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Development in context: the timely emergence of eco-devo

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Ecological development or 'eco-devo' examines the mechanisms of developmental regulation in real-world environments, providing an integrated approach for investigating both plastic and canalized aspects of phenotypic expression. This synthetic discipline brings a current understanding of environmentally mediated regulatory systems to studies of genetic variation, ecological function and evolutionary change. Eco-devo is emerging at a critical point in time, as researchers try to understand and predict the future of organisms in a changing world. Precise knowledge of the external and internal environmental cues, signaling pathways and genetic elements implicated in developmental outcomes will provide key insights to the immediate tolerance and potential evolutionary resilience of organisms to the altered physical and biotic conditions created by human activities.

A crucial moment for ecological development

Ecological developmental biology, or 'eco-devo', examines how organisms develop in 'real -world' environments [1–3]. Against a historical backdrop of separate developmental categories (adaptive plasticity, polyphenisms, canalization and instability), eco-devo aims to provide an integrated framework for investigating development in its ecological context. This means expanding research programs beyond standardized laboratory conditions to include the various environments in which development can occur, by incorporating both abiotic and biotic factors into studies of gene expression and regulatory pathways. It further entails studying the expression of traits important to function, fitness and ecological interactions in those environments. This expanded investigation can provide precise answers to questions about the developmental processes that lead to adaptive and maladaptive phenotypes in specific environments. These answers are particularly crucial as researchers consider the potential of diverse taxa to tolerate anthropogenic changes to their habitats in the immediate term, as well as their evolutionary potential to adapt to a dramatically altered physical and biotic landscape (Figures 1 and 2).

Eco-devo: toward a newer synthesis

Eco-devo is not simply a repackaging of plasticity studies under a new name but a more inclusive conceptual framework for understanding development in general. In 1965, when most geneticists considered developmental variability to be uninteresting noise, the genecologist A.D. Bradshaw coined the term 'phenotypic plasticity' to emphasize that environmentally contingent phenotypic expression could be a mode of individual adaptation to immediate challenges or stresses [4]. Over the past two decades, plasticity has been studied intensively, with the primary goals of characterizing phenotypic variation expressed under diverse environmental conditions and assessing its potential evolutionary impact [5–10]. This area of research has increased awareness that the context dependence of development is 'the rule rather than the exception' [11,12], and that it constitutes a fundamental mode of adaptive variation for many traits and taxa.

Whereas plasticity studies draw on quantitative genetic and phenotypic selection analyses to examine developmental outcomes and their evolution as adaptive traits, eco-devo adds an explicit focus on the molecular and cellular mechanisms of environmental perception and gene regulation underlying these responses, and how these signaling pathways operate in genetically and/or ecologically distinct individuals, populations, communities and taxa [13]. This emerging discipline definitively frames development as an environmentally contingent repertoire of potential phenotypes. Phenotypes might be similar across environments (canalized) or distinctly different (plastic); in either case, they reflect a complex chain of regulatory events that are informed by both external and internal environmental signals and feedbacks [14]. In other words, plasticity and canalization (whether adaptive or maladaptive) describe different outcome patterns but both arise from the same type of complex signaling networks informed by environmental inputs [12]; it is these regulatory systems, rather than any specific outcomes, that evolve [6,15–19].

Accordingly, eco-devo is a more inclusive field, and one that implicitly moves biologists toward an integrated, norm of reaction paradigm for studying developmental processes and their evolution [3,11] (Box 1). Implicit in this approach is the notion that gene function is environment specific and, therefore, requires 'ecological annotation' [20]. Eco-devo also connects the organism as a developmental system with its own ecological experience and that of interacting individuals and taxa. The morphological and life-history responses of an individual to the environment modify its phenotype and consequently its subsequent environment: for instance, plants that produce broad 'shade leaves' live in a more photon-rich environment by virtue of their own expanded surface area, and maternal adjustments to offspring germination behavior

