early studies of rapid evolution, that often involved adaptive evolution driven by trophic interactions. For example, a majority

of the studies of rapid evolution tabulated by Thompson (1998) involved gain or loss of defense traits — gains in response to selection pressure from predators or pathogens or losses when a threat is diminished (presumably to avoid an unnecessary cost of defense). Most of the other examples involve either the other end of a trophic interaction, rapid consumer or pathogen evolution to improve exploitation of available prey or hosts, or evolution of resistance to chemicals such as environmental toxins, herbicides and pesticides, and antibiotics.

Here we propose that it will be useful to conceptualize eco-evolutionary dynamics more broadly, integrating other kinds of evolutionary processes (including non-adaptive evolution) to understand better the full spectrum of feedbacks between ecology and evolution.

Drift and Mutation: The four fundamental processes in evolutionary dynamics are selection, migration, drift, and mutation. Selection (as noted above) and to a lesser extent migration (e.g., Farkas *et al.* 2013) have received due attention, but drift and mutation have been relatively neglected in studies of eco-evolutionary dynamics. Theory (Snyder & Ellner 2018; Snyder *et al.* 2021) and experimental data (Liu *et al.* 2019) suggest that the magnitude of random genetic drift is often far above that predicted by standard population genetic (Wright-Fisher or Moran) models. Even under tightly controlled laboratory conditions, Liu *et al.* (2019) found that the drift-effective population size for caged *Drosophila* populations was roughly 10 times smaller than the actual population size, because a small fraction of individuals (for unknown reasons, unrelated to genotype) monopolized reproduction. Such extreme reproductive skew is also seen in natural populations, for example Chen *et al.* (2019) observed vast variation in lifetime reproduction within one Florida scrub jay population, the top 10 individuals producing more total nestlings than the bottom 200, which could not be

ascribed to any known genetic differences between individuals. Whereas, the primary message of rapid evolution is that the deterministic component of evolutionary change is much larger than we formerly imagined, it may be equally true that the random component of evolutionary change is also much larger than we currently imagine, and too large to ignore when projecting evolutionary responses to changed ecological conditions.

Drift can also mediate eco-evolutionary feedback between population dynamics and deleterious mutations. For example, extinction vortex and mutational meltdown (Gilpin & Soulé 1986; Lynch & Lande 1993) is a positive feedback between decreased population density and greater fixation of deleterious mutations due to genetic drift. Once population density has decreased sufficiently, eco-evolutionary feedback drives extinction. Although the concept of an extinction vortex itself is not new, it will be intriguing to measure the speed of evolution driven by genetic drift and consider a conceptual eco-evolutionary framework incorporating selection and drift (Nabutanyi & Wittmann 2021). This will be especially important when studying eco-evolutionary dynamics in large organisms with small population sizes (e.g., Campbell-Staton *et al.* 2021) and in metapopulation and metacommunity dynamics with many small populations in separated habitats (De Meester *et al.* 2019) as the classical shifting balance theory (Wright 1982) implies.

Mutation may also have feedbacks with population density because the absolute rate at which mutations, favorable or unfavorable, arise in a population depends on population size. This relationship is embodied in the “fundamental (canonical) equation of Adaptive Dynamics” (Dieckmann & Law 1996), because Adaptive Dynamics theory posits that evolution is mutation-limited and operates on a slower time-scale than ecological dynamics. Absence of such a time-scale separation is a defining feature of eco-evolutionary dynamics (Bassar *et al.* 2021), but it still may be interesting to consider feedbacks involving mutation rate, especially in microorganisms such as bacteria. For example, if adaptive

evolution is important for population persistence in the face of changing conditions, could reduced population size lead to selection for higher mutation rates?

Theoretical studies of eco-evolutionary dynamics have often employed deterministic models such as ordinary differential equations (ODEs: Govaert *et al.* 2019). As drift and mutation are stochastic processes, we need to employ other modeling frameworks (e.g., stochastic differential/difference equations or individual-based models) to integrate drift and mutation into eco-evolutionary dynamics (e.g., Constable *et al.* 2016).

Disruptive selection causing diversification and fusion of lineages: Compared with directional and balancing selection, disruptive selection is underrepresented in studies of eco-evolutionary dynamics. Although disruptive selection and the resultant lineage diversification (evolutionary branching) have been examined in studies of Adaptive Dynamics theory (Geritz *et al.* 1998), the basic assumption there is that evolution is much slower than ecological processes. What will happen when that evolution is as fast as ecological processes?

