

## Review Article

# Plant Phenotypic Plasticity in Response to Environmental Factors

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Received 8 December 2013; Revised 21 February 2014; Accepted 24 March 2014; Published 22 April 2014

Academic Editor: Shoji Mano

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Plants are exposed to heterogeneity in the environment where new stress factors (i.e., climate change, land use change, and invasiveness) are introduced, and where inter- and intraspecies differences may reflect resource limitation and/or environmental stress factors. Phenotypic plasticity is considered one of the major means by which plants can cope with environmental factor variability. Nevertheless, the extent to which phenotypic plasticity may facilitate survival under environmental condition changes still remains largely unknown because results are sometimes controversial. Thus, it is important to identify plant functional traits in which plasticity may play a determinant role in plant response to global change as well as on the ecological consequences at an ecosystem level for the competition between wild and invasive species, considering that species with a greater adaptive plasticity may be more likely to survive in novel environmental conditions. In the near future, it will be important to increase long-term studies on natural populations in order to understand plant response to environmental factor fluctuations including climate change. There is the necessity to analyze variations at phenotypic and genetic levels for the same species and, in particular, for endemic and rare species because these could have drastic effects at an ecosystem level.

## 1. Introduction

Literature on phenotypic plasticity has increased expanding from the initial focus on abiotic factors to that of biotic ones [1–3] and, in recent years, taking into consideration plant response to global climate change, land use change and plant invasiveness [4, 5] (Table 1). Thus, fundamental questions for evolutionary ecologists in a global change context are how plant species will respond to these new scenarios and what mechanisms will be involved in the process [6, 7]. The understanding of phenotypic plasticity will be crucial for predicting changes in species distribution, community composition, and crop productivity under global change conditions [8, 9]. Nevertheless, the theme of phenotypic plasticity is complex and researchers do not always arrive at the same conclusions and results are sometimes controversial.

Phenotypic plasticity has been defined as a change in the phenotype expressed by a single genotype in different environments. Bradshaw [10] recognized that phenotypic plasticity could itself be under genetic control and therefore subjected to selective pressure. Scheiner and Goodnight [11]

show that there is no reason to believe that the selection of plastic and genetic variations need necessarily be coupled. Nevertheless, a population could respond to an extremely variable environment by becoming both more plastic and more genetically variable. Literature suggests that phenotypic plasticity can evolve when there is a sufficient genetic variation [12, 13] due to genetic correlations with other traits that are under selection or to genetic drift [14]. Since phenotypic plasticity influences environmental tolerance, different plastic responses may contribute to differences in the range of environments that species inhabit [15]. In particular, the environment can induce changes in the individual's behavior at a morphological and/or physiological level [16] and such changes may be crucial to survival in heterogeneous and variable conditions [17–20]. For certain morphological traits, phenotypic plasticity has been shown to reflect genetic correlations relatively well, and traits belonging to the same suite of characters are more highly genetically and phenotypically correlated than traits from different suites [21]. The selection for photosynthetic traits may often operate indirectly via correlation with other traits, emphasizing the importance of

TABLE 1: List of the mentioned species and corresponding references.

Species	References
<i>Abies alba</i>	[27]
<i>Acer pseudoplatanus</i>	[27]
<i>Acer saccharum</i>	[28]
<i>Betula papyrifera</i>	[28]
<i>Campanula thyrsoidea</i>	[29]
<i>Coffea arabica</i>	[30, 31]
<i>Corylus avellana</i>	[32–34]
<i>Crepis pygmaea</i> subsp. <i>pygmaea</i>	[35]
<i>Cyclobalanopsis multinervis</i>	[36]
<i>Epilobium fleischeri</i>	[29]
<i>Fagus sylvatica</i>	[27, 37–39]
<i>Fraxinus excelsior</i>	[32–34]
<i>Geum reptans</i>	[29]
<i>Glycine max</i>	[40]
<i>Glycine soja</i>	[40]
<i>Hedera helix</i>	[41]
<i>Ilex aquifolium</i>	[42]
<i>Isatis apennina</i>	[35]
<i>Lythrum salicaria</i>	[43, 44]
<i>Myrtus communis</i>	[45]
<i>Ostrya virginiana</i>	[28]
<i>Phillyrea latifolia</i>	[41, 46]
<i>Picea abies</i>	[27, 47]
<i>Pinus halepensis</i>	[48–50]
<i>Pinus nigra</i>	[48]
<i>Pinus pinaster</i>	[48]
<i>Pinus pinea</i>	[48]
<i>Pinus sylvestris</i>	[48, 51]
<i>Pinus uncinata</i>	[48]
<i>Pistacia lentiscus</i>	[46, 52–55]
<i>Poa alpina</i>	[29]
<i>Populus tremula</i>	[32, 33]
<i>Populus tremuloides</i>	[28]
<i>Quercus aliena</i> var. <i>acutiserrata</i>	[36]
<i>Quercus coccifera</i>	[50, 56]
<i>Quercus faginea</i>	[48]
<i>Quercus ilex</i>	[19, 46, 48, 55, 57–61]
<i>Quercus mongolica</i> var. <i>crispula</i>	[62, 63]
<i>Quercus petraea</i>	[48]
<i>Quercus pyrenaica</i>	[48]
<i>Quercus robur</i>	[48]
<i>Quercus suber</i>	[48]
<i>Rhododendron ponticum</i>	[42]
<i>Rubia peregrina</i>	[41, 64]
<i>Ruscus aculeatus</i>	[41]
<i>Sesleria nitida</i>	[65]
<i>Shorea disticha</i>	[66]
<i>Shorea trapezifolia</i>	[66]
<i>Shorea worthingtonii</i>	[66]

TABLE 1: Continued.

Species	References
<i>Smilax aspera</i>	[41]
<i>Stellaria longipes</i>	[67]
<i>Taraxacum officinale</i>	[68]
<i>Tilia cordata</i>	[32–34]
<i>Viburnum tinus</i>	[41]

viewing the phenotype as an integrated function of growth, morphology, life history, and physiology [22]. The timing of plant development can itself be plastic [23] and many phenotypic responses to environmental stress factors may be the consequence of growth reduction due to resource limitations [24, 25]. Differences among species and populations may reflect different selective pressures on plasticity, different limitations acting upon the maximization of plasticity, or a combination of both [26]. The potential plastic response of a given trait may be large but the observed plasticity may be lowered by resource limitations or environmental stress factors [14].

