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Plant–environment interactions through a functional traits perspective: a review of Italian studies

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ABSTRACT

Italy is among the European countries with the greatest plant diversity due to both a great environmental heterogeneity and a long history of man–environment interactions. Trait-based approaches to ecological studies have developed greatly over recent decades worldwide, although several issues concerning the relationships between plant functional traits and the environment still lack sufficient empirical evaluation. To draw insights on the association between plant functional traits and direct and indirect human and natural pressures on the environmental drivers, this article summarizes the existing knowledge on this topic by reviewing the results of studies performed in Italy adopting a functional trait approach on vascular plants, bryophytes and lichens. Although we recorded trait measurements for 1418 taxa, our review highlighted some major gaps in plant traits knowledge: Mediterranean ecosystems are poorly represented; traits related to belowground organs are still overlooked; traits measurements for bryophytes and lichens are lacking. Finally, intraspecific variation has been little studied at community level so far. We conclude by highlighting the need for approaches evaluating trait–environment relationship at large spatial and temporal scales and the need of a more effective contribution to online databases to tie more firmly Italian researchers to international scientific networks on plant traits.

KEYWORDS

Climate change; CSR plant strategy theory; forest management; intraspecific variability; land use change; plant traits; terrestrial and freshwater environments

Introduction

Process shaping vegetation patterns have traditionally been approached by analyzing spatial and temporal changes in plant species composition (McGill et al. 2006). Species identity provides important information for ecological and evolutionary studies, however, this information alone does not effectively contribute to

the understanding of ecosystem functioning (Westoby et al. 2002; Garnier et al. 2004). Considering the huge number of plant species and their uneven geographical distribution, models based on species identity cannot be generalized or easily transferred to areas with a different flora (Keddy 1992). Even though non-taxonomic classifications of plants have a very long history (Garnier et al. 2016), the trait-based approach in ecology has substantially developed over the last three decades and also thanks to the impulse of studies on global environmental changes (Smith, Shugart, and, Woodward 1997).

Plant functional traits are defined as ‘any morphological, anatomical, biochemical, physiological or phenological heritable feature measurable at the individual level, from the cell to the whole-organism level’ (Garnier et al. 2017) that impacts plant species fitness affecting growth, reproduction, resource use, establishment, etc. (Garnier and Navas 2012). Traits mediate the response of plants to the environment (Lavorel and Garnier 2002) and influence ecosystem functioning (Kattge et al. 2011). Accordingly, they are used in ecological research (Violle et al. 2007) to address fundamental questions including (i) the responses of functional traits to different environmental gradients at the species and community level, (ii) the identification of rules governing the assembly of communities, and (iii) the relationships between plant functional traits and ecosystem services (Garnier et al. 2016 and references therein). In spite of this, several major issues in trait-based ecology still lack sufficient empirical evaluation (Shipley et al. 2016).

Italy is the European country with the highest number of native vascular plant species and subspecies (Bartolucci et al. 2018); at the same time, it has a long history of human pressures on the environment that still influences a wide range of ecosystems. Such a high plant diversity derives from a wide latitudinal gradient and from the remarkable heterogeneity in terms of climate and physiography, along with a complex biogeographic evolution (Smiraglia et al. 2013; Blasi et al. 2014). These conditions allow for a broad variety of natural vegetation types (Blasi 2010) that is enriched by the occurrence of semi-natural ones, deriving from the long history of human activities (Capotorti et al. 2012). In parallel, global changes are shaping biodiversity and ecosystem functioning in Italy with different patterns and rates across the various environments (Chelli et al. 2017). For instance, because of the ongoing climate change, Italy results one of the European countries most prone to extreme drought (Spinoni et al. 2018) and temperature increase (Rogora et al. 2018). Its forests were subjected to timber exploitation since the Roman times (Vacchiano et al. 2017), and it is now undergoing land-use change at very high rate with a consistent process of reforestation and a steady decrease of pasture extent (Falcucci et al. 2007; Malavasi et al. 2018). Furthermore, its sandy shorelines have been heavily transformed in the last 60 years with considerable loss or modification of natural vegetation (Malavasi et al. 2013). For these reasons, the analysis of environmental and human-related gradients, as well as the mechanisms through which these gradients shape community composition and determine specific ecosystem services is particularly challenging in Italy. In this view, Italy may serve as a model region to test the effectiveness of trait-based approaches.

To draw general insights on the association between plant functional traits and direct and indirect natural and human pressures on environmental drivers, here we summarize the existing knowledge on this topic by reviewing the results of Italian studies that used the functional traits of vascular plants, bryophytes and lichens.

Especially, we aim to (1) assess the ‘state of the art’ of the relation between plant traits and both environmental or human drivers in Italy, (2) identify the most frequently investigated research fields, above all those dealing with global change drivers, summarizing major results, in order to contribute to their empirical evaluation and (3) identify knowledge gaps and suggest operative indications for the Italian research community to fill them.

To give more generality to the presented results, they could be compared with a global and more comprehensive review focusing on few relevant topics; regrettably, this kind of global review is beyond the scope of this article.

Materials and methods

We collected 164 papers during a workshop of the Italian Botanical Society specifically organized for this purpose (Plant traits 2.0: State of the art and future perspectives for research on plant functional traits in Italy, 9–10 February 2017, Bologna, Italy). In addition to this event, we carried out a literature search through ISI Web of Science and Google Scholar as well as through cross-referencing. The search terms for the query (11th October 2017) were 'plant functional trait_' AND 'Italy'. In the Web of Science, a total of 83 references were found; among them, 40 were already included, 23 were not relevant for the review, and the remaining 20 papers were added to our database. In Google Scholar only the first 300 items (ranked by relevance) were checked, and four additional studies matching the requested criteria were found.

In general, studies were included if meeting the following criteria: (i) performed in Italy, (ii) published in peer-reviewed journals, (iii) focused on the relationship of response and/or effect traits (sensu Lavorel and Garnier 2002) of vascular plants, bryophytes and lichens to environmental variables/ gradients. The review has a broad focus on the plant functional traits approach, it includes studies based on both field/greenhouse measurements of traits according to standard methods and on traits collected from databases aimed at gaining deeper insights into ecological functioning at species and community levels in terrestrial and freshwater environments. We excluded studies related to marine environments, crops, and those based on modelling, pollen analysis, bioaccumulation, phytoremediation, and dendroecology. Altogether, 188 articles were identified and included in the review (Supplementary Information Appendix 1). The following main topics were recognized: (a) impact of climate change on functional traits; (b) response of functional traits to forest management and eutrophication; (c) secondary grasslands, grazing and land-use change; (d) CSR plant strategy theory; (e) plant functional traits and ecological processes in coastal ecosystems; (f) plant functional traits and intraspecific variability; (g) aquatic environments and plant growth: evidence from river and shallow inland ecosystems (Tables 1 and 2).

