

Ecological consequences of phenotypic plasticity

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Phenotypic plasticity is widespread in nature, and often involves ecologically relevant behavioral, physiological, morphological and life-historical traits. As a result, plasticity alters numerous interactions between organisms and their abiotic and biotic environments. Although much work on plasticity has focused on its patterns of expression and evolution, researchers are increasingly interested in understanding how plasticity can affect ecological patterns and processes at various levels. Here, we highlight an expanding body of work that examines how plasticity can affect all levels of ecological organization through effects on demographic parameters, direct and indirect species interactions, such as competition, predation, and coexistence, and ultimately carbon and nutrient cycles.

Introduction

Phenotypic plasticity can be inclusively defined as the production of multiple phenotypes from a single genotype, depending on environmental conditions [1,2]. It is now clear that a wide diversity of organisms express phenotypic plasticity in response to biotic and abiotic aspects of their environments (reviewed in [3–7]). These plastic responses include changes in behavior, physiology, morphology, growth, life history and demography, and can be expressed either within the lifespan of a single individual [8] or across generations [9]. A fascinating literature has emerged documenting patterns of expression of plasticity and genotype x environment interactions (see Glossary), testing whether responses are adaptive, and modeling how evolution affects plasticity [6]. Here, we focus on an equally important but less well understood aspect of phenotypic plasticity: its ecological impact [10]. We review recent research showing how plasticity alters interactions between individuals and their environments in ways that influence the stability and local biodiversity of populations and communities. We argue that, because plasticity can alter a variety of direct and indirect interactions among individuals and their environments, it should ultimately affect many ecological processes, such as population and

community dynamics, and aspects of community and ecosystem functioning.

Some of the general ideas from this body of work are relatively new, whereas others were proposed decades ago but not widely appreciated by researchers working in other disciplines or systems. For instance, there is a long tradition of work on behavioral plasticity in animals and its population- and community-level effects, which has flourished as the distinct area of ‘behavioral ecology’. The

Glossary

Adaptive plasticity: plasticity maintained by natural selection.

Allee effect: when the per-capita birth rate increases with density but the per-capita death rate does not [59]. Low population sizes are therefore vulnerable to extinction because the birth rate is less than the death rate.

Density-mediated indirect interaction (DMII): when one species affects the density of another species by altering the density of an intermediate species (e.g. keystone predator effects, exploitative competition or trophic cascades).

Ecological trap: a specific type of evolutionary trap in which cues for habitat choice are altered and become less reliable [45].

Genotype-by-environment interaction (GxE): in population genetic experiments, phenotypic variance can be partitioned by apparent causal agents: the component of phenotypic variation owing to differences in genotype (G), the component of variation attributable solely to environmental factors (E), and the component of variation that is due to differences among genotypes in their response to environmental factors (GxE). GxE demonstrates genetic variability for phenotypic plasticity within a population. However, there need not be significant genetic variation within a population for individuals to be phenotypically plastic.

Inducible defense: phenotypically plastic traits that reduce the risk of consumption [4].

Inducible offense: phenotypically plastic traits that enhance consumptive or competitive ability.

Lag time: time between when an individual experiences a particular environment and when it responds to that environment [40]. In the case of plasticity that is reversible, lag time can refer to the response after which an individual experiences an inducing agent, or the response after the inducing agent is no longer present, or both.

Non-independent multiple predator effects: when the effects of different types of predator in combination cannot be predicted from the isolated effects of each predator [21]. Typically, investigators test for multiple predator effects of prey survivorship.

Paradox of enrichment: population models predict that adding nutrients to a system will cause large fluctuations in population size and will lead to stochastic species extinctions [60].

Reaction norm: the relationship between the environment and the phenotype of an individual or a group of individuals [7].

Trait-mediated indirect interaction (TMII): when one species affects the density of another species by altering the traits of an intermediate species (e.g. predator-induced reduction in herbivore foraging results in greater plant biomass) [61]. Behaviorally mediated indirect interactions are a TMII that involves a behavioral response.

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general framework for plasticity that we propose will make clear common principles that are relevant to diverse taxa as well as other types of phenotypic plasticity. For example, behavioral plasticity in animals and developmental plasticity in plants can have analogous effects on population stability and trophic interactions. Hence, our goal is to direct attention to the common ecological issues and questions that arise from an awareness of phenotypic plasticity as a general biological phenomenon.

