



Tansley review

Ecological limits to plant phenotypic plasticity

Author for correspondence:
Fernando Valladares
Tel: +34 917452500, ext. 1204
Fax: +34 915640800
Email: valladares@ccma.csic.es

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Fernando Valladares^{1,2}, Ernesto Gianoli^{3,4} and José M. Gómez⁵

¹Instituto de Recursos Naturales, Centro de Ciencias Medioambientales, CSIC Serrano 115, Madrid, E-28006, Spain; ²Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/Tulipán s/n, Móstoles, Madrid, E-28933, Spain;

³Departamento de Botánica, Universidad de Concepción, Casilla 160-C Concepción, Chile; ⁴Center for Advanced Studies in Ecology & Biodiversity (CASEB), P. Universidad Católica, Alameda 340, Santiago, Chile; ⁵Grupo de Ecología Terrestre, Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Granada, E-18071, Spain

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Summary

Key words: abiotic stresses, competition, complex environments, fitness, global change, herbivory, phenotypic integration, trait-mediated interactions.

Phenotypic plasticity is considered the major means by which plants cope with environmental heterogeneity. Although ubiquitous in nature, actual phenotypic plasticity is far from being maximal. This has been explained by the existence of internal limits to its expression. However, phenotypic plasticity takes place within an ecological context and plants are generally exposed to multifactor environments and to simultaneous interactions with many species. These external, ecological factors may limit phenotypic plasticity or curtail its adaptive value, but seldom have they been considered because limits to plasticity have typically addressed factors internal to the plant. We show that plastic responses to abiotic factors are reduced under situations of conservative resource use in stressful and unpredictable habitats, and that extreme levels in a given abiotic factor can negatively influence plastic responses to another factor. We illustrate how herbivory may limit plant phenotypic plasticity because damaged plants can only rarely attain the optimal phenotype in the challenging environment. Finally, it is examined how phenotypic changes involved in trait-mediated interactions can entail costs for the plant in further interactions with other species in the community. Ecological limits to plasticity must be included in any realistic approach to understand the evolution of plasticity in complex environments and to predict plant responses to global change.

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It is not the strongest of species that survive or the most intelligent but the ones most responsive to change'
Charles R. Darwin (1859)

I. Phenotypic plasticity: if so good, why so little?

Environments are highly heterogeneous both in space and time, and organisms must either acclimate to, or escape from, adverse conditions. Phenotypic plasticity, or the capacity of a given genotype to render different phenotypes under different environmental conditions, is a means to cope with environmental heterogeneity that is particularly adequate for sessile organisms (Bradshaw, 1965; Sultan, 2000). The ecological breadth of species may be partly explained by their capacity to show plastic responses to the environment (Sultan, 2001; González & Gianoli, 2004; Saldaña *et al.*, 2005). Besides, phenotypic plasticity is a source of ample phenotypic variation that may promote adaptive divergence and, thus, evolution and speciation (West-Eberhard, 2003). Many studies have shown that plants are plastic for numerous ecologically important traits, ranging from morphology, physiology and anatomy, to developmental and reproductive timing, breeding system and offspring developmental patterns (Sultan, 2000). In the last two decades phenotypic plasticity of plants has become a central issue of ecological and evolutionary research. There have been significant advances in the understanding of the genetic basis and potential adaptive value of reaction norms, which depict the variation in phenotypic expression with the environment (Scheiner, 1993; Sultan, 1995, 2001; Pigliucci, 2001; Schlichting, 2002; DeWitt & Scheiner, 2004; van Kleunen & Fischer, 2005; Valladares *et al.*, 2006).

Plastic responses of plants to contrasting environments have been frequently reported as adaptive (e.g. Poorter & Lambers, 1986; Valladares & Percy, 1998; Donohue *et al.*, 2003; Dudley, 2004), but this is not always the case (van Kleunen & Fischer, 2005), and examples of maladaptive plasticity do exist (Sánchez-Gómez *et al.*, 2006a; Ghalambor *et al.*, 2007). There is abundant evidence that plant species and populations may differ remarkably in the extent of their plastic responses to comparable environmental challenges (e.g. Schlichting & Levin, 1984; Valladares *et al.*, 2000, 2002a; Balaguer *et al.*, 2001; Sultan, 2001). Because phenotypic plasticity can be very advantageous for plants, the question arises of why plasticity is not always maximal. Differences among species and populations in their plasticity may reflect differential selective pressures on plasticity, differential limitations acting upon the maximization of plasticity, or a combination of both. Differential selective pressures on plasticity

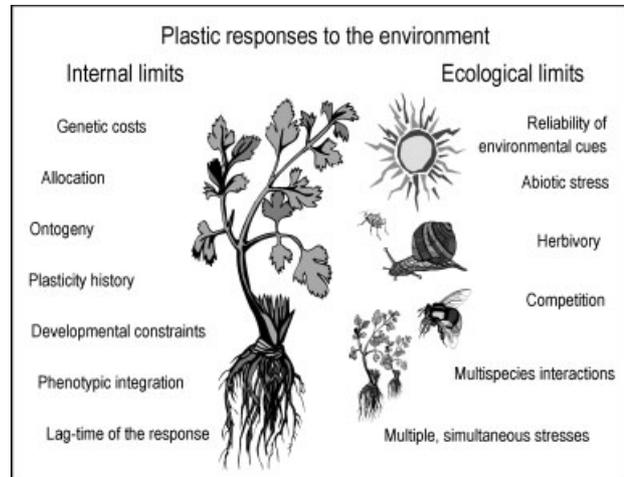


Fig. 1 Many internal and ecological factors can influence the capacity of plants to respond to a given environmental factor. While the internal limits to plasticity have received sustained attention, the ecological constraints and costs induced by multiple biotic and abiotic factors, which more often than not exert their influence simultaneously, have been explored in less detail, despite the growing evidence of their importance.

have been suggested for habitats differing in their environmental heterogeneity (Balaguer *et al.*, 2001; Donohue *et al.*, 2003; Gianoli & González-Teuber, 2005), although not all the environmental heterogeneity is functionally relevant for the plant (Gómez *et al.*, 2004). The fact that plasticity observed in nature is often lower than that expected suggests the existence of costs and limits of plasticity (Fig. 1). The costs and limits of phenotypic plasticity are not as well understood as its benefits (DeWitt *et al.*, 1998; Givnish, 2002).