Rapid evolution in response to disruptive selection may promote rapid speciation (Hendry *et al.* 2007). Interestingly, some theoretical studies have shown that rapid antagonistic coevolution can drive lineage diversification whereas slow coevolution results in continuous trait changes without divergence (Calcagno *et al.* 2010). The cessation of disruptive selection, on the other hand, may cause speciation reversal, a fusion of two distinct lineages, which have been described in several systems (Vonlanthen *et al.* 2012). It will be interesting to consider ecological consequences of disruptive selection and the resultant eco-evolutionary feedbacks, because rapid (micro)evolution may actually cause long-standing evolutionary change (i.e., macroevolution).

Selection that reduces population growth rate: Despite the recognition that selection is

driven by relative fitness within populations rather than absolute fitness (Metz *et al.* 1992), studies of eco-evolutionary dynamics have tended to focus on selection that increases absolute fitness, partly because of the prevalence of studies on evolutionary rescue, where adaptive evolution prevents population extinction (Gomulkiewicz & Holt 1995; Kinnison & Hairston 2007; Bell 2017). Theoretical studies on eco-evolutionary dynamics (e.g., Vasseur *et al.* 2011; Cortez 2018; Yamamichi & Letten 2021) often employ the model of Lande (1976) for quantitative trait evolution, in which a mean trait value (\bar{z}) evolves to increase the per-capita population growth rate:

$$\frac{d\bar{z}}{dt} = v \frac{\partial}{\partial \bar{z}} \left(\frac{1}{N} \frac{dN}{dt} \right), \quad (1)$$

where v is additive genetic variance and N is population density.

However, because selection acts on relative fitness, it can actually decrease population growth rate (Abrams *et al.* 1993). This can be incorporated in Equation 1 by considering frequency-dependent selection (Abrams 2001). Selection on relative fitness may cause extinction resulting in “evolutionary suicide” rather than “evolutionary rescue” (Henriques & Osmond 2020). Again, studies in Adaptive Dynamics theory have investigated evolutionary suicide (Parvinen 2005), but the basic assumption there has been that evolution is slow. In the context of community ecology, adaptation to intraspecific interactions such as sexual and social interactions may result in an evolutionary tragedy of the commons (Rankin *et al.* 2007a), and promote negative frequency-dependence by reducing the population growth rate of species with high abundance (“intraspecific adaptation load” *sensu* (Yamamichi *et al.* 2020)). In particular, there is currently a heated debate about whether sexual selection increases population growth rate (e.g., by selecting better adapted males) or not (e.g., by wasting energy or attracting predators via male-male competition and female mate choice)

(Kokko & Brooks 2003; Martins *et al.* 2018; Cally *et al.* 2019). Either may be the case depending upon the context of the interaction, and both can result in eco-evolutionary dynamics as population interactions result in evolution (driven by sexual selection) that feeds back to affect population growth rate. It will be important to consider evolution that maximizes geometric mean fitness (e.g., bet-hedging: Cohen 1966) as well, because it may also reduce the short-term population growth rate (unlike Equation 1).

Other evolutionary processes: There are many other aspects of evolution that have been considered relatively infrequently in the context of eco-evolutionary dynamics. For example, one of the central topics in evolutionary biology is evolution of cooperation due to kin or multilevel selection (Nowak 2006). By considering feedbacks between ecological and evolutionary processes, it will be possible to provide a new perspective on the evolution of cooperation: for example, laboratory experiments with yeast have shown transient eco-evolutionary cycles to a coexistence equilibrium of cooperators and cheaters (Sanchez & Gore 2013). Weitz *et al.* (2016) proposed a theoretical framework that combines evolution of cooperation and ecological dynamics, and found similar cycles. Bergstrom and Lachmann (2003) showed that a rapidly evolving species benefits less in coevolution with mutualist partners. On the other hand, Rankin *et al.* (2007b) using eco-evolutionary model simulations showed that interspecific competition may promote evolution of intraspecific cooperation, highlighting the potential importance of multi-level selection.