The effect of plasticity on individual–environment interactions

Direct interactions

The recognition that plasticity can be adaptive has stimulated a wealth of studies on how plasticity alters interactions between individual organisms and their environments [3–6]. Although this research program has been motivated largely by evolutionary questions, studies of adaptive plasticity such as inducible defenses and inducible offenses [4,10,11] (Box 1) also have clear ecological implications. For example, in East Africa, herbivory by elephants and giraffes induces longer and more numerous protective spines on *Acacia drepanolobium* trees [8], which enhances the survivorship and competitive ability of *A. drepanolobium* when subsequent herbivores arrive.

Studies examining how plasticity affects the interactions of organisms with their environments typically focus on (i) an abiotic or biotic environmental factor (e.g. temperature or predation); and (ii) an ecologically relevant aspect of a phenotypic response to that factor. The altered phenotypes, in turn, affect subsequent interactions. For example, barnacles exposed to greater water velocities produce shorter feeding appendages [12], which affect food acquisition. Similarly, plants alter the growth and structure of roots in response to different concentrations of nutrients, which maximizes nutrient foraging in patchy soils [13]. This response increases the capture of essential nutrients, such as phosphate and, in turn, affects competitive interactions among plant species [13]. Many studies have shown that plasticity affects direct interactions between individuals and their biotic (e.g. predation, herbivory and competition) and abiotic (e.g. temperature and light) environments in a variety of ways and in a wide range of taxa [3–7].

Indirect interactions

Recently, investigators have begun to consider how plasticity affects indirect interactions in multi-species assemblages. Before a decade ago, ecologists interested in indirect interactions were primarily concerned with the indirect effects of consumption [14]. A predator decreases the density of its prey, which in turn alters the strength of the interaction between the prey and a third species. Consequently, the predator, by consuming prey, indirectly affects the third species, typically referred to as a density-mediated indirect interaction. For example, predatory dragonfly larvae, through their consumption of frog tadpoles, indirectly interact with periphyton communities [15]. When dragonfly larvae are present, they consume

Box 1. Phenotypic plasticity in frog larvae

Frog tadpoles are an effective system for exploring the ecology of phenotypic plasticity. Frequently, predators induce tadpoles to reduce their foraging activity, which reduces detection by predators [62]. Predators also induce relatively larger tails and smaller bodies in tadpoles (Figure 1) [62], which reduce capture by predators [63] owing to faster swimming abilities and because a large tail lures predator strikes away from the vulnerable body [64]. However, both defenses come at the cost of slower growth [65], because predator-induced tadpoles have smaller mouthparts [66] and shorter, less efficient intestines, and spend less time foraging [67].

Predators are only part of the story. Competitors induce the opposite suite of traits, enabling faster growth but at the cost of increased vulnerability to predation [66,67]. Tadpoles can fine-tune their phenotypes to different combinations of predator and competitor densities and balance these opposing inductive forces [68]. The existence of two inductive processes (i.e. changes in predator and competitor densities) means that predators can induce phenotypes directly as well as indirectly by consuming tadpoles and reducing competition among tadpoles. The direct effect of predators scaring tadpoles is primarily responsible for changes in tadpole morphology, whereas the direct and indirect effects of predators are equally responsible for changes in tadpole behavior [69].

These responses are induced by chemical cues, and tadpoles can discriminate among predator species, exhibiting predator-specific phenotypes. This suggests that different predators emit unique chemicals [70]. Tadpoles can also discriminate among different diets for a given predator, suggesting that diet mediates these chemical signals [71]. Furthermore, the magnitude of defense induced by a predator consuming different diets is inversely related to the phylogenetic distance between tadpoles and the diet of that predator, which includes other species of tadpoles, insects and snails [72].

Because amphibians live in a heterogeneous landscape of predation and competition, plastic traits are favored owing to a tradeoff between predator resistance and growth. This tradeoff affects not only individuals, but also the community via trait-mediated indirect effects [16], and is one example of why amphibians are an excellent model system to use to study the ecology of phenotypic plasticity.