It is important to note that the observed phenotypic responses to the environment are the net result of active and passive responses. The potential plastic response in a given trait may be large but the observed plasticity can be lowered by resource limitation or environmental stress (van Kleunen & Fischer, 2005). Besides, many phenotypic traits change dramatically over the course of plant growth, a phenomenon termed ontogenetic drift (Evans, 1972). Thus, size- or age-dependent phenotypic variation must be taken into account when estimating true phenotypic plasticity (Coleman *et al.*, 1994; Valladares *et al.*, 2006). Ontogeny is also important in studies addressing plasticity because plants have been shown to express different levels of plasticity as they grow (e.g. Mediavilla & Escudero, 2004). Developmental reaction norms are a suitable approach to account explicitly for ontogeny in studies of plasticity (Pigliucci *et al.*, 1996; Schlichting & Pigliucci, 1998; Cheplick, 2003).

The most widely considered costs of plasticity are: (1) maintenance costs of the mechanisms of plasticity; (2) production costs of induced phenotypic features; (3) information acquisition costs; (4) developmental instability of environmentally contingent phenotypic features; and (5) genetic

costs via linkage (the tendency for genes to be inherited together because of their location near one another), pleiotropy (control by a single gene of several apparently unrelated aspects of the phenotype) or epistasis (masking of the phenotypic effect of alleles of one gene by alleles of another gene) (DeWitt *et al.*, 1998). Analyses addressing the limits to plasticity usually include: (1) low reliability of environmental information; (2) lag time in the response; (3) developmental range limit; and (4) epiphenotype problems or phenotypic add-on responses not integrated during early development (DeWitt *et al.*, 1998; Givnish, 2002). However, some of these limits and costs of plasticity are specific for actively moving organisms. Those that are most relevant for plants can be rearranged as: (1) genetic costs, including maintenance and developmental instability costs; (2) plasticity history limits (as shown by Weinig & Delph, 2001); (3) environmental reliability costs; and (4) lag-time costs (van Kleunen & Fischer, 2005). Costs may vary in magnitude depending on environmental conditions and they seem to be more significant in stressful environments (Steinger *et al.*, 2003).

Several additional, but less explored, factors can impose further limits on the full expression of plasticity. For example, phenotypic inertia induced by large propagules could lead to a reduced plasticity in the case of juvenile plants, as suggested by the study of Rice *et al.* (1993) on oak acorns. Besides, phenotypic plasticity may not always evolve because of its adaptive value: it can evolve as a result of genetic correlations with other traits that are under selection (Pigliucci *et al.*, 2006). The fact that plant traits are correlated gives rise to an integrated phenotype (Pigliucci & Preston, 2004) and could set limits to the full expression of plasticity for individual traits (Gianoli, 2001). The scant empirical studies on the ecological significance of phenotypic integration suggest that stressful environments lead to increased levels of phenotypic integration in plants (Schlichting, 1989; Waitt & Levin, 1993; Gianoli, 2004). This might also explain cases of reduced plasticity under stressful conditions, in addition to the already mentioned passive responses that counteract active plasticity, and the increased costs of plasticity under stress. However, we are far from a solid understanding of phenotypic integration in plants (Pigliucci & Preston, 2004), so there is still a need for more empirical evidence and further theoretical developments in order to define its role as a potential limit to plasticity for individual traits.

Although it is commonly accepted that plants must deal with several co-occurring ecological factors in natural conditions, most studies of phenotypic plasticity have been conducted considering phenotypic responses to a single factor, often an abiotic factor (e.g. light, water, temperature or nutrients). However, potential plasticity to a given factor can be influenced by other biotic and abiotic factors co-occurring in complex, multivariate environments (Sultan *et al.*, 1998; Valladares *et al.*, 2002b; Gianoli, 2003; Sánchez-Gómez *et al.*, 2006b; Gianoli *et al.*, 2007; Maestre *et al.*, 2007). The influence

of other environmental factors on the plastic responses to a given environmental factor frequently leads to a reduced expression of phenotypic plasticity, and this situation is what we refer to here as the ecological limits to phenotypic plasticity, in contrast to the more frequently addressed internal limits (Fig. 1; Van Kleunen & Fischer, 2005). Ecological limits also include information reliability issues but we will not extend on them because they have received detailed attention in previous studies (e.g. Weinig, 2000). We use limits as a comprehensive term, including both constraints, when maximal plasticity cannot be achieved, and costs, when actual plasticity is not beneficial or even negative in terms of fitness (Fig. 1).

Our general aim here is to address plant phenotypic responses to complex environments (i.e. when several ecological factors act simultaneously upon plants). We are particularly interested in understanding how plastic responses of plants to one factor are influenced by changes elicited or limitations imposed by other environmental factors. We will first address plastic responses in multifactor abiotic scenarios, then explore how biotic factors affect plastic responses to abiotic factors, and finally discuss how plasticity influences and is influenced by biotic interactions, with competition and herbivory as model biotic interactions. General hypotheses and conceptual models will be put forward at each level of analysis in order to refine our understanding of the rapidly expanding field of phenotypic plasticity and to foster novel research avenues. After revising our current understanding of plastic phenotypic responses from individual to community level processes, we will finish the review by discussing how all of this could be integrated to study plant responses to global change.

II. Ecological constraints caused by abiotic factors

Even though plastic responses of plants to changing abiotic factors tend to increase fitness across environments, low or even no plasticity might be adaptive when environmental change is not predictable or when no phenotypic response can overcome the environmental challenge (Henry & Aarssen, 1997; Huber *et al.*, 2004; Valladares *et al.*, 2005a,b; Ghalambor *et al.*, 2007). Cases of potentially maladaptive plasticity have been discussed for Mediterranean woody seedlings facing unpredictable changes in stressful semi-arid environments (Valladares *et al.*, 2002b, 2005). Analogously, plasticity of understory plants in response to light has been found to be low in tropical, shade-tolerant, woody species (Valladares *et al.*, 2000), in agreement with a stress-tolerance strategy (Grime & Mackey, 2002). A reduced plasticity in response to low light might not enhance light capture of understory plants but can avoid or minimize futile elongation in a situation where canopy trees cannot be overtopped (Valladares & Niinemets, *in press*). This agrees with the finding that the most plastic species in response to light exhibited the highest seedling mortality in deep shade in a comparative study of four Iberian tree species (Fig. 2; Sánchez-Gómez *et al.*, 2006a).