The particular way by which a genotype varies in its expression across a range of environments can be described by a reaction norm which is genetically determined [69]. The reaction norm for any specific trait of a genotype can be visualized as a line or a curve on a two-dimensional plot of the environmental value versus the phenotypic value (Figure 1). Phenotypic plasticity can be visualized as a change in the slope of the reaction norm between ancestral and derived populations or species [70, 71]. Such change has been shown to occur in nature between species subjected to different selection pressures [72–74]. Plasticity is what makes the appearance of an environmentally induced novel phenotype possible, and a process of selection on the expression of such phenotype in a new environment may end up “fixing” (genetically assimilating) it by altering the shape of the reaction norm [75]. Thus, plasticity could facilitate the expression of relatively well-adapted phenotypes under novel conditions (e.g., after migration to new geographical areas) improving the performance of the population and resulting in the genetic assimilation of the trait in the new environment. This has the potential to explain a variety of evolutionary ecological processes [14, 75].

Indexes can facilitate comparison of different studies [76, 77], set of species or populations within a given species by considering experimental data in research on plasticity [19, 56, 57]. However, at least 17 different indexes have been employed as a measure of the phenotypic plasticity but can be flawed and applied in different ways. Most of them cannot be standardized across traits or compared among different species [78] complicating comparison among studies [3, 79]. Moreover, measures of phenotypic plasticity are strongly related to the context and may not be comparable across different studies where different gradients and/or species have been used [77]. Since information about plasticity is structured in a way that makes it difficult for quantitative and comparative analysis, Poorter et al. [79] proposed a method to fill this gap by building a large database which currently

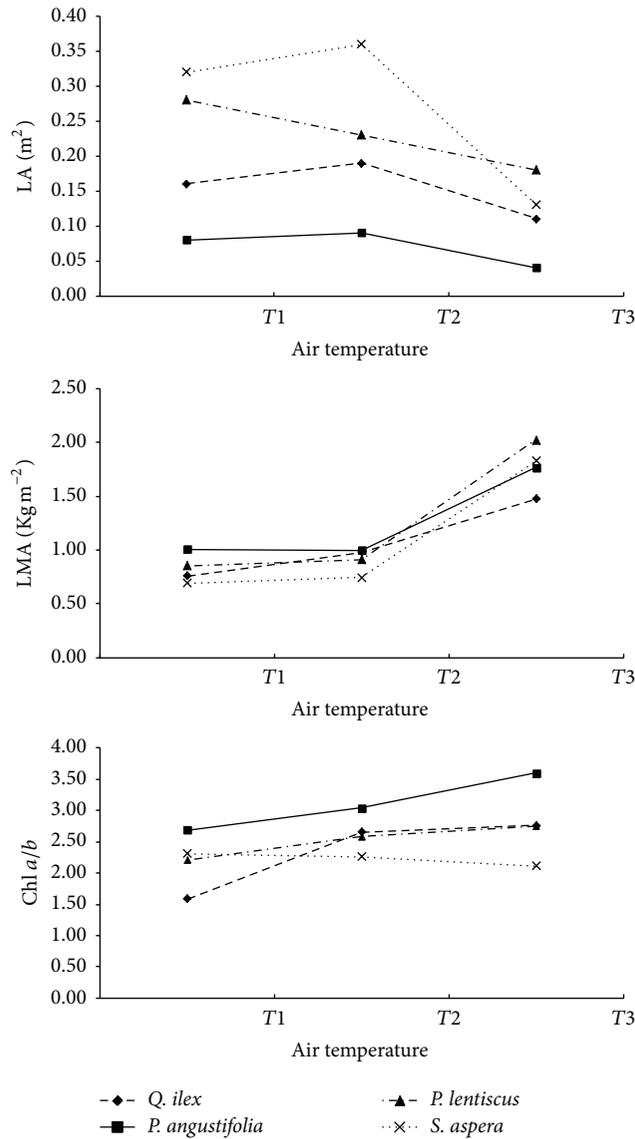


FIGURE 1: The reaction norm for any specific traits of a genotype can be visualized as a line on a plot of the environmental value versus the phenotypic value. In this example, the response of four evergreen species (*Quercus ilex*, *Phillyrea angustifolia*, *Pistacia lentiscus*, and *Smilax aspera*) in three different sites inside the Castelporziano Estate (Latium coast near Rome, Italy) to a gradient of air temperature ( $T1 = 16.5^{\circ}\text{C}$ ,  $T2 = 17.2^{\circ}\text{C}$ , and  $T3 = 21.9^{\circ}\text{C}$ ) is shown [55]. Lines represent the species and slope the phenotypic response. Among the cooccurring species, *S. aspera*, growing in the understory of the forest, has a larger morphological than a physiological plasticity. *Q. ilex* is the species with the largest morphological and physiological plasticity. Leaf area (LA), leaf mass area (LMA), and chlorophyll *a* to *b* ratio (Chl *a/b*) are shown.

contains data on 1000 experiments and 800 species. This approach could serve as a benchmark for future phenotyping efforts as well as for modelling global change effects on both wild species and crops [79].

## 2. Physiological, Anatomical, and Morphological Plasticity

Physiological, morphological, and anatomical plasticity may have a different role in plant adaption to environmental changes. In particular, plasticity for physiological and life-history traits may allow plants to grow and reproduce in

spatially or temporally variable environments [46, 80]. Physiological plasticity is more linked to an enhanced capacity to colonize gaps and open areas [81, 82] because it ensures adjustments of gas exchange in response to environmental factor changes in a short term. This aspect evidences the importance of physiological plasticity in plant acclimatization to adverse environments where morphological and anatomical plasticity play a secondary role [83]. In fact, plants growing in stress conditions tend to have a conservative leaf morphological pattern to avoid the production of structures too expensive to be sustained [84, 85]. Moreover, morphological plasticity is more linked to an enhanced plant capacity to

grow in forest understories [37, 82] by having an important role in resource acquisition [64, 86].

### 3. Plant Response to Light

The heterogeneous light environment within a plant canopy brings about different stress factors for leaves in different canopy positions. One of the expressions of plant phenotypic plasticity is the modification of leaf traits to the light gradient [87] and the reduced red/far red ratio [2] from the top to the bottom of the tree canopy, mainly during leaf formation [69]. One of the main morphological traits which changes in response to light variations is the specific leaf area (SLA, ratio between leaf area and leaf dry mass). The plasticity of SLA implies the morphogenetic control of leaves which tends to increase leaf area in the shade in order to intercept more light while on the contrary there is a genetic or physiological limitation to the total leaf volume as well as a resource limitation [88]. SLA reflects leaf thickness [89] and the relative proportion of assimilatory, conductive, and mechanical tissues [90]. In particular, the increased total lamina thickness in sun leaves compared to shade leaves is mainly due to the greater palisade parenchyma, spongy parenchyma, and epidermal tissue thickness, suggesting that leaf internal structure may play an important role in light capture [91]. In a research on leaf morphology of woody angiosperms, Wylie [92] shows that, as a result of shading, leaf thickness decreased, on an average, by 54%, the volume of the palisade parenchyma by 60%, and the epidermal thickness by 17%. McClendon [93] and Gratani et al. [46] showed a strong correlation between leaf thickness and the light-saturated rate of photosynthesis per unit of leaf area.