Figure 1. Morphological plasticity in tadpoles. Tadpole (a) has been exposed to predators, resulting in the induction of a colorful and relatively large tail. Tadpole (b) has not been exposed to predators and has a less colorful and relatively small tail. Reproduced with permission from Rick Relyea.

tadpoles, thereby reducing tadpole density, which decreases the grazing pressure of tadpoles on the algae.

Plasticity can also generate indirect interactions, typically referred to as trait-mediated indirect interactions. For example, in addition to eating tadpoles, dragonfly larvae also induce tadpoles to forage less, which causes an increase in algal densities [15]. Thus,

Box 2. Multiple predator effects

Studies of predator–prey interactions generally consider only a single type of predator, yet, prey are commonly threatened by more than one type of predator in nature. More than half of the empirical studies reviewed by Sih *et al.* [21] demonstrated multiple predator effects, whereby inclusion of additional types or species of predators altered (i.e. enhanced or reduced) the predation risk for the prey species. For example, two freshwater predators (sculpin *Cottus bairdi* and stonefly larvae *Agnatina capitata*) consume mayfly *Baetis tricaudatus* larvae. When both sculpin and stonefly larvae are present, each consumes fewer mayflies than when each predator is alone [73] (i.e. the presence of a predator weakens the strength of the interaction between the other type of predator and prey). This is because sculpin induce stonefly larvae to hide beneath rocks and reduce their foraging activity [74]. Thus, plasticity leads to risk reduction.

Multiple predators can also affect survivorship of prey across life histories. In an East African rainforest, the frog *Hyperolius spinigularis* lays its developing embryos on leaves that overhang ponds, and hatchlings drop into the pond and develop as tadpoles until metamorphosis [23]. While on the leaves, the presence of another frog *Afraxalus fornasini*, which preys on the embryos of *H. spinigularis*, induces them to hatch early and at a small size (i.e. life-history plasticity). Once in the pond, tadpoles are exposed to predatory larvae of the libellulid dragonfly *Trapezostigma basilaris*. Although the two predators do not interact directly, they interact indirectly through the prey. Thus, the presence of the arboreal predator reduced the effectiveness of the aquatic predator by 70% compared with the predicted survivorship from each predator in isolation (Figure 1a). This reduction in risk is caused equally by plasticity and density effects (Figure 1b).

