Ann. N.Y. Acad. Sci. ISSN 0077-8923

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Issue: *The Year in Evolutionary Biology*

Global change and the evolution of phenotypic plasticity in plants

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Global change drivers create new environmental scenarios and selective pressures, affecting plant species in various interacting ways. Plants respond with changes in phenology, physiology, and reproduction, with consequences for biotic interactions and community composition. We review information on phenotypic plasticity, a primary means by which plants cope with global change scenarios, recommending promising approaches for investigating the evolution of plasticity and describing constraints to its evolution. We discuss the important but largely ignored role of phenotypic plasticity in range shifts and review the extensive literature on invasive species as models of evolutionary change in novel environments. Plasticity can play a role both in the short-term response of plant populations to global change as well as in their long-term fate through the maintenance of genetic variation. In new environmental conditions, plasticity of certain functional traits may be beneficial (i.e., the plastic response is accompanied by a fitness advantage) and thus selected for. Plasticity can also be relevant in the establishment and persistence of plants in novel environments that are crucial for populations at the colonizing edge in range shifts induced by climate change. Experimental studies show taxonomically widespread plastic responses to global change drivers in many functional traits, though there is a lack of empirical support for many theoretical models on the evolution of phenotypic plasticity. Future studies should assess the adaptive value and evolutionary potential of plasticity under complex, realistic global change scenarios. Promising tools include resurrection protocols and artificial selection experiments.

Keywords: global change; phenotypic plasticity; natural selection; invasive plants, adaptive; constraints; novel environment

Global change and phenotypic plasticity in plants

Natural systems have been profoundly transformed by human activities since the nineteenth century, but over the last three decades these changes are occurring at an unprecedented rate. Fundamental questions for evolutionary ecologists in a global change context are how plant species will respond to these new and complex environmental scenarios and what mechanisms will be involved in the process.[1] Phenotypic plasticity is a proposed mechanism by which plant species may persist when faced with these rapid environmental changes.[2]

Although the term *global change* is widely used, there is no clear consensus on its definition, and many studies refer to *global change* and *climate change* indistinctly. However, a wider and more realistic definition is needed to accurately measure and predict plants' responses to global change.[3] In the context of this review, we define *global change* as any anthropogenic environmental change that alters the atmosphere, the oceans and terrestrial systems, including those changes that, although occurring

doi: 10.1111/j.1749-6632.2010.05704.x

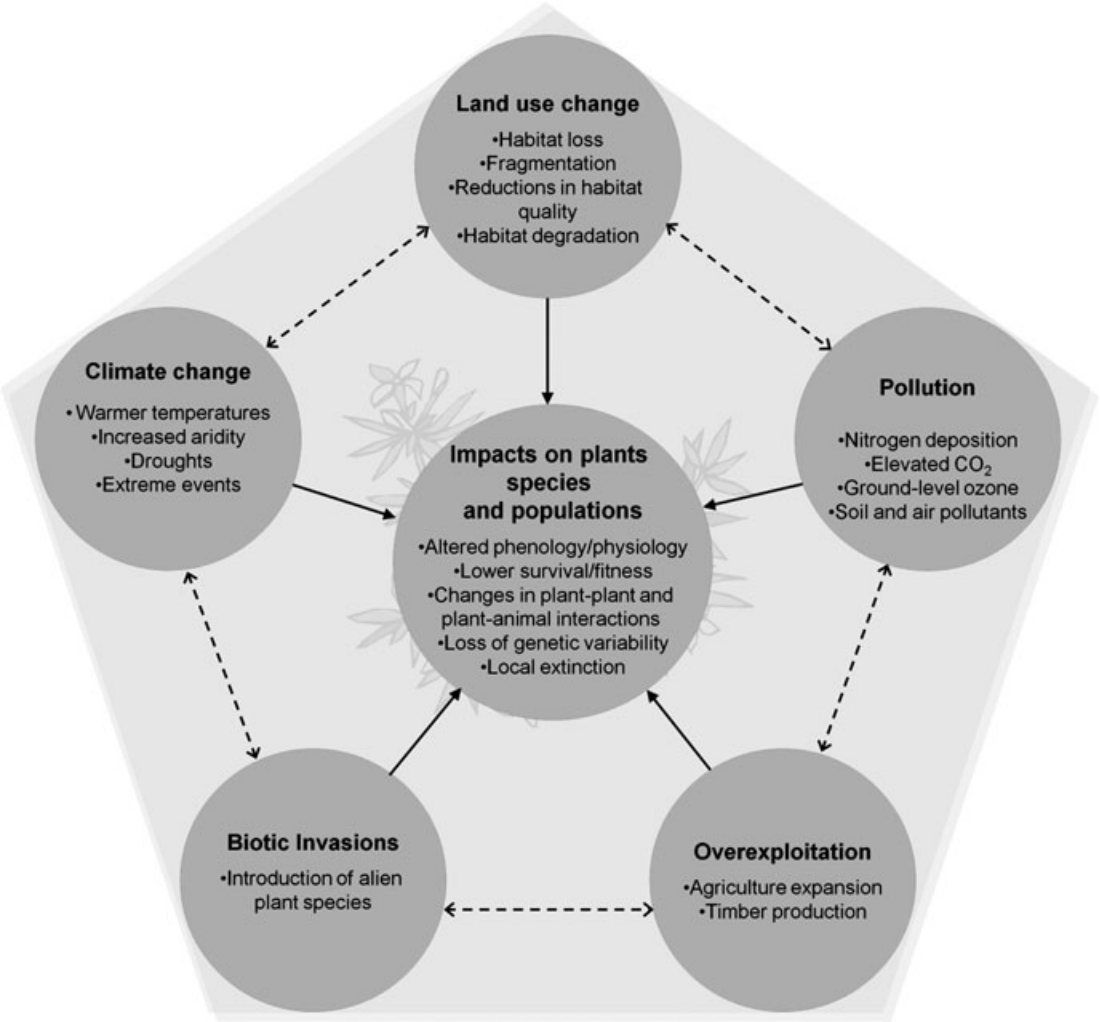

Figure 1. **Components of anthropogenic global change and their impacts on plant species and populations. The dashed arrows represent interactions between drivers and can occur between any drivers.**

locally, have global effects or are so widespread as to be considered global (e.g., land use changes) (modified from[4]). An obvious consequence of this definition is that global change does not refer exclusively to climate change. Global change components, or drivers, can be grouped in five categories:[5] climate change, land use change, overexploitation, pollution, and invasive species (see Fig. 1). These drivers of change impact plant species and communities in various and interacting ways and exert new selective pressures to which plants respond and possibly adapt.

