PERSPECTIVE

The role of phenotypic plasticity in shaping ecological networks

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Abstract

Plasticity-mediated changes in interaction dynamics and structure may scale up and affect the ecological network in which the plastic species are embedded. Despite their potential relevance for understanding the effects of plasticity on ecological communities, these effects have seldom been analysed. We argue here that, by boosting the magnitude of intra-individual phenotypic variation, plasticity may have three possible direct effects on the interactions that the plastic species maintains with other species in the community: may expand the interaction niche, may cause a shift from one interaction niche to another or may even cause the colonization of a new niche. The combined action of these three factors can scale to the community level and eventually expresses itself as a modification in the topology and functionality of the entire ecological network. We propose that this causal pathway can be more widespread than previously thought and may explain how interaction niches evolve quickly in response to rapid changes in environmental conditions. The implication of this idea is not solely eco-evolutionary but may also help to understand how ecological interactions rewire and evolve in response to global change.

KEYWORDS
ecological network, interaction niche, interaction strength, intraspecific trait variation, niche breadth expansion, niche shift, network plasticity, phenotypic plasticity, polyphenism

INTRODUCTION

Phenotypic plasticity, the ability of a genotype to produce alternative phenotypes when exposed to different environments (Pigliucci, 2001; Schlichting & Pigliucci, 1998), has important implications for understanding how organisms can rapidly cope with changing environments (Pfennig, 2021). Phenotypic plasticity is widespread, and its occurrence has already been documented in a myriad of organisms all across the tree of life (Pfennig, 2021). The ecological consequences of plasticity are paramount. Plasticity may expand species ranges (Berg & Ellers, 2010), accelerate colonization and invasion success (Davidson, Jennions, & Nicotra, 2011) and stabilize population dynamics in changing environments (Chevin, Lande, & Mace, 2010). Phenotypic plasticity might entail the emergence of novel phenotypes with new adaptive possibilities, which may be beneficial in some contexts (Snell-Rood & Ehlman, 2021; Sultan, 2021). Plastic responses include changes in different types of traits, such as those related to the physiology, morphology, behaviour and life history of species, and can be expressed across generations (Agrawal, Laforsch, & Tollrian, 1999; Donelson, Salinas, Munday, & Shama, 2018; Fox & Mousseau, 1998; Puy et al., 2022), within a generation (Agrawal, 2001; Green, 1967)

or within the lifespan of a single individual (Gómez et al., 2020; Karban & Baldwin, 1997).

Ecological interactions are important elicitors of plasticity (Westneat, Potts, Sasser, & Shaffer, 2019). The relationship between phenotypic plasticity and ecological interactions has a long tradition of research (Agrawal, 2001). It is well known that some, mostly antagonistic, interactions have played an important role in the evolution of plastic traits. This process has been extensively investigated in predator–prey, parasite–host and plant–herbivore interactions, and it is widely acknowledged that plasticity in this context favours the expression and evolution of defence and offence traits (Karban & Baldwin, 1997; Tollrian & Harvell, 1999). Competitive interactions are also a motor of phenotypic plasticity, favouring rapid niche segregation and enabling species coexistence (Callaway, Pennings, & Richards, 2003; Hess, Levine, Turcotte, & Hart, 2022; Turcotte & Levine, 2016). Although much less explored, it is increasingly acknowledged that mutualistic interactions may also elicit plastic responses and modulate plasticity (Callaway et al., 2003; Friesen et al., 2011; Goh, Veliz Vallejos, Nicotra, & Mathesius, 2013; Yamada et al., 2008).

Ecological interactions are not only a source of phenotypic plasticity but are also modified by the presence of plastic traits (Berg & Ellers, 2010). Although the dynamics of many ecological interactions depend on changes in abundance or density of the interacting organisms (*density-mediated interactions*), there is no longer any doubt that interactions in which their effects on other organisms depend on changes in phenotypic traits of the interacting individual (*trait-mediated interactions*) also play a relevant role in the structure and dynamics of ecological communities (Bolker, Holyoak, Křivan, Rowe, & Schmitz, 2003; Schmitz, Krivan, & Ovadia, 2004; Werner & Peacor, 2003). Trait-mediated interactions can be direct, occurring when the plastic change in one species alters the interaction strength in a second species. A classic example is the induction of defences in prey that modify the functional responses of predators (Tollrian & Harvell, 1999). Additionally, by prompting plastic responses in traits other than those directly involved in the interaction, phenotypic plasticity may indirectly affect the interaction of the target species with third species. For example, plant attractiveness to pollinators is altered by changes in floral traits caused by the damage by ungulates and folivorous insects (Gómez, 2003; Rusman, Poelman, Nowrin, Polder, & Lucas-Barbosa, 2019; Strauss, 1997; Strauss, Sahli, & Conner, 2005). Plasticity is, thus, also a major source of *trait-mediated indirect interactions* (Valladares, Gianoli, & Gómez, 2007; Werner & Peacor, 2003).

Plasticity can affect not only the dynamics of interactions but also their structure (Miner, Sultan, Morgan, Padilla, & Relyea, 2005). In particular, plasticity may have strong effects on the identity and size of the *interaction niche*, the region of the niche space that encompasses the interaction with the set of species that affect the reproductive success or population growth of the target species. This occurs because, by expressing different phenotypes in different environments, organisms can interact at each time or locality with different sets of species that differ in functional traits (Gómez et al., 2020, 2022).

Plasticity-mediated changes in interaction dynamics and structure may scale up and affect the ecological network in which the plastic species is embedded. In this study, we argue that, by affecting the strength of ecological interactions and the breadth and identity of interaction niches, phenotypic plasticity influences the topology and functioning of ecological networks. The rationale of our conceptual pathway is schematically illustrated in Figure 1. We first consider that plasticity, whether caused by abiotic agents or ecological interactions, has an immediate and direct effect on the magnitude of phenotypic variation within species. We hypothesize that, by enhancing the magnitude of intra-individual phenotypic variation, plasticity may have three possible direct effects on the interactions that the plastic species maintains with other species in the community. It (1) may expand the extent of the interaction niche (i.e., expands the niche breadth of the plastic species), (2) may cause a shift from one interaction niche to another one in the network, and, in its most extreme manifestation (3) may even cause the colonization of a novel niche. We, thus, predict that the combined action of these three effects scale to the community level and eventually expresses itself in modifying the topology and functionality of the entire ecological network. We tested this prediction by exploring the effect of plasticity on network topology (described as connectance, nestedness and modularity) in six idealized scenarios defined by the type of plasticity (continuous versus polyphenic) and its effect on the magnitude of intraspecific trait variation (ITV), and quantitatively validating these effects by simulating them in real-world networks. We propose that this causal pathway can be more widespread than previously thought and may explain why interaction niches evolve quickly in response to rapid changes in environmental conditions. The implication of this idea is not solely eco-evolutionary but also may help to understand how ecological interactions rewire and evolve in response to global change.