Results and discussion

Similarly to the temporal trend of the international scientific production on plant functional traits (source: ISI Web of Science, search terms 'plant functional trait_'), the vast majority of Italian studies using the functional approach were performed during the last decade (Figure 1(a)). Studies were mainly carried out in the Continental biogeographic region (sensu Roekaerts 2002; 42%), while a lower number of papers referred to the Alpine (32%) and the Mediterranean region (26%), despite the fact that the latter comprises >50% of the Italian territory. Semi-natural grasslands and forests (24 and 23%, respectively) were the most studied ecosystems, while only few studies have dealt with Mediterranean shrublands and agroforestry systems (3%), and alpine/sub-alpine peatlands (5%, Figure 1(b)).

For vascular plants, we discuss traits belonging to the following categories: whole-plant traits (Kleyer et al. 2008; Pérez-Harguindeguy, Diaz, and Garnier 2013), leaf traits (Pérez-Harguindeguy, Diaz, and Garnier 2013; Garnier et al. 2017), seed and dispersal traits (or regenerative traits, sensu Pérez-Harguindeguy, Diaz, and Garnier 2013), phenology and flowering traits (Kühn et al. 2004), clonal traits (Klimešová et al. 2017), root traits (or belowground traits, sensu Pérez-Harguindeguy, Diaz, and Garnier 2013; Garnier et al. 2017). Among these, leaf (28%) and whole-plant traits (27%) were used with a similar relatively high frequency. Phenological, seed and clonal traits were also well represented (17, 12 and 9%, respectively), while few papers dealt with root traits (2%). Canopy height, specific leaf area (SLA), flowering phenology, seed mass, leaf dry matter content (LDMC), leaf nitrogen, and vegetative propagation were the most frequently used plant functional traits (at least in 20 papers). These are commonly recognized as key traits related to fundamental plant challenges (dispersal, establishment, persistence; Weiher et al. 1999) and are inherent to major ecological strategy theories, such as (i) the Leaf-Height-Seed plant ecology strategy scheme (including SLA, canopy height and seed mass; Westoby 1998), (ii) the CSR strategy scheme (SLA,

LDMC; Grime and Pierce 2012; Pierce et al. 2013), and (iii) the Leaf Economics Spectrum (Wright et al. 2004).

For bryophytes, we selected the following categories according to Cornelissen et al. (2007): tissue chemistry traits, carbon gain related traits, traits related to carbon and nutrient losses (litter chemistry), other morphological and cytological traits. The most represented were tissue chemistry traits and traits related to carbon and nutrient loss, but only in studies conducted in the alpine biogeographic region. All functional traits considered were primarily measured from specimens collected in the field. In detail, traits were measured for 1080 vascular plant and 15 bryophyte species (Supplementary Information Appendix 2). Flowering phenology was the functional trait more frequently measured on vascular plant species (>800 species), followed by canopy height and SLA (>700 species; Figure 1(c)). In contrast, functional traits of lichens were obtained mainly from databases (i.e. *Italic 5.0*; Nimis and Martellos 2017). In Italy, plant functional traits have been used to answer many ecological questions (Table 1): many traits have been used in studies dealing with forest management, grazing and land-use change, but with discrepancies among biogeographic regions (Table 1). On the contrary, few traits were used in aquatic environments. Additionally, clonal and root traits were never considered in studies on climate change.

Impact of climate change on functional traits

Studies were conducted through manipulation experiments or observational approaches. Experiments dealing with seed traits were performed by exposing parental alpine plants or dispersed seeds to warming. Seeds produced by plants exposed to moderate warming ($+1.5\text{ }^{\circ}\text{C}$) were more resistant to heat (Bernareggi et al. 2015) and showed changed germination/dormancy responses as compared to controls, with deeper and less dormant seeds showing major changes in response to incubation temperatures and to cold stratification periods, respectively (Bernareggi et al. 2016). Alpine plant seeds directly exposed to warming after dispersal showed a general increase in germination rate both in spring and autumn, with a subsequent high percentage of seedling survival in winter (Mondoni et al. 2012, 2015; Orsenigo et al. 2015). Exposure of seeds of two Mediterranean annual species to water stress led to reduced and delayed germination with contrasting responses among populations, revealing a possible adaptation to drought stress in the southernmost population (Orsenigo et al. 2017).

Experiments focused on flowering time revealed a plastic response to changing micro-climatic conditions, both for snowbed-specialized and alpine generalist species (Petraglia et al. 2014b, Carbognani et al. 2016). Petraglia et al. (2014b) showed that for many species, flowering time was tuned by snowmelt date and temperature. However, Carbognani et al. (2016) highlighted the importance of timescale of the observations, with snowmelt time playing a major role at annual scale and temperature at the growing season timescale. Even observational approaches studying flowering of primary grasslands species in N-Apennines showed a plastic response of different species. In general, inflorescence production was affected by mean summer temperature, suggesting a change in reproductive strategies (e.g. changes in the ratio sexual/ clonal reproduction; Abeli et al. 2012a). However, snow cover persistence was also a relevant driver of the reproductive effort in some species, with a significant decrease of inflorescence production with reduced snow cover persistence both in primary grasslands (Abeli et al. 2012b) and dwarf-shrub heath (Gerdol et al. 2013).

The response of leaf traits to experimental extreme drought was studied in sub-Mediterranean secondary grasslands (Wellstein et al. 2017) and resulted in differential patterns (through phenotypic adjustment) of functional groups: grasses increased significantly their SLA under drought, indicating better growth performance of these species, which is most likely related to their strategy to allocate resources to belowground parts. In contrast, forbs showed a SLA reduction as a response to water stress.

Analysis of plant trait turnover through long-term observations revealed significant floristic and functional changes over the last 42 years in alpine and subalpine grasslands of central Apennines, with an increase in

thermophilous, nitrophilous and mesophilous plant species and an increment in the frequency of hemicryptophytes (Evangelista et al. 2016). These changes are likely attributable to the combined effect of higher temperatures and the increase in soil nutrients triggered by global change. A thermophilization trend has been also documented in several European mountains and has been related mainly to the effects of climate change (e.g. Britton et al. 2009; Engler et al. 2011; Gottfried et al. 2012; Frate et al. 2018). Accordingly, recent evidence (e.g. Spasojevic et al. 2013) suggests that variations in nutrient availability, soil moisture and temperature led to changes in the functional composition of alpine plant communities with a shift towards more resource acquisitive functional traits (e.g. hemicryptophytes with well-developed leaves).