Sun leaves with respect to shade leaves, on an average, have a higher photosynthetic rate on a leaf area basis which is associated to a higher chlorophyll (Chl) *a/b* ratio, a significantly lower light-harvesting Chl *a/b* protein (LHCII), a lower stacking degree of thylakoids [94, 95], and a higher nitrogen (N) content per unit of leaf area [46, 96, 97] since approximately half of N is invested in the photosynthetic proteins [96]. Hirose and Werger [98] suggest that N varies with light availability in plant canopies in such a way as to optimize the daily canopy photosynthesis. Thus, the N investment is related to light in that more N is allocated to carboxylation in sun leaves and to light harvesting in shade leaves with variations in the photosynthetic capacity [99] (Figure 2). The photosynthetic capacity and N content are generally both higher in leaves under high light conditions [96, 98, 100]. The higher photosynthetic rates of sun leaves are supported by higher stomatal conductance and stomatal density to maximize CO<sub>2</sub> absorption [101]. On the contrary, leaf trait adjustments to low light increase the capacity of light absorption at the expense of the photosynthetic capacity minimizing carbon loss through respiration [96].

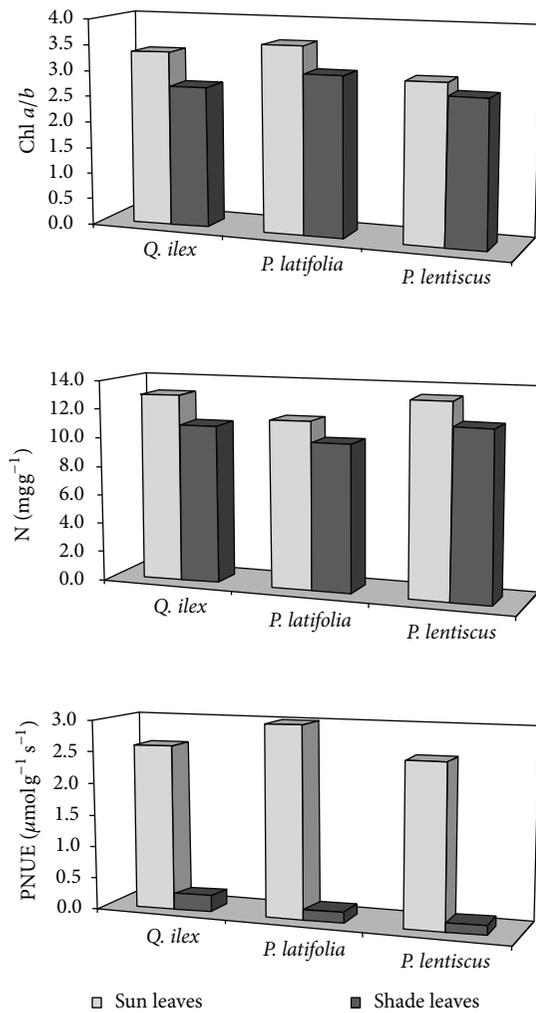
Changes in the efficiency of light interception and in the costs for light harvesting along the light gradient from the top to the bottom of the plant canopy are the major means by which an efficient light harvesting is achieved. In particular, at shoot scale, foliage inclination angle and

foliage spatial aggregation are the major determinants of light harvesting while, at the canopy scale branching frequency, foliage distribution and biomass allocation to leaves modify light harvesting significantly [102]. Intracopy plasticity has important impacts on many aspects of tree biology, potentially contributing to the whole-canopy performance via effects of light penetration through the canopy and on the energy, carbon, and water balance of the individual leaves [97, 103, 104]. Plasticity within the same plant, in a temporary heterogeneous environment, may play an adaptive role in strong seasonal climates such as the Mediterranean climate [20].

Moreover, leaf trait variations in response to the light gradient within the canopy change in different species and forest types [105–108]. In forests with dense foliage, the upper layers absorb the majority of the incoming radiation. In broadleaf and conifer forests of the temperate zone, on an average, 3–10% of the incident photon flux density (PFD) penetrates the tree canopy [69]. Gratani and Foti [109] show that SLA increases, on an average, by 21% from the dominant tree layer of a mixed deciduous broadleaf forest to the dominated layer in response to a decrease in the light level. The same trend is measured from the dominant tree layer of a Mediterranean evergreen forest to the dominated layer by the 54% SLA increase, associated with a 9.5% lower chlorophyll *a/b* ratio and 86% lower photosynthetic rate [110]. Mendes et al. [45] analyzed the large morphological and anatomical leaf trait variations to different light conditions for *Myrtus communis*, an evergreen sclerophyllous species which grows in Mediterranean areas from open clearings to understories, with a 26% increase of the SLA from sun to shade conditions. Nevertheless, taxonomically different species cooccurring in the same habitat often share common morphological and physiological traits, reflecting a convergent evolution in response to environmental factors [111]. The large plasticity in the structure of the mesophyll in concert with other traits seems to enable these species to cope with different environmental regimes (i.e., Mediterranean type climate), attaining a wider habitats range [111].

### 4. Shade Tolerance

Shade tolerance is one of the most important ecological factors with respect to interspecific competition among forest trees of the temperate climate zone. The shade tolerance of a given plant is defined as the minimum light under which a plant can survive; however, only a fraction of plants can reproduce under these conditions. Thus, a biological definition of shade tolerance must consider the whole life cycle of the plant from early survival and growth to reproduction [112]. In general, sun and shade leaves are thinner in tolerant species than in intolerant species [113]. The overall trend in literature suggests that early successional and light demanding species are more plastic than late-successional and shade-tolerant species [114–116]. Nevertheless, there is increasing evidence that indicates that adjustments are not necessarily related to the successional status of the species [117, 118] (Table 2).



