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Trait plasticity in species interactions: a driving force of community dynamics

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Abstract Evolutionary community ecology is an emerging field of study that includes evolutionary principles such as individual trait variation and plasticity of traits to provide a more mechanistic insight as to how species diversity is maintained and community processes are shaped across time and space. In this review we explore phenotypic plasticity in functional traits and its consequences at the community level. We argue that resource requirement and resource uptake are plastic traits that can alter fundamental and realised niches of species in the community if environmental conditions change. We conceptually add to niche models by including phenotypic plasticity in traits involved in resource allocation under stress. Two qualitative predictions that we derive are: (1) plasticity in resource requirement induced by availability of resources enlarges the fundamental niche of species and causes a reduction of vacant niches for other species and (2) plasticity in the proportional resource uptake results in expansion of the realized niche, causing a reduction in the possibility for coexistence with other species. We illustrate these predictions with data on the competitive impact of invasive species. Furthermore, we review the quickly increasing number of empirical studies on evolutionary community ecology and demonstrate the impact of phenotypic plasticity on community composition. Among others, we give examples that show that differences in the level of phenotypic plasticity can disrupt species interactions when environmental conditions change, due to effects on realized niches. Finally, we indicate several promising directions for future phenotypic plasticity research in a community context. We need an integrative, trait-based approach that has its roots in community and evolutionary ecology in order to face fast changing environmental conditions such as global warming and urbanization that pose ecological as well as evolutionary challenges.

Keywords Niche model · Resource acquisition trade-off · Community assembly · Functional traits · Invasion ecology · Phenotypic plasticity

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Introduction

One of the main goals of community ecology is to examine the patterns and processes that underly the distribution and abundance of populations, and interactions among populations and their environment of coexisting species at a particular site or in a specific area (McArthur 1972; Cody and Diamond 1975; Ricklefs and Schluter 1993). Community ecology has been successful in describing and explaining several patterns of species diversity and abundance in communities (McGill et al. 2006; Agrawal et al. 2007). However, at the same time community ecology has been questioned for lack of two important attributes. First, community ecology is short of general, mechanistic principles leading to quantitative predictions (Lawton 1999; Simberloff 2004; Lockwood 2008), presumably due to the multitude of direct and indirect interactions between the many species present. Second, community ecology has largely assumed homogeneous populations that are unreceptive to evolutionary change, thereby excluding any evolutionary community dynamics resulting from selection on traits of individuals. In other words, one of the key assumptions has been that life history traits of interacting species are uniform within species and unchanging over time (Agrawal et al. 2007). For a long time, it was assumed that the relatively slow time scale of evolutionary changes rendered an evolutionary perspective of community ecology unnecessary.

More recently, a growing number of ecologists have come to realize the value of an evolutionary perspective for addressing these limitations. For example, it has been suggested that general principles can be produced by a focus on species' traits. If traits of individuals can be functionally linked to interspecific interactions, this would provide a mechanistic approach to community structure. The use of species functional traits is well-established in the field of plant ecology, and species traits have been more or less successfully used as generalized predictors of vegetation composition response to herbivory (Diaz et al. 2007), climate (Lavorel and Garnier 2002; Wright et al. 2004), and invading species (Funk et al. 2008). However, the question remains whether fixed average trait values of species can be applied across a wide range of environments, and how much of the observed variation in vegetation composition they can actually explain. Compelling evidence shows that strong selection pressures and fast (co)-evolution are commonplace in nature (Thompson 2005), placing evolutionary and ecological dynamics on similar time-scales (Fussmann et al. 2007). As a consequence, functional trait values cannot be considered as fixed characteristics of species, and it will be necessary to consider the effects of trait evolution and trait plasticity in ecological studies. The value of an evolutionary perspective for addressing community ecological questions depends on the importance of genetic variation of traits and phenotypic plasticity of those traits for species interactions.

In this review, we consider variation in traits of individuals and species to be essential to understand and predict species interactions and community composition. First, we will show as a proof of principle that phenotypic plasticity applies to functional traits important in community ecology. Subsequently, we will address how such phenotypic plasticity can alter the realised niches of species in a community using niche models. We will particularly focus on phenotypic plasticity in traits involved in resource allocation and stress tolerance as these traits strongly influence the interaction between species. Finally, we will illustrate the effects of phenotypic plasticity on community properties. Among others, we will give examples that show that differences in the level of phenotypic plasticity between species can disrupt species interactions, and the composition of communities. To conclude our review we outline several promising directions for future phenotypic plasticity research in a community context. This review contributes to an emerging field of study,

evolutionary community ecology, which explores the possibilities to bridge the gaps between community ecology and evolutionary ecology (i.e. Vellend and Geber 2005; McGill et al. 2006; Johnson and Stinchcombe 2007; Emerson and Gillespie 2008; Urban et al. 2008).