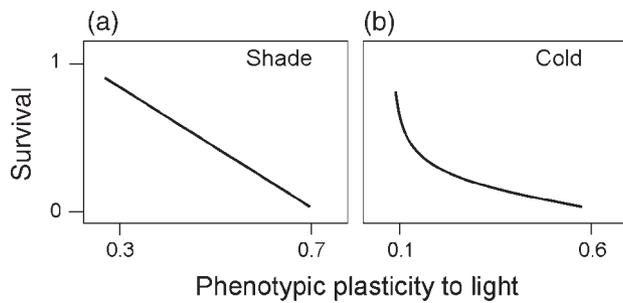


Fig. 2 Scenarios of negative fitness associated with phenotypic plasticity. Influence of phenotypic plasticity in response to available light on the survival of woody Mediterranean seedlings either under deep shade (a) or after unusually cold snaps over the winter (b). In both cases, species exhibiting highly plastic responses to light were those exhibiting low survival under limiting conditions of light or temperature. Survival in deep shade was quantified in four species (elaborated from data in Sánchez-Gómez *et al.*, 2006a,c), whereas survival after the cold snap was assessed in eight species (unpublished results from the experiment in Sánchez-Gómez *et al.*, 2006b). Plasticity is expressed by the plasticity index of Valladares *et al.* (2000) which spans from 0 (no plasticity) to 1 (maximal plasticity).

Highly heterogeneous environments often involve heterogeneity in multiple factors. Light, temperature, and soil fertility and moisture exhibit complex patterns in nature, frequently covarying in nonlinear ways. The spatial and temporal scales might be different for each factor, further complicating the notion of 'functional heterogeneity' (*sensu* Li & Reynolds, 1995, i.e. the heterogeneity perceived and functionally relevant for a given organism), and the interpretation of the associated plant responses (Gómez *et al.*, 2004; Gómez-Aparicio *et al.*, 2005). For example, while light heterogeneity can be relevant at the scale of meters (Valladares, 2003; Valladares & Guzmán, 2006), soil heterogeneity might be relevant at the scale of centimeters or less (Hodge, 2006). Frequently, the level of at least one of the environmental factors represents a stressful condition. As stress often operates in a temporary or fluctuating manner, facultative adaptations able to be produced within a single genotype through phenotypic plasticity are hypothesized to be adaptive (Bradshaw & Hardwick, 1989). However, the response of plants to a combination of two or more different abiotic stress factors is unique and cannot be directly extrapolated from the response to each factor operating singly (Valladares & Pearcy, 1997; Mittler, 2006). Empirical evidence on simultaneous plant responses to several abiotic factors has, in fact, revealed a complex picture. Those woody seedlings exhibiting greater elongation in the shade (i.e. being highly plastic in response to light) were severely affected by a cold snap taking place over the winter (Fig. 2). Drought significantly reduced the survival of woody seedlings in deep shade but, more interestingly, it also reduced plastic responses to light of both shade-tolerant and shade-intolerant species in a factorial experiment (Fig. 3). Most of these cases can be explained by the fact that phenotypes which are advantageous

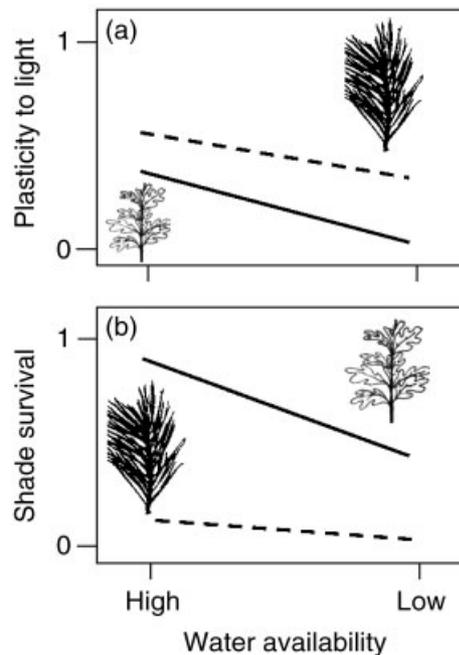


Fig. 3 Scenarios of constraints to plasticity imposed by abiotic factors (drought). Phenotypic plasticity in response to light (a) and shade survival (b) of seedlings of two oaks (continuous lines) and two pines (dashed lines) at two contrasting levels of water availability (elaborated from data in Sánchez-Gómez *et al.* (2006a,c). Oaks were less plastic but more shade tolerant than pines, and water stress significantly reduced not only survival but also plasticity to light in the two groups of species. Plasticity is expressed by the plasticity index of Valladares *et al.* (2000), which spans from 0 (no plasticity) to 1 (maximal plasticity).

under extreme values of a given abiotic factor can be maladaptive for extreme values of another factor. Thus, plasticity becomes detrimental when the extreme values of both factors take place simultaneously, as in the case of a dry understory. In fact, plant species capable of tolerating more than one abiotic stress are, in general, very scarce (Niinemets & Valladares, 2006), and the combination of low light and drought, in particular, has been argued to pose a very strong ecological filter (Valladares & Pearcy, 2002). The hazardous nature of a dry shade is further complicated in continental Mediterranean habitats by the cold snaps that take place over the winter and early spring, making questionable the notion of shade as a benign environment in these semi-arid ecosystems (Valladares *et al.*, 2005a,b).

Stem elongation in response to shade is one of the best studied cases of phenotypic plasticity in plants. Changes in the ratio of red to far-red wavelengths (R:FR) indicates neighbour proximity and influences stem elongation (Ballaré, 1999). However, because of the simultaneous variation of other environmental factors, such responses to R:FR might become maladaptive. This was shown by Weinig (2000a,b), who found that temperature and photoperiod set limits to adaptive R:FR responses in different populations of *Abutilon theophrasti*.

This is a clear example of multiple environmental factors varying simultaneously and limiting the adaptive value of responses to a single cue such as light quality. Plants can overcome this problem to some extent by responding to a combination of cues, and this is the case for shade avoidance (Pierik *et al.*, 2004a). Elongation can be the result of many factors acting in concert, including not only phytochrome-mediated responses to R:FR but also the integrated action of the plant hormones ethylene, auxin, gibberellin and abscisic acid (Voesenek *et al.*, 2004). Thus, maximal elongation in response to shade was observed when not only R:FR was modified but also when the atmospheric ethylene concentration was simultaneously enhanced (Pierik *et al.*, 2004a,b). These studies with transgenic tobacco revealed the interesting situation that responses to shade were mediated by a multisignal mode of neighbour detection, which can significantly reduce the information reliability limits of plasticity.