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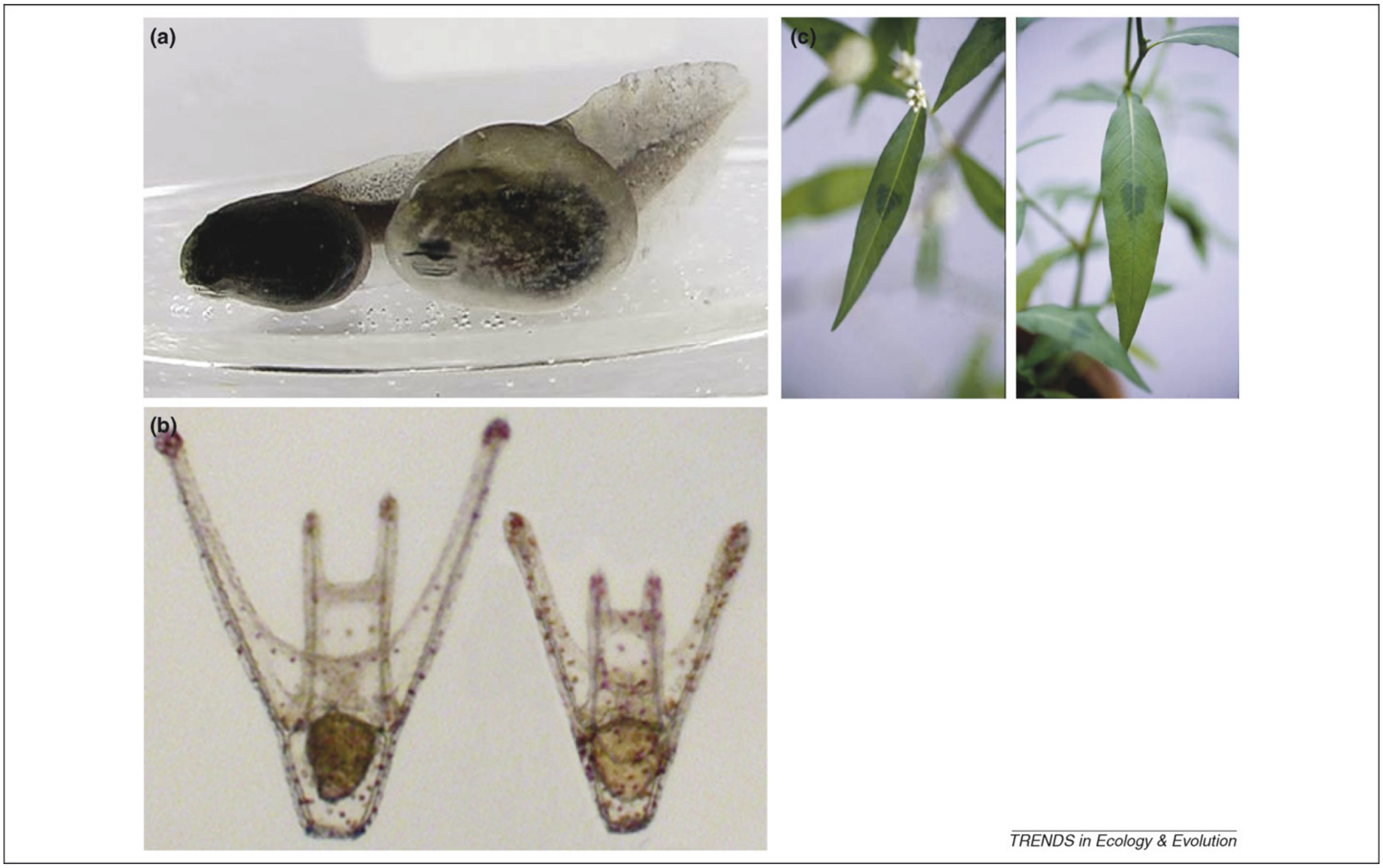