The relevance of considering plasticity in functional traits

Phenotypic plasticity is the ability of a genotype to modify phenotypic expression in response to environmental conditions such as temperature, drought, predation pressure, and resource availability (DeWitt and Scheiner 2004). Many of the functional traits that are thought to be important for the outcome of competition and the associated community composition are known to be highly plastic. For instance, root length and root demography respond strongly to supply levels of nutrients (Hodge 2004), leaf architecture and leaf number are highly dependent on light conditions (Pigliucci et al. 2003, Valladares and Niinemets 2008), and defence mechanisms are induced under predation pressure (Tollrain and Harvell 1999). Phenotypic plasticity has often been suggested to be costly and therefore limited to environments with predictable variation (DeWitt et al. 1998). Yet a recent meta-analysis demonstrated the costs of plasticity to be weak, explaining the ubiquitous occurrence of plastic traits (Van Buskirk and Steiner 2009). The level of phenotypic plasticity of traits can be measured by their reaction norm, which describes the change in trait values across environments. Steeper reaction norms indicate a higher degree of plasticity for a specific trait under influence of a specific environmental variable (see for example Fig. 1b; increase in stress intensity results in a strong increase in the uptake of a resource in one species, but less so in a second species). It is important to realise that not all traits of one individual have the same reaction norm, and similarly, not all environmental variables elicit the same degree of plasticity in a particular trait. Therefore, it is not

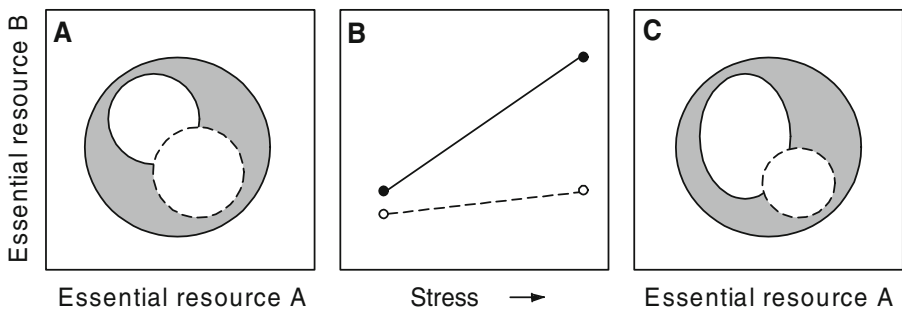


Fig. 1 The role of phenotypic plasticity in the relationship between fundamental and realized niches of species. The fundamental niche (dark grey circle, Fig. 1a) is the level of each factor needed (resource A and B) for a species to survive. Realized niches (light grey circles, Fig. 1a) for two species with respect to resource A and B are narrower than fundamental niches due to overlap and competition between the two species. Under increasing stress intensity due to an environmental change, both species show phenotypic changes in the uptake of resource B (Fig. 1b), but the two species differ in their plasticity, as indicated by differences in the slope of their reaction norms. As a consequence, species 1 (top light grey circle and solid line in the figure) is better able to tolerate higher stress levels (i.e. is the more plastic species for uptake of resource B), which leads to differentiation in realized niches of the two species under environmental change. Note that the fundamental niche does not change. Without loss of generality, the example can be extended to other environmental factors and to multiple species

possible to make a statement about the plasticity of one species compared to the other, unless particular traits and conditions are specified.