INTRASPECIFIC PHENOTYPIC VARIATION

It is widely acknowledged that intraspecific phenotypic variation has significant implications for several fundamental ecological processes and dynamics (Crawford, Jeltsch, May, Grimm, & Schlägel, 2019; Des Roches et al., 2018; Hausch, Vamosi, & Fox, 2018; Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012;
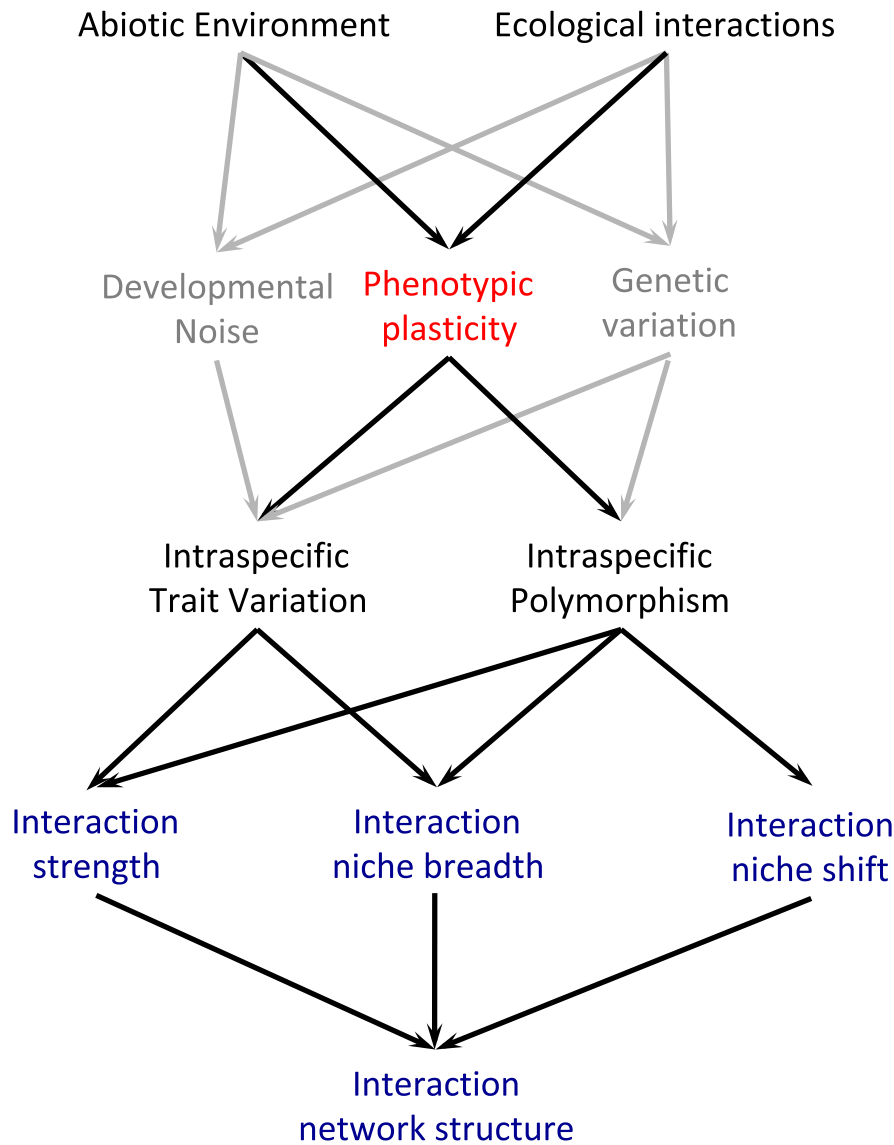
FIGURE 1   Causal links between plasticity and the structure of ecological interaction networks.

Moran, Hartig, & Bell, 2016; Spasojevic, Turner, & Myers, 2016; Westerband, Funk, & Barton, 2021). To understand how plasticity-mediated variation may affect ecological interactions and networks, it is convenient to take into account that intraspecific phenotypic variation can express in two different forms. First, traits may vary quantitatively among individuals, a phenomenon called ITV. Alternatively, intraspecific variation may emerge when individuals of the same population exhibit completely different discrete phenotypes, a phenomenon called *polymorphism*. Whereas the extent, frequency and eco-evolutionary importance of polymorphism have long been studied (Endler, 1986; Ford, 1945; Jamie & Meier, 2020; Mayr, 1963; Skulason & Smith, 1995), the existence of ITV has attracted the attention of community ecologists only in recent years (Bolnick et al., 2011; Des Roches et al., 2018; Kuppler et al., 2020; Violle et al., 2012) despite being

a phenomenon long recognized by evolutionary ecologists (Van Valen, 1965, 1978).

Plasticity as source of intraspecific phenotypic variation

The phenotypic variance of traits has two main components, a genetic and an environmental component (Charlesworth & Charlesworth, 2010; Falconer & Mackay, 1996; Lynch & Walsh, 1998). The genetic component is attributable to genetic variation caused primarily by mutation and recombination (Charlesworth & Charlesworth, 2010). The environmental component can be caused by several factors, although developmental noise and phenotypic plasticity are the most important environmental sources of variation (Graham, 2021; Mitchell & Bakker, 2014; Moran et al., 2016; Westerband

et al., 2021). Developmental noise, defined as random, unpredictable developmental variation (Graham, 2021; Westneat, Wright, & Dingemanse, 2015), is mostly due to somatic mutations, stochastic gene expression and differences in the diffusion of morphogens (Willmore & Hallgrímsson, 2005). It generates deviation from a target phenotype caused by phenotypic imprecisions due to error (Westneat et al., 2015).

Plasticity may affect both continuous and polymorphic traits, causing in this latter case the appearance of *polyphenism* (Wennersten & Forsman, 2012). A central question that remains to be solved is how much of the intraspecific phenotypic variation, whether continuous or discrete, is caused by phenotypic plasticity versus other sources of variation. Although many authors suggest that this proportion may be large (Lajoie & Vellend, 2015), it has only been formally accounted for in a few species. Whereas phenotypic plasticity accounts for about 5% of the variance in some life history traits in several mammalian and avian species (Nussey, Wilson, & Brommer, 2007), it can account for over 50% of the variance in the morphology of some fish species (Robinson & Wilson, 1996) or 60% of the variance in physiological, foliar and germination traits of some plant species (Arnold, Wang, Catling, Kruuk, & Nicotra, 2022). These few data suggest that plasticity may play in some systems a relevant role in the occurrence and maintenance of intraspecific phenotypic variation. The relative importance of phenotypic plasticity as an agent of intraspecific phenotypic variation will probably vary depending on the type of trait and organism and, most important, the graininess of the environment, the spatio-temporal scale of environmental variation relative to organism mobility and lifespan (Levins, 1968; Wennersten & Forsman, 2012).