As with evolution of cooperation, other adaptive evolution, driven by intraspecific interactions such as sexual selection and conflict, has been underrepresented until recently (Giery & Layman 2019; Svensson 2019; Yamamichi *et al.* 2020). Similarly, recent papers have highlighted the value in considering the difference between hard and soft selection (Bell *et al.* 2021) and population genetic aspects in eco-evolutionary dynamics (Osmond & Coop

2020; Yamamichi 2022). Soft selection is affected by environmental conditions as well as population composition and may result in counterintuitive effects on population growth (Bell *et al.* 2021). Seeking population genetic signatures of eco-evolutionary dynamics may be particularly pertinent in this era of “big genomic data.” We may be able to infer past eco-evolutionary dynamics by examining genomic patterns of populations (e.g., selective sweeps due to adaptive evolution in evolutionary rescue: (Osmond & Coop 2020)). It will also be possible to examine how genetic architecture of adaptive trait evolution affects eco-evolutionary dynamics in the future (Rudman *et al.* 2018; Yamamichi 2022).

Because natural selection is not the sole mechanism of rapid evolution, it will be important to integrate concepts in population genetics, evolutionary biology, and ecology carefully to better understand and predict ecological dynamics in nature. Despite the rise of studies of eco-evolutionary dynamics from at most one or two per year prior to 2007 to well over 100 per year since 2017 (Bassar *et al.* 2021), a recent co-citation network analysis by Réale *et al.* (2020) indicates that there has been no trend towards a stronger integration of ecology and evolutionary biology. This may partly be because the number of researchers is increasing and each subdiscipline has expanded. However, conceptual developments can be accelerated by considering analogies between ecology and evolutionary biology (Hairston *et al.* 1996; Vellend 2016). Studying eco-evolutionary dynamics as an interdisciplinary topic presents a great opportunity to promote a synthesis of population/community ecology and population/quantitative genetics as well as evolutionary (behavioral) ecology. In addition, it will be essential for deepening our understanding of microbiology and effects of ongoing environmental changes (Loreau *et al.* 2022). Through this process, considering eco-evolutionary dynamics will become essential not only for ecologists but also for geneticists and evolutionary biologists.

Funding

MY was supported by Japan Society for the Promotion of Science (JSPS) Grants-in-Aid for Scientific Research (KAKENHI) grant number 19K16223, 20KK0169, 21H02560, 22H02688, and 22H04983 and by Australian Research Council (ARC) Discovery Project DP220102040.

Conflict of interest

The authors declare no conflict of interest.

References

1.
Abrams, P.A. (2001). Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: An assessment of three methods. *Ecol. Lett.*, 4, 166-175.
2.
Abrams, P.A., Matsuda, H. & Harada, Y. (1993). Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.*, 7, 465-487.
3.
Bassar, R.D., Coulson, T., Travis, J. & Reznick, D.N. (2021). Towards a more precise – and accurate – view of eco-evolution. *Ecol. Lett.*, 24, 623-625.
4.
Bell, D.A., Kovach, R.P., Robinson, Z.L., Whiteley, A.R. & Reed, T.E. (2021). The ecological causes and consequences of hard and soft selection. *Ecol. Lett.*, 24, 1505-1521.
5.
Bell, G. (2017). Evolutionary rescue. *Annu. Rev. Ecol. Evol. Syst.*, 48, 605-627.
6.
Bergstrom, C.T. & Lachmann, M. (2003). The Red King effect: when the slowest runner wins the coevolutionary race. *Proc. Natl. Acad. Sci. U.S.A.*, 100, 593-598.
7.
Calcagno, V., Dubosclard, M. & de Mazancourt, C. (2010). Rapid exploiter-victim coevolution: The race is not always to the swift. *Am. Nat.*, 176, 198-211.
- 8.