The study of climate change–driven effects on plants has so far gained the bulk of attention. Changes in atmospheric CO_2 concentration, air and water temperatures, rainfall patterns, and even the amount of solar radiation reaching the Earth's surface have been altered owing to human activities,[6,7] and the associated impacts on plants have been extensively documented across biomes.[1,8,9] Overall, climate change has been shown to affect the phenology, abundance and distribution of plant species, and the composition of plant communities.[9,10] Other aspects of global change that have received great consideration are land use change and overexploitation, which refer to the alteration of ecosystems due to human activities like agriculture, industry, and forestry (Fig. 1). These changes

transform the landscape and cause habitat fragmentation, soil degradation, and desertification.[11,12] Since 1850, 6 million km^2 of forest and woodland surface worldwide have been cleared for croplands or extensively managed,[13] with dramatic consequences for the natural habitats of many plant species. For example, habitat fragmentation reduces the size and genetic variability of plant populations and may disrupt plant-pollinator interactions, eventually reducing individual plant fitness.[14,15]

Alongside climate change and land use changes, the introduction of alien species is considered among the greatest threats to biodiversity.[4] In Europe alone, more than 6,000 plant species have been classified as aliens.[16] Invasive species alter plant–plant interactions, reduce the abundance of or displace the native flora, and affect ecosystem functioning.[17] Finally, pollution, that is, contaminants introduced into the environment as well as naturally occurring substances—such as greenhouse gases or nitrogen—whose concentrations have increased because of human activities, can cause local extinction, affect physiology and biomass allocation and alter the composition of plant communities due to different sensitivities of species to the presence of pollutants (Fig. 1).[18]

Importantly, most plant species in natural conditions face multiple global change drivers simultaneously.[19,20] For example, plants in fragmented landscapes may also face increases in temperature or reductions in rainfall. Although the responses of plant species to interacting global change drivers remain largely unknown, there are some studies showing evidence of synergistic interactions that modify the response of plant species to multiple stresses.[3,21] For instance, Matesanz *et al.*[3] found that the interaction between fragmentation and habitat quality led to lower survival and lower relative growth in plants of the Mediterranean species *Centaurea hyssopifolia*.

Plants cope with these changing environments in different ways. One way in which plants respond to environmental variation is through phenotypic plasticity, that is, the capacity of a given genotype to express different phenotypes under different environmental conditions.[22] Plastic responses can affect the performance and reproductive success of individual plants and the ecological breadth of plant species.[23,24] Phenotypic plasticity is a trait itself and, therefore, is subject to evolution by natural selection or other evolutionary mechanisms.[22,25] If there is genetic variation for plasticity of functional traits (genotype by environment interaction),[22] and some response results in a fitness advantage, phenotypic plasticity can evolve by natural selection. Many empirical studies have shown evidence of plastic responses to key ecological factors of several functional and life-history traits, including morphology, physiology, and reproduction (e.g., Refs. 26–28). In cases where plasticity in these traits improves plant survival and reproduction, this plasticity is considered adaptive (see Section 3).[29] Phenotypic plasticity may be one of the main responses of plant populations to global change in the short term. Moreover, if there exists genetic variation for adaptive phenotypic plasticity in natural plant populations, the evolution of phenotypic plasticity may ultimately play a major role in the successful response of plants to global change.

Over the last decades, the study of phenotypic plasticity has received extensive attention from ecologists and evolutionary biologists. However, despite the theoretical and experimental effort devoted to this field, the evolution of phenotypic plasticity in plants and its implications in a global change context remain largely understudied. In this review, we address the role of adaptive phenotypic plasticity in plant adaptation to global change. We first summarize the accounts of plant plasticity in global change scenarios, particularly focusing on the studies showing evidence for selection on plasticity. We also review general studies on evolution of phenotypic plasticity in plants and discuss the insights that they provide for potential evolution of plasticity under global change. Moreover, we review the existing literature on the evolution of plasticity in invasive species, as they represent model systems to test rapid evolution in novel environments, and show how plasticity can be related to other described plant responses to global change such as range shifts. We discuss some important constraints for the evolution of phenotypic plasticity and identify promising approaches to study the evolution of plasticity. Finally, we identify key questions for future research.

Accounts of phenotypic plasticity in a changing world

As sessile organisms, plants exhibit a remarkable capacity to adjust their morphology, physiology, and

Table 1. Functional traits expected to be affected by different global change components. The traits listed under "invasive species" refer to those of the native species

Global change components	Traits expected to be affected
Land use change	Growth traits
	Phenology
	Reproductive traits
Climate change	Biomass allocation
	Phenology
	Physiological traits (Ps, g_s, WUE, R)
	Reproductive traits
	SLA
Invasive species	Biomass allocation
	Flowering morphology
	Herbivore defenses
	Phenology
	Physiological traits (Ps, g_s, WUE, R)
	Reproductive traits
	Tolerance to allelopathy
Pollution (including elevated CO_2 and N deposition)	C:N ratios, leaf N content
	Growth traits
	Phenology
	Physiological traits (Ps, g_s, WUE, R)
	Plant biomass and allocation
Overexploitation	Growth traits
	Survival

Notes: Ps, photosynthetic rate; g_s, stomatal conductance; WUE, water use efficiency; R, respiration; SLA, specific leaf area; C:N, carbon:nitrogen ratios.

reproduction to a particular set of environmental conditions by means of phenotypic plasticity. There is currently abundant evidence of plant plastic responses to global change drivers. Observed plastic responses span a broad variety of functional traits, as different components of global change affect different traits (Table 1). One of the most ubiquitous—and well studied—forms of phenotypic plasticity is the change in phenology in response to changes in climate, which has been observed in many plant species worldwide (reviewed in Refs. 1,9,30). For example, in a recent meta-analysis, Menzel *et al.*[10] reported a 2.5 days-per-decade advance in spring and summer events for 542 plant species as a response to the warming weather. Although these studies do not usually include a genetically structured sample and therefore can confound evolutionary and plastic responses, studies in phenological garden networks in which the same genotypes are observed every year show similar patterns.[31,32] As climate change elicits plastic responses in plant phenology, other global change drivers such as nitrogen deposition, elevated CO_2, habitat fragmentation, or pollution also affect plant phenology.[33,34] For example, Power *et al.*[34] found an advance in bud-burst in *Calluna vulgaris* plants that had an experimental manipulation of nitrogen availability, and Ryser and Sauder[35] found a delay in flowering date in plants growing in metal-contaminated soil. Similarly, Sigurdsson[36] reported plastic responses in the autumn phenology of seedlings of *Populus trichocarpa* as a response to a combination of nitrogen addition and elevated CO_2.