Interestingly, stem length is a phenotypic trait responsive to environmental factors other than shading. The capacity to elongate is an important selective trait in plants from flood-prone environments, with fast shoot elongation being a favourable trait only in environments with shallow and prolonged flooding events, because costs associated with this response prevent its expression in sites with either deep or very short-duration floods (Voesenek *et al.*, 2004). Stem elongation in terrestrial environments can result from competition, and taller plants are known to have a disproportionate advantage in dense stands (Dudley & Schmitt, 1996). However, plants must follow basic biomechanical laws and therefore must be able to carry their own weight and to resist wind forces, which is challenged by stem elongation. An elongated plant in a dense stand might only need to carry its own weight because the wind is shielded. When wind shield is not provided, stems might not grow as tall as would be required for outcompeting neighbour plants because part of the growth must be devoted to enhance self-support. There is a large fitness premium for plants elongating in response to both shading and wind shield (Anten *et al.*, 2005), but if wind shield disappears or decreases, as when a canopy gap is created, the more elongated individuals are more vulnerable to mechanical failure.

For some of the scenarios discussed above, reduced plasticity in response to one factor can render high fitness across a range of environments involving changes in other factors (i.e. plasticity is maladaptive). Alternatively, plasticity in response to a given factor can be directly limited by a given range of values of another factor (i.e. plasticity is functionally constrained). Summarizing, plastic responses to abiotic factors can be reduced under situations of a conservative resource use imposed by stressful habitats experiencing unpredictable environmental changes. Extreme or harmful levels in a given abiotic factor can negatively influence plastic responses to another, which has been seen in the low plasticity in response to light of woody seedlings under limiting water availability.

Finally, extreme or heavily modified phenotypes can be more vulnerable to further environmental changes, which is exemplified by the high mortality of elongated shade plants experiencing cold snaps or strong wind when shielding by a dense stand disappears.

III. Ecological constraints caused by biotic factors

Earlier work addressing external limitations to the evolution of adaptive reaction norms mostly considered characteristics of the abiotic environment (e.g. the magnitude of environmental heterogeneity or the reliability of cues; Bradshaw & Hardwick, 1989; van Tienderen, 1991; Scheiner, 1993; Sultan, 1995; Alpert & Simms, 2002; van Kleunen & Fischer, 2005). However, phenotypic plasticity takes place within an ecological community and therefore the modulating role of biotic components should not be overlooked (e.g. Stevens & Jones, 2006; Anderson *et al.*, 2007). In fact, herbivory and interspecific competition may limit plant responses to challenging environments, constraining phenotypic plasticity (see Callaway *et al.*, 2003). Thus, neighbour plants would be at the same time the modifying biotic factor and the main environmental factor. Unfortunately, while the environmental modulation of plant phenotypic responses to herbivory has been amply documented (Gianoli & Niemeyer, 1996; Cipollini & Bergelson, 2001; Gianoli, 2002; Izaguirre *et al.*, 2006; Roberts & Paul, 2006), the herbivore-induced constraints on plant phenotypic plasticity to abiotic factors have not been evaluated in detail (Miner *et al.*, 2005).

In this section, we will focus on the limits to plasticity imposed by herbivores. Our analysis concentrates mainly on above-ground herbivory, but there is some evidence that below-ground herbivores may also influence plant responses to environmental factors (e.g. Dunn & Frommelt, 1998).

Plant traits affected or induced by herbivory are very diverse; they include chemical defences (Agrawal, 1999, 2000), mechanical structures such as thorns, spines and trichomes (Gómez & Zamora, 2002; Young *et al.*, 2003), nutritional quality traits (Bi *et al.*, 1997), volatiles that attract predators and parasites of herbivores (Takabayashi & Dicke, 1996; De Moraes *et al.*, 1998), and extrafloral nectaries that attract defensive ants (Agrawal & Rutter, 1998; Huntzinger *et al.*, 2004). Compensatory responses of plants to damage also involve changes in plant phenotype that potentially affect the interactions of plants with other organisms. Finally, herbivores and pathogens may cause changes in plant traits not related at all with resistance or tolerance, often as a consequence of resource re-allocation in damaged plants. For example, it has been found that damage affects flowering phenology, flower display, flower morphology and size, pollen and nectar production, and plant architecture (Quesada *et al.*, 1995; Strauss *et al.*, 1996; Strauss, 1997; Aizen & Raffaele, 1998; Gómez, 2003). Examination of the potential effects of herbivory on plant phenotypic plasticity may contribute to the extensive

discussion on the ecological significance of herbivores for plant fitness (e.g. Marquis, 1992; Paige, 1992; Louda & Potvin, 1995; Crawley, 1997; Wise & Abrahamson, 2007).

The vast research on the changes in plant chemistry, physiology, morphology and development that occur following herbivory (Karban & Baldwin, 1997; Zangerl, 2003; Agrawal, 2005) might be useful for understanding how these responses interact with plant phenotypic plasticity (Cipollini, 2004, 2007; Roberts & Paul, 2006). For instance, the biosynthesis of indole glucosinolates and indole alkaloids, defensive metabolites that may be induced upon herbivory (Karban & Baldwin, 1997), includes indole-acetaldoxime, a precursor of the hormone indole-acetic acid (Hansen & Halkier, 2005), which plays a central role in the stem-elongation response to shading (Morelli & Ruberti, 2000). Similarly, leaf wounding may elicit both an increase in proteinase inhibitors, which may deter herbivores (Broadway *et al.*, 1986), and a decrease in the levels of indole-acetic acid (Thornburg & Li, 1991), which may limit plastic responses to shade. A field study with genetically modified plant varieties found some evidence that mutant plants constitutively expressing the shade-avoidance response suffer more herbivory than wild types (McGuire & Agrawal, 2005). Translocation to leaves of nonstructural carbohydrates stored in stems and roots allows plants to overcome the negative carbon balance imposed by deep shade or herbivory (Myers & Kitajima, 2007). This suggests that the occurrence of herbivore damage could compromise the capacity of plants to express metabolic responses to shading. Nonstructural carbohydrates are also involved in plant tolerance to extreme cold (Bravo *et al.*, 2001), and herbivory may affect the sugar metabolism of plants involved in freezing protection (Bravo *et al.*, 1997). Finally, several types of compensatory responses associated with tolerance to herbivory have been reported (Strauss & Agrawal, 1999; Stowe *et al.*, 2000), including increased relative allocation of resources to shoots (Mabry & Wayne, 1997), increased photosynthesis (Nowak & Caldwell, 1984) and delayed flowering (Lennartsson *et al.*, 1998). These patterns may counteract the functional responses to drought, such as early flowering (Bennington & McGraw, 1995; Gianoli, 2004), decreased stomatal conductance that reduces both water loss and photosynthesis (Schulze, 1986), and the increased root:shoot ratio of biomass allocation (Lloret *et al.*, 1999; Gianoli & González-Teuber, 2005).

