

Eco-Evolutionary Dynamics: The Predator-Prey Adaptive Play and the Ecological Theater

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The emerging field of eco-evolutionary dynamics has demonstrated that both ecological and evolutionary processes can occur contemporaneously. Ecological interactions, such as between predator and prey, are important focal areas where an eco-evolutionary perspective can advance understanding about phenotypically plastic and adaptive evolutionary responses. In predator-prey interactions, both species reciprocally respond and adapt to each other in order to simultaneously ensure resource consumption and predation avoidance. Here we sketch out a way to help unify experimental and analytical approaches to both eco-evolutionary dynamics and predator-prey interactions, with a specific focus on terrestrial systems. We discuss the need to view predator-prey eco-evolutionary dynamics as a perpetually adaptive interplay with constantly shifting pressures and feedbacks, rather than viewing it as driving a set evolutionary trajectory. We then outline our perspective on how to understand eco-evolutionary patterns in a predator-prey context. We propose initiating insight by distinguishing phenotypic plasticity against genetic change (*i.e.*, “molecular reductionism”) and further applying a landscape-scale perspective (*i.e.*, “landscape holism”). We believe that studying predator-prey interactions under an eco-evolutionary lens can provide insights into how general and, consequently, predictable species’ evolutionary responses are to their contemporary environments.

INTRODUCTION

The fields of ecology — the study of how populations and species interact with one another and their environment — and evolution — the study of how heritable characteristics of populations and species change over time — are naturally paired in university departments, journal titles, and professional societies. After all, ecological and evolutionary processes are intrinsically linked as ecological relationships provide the context for

evolutionary change. As Yale Professor G.E. Hutchinson (1965) famously expressed, the “ecological theater” sets the stage for the “evolutionary play”. Nevertheless, the subfields of ecology and evolutionary biology have long operated in a surprising degree of isolation, largely because scientists, including Hutchinson himself, believed that evolutionary processes operated too slowly to alter contemporary ecological dynamics [1]. New research has, however, begun to illuminate how both processes can not only operate on contemporaneous timescales but

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†Abbreviations: eco-evo, eco-evolutionary; LCG, Landscape community genomics; GWAS, genome-wide association mapping studies.

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also influence one another [2-6]. Thus, as the paradigm is shifting to recognize that both evolutionary and ecological processes can occur simultaneously in a wide range of systems, the study of their interaction is growing as a field in its own right [7].

Eco-evolutionary processes (hereafter, “eco-evo”) occur via reciprocal interactions between ecological and evolutionary processes which enable organisms to both shape and adapt to their environment [8,9]. Ecological processes, such as species interactions and environmental changes, can influence evolutionary change by altering natural selection. This, in turn, can alter the genetic frequency underlying phenotypic traits. These evolutionary trait changes could further alter ecological dynamics, including the nature and strength of species interactions with their environment, competitors, and predators — thereby instigating a new round of evolutionary change and ultimately resulting in an eco-evo feedback loop [10,11]. Eco-evo studies have extensively reported how ecology influences evolution (“eco to evo”), while newer studies investigate the reverse process (“evo to eco”) [4,12,13]. Few studies have examined a complete feedback loop (but see [14]) [8,9,11,15].

A pressing challenge is to integrate an eco-evo dynamics perspective with community ecology, and particularly for terrestrial predator-prey interactions. Aquatic systems have historically been the focus of eco-evo studies, as aquatic food webs contain many microscopic species with rapid reproduction and short lifespans which facilitate the use of mesocosm studies that track population evolution over many generations [14,16]. In these cases, eco-evolutionary processes and feedbacks on predator-prey systems can often be fully examined in the context of long-term (relative to species generation time) dynamics that can happen within the span of weeks or months. Nevertheless, recent analyses of megafaunal communities have revealed that species with decadal generation times are also undergoing contemporary evolutionary change [17-19]. Thus, while it would be logistically challenging to study eco-evolutionary feedbacks in the context of long-term dynamics in these systems, it is nonetheless still possible to begin understanding the basis by which environmental variation and change may drive evolutionary change in those traits of predator and prey species that ultimately shape their interactions and temporal dynamics [e.g. 20]. But, how environmental variation and change drive such trait evolution in these kinds of systems has received far less attention [21,22].

We make the case here that an eco-evo framework aimed at understanding the evolutionary trajectory of large predator and prey traits, as well as their interactions, is needed in order to fully understand the fate of these species and their ecological function in an era where ecological systems are continually being altered by natural

and anthropogenic environmental change. Specifically, rapid changes to the environment (e.g. climate change, urbanization) may fundamentally alter the ecological stage upon which natural selection acts. In turn, this may drive evolutionary change in predator or prey traits (e.g. rate and timing of development, camouflage coloration, biomechanical hunting, and escape performance) which may further cascade to impact interacting species [23]. For example, climate warming can hasten the emergence of larval insects in spring, causing a mismatch between the timing of insect availability and the arrival of migrant songbirds that rely on this food source [24]. Resultant selection on songbird migration and breeding behavior could then drive changes in gene frequencies between generations, which may further alter their predation of insect prey as well as their interactions with other species in food webs across their seasonal and migratory ranges [25-27]. Additionally, shrinking species populations due to direct (e.g. hunting and harvesting) or indirect (e.g. habitat fragmentation, pollution) human impacts can lead to genetic drift, which can similarly alter the frequency of genes encoding traits that influence predator-prey interactions [16,18].