Among the papers dealing with lichens, photobiont type, thallus growth forms and dispersal strategy were the most studied functional traits, at national (Marini et al. 2011; Giordani et al. 2012) or local level, spanning from glacier forelands to Mediterranean systems (Favero-Longo et al. 2014; Nascimbene and Marini 2015; Nascimbene et al. 2017; Giordani et al. 2014c). Thallus growth form and photobiont type were responsive to climate factors in several ecosystems both at national (Marini et al. 2011; Giordani et al. 2012) and local level (Nascimbene and Marini 2015; Nascimbene et al. 2017), representing a promising tool for detecting the effects of climate change on lichen species. For instance, thallus growth forms showed contrasting patterns related to temperature in forest ecosystems, with crustose species being enhanced by warming, and fruticose and foliose lichens being negatively impacted by warming (Nascimbene and Marini 2015). Also photobiont type (i.e. the photosynthetic partner of the lichen symbiosis) showed differential response to climate variables; despite the general dependence of lichens on water supply, lichens characterized by Trentepohlia algae were further enhanced by warming, while species richness of lichens characterized by cyanobacteria was only related to precipitation (Marini et al. 2011).

Response of functional traits to forest management and eutrophication

Understorey species compositional changes during the regeneration phases after coppicing appeared to be driven by plant functional traits, in particular leaf, clonal and reproductive traits (Canullo et al. 2011, 2017; Campetella et al. 2011; Catorci et al. 2012a). In detail, changes in environmental conditions during the forest regeneration after coppicing filtered species with high SLA values (Campetella et al. 2011; Catorci et al. 2012a), short-distance dispersal (Campetella et al. 2011), early leaf and flower production (Catorci et al. 2012a) and high mobility due to stem-derived clonal growth organs (i.e. hypogeous rhizomes; Canullo et al. 2011, 2017). Additionally, understorey traits composition was influenced by the presence of the alien trees *Prunus serotina* and *Robinia pseudoacacia* but with different impact, suggesting the importance of different management and control strategies (Terwei et al. 2016).

Papers comparing different types of forest management, namely old coppice vs. high forest, showed contrasting results: the understorey herbaceous layer did not show significant differences in leaf, flowering, whole-plant and seed attributes (Scolastri et al. 2017); in contrast, belowground traits (i.e. fine-root traits) of tree species (*Fagus sylvatica*) were sensitive to management. In particular, fine-root standing biomass decreased and nitrogen concentration increased with the reduction of the stand density. Furthermore, both fine-root production and turnover rate were lower, and C:N ratio higher, in dense old coppice than in thinned high forest stands (Montagnoli et al. 2012a; Terzaghi et al. 2013), suggesting the importance to explore belowground traits in future studies. In absence of management, local ecological continuity favoured species with low dispersal ability (i.e. large seeds with low persistence in the soil, and short-distance animal dispersion; Ricotta and Burrascano 2008; Burrascano et al. 2009). However, despite differences in terms of functional traits between unmanaged and managed forests, the difference in their functional beta diversity values are only marginally significant, probably due to the different spatial scale at which ecological variations occur in forest stands with different management histories (Ricotta and Burrascano 2008).

For lichens, three functional traits were mainly considered, namely photobiont type, thallus growth forms and dispersal strategy. Lichens were sensitive to forest management (Nascimbene et al. 2007, 2008). In particular, the release of deadwood in managed forests was a key factor for the maintenance of lichens functional diversity. The occurrence of deadwood in different decay status supported a broad lichen community (Nascimbene et al. 2008). Lichen growth form was the most responsive trait and was considered a reliable indicator for evaluating and comparing the responses of epiphytic lichens to atmospheric deposition in forests across diverse regions (Giordani et al. 2012, 2014). In particular, Giordani et al. (2014) showed that the percentage of macrolichens was the most reliable indicator, since 56.7% of its variation could be explained by nitrogen deposition. Moreover, both narrowly lobed and broadly lobed foliose lichens were negatively affected by acidic deposition, while narrowly lobed species were also negatively influenced by increasing concentrations of SO₄²⁻ (Giordani et al. 2012). Under high eutrophication levels, differences in tree-related factors were not related to significant differences in epiphytic lichen communities' composition (Giordani and Malaspina 2017). In fact, different epiphytic lichen functional groups with different nitrogen tolerances responded to several atmospheric pollutants, which had both independent and joint effects, whereas they did not show significant differences depending on bark pH.

Secondary grasslands, grazing and land-use change

Changes in grazing intensity produced significant changes in species and functional traits composition in montane grasslands (Catorci et al. 2016; Giarrizzo et al. 2017). The increase in grazing pressure produced an increase in species showing traits associated with frequent disturbance (Giarrizzo et al. 2017), usually poorly palatable and characterized by strong grazing avoidance strategies (Catorci et al. 2016). In lichens, Giordani et al. (2014a) found a similar shift, with a significant increase in the similarity of the oligotrophic component of lichen communities due to nitrogen accumulation. Grazing cessation leads to an overall reduction of functional diversity together with an increase in productivity through a shift from functional strategies devoted to grazing avoidance and tolerance to those devoted to competition for light and resource acquisition (Tardella and Catorci 2015). In fact, in abandoned grasslands, several studies assessed how the dominance of some grasses (e.g. *Brachypodium genuense*, Tardella et al. 2017; *Sesleria nitida*, Wellstein et al. 2014) influence community composition by competitive exclusion of subordinate species. Such dominance proved to be context dependent and related to functional traits. For instance, in central Apennines, *Brachypodium genuense* populations showed different strategies under different conditions (mesic vs. xeric), with a fast-growing strategy and high competitive ability (high SLA and plant height) in productive environments (Tardella et al. 2017). Even subordinate species, which often are highly palatable for wild herbivores (Corazza et al. 2016), showed different context-dependent trait-based strategies to coexist and to cope with the dominant species. Here, flowering, whole plant, seed, clonal and belowground traits played a key role (Halassy et al. 2005; Catorci et al. 2012b; Wellstein et al. 2014; Corazza et al. 2016). However, the impact of grazing on functional composition of grasslands may vary with climate, productivity, dominant life forms and may not be functionally related to direct herbivore damage (McIntyre et al. 1999 and references therein).

CSR plant strategy theory

Competitor, stress-tolerator, ruderal (CSR) plant strategy theory was conceived by Grime (1974, 1977, 2001) as a trade-off between three extreme adaptive trait syndromes that have evolved in response to competition (biotic limitations to biomass production), stress (abiotic limitations to productivity) and disturbance (biomass destruction). In Grime's most modern definition (Grime and Pierce 2012), these trait syndromes are supposed to facilitate the survival of genes via: '(C) the survival of the individual using traits

that maximise resource acquisition and resource control in consistently productive niches, (S) individual survival via maintenance of metabolic performance in variable and unproductive niches, or (R) rapid gene propagation via rapid completion of the lifecycle and regeneration in niches where events are frequently lethal to the individual'. This formulation has the advantage of being the only trait-based ecological strategy theory with empirical support across major taxonomic groups (Grime and Pierce 2012).