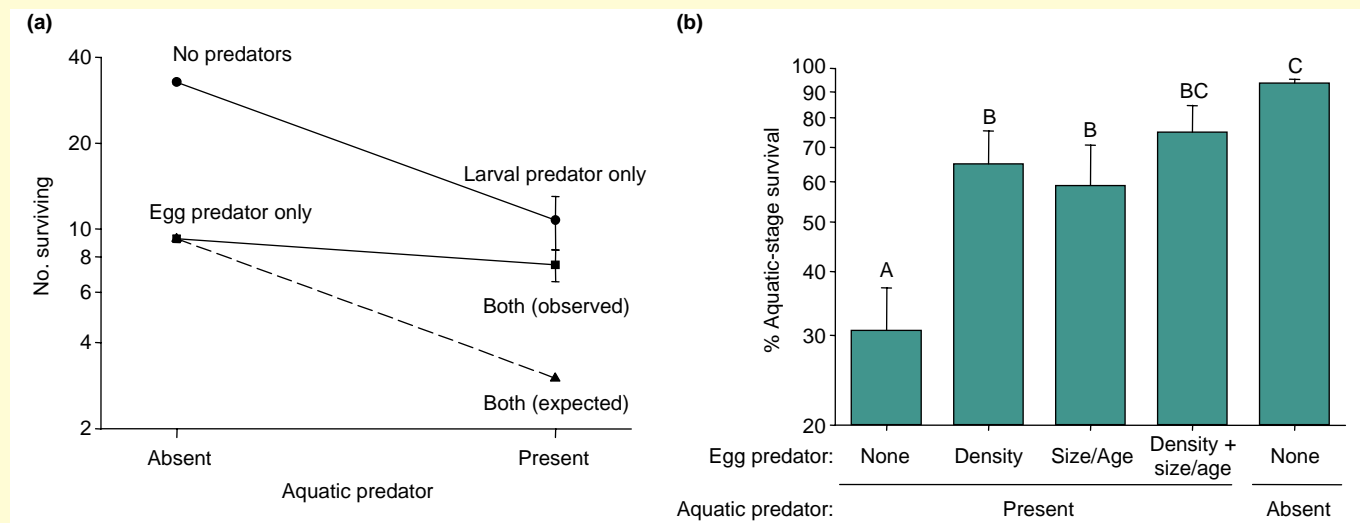


Figure 1. Multiple predator effect across life-history stages. (a) The survivorship of frog *Hyperolius spinigularis* embryos on exposure to four combinations of predators. Circles represent the absence of the egg predator, and squares represent the presence of the egg predator. (b) The survivorship of prey when the effects of density and plasticity are isolated. Letters indicate significant differences among treatments. Reproduced, with permission, from [23].

dragonfly larvae also indirectly interact with algae by altering the behavior of the tadpoles. This area of research is rapidly increasing (recently reviewed in [16–19]), and demonstrates that plasticity, by altering indirect interactions, can influence the strength of competition [20], facilitation [21] and trophic cascades [22], as well as cause non-independent multiple predator effects [23] (Box 2). To date, most research on indirect interactions via plasticity has examined anti-predator behavior. However, morphological plasticity can also cause indirect interactions [24], and it is likely that any type of plasticity can alter the direction and strength of indirect interactions.

Although most research has focused on plastic responses to biotic conditions, plastic responses to abiotic factors can also result in indirect effects. For example, plants might respond phenotypically to predicted atmospheric change. Plants respond to elevated CO₂ through changes in leaf chemistry, which reduce tissue nutritional quality for herbivores. This affects herbivore feeding behavior, development time and predation risk [25], leading to larger effects on community dynamics [26].

Niche construction

Many organisms have the ability to modify the environments that they experience, called ‘niche construction’

[27]. Recently, work has demonstrated that plasticity can result in niche construction [28], and it is especially interesting when environmental modifications lead to improvements [28]. For example, in response to shading by neighboring plants, many plants elongate shoot internodes to overtop these competitors, a developmental response that brings the photosynthetic organs of that individual into a more favorable light environment [29]. In *Arabidopsis thaliana*, shading by neighbors also induces a change in phenology by accelerating reproductive onset [29]. This plastic response enhances the resource environment of the plant during the crucial period of seed and fruit maturation, because, in most habitats, light as well as nutrient availability decline later in the growth season [29].

Niche constructions can also create feedbacks that shape subsequent interactions between the individual and its environment. For example, *A. thaliana* disperses seeds at different spatial scales depending on the density of conspecifics. Thus, the current density of conspecifics affects the future density of conspecifics through plasticity in dispersal, and thus alters subsequent dispersal [28]. The research on plasticity influencing niche construction has primarily focused on plants and the effects of morphological and life-history plasticity [28,29]. This research demonstrates that individual–environment

interactions might be more complex than was previously thought.

Altered interactions have consequences for populations and communities

Population stability and species co-existence

The idea that behavioral and physiological plasticity can affect population dynamics was suggested >20 years ago (reviewed in [3,30]). However, there is an increasing interest in the effects of plasticity on population dynamics, and early ideas are being re-discovered or investigated for different types of plasticity. For example, a variety of inducible defenses and offenses can affect the amplitude of population fluctuations, and increase the stability of a population within a community with two or three trophic levels [31–38].

Plasticity can stabilize a population because plastic responses are often density dependent. In a simple predator–prey system, the size of the prey population initially increases followed by an increase in the size of the predator population. The increase in the predator population induces prey defenses, which can reduce the population growth rate of the prey. The increase in prey defenses also slows the size increase of the predator population because prey are now better defended, slowing per-capita consumption rates. The opposite is true when population sizes decrease. Thus, the phenotypic response of a prey to predator density results in a negative feedback that can stabilize the population size of both predator and prey [35]. In a similar manner, phenotypic responses of a predator to prey can also stabilize population sizes [39].

The ability of plasticity to stabilize a population is strongly dependent on the lag between the induction time of a plastic response and the timing of environmental changes [32,39,40]. As the lag time increases, the ability of plasticity to stabilize a population decreases, increasing the amplitude of population fluctuations [32,39,40]. Interestingly, the ability of inducible defenses to stabilize a population can explain the absence of the paradox of enrichment, and might resolve the discrepancy between theoretical and empirical studies [36,37] (Box 3).