Phenotypic plasticity may be limited both by the direct effects of herbivory on the plant (biomass loss that compromises future growth or differentiation) and by the plastic responses triggered by herbivores, such as the induction of costly chemical defences or changes in above-ground/below-ground resource allocation. Our general graphical analysis (Fig. 4) does not distinguish between direct and indirect effects of herbivory. This analysis focuses on the consequences of herbivory for the plant in terms of the change in slope (and elevation) of the reaction norm of a phenotypic trait whose variation allows a better resource use in the novel

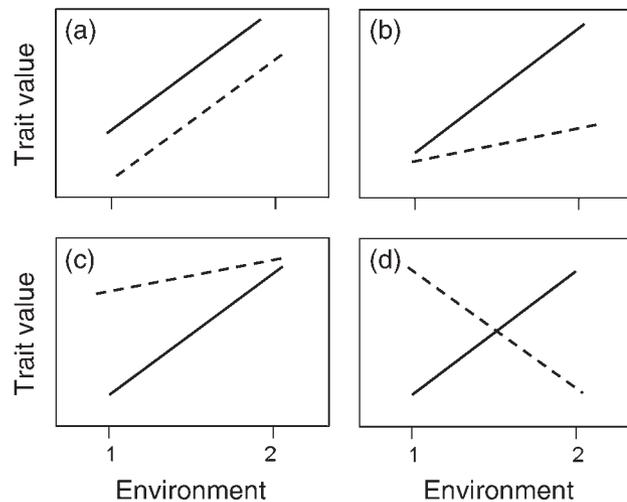


Fig. 4 Scenarios of constraints on plasticity imposed by biotic factors (herbivory). The panels show the reaction norms in the absence (continuous line) and presence (dashed line) of herbivores. It is assumed that the continuous line depicts the functionally optimal response of the plant to the environment (i.e. the phenotype of greatest fitness in each environment). In panel a there is no effect of herbivory on the slope of the reaction norm (i.e. on plasticity) but its elevation is changed, causing a slight departure from the optimal phenotype in each environment. In panels b and c there is a significant reduction in the slope of the reaction norm caused by herbivores. Whereas in b reduced plasticity results in a maladaptive phenotype in environment 2, in c reduced plasticity causes a maladaptive phenotype in environment 1. In d there is a change in the direction, but not in the slope, of the reaction norm, causing a maladaptive phenotype in both environments. If environments 1 and 2 are equally stressful, then the examples shown in b and c are similar in terms of plant fitness losses. If environment 2 is more stressful than environment 1, then b depicts a scenario of greater fitness losses than c. The most injurious case is shown in d.

environment. Following early suggestions on the use of the term constraint (Antonovics & van Tienderen, 1991), herbivory is herein considered a constraint to plasticity with reference to a null hypothesis. Thus, such constraint is evidenced by significant departures of the reaction norm of damaged plants from the reaction norm of undamaged plants (the null hypothesis, continuous line in Fig. 4). This reaction norm is therefore preliminary assumed to be the 'right', functional response of the plant's trait to the environmental gradient, regardless of the presence of herbivores. The fact that the joint effect of herbivory and resource limitation often has detrimental consequences for plant fitness (Hawkes & Sullivan, 2001) suggests that the reaction norm of damaged plants should reflect constrained phenotypic trait values rather than optimized ones, particularly in the challenging environment.

In spite of the abundance of studies addressing the interactive effects of herbivory and environmental factors on plants, few studies have explicitly evaluated the effect of damage on

plant phenotypic plasticity. The latter studies, together with a noncomprehensive sample of other studies where such an effect could be inferred *a posteriori*, are summarized in Table 1. Selected cases include plasticity to five key environmental factors for plants: shade; drought; CO₂; soil nutrients; and flooding (Table 1). The most common pattern found is a reduction in the slope of the reaction norm of damaged plants (the case shown in Fig. 4b). Although in some cases the resulting constrained phenotype might be explained, invoking stress amelioration as a result of herbivory (e.g. a reduced slope in the reaction norm of water use efficiency may be a consequence of a decreased water loss owing to consumption of leaf area), an ecophysiological analysis of most of the cases in Table 1 indicates that damaged plants could not attain the target phenotype in the challenging environment. This supports our assertion of the preceding paragraph regarding the constrained nature of the reaction norm of plants suffering herbivory.

Several research lines may complement the approaches to biotic modulation of phenotypic plasticity to abiotic factors outlined herein. There is some evidence that symbiotic endophytic fungi may affect the phenotypic plasticity of host plants in response to soil nutrients, the net effect being genotype specific (Cheplick *et al.*, 1989; Cheplick, 1997). Mycorrhizal infection may modify plant responses to phosphorous addition (re-analysis of the data from Lu & Koide, 1994), leading to reaction norms of reduced slope but increased elevation (the case shown in Fig. 4c). These findings broaden our perspective and call for the inclusion of beneficial species in future analyses of the effects of biotic factors on phenotypic plasticity. Moreover, this also suggests that further research should explore whether there is genetic variation for the sensitivity of reaction norms to herbivory, both within and among populations. Another unexplored and potentially important aspect involved in the modulation of plant phenotypic plasticity by biotic factors is the capacity of allelopathic compounds to limit reaction norms. This would allow us to quantify in greater detail the negative impacts of competition on the target plant, constituting another avenue for insights on the ecological limits of plasticity.