Here we offer, after consideration of the eco-evo and predator-prey literature, a perspective on how the two fields of study can be more comprehensively combined to advance understanding of the improvisational nature of the evolutionary play and ecological theater. We develop the case that an eco-evolutionary program ought to be applied to systems in which long-term dynamics cannot be measured — owing to predator and prey species having long (year to decades) generations times — but nonetheless exhibit the potential for rapid trait change that could shape the future trajectory of their dynamics [e.g. 20]. We highlight that predators are both reactors to ecological change and drivers of evolutionary change. Further, we develop the case that the key steps for the thoughtful integration of eco-evolutionary and predator-prey processes are: (1) disentangling genetic change from trait plasticity (i.e., “molecular reductionism”) and (2) considering variation in the spatial, in addition to the temporal, context in which these eco-eco dynamics play out (i.e., “landscape holism”) [21,22].

EXTENDING ECO-EVOLUTIONARY DYNAMICS TO PREDATOR-PREY INTERACTIONS

Eco-evo studies, especially when coupled with predator-prey interactions, are important in the study of the flow of energy and matter through communities and food webs [15,28,29]. Eco-evo studies are helpful in linking organismal traits to biophysical processes, including prey behavioral and physiological responses associated

with predation risk [28,30]. When predator and prey evolutionary responses are shaped by their interactions with one another, these responses can cascade to shape the properties and functions of the ecosystems in which they reside [1,5,31]. Studies of predator-prey dynamics have typically observed predators as “instigators” of prey adaptation rates, in which prey respond faster due to their shorter generation times, faster population dynamics, and quicker life history strategies [8,5,32-34]. Predators effectively act as an environmental stressor on their prey who, in turn, respond through an active modification of functional traits (*e.g.* changes in metabolism, behavioral changes) [23,35]. Thus, predators instigate evolutionary change in prey by propagating a sequence of reaction, response, and adaptation [30,34,36-38]. For example, chronic predation stress can cause a change in prey nutrient demands, thereby altering the distribution of nutrients within ecosystems via an “adaptive game involving changes and feedbacks between predator and prey traits” [39].

Consider, for example, changes in biomechanical performance in an *Anolis* lizard species. As a clade, *Anolis* lizard species have adapted to occupy different habitat locations including the ground, trunks of bushes, and branches. Body and limb morphology reflects specialized habitat adaptations (more comprehensively, this morphology-habitat relationship is a continuous feedback). Experimental introductions of a ground-dwelling predatory lizard onto small islands revealed that such differentiation in ecomorphology-habitat association could evolve within-species as well [4]. The introduced predator selected those individuals of a ground-dwelling *Anolis* species that had a low behavioral propensity to avoid predators by climbing up on trunks and thinner branches [4]. This selective pressure triggered the survivors to exhibit plastic changes in morphology toward shorter limbs and longer digits to facilitate active maneuvering on thin branches and catching prey in the higher vegetation canopy. Plasticity in turn became an antecedent to locally adaptive evolutionary change in these *Anolis*' functional traits. This changed their functional role in the island ecosystem within about 10 to 15 years, relative to those on control islands [4]. More generally, inducible prey responses and potential adaptive response by the predator to enhance capture of the surviving prey can lead to ensuing reactive, eco-evolutionary cycles [34,40,41].

Trait-centric studies of predator-prey interactions have historically focused on interspecific interactions that promote fitness (*e.g.* growth, survival, and reproduction) [42-44]. Though not considered in an explicitly eco-evo context, these processes nevertheless have elements of adaptive responses and feedbacks [23,37]. For instance, predators have a negative consumptive effect on prey and prey provide a positive nutritional benefit to predators.

However, the success of the predator in capturing and consuming prey in the first place is contingent on predator morphology (*e.g.* gape width) in relation to prey morphology (*e.g.* body size) [37], or predator behavior (*e.g.* stealth and hunting mode) in relation to prey behavior (*e.g.* vigilance and escape mode) [23]. The consumption of prey supports predator physiological needs (the nutrient balance between maintenance, growth, and reproduction). Predator physiology then directly determines predator morphology (*e.g.* increased size) and behavior (*e.g.* increased aggression) [45]. While direct predation clearly results in death, predators can also indirectly influence live prey through non-consumptive risk effects and the induction of stress responses [23]. Stress, in turn, alters prey physiology (*e.g.* elevated increased heightened metabolism), behavior (*e.g.* alertness and vigilance) and morphology (*e.g.* induction of escape morphology).

The combination of consumptive and non-consumptive interactions leads to a complex predator-prey interaction that becomes an adaptive game, involving changes and feedbacks between predator and prey functional traits [19,23,37]. The strengths of predator effects on prey may depend on the capacity for and magnitude of physiological (*e.g.* good vs. poor physiological condition), morphological (*e.g.* large vs. small bodied) and behavioral (*e.g.* bold vs. shy) trait responses. Accordingly, Hutchinson's metaphor of the ecological theater and evolutionary play is prime for updating. A play connotes a scripted performance, with the actors following each line and letter dutifully. But as we discuss, species in “ecological theaters” seem to improvise more than follow a fixed script. How the actors (interacting species) perform their parts depends on their physical, physiological, or behavioral states as determined by constraints in the expression of their functional traits in different environmental contexts. This adaptive performance could in turn transform the theater. As a result, the improvisational evolutionary play may again change with the shifting characteristics of the ecological theater, and both the stage and actors may appear very different as the curtain closes [29].