A reaction norm describes the pattern of phenotypic expression of a single genotype across different environments and provides information on the direction and magnitude of phenotypic change elicited in response to environmental variation (Arnold, Kruuk, & Nicotra, 2019). Reaction norms can help infer whether phenotypic plasticity is behind the observed intraspecific phenotypic variation (Figure 2). Thus, when the slopes of the reaction norms are all zero, the trait is not plastic, and, thus, plasticity is not the source of the observed variation (Figure 2a). When the trait is plastic, but all reaction norms are parallel and the $G \times E$ effect is not significant (Figure 2b), we assume that plasticity is also not the source of the observed trait variation. Only when $G \times E$ is significant can we conclude that plasticity is the source of the intraspecific phenotypic variation (Figure 2c,d). The magnitude of plasticity-mediated intraspecific phenotypic variation may remain similar between environments (Figure 2c) or, conversely, may change (Figure 2d). In the latter scenario, plasticity is the source not only of intraspecific phenotypic variation but also of its differences in magnitude between environments.
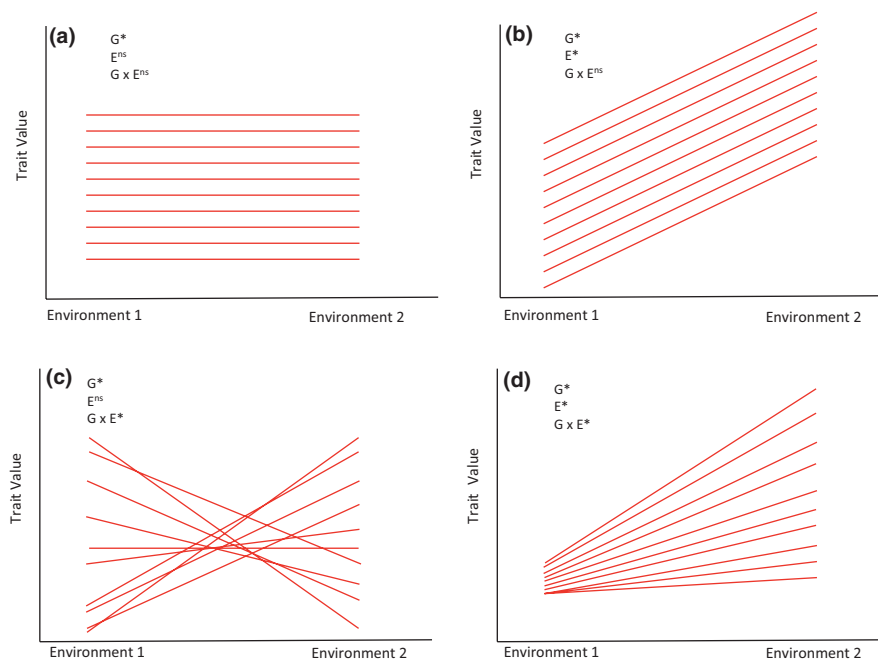

FIGURE 2 Relationship between intraspecific trait variation (ITV) and reaction norms. (a) No plasticity; non-plastic ITV; no between-environment change in ITV magnitude. (b) Plasticity; non-plastic ITV; no between-environment change in ITV magnitude. (c) Plasticity; plastic ITV; no between-environment change in ITV magnitude; (d) Plasticity; plastic ITV; between-environment change in ITV magnitude. G = genetic effect on a trait, E = environmental effect on a trait, $G \times E$ = interaction between environment and genetic effects on a trait. * = significant effect; ns = non-significant effect.

Differences between plastic and non-plastic trait variation

The phenotypic variation caused by phenotypic plasticity differs from other types of variation in several fundamental features. First, unlike the variation caused by developmental noise, which occurs when genotype and environment are fixed, phenotypic plasticity occurs when the same genotype faces different environments (Schlichting & Pigliucci, 1998). This is a fundamental difference that may have paramount implications on how each of the two types of environmentally determined phenotypic variation affect the interactions among species. In addition, plastic responses may anticipate environmental changes (Agrawal, 1999, 2001). In fact, many plastic changes are active and involve multiple regulatory genes and processes acting in different hierarchies to produce a complex, coordinated change adjusted to the environmental conditions that the next generations will experience (Agrawal, 2001). Finally, unlike developmental noise, phenotypic plasticity can be adaptive, eliciting new phenotypes that can be beneficial in certain contexts (Ghalambor, McKay, Carroll, & Reznick, 2007; Snell-Rood & Ehlman, 2021; Sultan, 2021).

Contrasting with genetic variation, phenotypic plasticity can prompt the quick rise of new traits (Pfennig, 2021). This difference in the time required to produce novel phenotypes may have overriding consequences for how coevolutionary processes shape the species assembly in ecological communities (Snell-Rood & Ehlman, 2021; Snell-Rood, Kobiela, Sikkink, & Shepherd, 2018; Turcotte & Levine, 2016). Thus, plastic species are more likely to interact with new non-coevolved partners than non-plastic species.

PLASTICITY EFFECTS ON ECOLOGICAL INTERACTIONS

Intraspecific phenotypic variation can significantly affect three features of ecological interactions: interaction strength, breadth of interaction niche and shift between interaction niches (Bolnick et al., 2011; Clegg, Ali, & Beckerman, 2018; Cope et al., 2022; Melián et al., 2018; Pfennig & McGee, 2010; Smith & Skulason, 1996). By altering the pattern and magnitude of intraspecific phenotypic variation, phenotypic plasticity can be responsible for these three interaction parameters, at least in certain circumstances, although this causal pathway has been little explored. In the following sections, we will describe how plasticity may influence these interaction parameters.

Plasticity and interaction strength

It has long been recognized that plasticity can affect the strength of many interactions (Miner et al., 2005).

Plasticity may first affect interaction strength by entailing the production of a novel phenotype that alters the impact of the interaction. Many studies show that prey can change their behaviour in the presence of predators to counteract the cost of predation, an idea that was coined as the *ecology of fear* (Brown, Laundré, & Gurung, 1999). Plasticity in foraging and vigilance behaviour results in a change in predation rate and strength of interaction with the predator (Brown et al., 1999; Zanette & Clinchy, 2019). Likewise, it has long been recognized that many defensive and offensive traits are plastic (Agrawal, 1999, 2001; Benard, 2004; Karban, 2011). The induction of chemical and physical defences significantly impacts the behaviour and feeding rate of many predators (Karban, 2011), weakening the interaction strengths and boosting the stability of the pairwise interactions (Hess et al., 2022; Mougi & Kishida, 2009).