Plasticity index	<i>Q. ilex</i>	<i>P. latifolia</i>	<i>P. lentiscus</i>
<b>Morphological traits</b>			
DM	0.16	0.11	0.14
LA	0.50	0.38	0.32
LMA	0.41	0.28	0.24
SLA	0.41	0.29	0.24
Mean value	0.37	0.26	0.23
<b>Anatomical traits</b>			
Leaf thickness	0.41	0.30	0.20
Palisade parenchyma thickness	0.47	0.37	0.28
Spongy parenchyma thickness	0.41	0.25	0.12
Adaxial cuticle thickness	0.19	0.31	0.28
Abaxial cuticle thickness	0.31	0.33	0.27
Adaxial epidermis thickness	0.27	0.28	0.18
Abaxial epidermis thickness	0.14	0.05	0.01
Stomatal density	0.28	0.20	0.08
Guard cell length	0.08	0.12	0.00
Mean value	0.28	0.25	0.16
<b>Biochemical traits</b>			
N	0.15	0.12	0.12
Chl <i>a + b</i>	0.35	0.40	0.47
Chl/Car	0.32	0.32	0.42
Chl <i>a/b</i>	0.16	0.15	0.08
Chl/N	0.44	0.43	0.51
Mean value	0.28	0.28	0.32
<b>Physiological traits</b>			
$P_N$	0.96	0.97	0.95
$g_s$	0.67	0.56	0.59
WUE	0.86	0.92	0.85
PNUE	0.92	0.95	0.93
$\Psi_m$	0.14	0.12	0.10
Mean value	0.71	0.70	0.69

FIGURE 2: Leaf trait variations in response to the light gradient from the top to the bottom of the canopy of three evergreen shrubs (*Pistacia lentiscus*, *Phillyrea latifolia*, and *Quercus ilex*) cooccurring in the Mediterranean maquis [46]. All the considered species have significantly thicker sun leaves compared to shade leaves (on an average 0.45 times) due to the palisade parenchyma (61%, mean value), spongy parenchyma (38%, mean value), and the adaxial cuticle (36%, mean value) thickness. The higher leaf consistency (i.e., higher leaf mass area, LMA) of sun leaves can be used as a measure of investment per unit of leaf area in conditions of full sun. Moreover, shade leaves have a lower chlorophyll *a* to *b* ratio (Chl *a/b*) (13%, mean of the considered species) due to the higher chlorophyll *b* content (89%, mean of the considered species) since it is usually the main component of the LHCP (light-harvesting protein), which is higher in the shade conditions. Sun leaves allocate, on an average, 16% higher nitrogen (N) content than shade leaves reflecting an increase in carboxylating enzymes (RUBISCO) and proteins, responsible for the photosynthetic electron transport in full sun. The phenotypic plasticity of the considered species is higher for leaf physiological traits (0.86), and among them, net photosynthesis ( $P_N$ ) and the photosynthetic nitrogen use efficiency (PNUE) have a larger plasticity (0.96 and 0.93, resp.). The largest phenotypic plasticity of *Q. ilex* (0.41) among the cooccurring species (0.36, mean value) reflects its wider ecological distribution area. Leaf dry mass (DM), leaf area (LA), specific leaf area (SLA), total chlorophyll *a + b* content (Chl *a + b*), chlorophyll to carotenoid ratio (Chl/Car), chlorophyll to nitrogen ratio (Chl/N), net photosynthesis ( $P_N$ ), stomatal conductance ( $g_s$ ), water use efficiency (WUE), and leaf water potential at midday ( $\Psi_m$ ) are shown.

Numerous studies focus on acclimation of the photosynthetic properties of plant species to different light conditions; nevertheless, results sometime disagree. For example, *Coffea arabica* is an evergreen perennial tree from the African forest understory which is considered an obligatory shade species. Matos et al. [30] show that plasticity of physiological and biochemical traits in *C. arabica* is more important for acclimation to intracopy light variations than morphological

and anatomical trait plasticity. Nevertheless, Araujo et al. [31] show that the apparent inability of *C. arabica* shade leaves to optimize carbon gain under low light and the successful ability of sun leaves to prevent photoinhibition of photosynthesis under high light conditions are consistent with the findings that it performs well at full sun exposure. Niinemets et al. [32] showed that in temperate deciduous forests species differ in their shade tolerance with *Corylus avellana* having the

TABLE 2: Phenotypic plasticity of morphological and physiological leaf traits for the mentioned shade-tolerant, shade-intolerant, and intermediate species and corresponding references.

	Species	Morphological plasticity	Physiological plasticity	References
Shade-tolerant	<i>Fagus sylvatica</i>	0.46	0.39	[37]
	<i>Acer pseudoplatanus</i>	0.31	0.34	[27]
	<i>Ilex aquifolium</i>	0.54	0.24	[119]
	<i>Quercus ilex</i>	0.33	0.5	[46]
	<i>Acer saccharum</i>	0.3	0.3	[108]
Intermediate	<i>Acer rubrum</i>	0.41	0.26	[108]
	<i>Betula alleghaniensis</i>	0.29	0.32	[108]
	<i>Picea abies</i>	0.13	0.22	[27]
	<i>Quercus rubra</i>	0.41	0.27	[108]
Shade-intolerant	<i>Quercus robur</i>	0.24	0.6	[37]
	<i>Cistus incanus</i>	0.18	0.38	[120]
	<i>Abies procera</i>	0.29	0.32	[108]

largest tolerance, followed by *Tilia cordata*, *Fraxinus excelsior*, and *Populus tremula* [33, 34]. Wyka et al. [27] by comparing seedlings of two conifers (the shade-tolerant *Abies alba* and the moderately shade-tolerant *Picea abies*) and two deciduous angiosperms (the highly shade-tolerant *Fagus sylvatica* and the moderately shade-tolerant *Acer pseudoplatanus*) in two-year studies, tested the hypothesis that light-induced plasticity of physiological and anatomical traits was lower in highly shade-tolerant species than in moderate shade-tolerant ones. The authors concluded that shade tolerance was not a consistent predictor of anatomical plasticity and that, for many traits, differences between the light treatments were magnified in the second year, showing that anatomical and physiological adjustment to shade is a long-term process. Valladares et al. [37] investigated phenotypic plasticity of two species differing in their shade tolerance (the most shade-tolerant *Fagus sylvatica* and the more light-demanding *Quercus robur*) hypothesizing a lower plasticity in the species of deep shade than in the more light-demanding species, according to comparative studies of others woody plants [56, 85, 105]. Moreover, the authors suggested that an alternative hypothesis was also feasible (i.e., that shade tolerance can be achieved by enhanced plasticity) as argued previously for the same two species [121]. The results showed a mean phenotypic plasticity similar to the two species (*Q. robur* and *F. sylvatica*) due to the fact that while *Q. robur* has a higher physiological plasticity, *F. sylvatica* has a higher morphological plasticity, with one group of traits counteracting the effect of the other group on the mean plasticity index [37].