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Figure 1. Developmental outcomes depend on ecological context. Dramatic examples of environmentally contingent development include adaptive plasticity, whereby phenotypes produced in alternative environments are adaptive to particular ecological demands. Examples of such plasticity are common in a broad range of animals, plants and other taxa. **(a)** Tadpoles of the brown frog *Rana pirica* develop a bulging body type (right) in the presence of the gape-limited predatory salamander *Hynobius retardatus* that is impossible for *Hynobius* to swallow. **(b)** When food is relatively scarce, larvae of the sea urchin *Lytechinus variegatus* allocate more tissue to their feeding structures, ciliated larval 'arms' (left). **(c)** Annual plants in the genus *Polygonum* produce large, thin leaves in low light (which enhance photosynthetic photon harvest) and narrow, thicker leaves (which conserve water) in high light. Sun- (left) and shade- (right) produced leaves of a single *P. persicaria* genotype differ markedly when grown in contrasting environments. (a) reproduced with permission from Osamu Kishida. (b) reproduced with permission from Justin Mc Alister and Robert Podolsky.

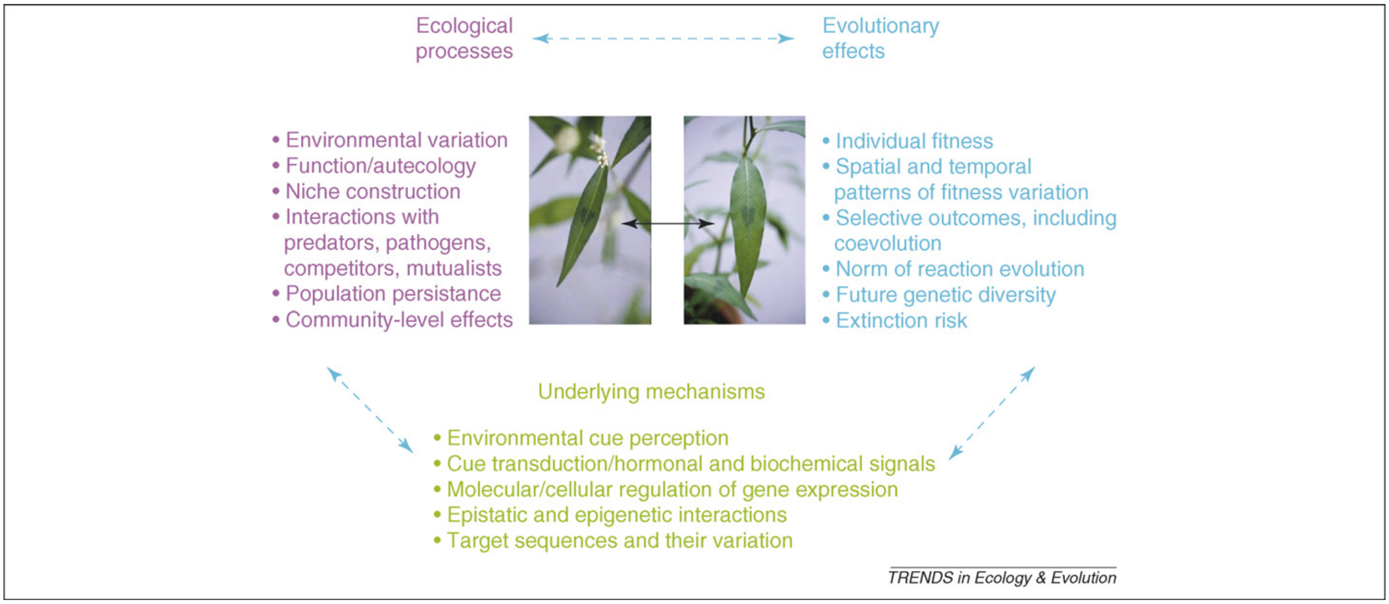

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Figure 2. The integrative ecological development approach. Environmentally contingent, 'eco-devo' variation can be exemplified as the production by a single *Polygonum persicaria* genotype of narrow sun leaves in high light (left), versus broad, thin shade leaves in low light (right). Such alternative developmental outcomes reflect underlying regulatory mechanisms (shown in green), and result in both ecological (pink) and evolutionary (blue) consequences at individual, popuation and community levels. As indicated by dashed arrows, complex reciprocal effects and feedbacks occur among these aspects of eco-devo variation; for instance, individual functional consequences affect fitness and consequently selective outcomes, which in turn shape subsequent developmental pathways and their ecological effects. This simple diagram provides a very general framework, rather than an exhaustive list of possible elements in eco-devo research.