In addition to changes in phenology, many studies have documented morphological and physiological plastic responses to other components of environmental change such as drought,[37–41] light gradients,[42–46] changes in temperature,[47] elevated CO_2,[48–50] pollution,[51–54] or combinations of global change drivers.[3,43,55,56] These plastic responses range from changes at the leaf level, such as adjustments in stomatal conductance or increases in water use efficiency, to whole-plant responses, including changes in growth patterns or biomass allocation, and may be beneficial for plant performance in stressful and/or changing environments, reducing the fitness consequences of anthropogenic environmental change.[57] For example, allocation to root mass or increases in root length maximize water acquisition under drought conditions,[40,41,58,59] and advances in phenology when conditions are stressful may enable plant species to escape stress and reproduce.[60,61]

Although the mere observation of a plastic response to a given environment does not necessarily mean that this response is adaptive,[39,62] if plants achieve greater fitness in the new environment—or maintain fitness in a stressful environment—as a consequence of plasticity, then plasticity is adaptive. In such cases, plastic responses to the human-induced environmental change may alter the phenotypes without genetic change to the population,

buffering the strength of selection and consequently preventing plant populations from losing genetic variability.[57,63–65] This is of critical importance in a global change context, as the maintenance of genetic variation increases the potential for adaptation to new environments.[66] It is also noteworthy that even in the case that the plastic response does not produce an optimum phenotype in the novel environment, plasticity may allow plants to survive and establish, at least initially, under the new conditions.[63,67]

In conclusion, both observational and experimental studies show that plastic responses to environmental variation are common, not only as a response to climate change but also to other global change drivers. Moreover, phenotypic plasticity may play a role both in the short-term response of plant populations to global change as well as in the maintenance of genetic variation. Altogether, this suggests that the standing phenotypic plasticity might be an important mechanism to deal with global change.

Selection on phenotypic plasticity and global change

So far, studies on plant responses to global change have mostly focused on the role of existing plasticity—usually considering plasticity as an alternative to evolution—[20,57] or on the evolution of mean traits as a response to new selective forces.[1,9,68] We have shown evidence that plants are responding plastically throughout the world to the new environmental conditions. However, usually overlooked is the possibility that plants are evolving new plastic responses, a potentially important component of plant response to global change.[69]

Phenotypic plasticity is a trait under genetic control, and therefore is subject to evolutionary mechanisms such as natural selection or drift.[22,25,29,62] One of the most critical characteristics of anthropogenic global change is that it is leading to a completely new array of environmental scenarios that plants may have not experienced before,[70] creating new and strong selective pressures. If the new environmental conditions are different from the original conditions, some plasticity of functional traits may be beneficial and therefore selected for.[22,71]

For evolution of phenotypic plasticity by natural selection to occur, several conditions need to be satisfied. First, there is a need for environmental heterogeneity.[22] In nature, this is hardly a limitation, because constant environments, either spatially or temporally, are virtually nonexistent. This is especially relevant in a climate change context, since increases in the interannual variation of temperature and rainfall and in the frequency of extreme climatic events have been predicted for different regions.[72] Consequently, it has been proposed that there will be selection for increased plastic responses.[67,73] In this context, some studies have shown greater adaptive plasticity in plants occurring in heterogeneous environments compared to more homogeneous ones,[39,74–76] suggesting that the evolution of phenotypic plasticity can indeed be favored in heterogeneous environments as long as the environmental cues that promote the plastic response remain reliable and plastic responses can take place on time (see Section 6).[22,69]

Second, phenotypic plasticity of functional traits can evolve only when there is within-population genetic variation for plasticity in the functional traits, that is, different genotypes respond differently to the same set of environments. Many studies have reported genetic variation for plasticity, measured as the genotype-by-environment interaction.[45,74,77–80] Recent studies have also shown that a certain amount of cryptic genetic variation may exist in plant genomes, being expressed when the organism encounters rare or novel environments.[81,82] The concept of the "hidden reaction norm" arises from the idea that parts of these unexpressed sources of variation would be expressed when environmental change occurs (see Ref. 81; Fig. 2 for a graphical example). This hidden genetic variation may play a critical role in phenotypic evolution to global change, as it may modulate the potential for evolution to novel environments.

Third, and most importantly, for plasticity to be adaptive, and therefore selected, it needs to have an impact on plant fitness. There are now numerous examples showing evidence of adaptive plasticity as a response to different environmental factors.[27,39,40,44,45,74,77–80,83–85] For example, Heschel *et al.*[40] found that plastic responses in water use efficiency were adaptive under drought conditions in the species *Polygonum persicaria*, and in a recent study, van Kleunen *et al.*[85] found that plastic responses of morphological traits of *Ranunculus reptans* to flooding were adaptive and had evolved in response to direct selection on plasticity.

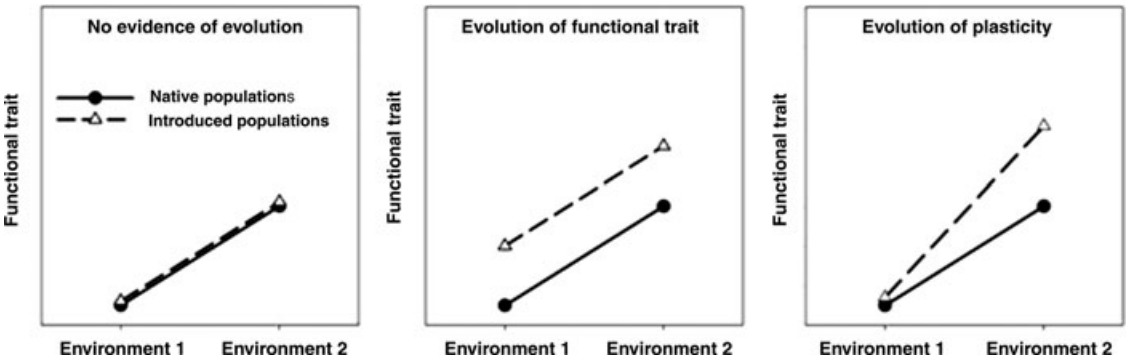

Figure 2. Evolution of a functional trait and its norm of reaction after the introduction of alien species.