- 245 Cally, J.G., Stuart-Fox, D. & Holman, L. (2019). Meta-analytic evidence that sexual selection
246 improves population fitness. *Nat. Commun.*, 10, 2017.
247 9.
- 248 Campbell-Staton, S.C., Arnold, B.J., Gonçalves, D., Granli, P., Poole, J., Long, R.A. *et al.*
249 (2021). Ivory poaching and the rapid evolution of tusklessness in African elephants.
250 *Science*, 374, 483-487.
251 10.
- 252 Chen, N., Juric, I., Cosgrove, E.J., Bowman, R., Fitzpatrick, J.W., Schoech, S.J. *et al.* (2019).
253 Allele frequency dynamics in a pedigreed natural population. *Proc. Natl. Acad. Sci.*
254 *U.S.A.*, 116, 2158-2164.
255 11.
- 256 Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*,
257 12, 119-129.
258 12.
- 259 Constable, G.W., Rogers, T., McKane, A.J. & Tarnita, C.E. (2016). Demographic noise can
260 reverse the direction of deterministic selection. *Proc. Natl. Acad. Sci. U.S.A.*, 113,
261 E4745-E4754.
262 13.
- 263 Cortez, M.H. (2018). Genetic variation determines which feedbacks drive and alter predator-
264 prey eco-evolutionary cycles. *Ecol. Monogr.*, 88, 353-371.
265 14.
- 266 Coulson, T., Kendall, B.E., Barthold, J., Plard, F., Schindler, S., Ozgul, A. *et al.* (2017).
267 Modeling adaptive and nonadaptive responses of populations to environmental change.
268 *Am. Nat.*, 190, 313-336.
269 15.
- 270 Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation*
271 *of Favoured Races in the Struggle for Life*. John Murray, London.
272 16.
- 273 De Meester, L., Brans, K.I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H. *et al.* (2019).
274 Analysing eco-evolutionary dynamics—The challenging complexity of the real world.
275 *Funct. Ecol.*, 33, 43-59.
276 17.
- 277 Dieckmann, U. & Law, R. (1996). The dynamical theory of coevolution: a derivation from
278 stochastic ecological processes. *J. Math. Biol.*, 34, 579-612.
279 18.

280 Farkas, T.E., Mononen, T., Comeault, A.A., Hanski, I. & Nosil, P. (2013). Evolution of
281 camouflage drives rapid ecological change in an insect community. *Curr. Biol.*, 23,
282 1835-1843.

283 19.

284 Fussmann, G.F., Loreau, M. & Abrams, P.A. (2007). Eco-evolutionary dynamics of
285 communities and ecosystems. *Funct. Ecol.*, 21, 465-477.

286 20.

287 Geritz, S.A.H., Kisdi, É., Meszéna, G. & Metz, J.A.J. (1998). Evolutionarily singular strategies
288 and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12, 35-57.

289 21.

290 Giery, S.T. & Layman, C.A. (2019). Ecological consequences of sexually selected traits: An
291 eco-evolutionary perspective. *Q. Rev. Biol.*, 94, 29-74.

292 22.

293 Gilpin, M.E. & Soulé, M.E. (1986). Minimal viable populations: processes of species
294 extinction. In: *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé,
295 ME). Sinauer, pp. 19-34.

296 23.

297 Gomulkiewicz, R. & Holt, R.D. (1995). When does evolution by natural selection prevent
298 extinction? *Evolution*, 49, 201-207.

299 24.

300 Govaert, L., Fronhofer, E.A., Lion, S., Eizaguirre, C., Bonte, D., Egas, M. *et al.* (2019). Eco-
301 evolutionary feedbacks—Theoretical models and perspectives. *Funct. Ecol.*, 33, 13-30.

302 25.

303 Hairston, N.G., Jr., Ellner, S. & Kearns, C.M. (1996). Overlapping generations: the storage
304 effect and the maintenance of biotic diversity. In: *Population Dynamics in Ecological
305 Space and Time* (eds. Rhodes, OE, Jr., Chesson, RK & Smith, MH). University of
306 Chicago Press Chicago, IL, pp. 109-145.

307 26.

308 Hairston, N.G., Jr., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005). Rapid evolution
309 and the convergence of ecological and evolutionary time. *Ecol. Lett.*, 8, 1114-1127.

310 27.

311 Hart, S.P., Turcotte, M.M. & Levine, J.M. (2019). Effects of rapid evolution on species
312 coexistence. *Proc. Natl. Acad. Sci. U.S.A.*, 116, 2112-2117.

313 28.