Given that plasticity can affect the stability of populations, it is not surprising that plasticity can also affect species coexistence within communities. Recent theoretical work suggests that adaptive plasticity, both inducible offenses and defenses, can increase species permanence by enlarging the conditions in which species can coexist [36,37,41–43]. For example, with a mathematical model, Krivan [43] demonstrated that a community with a top predator, two consumer species, and a resource species was more likely to persist when the predator had adaptive behavioral plasticity and could switch its prey preference to maximize its growth, compared with when the predator had a fixed behavior.

For the stability and permanence of species, whether plasticity is adaptive probably has a large effect. This is because longer lag times of plasticity can destabilize populations, and increase the likelihood that plasticity will be non-adaptive [40]. However, if the response is adaptive, then the type of plasticity (e.g. behavioral, morphological, or physiological) might have relatively

Box 3. The paradox of enrichment

Population models predict that adding nutrients to a system will cause large fluctuations in population size and lead to stochastic species extinctions. This is referred to as the ‘paradox of enrichment’. However, populations are often more stable when nutrients are added to natural systems than models predict [36,37,75]; a possible explanation for this is plasticity. In theoretical models, inducible defenses can stabilize population fluctuations, reducing the probability that populations will go extinct and, thus, eliminating the paradox of enrichment [36,37,75].

In an empirical test of the predictions of theoretical models, Verschoor *et al.* found similar results in experiments with aquatic organisms [37]. They demonstrated that population fluctuations were much less in a system with an alga, herbivorous zooplankton, and carnivorous zooplankton when the species of alga had an inducible defense than when it did not (Figure 1).

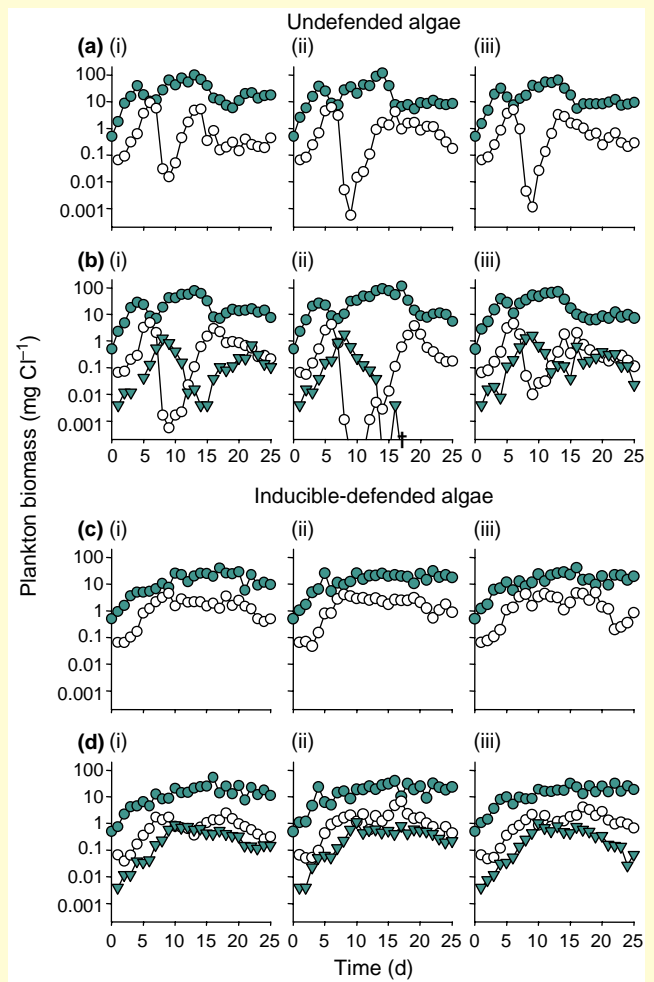


Figure 1. Inducible defenses lead to the absence of the paradox of enrichment. The symbols indicate algae (filled circles), herbivorous zooplankton (open circles) and carnivorous zooplankton (filled triangles). (a) and (b) represent experiments with an undefended alga, whereas (c) and (d) represent experiments with an alga with inducible defenses. (a) and (c) represent an experiment with two trophic levels, and (b) and (d) represent one with three trophic levels. (i–iii) indicate the replicate. Reproduced, with permission, from [37].