Some global change scenarios may alternatively lead to the evolution of reduced plasticity. For instance, there may be certain functional traits for which the expression of a flat norm of reaction in a specific set of environments is adaptive. For example, maintaining high photosynthetic rates in both moist and dry conditions is likely to be adaptive in both environments. If there is genetic variation for plasticity in the population, the genotypes expressing the most canalized (flat) norm of reaction will be selected, that is, evolution of reduced plasticity.

Similarly, evolution of reduced plasticity may occur through genetic assimilation. Plasticity may initially allow the establishment of a plant species in a new environment (see Section 4). Over time, selection will favor the most successful phenotype in the new environment and, if the original environment is not experienced anymore and/or there are costs to plasticity, genetic variation for plasticity (and for mean traits) may be lost from the population.[63,66,67,71,86] If low gene flow limits the arrival of new genetic variation into the population, this process will compromise the potential for adaptation of the population to further changes in the environment.[66,67] For example, a prolonged (more than one season) and intense drought may act as a strong selection force in a population of an annual species, quickly favoring genotypes that have higher fitness in the dry environment, therefore removing genetic variability from the population. Besides increased inbreeding,[15] reduced genetic variability will also affect the persistence of the population in moist years and microhabitats.

A survey of the literature leads to two main conclusions. First, studies showing adaptive plastic responses are usually performed in simple environments varying mainly in one or two abiotic factors such as light and water. As we have shown in Section 2, plastic responses to other global change drivers like elevated CO_2 or nitrogen availability have been addressed in a number of studies (e.g., Refs. 50,87–90), but hardly any of these studies have tested whether these plastic responses are adaptive by assessing fitness consequences (but see Refs. 83,91,92). Second, plasticity is in itself a trait that can evolve as a response to environmental variation, and there is some evidence that plasticity may be adaptive and selected for. Moreover, there is evidence that there can be cryptic genetic variation that could be expressed in novel global change scenarios. This, together with the predicted increase of the environmental heterogeneity, suggests significant opportunities for selection on plasticity under global change. Therefore, it becomes clear that phenotypic plasticity may play a relevant role both in short-term responses but also in plant adaptation to global change. However, it also stands out that our understanding of the potential for evolution of phenotypic plasticity as a response to global change is still very limited, primarily because of the lack of experimental data testing the predictions from the numerous theoretical studies on this subject.[93] Future research should be aimed at empirically testing whether plasticity is adaptive in different global change scenarios, including more complex and novel environments where different stresses occur simultaneously (see Section 7 for promising approaches to study the evolution of plasticity).[20]

Phenotypic plasticity and range shifts

One of the most documented responses of plant species to climate change are range shifts, that is,

the dispersal or migration of plant species toward higher latitudes and altitudes, where environmental conditions are more similar to environments in the species' historic range,[94–98] and great effort has been devoted to the simulation and prediction of future species distributions and local extinctions.[99,100] Although such simulations are very helpful in a global change context, an important limitation is that they often fail to account for the role that phenotypic plasticity may play in the persistence and later adaptation of plants to novel environments.[99,100]

Phenotypic plasticity may play an important role in the establishment of plant populations in novel environments, either after colonization of a new habitat or as a response to change in the *in situ* environmental conditions.[22,71,74] If plasticity has evolved as a response to environmental heterogeneity in a specific habitat, and this within-habitat variation resembles the differences between two different habitats, plasticity may allow the establishment and persistence of the population in the altered environment.[74] For example, plasticity may evolve in a population as a response to spatial (different microhabitats) or temporal (seasonal) heterogeneity in water availability. If some of the genotypes from this population colonize a consistently drier (or moister) habitat and are able to express plastic responses that lead to functional (although maybe not the fittest) phenotypes, plasticity may allow them to persist.[101,102]

In the same context, phenotypic plasticity may further facilitate local adaptation to novel habitats that arise as a result of global change.[63] For example, if the colonizing genotypes express a suboptimal phenotype in the new environment,[22] directional selection will favor the phenotypes closest to the optimum in the new environment, therefore facilitating adaptation to the new conditions.[63,65] As we have mentioned in Section 3, plasticity may or may not be lost after establishment in the new conditions.[63]

Similarly, plasticity may also favor adaptation to new environments by limiting gene flow between the original and the newly colonized population. In a recent study, Levin[103] showed that individuals colonizing new habitats often experience plastic phenological shifts, delaying or advancing flowering and reproduction in response to the new conditions. This environment-driven change in flowering time results in assortative (nonrandom) mating within populations, reducing gene flow between populations and promoting the evolution of local adaptation in a newly colonized environment.

In this context, it is noteworthy mentioning that plasticity may also be relevant as an indirect response to global change. For example, if a plant species shifts its distribution to track changes in climate, it might be exposed to other new environmental conditions to which it may also respond plastically. For example, a plant species may migrate northward to keep the climatic conditions constant. However, soil features and the composition of the plant community in the new environment may be different, as species differ in the ability to track changes in climate.[100–104] Thus, species interactions and soil nutrient availability can be rather different in the new environment, despite similarities in climate.

Alongside the role of plasticity in colonization and adaptation to novel environments, the evolution of phenotypic plasticity may be critical for the persistence of plant populations in complex scenarios where different global change drivers interact. In cases where opportunities for dispersal and distribution shifts are limited by natural barriers or habitat fragmentation, rapid adaptation may be necessary to prevent extinction of plant species subject to global change[1,70] For example, in fragmented or alpine habitats where dispersal and migration to other favorable sites are limited or even prohibited, evolutionary processes, including the evolution of plasticity, play a more important role in adaptation to changing environmental conditions.[61,67]

Another relatively unknown form of plasticity that may be beneficial in these situations is transgenerational plasticity, that is, the effects of the maternal environment on the development of the offspring. Some studies have reported adaptive transgenerational plasticity when the maternal and the offspring environments are correlated.[105] For example, in a recent study, Sultan *et al.*[59] found that drought-stressed plants of *Polygonum persicaria*, a plant that occurs in a wide variety of moisture conditions, produced offspring that grew longer roots and greater biomass when grown in dry conditions.[59] Similarly, it has been shown that once they find physical support, *Ipomoea purpurea* twining vines develop thicker stems and shorter internodes compared to prostrate vines, and the attained phenotype is associated with better performance;[106] interestingly, the offspring of supported mother plants also

showed thicker stems and shorter internodes than those of unsupported plants.[107]

The role of phenotypic plasticity in colonization and adaptation has important consequences for simulations of changes in species distributions and predictions of local extinctions due to global change. Phenotypic plasticity not only allows colonization and adaptation to novel environments but also may be very beneficial in critical situations where dispersal is limited. Altogether, this suggests that the projections of shrinkage of species ranges or local extinctions may be overestimated or misleading. Future research should be aimed at combining multispecies studies on range shifts with focused studies that incorporate the role of plasticity.