The relevance of considering plasticity of functional traits in community ecology has become more urgent since an increasing number of studies turn to trait databases to explain community patterns, both in plant and animal ecology (Heemsbergen et al. 2004; Ozinga et al. 2007). Trait databases, such as the Globnet leaf economics database (Wright et al. 2004) or the LEDA trait database for the Northwest European flora (Kleyer et al. 2008), are used extensively to analyse vegetation compositional responses to changing environments. Similarly, the SPEAR trait database for European aquatic macroinvertebrates (Liess et al. 2008) or the database for lotic invertebrates traits for North America (Vieira et al. 2006), are increasingly exploited to understand community compositional changes in disturbed streams and ponds. Often these databases contain key morphological and life history traits, which are precisely the type of traits that are highly plastic in response to environmental change (Roff 2002). However, almost without exception, these databases only contain fixed, mean values, discarding trait plasticity that may result from the changing environment. Although studies using fixed-trait databases have been successful in explaining vegetation patterns across time and space, often much of the observed variance in vegetation composition is left unexplained. Possibly the traits included in the database do not capture all of the relevant functional phenotypic variation or the lack of fit is due to large intraspecific trait variability in traits, caused by either genetic variation or phenotypic plasticity (Hodge 2004; Valladares and Niinemets 2008). Trait diversity within a community is a regularly used metric to predict community patterns, but empirical studies show that functional traits can vary as much within as between species (Hodge 2004; Valladares and Niinemets 2008). For instance, a comparative study on plant traits such as leaf mass per unit area, relative growth rate, and photosynthetic capacity of 16 congeneric rainforest shrubs, revealed that the magnitude of trait variation caused by plastic phenotypic responses to light was equally large as the variation in plant traits among species (Valladares et al. 2000). Therefore, to ignore the effect of phenotypic plasticity in trait values can significantly impair the explanatory power of trait-based analyses.

Another realm of community ecology to which the concept of phenotypic plasticity can contribute is the study of community assembly (Funk et al. 2008). Community composition is thought to result from ecological filters which ‘sort out’ those species from the regional species pool which have traits adapted to a local environment. This process leads to a coupling between the environment and functional traits that determine a species’ ecological strategy (McGill et al. 2006; Westoby and Wright 2006). Such environmental filters will locally limit the range of viable ecological strategies and will result in trait convergence of species within a community (McArthur and Levins 1967; Grime 2006; Funk et al. 2008). However, phenotypic plasticity allows organisms to adjust to a large range of conditions without evolutionary change. As a consequence, trait convergence within a habitat is not solely due to genetic similarities between species, but can often be explained for a significant part by plastic responses, i.e. phenotypic similarity despite genetic divergence. Trait plasticity may allow species to shift their ecological strategy to fit current environmental conditions and enable them to pass the ecological filter. Likewise, trait divergence *among* communities is often thought to be a consequence of community assembly rules, but may equally well be due to phenotypic plasticity induced by divergent environmental conditions. Indeed, a survey of leaf, stem, and root traits of woody plant species across an environmental gradient in coastal California, showed a restricted range of trait values within sites and a shift in mean trait value across the gradient. Although the larger part of trait variation along the gradient was due to species turnover, intraspecific

variation due to plasticity explained a significant part of the shift in mean trait values across the gradient (Cornwell and Ackerly 2009). Hence, it can be expected that species that show extensive trait plasticity will be favoured more frequently by ecological filters and be assembled in communities in a wide range of environments.

These are just a few examples of the impact that phenotypic plasticity can have on community dynamics. In the following paragraphs we aim to present a conceptual framework that can bring together the evolutionary perspectives of trait plasticity with community ecological approaches using the concept of fundamental versus realized niches (Hutchinson 1975).

Community niche models and phenotypic plasticity

The key concept of niche theory states that the conditions under which a particular species can successfully exist, change with the presence of other species (Hutchinson 1959, MacArthur and Levins 1967). A species' potential or fundamental niche is defined by the range of environmental factors under which it can survive, grow and reproduce in the absence of other species. The realized niche is the part of the fundamental niche occupied in the presence of other species (Fig. 1a). Consequently, the realised niche of species is directly affected by changes in the species composition of its community. In addition, realized niches can be affected indirectly by environmental factors if environmental change affects constituent species in the community differentially, which may cause a shift in community composition. For example, species may differ in the level of phenotypic plasticity (Fig. 1b), determining their ability to cope with environmental change and adjust their realised niche accordingly (Fig. 1c).

To evaluate the consequences of phenotypic plasticity for species interactions and the composition of the community we use the community niche models developed by Tilman (1982) and further explored by Chase and Leibold (2003). These mechanistic models show how supply of resources and species' requirements interact to determine the possibility for coexistence of species (Fig. 2a). Each species is characterized by a zero net growth isocline (ZNGI) that defines the minimum resource requirement for a species to maintain itself, and by an impact vector (I), which specifies the relative rate of consumption of resources (Chase and Leibold 2003). The slope of the impact vector gives the proportional uptake of the two resources, and delineates the resource supply conditions under which the two species will coexist at equilibrium or drive each other to extinction due to resource competition.