In summary, we have shown that: (1) herbivory may constrain the expression of plant phenotypic plasticity in response to abiotic factors; (2) symbiotic species also affect plastic responses of plants to abiotic factors; (3) the elucidation of underlying mechanisms is at hand; and (4) these phenomena remain largely underexplored despite the availability of suitable data to test for their occurrence and relevance.

IV. Ecological costs: influence of plasticity on species interactions

Ecologists are starting to recognize the importance of trait-mediated interactions (TMI), namely the effects that occur on the interacting organisms as a consequence of changes in their phenotypes (Bolker *et al.*, 2003; Dill *et al.*, 2003;

Luttbeg *et al.*, 2003; Trussell *et al.*, 2003; Werner & Peacor, 2003; Schmitz *et al.*, 2004). Plants are frequently involved in TMIs as their phenotype is modified by the effect of herbivores and pathogens in a variety of ways (Gómez & González-Megías, 2007). While in the preceding section we addressed the effects of above-ground herbivory on plant phenotypic responses to abiotic factors, in this section we summarize how changes in plant phenotype elicited by a given plant or animal species may play a role in the interactions between the plant and other organisms. We will describe cases in which phenotypic modifications of plants following damage affect the interactions between plants and both natural enemies and mutualistic species. It is important to distinguish between the inevitable effects of damage and active responses to it, which include inducible defences and compensation. The latter are putative cost-saving mechanisms and, thereby, can be considered as adaptive phenotypic plasticity allowing plants to maximize fitness in each environment (Karban & Baldwin, 1997; Cipollini, 2004).

Plants usually interact with many organisms simultaneously. While plants are pollinated by many different and disparate animals, from insects to birds and mammals, they are also attacked by many different kinds of herbivores, from large ungulates to tiny bugs, beetles or flies, and can be infected with many different types of microscopic pathogens. In these multispecific scenarios, the modification of the plant phenotype can indirectly affect the interaction that the plant maintains with other species, an effect named trait-mediated indirect interaction (TMII) that is a particular case of TMI. From a plant perspective, the occurrence of TMII may mean either a cost or a benefit of phenotypic plasticity (Fig. 5). For instance, phenotypic plasticity is costly when the modification of trait values caused by one herbivore increases the interaction with a second or subsequent-acting herbivore (Fig. 5b). For example, Danell & Huss-Dannell, 1985) reported that *Betula pendula* trees browsed by moose (*Alces alces*) were preferred over unbrowsed trees by some phytophagous insects such as aphids, psyllids, leaf-miners and leaf-gallers. Martinsen *et al.* (1998) similarly found that the leaf beetle *Chrysomela confluenta* prefers the resprouts from *Populus fremontii* and *P. angustifolia* individuals damaged by the beaver *Castor canadensis* because they are richer in nitrogen. This increase in insect attack occurs because damage by mammalian herbivores can provoke overcompensatory growth in plants and/or rejuvenation of plant tissues. Overcompensation increases food availability for insects, whereas rejuvenation leads to plant tissue of higher quality (Kruess & Tschardt, 2002a).

Phenotypic plasticity is also costly when the modification of the plant phenotype decreases the interaction with mutualistic organisms (Fig. 5c). For instance, there is evidence that herbivory by ungulates (Gómez & Zamora, 2000; Gómez, 2003), caterpillars (Strauss *et al.*, 1996; Lehtilä & Strauss, 1997), spittle bugs (Hämbäck, 2001) or mechanical damage (Mothershead & Marquis, 2000) may decrease plant attractiveness

Table 1 Examples of studies finding an effect of herbivory or damage on plant phenotypic plasticity

Plant species	Herbivory treatment	Environmental gradient	Effect of herbivory on reaction norm (scenario in Fig. 4)	Source
<i>Chenopodium album</i>	Caterpillars: 34% leaf area	Shade: 100% vs 62% PAR	Stem length: unchanged slope, reduced elevation [A]	1
	<i>Convolvulus arvensis</i> Clipping: 25% leaf area	Shade: 100% vs 5% PAR	Internodes length: reduced slope [B]	2
<i>Convolvulus demissus</i>	Clipping: 50% leaf area	Drought: watering every 10 d vs every 3 d	Petiole length: reduced slope [B]	3
			Leaf shape: reduced slope [B]	
<i>Convolvulus demissus</i>	Leaf beetles: 50% leaf area	Drought: watering every 10 d vs every 3 d	Root:shoot ratio: reduced slope [B]	4
			Xylem water potential: reduced slope [B]	
<i>Solanum dulcamara</i>	Aphid colony during 4 wk	CO ₂ : 350 vs 700 µl per litre	Root biomass: inversed slope [D]	5
			Water use efficiency: reduced slope [B]	
<i>Asclepias syriaca</i>	Aphid colony during 5 wk	CO ₂ : 350 vs 700 µl per litre	Root:shoot ratio: reduced slope [B]	5
			Leaf area: reduced slope [B]	
<i>Rumex obtusifolius</i>	Leaf beetles: 3% leaf area	CO ₂ : ambient vs elevated (+ 250 µmol)	Water use efficiency: reduced slope [B]	6
			Total leaf area: reduced slope [B]	
<i>Ambrosia artemisiifolia</i>	Aphid colony during 2 months	Soil N: medium (1.0 mM) vs low (0.2 mM)	Root:shoot ratio: unchanged slope, reduced elevation [A]	7
			Dark respiration: inversed slope [D]	
<i>Scirpus ancistrochaetus</i>	Clipping: 50% stem height	Neutral shade: 70% vs 37% PAR	Stomatal conductance: reduced slope [C]	8
			Root:shoot ratio: reduced slope [B]	
<i>Festuca ovina</i>	Repeated defoliation	Soil N: high (2.0 mM) vs low (0.02 mM)	Primary root diameter: reduced slope [B];	9
			Length of root axis: unchanged slope, reduced elevation [A]	
<i>Lolium perenne</i>	Repeated defoliation	Soil N: high (2.0 mM) vs low (0.02 mM)	Primary root diameter: reduced slope [B];	9
			Root:shoot ratio: reduced slope [B]	
<i>Madia sativa</i>	Clipping of apical bud	Drought: watering every 8 d vs every 4 d	Root:shoot ratio: reduced slope [C]	10
			Leaf area ratio: reduced slope [C]	
<i>Heliconia acuminata</i>	Clipping: 50% leaf area	Shade: canopy gaps vs forest understory	Root:shoot ratio: reduced slope [B]	11
			Root:shoot ratio: reduced slope [C]	
<i>Salix nigra</i>	Clipping: one-third stem height	Flooding: control vs continuous flooding	Root:shoot ratio: reduced slope [B]	12

Capital letters in brackets at the end of the fourth column [A, B, C, D] refer to the possible scenarios of constraints on plasticity outlined in Fig. 4. Only those studies with bold numbers (1–5) in the last column explicitly addressed the effect of herbivory on plasticity.