Phenotypic plasticity and invasive species

Biological invasions have long been considered a widespread component of human-caused global change.[4] The number of plant species accidentally or purposely transported by humans across continents has significantly increased in the last centuries.[17] Some of these species become abundant in their introduced range and spread rapidly across diverse habitats, outcompeting native species, changing the structure and functioning of native plant communities, and causing both environmental and economic problems.[108,109]

Despite the enormous effort over the last two decades dedicated to the study of invasive plant species, the evolutionary mechanisms that lead to invasiveness in introduced species remain unclear in many cases.[110] It is commonly thought that if a species is able to maintain fitness across a broad variety of environmental conditions it is more likely to become invasive.[71,111] A major way that plants achieve this kind of niche breadth is by means of adaptive phenotypic plasticity.[24,74,112] Two main nonexclusive hypotheses have been posed to explain the role of phenotypic plasticity in plant invasions.[71,113] First, invasive species may be more plastic than native or alien noninvasive species, and second, invasive populations may be more plastic compared to populations in the native range. The last hypothesis is especially interesting as it allows for tests of the evolution of phenotypic plasticity in the introduced range.

To test the first hypothesis, previous studies have compared plasticity and performance of invasive and native species (reviewed in Refs. 71,114). Some studies used related species to compare the differences in plasticity between native and introduced species to account for the phylogenetic history of the species. While several studies support the idea that invasive species are more plastic for physiological and morphological traits affecting fitness in response to ecologically relevant environments than their native counterparts,[71] recent evidence challenges the generality of this pattern (Gianoli, personal communication).[115,116]

It has also been hypothesized that invasive species are able to undergo rapid evolutionary change.[117–120] Invasions of novel environments usually involve changes in selection forces that may lead to evolutionary change.[118,119] In this context, rapid evolution of plasticity may play an important role in the success of introduced species in introduced habitats if plasticity in functional traits is accompanied by a fitness advantage in the novel environment.[71] Alternatively, phenotypic plasticity may grant initial survival in novel habitats, and then natural selection could operate at the local scale, driving evolution of ecotypes (see Section 4).[121]

As mentioned before, an experimental approach to test for the evolution of plasticity in invasive species is the comparison of a sample of populations of a particular species from both the introduced and the native range.[71,120] In the introduced range, selection may act on mean trait values and/or on the plasticity of functional traits, that is, it may drive the evolution of both the elevation and the slope of the reaction norm (Fig. 2). While a number of studies have focused on differences in mean functional traits between populations of different origin (e.g., tests on the evolution of increased competitive ability, EICA hypothesis[122,123]), only a few studies have compared patterns of phenotypic plasticity in native versus introduced populations (Table 2). These studies span a wide variety of taxa and growth forms and assess changes in plasticity to several ecologically relevant factors such as water, light and nutrient availability, soil pH, and presence of predators. While all studies showed significant plastic responses of the invasive species from both the native and introduced range, there is no clear pattern as to whether phenotypic plasticity is higher in introduced populations, as only half of the studies showed evidence for an increased plasticity in the populations of the introduced range. Moreover, the observation of increased plasticity

Table 2. Evidence of changes in phenotypic plasticity in introduced versus native populations of invasive plant species

Species	Growth form	Number of populations	Experimental treatments	Functional traits measured	Fitness traits measured	Evidence of changes in plasticity	Reference
Cynoglossum officinale	Biennial herb	10 native/10 introduced (N)	3 levels of nutrient availability	Plant size and flowering date	Plant fecundity	Phenotypic plasticity for size and fecundity was higher among introduced populations, but due to founder effects	126
Taraxacum officinale	Annual herb	2 native/2 introduced (N)	2 levels of water and 3 levels of nutrient availability	Biomass and root:shoot ration	Survival and reproduction	No evidence of increased plasticity in the introduced populations	176
Sapium sebiferum	Tree	5 native/5 introduced (N)	4 combinations of water and light availability	Height growth, leaf area, leaf biomass, and aboveground biomass	–	Increased plasticity of leaf area and biomass to light in the introduced range	113
Senecio inaequidens	Perennial herb	12 native/11 introduced (N)	4 levels of nutrients availability and presence of aphids	Branch number and shoot and root biomass	Flower number	Increased plasticity of root biomass to fertilization in the introduced range	124
Senecio pterophorus	Perennial shrub	4 native/4 introduced (N)	4 levels of disturbance and water availability	Leaf morphology, chlorophyll fluorescence, and reproduction	Plant fecundity	Increased plasticity of morphological and reproduction traits to disturbance and water availability	129
Mimulus guttatus	Perennial herb	17 native/7 introduced (Y)	2 levels of water availability	Growth	Plant fecundity	No	128
Phalaris arundinacea.	Perennial grass	6 native/6 introduced (N)	Moisture gradient	Stem height, tillering rate, and leaf number	–	Increased plasticity of morphological traits to water conditions in the introduced range	110
Hypericum perforatum	Perennial forb	18 native/17 introduced (N)	Cross-continental common gardens	Leaf physiology and morphology	Plant fecundity	No	125
Clidermia hirta	Perennial shrub	4 native/4 introduced (N)	2 levels of light availability	Growth rate, biomass allocation, and physiological traits	–	No	177
Melaleuca quinquenervia	Tree	3 native/4 introduced (Y)	6 levels of water availability and pH	Seedling biomass and growth rate	–	Increased plasticity to soil pH in the introduced range	127

Notes: Also shown are species name, growth form, sample size, treatments, and traits measured. Only studies specifically assessing changes in phenotypic plasticity are included. (Y) and (N) indicate whether within-population genetic variation for plasticity was or was not quantified, respectively.

in the introduced populations does not necessarily mean that plasticity has evolved as adaptation after the introduction.[124] Other processes such as the filtering of genotypes that are not preadapted or founder effects may account for higher plasticity in the introduced range.[125,126] For example, Bossdorf *et al.*[124] found greater plasticity for root biomass as a response to fertilization in the introduced populations of *Senecio inaequidens*, but they were also less genetically variable and similar to a group of the native populations, suggesting that plastic preadapted genotypes from the native range have been able to invade the introduced range, without undergoing adaptive evolution of plasticity, that is, although strictly speaking the population has evolved, there has not been adaptive evolution in the population, as the surviving genotypes were already present in the population.