The most frequent application of the model is resource competition between two species for two essential resources, where species show a trade-off in the minimum requirement for (ZNGI) and their impact (I) on each resource (Fig. 2a). In other words, species with a low requirement for one of the resources have a high demand for the other resource. For example, plants can lower their light requirements by increasing the concentration of chlorophyll in their leaves, but this requires a higher amount of nitrogen per leaf (Valdadares and Niinemets 2008). The trade-off in requirements for the two resources enables multiple competitors to coexist and shapes the structure of the community (Bonsall et al. 2004; Tilman 2004; Gilbert et al. 2006). The level of divergence in realised niches depends on the relative position a species takes on the trade-off surface, and is maximal if the species are at opposite ends of the trade-off surface. The original model assumes that resource requirements and the proportional uptake of resources are fixed for each species,

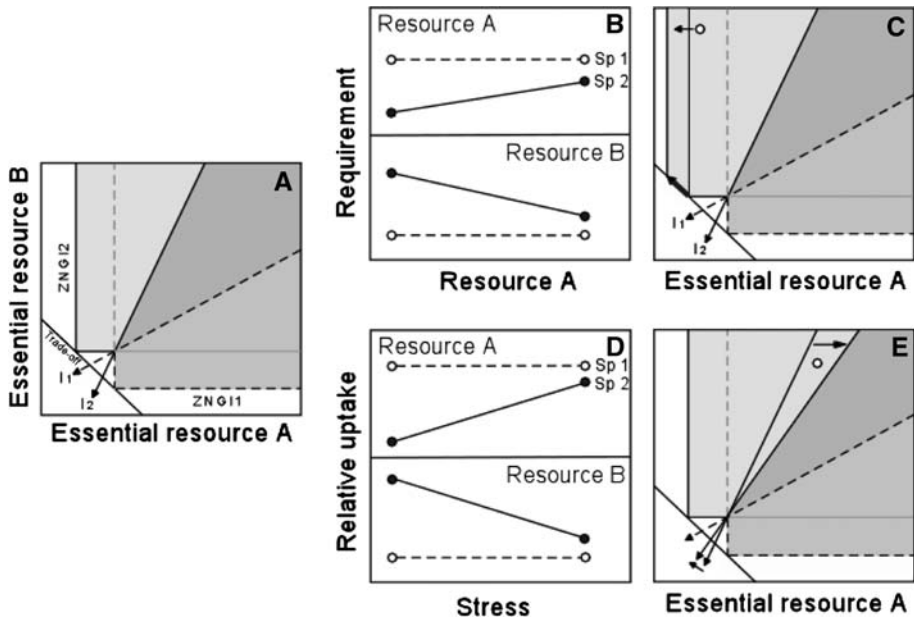


Fig. 2 The effect of phenotypic plasticity in resource requirement and proportional resource uptake on the niche space of two species competing for two essential resources. In **a**, the requirement niche for each of two species and for two essential resources is represented by the *shaded areas*. The *vertical* and *horizontal lines* indicate the average zero-net-growth isoclines (ZNGI's; where $dN/dt = 0$) for species 1 (*dashed line*) and species 2 (*solid line*). The *arrows* indicate the average impact of a species on the two resources, the impact vector (*I*). There is a trade-off in the requirement for the two resources. Any combination of resource supplies in the *light grey* area excludes species 1 from the system, while in the *dark grey* area any range of resource supplies allows coexistence of both species 1 and 2. In **b**, phenotypic plasticity in ZNGI (in this particular case a lower requirement of species 2 for resource A when resource A declines) will shift the ZNGI of individuals of species 2 across the trade-off surface. The new trade-off value in the requirement for the two resources of species 2 enlarges the fundamental niche of species 2 when sufficient amount of resource B is available (area indicated by the *white dot*, **c**). In **d**, phenotypic plasticity in resource uptake induced by environmental stress results in a higher proportional uptake of resource A over B by species 2. The change in the direction of the impact vector of individuals of species 2 reduces the area of resource supply points that allow coexistence of the two species (*dark grey*, Fig. 2e). This example correspond to an enlargement of the realised niche of species 2 at the expense of the realised niche of species 1 (area indicated by the *white dot*). The fundamental niches of the two species will not change

but the model can be adjusted to allow different forms of plasticity, which may change predictions on coexistence of species (Chase and Leibold 2003).