Plasticity may also affect the interaction strength by increasing the diversity of phenotypes with different impacts on the interacting partners. Several individual-based and trait-based population models have shown that trait variation alters the strength of ecological interactions (Doebeli, 1997; Gibert & Brassil, 2014; Okuyama, 2008; Pachepsky et al., 2007; Schreiber, Bürger, & Bolnick, 2011). It seems that ITV decreases the overall interaction strength of specialist predators and promotes weak interactions (Gibert & Brassil, 2014; Gibert & DeLong, 2017). Because the presence of weak interactions tends to stabilize communities (McCann, 2000; McCann, Hastings, & Huxel, 1998), increased ITV might lead to more stable population dynamics with a higher probability of persistence (Gibert & Brassil, 2014; Gibert, Dell, DeLong, & Pawar, 2015; Wright, Ames, & Mitchell, 2016; but see Noto & Gouhier, 2020). This concurs with the general observation that plasticity favours stability (Mougi & Kishida, 2009).

Plasticity and interaction niche

The consequences of plasticity on niche breadth and/or shift have also long been recognized (Miner et al., 2005; Wennersten & Forsman, 2012). Most studies to date have explored the effect of plasticity on climatic or abiotic niches (Sexton, Montiel, Shay, Stephens, & Slatyer, 2017; Snell-Rood & Ehlman, 2021). However, fewer studies have investigated how plasticity may affect the number, frequency or identity of species that a given species interacts with, a feature that informs us of the breadth of the interaction niche and that can shed some light on the plasticity-mediated evolution of interaction generalization.

The consequences of plasticity on interaction niche expansion or shift can be observed between populations in coarse-grained environments. However, a more relevant situation emerges when interaction niches change within populations. In these fine-grained environments, niches

may expand or change: (i) when individuals of the same genotype express different developmental plasticity because they are exposed to different conditions during development; (ii) when all individuals of a given genotype express reversible traits in response to fine-grained temporal heterogeneity or (iii) when all individuals of a genotype of a modular organism express reversible plasticity at the level of modules in response to fine-grained spatial heterogeneity (Wennersten & Forsman, 2012). The way interaction niches expand or change will depend on the type of plasticity (continuous versus polyphenic) and on whether plasticity causes an increase in ITV. Taking into account this differentiation, we envision the following idealized scenarios:

a. No plasticity (Figure 3a). The null situation happens when the species is not plastic for the trait mediating the interaction (the *interaction trait*). In this scenario, we would expect all individuals of the target species to interact with a very similar pool of interacting organisms in any environment. Consequently, the genotype and population-level identity and breadth of the interaction niche remain similar.

b. Plasticity in continuous traits, no change in ITV (Figure 3b). This occurs when the interaction traits are plastic but change equally in all genotypes of the population, causing all genotypes to interact with different sets of species in each environment with no intra-environment variation in the interaction niche. Therefore, the overall, across environments niche of each individual will be broader than the niche within each environment. Since it is expected that all genotypes change in the same way between environments, the genotype-level interaction niches and the population-level niche will all be very similar to each other (Figure 3b).

c. Plasticity in continuous traits, change in ITV (Figure 3c). Another scenario emerges when the interaction traits are plastic, but the magnitude of plasticity varies among genotypes, causing a
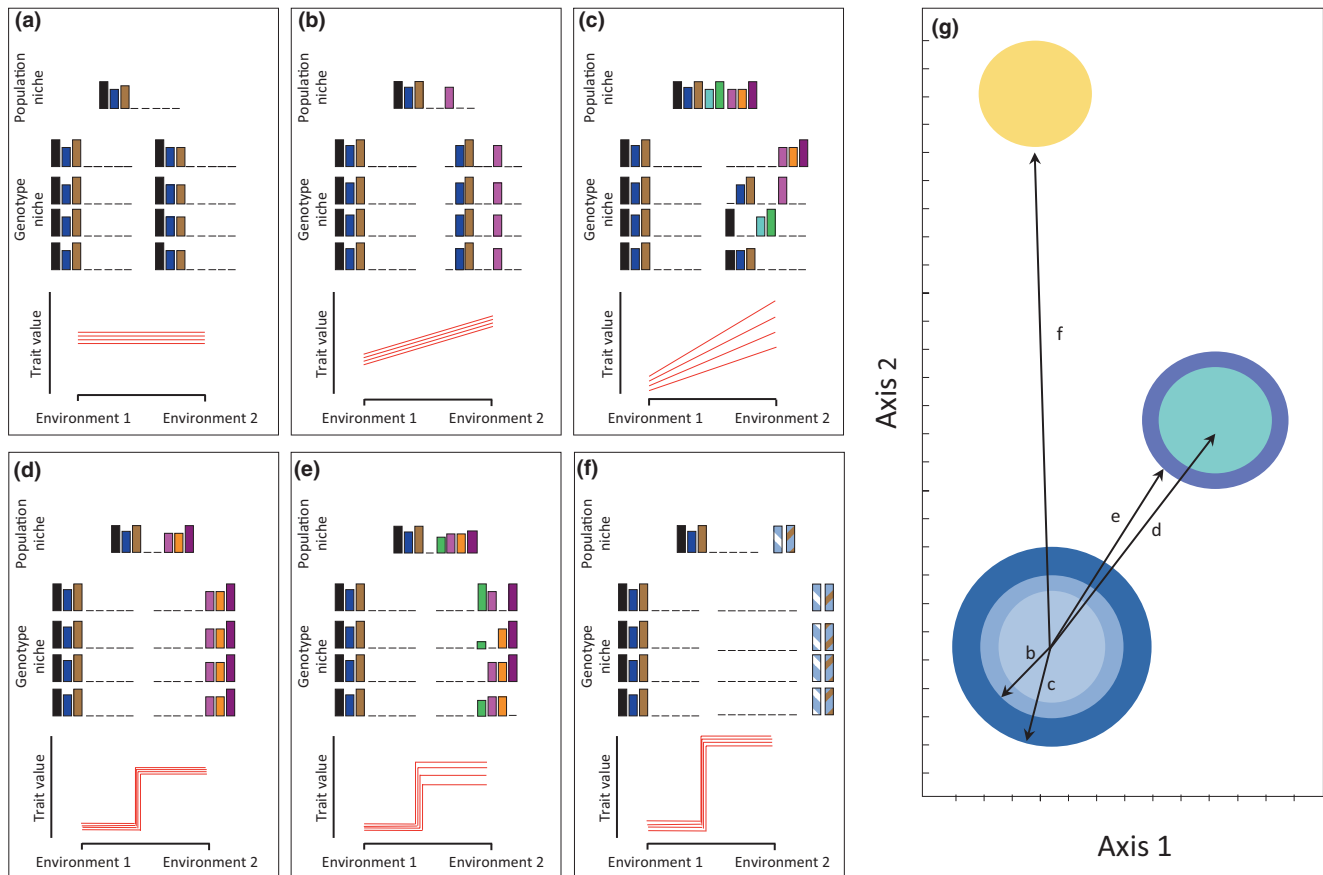