In terms of traits, the fundamental characters that can universally link CSR strategies in all organisms are the proportions of essential elements (especially carbon, nitrogen and phosphorus) 'invested in traits involved in resource acquisition, maintenance or regeneration'. Thus, the quantity of biomass produced is related to the amount of carbon acquired by organisms, and tissue density to the way in which essential elements are deployed for primary metabolism or reproduction. In a practical sense, plant traits that are measured include size traits such as leaf area or canopy height, resource-use and tissue density traits such as SLA and LDMC, respectively, or reproductive traits, particularly those involved in flowering and fruiting phenology (Hodgson et al. 1999; Pierce et al. 2013, 2017). These trait relationships have been confirmed to reflect fundamental underlying trade-offs throughout vascular plants (Diaz et al. 2016). Crucially, it is important to avoid the misconception that each trait is measured to represent either C, S or R: CSR values represent the balance between traits and thus the three-way trade-off. For example, the degree of 'C-selection' is never calculated from a single trait, but is weighted by all of the traits measured (Pierce et al. 2017).

The CSR approach proved to be suitable outside its original area of development (Britain), and to be consistent with traits variation in a broad sample of Italian species (including aquatic plants, Pierce et al. 2012) of the continental, sub-alpine and alpine bioclimatic zones (Cerabolini et al. 2010b), but also in coastal habitats (Ciccarelli 2015). Specifically, high elevation species were predominantly stress-tolerators but included some competitive-ruderals and ruderals (Figure 2(a); Caccianiga et al. 2006; Pierce et al. 2007a, 2007b; Gentili et al. 2013). Here, both abiotic stress resulting from a scarcity of resources and physical disturbance limited plant growth. Several studies conducted along transects in glacier forelands demonstrated a functional shift from broadly ruderal pioneers towards stress tolerance in late succession (Caccianiga et al. 2006; Gobbi et al. 2010). This shift was also reflected in phylogenetic changes, indicating that species sorting by environmental filtering tends to favor the co-occurrence of phylogenetically related species (Ricotta et al. 2015). Additionally, the progressive substitution of ruderal species by stress tolerators was accompanied by a constant and significant decrease in community-level functional diversity and uniqueness, meaning that the increased uniformity of vegetation structure over time goes together with an increase in functional redundancy (Ricotta et al. 2016). Till deposited at the retreating glacier terminus provides a substrate that can support faster growing species (with high foliar N contents), but is only tenable to those that can avoid physical disturbance via rapid phenological development (i.e. ruderals), while stress-tolerance (and lower N contents) in late succession suggested selection for efficient nutrient use (Caccianiga et al. 2006; Gobbi et al. 2010). Interestingly, such functional shifts (from R-strategists to Sstrategist) have been confirmed also in coastal dune primary successions (Ciccarelli 2015), suggesting that during primary successions there is a shift from ruderality to stress-tolerance across ecosystems (Figure 2(b)).

In sub-alpine secondary grasslands, the most abundant species were stress-tolerators, ruderals and competitive-ruderals, demonstrating the existence of contrasting opportunities for survival, based on nutrient availability and grazing pressure (Figure 2(c); Pierce et al. 2007a; Cerabolini et al. 2010a). In contrast, in lowland grasslands, species were predominantly competitive-ruderals but included some stress-tolerators (Pierce et al. 2007b). However, the number of strategies strongly depended on biomass production, with the higher values (also in terms of species richness and trait variance) occurring at intermediate biomass, while extremes of biomass production were associated with relatively few taxa exhibiting similar trait values and specialised strategies (Cerabolini et al. 2016).

Plant functional traits and ecological processes in coastal ecosystems

Plant functional traits gave useful insights into the temporal trends and into the conservation status of sandy coastal systems. Prisco et al. (2016) showed that a general increase in natural vegetation cover occurred in recent years in coastal protected areas, although this increase was mainly in the wooded dune habitats. Here, late-successional, tall-growing and large-seeded species showed the clearest signs of cover expansion. However, this expansion occurred in part at the expense of coastal dune grasslands, which thrive under the natural disturbance regimes of healthy coastal dune systems and have declined since the 1960s. In fact, the total cover of therophytes and species with high LDMC values has tended to decrease (Prisco et al. 2016). Then, by analyzing temporal trends in functional traits, Prisco et al. (2016) were able to determine which type of species were favoured and which were not, and why. Similarly, the functional approach was better than focusing solely on taxonomic diversity, for capturing the response of plant communities to spatial and temporal landscape patterns in coastal sand dunes. In fact, while taxonomic diversity only seemed to be moderately affected by landscape processes, this was not the case for functional diversity (Malavasi et al. 2016). In addition, Jucker et al. (2013) also found a negative association of both the taxonomical and the functional diversity of coastal dune communities with the level of invasion by a highly invasive alien species from South Africa (*Carpobrotus* spp.). By examining trait patterns, the authors hypothesized that this is likely the result of the selective exclusion of specific functional groups from the native community by this highly competitive alien plant, through a combination of niche- and fitness-related processes. Moreover, Stanisci et al. (2010) using a functional approach including belowground traits, pinpointed the characteristics of the most successful invaders among alien taxa in coastal sand dunes: large leaf area, biennial/annual life cycle, and thick and long roots.

Plant functional traits have also been useful to infer assembly rules in plant communities particularly along natural stress gradients, which have been extensively studied in coastal sand dunes. Specifically, by allowing the quantification of species' ecological niches, functional traits can be used to test the predominance of certain ecological filters along gradients, thereby allowing to make inferences on the processes behind the co-existence of species under different levels of abiotic stress. For example, coastal habitats closer to the sea (higher levels of environmental stress) were found to have higher proportions of specialized species. On the contrary, sheltered backdune habitats, at the other end of the gradient, were mostly dominated by generalists (Carboni et al. 2016). Recently, Conti et al. (2017) suggested that in order to assess the assembly processes underlying community patterns, it is revealing to analyze jointly the functional and the spatial patterns of species co-occurrences, as they can convey complementary information, while also accounting for the so-far overlooked role of micro-environmental heterogeneity. For example, in Central Italian coastal dunes, spatial segregation of species within communities was more common farther from the sea, suggesting the dominance of competitive processes in the least stressed communities. But in addition, whether the species coexisting within communities shared similar or highly divergent functional traits (i.e. plant height, seed mass, SLA), depended not only on the average stress level along the gradient, but also on the environmental heterogeneity within the community. Finally, functional patterns in coastal plant communities were also partly linked to phylogeny. At the overall species pool level, there was evidence of a phylogenetic signal in species traits (i.e. closely related species shared similar traits). However, while functional diversity among communities was closely mirrored by their phylogenetic variability, this was not the case for the communities' functional composition (Carboni et al. 2013). In conclusion, functional trait patterns have been shown to be useful to gain insights into the processes of both plant community assembly and invasion in coastal dune systems.

Plant functional traits and intraspecific variability

Most of the studies included species of montane primary and secondary grasslands (Wellstein et al. 2013; Catorci et al. 2014; Gratani et al. 2012, 2014; Puglielli et al. 2015a), with *Sesleria nitida* (Wellstein et al.