little effect because selection should favor short lag times for any type of plasticity. Although it is typically assumed that morphological plasticity has longer lag times compared with more immediate types of responses, such as behavioral plasticity, lag times are a product of the time it takes to induce a particular phenotype and the timing

Box 4. Ecological realism in plasticity experiments

Controlled experiments are required to document precisely plastic responses to specific environmental variables. However, the results of such studies are ecologically meaningful only if experimental conditions match salient aspects of natural environmental variation. Plasticity studies explicitly recognize that the researcher's choice of environmental manipulations can profoundly influence experimental results. Hence, the key to designing ecologically informative plasticity experiments is to recreate the kind of environmental variation that elicits plastic responses in the natural setting of the organism; in other words, careful attention to ecological realism.

Identifying environmental factors that cue plasticity

Identifying the precise cue or cues that induce a plastic response can be challenging. For instance, submerged tadpoles might sense imminent pond drying through changes in temperature or chemical concentration, visual effects of surface proximity, or increased swim contact to induce accelerated metamorphosis [76]. Moreover, plasticity cues can consist of specific aspects of environmental variables, such as the spectral quality of shade treatments [77]. Recognizing these specific factors is crucial because their correlations with particular ecological pressures can vary from one habitat or site to another, shaping the expression and evolution of plasticity in distinct populations [78]. In some cases, a known proximal cue can be experimentally separated from its natural context, enabling a plastic response to be tested in alternative ecologically relevant environments [79].

Implementing appropriate treatments

Ecologically meaningful data also demand realistically designed levels of relevant environmental factors, ideally based on naturally occurring states. Arbitrary treatment levels (e.g. stressful versus favorable) can produce ecologically misleading results for two reasons. First, because the relationship between phenotypic responses and environmental variation is often nonlinear [80], responses to arbitrary treatments cannot be simply extrapolated to field conditions. Second, variance among genotypes, populations or taxa will depend upon the environmental states studied [81]. The timing and pattern of applying experimental treatments is also important [82]. In some cases, it is important to alter the variance, range or frequency of environmental states rather than the mean [83]. This information requires careful, repeated measurements of field conditions, but can provide a useful interpretive context for ecological and evolutionary questions [54,80].

Accounting for real-world complexity

Perhaps the most important (and most difficult) step in creating ecologically realistic plasticity experiments is to incorporate the real-world complexity of multiple biotic and abiotic variables. The ecological impact of any plastic response depends on the functional and fitness tradeoffs that it creates in the context of these environmental demands. Although controlled experiments can incorporate several interacting factors, it is only through field experiments that the ability of the organism to integrate all of its environmental demands through plasticity can be tested. Field studies can also identify interacting environmental factors (e.g. local consumers or competitors), suggest additional plastic traits that merit study, and reveal specific life-cycle stages at which various plastic traits are most ecologically important and therefore should be measured. In this way, results of field experiments can be invaluable in shaping the controlled studies needed to characterize precisely specific aspects of plasticity, as well as in testing their functional and fitness consequences.

and rate of environmental change. It is therefore possible that a quick behavioral response can result in a longer lag time than can a slow morphological response, and there is currently no evidence that responses that can occur more quickly have shorter lag times. Studies of behavioral and morphological plasticity [36,37,41–43], as well as

plasticity that affects of niche construction [44], demonstrate that plasticity can promote stability, species coexistence or both. However, any type of plasticity has the potential to promote stability and species coexistence as long as there is an appropriate density-dependent response.

Ecological and evolutionary traps

Plastic responses are often induced by environmental cues. However, these have the potential to become less reliable (e.g. as a result of anthropogenic effects) and negatively affect populations. When this happens, it is referred to as an evolutionary trap [45]. For example, mayflies use polarized light, which indicates the presence of water, as a cue for where to lay their eggs. However, dry asphalt and black plastic used to cover agricultural fields also reflect polarized light, and mayflies have been observed laying their eggs on roads or plastic sheets [46]. Although evolutionary traps can arise whenever an organism that is plastic uses a cue that becomes less reliable, negative effects are likely to be larger when cues for neutral or adaptive plasticity are altered, because what were beneficial or neutral responses are now detrimental responses. Given that many species have adaptive inducible defenses and offenses to other species, invasive species might be a common and important cause of evolutionary traps [47].