Understanding improvisational eco-evo feedbacks requires a combination of reductionism and holism [29]. That is, it requires linking an understanding of the evolutionary mechanisms driving phenotypic variation (*i.e.*, “molecular reductionism”) and change, with and understanding of how those mechanisms play out in different ecological contexts — theaters — across landscapes (*i.e.*, “landscape holism”). Doing this requires considering species populations effectively as ensembles of individuals that exhibit phenotypic variation in their functional traits. We next explain how to integrate molecular reductionism with landscape holism in the context of exploring phenotypic variation in functional traits within populations.

ADVANCING MOLECULAR REDUCTIONISM

A Molecular Perspective for Eco-Evo Dynamics in Predator-Prey Systems

A molecular reductionism approach seeks to disentangle the two forms of trait variation: phenotypic plasticity and genetic change [21,46]. Hendry [47] describes phenotypes as the “nexus of eco-evo dynamics”. Indeed, phenotypic plasticity is likely to be one of the first individual responses expressed under environmental change. Yet, the environmental “stage” is always changing, and it is important to parse out the extent to which species adaptations are based in trait plasticity, selection-driven evolutionary change, or a feedback between the two [21,22]. From a predator-prey perspective, trait variation is influenced by both strong prey preferences made by predators and the consequential evolution of anti-predation traits within prey; one species is expected to provoke an evolutionary ecological response in the other species [9]. This can set up an adaptive “arms race”, as occurs when predators improve their biomechanical athleticism to pursue prey and prey adjust their maneuvering abilities to avoid predators [19,23]. Alternatively, prey may also modify plastic (*i.e.* inducible) antipredator defense morphologies in response to predation risk, and predators modify their offenses in response to changes in prey catchability [41]. Ignoring plasticity in contemporary evolution can lead to incomplete insight into local adaptation and new trait evolution [30,48–50], including in predator-prey systems where eco-evo processes affect community-level dynamics [51,52]. For example, Yamamichi *et al.* [53] concluded that phenotypic plasticity tends to stabilize population dynamics faster than does rapid evolution. Given both the short-term plastic and long-term evolutionary species responses to predator-prey interactions, an assessment of how genotype and allele frequencies change over time as a result of ecological change is critical to an eco-evo perspective [9,54].

The use of reciprocal translocation experiments offer the experimental foundation upon which we can study the adaptive potential of traits, thereby determining whether a trait is plastic or genetic [48]. For example, phenotypically plastic individuals which are translocated will exhibit traits shaped by conditions in the new site rather than those that are adaptive to their site of origin. Alternatively, a trait of interest is genetically based if it varies amongst individuals reared in the same environment, but originating elsewhere [55]. Studies have only recently begun studying trait selection at *both* the phenotypic and genetic level [8,56–58], and more are needed. But, such experiments may be challenging to complete with large vertebrate predators and prey that roam widely across landscapes. Thus, alternative means to track the molecular genetic makeup of populations and associate that with

predator and prey functional traits may offer complementary insights. Below, we outline two molecular fields of study that are particularly promising for predator-prey eco-evolutionary studies.

Applications of Community Genetics and Genomics

Community genetics is an emerging molecular lens through which to assess eco-evolutionary change in predator-prey systems. Community genetics builds off of a traditional population genetic approach which studies how populations are evolving at the pace of a few generations, as well as how any genetic divergences might be attributed to ecological versus demographic factors [59]. A community genetics approach extends the molecular focus to the genetic interactions of multiple species and their abiotic environment [60]. Community genetics aids in the investigation of contemporary evolution (*i.e.*, genetic variation) amidst simultaneous environmental and community compositional changes [60,61]. For example, Bailey *et al.* [62] used a community genetics study to demonstrate a correlation between plant traits (phytochemistry genotypes) and predator-prey interactions and community composition (herbivore density and predator foraging). In another example, flowers evolved chemical signals as a defense mechanism to attract spiders to prey on their predatory folivores [63]. Both studies show that interspecific interactions are important in shaping heritability and the nature of ensuing ecosystem processes. A community genetics perspective can help address questions about how abiotic and biotic factors influence selection in multiple, interacting species and how consistent these genetic patterns are across different environmental conditions thereby enhancing predictability.

As another option, genomics research investigates the entire range of molecular structure and function within an organism. It offers promising breakthroughs in understanding the genomic bases of phenotypes at the pace at which molecular evolution is occurring [64–66]. Genomic data allow a greater capacity to resolve evolutionary processes underlying ecological patterns, thereby improving the predictability of eco-evolutionary dynamics. Approaches such as genome-wide association mapping studies (GWAS) have opened doors into the investigation of loci location, the number of loci involved in trait adaptation, the strength of loci associated with phenotypic traits (*e.g.* major and minor effect loci/alleles), and the divergence and variation of traits in nature [67–69]. These genomic advances make it possible to study both the abiotic (the “stage”) and biotic (the “actors”) factors within the evolutionary play [70]. In addition, genomics research facilitates the study of multiple traits — a helpful approach because covarying traits can both speed-up or slow-down the rates of evolution.