In this context, it is also worth mentioning that plasticity may evolve in the introduced range, but the resulting plasticity does not necessarily need to be higher than in the native populations. As we have mentioned in Section 3, there may be functional traits for which the expression of a flat norm of reaction is adaptive. This suggests that the expected outcome of these comparisons does not necessarily need to be evolution of increased plasticity, as it is both trait and environment dependent. Formal tests of whether the change in plasticity translates into fitness advantages and knowledge of the introduction history and genetic relatedness of the populations may help to elucidate whether plasticity has evolved in the introduced range.

Surprisingly, only the studies by Kaufman and Smouse[127] and van Kleunen and Fischer[128] assessed within-population genetic variation for phenotypic plasticity (Table 2), that is, differences in plasticity among genotypes (maternal families) within each population. Both found significant genetic variation for phenotypic plasticity. It is generally recognized that increasing the number of sampled populations at the expense of maintaining maternal families within each population results in a better knowledge of the differences in plasticity between the introduced and the native range of the invasive species.[71,129] Maintaining maternal families within each poulation require that different replicates (siblings or clones) of the same genotype (maternal family) are assigned to the different experimental environments—as opposed to creating a seed mixture for each population—therefore significantly increasing the size of the experiment. However, the evolutionary implications of within-population variability highlight the need for studies accounting for this source of variation. As outlined in previous sections, within-population genetic variation for plasticity ($G \times E$) is a measure of its potential for evolution in the population. This parameter can aid in understanding the dynamics of the invasive species in the introduced range and its potential for adaptation to new environmental conditions.

Finally, the invasive species also represents new environments for the native species, and might thus affect the evolution of plasticity in native species.[64] For example, Lau[130] found that the exotic plant *Medicago polymorpha* and an exotic herbivore altered the strength and direction of natural selection on the competitive ability and antiherbivore defenses of the native plant *Lotus wrangelianus*. Evolution of plasticity in the native species in traits involved in the persistence in invaded communities may therefore be a critical component of the evolutionary response of native plants to invasive species.

Constraints on the evolution of phenotypic plasticity

The expression and evolution of phenotypic plasticity in plants may be limited by both intrinsic and extrinsic factors, which have been extensively listed and discussed (See Refs. 62,102,131–135; see Valladares *et al.*[2] Fig. 1 for a summarizing scheme). Moreover, evolution of phenotypic plasticity, being itself a trait,[78,136,137] is subject to the typical constraints to evolution of any phenotypic trait, which has been comprehensively studied.[138–141] We will focus here on two constraints to the evolution of plasticity in plants. The first one limits the expression of phenotypic plasticity and hence its possibility of being a target of natural selection. This constraint is phenotypic integration—the network of character correlations—and, to our knowledge, it has not been explicitly considered in earlier lists of costs and limits of phenotypic plasticity. The study of phenotypic integration as a likely constraint to the evolution of plasticity may be relevant in the context of global change because of the simultaneous occurrence of potential selective factors—namely global change drivers—that affect different target traits that could

be correlated. The second constraint is related to the adaptive value of phenotypic plasticity in the novel environment in connection to the environmental cue triggering the plastic response. This is one of a few specific unambiguous plasticity costs, that is, distinct from those ascribable to any phenotypic trait. Addressing the relationship between environmental heterogeneity and phenotypic plasticity has significant bearing on global change research in view of the unpredictability of developing climatic regimes.

Phenotypic integration refers to the pattern and magnitude of character correlations[142] and is usually estimated as the number of significant phenotypic correlations between traits.[102,143,144] A classic study on phenotypic integration by Berg[145] showed a decoupling between correlation pleiades of reproductive and vegetative traits in several herbaceous plants. Such patterns of trait variation and covariation may be a consequence of correlational selection or, alternatively, of the genetic/developmental architecture of the organism.[146] It has been recently shown that phenotypic plasticity may be inversely related to phenotypic integration. Gianoli and Palacio-López[147] reported for the perennial species *Convolvulus chilensis* and *Lippia alba* that plasticity of a given trait to shading and drought, respectively, decreased with the number of significant correlations that it had with the other phenotypic traits. The notion that phenotypic integration might constitute an internal constraint to phenotypic plasticity was suggested in earlier studies,[2,106,137,143,148,149] but experimental evidence has been lacking. This finding reveals an apparent tradeoff between two essential features of organism functioning, namely flexibility and coherence, whose evolutionary implications should be further investigated,[147] particularly if phenotypic correlations reflect genetic correlations, as has been shown for several plant species.[150] Progress in this area requires a better understanding of the ecological and evolutionary significance of phenotypic integration, which can be viewed as a constraint as well as an adaptation.[151] While there is some evidence of pollinator-mediated selection on intrafloral integration (Ref. 152, but see Ref. 153), evidences of the adaptive value of phenotypic integration at the whole-plant level are lacking. It has been reported for several plant species that phenotypic integration increases with environmental stress,[75,143,154–156] but it is currently unknown whether this pattern reflects a functional response or it is merely a stress symptom. Furthermore, in order to gain insights into the nature (and possibly, hierarchy) of relationships between traits in the context of phenotypic plasticity, we need a—not yet available—tractable quantitative framework where the outcome of the complex network of interactions among characters and the environment may be represented in multivariate phenotypic space (see Ref. 157).

