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...
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 microscop ic 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-evo 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 consequent 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 may 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-
nomic 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-geo 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 hetero-
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-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. mega fauna) 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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