Box 1. Development in context: the norm of reaction

The key conceptual tool for studying development in environmental context is the 'norm of reaction': the pattern of phenotypic expression realized by a given genotype across a range of conditions. This approach makes explicit two important points: first, the phenotype expressed by a given genotype depends on the environmental context and, second, the phenotypic effect of a given environment depends on the genotype in question, as a particular developmental response system.

These individual response patterns and their underlying regulatory mechanisms are heritable properties of the genome and, accordingly, evolve [3,5–7,12,15–19]. As are other products of evolution, they are shaped by phylogenetic history and genetic constraints as well as by natural selection and drift: norms of reaction to a given environmental cue can vary among genotypes, populations, or closely related taxa. The adaptive value of norms of reaction can be assessed using phenotypic selection analysis for genotypic means, or by manipulating trait expression, environmental cues or specific loci involved in cue perception and transduction.

cause those offspring to encounter a different seasonal climate [21]. Ecological development thus includes many aspects of niche construction – that is, the ways in which organisms themselves shape their environmental experience [22]. Individual responses to environment also constitute phenotypic or 'trait-mediated' effects that directly or indirectly shape a range of higher-order ecological interactions, from bacterial endosymbionts and their hosts to reciprocal or cascading effects among competitors, predators and prey [1,23–25]. Based on common induction cues, regulatory pathways or ecological consequences, eco-devo traits can include behavioral, physiological, or biochemical responses to environment that are not traditionally considered 'developmental' [13].

A focus on mechanisms: eco-devo approaches

Environmentally contingent development arises from a cue perception and response system, mediated by a complex signaling network. Although, currently, the underlying signaling pathways have been characterized in relatively few cases [12,18], several exciting research programs are studying molecular mechanisms in the context of naturally occurring environmental variation, in both plants and animals. One international effort [26,27] has investigated the molecular regulation of an ecologically important developmental transition, reproductive timing, in natural populations of the well-studied model genetic system *Arabidopsis thaliana*. Spring flowering in this winter annual plant is cued by both cold exposure ('vernalization') and day length, signals that vary latitudinally across the broad geographical range of the species [27]. The *Frigida* (*FRI*) locus mediating the cold requirement of the plant interacts epistatically with a chromosomally distinct flowering-repressor locus, *FLC*. Through this regulatory interaction, allelic variation at the *FRI* locus is associated with a geographical cline in flowering time from Mediterranean to Northern European ecotypes [26]. Because epistatic loci can show constrained responses to natural selection, this signaling interaction could hinder the evolution of appropriate phenological shifts in *Arabidopsis* populations as springs become warmer under global climate change. This finding confirms the general prediction that the genetic regulation of eco-devo responses involves complex epistatic elements [16]; however, to date, we know little about the genetic architecture of these responses [27].

Identifying environmental cues and their perception and transduction mechanisms is another central focus of eco-devo research (the specifically hormonal aspects of these mechanisms have recently been termed 'hormonal ecology' [28]). A specific environmental cue can initiate a suite of integrated developmental adjustments. For instance, young wood frog *Rana sylvatica* tadpoles that receive a chemical signal that predators are present produce a longer tail (for faster escape) and a correspondingly shorter body and gut [29]. The same trait or set of traits can be influenced by an entirely distinct environmental signal: these tadpoles also alter gut length adaptively in response to competition, presumably signaled by individual food intake rate [29].

Because regulatory pathways are often shared among distinct environmental cues and/or developmental traits in even broadly related taxa, deconstructing the interplay of conserved and novel elements in these pathways can provide important insights into adaptive responses and constraints at both individual and species levels. In plants, for instance, components of the same hormonal pathway are involved in stem elongation in response to flooding (which rescues the shoot from submergence and consequent low gas exchange) and stem elongation in response to shade by neighboring plants (which maintains access to sunlight in dense populations) [30]. However, these similar adaptive growth responses are initiated by distinct internal signals: the flood response is triggered by a build-up of the gaseous hormone ethylene in submerged tissues, and the shade response is cued by photosensitive phytochrome molecules. Species-specific refinements of shared pathways can result in characteristic developmental repertoires associated with different ecological scenarios. For example, as a result of differences in the ethylene-mediated pathway mentioned above [31], plant species show different capacities for elongation in response to submergence, resulting in different ecological distributions across flood-prone habitats [30].