We modify the assumptions of the model to allow plasticity in the resource requirement and proportional resource uptake as a consequence of environmental change. Phenotypic plasticity in resource requirements can be brought about by morphological or physiological adaptations to a changing environment that lower the requirement for a resource (Fig. 2b). The magnitude of the shift in ZNGI is dependent on the magnitude of environmental change as well as the steepness of the reaction norm for that trait (Fig. 2b). As a result of plasticity the ZNGI for this resource will shift along the trade-off surface and change the resource conditions under which the plastic species can survive. In many cases shortage of one of the essential resources itself induces plasticity that lowers the requirement for this resource (Fig. 2c). For example, dry conditions induce a decrease in stomatal conductance in a dry forest tree species, which reduced water loss and lowered its water requirements

during the dry season (Stratton & Goldstein 2001). Two important consequences arise from plasticity induced by essential resource availability. First, even though the trade-off in minimum requirement for each essential resource will lead to an increased requirement for resource B if the requirement for resource A is lowered, if resource B is in sufficient supply and available far above its minimum requirement (i.e. in the upper left hand corner of Fig. 2c), no actual limitation in performance will result. Second, because phenotypic changes in resource requirement occur only under shortage of one of the essential resources, under more abundant resource supply conditions the requirement (ZNGI resource B) of the species is not affected (i.e. in the lower right hand corner of Fig. 2c). Hence, plasticity in ZNGI under low resource availability enlarges the fundamental niche of the species but does not alter the conditions under which the species can coexist with other species (Fig. 2c).

Phenotypic plasticity in relative resource consumption is also likely to occur (Fig. 2d), for example through predator-induced changes in foraging activity, or root plasticity that affects the uptake efficiency of essential nutrients (Callaway et al. 2003; Steiner 2007). Plasticity in the proportional resource uptake affects the slope of the impact vector I ; therefore it affects the realized niche primarily by changing the occurrence of competitive exclusion and coexistence of both species (Fig. 2e). A prime example is the occurrence of complementary chromatic adaptation in cyanobacteria which changes the pigment composition and hence light absorption spectra of species (Stomp et al. 2008). The light conditions for coexistence between cyanobacteria with fixed red or green phenotypes are less stringent than for coexistence between the phenotypically plastic species and either of the fixed phenotypes (Stomp et al. 2008).

Hence, two general predictions arise from considering trait plasticity in the model: Under environmental change: (1) plasticity in resource requirement induced by availability of resources enlarges the fundamental niche of species and causes a reduction of vacant niches for other species and (2) plasticity in the proportional resource uptake results in expansion of the realized niche, causing a reduction in the possibility for coexistence with other species. To our knowledge, explicit experiments testing these predictions have not been carried out yet. Most competition experiments lack detailed information on the physiological mechanism involved, and only measure the ecological consequences of competition. However, indirect evidence can be obtained from competition experiments on native and invasive species. Phenotypic plasticity in requirement of essential resources may increase an invader's success if its plastic response to resource availability allows it to occupy a wider range of niches in comparison to competitors in the local community (Baker 1965; Richards et al. 2006). For example, native and invasive subtropical grassland species showed a significant difference in growth response to light conditions. Native and invasive species had a similar growth when grown under ambient light conditions, but the invasive species had a higher biomass when the conditions changed to a shaded environment, indicative of a reduced requirement for light (Zou et al. 2009). The significantly steeper reaction norm of the invasive species allowed it to cope with a larger range of environmental conditions than the native species, which may explain the range expansion.

Another example shows realized niche enlargement as a result from phenotypic plasticity in resource uptake traits. The rapidly colonizing non-native *Schinus terebinthifolius* showed a strong phenotypic plasticity for water uptake under different conditions of water availability, resulting in increased stem growth in the wet season (Stratton and Goldstein 2001). This high plasticity enabled the invasive species to utilize available resources more efficiently than the native species, and hence broaden its trait space and associated niche width (Richards et al. 2006; Funk et al. 2008). Interestingly, a recent computational model

showed that phenotypic plasticity of an invader adds to its ability to displace residents, while plasticity of a resident species enhances its ability to oppose invaders, due to increased fitness associated with plasticity (Peacor et al. 2006). The phenomenon that invasive species have higher trait plasticity than indigenous species seems to be widespread in both plants and animals (Callaway et al. 2003; Chown et al. 2007; Funk 2008; Engel and Tollrian 2009). Contrary to the wealth of information on trait plasticity of invaders, as far as we know there is no empirical evidence for invasion resistance due to the presence of plastic native species. More information is urgently needed on how trait plasticity of invaders and resident species shape communities under environmental change.