In short, the use of community genetics and/or ge-

omic techniques can contribute to the identification of the genetic architecture underlying key ecological traits. As discussed next, these insights facilitate analysis of eco-evolutionary feedbacks through evaluation of correlations between genetic variation in natural populations and environmental variation.

ADVANCING LANDSCAPE HOLISM

A Landscape Perspective for Eco-Evo Dynamics in Predator-Prey Systems

Predator-prey interactions and their cascading effects on food webs have most commonly been understood through the lens of dynamical models, and many important insights in food web ecology have been developed within this framework [71,72]. Nevertheless, these models in their most standard form dilute the variation in predator-prey interactions across space and time to meet model assumptions that preclude environmental and evolutionary change. We join a growing cohort of scientists [14,73-76] stressing the importance of understanding predator-prey interactions in a spatially and temporally explicit context. Specifically, we advocate the use of landscape-scale approaches to elucidate the eco-evo processes that shape predator and prey traits in ways that both result from and maintain variation in predator-prey interactions.

Predator-prey interactions play out in a heterogeneous mosaic of habitats in which the physical and behavioral traits of each species, as well as the nature and frequency of interspecific encounters, may vary [74-77]. The heterogeneity of landscapes provides an opportunity to investigate whether apparent trait differences among populations of species are the contextual expression of inherent trait variation or, rather, the result of evolutionary divergence [78,79]. Questions of how a landscape-scale perspective changes the ecological and/or evolutionary elements that we observe have not been fully addressed (but see [15]). Historically, the outcomes of predator-prey eco-evolutionary dynamics have been considered highly context dependent. However, opportunity to make broader conclusions and connections can come from considering ecological and evolutionary processes across a generalizable environmental gradient [35,80]. For example, ambient temperatures are warming globally, with the rate and intensity of warming varying between distinct ecosystems. Rising temperatures can increase animal metabolism, increasing demand for soluble carbon and altering herbivore body stoichiometry [81]. However, research has also demonstrated that the non-consumptive effects of predators on prey metabolism and stoichiometry can also increase with temperature, and these stoichiometric and trait shifts cascade to influence ecosystem functioning [28,81,82]. Accordingly, with

these compounded stressors, the adaptive peak for prey physiological responses to predation risk may fluctuate along a temperature gradient, driving local adaptation along temperature gradients and the evolution of distinct antipredator responses under rising regional and global temperatures [83].

Therefore, identifying unified “eco” and “evo” environmental gradients (such as temperature in a warming world) will be necessary to study eco-evo feedbacks within a predator-prey context [35,84]. Landscape-level heterogeneity provides natural experiments for teasing apart the ecological versus evolutionary differences within a community. Specifically, reciprocal transplant experiments that translocate conspecific individuals between distinct environments can help elucidate whether phenotypic variation between locations is the result of local adaptation or contextual phenotypic expression of variable traits [79]. For example, *Agelenopsis aperta* spiders exhibit variation in behavioral traits, and the fitness associated with these traits is context-dependent; boldness is favored in open desert environments with low predation risk and low prey availability, while fearful behavior is advantageous in riparian areas with more abundant avian predators [85]. Genetic analyses paired with reciprocal transplant experiments revealed that the behavioral differences observed in riparian and desert spiders were due to selection and genetic differentiation, as opposed to individual plasticity. However, directional gene flow from open desert areas maintained behavioral variation in riparian populations [85]. Thus, landscape heterogeneity facilitated genetic divergence between populations under different predation regimes. All the while, landscape connectivity has prevented more complete divergence and ensured that riparian predators of these spiders remain exposed to bold individuals, potentially facilitating predation. Genomic studies, in addition to translocation experiments, allow measurement of adaptive genes and estimations of selection gradients across an area [86].

The strength of a predator-prey interaction depends on the magnitude of organismal functional traits. Further, the magnitude of these traits dictates the spatial scale at which these interactions are detectable [23]. For example, whether predator-prey pairings initially interact depends on relative body sizes (e.g. complementary predator gape and prey shape; “size selectivity” [23]). Therefore, an appropriate spatial scale of a study would depend on predator hunting ranges in addition to prey mobility [23]. Hence, the spatial context of “form and function” necessitates knowing whether predators in a system are sit-and-wait or wide-roaming, and knowing prey foraging behavior as this determines the degree of spatial movement.

Ultimately, the ecological heterogeneity of a landscape affects both the phenotypic and genetic heteroge-

neity of species. Hence the idea of “adaptive landscapes” becomes useful a conceptual framework for describing ecological effects on contemporary evolutionary [7,87]. We expect selective pressures on species phenotypes to alter traits and genes across space. A spatial-genetic approach to studying these eco-evolutionary feedbacks is necessary and, as we outline below, landscape community genomics offers a further window of insight.