2013; Gratani et al. 2014; Puglielli et al. 2015a), an endemic grass of the montane belt of the Apennines, being the most represented. Such species showed significant intraspecific differences in trait attributes. In detail, leaf traits (mainly SLA or its inverse LMA, leaf tissue density, LTD, and leaf thickness, LT) of *S. nitida* were highly responsive to light availability (Puglielli et al. 2015a) and elevation (as proxy of temperature, Gratani et al. 2014), with mean plasticity index (PI, sensu Valladares et al. 2000) ranging from 0.05 to 0.32 (for SLA plasticity see Figure 3). However, Wellstein et al. (2013) showed a relatively low plasticity of leaf traits and plant height in two contrasting grasslands (mesic vs. xeric), while clonal traits demonstrated to be highly plastic. The investigated clonal traits were related to space occupancy and multiplication frequency and were regulated by soil nutrient and moisture availability.

Different studies focused on species of Mediterranean ecosystems using field observations (Crescente et al. 2002; Puglielli et al. 2017a; Gratani et al. 2018) and common garden approaches (Gratani et al. 2003; Catoni and Gratani 2013; Puglielli et al. 2017b). In particular, Crescente et al. (2002), Gratani et al. (2003) and Peguero-Pina et al. (2017) revealed significant levels of phenotypic plasticity for plant and leaf traits in *Quercus ilex* ecotypes. For example, PI for plant height was 0.50 for *Q. ilex* individuals growing at a climax area and at the northern distribution limit of the species in Italy (Crescente et al. 2002). At the leaf level, PI values for SLA and LTD ranged between 0.15–0.27 and 0.15–0.32, respectively, in *Q. ilex* plants grown from acorns sampled along an aridity gradient (Gratani et al. 2003). A remarkable leaf morphological plasticity of SLA and LT was also found in the widespread Mediterranean shrub *Cistus salvifolius* in response to a reduced light environment (Puglielli et al. 2017a). Moreover, SLA changes were also mostly related to changes in physiological and biochemical leaf traits revealing a long-term acclimation process of *C. salvifolius* to a low light environment. Also, within species inter-annual variability in anatomical components of LMA has been demonstrated to reduce net photosynthesis (on area basis) responsiveness to air temperature changes (Gratani et al. 2018). However, such relationship held only for evergreen sclerophyllous species compared to semi-deciduous ones, highlighting that interannual leaf plasticity patterns in response to temperature (and their relationship with photosynthesis) depend on leaf habitus within Mediterranean communities. At the within individual level, Puglielli et al. (2017b) demonstrated that different leaf cohorts of *Cistus* spp. are characterized by differences in leaf trait coordination patterns. Such strategy allows species to modulate resource-acquisition and use strategies with varying environmental conditions, highlighting another level of phenotypic plasticity. Relevant levels of phenotypic plasticity in leaf traits have been found also in *Fagus sylvatica*, *Picea excelsa* and *Populus nigra* along biogeographical gradients in studies conducted at continental scale, including Italy (Bauer et al. 1997; Kang et al. 2011; Guet et al. 2015).

The increased interest paid to the inclusion of intraspecific variability in ecological studies raised also the question whether different spatial levels could account for different proportion of traits' variability. As an example, Petruzzellis et al. (2017) compared variability patterns across multiple spatial scale of one morphological (SLA) and one physiological (leaf osmotic potential, p) functional trait in a population of *Q. ilex*. They found that the variability of SLA was mainly spread within individuals, while the variability of p was much higher between rather than within individuals of the same species. This difference opens interesting questions about the patterns of intraspecific trait variability in different species, encouraging future analyses including more traits and more species.

Aquatic environments and plant growth: Evidence from river and shallow inland ecosystems

River stretches, wetlands and eutrophic shallow lakes of the continental biogeographic region in northern Italy were the most studied environments. Several papers were focused on single species. Studies related to growth form and performance of *Phragmites australis* found significant differences in attributes according to site-specific ecological status. Flooded stands or sites with permanent submersion were characterized by high rates of clumping habit and dead apical bud, and lower culm diameters, showing

clear signs of plants dieback (Lastrucci et al. 2016, 2017). Other studies addressed the growth response of a rare fern, *Marsilea quadrifolia*, and a widespread opportunistic species, *Vallisneria spiralis*, respectively to sediment trophic level and physico-chemical water features, demonstrating a certain capacity of both species to grow under varying levels of nutrients in water and sediment (Bolpagni et al. 2015; Bolpagni and Pino 2017).

Finally, two studies focusing on plant-mediated gas exchange of *Trapa natans* clarified its pivotal role in inducing persistent hypoxia and anoxia in the colonized water bodies, and in conditioning CO₂ and CH₄ stand fluxes at the water-atmosphere interface (Bolpagni et al. 2007; Pierobon et al. 2010).

At community level, Oglio river wetlands (northern Italy) were studied in order to assess the effect of wetland origin (natural vs. artificial) and hydrology (lotic vs. lentic) in shaping growth forms composition of riverine wetland vegetation. In general, data revealed the predominance of terrestrial herbaceous species and the deterioration of the obligate aquatic plant contingent and the helophyte representativeness in such ecosystems (Bolpagni et al. 2013; Bolpagni and Piotti 2015, 2016). Wetlands origin and their structural complexity rather than hydrological features seemed to condition community composition in terms of growth forms (Bolpagni et al. 2013; Bolpagni and Piotti 2016).

Furthermore, some studies coupled the remote sensing approaches with field sampling in order to assess macrophyte growth forms distribution at different spatial scales along time or water feature gradients in lakes (Bolpagni et al. 2014; Villa et al. 2015, 2017). This constitutes a step forward for macrophyte traits mapping going beyond the local scale and can be used for supporting regional to continental monitoring of spatial and temporal dynamics of primary producers in freshwater ecosystems (Villa et al. 2015, 2017). Only one study was related to lichens (Nascimbene et al. 2009), evaluating the effectiveness and life-strategies of freshwater lichens in colonizing newly constructed stone structures in low-elevation streams. Size of thalli, morphological and ontogenetic traits of the species were influenced by the age of restored habitats.

Conclusions and future research perspectives

Our review represents the first comprehensive overview of the main findings in studies linking plant functional traits to environmental and human drivers in Italy. It can be a stepping stone to develop functional quantitative analyses of plant communities based on plant traits, especially in ecosystem services evaluations, and it can be a starting point to extend this comprehensive perspective beyond the national scale, to tie more firmly Italian researchers to international scientific networks on plant traits. We took note of species encountered while working at this review (looking at the considered papers and related supplementary materials), which traits have been studied at least once on a population located in Italy; we supply the species list in Supplementary Information Appendix 2. We found a surprisingly high number of traits available for 1080 vascular plants (of which only 3.2% endemics), mainly related to whole-plant, leaf, seed, phenology and flowering traits. On the contrary, we registered a lack of traits measurements for bryophytes and lichens. We also observed that functional traits of belowground organs (root and clonal traits) have been often neglected, despite the fact that these traits are extremely informative on resource acquisition strategies and other key functions, such as space occupancy, recovery after damage (Lambers et al. 2006; Lalibert_e 2017; Ottaviani et al. 2017) as well as other fundamental mechanisms such as plant–plant, plant–soil and plant–climate interactions. Also the availability of wood traits measured in Italy, which include a time factor since they can be dated within tree ring series (Baas et al. 2016; Beeckman 2016), could represent a valuable step forward in plant functional analysis at local scale. In the meantime, wood traits are available in TRY database (Kattge et al. 2011), or could be easily obtained from other sources (see Beeckman 2016).