The examples described above concentrate on phenotypic plasticity in resource requirement of species-pairs competing for essential resources. However, a wide variety of organisms express phenotypic plasticity in response to biotic factors, such as induced plant responses to herbivory and induced prey responses to predators (Karban and Baldwin 1997; Tollrain and Harvell 1999; Agrawal 2001; Miner et al. 2005; Heil 2010). For example, herbivory induces an increase in the number and length of protective spines on *Acacia drepanolobium*, which enhances the competitive ability and fitness of *Acacia* under grazing pressure (Young et al. 2003). On the other hand, induced defences often result in reduced foraging and a lower growth rate due to adaptive behavior and resource allocation to defensive structures (Sih et al. 1998; Schmitz et al. 2004; Hoverman and Relyea 2008). The changes in the trade-off between growth and defence resulting from phenotypic plasticity can be incorporated in the niche models in the same way as illustrated above for the case of resource competition. For a mathematical underpinning of this subject we refer to Chase and Leibold (2003).

Incorporating effects of phenotypic plasticity in community diversity and structure

Phenotypic plasticity can only provide a mechanistic explanation for community ecological processes if the predictions from plastic responses in interacting species-pairs can be extrapolated to multi-species assemblages. Here we identify three developing fields of community ecology research that may benefit from recent insights in how trait plasticity affects interacting species in ecological communities.

It is often ignored that the historical sequence of species assembly may affect species establishment (Jenkins and Buikema 1998; Chase 2003; Fukami 2004). This so-called priority effect interacts with phenotypic plasticity. Community assembly is affected by inhibitive or facilitative interactions between the resident and the arriving species. For example, the response of prey to resident predators can facilitate predation by a second, later arriving predator (Hoverman and Relyea 2008). In the case of aquatic snails, morphological and behavioural defences induced by earlier exposure to fish and crayfish led to a higher predation when water bugs colonised the system later on. It suggests that the impact of a colonizing species will depend on the historical build-up of the community. Other aquatic studies confirm that induced responses in prey species vary according to species of prey and predator present (i.e. Laurila et al. 2002; Werner and Peacor 2003). These prey-predator examples indicate that to understand community assembly more information is badly needed on how trait plasticity of community inhabitants and arriving species interacts with priority effects.

However, if a species modifies its phenotype as a reaction to the presence of another species, a change in its traits can alter the per capita intake rate of other species, even in the absence of density effects on the reacting species. Recently, it has become apparent that

non-lethal effects of predators, such as an impact on its prey growth rate or defence traits, can also cascade through the food chain and affect food web architecture. One possible mechanism is a foraging-predation risk trade-off for intermediate species in the food chain (Agrawal 2001; Werner and Peacor 2003; Schmitz et al. 2004), where the prey shows phenotypic plasticity in morphological and behavioral defense traits. For instance, a rocky intertidal shore study showed that predation risk by crabs significantly suppressed snail grazing of fucoid algae, which in turn strongly affected algae succession and dynamics (Trussell et al. 2002). Similarly, in an old-field terrestrial food chain the presence of spider cues also results in altered feeding behavior of leaf-chewing grasshoppers, which increased herb damage (Beckerman et al. 1997). Non-lethal plasticity effects in food chains do not only cascade top-down, but can also cascade bottom-up through the food chain. Plasticity in plant defenses can directly affect development and body size of herbivore populations and their subsequent predators, up to the fourth trophic level (Soler et al. 2005) or indirectly affect the food chain when herbivore-damaged plants attract predators by induced emission of volatile plant compounds (Price et al. 1980; Agrawal 2001; Havill and Raffa 2000). Although cascading trait plasticity effects have received little attention so far, they are probably common and are therefore increasingly appreciated as a structuring force in food web topology.

