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3 PLANT-ENVIRONMENT INTERACTIONS THROUGH A FUNCTIONAL TRAITS
4 PERSPECTIVE: A REVIEW OF ITALIAN STUDIES
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71 **Abstract**

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

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88 **Keywords:** Climate change; CSR plant strategy theory; Forest management; Intraspecific
89 variability; Land use change; Plant traits, Terrestrial and Freshwater environments.

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106 **1. INTRODUCTION**

107 Processes shaping vegetation patterns have traditionally been approached by analyzing spatial and
108 temporal changes in plant species composition (McGill et al. 2006). Species identity provides
109 important information for ecological and evolutionary studies, however, this information alone does
110 not effectively contribute to the understanding of ecosystem functioning (Westoby et al. 2002;
111 Garnier et al. 2004). Considering the huge number of plant species and their uneven geographical
112 distribution, models based on species identity cannot be generalized or easily transferred to areas
113 with a different flora (Keddy 1992). Even though non-taxonomic classifications of plants have a
114 very long history (Garnier et al. 2016), the trait-based approach in ecology has substantially
115 developed over the last three decades, thanks also to the impulse of studies on global environmental
116 changes (Smith et al. 1997).

117 Plant Functional Traits are defined as "any morphological, anatomical, biochemical, physiological
118 or phenological heritable feature measurable at the individual level, from the cell to the whole-
119 organism level" (Garnier et al. 2017) that impacts plant species fitness affecting growth,
120 reproduction, resource use, establishment, etc. (Garnier and Navas 2012). Traits mediate the
121 response of plants to the environment (Lavorel and Garnier 2002), and influence ecosystem
122 functioning (Kattge et al. 2011). Accordingly, they are used in ecological research (Violle et al.
123 2007) to address fundamental questions including i) the responses of functional traits to different
124 environmental gradients at the species and community level, ii) the identification of rules governing
125 the assembly of communities, and iii) the relationships between plant functional traits and
126 ecosystem services (Garnier et al. 2016 and references therein). In spite of this, several major issues
127 in trait-based ecology still lack sufficient empirical evaluation (Shipley et al. 2016).

128 Italy is the European country with the highest number of native vascular plant species and
129 subspecies (Bartolucci et al. 2018); at the same time it has a long history of human pressures on the
130 environment that still influences a wide range of ecosystems. Such a high plant diversity derives
131 from a wide latitudinal gradient and from the remarkable heterogeneity in terms of climate and
132 physiography, along with a complex biogeographic evolution (Smiraglia et al. 2013; Blasi et al.
133 2014). These conditions allow for a broad variety of natural vegetation types (Blasi et al. 2010) that
134 is enriched by the occurrence of semi-natural ones, deriving from the long history of human
135 activities (Capotorti et al. 2012). In parallel, global changes are shaping biodiversity and ecosystem
136 functioning in Italy with different patterns and rates across the various environments (Chelli et al.
137 2017). For instance, due to the ongoing climate change, Italy results one of the European countries
138 most prone to extreme drought (Spinoni et al. 2018) and temperature increase (Rogora et al. 2018).
139 Its forests were subjected to timber exploitation since the Roman times (Vacchiano et al. 2017), and
140 it is now undergoing land-use change at very high rate with a consistent process of reforestation and

141 a steady decrease of pasture extent (Falcucci et al. 2007; Malavasi et al. 2018). Furthermore, its
142 sandy shorelines have been heavily transformed in the last 60 years with considerable loss or
143 modification of natural vegetation (Malavasi et al. 2013). For these reasons, the analysis of
144 environmental and human-related gradients, as well as the mechanisms through which these
145 gradients shape community composition and determine specific ecosystem services is particularly
146 challenging in Italy. In this view, Italy may serve as a model region to test the effectiveness of trait-
147 based approaches.

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

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

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

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161 **2. MATERIALS AND METHODS**

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

171 In general, studies were included if meeting the following criteria: i) performed in Italy, ii)
172 published in peer-reviewed journals, iii) focused on the relationship of response and/or effect traits
173 (sensu Lavorel and Garnier 2002) of vascular plants, bryophytes and lichens to environmental
174 variables/gradients. The review has a broad focus on the plant functional traits approach, it includes
175 studies based on both field/greenhouse measurements of traits according to standard methods and

176 on traits collected from databases aimed at gaining deeper insights into ecological functioning at
177 species and community levels in terrestrial and freshwater environments. We excluded studies
178 related to marine environments, crops, and those based on modelling, pollen analysis,
179 bioaccumulation, phytoremediation, and dendroecology.