We explored the TRY database (a global archive of plant traits, Kattge et al. 2011) found trait values for about 900 species deriving from Italian datasets (i.e. contributors with traits measurements carried out in

Italy). They were mainly related to leaf traits (Pierce et al. 2007a, 2007b, 2012, 2013, 2014b; Cerabolini et al. 2010a, 2010b; Campetella et al. 2011; Burrascano et al. 2015; Ciccarelli 2015; Giarrizzo et al. 2017). Combining the abovementioned information and the data collected in this review (Supplementary Information Appendix 2), we gathered information on plant traits measured on Italian populations for an overall total of 1418 taxa, which represent almost the 20% of the entire Italian vascular flora (Bartolucci et al. 2018). Most of this information is shared in TRY database, but not all (Figure 4). About 500 species whose traits measurements have been published in papers considered in this review are not available in TRY.

Moreover, 113 species among these (8% of the 1418 taxa) are totally missing in TRY database. Additionally, we explored the correspondence between the functional trait database for Mediterranean Basin plants (BROT 2.0, Tavs_ano_glu and Pausas 2018) and our data related to the Mediterranean biogeographic region (Supplementary Information Appendix 2, 126 taxa), assessing that 32 species (25% of the 126 taxa) are totally missing in BROT 2.0 database. It is therefore evident that Italian researchers can easily give a more effective contribution to TRY and BROT 2.0 databases and to global research, by sharing their own already published trait measurements. This could lead to an improving of the spatial coverage of the global and regional archives of plant traits and give a crucial contribution regarding plant communities still poorly investigated such as those of the Mediterranean region.

The plant traits approach holds promises in disentangling several issues still controversial in plant ecology. For example, the assessment of determinants responsible for the invasion potential of alien species is crucial in the light of the ongoing climate change. Recently, Petruzzellis et al. (2018) compared several functional and mechanistic (*sensu* Brodribb 2017) traits in a native and in an alien species in sites under different light regimes and suggested that a trade-off between hydraulic safety and resource acquisition and use efficiency could promote invasion by alien species.

Plant–animal interactions in pollination and dispersal, which influence the maintenance of plant populations and communities (Morales and Traveset 2008; Fantinato et al. 2018a) have been scarcely investigated by means of plant traits.

Recently floral traits, such as flowering phenology, floral morphology and anther position, have been proved to influence the co-existence of co-flowering species in species-rich communities (Fantinato et al. 2018b). Further investigations of trait-driven interactions might open new perspectives on plant–plant co-existence (Pauw 2018).

Intraspecific trait variability, which has a strong effect on the sampling size and effort (Petruzzellis et al. 2017), is still scarcely considered at population and community level, while intraspecific variability is often considered in ecophysiological studies. Moreover, we underline the need of approaches evaluating trait–environment relationships at broad spatial and temporal scales, possibly resulting from the collaboration of several research groups at national level, as well as analysis of traits variations along ecological gradients, in order to make predictions about land use and climate change impacts.

Italy could be a good regional model to explore emerging research fields in plant ecology, like those related to ecosystem services and functional biogeography. There is a growing evidence that plant traits considered at community level have strong effects on ecosystem processes underlying important ecosystem services (Suding and Goldstein 2008; Lavorel et al. 2011). Also functional biogeography (*i.e.* the study of the geographic distribution of trait diversity across organizational levels; Violle et al. 2014) could find a fertile ground in Italy, given its broad biogeographical range.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. Application fields of the most used plant functional traits in Italy with indications of the number of papers and biogeographic region (A: Alpine; C: Continental; M: Mediterranean; Roekaerts 2002).

Functional trait	Section						
	Impact of climate change on functional traits	Response of functional traits to forest management and eutrophication	Secondary grasslands, grazing and land-use change	CSR plant strategy theory	Plant functional traits and ecological processes in coastal ecosystems	Plant functional traits and intraspecific variability	Aquatic environments and plant growth: evidence from river and shallow inland ecosystems
Whole-plant traits							
Growth form		1 ^M	1 ^A		1 ^C , 4 ^M		5 ^C , 1 ^M
Life form	1 ^C	4 ^C , 1 ^M	1 ^A , 5 ^C	1 ^C	1 ^C , 6 ^M		
Canopy height		2 ^C , 1 ^M	1 ^A , 7 ^C	10 ^A , 3 ^C , 1 ^M	1 ^C , 10 ^M	4 ^C , 2 ^M	1 ^M
Leaf traits							
Specific leaf area	1 ^A , 1 ^C	2 ^C , 1 ^M	1 ^A , 4 ^C	11 ^A , 4 ^C , 1 ^M	1 ^C , 11 ^M	3 ^C , 2 ^M	
Leaf dry matter content	1 ^A		2 ^C	11 ^A , 4 ^C , 1 ^M	1 ^C , 10 ^M	1 ^C	
Leaf anatomy		3 ^C	3 ^C				
Leaf N	4 ^A , 1 ^C		2 ^C	3 ^A , 2 ^C		1 ^A , 1 ^C , 1 ^M	
Leaf persistence		1 ^C	5 ^C		1 ^C , 3 ^M	1 ^C , 1 ^M	
Leaf thickness			1 ^M		3 ^M	3 ^C , 4 ^M	
Leaf mass per area	2 ^M					4 ^C , 6 ^M	
Seed / Dispersal traits							
Seed germination	6 ^A , 1 ^C , 1 ^M					1 ^C	
Seedling recruitment	1 ^A						
Seed dormancy	2 ^A						
Seed mass	1 ^A	5 ^C , 1 ^M	1 ^A , 3 ^C	1 ^A , 2 ^C	1 ^C , 6 ^M	1 ^C	
Seed dispersal		4 ^C , 2 ^M			1 ^C , 6 ^M		1 ^A
Phenology / Flowering traits							
Inflorescence production	4 ^A , 1 ^C		4 ^C				1 ^M
Flowering time	3 ^A	4 ^C	7 ^C , 1 ^M	8 ^A , 3 ^C , 1 ^A	1 ^C , 3 ^M		
Pollination system		2 ^C	1 ^A , 1 ^C		1 ^C , 4 ^M		
Clonal traits							
Vegetative propagation		3 ^C , 2 ^M	7 ^C		1 ^C , 4 ^M		
Lateral spread		3 ^C	1 ^C	4 ^A , 2 ^C		1 ^C	
Spacers length		2 ^C	1 ^C			1 ^C	
Multiplication frequency		2 ^C				1 ^C	
Root traits							
Fine-root biomass		2 ^A	1 ^A			1 ^A , 1 ^C	
Fine-root turnover rate		2 ^A					
Fine-root C:N ratio		2 ^A	1 ^A				
Fine-root seasonal pattern		2 ^A					
Specific root length		2 ^A			1 ^M	1 ^M	
Biogeogr. Region representativeness (%)							
A	77	18	13	62	0	5	11
C	13	66	85	32	12	54	56
M	10	16	3	6	88	41	33