Differences in forest structure determine changes in the light gradient and, consequently, in the presence of shade-tolerant and intolerant species. In particular, the deciduous forests may consist of an upper layer with shade-intolerant tree species and a lower layer with shade-tolerant tree species [32], while in mixed forests, deciduous and evergreen species with contrasting ecological potentials can occupy different layers [122]. Poorter et al. [48] analyzed shade tolerance in tree species growing in some forests of Continental Spain showing that the wider canopy, lower height, and flat leaves of the Fagaceae (*Quercus faginea*, *Quercus ilex*,

*Quercus petraea*, *Quercus pyrenaica*, *Quercus robur*, and *Quercus suber*) enhanced their shade tolerance compared to Pinaceae (*Pinus halepensis*, *Pinus nigra*, *Pinus pinaster*, *Pinus pinea*, *Pinus sylvestris*, and *Pinus uncinata*). On the contrary, resistance to fire [123], drought tolerance [124], and allometric plasticity of the shade-intolerant pines increased their rapid occupation of open spaces [125] and could be relevant to explain species ecological dominance. The shade-intolerant *Populus tremuloides* and *Betula papyrifera*, common species of the broad ecotone between the boreal and cold-temperate forests of central and eastern North America, possess traits that maximize whole plant carbon dioxide (CO<sub>2</sub>) exchange leading to long-term growth and survival disadvantages in very low light, while the shade-tolerant *Acer saccharum* and *Ostrya virginiana* minimize CO<sub>2</sub> losses in low light at the expense of maximizing CO<sub>2</sub> gains in high light [28]. The same authors conclude that the shade-intolerant species have a larger plasticity than the shade-tolerant species. Ke and Werger [36] showed that the deciduous *Quercus aliena* var. *acutiserrata* is a gap-dependent species having advantage over the evergreen *Cyclobalanopsis multinervis* in forest gaps and clearings by the greater morphological and physiological plasticity of seedlings. The ability to acclimate to contrasting light environments is particularly important for tropical woody species because tree seedlings grown in the forest understory are prone to experience photoinhibition under an increased light level through formation of a gap [126]. High irradiance in tropical latitudes can cause chronic photoinhibition through impairment of photosystem II (PSII) reaction centres in the leaves of plants that have experienced gap openings [127, 128]. Nevertheless, species vary in their shade tolerance to the increased light after a gap creation. For example, in deciduous broadleaf forests of northern Japan, *Quercus mongolica* var. *crispula* is a gap-dependent species because its seedlings could survive at most a dozen years under a closed canopy even though they can germinate in low light environments [62, 63]. Koike et al. [129] in a research on early successional species, gap phase species, mid-successional species, and late successional species showed that acclimation potential of the species was

expressed by their plasticity which was closely linked to the photosynthetic capability [130].

Despite the assumption that shade leaves develop in response to reduced light, other factors may also be involved, such as temperature and water stress [113]. It has been hypothesized that plants cannot tolerate combined shade and drought, as a result of a morphological trade-off [49, 131]. Nevertheless, Sack et al. [41] investigated six species (*Phillyrea latifolia*, *Viburnum tinus*, *Rubia peregrina*, *Ruscus aculeatus*, *Hedera helix*, and *Smilax aspera*) that cope with strong summer drought in the understory of mixed *Quercus* forests in southern Spain. All the species persisted in the shade (ca 3% daylight) and converged in features that conferred tolerance to shade plus drought by reducing the demand for resources. In particular, demand for water was reduced through a moderate-to-high below-ground mass fraction and low-to-moderate SLA, while demand for both low irradiance and water was reduced through a low-to-moderate leaf N content and leaves with a long life span. On an average, SLA is the trait most strongly correlated to shade tolerance [132].

Generalist species that grow in a range of moisture and light conditions within a forest, on an average, have a larger morphological plasticity than specialist species [66]. In particular, the more generalist *Shorea disticha* occurring on most sites within the evergreen forests and extending over most areas of the South and Southeast Asia has a greater plasticity than *Shorea trapezifolia*, which is restricted to the lower slopes of the valley within the forest, and *Shorea worthingtonii* which is restricted to the ridge-tops.

## 5. Ecotypes

Long-term selection can lead to the development of morphological and physiological adaptations to the local environment generating ecotypic differentiation in functional traits [133, 134]. Genotypes adapted to local environmental conditions are referred to as ecotypes [135]. When environments within the distribution area of a species differ, it is unlikely that any single phenotype confers high fitness in all situations. The distinction between phenotypic plasticity and local adaptation of an ecotype is based primarily upon genetic analysis and transplantation experiments [52]. In particular, spatial genetic differentiation along climatic gradients has been documented for many species [136–138] as well as for ecotype formations [52, 136, 138]. For example, ecotypes of *Pinus taeda* [139], *Picea abies* [47], *Pinus sylvestris* [51], *Fagus sylvatica* [38, 39], and *Quercus coccifera* [50] have adaptive features which are probably driven by the climate of the locality from which they originate. Moreover, species with extensive geographical ranges have the potential to exhibit a larger intraspecific variation in physiology, morphology, phenology, and growth rate [140]. Gratani et al. [19], Bonito et al. [57], and Pesoli et al. [58] compared plant and leaf trait plasticity in *Quercus ilex* seedlings from different provenances in Italy and grown in a common garden (Figure 3). *Quercus ilex* is a deep-rooted evergreen species widely distributed in the Mediterranean Basin [59] extending 6,000 km longitudinally from Morocco to France.

This species seems to be limited to the southern range due to increased summer drought, and in altitude (it is distributed from the sea level to 1,100 m a.s.l.) by factors associated with low temperature [60]. The results show that seedlings from the more xeric provenance have a higher tolerance to drought stress by a higher leaf mass area (LMA) limiting transpiration and a higher stomata sensitivity to changes in water potential allowing a higher relative leaf water content (RWC). On the contrary, the reduced leaf area appears to be the best adaptive trait in response to winter cold stress at the northern limit of the distribution area, while the largest shoot production reflects the more favorable climatic conditions at the centre of the distribution area. Thus, while the favorable environmental conditions increase the phenotypic plasticity of *Q. ilex* morphological and physiological traits, the less favorable conditions (i.e., cold and drought stress) allow specialization. Michaud et al. [61] observed a homogeneous genetic structure of *Q. ilex* in the Mediterranean region with only slight geographic variations due to isolation (i.e., North Africa and Sicily) which supports the hypothesis that *Q. ilex* corresponds to a single genetic entity. According to these hypotheses, Balaguer et al. [56] show that phenotypic plasticity varies across the geographical range of *Quercus coccifera*, and among populations, suggesting that *Q. coccifera* ecotypic differentiation accounts for its occurrence in contrasting habitats. Wen et al. [40] studied the origin and evolution of cultivated soybean. They investigated genetic diversity, geographic differentiation, and genetic relationship among geographic ecotypes of cultivated (*Glycine max*) and wild (*G. soja*) soybeans growing in South-Central China, South-West China, and South China. The results showed that the wild accessions had relatively small genetic distances with all cultivated accessions and the Middle and Lower Changjiang valleys wild ecotypes were smaller compared to other wild ones, including their local wild counterparts. Therefore, it is inferred that the wild ancestors in southern China, especially those from Middle and Lower Changjiang valleys, might be the common ancestors of all cultivated soybeans. Nevertheless, exploitation of new habitats may be associated with the loss of plasticity and evolution of specialization [16]. Adaptation of species to geographic environmental variations often depends on genetic variations among seed sources [19, 141]. Nahum et al. [52] showed that *Pistacia lentiscus* ecotypes growing in diverse habitats along a climatic gradient in Israel do not have any pattern of ecologically related genetic differentiation, and morphological and physiological differences are probably due to phenotypic plasticity. Thus, adaptive plasticity can expand environmental tolerance contributing to a wide distribution [53] of *P. lentiscus* around the Mediterranean region [52, 54]. Emery et al. [67] show that ecotypes of *Stellaria longipes*, an herbaceous perennial species growing along an altitudinal gradient on Plateau Mountain (Alberta) from the alpine tundra (i.e., higher altitude), has a lower plasticity than the ecotype from the prairie (i.e., lower altitude).