FIGURE 3 Effects of plasticity on interaction niches of both the individual genotypes and the across-environment population. (a) No plasticity. The set of species interacting with the target species remains the same in each environment. (b) Plasticity in continuous traits, no change in ITV. The set of interacting species changes slightly across environments but there is no between-genotype variation. (c) Plasticity in continuous traits, change in ITV. There is between-genotype variation in the set of species interacting with in each environment. (d) Polyphenism, no change in ITV. The set of interacting species changes significantly across environments, causing a shift of the interaction niche. (e) Polyphenism, change in ITV. There is both a between-environment change in the identity and a between-genotype variation in the set of interacting species, causing simultaneously a shift and an expansion of the interaction niche. (f) Extreme polyphenism. The interacting species in the novel environment are new for the community, causing an extreme niche shift. (g) Schematic representation of each scenario in a two-axis niche space (each letter refers to each of the previous scenarios).

change in the magnitude of ITV. This scenario occurs when different genotypes respond in different ways to environmental changes. As genotypes differ in the value of interaction traits in that second environment, they will interact with a slightly different set of species. In this situation, the expansion of the interaction niche will be even greater at the population level (Figure 3c). Many empirical and theoretical studies support the idea that plasticity broadens the niche mostly due to the effect of plasticity on intraspecific phenotypic variation, an important motor of niche breadth (Carscadden et al., 2020; Gibert & DeLong, 2017; Kang et al., 2022; Le Bagousse-Pinguet, de Bello, Vandewalle, Leps, & Sykes, 2014; Sides et al., 2014). This relationship between plasticity-mediated ITV and niche breadth has long been recognized (Van Valen, 1965). One mechanism by which plasticity-mediated ITV can expand the interaction niche is by triggering the emergence of individual specialization in novel environments and favouring the emergence of individualized niches (Trappes et al., 2022).

d. Polyphenism, no change in ITV (Figure 3d). Plasticity may also trigger the shift of individual interaction niches. According to the niche divergence hypothesis, polymorphism is more frequent in species inhabiting heterogeneous environments because individuals can better locally adapt to different ecological niches (Dreiss et al., 2012; Passarotto, Parejo, Penteriani, & Avilés, 2018). Polyphenic individuals may, thus, interact with alternative sets of species depending on the expressed phenotype (Mason, 2016). For example, the polyphenic tadpoles *Spea bombifrons* Cope, 1863 and *Spea multiplicata* Cope, 1863 exhibit two morphs that differ in trophic niches (Pfennig, 2021). Plasticity-mediated niche shifts can also occur within individuals. Different morphs of the polyphenic flowers of *Moricandia arvensis* DC. are visited by different pollinators (Gómez et al., 2020, 2022).

e. Polyphenism, change in ITV (Figure 3e). Another scenario may occur when the interaction traits are polyphenic, but the phenotypes differ more intensely among individuals in one environment than in the other. This pattern would simultaneously cause a shift and an expansion of the individual niches (Figure 3e). It is known that interactions among species can vary during lifetime (Poisot, 2013; Segar et al., 2020) and that the strength of phenotypic plasticity can also vary if environmental conditions change (Chevin et al., 2010). Thus, the expected plasticity-mediated niche shift could also originate niche expansion in highly variable environments. The peppered moth *Biston betularia* L., 1758 exhibits a reversible polyphenism for the body colour, being brown when eating on birches and green when eating on willows.

Plasticity-mediated ITV was significantly larger in the green environment, being behind the observed expansion of the host range of the moth (Noor, Parnell, & Grant, 2008).

f. Extreme polyphenism (Figure 3f). Another scenario may occur when polyphenism is so radical that the organisms start to interact with novel species completely unrelated to their previous hosts (De Fine Licht, 2018) (Figure 3f). The outcome here is also a niche shift, but the location of this new niche in the niche space is farther away from the original niche (Figure 3g). For example, phenotypic plasticity seems to have helped some populations of the three-spine stickleback *Gasterosteus aculeatus* L., 1758 to exploit pelagic and benthic prey, thereby broadening their trophic niche substantially (Svanbäck & Schluter, 2012).

PLASTICITY EFFECTS ON ECOLOGICAL NETWORKS

Most ecological networks are topologically dynamic, expressed by changes in the architecture of the web along spatial and temporal axes (Delmas et al., 2019; Tylianakis & Morris, 2017). Two main factors regulate the spatiotemporal dynamics of network topology. First, the structural properties of ecological networks vary due to changes in species composition caused by the non-random extinction of some species and the invasion of new ones (Tylianakis & Morris, 2017). In addition, network topology also varies as a consequence of changes in the reconnection pattern among the existing species (Tylianakis & Morris, 2017). The topological variation due to the rewiring of interactions among species has been recently coined as network topological plasticity or just network plasticity (D'Alelio et al., 2015; Ramos-Jiliberto, Valdovinos, Moisset de Espanés, & Flores, 2012; Schwarz, Dormann, Vázquez, & Fründ, 2021; Sheykhali et al., 2020).

An emerging literature is starting to show that the topological plasticity of ecological networks may have relevant consequences on the structure and functioning of the entire network (Gray et al., 2021; Ramos-Jiliberto et al., 2012). The reassembly of interactions among species influences several global network properties. Thus, topological plasticity modulates the robustness, defined as the capacity of the network to maintain functionality or connectivity against species extinction, of both mutualistic and antagonistic networks (Nuwagaba, Zhang, & Hui, 2017; Ramos-Jiliberto et al., 2012; Sheykhali et al., 2020; Thierry et al., 2011; Vizentin-Bugoni, Debastiani, Bastazini, Maruyama, & Sperry, 2019). In addition, because rewiring is more frequent among generalist species than among specialist ones, topological plasticity significantly impacts the pattern of network generalization

(Olesen, Stefanescu, & Traveset, 2011) and may facilitate networks to respond to changing environments (D'Alelio et al., 2015).