Applications of Landscape Community Genomics

Landscape community genomics (LCG) can offer a way to detect and quantify the spatial variation in trait evolution, thereby providing further opportunity to study the eco-evolutionary dynamics of interspecific interactions. At its core, a landscape genomics approach investigates how environmental heterogeneity affects spatial patterns of adaptive genetic variation (*e.g.* loci under selection) [88-90]. Landscape genomics requires a large number of molecular markers to be genotyped for each individual sampled in order to conduct genome-wide scans. The advantage of working with a large number of (often unlinked) loci is the increase in power to identify outlier loci under selection, thereby facilitating an investigation of adaptive genetic variation using demographic and population dynamic inferences [86]. Moving beyond common isolation-by-distance measurements, landscape genomics opens up the possibility for isolation-by-environment metrics in which questions of local genetic adaptation, biased dispersal, and habitat choice can be pursued [90,91].

Building off of this, LCG investigates the genomic evolution of multi-species communities (*e.g.* predator-prey interactions) in complex environments [70,92]. An LCG study can provide insight into how abiotic and biotic factors influence gene flow, drift, selection in multiple interacting species. Further, it supports inquiry into how environmental changes impact community composition and genomic co-evolution [70]. An LCG study with an eco-evo perspective will necessitate genetic and ecological data to be sampled across a gradient of abiotic (*e.g.* environmental) and biotic (*e.g.* areas of sympatry vs. allopatry) factors [70]. Ultimately, the aim of applying LCG to eco-evolutionary questions is to determine how consistent patterns of eco-evolutionary dynamics are in separate communities under different environmental conditions; generalizable patterns will result in greater eco-evo predictions. LCG offers techniques to pursue questions about the magnitude of evolutionary change affected by specific loci, the ecological forces associated with evolutionary change, and whether such change is beneficial or detrimental to a population.

SUMMARY

Species are not static, their traits are not fixed, and they do not operate in isolation. Interspecific interactions like predator-prey relationships highlight that biotic factors, in addition to the abiotic environment, play a critical role in the contemporary relationship between ecology and evolution. The concept of a terrestrial eco-evolutionary predator-prey study may seem theoretically comprehensive, yet too hefty for plausible experimentation. However, by addressing the natural links between eco-evolutionary dynamics and predator-prey interactions, we believe that an experimental design can be established so as to track predator-prey adaptive responses and to determine whether observed phenotypic change is the result of plasticity or adaptive evolution. Determining the spatiotemporal scale at which to study the eco-evo dynamics of a predator-prey system will require knowledge about population dynamics, quantity, and diversity of traits, as well as evolutionary history. We propose two necessary guidelines for a predator-prey eco-evolutionary study to be applicable across spatiotemporal scales: a trait-based approach (“molecular reductionism”) and an imposed ecological gradient (“landscape holism”).

First, a trait-based approach which specifically focuses on variation in adaptive functional traits within and among populations of predator and prey species [23] is important for discerning the species characteristics involved in eco-evolutionary feedbacks. Translocation experiments with imposed changes in different contexts facilitate observations of local adaptation in nature and the strength of phenotypically plastic responses [15]. Molecular reductionism — by way of community genetics or genomics methodology — enhances an eco-evolutionary study to discern whether or not species’ trait changes are evolutionary adaptations. Second, studies should be conducted in ways that evaluate changes across different ecological contexts (*e.g.* environmental gradients and combinations of predator-prey presence and absence) [23,35]. For example, studies can be conducted over temperature gradients to observe differences in physiological or metabolic response [28,93]. To this end, heterogeneity at the landscape scale provides a natural experiment for teasing apart evolutionary versus ecological differences (*i.e.*, are trait differences due to evolutionary divergence or contextual expression of inherent variation?). Research using species that are amenable to experimentation within mesocosms can additionally inform how adaptive, plastic processes become manifest at the landscape scale. Ideally, traditional factorial experiments ought to be replicated in different landscape-scale environmental contexts *and* interspecific magnitudes where focal species exist in sympatry and allopatry [70]. Landscape holism — by way of landscape community genetics — can facilitate

the connection between predicted behavioral, physiological, and other changes in predator-prey interactions and community function [39].

While insight from experimentation across a series of environmental gradients could also offer the promise of repeatability [11], completing such experiments may prove to be difficult to achieve on the landscape scale and in natural systems. Such logistics are even more challenging when examining species (e.g. megafauna) that do not have short generation times and thus do not afford the opportunity to run experiments that alter selective pressures [11]. Insights at larger scales may need to enlist genomic research within an eco-evolutionary context. Genomic research can facilitate comparisons in contexts where transplant experiments are not financially or ethically possible. Distinguishing the genetic mechanism tying phenotypic trait change and population dynamics changes can be valuable for population management plans [53,20]. Such an integrative approach to understand predator-prey eco-evolutionary research can enhance our understanding of the interplay between species interactions, environmental changes, and evolutionary adaptations [3,33,36,52,53], and offer insights to meet the call to maintain evolutionary processes as part of landscape-scale biodiversity conservation [94].