In cases where environmental cues are indirect and predictive rather than immediate – for example, when cues initiate a life-history transition in advance of an environmental change – they can be difficult to identify. In amphibians, for instance, a similar hormonal pathway to induce metamorphosis is activated by different environmental signals in taxa that face the common challenge of producing their terrestrial form before the larval pool dries up. In the spadefoot toad *Spea hammondii*, tadpoles recognize imminent pond drying through their own reduced movement in a decreasing volume of water, and by proximity to the surface of the water, sensed by pressure and visual stimuli [32]. In another spadefoot toad, *Scaphiopus couchii*, more frequent physical contact among crowded tadpoles in a diminishing volume of water serves to cue the metamorphic response [33]. These distinct sensory cues are transduced through the neuroendocrine system to elicit similar hormonal events that initiate metamorphosis, including release of thyroid hormone to regulate the expression of genes involved in limb development, gut remodeling and other morphogenetic changes [34]. The congeneric *Spea multiplicatus* relies on a third cue system: as prey density rises with shrinking pool volume, tadpoles receive a direct cue in the form of increased ingestion of brine shrimp with their high constituent levels of thyroid hormone [35].

Phytochrome-mediated plant growth responses are a uniquely well understood eco-devo system, from gene sequences at specific loci encoding phytochrome proteins, to the light-sensing and regulatory functions of the proteins, to phenotypic outcomes and their autecological and microevolutionary consequences [17,36,37]. Changes in light spectral quality during shade filtering from nearby plants trigger photoconvertible phytochrome molecules to send a chemical signal. This signal quickly induces expression of a host of growth-related genes, resulting in elongation and other growth adjustments that enable the individual adaptively to avoid shade from its neighbors [36,38]. Recent studies of this regulatory cascade have revealed complex interactions between endogenous hormones including gibberellins and ethylene with growth-suppressor proteins [39]. These developmental responses differ in populations from open sites (where the adjustments are adaptive) compared with populations under canopy shade, where the elongated phenotype is maladaptive [40]. Other photoreceptors in the phytochrome gene family have been characterized through mutant analysis and transgenic constructs [17,36,38]; in some cases, these are implicated in ecologically distinct aspects of environmental response, such as negatively phototropic (i.e. downward) growth of roots [41]. This impressive body of work illustrates, on the one hand, how gene duplication and regulatory diversification can lead to novel, adaptive aspects of environmental response and, on the other hand, how norms of reaction for a given response pathway can evolve differently in contrasting habitats.

Eco-devo insights to a changing world

An eco-devo approach is particularly crucial as organisms are increasingly faced with anthropogenically altered ecosystems. New challenges include a myriad of local and global abiotic changes, resulting shifts in the presence and abundance of interacting organisms, and the introduction of countless alien taxa, which, by definition, are in novel environments, and which, in turn, create novel biotic conditions for natives in their new ranges [42]. By identifying the environmental cues, genetic elements and signaling pathways implicated in phenotypic expression patterns, eco-devo studies can reveal specific opportunities and constraints on organisms in their immediate and evolutionary responses to these new conditions.

Immediate impacts

In the short term, existing phenotypic repertoires will determine individual responses and, hence, population and species persistence. If the salient cues remain, adaptive plastic or canalized responses can promote survival and reproduction under altered conditions [40,43], enabling organisms with such reaction norms to persist long enough for further selective change to occur [44–46,47]. For instance, red squirrels in the Canadian Yukon *Tamiasciurus hudsonicus* can advance parturition date in response to warmer spring temperatures and earlier food availability [48]. Broadly adaptive norms of reaction based on the ability to sample multiple aspects of the environment might be particularly valuable to organisms facing novel conditions [44]. Such broadly adaptive response repertoires might also contribute to the invasiveness of species [43]; thus, characterizing eco-devo responses could help to predict whether non-native species are likely to spread invasively in a new range [49–51].