Two main mechanisms govern the emergence and maintenance of topological plasticity in ecological networks. First, network plasticity can arise when organisms alternate between different interacting species partners based on temporal or spatial changes in their relative abundance, availability, probability of encounter or detectability (CaraDonna et al., 2017; Schwarz et al., 2021; Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009). Alternatively, interaction rewiring can also be triggered by the environmental modification of traits relevant to the interaction occurring in the species belonging to the network (D'Alelio et al., 2015). In this latter scenario, the topological plasticity of networks is mediated by the phenotypic plasticity of the interacting species. Indeed, by facilitating the expansion of niche breadth and driving niche shifts, phenotypic plasticity may promote the appearance of new connections or the reconnection between new pairs of species (Barbour & Gibert, 2021). This process is more noticeable when plasticity is intraindividual, since the same organism confront different environments and undergo significant changes in their interaction networks (Gómez et al., 2020, 2022). Despite the potential importance of this process for understanding the structure and dynamics of ecological networks in changing environments, the consequences of phenotypic plasticity for the pattern of interaction rewiring have been largely overlooked (Barbour & Gibert, 2021; Gray et al., 2021).

We hypothesize that plasticity-mediated rewiring can affect the architecture of ecological networks in three main ways, depending on whether the phenotypic plasticity: (1) expands the niche breadth of the plastic species, (2) causes a shift between existing niches in the network or (3) causes a jump to a novel niche (Figure 4). These effects will also depend on the generalization degree of the plastic species. To explore these ideas, we predict in the following sections the potential effects that plasticity has on network connectance, nestedness and modularity, three important metrics describing network topology. Afterwards, we quantitatively tested our predictions by simulating these effects in 10 real-world networks downloaded from the 'web of life' database (https://www.web-of-life.es) (Appendix S1; R scripts and networks are in Tables S1 and S2). We want to note that a comprehensive analysis of the effect of plasticity on network topology is beyond the scope of this paper, our intention here being only to draw attention to the potential consequences of phenotypic plasticity for network properties. We hope these ideas will serve as a basis for future theoretical and empirical studies that can reliably establish the effect of phenotypic plasticity on the structural properties and evolution of ecological networks.
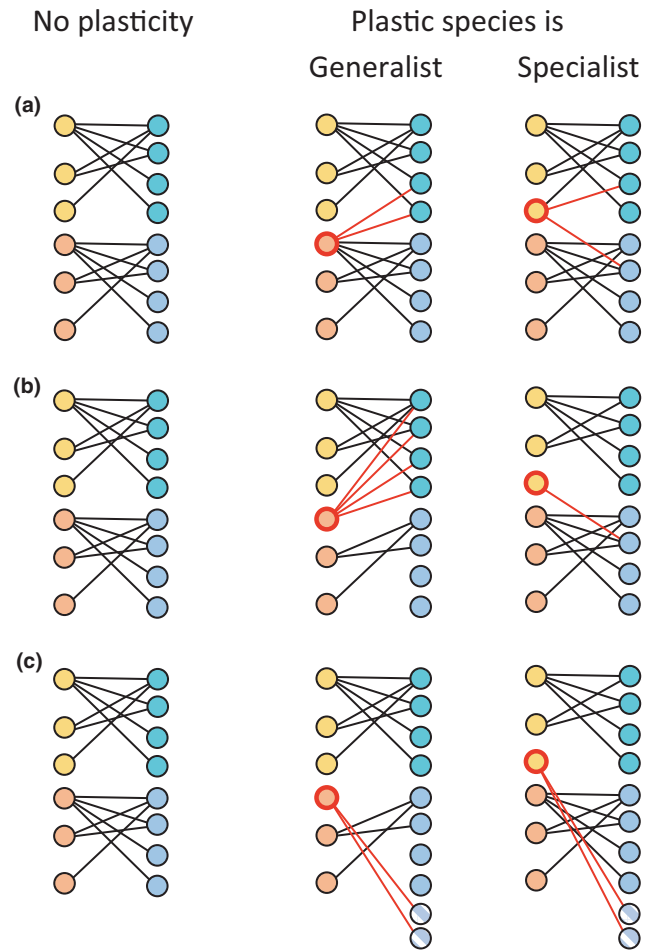

FIGURE 4 Potential ways by which phenotypic plasticity may affect the structure of ecological networks. A hypothetical bipartite modular network (two modules in each set of species) with no plastic species is represented in the left column. From this network, we illustrate different scenarios allowing one species to be plastic (red-circled node). The plastic species can be generalist (middle column) or specialist (right column). Depending on how plasticity affects interaction niche, there are three possibilities: (a) Interaction niche expansion. A network where the plastic species expands its niche by augmenting the number of interacting species from the same or other niches (modules). (b) Shift to an existing interaction niche. A network where the plastic species jumps from one interaction niche to another. (c) Jump to a new interaction niche. A network where the plastic species starts interacting with new species conforming a new interaction niche.

Effects of plasticity-mediated niche expansion on network properties

Plasticity can first affect the structure and functioning of ecological networks by enhancing the phenotypic variation of interacting species (Figure 4a). In fact, it is known that ITV influences the structure and dynamics of many ecological networks (Baruah, 2022; Clegg et al., 2018; Gibert, Debat, & Ghalambor, 2019; Gilljam et al., 2011; Melián et al., 2018; Segar et al., 2020).

When plasticity increases the ITV of interacting species and, consequently, promotes the expansion of niche breadth, the most likely outcome is an increase

in the *degree* of the plastic species irrespective of their generalization intensity (Figure 4a). When this happens, because plastic species become functionally more generalized, network *connectance*, defined as the proportion of established interactions relative to the possible number of interactions, is expected to increase (Blüthgen, Fründ, Vázquez, & Menzel, 2008). Our simulations suggest that this prediction is especially evident when the plastic species is a specialist (Figure 5a). Plasticity-mediated increase in ITV also causes an increase in the among-individual variance in degree because different individuals of the same species will differ in the number of links they have (*interaction heterogeneity*). Consequently, different individuals of the same species will occupy different positions in the community network, diluting the overall *role* of the