PAR, photosynthetically active radiation.

1, Kurashige & Agrawal (2005); 2, Gianoli *et al.* (2007); 3, Quezada & Gianoli (2006) (The study lacked a control environment and damage treatment; the reaction norm of damaged plants is inferred after results of similar studies in the plant species with a complete factorial design. The same applies for the next reference.); 4, E. Gianoli *et al.* unpublished; 5, Hughes & Bazzaz (2001); 6, Pearson & Brooks (1996) (there was a significant herbivory-by-CO₂ interaction, and slopes were crossed); 7, Throop (2005) (our analysis of the slopes indicated reduced plasticity, which was not concluded by the authors. The herbivory-by-nitrogen interaction was not significant, but the authors did not conduct a separate statistical analysis for aphids, which were pooled with beetles, and the analysis included three levels of soil N); 8, Lentz & Cipollini (1998) (the herbivory-by-light interaction was significant but included four levels of shading. Our analysis of the slopes indicated reduced plasticity, which was not specifically concluded by the authors); 9, Dawson *et al.* (2003) (evaluation of slopes indicated reduced plasticity following the results of a posthoc test across herbivory and soil N treatments, but this was not explicitly concluded by the authors); 10, W. L. González *et al.* unpublished (the herbivory-by-watering interaction was significant. Our analysis of the slopes indicated reduced plasticity, which was not specifically concluded by the authors); 11, Bruna & Ribeiro (2005) (the herbivory-by-habitat interaction was significant. Comparison of the slopes indicated reduced plasticity, which was not stated by the authors); 12, Li *et al.* (2005) (the herbivory-by-flooding interaction was significant. Our analysis indicated reduced slope of plants suffering light herbivory compared with undamaged plants, when considering plasticity to continuous flooding. This was implied but not explicitly concluded by the authors).

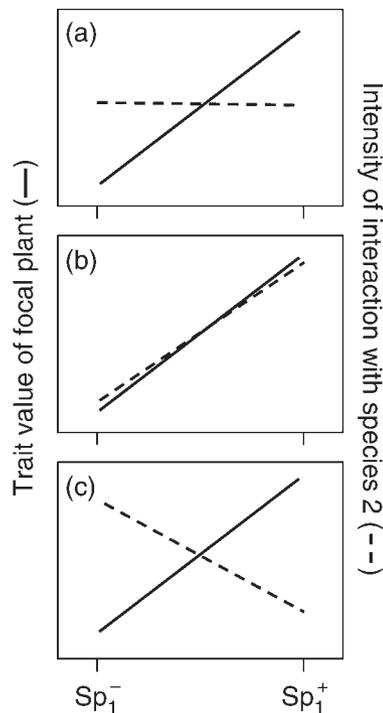


Fig. 5 Potential outcomes of the effect of one species (species 1) on the value of a trait of a focal plant (continuous line) and on its indirect, trait-mediated effect on a second species (dashed lines, representing intensity of interactions between focal plant and species 2; abundance of species 2 could be a valid surrogate of intensity of interaction in certain situations). For the sake of simplicity, the main assumption of this model is that trait value is a sole function of the presence of species 1. (a) No cost of phenotypic plasticity because changes in trait value induced by species 1 have no effect on species 2; (b) phenotypic plasticity is beneficial if species 2 is mutualist and costly if species 2 is antagonist; and (c) phenotypic plasticity is costly if species 2 is mutualist and positive if species 2 is antagonist. The shift from a situation depicted in one panel to that depicted in another one can take place as the result of a change in the identity of the interacting species, the abiotic conditions, or both.

to pollinators via changes in the plant phenotype, particularly in floral traits (see Strauss, 1997). On the contrary, phenotypic plasticity is beneficial when the modification of plant phenotype as a consequence of prior damage decreases the interaction with subsequent antagonist organisms (Fig. 5c). For example, the architectural modification caused by ungulate damage to some woody plants severely affects those insects dependent on complex structures, such as sap-suckers and caterpillars (Tschardt & Greiler, 1995; Abensperg-Traun *et al.*, 1996; Bestelmeyer & Wiens, 1996; Dennis *et al.*, 1997; Tschardt, 1997; Kruess & Tschardt, 2002a,b). Mammalian herbivores also induce the production of defensive responses by plants that could negatively affect insects (Gómez & González-Megías, 2002). Some studies have demonstrated that many insect herbivores are able to discriminate among damaged and undamaged plants (Reznik,

1991; Dolch & Tschardt, 2000). For example, experimental defoliation on alder *Alnus glutinosa*, simulating damage by ungulates, reduces consumption by the leaf beetle *Agelastica alni* (Dolch & Tschardt, 2000). Insects could also have a significant counter-effect on mammal herbivores by inducing defence responses in plants (Karban & Baldwin, 1997, and references therein). In this case, the occurrence of TMIs might change the usually asymmetrical outcome of the mammal–insect competition, because it would cause the smaller organisms to outcompete the larger ones. Unfortunately, to our knowledge, no study has yet been conducted to explore these potential indirect effects of insects on mammals via induced plant responses.

The ideas on plasticity and TMIs can be extended to situations where the first species is also a plant. For example, when the focus plant is a protégée of a nurse plant, the former modifies its phenotype in response to the latter, affecting plant quality and thus the intensity of the interaction with the herbivores. Therefore, the reasoning regarding Fig. 5 can apply equally well to the situation of species 1 being a plant, which can be beneficial (facilitation) or detrimental (competition) for the focus plant. It has been shown that certain plants can protect other plant species from herbivory (e.g. Smit *et al.*, 2007) but little is known about the role that the plastic responses of the protégée can play on the overall outcome of all the interactions involved. This is because plasticity and interactions of plants have only been addressed for direct plant–plant TMIs (Callaway *et al.*, 2003). Interestingly, plant–plant interactions have been found to exhibit an ontogenetic drift (Miriti, 2006), which takes place in parallel to the better explored ontogenetic drift in plasticity itself (Coleman *et al.*, 1994; Valladares *et al.*, 2006). Thus, future studies on the limits of plastic responses should focus not only on differences in responses between life-history stages and how this might affect competition and plant community structure and dynamics via TMIs, as suggested by Strand & Weisner (2004), but also explore how TMIs themselves change over the ontogeny of a plant. Although we have focused on the ecological consequences of phenotypic modifications triggered by animals and plants interacting with the target plant, there is also evidence that interactions with mutualistic mycorrhizal species differentially affect plant phenotype, modifying plant tolerance to herbivores (Bennet & Bever, 2007) and attractiveness to pollinating insects (Gange & Smith, 2005).