Eco-devo cue and response systems for traits with long lag times reflect past correlations between embryonic or juvenile environmental signals and selective conditions later in the life cycle. When habitat disturbance or climatic shifts disrupt these correlations, organisms can express adult morphologies or behaviors that are maladaptive to the altered conditions [52]. This is of concern in managed populations such as salmon fisheries, where rearing juveniles in a structurally homogeneous hatchery results in adults that are unable to alter their exploratory behavior appropriately in response to predator presence [53]. More generally, as the global climate changes, photoperiodic life-history cues used by a diverse array of organisms are becoming unlinked from local seasonal patterns, leading to population declines and the breakdown of synchronized ecological interactions [54]. In the insectivorous great tit *Parus major*, for instance, the timing of reproductive onset is cued by photoperiod and temperature signals, such that offspring will hatch when their caterpillar food supply is at its peak [55]. Owing to warmer early spring temperatures in recent decades, the timing of caterpillar growth has advanced, and the period of highest food demand by *P. major* populations no longer coincides with peak supply [56]. Because species differ in their abilities to shift phenologically in accord with climate warming, knowledge of eco-devo patterns will provide crucial predictive information regarding potentially destabilizing disruptions to food webs and other ecological interactions.

Evolutionary response

In the longer term, we face an urgent question: will phenotypic expression patterns evolve quickly enough in most taxa to accommodate these myriad environmental challenges? Assessing the potential for adaptive evolutionary response requires information about patterns of eco-devo variation within and among populations. For instance, one intensively studied European population of great tits has been shown to contain genetic variation for greater temperature plasticity in reproductive timing, providing the potential, in this population at least, for phenological reaction norms to evolve adaptively to keep pace with the shifting climate and its effect on food availability [57]. Another recent study showed that variation among genotypic reaction norms for traits affecting growth rate and survival in saline and fresh water enabled a salt marsh copepod to invade a novel freshwater habitat [58]. Such genetic variation in reaction norms (termed genotype x environment variation, or GxE) is the essential raw material for selective change in ecological developmental traits (Box 2). In addition to measuring GxE variation, information about its molecular basis and genetic architecture

Box 2. Genetic diversity for environmental response patterns

Evolutionary predictions regarding adaptation to anthropogenic change depend on genetic variation, as expressed across the possible range of environments; in other words, on genetic diversity for norms of reaction. In some cases, genotypes converge on identical norms of reaction for a given trait (Figure Ia), owing to previously strong selection and/or inherent constraints. In such cases, or in the unlikely case of strictly parallel genotypic responses (Figure Ib), there is no genetic variation for the shape of an environmental response pattern and, hence, no potential for adaptive evolution of eco-devo traits. In many cases, however, norms of reaction show GxE interaction: non-parallel patterns of trait expression from one environment to another (Figure Ic,d). This type of genetic diversity affects proximate selective outcomes on environmental response patterns and constitutes the raw material for future adaptive evolution of reaction norms.

In many cases of GxE variation, the magnitude of trait differences among genotypes varies, such that genotypes are similar or identical in certain environments and markedly different in others (Figure Ic). In these cases, the selective outcome will depend on the relative frequency of environments encountered. Consequently, adding a previously rare or unknown environment to the ecological experience of a population can either make previously cryptic genetic variation available to selection, or buffer the population from selective change, depending on whether genotypes differ or converge in the new conditions. A second aspect of GxE interaction is that the rank order of genotypes for a given trait can vary from one environment to another (Figure Id). If environmental conditions vary within a site or there is gene flow among sites, selection will favor 'generalist' genotypes, whose response pattern maximizes relative fitness across the entire range of conditions encountered. If human disruptions to natural systems reduce gene flow among previously linked populations in different environments, this can promote the evolution of local specialization over broad adaptive plasticity.