314 Hendry, A.P. (2016). *Eco-evolutionary Dynamics*. Princeton University Press, Princeton, NJ.

315 29.
316 Hendry, A.P., Nosil, P. & Rieseberg, L.H. (2007). The speed of ecological speciation. *Funct.*
317 *Ecol.*, 21, 455-464.
318 30.
319 Henriques, G.J.B. & Osmond, M.M. (2020). Cooperation can promote rescue or lead to
320 evolutionary suicide during environmental change. *Evolution*, 74, 1255-1273.
321 31.
322 Hoffmann, A.A. & Sgrò, C.M. (2011). Climate change and evolutionary adaptation. *Nature*,
323 470, 479-485.
324 32.
325 Johnson, M.T.J. & Stinchcombe, J.R. (2007). An emerging synthesis between community
326 ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250-257.
327 33.
328 Jones, E.I., Ferrière, R. & Bronstein, J.L. (2009). Eco-evolutionary dynamics of mutualists and
329 exploiters. *Am. Nat.*, 174, 780-794.
330 34.
331 Kinnison, M.T. & Hairston, N.G., Jr. (2007). Eco-evolutionary conservation biology:
332 contemporary evolution and the dynamics of persistence. *Funct. Ecol.*, 21, 444-454.
333 35.
334 Kokko, H. & Brooks, R. (2003). Sexy to die for? Sexual selection and the risk of extinction.
335 *Ann. Zool. Fenn.*, 40, 207-219.
336 36.
337 Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution.
338 *Evolution*, 30, 314-334.
339 37.
340 Liu, J., Champer, J., Langmüller, A.M., Liu, C., Chung, J., Reeves, R. *et al.* (2019). Maximum
341 likelihood estimation of fitness components in experimental evolution. *Genetics*, 211,
342 1005-1017.
343 38.
344 Loreau, M., Jarne, P. & Martiny, J. (2022). Breaking down the wall between ecology and
345 evolution. *Authorea Preprints*.
346 39.
347 Lynch, M. & Lande, R. (1993). Evolution and extinction in response to environmental change.
348 In: *Biotic Interactions and Global Change* (eds. Kareiva, PM, Kingsolver, JG & Huey,
349 RB). Sinauer Associates, Inc. Sunderland, MA, pp. 234-250.

- 350 40.
- 351 Martins, M.J.F., Puckett, T.M., Lockwood, R., Swaddle, J.P. & Hunt, G. (2018). High male
352 sexual investment as a driver of extinction in fossil ostracods. *Nature*, 556, 366-369.
- 353 41.
- 354 Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M. *et al.* (2011).
355 Toward an integration of evolutionary biology and ecosystem science. *Ecol. Lett.*, 14,
356 690-701.
- 357 42.
- 358 Metz, J.A.J., Nisbet, R.M. & Geritz, S.A.H. (1992). How should we define ‘fitness’ for general
359 ecological scenarios? *Trends Ecol. Evol.*, 7, 198-202.
- 360 43.
- 361 Nabutanyi, P. & Wittmann, M.J. (2021). Models for eco-evolutionary extinction vortices under
362 balancing selection. *Am. Nat.*, 197, 336-350.
- 363 44.
- 364 Northfield, T.D. & Ives, A.R. (2013). Coevolution and the effects of climate change on
365 interacting species. *PLOS Biol.*, 11, e1001685.
- 366 45.
- 367 Nowak, M.A. (2006). *Evolutionary Dynamics*. Harvard University Press, Harvard, MA.
- 368 46.
- 369 Osmond, M.M. & Coop, G. (2020). Genetic signatures of evolutionary rescue by a selective
370 sweep. *Genetics*, 215, 813-829.
- 371 47.
- 372 Parvinen, K. (2005). Evolutionary suicide. *Acta Biotheoretica*, 53, 241-264.
- 373 48.
- 374 Pastore, A.I., Barabás, G., Bimler, M.D., Mayfield, M.M. & Miller, T.E. (2021). The evolution
375 of niche overlap and competitive differences. *Nat. Ecol. Evol.*, 5, 330–337.
- 376 49.
- 377 Pimentel, D. (1961). Animal population regulation by the genetic feed-back mechanism. *Am.*
378 *Nat.*, 95, 65-79.
- 379 50.
- 380 Post, D.M. & Palkovacs, E.P. (2009). Eco-evolutionary feedbacks in community and
381 ecosystem ecology: interactions between the ecological theatre and the evolutionary
382 play. *Philos. Trans. R. Soc. B*, 364, 1629-1640.
- 383 51.
- 384 Rankin, D.J., Bargum, K. & Kokko, H. (2007a). The tragedy of the commons in evolutionary