To accurately determine patterns of plasticity and investigate the ecological and evolutionary implications, it is important to better understand the environmental context in which phenotypes are expressed [2].

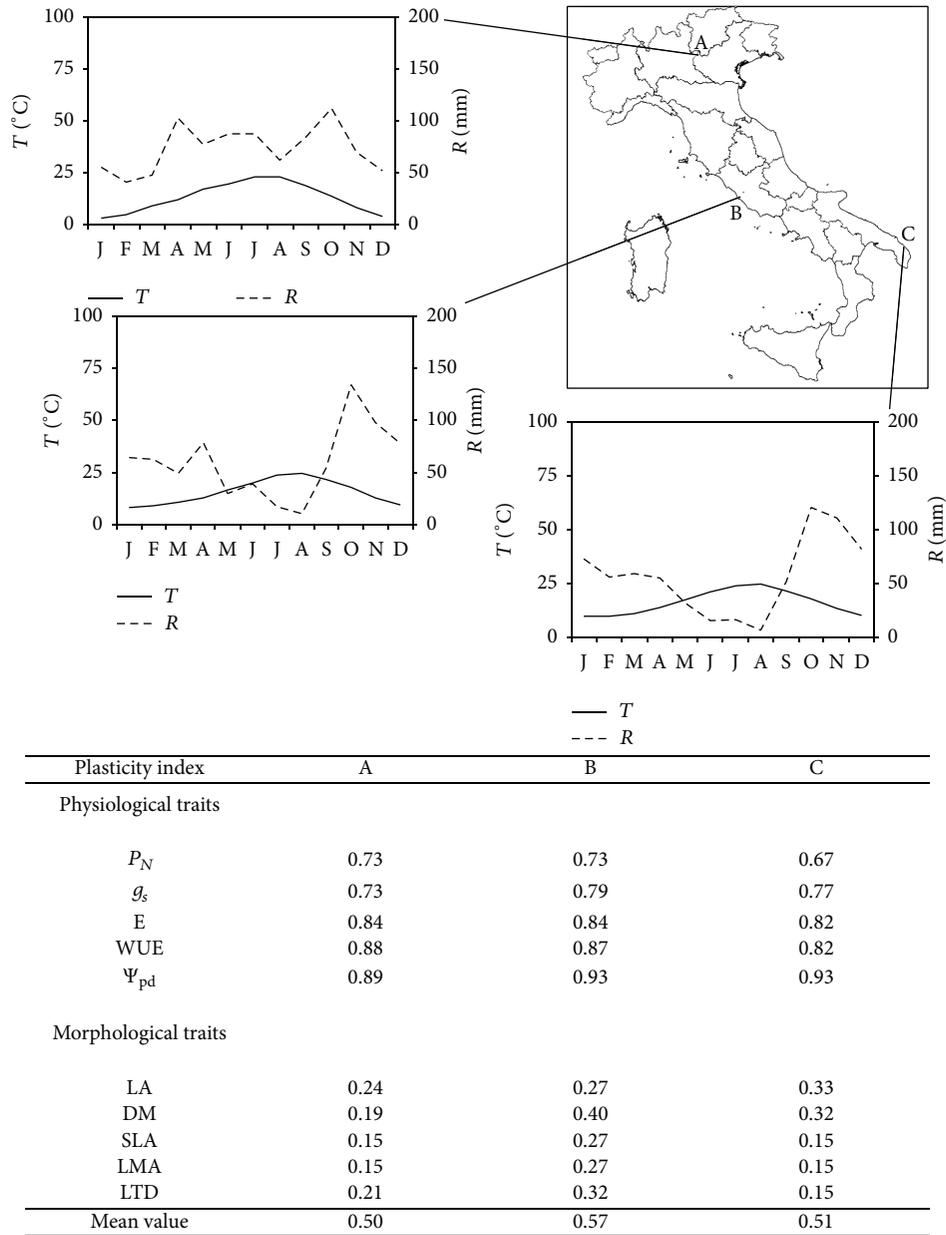


FIGURE 3: Physiological, morphological, and anatomical leaf trait variations of *Quercus ilex* ecotypes from different provenances in Italy, grown from seeds collected in the native environments. Seedlings from the more xeric provenance (Frassanito, 40°13'N, 18°26'E, at sea level, site C) have a larger tolerance to drought by a larger leaf mass area (LMA) and leaf tissue density (LTD) and a higher stomatal sensitivity to changes in leaf water potential at predawn ( $\Psi_{pd}$ ) contributing to a better water use efficiency (WUE) than the other seedlings [58]. In particular, the reduced leaf area (LA) appears to be the best adaptive trait in response to the winter stress at the northern distribution limit (Nago, 45°55'N, 10°53'E, 260 m a.s.l., site A) while the larger shoot and leaves production of Castelporziano seedlings reflects the favorable climatic condition of this locality (41°45'N, 12°26'E, at sea level, site B). The favorable environmental conditions at Castelporziano are expressed throughout a larger phenotypic plasticity while the cold stress at Nago and the drought stress at Frassanito allow specialization. Moreover, *Q. ilex* phenotypic plasticity is larger for physiological than for morphological and anatomical traits due to the capability of this species to grow in full sun as well as in shade conditions and colonize successfully new areas after fire by vegetative regeneration [142]. Frassanito shrubs by their larger tolerance to high temperature and limited water availability might have an advantage in response to the forecasted increase of air temperature and drought in the Mediterranean Basin. Net photosynthesis ( $P_N$ ), stomatal conductance ( $g_s$ ), leaf transpiration (E), and specific leaf area (SLA) are shown.