For plasticity to be adaptive there should be a good match between the attained phenotype and the environment. Consequently, phenotypic plasticity will not be adaptive when the environmental cues eliciting plant responses are unreliable, that is, when these cues are not significantly associated with the environment of selection.[76,132,158–160] Such a mismatch may occur when the response time of the trait is similar to or longer than the duration of the environmental state that triggered the response. This is more relevant for developmental plasticity, which is hardly reversible, than for physiological responses, which may be reversed over short time scales. When should temporal heterogeneity select for phenotypic plasticity? Pigliucci[22] provides a thoughtful analysis of evolutionary outcomes regarding plasticity in the presence and absence of environmental cues and depending on the duration of temporal fluctuation as compared to generation time. Empirical support for these theoretical expectations is needed.[22] In fact, at this point there is little quantitative evidence for a significant and positive relationship between temporal environmental heterogeneity and phenotypic plasticity in plant populations. Table 3 shows nine studies where this relationship was evaluated or could be inferred, and in five cases it was verified, although not all of these five cases reported adaptive phenotypic plasticity. We stress the need to gather more empirical information on the relationship between temporal heterogeneity and phenotypic plasticity, which perhaps has been overtheorized, in order to adequately address some basic issues: (1) Under which conditions is this relationship verified? (2) Which is the more relevant temporal scale selecting for plasticity, within-year or between years? and (3) Does growth habit influence this hypothesized relationship? Table 3 shows that all four perennials verified the hypothesis, but this evidence is clearly insufficient to draw any conclusion. These issues are particularly

Table 3. Studies evaluating phenotypic plasticity in plant populations with contrasting temporal environmental heterogeneity[a]

Species	Growth form	N pop	Environmental factor/ Heterogeneity scale	Plant traits	Result	Adaptive phenotypic plasticity?	Reference
Convolvulus arvensis	Perennial herb – weed	2	Soil moisture/ Within year	Leaf and stem morphology; shoot biomass; flowering time; seed size and number	Greater plasticity in the population from the more variable habitat	Yes	75
Convolvulus chilensis	Perennial herb	3	Soil moisture/ Between years	Leaf morphology; foliar trichome density	Greater plasticity in the population from the more variable habitat	Yes	39
Ranunculus flammula	Perennial herb	10	Water level/ Between years	Heterophylly (blade:petiole width above water / blade:petiole width below water)	Degree of heterophylly positively associated with habitat heterogeneity	Yes	178
Taraxacum officinale	Perennial herb – weed	2	Soil moisture/ Within year	Photosynthetic performance; flowering time	Greater plasticity in the population from the more variable habitat	No	179
Polygonum persicaria	Annual – weed	2	Light intensity/ Between years	Photosynthetic rate; leaf morphology; biomass allocation; plant biomass; fruit number and size	Similar plasticity in both populations[b]	Yes	45
Polygonum persicaria	Annual – weed	2	Soil moisture/ Between years	Leaf morphology; biomass allocation; plant biomass; fruit number and size	Similar plasticity in both populations[b]	Yes	41
Polygonum persicaria	Annual – weed	3	Soil moisture/ Within year	Photosynthetic rate; stomatal conductance; water use efficiency; leaf size; biomass allocation; # fruits	Similar plasticity in all three populations	Yes	40
Abutilon theophrasti	Annual – weed	4	Late-season neighbor shade/ Within year	Internodes length at later growth stage	Greater plasticity in the population from the more variable habitat	Yes	76
Solanum ptycanthum	Annual – weed	4	Soil nutrients/ Between years	Shoot morphology; biomass allocation; life history traits	Similar plasticity in populations from two contrasting habitats	Yes	180

[a] *Adaptive phenotypic plasticity* refers to positive associations between plasticity and plant fitness, or congruence between phenotypic patterns and ecophysiological predictions regarding optimal resource allocation/exploitation. ***Yes*** indicates that adaptive plasticity was verified at least for one plant trait.
[b] The authors did not compare plasticity levels between populations. Outcome inferred after statistical comparison of F-ratios.

important in view of the rapid rate of climate change and complex pattern of environmental variation associated with its strengthening, which includes increased unpredictability in within-year and between-years regimes of rainfall and temperature, and increased frequency of extreme climatic events.[72] A comprehensive understanding of the ecological scenarios under which plasticity can evolve and what factors may constrain its evolution will help us to estimate the chances of plant species and populations to successfully cope with the current rapid rate of global environmental change.

Promising approaches to test for the evolution of phenotypic plasticity

The evolution of phenotypic plasticity has been treated extensively in the literature from a theoretical standpoint.[131,159,161–168] How should we experimentally approach the evolution of phenotypic plasticity in plants in the context of global change? Here, we advocate the use of two particularly promising approaches to test for the evolution of phenotypic plasticity: artificial selection and resurrection experiments. We recommend these methods because they both involve experimental tests of the evolution of plasticity, and because they allow determining whether evolution has occurred and the presence of genetic variation for plasticity.

Selection experiments can be classified in two categories: artificial selection and quasi-natural selection.[93] In an artificial selection experiment, a specific and known selective force is imposed on a phenotypic trait (or on phenotypic plasticity as a trait itself) by selecting those individuals that show extreme values for the trait.[93,169,170] In contrast, in a quasi-natural selection experiment, specific environmental conditions are established and selection acts on the whole organism, that is, evolution occurs as a function of fitness. Studies selecting for phenotypic plasticity require the estimation of phenotypic plasticity by measuring a target trait and the plasticity of that trait across environments (more than two is best) in replicates of the same genotypes. There are a number of limitations associated with such experiments. For example, it is not feasible to perform artificial experiments using species with long juvenile periods. Also, in the case of fast-growing annual species, the high amount of resources required to perform long-term experiments can be a constraint. Despite these limitations, artificial selection is the best way to determine if and how fast a target trait will evolve under a given strength of selection.[20,93,169,170] It also allows testing for the ability of species or populations to adapt to novel environments, and therefore, this approach may be very useful to test the short-term evolutionary effects of global change on plants.

Table 4 reports results of artificial selection studies assessing the evolution of phenotypic plasticity in plants, either when measured as a correlated response or as the target of selection. The number of studies available is quite limited, probably owing to the fact that the design, protocols, and interpretation of the results of these studies can be extremely challenging.[169] It is noteworthy that many studies focus on model plants like *Arabidopsis thaliana* or other Brassicaceae relatives. More than half of the studies showed either low heritability of plasticity compared to mean trait heritability, or no response of plasticity to selection whatsoever. These results may be due to a combination of different factors. First, initial genetic variation for plasticity in the base populations may be low (i.e., studies showing low heritabilities), which may drastically limit the potential for evolution. Second, the number of generations included in these studies is usually low (in most cases three or fewer), which may also limit the capacity to observe a response to selection.[62] Finally, there may be limits and costs of plasticity constraining its evolution (see Section 6).[62,93] More studies are required to assess the response of plasticity to selection by global change drivers, including long-term studies assessing the potential for evolution of nonmodel species in complex and realistic global change scenarios.