180 Altogether, 188 articles were identified and included in the review (Appendix 1). The following
181 main topics were recognized: (a) impact of climate change on functional traits; (b) response of
182 functional traits to forest management and eutrophication; (c) secondary grasslands, grazing and
183 land-use change; (d) CSR plant strategy theory; (e) plant functional traits and ecological processes
184 in coastal ecosystems; (f) plant functional traits and intraspecific variability; (g) aquatic
185 environments and plant growth: evidence from river and shallow inland ecosystems (Table 1, 2).

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187 **3. RESULTS AND DISCUSSION**

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

197 For vascular plants, we discuss traits belonging to the following categories: whole-plant traits
198 (Kleyer et al. 2008; Pérez-Harguindeguy et al. 2013), leaf traits (Pérez-Harguindeguy et al. 2013;
199 Garnier et al. 2017), seed and dispersal traits (or regenerative traits, *sensu* Pérez-Harguindeguy et al.
200 2013), phenology and flowering traits (Kühn et al. 2004), clonal traits (Klimešová et al. 2017), root
201 traits (or belowground traits, *sensu* Pérez-Harguindeguy et al. 2013; Garnier et al. 2017). Among
202 these, leaf (28%) and whole-plant traits (27%) were used with a similar relatively high frequency.
203 Phenological, seed and clonal traits were also well represented (17%, 12% and 9%, respectively),
204 while few papers dealt with root traits (2%). Canopy height, specific leaf area (SLA), flowering
205 phenology, seed mass, leaf dry matter content (LDMC), leaf nitrogen, and vegetative propagation
206 were the most frequently used plant functional traits (at least in 20 papers). These are commonly
207 recognized as key traits related to fundamental plant challenges (dispersal, establishment,
208 persistence; Weiher et al. 1999) and are inherent to major ecological strategy theories, such as (i)
209 the Leaf-Height-Seed plant ecology strategy scheme (including SLA, canopy height and seed mass;
210 Westoby et al. 1998), (ii) the CSR strategy scheme (SLA, LDMC; Grime and Pierce 2012; Pierce et

211 al. 2013), and (iii) the Leaf Economics Spectrum (Wright et al. 2004).

212 For bryophytes, we selected the following categories according to Cornelissen et al. (2007): tissue
213 chemistry traits, carbon gain related traits, traits related to carbon and nutrient losses (litter
214 chemistry), other morphological and cytological traits. The most represented were tissue chemistry
215 traits and traits related to carbon and nutrient loss, but only in studies conducted in the alpine
216 biogeographic region.

217 All functional traits considered were primarily measured from specimens collected in the field. In
218 detail, traits were measured for 1080 vascular plant and 15 bryophyte species (Appendix 2).
219 Flowering phenology was the functional trait more frequently measured on vascular plant species
220 (>800 species), followed by canopy height and SLA (>700 species; Fig. 1c). In contrast, functional
221 traits of lichens were obtained mainly from databases (i.e. *Italic 5.0*; Nimis and Martellos 2017).

222 In Italy, plant functional traits have been used to answer many ecological questions (Table 1): many
223 traits have been used in studies dealing with forest management, grazing and land-use change, but
224 with discrepancies among biogeographic regions (Table 1). On the contrary, few traits were used in
225 aquatic environments. Additionally, clonal and root traits were never considered in studies on
226 climate change.

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228 **3.1. Impact of climate change on functional traits**

229 Studies were conducted through manipulation experiments or observational approaches.
230 Experiments dealing with seed traits were performed by exposing parental alpine plants or
231 dispersed seeds to warming. Seeds produced by plants exposed to moderate warming (+1.5°C) were
232 more resistant to heat (Bernareggi et al. 2015) and showed changed germination/dormancy
233 responses as compared to controls, with deeper and less dormant seeds showing major changes in
234 response to incubation temperatures and to cold stratification periods, respectively (Bernareggi et al.
235 2016). Alpine plant seeds directly exposed to warming after dispersal showed a general increase in
236 germination rate both in spring and autumn, with a subsequent high percentage of seedling survival
237 in winter (Mondoni et al. 2012, 2015; Orsenigo et al. 2015). Exposure of seeds of two
238 Mediterranean annual species to water stress led to reduced and delayed germination with
239 contrasting responses among populations, revealing a possible adaptation to drought stress in the
240 southernmost population (Orsenigo et al. 2017).