species (Gómez & Perfectti, 2012; Kuppler et al., 2017). Under these circumstances, we suggest that the expansion of niche breadth of plastic species will decrease the prevalence of reciprocal specialization in the overall network because rewiring tends to connect previously unconnected and formerly specialized species with more generalist species (Sheykhali et al., 2020). This process will intensify the magnitude of specialization asymmetry that will inflate *nestedness*, defined as the tendency of species to interact with the subsets of better-connected species, and deflate *modularity*, defined as the occurrence of structure in the network (Figure 4a). Both ideas are supported by our simulations, showing again that these effects are stronger when the plastic species is specialist (Figure 5a). It is widely acknowledged that the stability of ecological
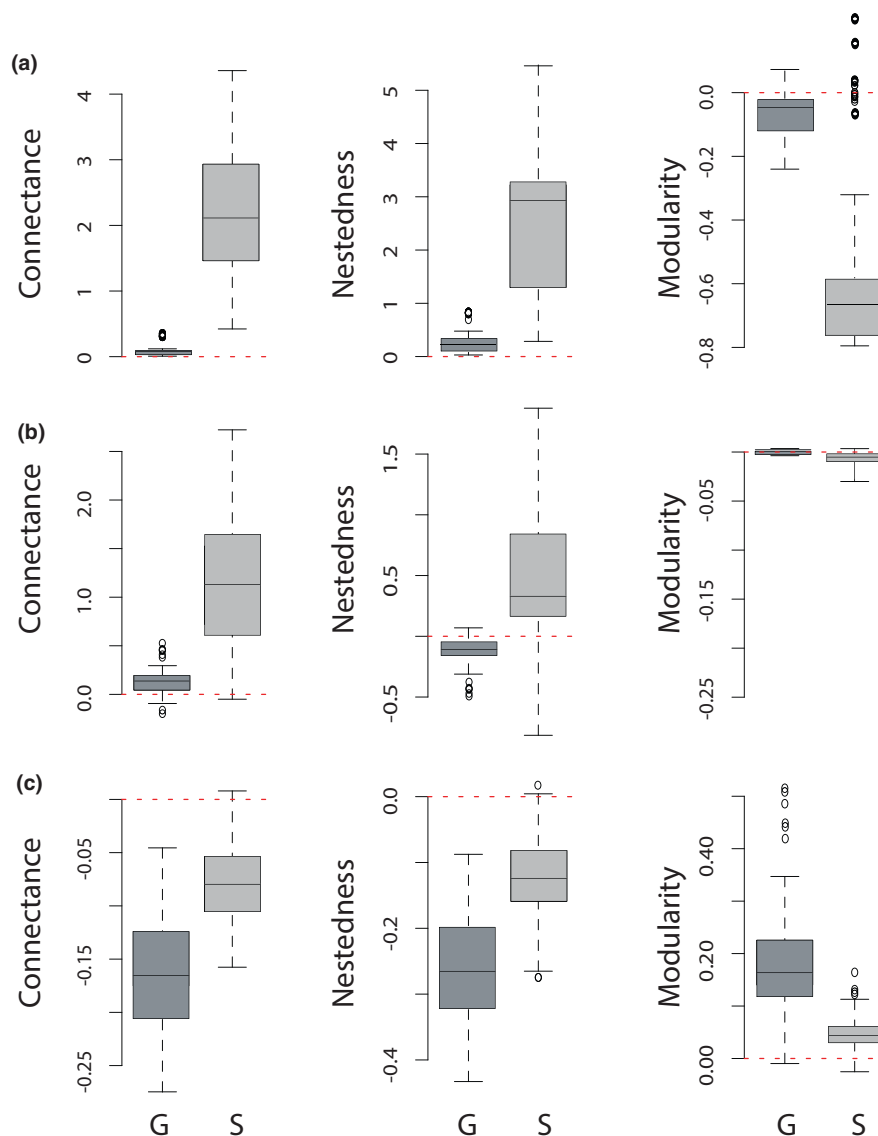

FIGURE 5 Outcome of the analyses simulating the three scenarios described in Figure 4 ((a) Interaction niche expansion; (b) Shift to an existing interaction niche; (c) Jump to a new interaction niche) using 10 real-world ecological networks (see Appendix S1) on three main network metrics: connectance, nestedness and modularity. The box plots show the medians, the interquartile ranges and the interval confidences. G = Generalist species; S = Specialist species.

communities and the robustness of networks are associated with an increase in connectance (Dunne, Williams, & Martinez, 2002; Estrada, 2007; May, 1972) and nestedness (Bascompte, Jordano, Melian, & Olesen, 2003; Bascompte, Jordano, & Olesen, 2006). Consequently, we predict that plasticity-mediated niche expansion will make networks more stable and robust, enabling the maintenance of network functionally even after species extinction due to global change.

Effects of plasticity-mediated niche shift on network properties

When plasticity expresses as a considerable variation in a continuous trait or, more frequently, as a discrete change in polyphenic traits, a likely outcome is a shift in the interaction niche of the plastic species (see previous section). Most frequently, this niche shift entails a change between niches already existing in the community (Figure 4b). For example, a change from a host to another host already embedded in the food web (Agrawal, 2001; Prokopy, Averill, Cooley, & Roitberg, 1982), a change from one prey to another prey from the existing pool of preys of the community (Robinson, Booms, Bechard, & Anderson, 2019) or a change from one functional group of pollinators to another group already visiting the flowers of co-occurring plants (Gómez et al., 2020, 2022). Assuming that the plastic generalist species remains generalist, a niche shift of generalist species will likely involve rewiring the existing links without a significant change in the total number of links in the network. In agreement with this idea, our simulations suggest that there is no substantial change in the connectance for the plastic generalist species (Figure 5b). Conversely, a niche shift in a plastic specialist species will likely imply a change in the degree of generalization because the plastic species would not have had enough time to co-evolve with the new set of species (Gómez et al., 2022). Supporting this idea, our simulations show an increase in connectance when the plastic species is specialist (Figure 5b). Nestedness will change depending on the generalization pattern of the plastic species. If the plastic species that shifts among modules is specialist, we would expect it to reconnect with a generalist of the new niche, increasing the nestedness of the entire network (Figure 4b). If the plastic species is generalist, nestedness will probably decrease because highly connected species from certain modules will receive an extra number of links from the species entering into those modules. Our simulations seem to support these expectations, showing a slight decrease in nestedness when the plastic species is generalist but an increase when the plastic species is specialist (Figure 5b). In addition, because plastic species will shift to pre-existing niches, it will cause the accumulation of some species

in certain network modules that will become larger and more connected without significantly affecting the modularity of the entire network (Figure 4b). Again, our simulations support this expectation (Figure 5b).

It appears that plasticity-mediated niche shift will have two main consequences for the structure of ecological networks, a change in nestedness and, more importantly, a redistribution of species among network modules. A reduction in nestedness makes networks more sensitive to perturbations (Bascompte et al., 2003, 2006; Baumgartner, 2020). In addition, the accumulation of species in certain niches will strengthen competitive interactions in those niches that, if strong enough, will threaten coexistence and favour the extinction of low-competitive species (Hess et al., 2022). We predict that, due to the combination of these effects, in cases where plastic species shift to a different interaction niche without retaining interactions with the original niche (i.e. pure niche shift without niche expansion), the resulting network will be less robust and prone to species loss. However, this effect will probably depend on the generalization/specialization degree of the plastic species.