Genetic diversity for patterns of environmental response is the necessary raw material for eco-devo responses themselves to evolve adaptively to changing ecological situations. As with any aspect of genetic variation, related species, in addition to local populations, might contain different types and amounts of GxE variation. Hence, the evolution of adaptive reaction norms to new environmental conditions might be differently constrained in distinct populations or taxa.

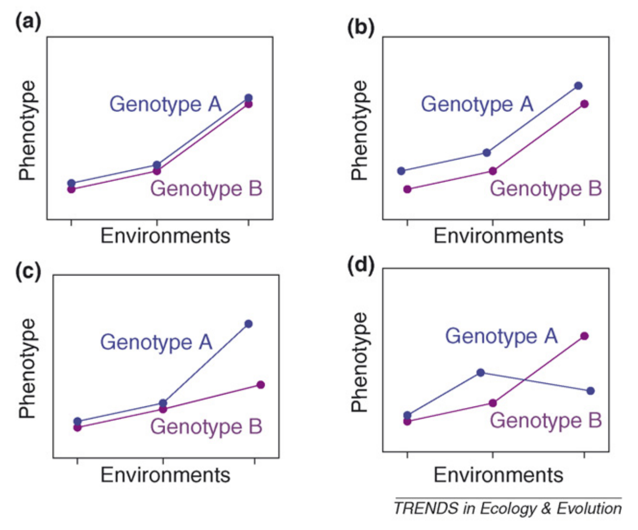

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Figure I. Patterns of norm of reaction diversity. For any phenotypic trait of interest, each genotype expresses a characteristic response to environmental states or 'norm of reaction'. Within a population, genotypes can converge on identical norms of reaction across a set of environments **(a)** or can differ consistently in all environmental states, resulting in parallel norms **(b)**. When genotypic differences vary from one environment to another, GxE variation is present and can occur in either or both of two ways. Genotypes might differ in the magnitude of environmental response to certain environments, expressing different phenotypes only in some environmental states **(c)**. The rank order of genotypic differences can also vary from one environment to another **(d)**, a pattern that can promote selective diversification among distinct habitats in the absence of gene flow.

in specific taxa will enhance our ability to predict the evolution and spread of new adaptations in those systems.

One crucial element of population and species persistence despite anthropogenic change might be GxE variation specifically for genotypes that are less phenotypically disrupted than others in unfavorable new conditions, perhaps owing to mutations for particular steps in transduction pathways. Such variation will allow selection for more canalized or homeostatic norms of reaction for key traits. Conversely, if all genotypes reduce fitness equally in a stressful environment, no raw material is present for the evolution of responses that buffer the stress. As with other aspects of genetic variation, available GxE variation for a trait (and its molecular components) can vary among populations and species, so taxa will have different potentials for coping with change through adaptive evolution of reaction norms. The availability of GxE for adaptive evolution also varies from one trait or type of trait to another, sometimes with different ecological implications. For example, if natural systems tend to contain more genetic variation for life-history traits than for central aspects of physiology such as metabolic and cellular processes, climate warming will selectively promote phenological shifts rather than heightened thermal tolerance. Unlike an evolutionary change in tolerance *per se*, these species-specific shifts are likely to disrupt ecological interactions in ways that might cascade through communities and ecosystems [55].

Evolutionary predictions depend not only on the presence of GxE variation, but also on its precise patterns of expression in relation to environmental conditions. This is because, as a result of environmentally contingent gene expression, the magnitude of fitness differences among genotypes varies from one environment to another [20,59]. As a result, adding a previously rare or unknown environment to the ecological experience of a population can either trigger a selective event by releasing otherwise hidden genetic variation, or buffer the population from selective change, depending on whether the genotypic norms are different or similar in that environment. In some cases, expressed genetic variation is greater under stressful novel conditions, a situation that facilitates selective change [60]. For example, steelhead salmon expressed greater behavioral variation when reared in a hatchery environment [53], and greater genetic variance for growth rate was expressed in *Pieris* butterflies at unfavorably high temperatures [61]. Bazzaz and colleagues [62] found greater variance for growth rate among genotypes of both a herbaceous annual plant and a forest tree, when grown in a combination of competitive conditions and elevated CO_2. Furthermore, genetic correlations among traits also vary from one environment to another, thus understanding potential genetic constraints on adaptive evolution requires documenting these correlations in the full range of prospective conditions [63,64]. In the plant study just described [62], the typical genetic correlation between total growth rate and reproductive fitness did not hold at elevated CO_2 at a naturalistic plant density, indicating that selection will not lead to the evolution of genotypes with enhanced abilities to fix atmospheric carbon through increased vegetative growth rates. The evolution of adaptive eco-devo patterns might also be constrained by phylogenetically conserved pleiotropy – for instance, when different functional or life-history traits are regulated by common cues or pathways, such as the endocrine system in vertebrates [25,48], or shared growth regulators, such as ethylene or abscisic acid, in plants [39].