Ecological traps, which are a specific type of evolutionary trap, can also lead to allee effects that increase the probability of a population going extinct [48]. Take the situation in which a cue for habitat choice is altered so that individuals now prefer low-quality sites. When populations are large, individuals can compete for preferred sites but ones of a low quality, which can lead to individuals occupying sites that are less preferred but higher quality [48]. However, when a population is small, individuals only occupy preferred, low-quality sites; thus, population growth is reduced because a greater proportion of the population occupies low-quality sites.

Local biodiversity

Recently, studies have demonstrated that plasticity can affect local biodiversity by altering indirect interactions [49–51]. For example, in a New England field, the presence of spiders increases local biodiversity because spiders induce several species of herbivores to seek refuge in and graze on a competitively dominant plant species, which enables competitively inferior plant species to increase [49]. Thus, by altering indirect effects, behavioral plasticity can affect biodiversity. However, it remains to be seen whether plasticity can alter biodiversity in other ways [49–51]. In addition, the effects of plasticity might have important ecological consequences on the health and persistence of communities, because biodiversity can influence community and ecosystem functioning [52].

Future directions

We have highlighted several ways in which plasticity can alter ecological patterns and processes at the level of individuals, populations and complex communities. However, it remains to be seen whether these higher-level

effects of individual plasticity are widespread in natural systems. Several aspects of plasticity deserve attention because they influence the direction and the strength of individual–environment interactions, and are, consequently, likely to alter the ecological impact of plasticity. These include: (i) time lags between environmental cues and plastic responses [4,40]; (ii) reversibility of response [53]; and (iii) the shape of reaction norms with respect to environmental gradients [6,7]. An important contribution will be made by studies of plasticity that focus explicitly on these factors to consider general principles for understanding plasticity in its ecological context. At present, studies on various types of plasticity (i.e. behavioral, physiological, morphological or life historical) are generally considered separately. Yet, it is unclear whether the ecological consequences of different types of plasticity will differ. For example, behavioral, physiological and morphological plasticity can all stabilize populations. We need a better understanding of whether different types of plasticity have similar ecological effects, which will require not only further research, but also well designed experiments (Box 4) and better communication among researchers.

Most plasticity research focuses on putatively adaptive responses to environmental challenges, such as inducible defenses and offenses. However, it is equally important to investigate the ecological consequences of non-adaptive environmental responses [10,54], which are likely to be common [55,56]. This is especially true for maladaptive plasticity that should amplify the effects of environmental change through the negative effects on individuals. For example, the snail *Physella virgata* flees and produces a more rotund shell when in the presence of certain non-molluscivorous sunfish that pose no risk. This maladaptive response slows the growth of individuals and is likely to alter population and community dynamics [55].

The consequences of plasticity for whole-community structure and dynamics, and ecosystem processes remain largely unknown. Nonetheless, plasticity is likely to have important effects, including the transfer of energy, numbers of trophic levels, and habitat interactions and feedbacks. Carbon cycles, nutrient cycles and primary productivity are likely to be altered by plastic effects on growth and morphology of ‘ecosystem engineers’ and other keystone species, as well as more subtle effects on community composition [57]. For example, induced behavioral responses in organisms, such as diel vertical migrations [4], will affect the transport and cycling of carbon and nutrients in aquatic systems. A more complex case is posed by feedbacks between nutrient availability and inducible defenses in terrestrial plants and marine algae: in these situations, carbon and nutrient availability affects the expression of inducible defenses, which in turn alter carbon and nitrogen balance through interspecific effects [58]. Exciting new avenues for research include the effects of plasticity on community diversity, resilience, zonation and patchiness, as well as rates of energy transfer throughout ecosystems and ecosystem functioning [52].

Conclusions

Interest in the ecological consequences of plasticity is increasing. By adopting an inclusive definition for the term ‘phenotypic plasticity’, we hope that researchers will recognize the broad implications of their work for a diversity of taxa and biological disciplines. Studies of plasticity in its ecological context provide a rich opportunity for interdisciplinary collaborations, to reveal not only patterns and mechanisms of environmental response, but also the direct and indirect effects of those responses on the relationship of organisms to their abiotic and biotic environments and, consequently on higher-level ecological processes.

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