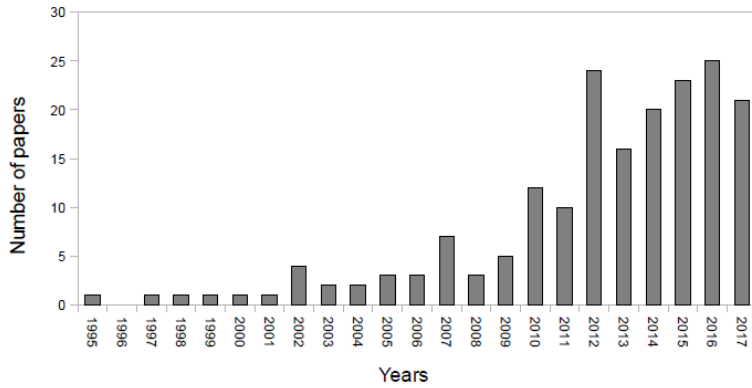
Table 2. Main topics 1195 and related papers for each section.

Section	Topic	n	References
3.1. Impact of climate change on functional traits	Manipulation experiments: warmer conditions	8	Mondoni et al. 2012, 2015; Wellstein & Cianfaglione 2014; Orsenigo et al. 2015; Bernareggi et al. 2016, 2016; Carbonegani et al. 2016; Gavrichkova et al. 2017
	Manipulation experiments: drought	3	Wellstein & Cianfaglione 2014; Orsenigo et al. 2017; Wellstein et al. 2017
	Manipulation experiments: reduced snow cover	1	Gerdol et al. 2013a
	Manipulation experiments: N and P deposition	6	Gerdol et al. 2002, 2008; Bragazza et al. 2012; Petraglia et al. 2013, 2014a,b
	Temporal gradients and space-for-time substitution	6	Bussotti et al. 2002; Abeli et al. 2012a,b; Dainese 2012; Salvatori et al. 2016; Evangelista et al. 2016
3.2. Response of functional traits to forest management and eutrophication	Effects of climate change on lichens	6	Marini et al. 2011; Giordani et al. 2012; Favero-Longo et al. 2014; Nascimbene & Marini 2015; Nascimbene et al. 2017; Giordani et al. 2014c
	Regeneration after coppicing	4	Canullo et al. 2011, 2017; Campetella et al. 2011; Catorci et al. 2012a
	Comparison between types of management	8	Scolastri et al. 2017; Montagnoli et al. 2012a; Terzaghi et al. 2013; Ricotta & Burrascano 2008; Burrascano et al. 2009; Nascimbene et al. 2007, 2008; Terwei et al. 2016
	Response to atmospheric deposition	3	Giordani et al. 2012, 2014; Giordani & Malaspina 2016
3.3. Secondary grasslands, grazing and land-use change	Comparison between land-uses	8	Catorci et al. 2011b,c,d; Catorci et al. 2012d; 2014a,b; 2013b; Targetti et al. 2013
	Gradients of stress and disturbance	6	Bagella et al. 2013a; Giordani et al. 2014a; Tardella & Catorci 2015; Catorci et al. 2016, 2017; Giarrizzo et al. 2017
	Abandonment under different environmental conditions	4	Halassy et al. 2005; Wellstein et al. 2014; Corazza et al. 2016; Tardella et al. 2017
	Belowground and flowering traits	3	Montagnoli et al. 2010; Catorci et al. 2012b; Bagella et al. 2013b
3.4. CSR plant strategy theory	Environmental and climatic gradients	6	Pierce et al. 2007b, 2012; Cerabolini et al. 2010b, 2016; Gentili et al. 2013; Ciccarelli 2015
	Disturbance gradients	2	Pierce et al. 2007a; Cerabolini et al. 2010a
	Primary successions	4	Caccianiga et al. 2006; Gobbi et al. 2010; Ricotta et al. 2015, 2016
	Biotic gradients and relationships	3	Pierce et al. 2014a,b; Caccianiga et al. 2012
	Forest management and fragmentation	2	Catorci et al. 2011a; Buffa & Villani 2012
3.5. Plant functional traits and ecological processes in coastal ecosystems	Conservation status and invasive species	7	Malavasi et al. 2016; Prisco et al. 2016; Acosta et al. 2006; Stanisci et al. 2010; Pisanu et al. 2011; Jucker et al. 2013; Marcantonio et al. 2014
	Assembly rules	5	Carboni et al. 2013, 2016; Ricotta et al. 2014, 2015; Conti et al. 2017
	Functional aspects of specific taxa	3	Pisanu et al. 2011, 2012; Giordani et al. 2015a; Ciccarelli et al. 2016
3.6. Plant functional traits and intraspecific variability	Bryophytes	4	Gerdol 1995, 2002; Gerdol & Bragazza 2006; Spitale & Petraglia 2010
	Vascular plants under field conditions	12	Crescente et al. 2002; Gratani et al. 2012, 2014, 2018; Wellstein et al. 2013; Catorci et al. 2014c; Bauer et al. 1997; Kang et al. 2011; Montagnoli et al. 2012b, 2014; Puglielli et al. 2015a, 2017a
	Vascular plants under common garden conditions	5	Gratani et al. 2003; Catoni & Gratani 2013; Guet et al. 2015; Puglielli et al. 2017b; Peguero-Pina et al. 2017
3.7. Aquatic environments and plant growth: evidence from river and shallow inland ecosystems	Wetland origin, hydrology, water levels, biogeography	6	Bolpagni et al. 2013; Bolpagni & Piotti 2015, 2016; Lastrucci et al. 2016, 2017; Villa et al. 2015
	Physico-chemical water features	2	Bolpagni et al. 2014, 2015
	Sediment trophic level and chemistry	2	Lastrucci et al. 2016; Bolpagni & Pino 2017
	Time/seasons and phenological phases	3	Bolpagni et al. 2007; Pierobon et al. 2010; Villa et al. 2015
	Trade offs	1	Pierce et al. 2012