V. Plasticity and global change

Plasticity is frequently invoked in studies exploring the impact of global change on key plant species and communities (Bawa & Dayanandan, 1998; Rehfeldt *et al.*, 2001; Maron *et al.*, 2004). The importance of phenotypic plasticity as a buffer against extinction has not been widely appreciated. In fact, the extent of species' losses may have been overestimated in many simulations of distribution shifts induced by global change

because the plasticity of individuals in populations of threatened species is not considered (Thuiller *et al.*, 2005). In an environment rapidly changing on local and global scales, narrowly adapted populations with low plasticity in selectively important characters might be at a higher risk of extinction (Valladares, in press).

Various pieces of evidence suggest that global change should in principle favor high levels of phenotypic plasticity in plants (Parmesan, 2006). However, global change often involves simultaneous changes in two or more abiotic and biotic factors, which – as discussed above – may impose restrictions on plastic responses to the environment. Consequently, we observe in nature a wide range of imperfect solutions to the conflicting situations faced by plants in changing and complex environments. As shown in Fig. 5, only three interacting species can lead to a broad range of adaptive values of plasticity for the focus plant, a situation that can be further complicated by the spatial and temporal heterogeneity of the main abiotic factors. This complexity emerging from the simultaneous consideration of several species and factors, together with the interactions among them, can explain the co-existence of species with contrasting plasticities and questions the notion that plastic phenotypic responses to global change are always adaptive. Global change might alter phenotypic integration, as suggested by the uncoupling of growth, foliage dynamics and cone production induced by midterm climatic variability in a Scots pine population at its southern range (Martínez-Alonso *et al.*, in press). Thus, global change may both induce differential plastic responses in co-occurring species and influence features such as phenotypic integration that may in turn influence plasticity for certain traits.

Global change may also indirectly affect plants through effects on phytophagous insects (Hódar & Zamora, 2004), or, more generally, through pronounced effects on other co-occurring animal and plant species (Peñuelas *et al.*, 2002). Climate change has been claimed to be responsible for the range shifts northward and upward of many species in northern hemisphere ecosystems (Thuiller *et al.*, 2005), but because species differ in their sensitivity to climate, shifts vary across species and thus species interactions can be significantly modified. Furthermore, global change involves more environmental changes than just global warming and altered precipitation patterns. For instance, increased levels of CO₂ in the atmosphere involve an increase of the C:N balance of plant tissues, lowering the food quality for most herbivores. Herbivores may respond by increasing the level of leaf consumption and consequently the damage to the plant or may simply show lower performance, and the level of plant chemical defences can also be affected by a change of CO₂ (Arnone *et al.*, 1995). Warmer temperatures differentially affect co-existing species and alter the synchronizations among plants, herbivores and other interacting animals (Battisti, 2004). If damage by herbivores actually constrains the ability of plants to respond to environmental pressures, as discussed in previous sections,

then the consequences of herbivory on plant performance may scale up in a scenario of changing environments. Two important components of global change are the invasion by exotic herbivores and the increased unpredictability and stressfulness of climate. Therefore, concurrent selective pressures on plant populations by herbivory and environment can be expected to become more common and intense.

Because plasticity of many plant species might not be able to compensate for the current rate of environmental change, the option would be to take advantage of the capacity for rapid microevolutionary change. Climate change has been shown to be a potent selective factor leading to the adaptive evolution of key plant traits for an annual species in just a few generations (Franks *et al.*, 2007). However, the challenge might be out of reach for slow-growing species with a long generation time, such as trees (Parmesan, 2006; Valladares, in press). Rapid climate change coupled with habitat fragmentation is leading to intense selective pressure and decreased genetic flow, respectively, which in turn leads to a decreased genetic diversity in slow-growing species (Jump & Peñuelas, 2005). Global change is thus imposing complex and opposing selective pressures to slow-growing, long-living species, which in turn limits the extent and ecological benefits of phenotypic plasticity, modifies species interactions, and decouples climate and local adaptation, leading to an increased vulnerability to extreme climatic events and to a higher risk of mortality of trees under the new climatic scenarios (Valladares, in press).

Collectively, all these results reveal that our current knowledge about the role of phenotypic plasticity in either buffering or amplifying the impact of global change on plant species and communities is not yet enough to enhance significantly the predictions of future biodiversity scenarios because of the intrinsic complexity of the ecological limits to plasticity.

VI. Concluding remarks

It is clear that the concept of phenotypic plasticity has become an important part of modern evolutionary and ecological research (Pigliucci & Kaplan, 2006; Valladares *et al.*, 2006), and it is now recognized as central to evolution rather than a minor phenomenon, as was the case not very long ago (Sultan, 1992). We are beginning to understand the patterns and mechanisms involved in plastic responses of plants to single environmental factors, but we are still far from unraveling the pattern and extent of plasticity in ecologically realistic settings and, above all, the ecological limits and implications of the various potential responses of plants to complex, multifactor environments.

Despite the growing interest in the costs and limits of plasticity, it is widely accepted that they are difficult to demonstrate (DeWitt *et al.*, 1998). The same applies to the case of adaptive plasticity, which is taken for granted in most studies (Gianoli & González-Teuber, 2005; Ghalambor *et al.*, 2007). To understand why plasticity is not more universal we need

not only studies of fitness–plasticity relationships from gene expression to the phenotype, as recommended by van Kleunen & Fischer (2005) but also mechanistic and ecophysiological studies unveiling trade-offs and functional limits to plasticity (e.g. Atkin *et al.*, 2006). Future studies aimed at unravelling why plasticity is not more universal should be tackled with a broad ecological perspective and the experimental design should take explicitly into account the otherwise obvious realizations that species are not alone and that many environmental factors act in concert.

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