Effects of adding new niches on network properties

Phenotypic plasticity might elicit the emergence of novel phenotypes with new adaptive possibilities, which may be beneficial in new contexts (Snell-Rood & Ehlman, 2021; Sultan, 2021). Under these circumstances, we predict that plasticity will cause a shift to a completely new niche previously unexplored by the group of species composing the ecological community. This occurs when the plastic change is so extreme that it allows the organisms to interact with new species unrelated to previous partners (Figure 3f). The new plastic phenotype might allow the interaction with a local species formerly not interacting with any of the species in the community, or promote the establishment of a new species in the community. For example, the plasticity of pollination-associated traits can facilitate both plant and animal invasions into native ecological networks (Danieli-Silva et al., 2012; Kaiser-Bunbury, Traveset, & Hansen, 2010; Olesen, Eskildsen, & Venkatasamy, 2002). Likewise, plasticity-mediated changes in flowering or fruiting phenology may promote interaction with generalist species consuming other types of resources during other seasons and that becomes new elements of the dispersal or pollination networks (Levin, 2009). We suggest that under these circumstances, new species in the network will interact with the plastic species. In principle, for the sake of simplicity, the plastic species is chosen randomly from the set of species (although we acknowledge that the consequences could differ if the plastic species is the most generalist or, on the contrary, the least connected species).

Network size will increase in this scenario due to the addition of new species, regardless of whether the plastic species is specialist or generalist, while the number of links will remain similar or even smaller if the new niche is composed of fewer species (Figure 4c). Consequently, due to the universal negative relationship between network size and connectance (Delmas et al., 2019), a reduction in connectance is expected. This prediction was supported by our simulations, which showed that connectance decreased, albeit slightly, after the jump of any type of plastic species to a new niche (Figure 5c). In this scenario, a decrease in nestedness is expected due to the increase in link specificity and the consequent increase in reciprocal ecological specialization. Finally, modularity is expected to increase because a new niche is added to the overall network, causing an increase in link specificity (Olesen, Bascompte, Dupont, & Jordano, 2007). Our preliminary simulations support these two predictions (Figure 5c). The overall outcome of this scenario is the opposite of the first scenario, with plasticity promoting lower connectance, lower nestedness and higher modularity. Consequently, plasticity-mediated addition of new niches would make networks less stable and robust.

FUTURE DIRECTIONS

We have advocated in this article that phenotypic plasticity can affect not only organisms but also the networks where they are embedded. Unfortunately, this topic remains largely unexplored despite its potential importance for understanding how ecological networks respond to external perturbations. To better comprehend the influence of phenotypic plasticity on ecological networks, we propose that future research should address three relevant aspects: how intraspecific phenotypic variation emerges from plasticity, how plasticity influences interaction niches and how plasticity explicitly shapes the architecture and functioning of the networks.

Although there is a long tradition of studies partitioning the variance of phenotypic traits (Coleman, McConnaughay, & Ackerly, 1994; Westneat et al., 2015), the number of studies that include phenotypic plasticity as a component of variation is scarce, and most have been done in controlled conditions (Westneat et al., 2015). This precludes us from knowing the real importance of plasticity as a motor of the phenotypic variation observed in nature. Moreover, it is important to know not only the quantity but also the distinctiveness of the plastic variation. Phenotypic plasticity alters intraspecific phenotypic variation in different ways than other sources of phenotypic variation. For example, it is widely acknowledged that plastic variation can arise faster than genetic variation (Snell-Rood et al., 2018; Snell-Rood & Ehlman, 2021), which may have enormous consequences for how ecological networks respond to changing environments. Plastic variation might enable a much quicker

rewiring, even with non-coevolved partners, than the genetically mediated variation. These and other potential consequences of exhibiting plastic-mediated variation should be incorporated into future studies dealing with assembly rules of plastic networks (D'Alelio et al., 2015; Ramos-Jiliberto et al., 2012; Schwarz et al., 2021; Sheykhali et al., 2020).

The development of a framework aimed at explaining the consequences of phenotypic plasticity on ecological networks will require a thorough understanding of how phenotypic plasticity influences interaction niches. Evidence is accumulating that phenotypic plasticity may promote the rapid evolution of interaction niches in response to immediate environmental changes (Gómez et al., 2022; Susoy, Ragsdale, Kanzaki, & Sommer, 2015). However, we do not yet know how frequent this phenomenon is and how important plasticity is in explaining the evolution of interaction niches. In relation with this, it would be fundamental to ascertain whether plasticity magnitude varies with the degree of the species belonging to the same ecological network. It is even unknown whether the niche consequence of plasticity differs between generalist and specialist species. Although based on a limited set of species within the generalization-specialization continuum, our simulations suggest that consequences are far more dramatic when plasticity affects specialist species. It will be desirable to expand both theoretical and empirical studies to a broader range of generalist and specialist species and analyse how interaction niches respond to the presence of plastic species along this continuum.

Finally, many questions remain open on how phenotypic plasticity influences the architecture and functioning of ecological networks. In particular, a future line of work should be that of determining how network properties change as a result of phenotypic plasticity relative to other sources of trait variation. For this, it would be convenient to obtain information from multiple networks about the ability that plastic species to disrupt reciprocal specialization, to affect the magnitude of nestedness and modularity, to alter the degree distributions and to facilitate the establishment of new interacting species. Having this information at hand will be fundamental in predicting how networks could face human-made global change. We presume that a key advance could come from the use of individual-based ecological networks (Gómez & Perfectti, 2012; Guimaraes Jr, 2020; Woodward et al., 2010). Individual-based ecological networks are remarkably versatile because they allow independent characterization of every individual for any interacting species (Gómez & Perfectti, 2012; Isla, Jácome-Flores, Pareja, & Jordano, 2022; Valverde, Gómez, & Perfectti, 2016). Consequently, individual-based ecological networks can incorporate the intensity of plasticity exhibited not only at the level of species but also at the level of genotype and individual (Gómez et al., 2020, 2022). Future research should focus on the

development of precise methodological and analytical tools to include phenotypic plasticity in individual-based ecological networks. The development of such a framework that explicitly considers the signal that the phenotypic plasticity of organisms leaves in ecological networks may give a more realistic view of how networks rewire and are assembled under natural conditions.

AUTHOR CONTRIBUTIONS

JMG and AGM wrote the manuscript, and all authors contributed substantially.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.