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REFERENCES

- Hutchinson GE. The Ecological Theater and Evolutionary Play. New Haven: Yale University Press; 1965. p. 53.
- Thompson JN. Rapid evolution as an ecological process. *Trends Ecol Evol.* 1998;13:329–32.
- Hairston NG, Ellner SP, Geber MA, Yoshida T, Fox JA. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett.* 2005;8:1114–27.
- Shoener TW. The newest synthesis: understanding the inter-play of evolutionary and ecological dynamics. *Science.* 2011;331:426–9.
- Post DM, Palkovacs EP. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos Trans Royal Soc B: Biol Sci.* 2009;364(1523):1629–40.
- Grant PR, Grant BR. Unpredictable Evolution in a 30-Year Study of Darwin's Finches. *Science.* 2002;296(5568):707–11.
- Hendry AP. *Eco-Evolutionary Dynamics.* Princeton: Princeton University Press; 2017.
- Becks L, Ellner SP, Jones LE, Hairston NG. The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics: Functional genomics of eco-evo feedback loop. *Ecol Lett.* 2012;15(5):492–501.
- Travis J, Reznick D, Bassar RD, López-Sepulcre A, Ferriere R, Coulson T. Chapter One - Do Eco-Evo Feedbacks Help Us Understand Nature? Answers From Studies of the Trinidadian Guppy. In: Moya-Laraño J, Rowntree J, Woodward G, editors. *Eco-Evolutionary Dynamics.* London: Academic Press; 2014. pp. 1–40.
- Levins R. *Evolution in Changing Environments.* Princeton: Princeton University Press; 1968.
- Rodríguez-Verdugo A, Buckley J, Stapley J. The genomic basis of eco-evolutionary dynamics. *Mol Ecol.* 2017;26(6):1456–64.
- Matthews B, Narwani A, Hausch S, Nonaka E, Peter H, Yamamichi M, et al. Toward an integration of evolutionary biology and ecosystem science: integration of evolutionary biology and ecosystem science. *Ecol Lett.* 2011;14(7):690–701.
- Pantel JH, Duvivier C, Meester LD. Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. *Ecol Lett.* 2015;18(10):992–1000.
- Yoshida T, Jones LE, Ellner SP, Fussmann GF, Jr NGH. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature.* 2003;424:4.
- Hiltunen T, Becks L. Consumer co-evolution as an important component of the eco-evolutionary feedback. *Nat Commun.* 2014;5:5226.
- Stoks R, Govaert L, Pauwels K, Jansen B, De Meester L. Resurrecting complexity: the interplay of plasticity and rapid evolution in the multiple trait response to strong changes in predation pressure in the water flea *Daphnia magna.* *Ecol Lett.* 2016;19(2):180–90.
- Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. Human predators outpace other agents of trait change in the wild. *Proc Natl Acad Sci USA.* 2009;106(3):952–4.
- Sullivan AP, Bird DW, Perry GH. Human behaviour as a long-term ecological driver of non-human evolution. *Nat Ecol Evol.* 2017;1(3), 0065.
- Wilson AM, Hubel TY, Wilshin SD, Lowe JC, Lorenc M, Dewhurst OP, et al. Biomechanics of predator-prey arms race in lion, zebra, cheetah and impala. *Nature.* 2018;554(7691):183–8.
- Coulson T, MacNulty DR, Stahler DR, vonHoldt B, Wayne RK, Smith DW. Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History. *Science.* 2011;334(6060):1275–8.
- Govaert L, Pantel JH, De Meester L. Eco-evolutionary partitioning metrics: assessing the importance of ecological and evolutionary contributions to population and community change. *Ecol Lett.* 2016;19(8):839–53.
- Ezard TH, Cote SD, Pelletier F. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Phil Trans R Soc B: Biol Sci.* 2009;364(1523):1491–8.
- Schmitz O. Predator and prey functional traits: understanding the adaptive machinery driving predator-prey interactions. *F1000 Res.* 2017;6:1767.
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Vissler ME. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol.* 2009;78(1):73–83.