Above we discussed the importance of trait plasticity for local ecological communities and food webs. However, a growing body of evidence reveals that local communities are connected at the regional scale through dispersal, resulting in metacommunities (Holyoak et al. 2005). Although changing conditions may lead to stressful conditions in local communities, dispersal ability provides the potential to escape adverse direct and indirect consequences of environmental changes by colonizing new habitats (Watkinson and Gill 2002). However, spatial associations are disrupted due to a wide range in dispersal ability of species (Berg et al. 2010). Moreover, differential dispersal of phenotypes with different trait plasticities, may provide local populations with better adapted individuals, and rescue the population from extinction (Urban et al. 2008). We are not aware of studies that have shown that dispersive individuals differ in a consistent manner in trait plasticity, but given the importance of dispersal for community assembly and metacommunity dynamics we urgently need empirical data on plasticity in dispersal traits, and how this affects plasticity in competitive traits. The integration of plasticity in life history traits with metacommunity ideas is a great challenge (Urban et al. 2008).

Future directions

It is clear to most ecologists that evolutionary processes in community ecology can no longer be ignored (Ellers 2009). The empirical evidence presented here undeniably calls not only for a trait-based community perspective (McGill et al. 2006; Suding et al. 2008; Funk et al. 2008), but also for a framework that takes plasticity of traits of interacting species into account. Combined this will provide a more mechanistic and quantitative insight into how phenotypic plasticity of component species can affect population persistence and shape community structure. However, we are only at the beginning of the difficult process of integrating evolutionary principles with the community level. There is an obvious need for a greater number of trait plasticity studies on natural communities to show long-term effects of trait plasticity (Hoverman and Relyea 2008). Short-term experiments might show strong plasticity effects, for instance in identifying trait-mediated

indirect effects when predators are added to a predator-free system (Werner and Peacor 2003). However, it is not clear if these plasticity effects are long lasting. Also, the range of taxa involved in these studies needs to be expanded, because the majority of studies on phenotypic plasticity of concern plants. It will be particularly challenging to include an often ignored but key component of ecosystems, i.e. belowground communities in trait plasticity studies (Sugden et al. 2004; Chown et al. 2007; Liefing and Ellers 2008). Below we identify some challenges for future research.

A methodological challenge will be to identify which traits are relevant for species interactions and measure the relative variability in trait plasticity between species. The focus should be on functional traits that define the realized niche of species and limit niche similarity between coexisting species (McGill et al. 2006; Suding et al. 2008; Funk et al. 2008). To estimate the dissimilarity in trait plasticity between species the shape of the reaction norms can be compared, preferably along environmental gradients (Miner et al. 2005). Several studies have demonstrated that the shape of the reaction norm differs between, for instance, native and invasive species; however, the form of changes and the type of traits showing differences in plasticity levels seem to be idiosyncratic (Chown et al. 2007; Muth and Pigliucci 2007). Moreover, to assess the importance of trait plasticity for pair-wise species interactions dissimilarity in the shape of reaction norms can be used to manipulate the magnitude of trait plasticity in mesocosm studies. A second major undertaking is the extrapolation of trait plasticity in pair-wise interactions in mesocosm studies to multi-species ecological communities. The relative simple approach of pair-wise comparisons yields accurate qualitative predictions on the outcome of mesocosm experiments (Agrawal 2001; Relyea and Yurewicz 2002; Miner et al. 2005), but it may not be that simple to scale it up to communities. Identifying for all components species how they adapt their traits to many environmental factors will be a Herculean task, and density effects of interacting species are often not taken into account. A careful choice of study systems as well as inventive use of molecular tools is necessary to scale these pair-wise comparisons to ecological communities (Ellers 2009).

To conclude, many community ecological issues, such as assembly, invasions, food web cascades are affected by plasticity of traits that relate to competition, tolerances and dispersal. We therefore need an integration of evolutionary principles with community ecological theory, i.e. evolutionary community ecology, in order to understand how changes in the environment affect community composition and species distributions. What's more, the new discipline of evolutionary community ecology can be mutually beneficial to community ecology and evolutionary biology. Most evolutionary studies perform experiments with single individuals in isolation, or only in direct interaction with another species, such as studies on co-evolution. Far fewer studies have addressed the effect of community diversity on genetic and phenotypic diversity of single species (Vellend and Geber 2005; Urban et al. 2008; Ellers 2009). Evidence suggests that species diversity can act as a source of diversifying selection on single species, through fine-scale competitive interactions among individuals (Vavrek 1998; Callaway and Aschehoug 2000; Fridley et al. 2007). Phenotypic plasticity in a community context is a fascinating area of biology, and a true integrative approach has the exciting potential to obtain a better understanding of pure and applied problems in biology.

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