385 biology. *Trends Ecol. Evol.*, 22, 643-651.
 386 52.
 387 Rankin, D.J., López-Sepulcre, A., Foster, K.R. & Kokko, H. (2007b). Species-level selection
 388 reduces selfishness through competitive exclusion. *J. Evol. Biol.*, 20, 1459-1468.
 389 53.
 390 Réale, D., Khelfaoui, M., Montiglio, P.-O. & Gingras, Y. (2020). Mapping the dynamics of
 391 research networks in ecology and evolution using co-citation analysis (1975–2014).
 392 *Scientometrics*, 122, 1361-1385.
 393 54.
 394 Rudman, S.M., Barbour, M.A., Csilléry, K., Gienapp, P., Guillaume, F., Hairston, N.G., Jr. *et al.*
 395 (2018). What genomic data can reveal about eco-evolutionary dynamics. *Nat. Ecol.*
 396 *Evol.*, 2, 9-15.
 397 55.
 398 Rudman, S.M., Greenblum, S.I., Rajpurohit, S., Betancourt, N.J., Hanna, J., Tilk, S. *et al.*
 399 (2022). Direct observation of adaptive tracking on ecological time scales in *Drosophila*.
 400 *Science*, 375, eabj7484.
 401 56.
 402 Sanchez, A. & Gore, J. (2013). Feedback between population and evolutionary dynamics
 403 determines the fate of social microbial populations. *PLOS Biol.*, 11, e1001547.
 404 57.
 405 Schoener, T.W. (2011). The newest synthesis: understanding the interplay of evolutionary and
 406 ecological dynamics. *Science*, 331, 426-429.
 407 58.
 408 Slobodkin, L.B. (1961). *Growth and Regulation of Animal Populations*. Holt, Rinehart and
 409 Winston, New York.
 410 59.
 411 Snyder, R.E. & Ellner, S.P. (2018). Pluck or luck: does trait variation or chance drive variation
 412 in lifetime reproductive success? *Am. Nat.*, 191, E90-E107.
 413 60.
 414 Snyder, R.E., Ellner, S.P. & Hooker, G. (2021). Time and chance: using age partitioning to
 415 understand how luck drives variation in reproductive success. *Am. Nat.*, 197, E110-
 416 E128.
 417 61.
 418 Svensson, E.I. (2019). Eco-evolutionary dynamics of sexual selection and sexual conflict.
 419 *Funct. Ecol.*, 33, 60-72.

62.
Thompson, J.N. (1998). Rapid evolution as an ecological process. *Trends Ecol. Evol.*, 13, 329-332.
63.
Vasseur, D.A., Amarasekare, P., Rudolf, V.H.W. & Levine, J.M. (2011). Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am. Nat.*, 178, E96-E109.
64.
Vellend, M. (2016). *The Theory of Ecological Communities*. Princeton University Press, Princeton, NJ.
65.
Vonlanthen, P., Bittner, D., Hudson, A.G., Young, K.A., Müller, R., Lundsgaard-Hansen, B. *et al.* (2012). Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature*, 482, 357-362.
66.
Weitz, J.S., Eksin, C., Paarporn, K., Brown, S.P. & Ratcliff, W.C. (2016). An oscillating tragedy of the commons in replicator dynamics with game-environment feedback. *Proc. Natl. Acad. Sci. U.S.A.*, 113, E7518-E7525.
67.
Wright, S. (1982). The shifting balance theory and macroevolution. *Annu. Rev. Genet.*, 16, 1-19.
68.
Yamamichi, M. (2022). How does genetic architecture affect eco-evolutionary dynamics? A theoretical perspective. *Philos. Trans. R. Soc. B*, 377, 20200504.
69.
Yamamichi, M., Kyogoku, D., Iritani, R., Kobayashi, K., Takahashi, Y., Tsurui-Sato, K. *et al.* (2020). Intraspecific adaptation load: a mechanism for species coexistence. *Trends Ecol. Evol.*, 35, 897-907.
70.
Yamamichi, M. & Letten, A.D. (2021). Rapid evolution promotes fluctuation-dependent species coexistence. *Ecol. Lett.*, 24, 812-818.
71.
Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G., Jr. (2003). Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, 424, 303-306.