## 6. High Altitude Mountain Plants

The impact of global warming on terrestrial ecosystems has been shown to be greater in arctic tundra and high mountain regions than in low latitude areas [143]. In particular, the projected rate of global warming in mountain ecosystems is expected to be up to three times higher than the global average rate of warming recorded during the 20th century [144]. The biodiversity scenarios for the 21st century forecasts the reduction of alpine habitat and loss of many European high-mountain plants [145, 146]. Dirnböck et al. [147] hypothesize a rapid increase in plant species extinction risk. Moreover, species-specific reduction in fitness and diversity could change community dynamics by altering species competitive abilities. Recent studies [35] indicate substantial adaptive potential as reflected by high heritability estimates for traits likely to be selected [148]. Nevertheless, there is little information on the adaptive potential in environments that are particularly threatened by climate change such as high altitude mountain areas. One of the predicted consequences of global climate change is the movement of plant species to higher elevations and latitudes as the climate to which they are adapted is displaced [149]. A drastic decrease of the distribution area or even extinction of plant species can be the consequence of migration processes towards higher altitudes. Rates and patterns of these dynamics will be highly dependent on the habitat preference of a particular species and on its functional traits [150]. Steep environmental gradients and patchy distribution of habitats lead to small size and spatial isolation of populations and restrict gene flow [29]. It has been hypothesized that plant species populations may persist in their current areas and withstand environmental changes if they have a large adaptive capacity [151]. Gratani et al. [35], in a comparative study on two populations of *Crepis pygmaea* subsp. *pygmaea* and *Isatis apennina* growing at different altitudes on the Gran Sasso massif (Italy), addressed the question whether plasticity of morphological and physiological traits could be indicative of their future adaptive potential to survive global warming. The results underline that *C. pygmaea* has a significantly higher plasticity of both physiological and morphological traits than *I. apennina*. Thus, the hypothesized air temperature increase could drive *C. pygmaea* and *I. apennina* to higher altitudes in the Gran Sasso massif with *C. pygmaea* being favored by the highest plasticity. Studies on *Sesleria nitida*, a perennial herbaceous species growing at different altitudes along a narrow altitudinal gradient in the Central Apennines (Monte Terminillo, Italy), show that the lower photosynthetic rates at the higher elevation are justified by the stronger wind action and the lower soil water content of this site, while the lower SLA (i.e., the highest leaf mass area, LMA) contributes to limit leaf transpiration [65]. The extent to which SLA is phenotypically plastic or genetically fixed has important implications for the survival of populations under environmental condition changes [152]. Moreover, the results show a larger plasticity for physiological than for morphological and anatomical leaf traits of *S. nitida* the first being more useful under strong stress conditions which change in a short-term (Table 3). The relatively large

phenotypic plasticity of *S. nitida* reflects its capability to maintain function under different environmental stress conditions and sustain the air temperature increase through a potential shift toward higher elevations. Stöcklin et al. [29] studied the consequences for the alpine landscape due to the evolutionary processes in four typical alpine plant species (*Epilobium fleischeri*, *Geum reptans*, *Campanula thyrsoides*, and *Poa alpina*). The within-population genetic diversity of the four species is large and mostly not related to altitude and population size. Nevertheless, genetic differentiation among populations is strongly increased with distance, thus suggesting considerable genetic drift among populations of alpine plants. Phenotypic variability is shaped by adaptive as well as by random evolutionary processes, and plastic responses to growth conditions seem to be crucial for survival of plants in the alpine landscape.

## 7. Competition between Invasive and Native Species

The increase of air temperature and carbon dioxide (CO<sub>2</sub>) concentration over recent decades has determined novel environmental conditions [153] which might act as a potent agent of natural selection among species favoring more phenotypically plastic species [154] and resulting in a competition between invasive over cooccurring native species [153, 155]. The phenotypic plasticity of cooccurring native and invasive species in the broadleaf forest developing in the Natural Reserve Siro Negri (45°12'39" N, 9°3'26" E, Italy) attests to the considered species responsiveness to light variations. *Q. robur* (a native species) and *R. pseudoacacia* (an invasive species) have a similar physiological plasticity. Nevertheless, the significantly higher morphological and anatomical plasticity of *R. pseudoacacia* than *Q. robur* confirms its past capability of colonizing the forest and then growing successfully into both the dominant and dominated layers (data Catoni et al. not published).

Introduced species frequently exhibit little genetic variations in the new environment due to the genetic bottleneck and drift experienced by the small founding populations [156]. Even with genetic variations, local adaptation may not arise if selection is weak or unpredictable, or if considerable gene flow occurs among populations [157]. Despite these limitations, local adaptation often contributes to the success of plants introduced in the new environments [158–162]. In agreement with this hypothesis, Niinemets et al. [42] show higher plasticity of the invasive *Rhododendron ponticum* in respect to the native *Ilex aquifolium* in high light environments by its higher N investment in light harvesting and in photosynthetic machinery allowing the production of more leaf area with equal photosynthetic and light-harvesting characteristics. The high phenotypic plasticity in photoprotective strategies and performance of the invasive *Taraxacum officinale* enhances its competitive ability in alpine environments [68] considering that light intensity is one of the most changing conditions along altitudinal gradients. The *T. officinale* plants from higher altitudes, where light conditions are more variable, possess greater plasticity

TABLE 3: Plasticity index (PI) of morphological and physiological leaf traits for *Crepis pygmaea* subsp. *pygmaea*, *Isatis apennina* [35], and *Sesleria nitida* [65].

	Morphological traits	PI	Physiological traits	PI	
<i>Crepis pygmaea</i> subsp. <i>pygmaea</i>	LA	0.20	$P_N$	0.63	
	DM	0.39	$g_s$	0.65	
	LMA	0.38	$R$	0.53	
	LTD	0.42	WUE	0.36	
			$\Psi_m$	0.73	
			Chl	0.31	
			RWC	0.21	
			$P_g$	0.55	
		<b>Mean value</b>	<b>0.35</b>	<b>Mean value</b>	<b>0.50</b>
	<i>Isatis apennina</i>	LA	0.25	$P_N$	0.42
DM		0.32	$g_s$	0.48	
LMA		0.30	$R$	0.72	
LTD		0.33	WUE	0.26	
			$\Psi_m$	0.48	
			Chl	0.17	
			RWC	0.15	
			$P_g$	0.37	
		<b>Mean value</b>	<b>0.30</b>	<b>Mean value</b>	<b>0.38</b>
<i>Sesleria nitida</i>		Leaf thickness	0.24	$P_N$	0.18
	Height of the major lateral vascular bundle	0.30	$g_s$	0.39	
	Width of the major lateral vascular bundle	0.24	$E$	0.33	
	Height of the major lateral vascular bundle	0.39	$R$	0.37	
	Width of the central vascular bundle	0.32	$R/P_N$	0.47	
	Diameter of the xylematic vessels	0.18			
	Mesophyll cell density	0.19			
	Thickness of the upper sclerenchyma layers	0.31			
	Total surface area of bulliform cells	0.07			
	Adaxial stomatal length	0.06			
	Abaxial epidermis thickness	0.06			
	Adaxial epidermis thickness	0.07			
	Leaf mass area	0.15			
	Leaf width	0.21			
		<b>Mean value</b>	<b>0.20</b>	<b>Mean value</b>	<b>0.35</b>