Future directions

Studying developmental transduction and regulatory pathways in the context of ecologically meaningful conditions is a key step toward synthesizing a contemporary understanding of these mechanisms with both ecology and evolution [2,13,20,65]. Assembling this integrated biological picture calls for collaborations between the traditionally distinct disciplines of molecular development and evolutionary ecology [66] to bring relevant aspects of environmental variation into developmental studies.

Insights into real-world scenarios require studies that go beyond the precise, single-factor tests characteristic of many earlier norm of reaction studies. Enhancing the ecological realism of eco-devo studies calls for careful measurement of field parameters and experiments that recreate variation in several interacting environmental factors [23,67]. Multifactorial studies can reveal important and sometimes surprising interaction effects. For instance, recent ecotoxicology studies (e.g. by Relyea and Hoverman [68]) have revealed a powerful synergy between toxic agrochemicals such as herbicides and the presence of stress owing to chemical predator cues. Such studies make it clear that realistic predictions regarding the impact of contaminants and other anthropogenic factors on natural communities require tests that incorporate interacting aspects of field conditions. We also need to know more about how eco-devo responses to altered environments, in turn, affect interactions among ecological competitors and facilitators, predators and prey, parasites, pathogens and their hosts, and mutualists [23,69].

Because organisms must either adapt to a rapidly (and radically) changing world or face extinction in the wild, and because existing ecosystems are being threatened by alien invasives, the once speculative question of adaptive evolutionary potential is now an urgent one. Rapid adaptive change has been documented in a range of organisms, particularly in populations facing novel conditions [70,71]. In some cases, these phenotypic changes reflect ‘contemporary evolution’ or rapid selective change in the genetic composition of populations, as in the well-studied cases of grasses that quickly evolve tolerance to metal-contaminated soils, and salmon populations with reduced size at maturity owing to selective harvesting. However, much of this very rapid adaptive response is not seen in common-garden comparisons, and thus is evidently the expression of existing functionally adaptive plasticity [47]. Of course, existing norms of reaction can also produce maladaptive phenotypes in extreme or new conditions, particularly because selection has not previously acted on those parts of the reaction norm. Eco-devo studies in existing and projected environments are needed to evaluate the degree to which various taxa are likely to withstand immediate anthropogenic changes to their habitats through existing response repertoires. Adaptive and random population-level differences in norms of reaction might have a crucial role in determining which populations persist or become extinct.

In the longer term, and as environments are further altered, a key aspect of species persistence will be the ability to evolve adaptive norms of reaction for human-altered ecosystems. As yet, relatively little is known about evolutionary potential for adaptive eco-devo response patterns. A few recent studies suggest that plasticity can evolve rapidly [58,72,73]. Genetic diversity for adaptive norms of reaction might be more available for certain fitness-related traits than for others; for instance, shifts in seasonal phenology might be a more probable selective response to global climate change than are changes in thermal tolerance *per se* [54]. Comparative studies of GxE variation might provide some general evolutionary predictions. Such studies should include prospective, in addition to existing, environmental states because genes expressed in harsh or novel environments can show unanticipated phenotypic effects and variance patterns [20]. Eco-devo insights will also inform our understanding of introduced invasive species, which are often predicted to express broadly adaptive norms of reaction to several environmental factors [43,46], possibly obviating selective change in new ranges.

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