An emerging approach to test for the evolution of plasticity is the use of resurrection experiments,[68] which allow for comparisons between plant genotypes from different generations within the same populations, stored as seeds, and grown simultaneously under controlled conditions. There are some limitations inherent to this approach, such as the confounding effects of gene flow or the possibility that the genotypes sampled at each generation are a biased sample of the population (owing to interannual variations in climate and/or persistent seed banks[68]). However, this protocol can provide some evidence of evolutionary change within natural populations over a known period of time. In this regard, preliminary results of a series of resurrection

Table 4. Artificial selection studies (including quasi-natural selection) on plants[a]

Species	Growth form	Evolution in response to?	Traits under selection	Number of generations	Results	Reference
Nicotiana rustica	Annual herb	Different sowing dates	Flowering date and height. Selection on both trait means and their plasticities	2	Lower realized heritability of plasticity compared to that of the traits mean. Mean trait value and plasticity were positively genetically correlated	181
Brassica juncea	Annual herb	Increased CO_2 concentrations	Fruit biomass. 14 morphological and reproductive traits in common garden after selection	7	Small evidence of evolutionary response of the measured traits or adaptive plasticity	182
Plantago lanceolata	Perennial herb	Light quality environments	Leaf length	4	Selection for leaf length affected plasticity in seed germination. Evidence that plasticity can evolve as a correlated response to mean trait values	183
Sinapis arvensis	Annual herb	Several abiotic stresses (low nutrients, low water, low light, etc)	Plant fecundity	3	Evidence of evolution of trait means that enhanced fitness in stressful habitats, but plastic responses to stress conditions were not consistent with adaptive phenotypic plasticity	184
Ranunculus reptans	Clonal herb	Competition with a coexisting species	Allocation to reproductive biomass an its plasticity	2	High heritability and potential for further evolution of the proportion of flowering rosettes but not for its plasticity	185
Ranunculus reptans	Clonal herb	Competition with a coexisting species	Growth form and its plasticity	2	No significant direct response of plasticity	186
Arabidopsis thaliana	Annual herb	Light quality environments	Plasticity in leaf number	3	Evidence of moderate evolution of plasticity	187

[b]Selection environments, traits target of selection, and number of generations of selection are also shown. Only studies assessing evolution of plasticity (either as the focal trait or as a correlated response) are shown. See Reusch *et al.*[20] for a review of selection experiments simulating global change selecting on mean traits.

experiments suggest the potential for rapid evolution in the increasingly invasive annual *Polygonum caespitosum* (s.l.), introduced in North America. One experiment compared genotypes collected from the same three field populations in 1994 and in 2005 grown at ambient and elevated CO_2 concentrations at a Free Air Concentration Enrichment (FACE) site. Although there was no evidence of recent evolution for the number of fruits each plant produced, plants from two of the populations had evolved to produce larger fruits in both CO_2 treatments, with a more pronounced increase in plants grown at elevated CO_2. Results also suggest that both physiological and life-history traits are evolving rapidly in populations of this species in ways that affect performance in ambient but not elevated CO_2 conditions (T. Horgan-Kobelski, S.E. Sultan and S.P. Long, unpublished data).

In conclusion, despite their limitations, the two proposed approaches can be very useful to understand whether plasticity has evolved as a response to the change in environmental conditions but also can shed light on the evolutionary potential for plant phenotypic plasticity to enhance performance under global change scenarios.

Concluding remarks

The aim of this review was to understand phenotypic plasticity of plants in a global change context. We have shown that plastic responses to global change scenarios are abundant and occur at different levels across individuals, populations, and species. However, evidence of adaptive plasticity remains scarce, particularly under novel environmental conditions. The understanding of phenotypic plasticity—and particularly of its evolution—in a changing world is still very limited, primarily because of the lack of experimental data. Future research should aim at filling this gap with experimental rather than theoretical studies, testing for adaptive plasticity as a response to complex and realistic environments. In this context, field studies are crucial to understand the complex environments where plants evolve. This knowledge, together with the predictions of climatic conditions that plants will face in the future can be used as the basis for controlled common garden experiments. Also, we want to stress the importance of a reliable genetic sampling within populations to understand the potential for evolution of plasticity. In this sense, comparisons of less than six to eight genotypes per population may lack the statistical power to detect differences in mean traits and plasticity across genotypes.[40]

Important questions involving promising future research emerged from this review. A relatively unexplored field in the context of phenotypic plasticity and global change is to understand whether populations of different cooccurring species have different genetic variation for plasticity and thus have different potential for evolution of plasticity as a response to the same changing environment. This may have important consequences as it may affect plant–plant interactions and alter plant community composition, as some species are likely to express and evolve plasticity faster than others. Multispecies comparisons of plasticity patterns with a good population sampling can provide relevant information in this regard (see Ref. 171 for a discussion on comparisons of plasticity patters across species).

Finally, a paramount question in the face of plant adaptation to global change that still remains open and controversial is whether phenotypic changes are due to plasticity, genetic change, or a combination of both. As we have shown, plasticity may prevent evolutionary change by shielding populations from natural selection[172] but also may promote evolution.[63,173] We have also shown that global change is leading to important phenotypic changes, and it has been suggested that the rate of environmental change imposed by human activities is so rapid that most phenotypic changes observed in natural populations are due to plasticity.[57] But plasticity itself and its potential for evolution is challenged by global change. Global change typically involves simultaneous changes in several environmental factors, usually imposing multifactor stresses (e.g., extreme temperatures and altered water and nutrient availabilities), and plasticity is expected to be limited by several cooccurring stresses.[2,42] In this regard, studies of climate change effects on birds are particularly illustrative. These studies show contrasting results: while Visser (see Ref. 174 for a synthesis) concluded that phenotypic plasticity is not sufficient to keep up with a warming world, Charmantier *et al.*[175] showed that plastic behavior enabled the great tit to track rapid climatic changes very closely. It is thus clear that more empirical information is needed to interpret the evolutionary implications of the large contribution of phenotypic plasticity to the rapid

phenotypic changes already observed in response to global change.

Acknowledgments

The authors would like to thank Tim Horgan-Kobelski and Sonia Sultan for the data presented in this manuscript and for the fruitful discussions about phenotypic plasticity. SM was funded by a Marie Curie IOF fellowship (7th Framework Programme EC-PEOPLE-IOF-2008). Funding was provided by Acción Bilateral Convenio CSIC-CONYCIT (2007CL0031) and by the grants REMEDINAL-CM (S-0505/AMB/000335) and CONSOLIDER Montes (CSD 2008-000400) from the Spanish Ministry of Science and Innovation.

Conflicts of interest

The authors declare no conflicts of interest.

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