Leaf area (LA), leaf dry mass (DM), leaf mass area (LMA), leaf tissue density (LTD), net photosynthesis ( $P_N$ ), stomatal conductance ( $g_s$ ), leaf respiration ( $R$ ), water use efficiency (WUE), leaf water potential at midday ( $\Psi_m$ ), total chlorophyll content (Chl), relative water content (RWC), gross photosynthesis ( $P_g$ ), leaf transpiration ( $E$ ), ratio between leaf respiration, and net photosynthesis ( $R/P_N$ ) are shown.

than plants from lower altitudes, suggesting that plasticity in ecophysiological traits will be one of the main strategies to colonize environments with variable light conditions. High adaptability can be due either to the adaptive strategy to cope with resource fluctuations in the native region [163, 164] or to a rapid evolution in novel environments after colonization [165]. Davidson et al. [153] show that invasive species are more plastic in their response to greater resource availability than noninvasives, but this plasticity is only sometimes associated with a fitness benefit, and noninvasive species maintain greater fitness homeostasis when comparing growth between low and average resource availabilities. Funk [166] investigated the plastic responses of five invasive-native pairs in low resource environments of the Hawaiian

Islands and found that the maximum photosynthetic rate and the organic leaf N concentration were positively related to the invasive species fitness in response to N availability. Since adaptive plasticity may allow certain species to colonize environmentally diverse areas without the lag time required for local adaptation, it may enhance their invasiveness and rapid geographic spread contributing to the displacement of native species [4].

Nevertheless, despite the effort over the last decades, the evolutionary mechanisms leading to invasiveness remain unclear [167]. Molina-Montenegro et al. [68] show that invasive species have significantly greater plasticity than native species. On the contrary, Drenovsky et al. [168] suggest that native and invasive species may converge on

functionally similar traits demonstrating comparable ability to respond to change in resource availability. In addition, Godoy et al. [169] show that despite reasonable arguments in favour of linking phenotypic plasticity to plant invasion, no general pattern between phenotypic plasticity and invasiveness emerged. DeWalt et al. [170] tested the hypothesis that the tropical shrub *Clidemia hirta* is more abundant in the introduced (Hawaiian Islands) than in the native range (Costa Rica) because of genetic differences in resource acquisition, allocation, and phenotypic plasticity between native and introduced genotypes. Nevertheless, the results underline the fact that genetic shifts in resource use, resource allocation, or plasticity do not contribute to differences in habitat distribution and abundance. An increased plasticity may not increase fitness (nonadaptive plasticity) or may even decrease it, and the correlation among different plant traits may confers invasiveness by reducing the cost of maladaptive and/or nonadaptive plastic traits [14, 171]. Bastlová and Květ [43] evidenced the phenotypic variability in native populations of *Lythrum salicaria*, a Eurasian species which successfully invaded north American wetlands competing with native plant species [44]. The authors showed that plants originating from more southern Eurasian localities were more similar to the invasive plants in North America than to plants from northern Eurasian localities. Variability in growth characteristics across the north-south gradient within the native range could result from long-term adaptation to prevailing environmental conditions, particularly day-length. Moreover, variability for some growth characteristics (i.e., dry weight and number of lateral branches, root dry weight), both between and within Eurasian populations, indicates a plastic growth response to the local environmental conditions.

## 8. Conclusions

Overall, climate change has been shown to affect abundance and distribution of plant species, as well as plant community composition [172, 173]. Recent studies indicate that under rapid climate change phenotypic plasticity rather than genetic diversity is likely to play a crucial role in allowing plants to persist in their environments [174]. Different responses to climate occur not only between populations throughout a species range but also between cooccurring individuals within a population [149]. Nevertheless, studies of genetic structure based on enzyme polymorphism in populations of forest trees have shown significant levels of intrapopulation variability and little interpopulation differentiation [61, 175, 176]. Increased summer drought will exacerbate the regeneration of many tree species at their lower latitudinal and altitudinal distribution limits and the introduction of more drought tolerant species in vulnerable habitats is considered to facilitate forest persistence [177]. Nevertheless, introducing more drought tolerant species to mitigate climate change might not necessarily be successful due to trade-offs between drought tolerance and growth plasticity. Nicotra et al. [178] sustain the fact that autochthonous provenances have the potential for resistance to change in climatic conditions

as a function of both phenotypic plasticity and genotypic variations.

Assessment of vegetation vulnerability and climate change resilience require understanding of the diversity among plant species in the current vegetation and their growth strategies in response to fluctuating resource availability [179]. Since species with extensive geographical range have the potential to exhibit large intraspecific variations in physiology, morphology, and phenology, they may be good models for the study of local and regional adaptations [140]. Nevertheless, adaptation to future global change could require the evolution of a number of different traits that may be constrained by correlations between them [180]. Thus, it is necessary to identify plant functional traits in which plasticity is likely to be a determinant in plant response to global change contributing to predict species distribution changes and shifts [178]. Moreover, it is important to fully understand the ecological consequences at a species and ecosystem level considering that species with a greater adaptive plasticity may be more likely to survive novel environmental conditions, since such changes typically occur too rapidly to allow for an evolutionary (or in some cases a migratory) response. Plasticity is recognized to be a major source of phenotypic variations in the real world because it will influence natural selection and, consequently, patterns of diversification among populations and, ultimately, species [2, 181]. Plasticity promotes evolutionary diversification if the produced phenotypes provide adaptive diversity that under selection becomes evolutionarily fixed [2, 182, 183]. Nevertheless, the extent to which phenotypic plasticity may facilitate survival under changing environmental conditions still remains largely unknown. Although phenotypic plasticity may facilitate short-term adaptation to environmental changes, genetic adaptation might ultimately be necessary for the persistence of species in extreme habitats [177].

In the near future it will be important to collect data by working in the field and, in particular, in primary forests and/or in well-conserved habitats where new stress factors are limited in order to define standard protocols useful for comparative studies. Among the strategies, environment conservation should protect heterogeneity between and within habitats in order to maintain larger intraspecific variability and, thereby conserving a variety of phenotypic specializations that will be able to buffer future environmental extremities due to climate and land-use changes [184].

## Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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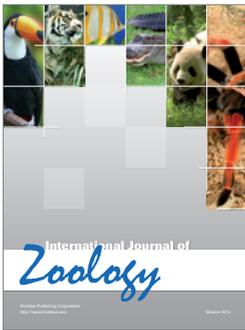
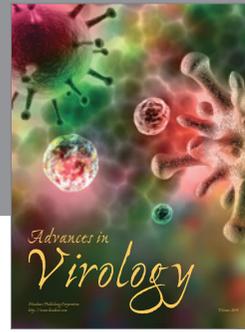
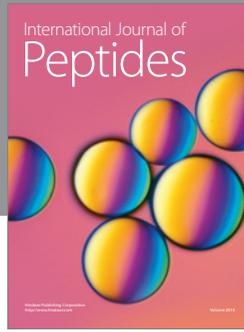
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