25. Both C, Visser ME. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*. 2001;411:296–8.
26. Forrest J, Miller-Rushing AJ. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philos Trans Royal Soc B: Biol Sci*. 2010;365(1555):3101–12.
27. Charmantier A, Gienapp P. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evol Appl*. 2014;7(1):15–28.
28. Schmitz OJ, Rosenblatt AE. The Temperature Dependence of Predation Stress and Prey Nutritional Stoichiometry. *Front Ecol Evol*. 2017;5:73.
29. Schmitz OJ. Resolving Ecosystem Complexity (MPB-47). Princeton University Press. Monographs in Population Biology; 2010.
30. West-Eberhard MJ. Phenotypic Plasticity and the Origins of Diversity. *Annu Rev Ecol Syst*. 1989;20:249–78.
31. Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, Ritchie ME, et al. Animating the Carbon Cycle. *Ecosystems* (N Y). 2014;17(2):344–59.
32. Abrams PA. Adaptive foraging by predators as a cause of predator-prey cycles. *Evol Ecol*. 1992;6(1):56–72.
33. Abrams PA. The Evolution of Predator-Prey Interactions: theory and Evidence. *Annu Rev Ecol Syst*. 2000;31(1):79–105.
34. Cortez MH, Ellner SP. Understanding Rapid Evolution in Predator-Prey Interactions Using the Theory of Fast-Slow Dynamical Systems. *Am Nat*. 2010;176(5):E109–27.
35. Schmitz OJ, Trussell GC. Multiple stressors, state-dependence and predation risk — foraging trade-offs: toward a modern concept of trait-mediated indirect effects in communities and ecosystems. *Curr Opin Behav Sci*. 2016;12:6–11.
36. Kishida O, Trussell GC, Mougi A, Nishimura K. Evolutionary ecology of inducible morphological plasticity in predator-prey interaction: toward the practical links with population ecology. *Popul Ecol*. 2010;52(1):37–46.
37. Reger J, Lind MI, Robinson MR, Beckerman AP. Predation drives local adaptation of phenotypic plasticity. *Nat Ecol Evol*. 2018;2(1):100–7.
38. Rosenzweig ML, MacArthur RH. Graphical Representation and Stability Conditions of Predator-Prey Interactions. *Am Nat*. 1963;97(895):209–23.
39. Hawlena D, Schmitz OJ. Physiological Stress as a Fundamental Mechanism Linking Predation to Ecosystem Functioning. *Am Nat*. 2010;176(5):537–56.
40. Connell JH. Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. *Oikos*. 1980;35(2):131–8.
41. Mougi A, Kishida O, Iwasa Y. Coevolution of phenotypic plasticity in predator and prey: why are inducible offenses rarer than inducible defenses? *Evolution*. 2011;65(4):1079–87.
42. Abrams PA, Matsuda H. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evol Ecol*. 1997;11:1–20.
43. Schmitz OJ, Krivan V, Ovadia O. Trophic cascades: the primacy of trait-mediated indirect interactions: Primacy of trait-mediated indirect interactions. *Ecol Lett*. 2004;7(2):153–63.
44. Bolnick DI, Preisser EL. Resource Competition Modifies the Strength of Trait-Mediated Predator-Prey Interactions: A Meta-Analysis. *Ecology*. 2005;86(10):2771–9.
45. Chubaty AM, Ma BO, Stein RW, Gillespie DR, Henry LM, Phelan C, et al. On the evolution of omnivory in a community context. *Ecol Evol*. 2014;4(3):251–65.
46. Ellner SP, Geber MA, Hairston NG. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics: how much does rapid evolution matter? *Ecol Lett*. 2011;14(6):603–14.
47. Hendry AP. Key questions in the genetics and genomics of eco-evolutionary dynamics. *Heredity*. 2013;111(6):456–66.
48. Gordon SP, Hendry AP, Reznick DN. Predator-induced Contemporary Evolution, Phenotypic Plasticity, and the Evolution of Reaction Norms in Guppies. *Copeia*. 2017;105(3):514–22.
49. Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA. Ecological consequences of phenotypic plasticity. *Trends Ecol Evol*. 2005;20(12):685–92.
50. Hendry AP, Gotanda KM, Svensson EI. Human influences on evolution, and the ecological and societal consequences. *Philos Trans Royal Soc B: Biol Sci*. 2017;372(1712):20160028.
51. Farkas TE, Mononen T, Comeault AA, Hanski I, Nosil P. Evolution of Camouflage Drives Rapid Ecological Change in an Insect Community. *Curr Biol*. 2013;23(19):1835–43.
52. Cortez MH, Weitz JS. Coevolution can reverse predator-prey cycles. *Proc Natl Acad Sci USA*. 2014;111(20):7486–91.
53. Yamamichi M, Yoshida T, Sasaki A. Comparing the Effects of Rapid Evolution and Phenotypic Plasticity on Predator-Prey Dynamics. *Am Nat*. 2011;178(3):287–304.
54. Barraclough TG. How Do Species Interactions Affect Evolutionary Dynamics Across Whole Communities? *Annu Rev Ecol Evol Syst*. 2015;46(1):25–48.
55. Donihue CM, Lambert MR. Adaptive evolution in urban ecosystems. *Ambio*. 2015;44(3):194–203.
56. Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, et al. The Strength of Phenotypic Selection in Natural Populations. *Am Nat*. 2001;157(3):245–61.
57. Mojica JP, Lee YW, Willis JH, Kelly JK. Spatially and temporally varying selection on intrapopulation quantitative trait loci for a life history trade-off in *Mimulus guttatus*. *Mol Ecol*. 2012;21(15):3718–28.
58. Cortez MH. How the Magnitude of Prey Genetic Variation Alters Predator-Prey Eco-Evolutionary Dynamics. *Am Nat*. 2016;188(3):329–41.
59. Hartl DL, Clark AG. Principles of Population Genetics. Sunderland: Sinauer Associates, Inc; 2007.
60. Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangerter RK, LeRoy CJ, et al. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat Rev Genet*. 2006;7(7):510–23.
61. Johnson MT, Stinchcombe JR. An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol Evol*. 2007;22(5):250–7.
62. Bailey JK, Wooley SC, Lindroth RL, Whitham TG. Importance of species interactions to community heritability:

- a genetic basis to trophic-level interactions. *Ecol Lett.* 2006;9:78–85.
63. Knauer AC, Bakhtiari M, Schiestl FP. Crab spiders impact floral-signal evolution indirectly through removal of florivores. *Nat Commun.* 2018;9(1):1367.
 64. Storfer A, Murphy MA, Spear SF, Holderegger R, Waits LP. Landscape genetics: where are we now? *Mol Ecol.* 2010;19(17):3496–514.
 65. Allendorf FW, Hohenlohe PA, Luikart G. Genomics and the future of conservation genetics. *Nat Rev Genet.* 2010;11(10):697–709.
 66. Legrand D, Cote J, Fronhofer EA, Holt RD, Ronce O, Schtickzelle N, et al. Eco-evolutionary dynamics in fragmented landscapes. *Ecography.* 2017;40(1):9–25.
 67. Stinchcombe JR, Hoekstra HE. Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity.* 2008;100(2):158–70.
 68. Segura V, Vilhjálmsson BJ, Platt A, Korte A, Seren Ü, Long Q, et al. An efficient multi-locus mixed-model approach for genome-wide association studies in structured populations. *Nat Genet.* 2012;44(7):825–30.
 69. Comeault AA, Soria-Carrasco V, Gompert Z, Farkas TE, Buerkle CA, Parchman TL, et al. Genome-Wide Association Mapping of Phenotypic Traits Subject to a Range of Intensities of Natural Selection in *Timema cristinae*. *Am Nat.* 2014;183(5):711–27.
 70. Hand BK, Lowe WH, Kovach RP, Muhlfeld CC, Luikart G. Landscape community genomics: understanding eco-evolutionary processes in complex environments. *Trends Ecol Evol.* 2015;30(3):161–8.
 71. Lotka AJ. *Elements of Physical Biology.* Baltimore: Williams and Wilkins; 1925.
 72. Loreau M. *From Populations to Ecosystems.* Princeton, Oxford: Princeton University Press; 2010.
 73. Urban M, Leibold M, Amarasekare P, Demeester L, Gomulkiewicz R, Hochberg M, et al. The evolutionary ecology of metacommunities. *Trends Ecol Evol.* 2008;23(6):311–7.
 74. Schmitz OJ, Miller JR, Trainor AM, Abrahms B. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. *Ecology.* 2017;98(9):2281–92.
 75. Fortin D, Buono PL, Schmitz OJ, Courbin N, Losier C, St-Laurent MH, et al. A spatial theory for characterizing predator–multiprey interactions in heterogeneous landscapes. *Proc R Soc B.* 2015;282(1812):20150973.
 76. Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecol Lett.* 2007;10(8):690–700.
 77. Hastings A. Spatial heterogeneity and the stability of predator-prey systems. *Theor Popul Biol.* 1977;12(1):37–48.
 78. Via S, Lande R. Genotype-Environment Interaction and the Evolution of Phenotypic Plasticity. *Evolution.* 1985;39(3):505–22.
 79. Kawecki TJ, Ebert D. Conceptual issues in local adaptation. *Ecol Lett.* 2004;7(12):1225–41.
 80. Urban MC. The evolution of species interactions across natural landscapes. *Ecol Lett.* 2011;14(7):723–32.
 81. Schmitz OJ. Global climate change and the evolutionary ecology of ecosystem functioning. *Ann N Y Acad Sci.* 2013;1297(1):61–72.
 82. Barton BT, Beckerman AP, Schmitz OJ. Climate warming strengthens indirect interactions in an old-field food web. *Ecology.* 2009;90(9):2346–51.
 83. Barton BT. Local adaptation to temperature conserves top-down control in a grassland food web. *Proc R Soc B.* 2011;278(12):3102–7.
 84. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. A framework for community interactions under climate change. *Trends Ecol Evol.* 2010;25(6):325–31.
 85. Riechert SE, Hall RF. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. *J Evol Biol.* 2000;13(3):541–50.
 86. Schwartz MK, McKelvey KS, Cushman SA, Luikart G. Landscape Genomics: A Brief Perspective. In: Cushman SA, Huettmann F, editors. *Spatial Complexity, Informatics, and Wildlife Conservation.* Tokyo: Springer Japan; 2010. pp. 165–74.
 87. Palkovacs EP. The value and intrigue of eco-evolutionary dynamics. *Ecology.* 2017;98(7):1977–8.
 88. Joost S, Bonin A, Bruford MW, Després L, Conord C, Erhardt G, et al. A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Mol Ecol.* 2007;16(18):3955–69.
 89. Manel S, Holderegger R. Ten years of landscape genetics. *Trends Ecol Evol.* 2013;28(10):614–21.
 90. Li Y, Zhang XX, Mao RL, Yang J, Miao CY, Li Z, et al. Ten Years of Landscape Genomics: challenges and Opportunities. *Front Plant Sci.* 2017;8:2136.
 91. Wang IJ, Bradburd GS. Isolation by environment. *Mol Ecol.* 2014;23(23):5649–62.
 92. Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, Shuster SM, et al. Community and Ecosystem Genetics: A Consequences of the Extended Phenotype. *Ecology.* 2003;84(3):559–73.
 93. Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson M, Brose U. Temperature, predator-prey interaction strength and population stability. *Glob Change Biol.* 2009;16(8):2145–57.
 94. Stockwell CA, Hendry AP, Kinnison MT. Contemporary evolution meets conservation biology. *Trends Ecol Evol.* 2003;18(2):94–101.