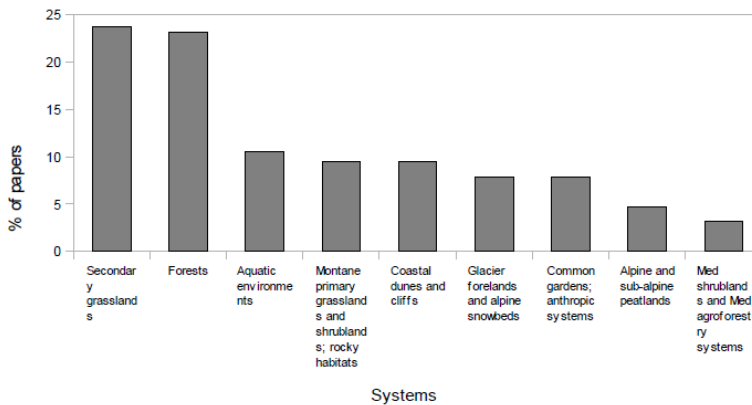
FIGURES

Figure 1. Italian studies on functional traits in relation to environmental variables/gradients: (a) temporal trend in the number of papers published per year; (b) distribution of the collected papers regarding studied ecosystems; (c) number of vascular plant species accounted for the most frequently investigated functional traits.

(a)



(b)



(c)

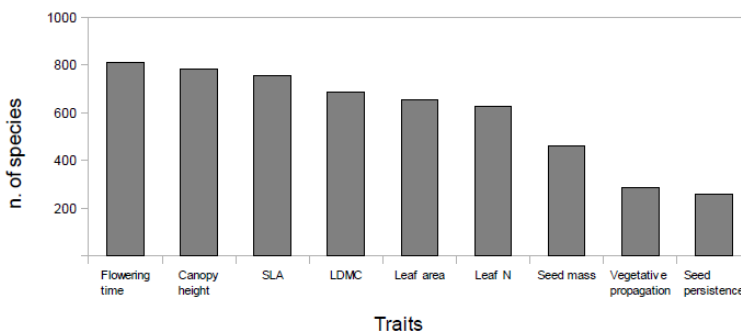


Figure 2. CSR triangles synthesizing general mean strategies and shifts of vegetation along gradients of (a) increasing elevation (based on Caccianiga et al. 2006; Pierce et al. 2007a,b; Gentili et al. 2013), (b) primary successions, including glacier forelands and coastal dunes (based on Caccianiga et al. 2006; Gobbi et al. 2010; Ciccarelli 2015), and (c) grazing abandonment (based on Pierce et al. 2007a; Cerabolini et al. 2010a).

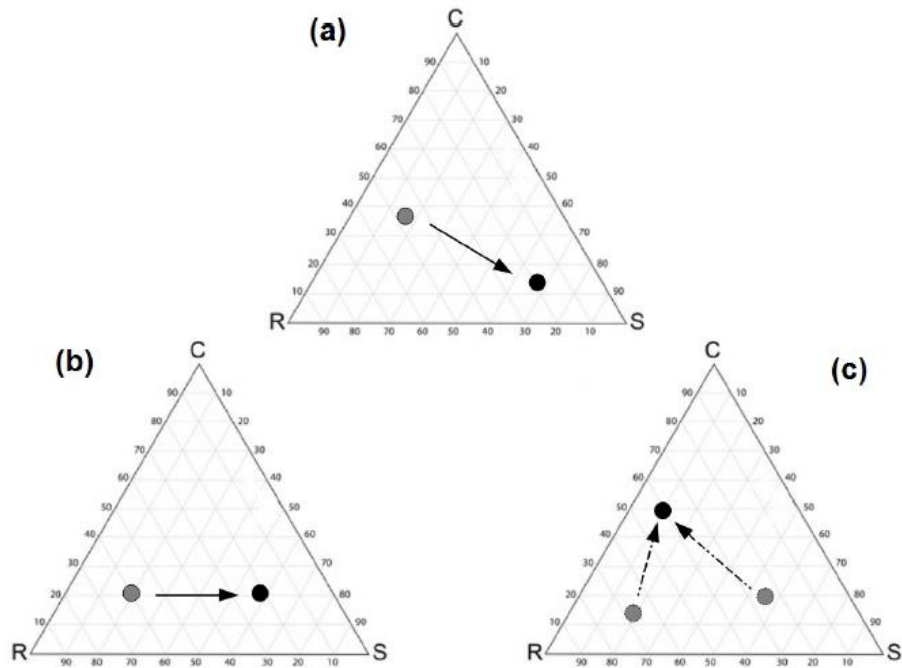


Figure 3. Maximum values of plasticity index (PI, sensu Valladares et al. 2000) of Specific Leaf Area for the endemic *Sesleria nitida* in different environments or along gradients (altitude, Gratani et al. 2014; natural environment vs. pot grown plants, Puglielli et al. 2015b; Light, Puglielli et al. 2015a; soil nutrient and moisture, Wellstein et al. 2013; rainfall manipulation, Wellstein et al. 2017).

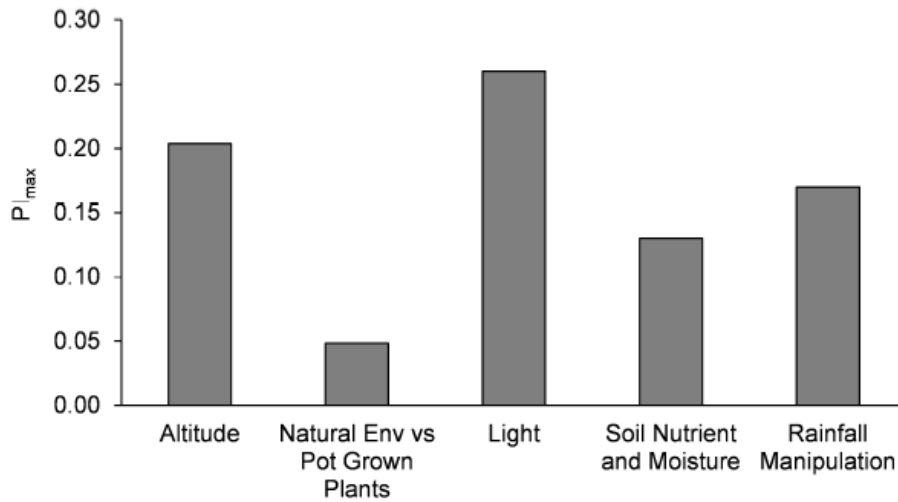


Figure 4. Gathered information on plant traits of Italian populations deriving from our review (Appendix 2) and the Italian contributors to TRY, for an overall total of 1418 taxa, almost the 20% of the entire Italian vascular flora (Bartolucci et al. 2018). Traits measurements of about 900 species (65% of the 1418 taxa) are already shared in TRY database (i.e. species found both in the reviewed papers and in the Italian datasets contributing to TRY, or species found only in the Italian datasets contributing to TRY), while trait values for 502 species (35% of the 1418 taxa) recorded by this review are not available in TRY; among these latter, 113 species (8% of the 1418 taxa) are totally missing in TRY.