241 Experiments focused on flowering time revealed a plastic response to changing micro-climatic
242 conditions, both for snowbed-specialized and alpine generalist species (Petraglia et al. 2014b,
243 Carbognani et al. 2016). Petraglia et al. (2014b) showed that for many species, flowering time was
244 tuned by snowmelt date and temperature. However, Carbognani et al. (2016) highlighted the
245 importance of timescale of the observations, with snowmelt time playing a major role at annual

246 scale and temperature at the growing season timescale. Even observational approaches studying
247 flowering of primary grasslands species in N-Apennines showed a plastic response of different
248 species. In general, inflorescence production was affected by mean summer temperature, suggesting
249 a change in reproductive strategies (e.g. changes in the ratio sexual/clonal reproduction, Abeli et al.
250 2012a). However, snow cover persistence was also a relevant driver of the reproductive effort in
251 some species, with a significant decrease of inflorescence production with reduced snow cover
252 persistence both in primary grasslands (Abeli et al. 2012b) and dwarf-shrub heath (Gerdol et al.
253 2013a).

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

260 Analysis of plant trait turnover through long-term observations revealed significant floristic and
261 functional changes over the last 42 years in alpine and subalpine grasslands of central Apennines,
262 with an increase in thermophilous, nitrophilous and mesophilous plant species and an increment in
263 the frequency of hemicryptophytes (Evangelista et al. 2016). These changes are likely attributable
264 to the combined effect of higher temperatures and the increase in soil nutrients triggered by global
265 change. A thermophilization trend has been also documented in several European mountains and
266 have been related mainly to the effects of climate change (e.g. Britton et al. 2009; Engler et al.
267 2011; Gottfried et al. 2012; Frate et al. 2018). Accordingly, recent evidence (e.g., Spasojevic et al.
268 2013) suggests that variations in nutrient availability, soil moisture and temperature led to changes
269 in the functional composition of alpine plant communities with a shift towards more resource
270 acquisitive functional traits (e.g., hemicryptophytes with well-developed leaves).

271 Among the papers dealing with lichens, photobiont type, thallus growth forms and dispersal
272 strategy were the most studied functional traits, at national (Marini et al. 2011; Giordani et al. 2012)
273 or local level, spanning from glacier forelands to Mediterranean systems (Favero-Longo et al. 2014;
274 Nascimbene and Marini 2015; Nascimbene et al. 2017; Giordani et al. 2014c). Thallus growth form
275 and photobiont type were responsive to climate factors in several ecosystems both at national
276 (Marini et al. 2011; Giordani et al. 2012) and local level (Nascimbene and Marini 2015;
277 Nascimbene et al. 2017), representing a promising tool for detecting the effects of climate change
278 on lichen species. For instance, thallus growth forms showed contrasting patterns related to
279 temperature in forest ecosystems, with crustose species being enhanced by warming, and fruticose
280 and foliose lichens being negatively impacted by warming (Nascimbene and Marini 2015). Also

281 photobiont type (i.e. the photosynthetic partner of the lichen symbiosis) showed differential
282 response to climate variables: despite the general dependence of lichens on water supply, lichens
283 characterized by Trentepohlia algae were further enhanced by warming, while species richness of
284 lichens characterized by cyanobacteria was only related to precipitation (Marini et al. 2011).

285

286 **3.2. Response of functional traits to forest management and eutrophication**

287 Understory species compositional changes during the regeneration phases after coppicing appeared
288 to be driven by plant functional traits, in particular leaf, clonal and reproductive traits (Canullo et al.
289 2011, 2017; Campetella et al. 2011; Catorci et al. 2012a). In detail, changes in environmental
290 conditions during the forest regeneration after coppicing filtered species with high SLA values
291 (Campetella et al. 2011; Catorci et al. 2012a), short-distance dispersal (Campetella et al. 2011),
292 early leaf and flower production (Catorci et al. 2012a) and high mobility due to stem-derived clonal
293 growth organs (i.e. hypogeogenous rhizomes; Canullo et al. 2011, 2017). Additionally, understory
294 traits composition was influenced by the presence of the alien trees *Prunus serotina* and *Robinia*
295 *pseudoacacia* but with different impact, suggesting the importance of different management and
296 control strategies (Terwei et al. 2016).

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

311 For lichens, three functional traits were mainly considered, namely photobiont type, thallus growth
312 forms and dispersal strategy. Lichens were sensitive to forest management (Nascimbene et al. 2007;
313 Nascimbene et al. 2008). In particular, the release of deadwood in managed forests was a key factor
314 for the maintainance of lichens functional diversity. The occurrence of deadwood in different decay
315 status supported a broad lichen community (Nascimbene et al. 2008). Lichen growth form was the

316 most responsive trait and was considered a reliable indicator for evaluating and comparing the
317 responses of epiphytic lichens to atmospheric deposition in forests across diverse regions (Giordani
318 et al. 2012; Giordani et al. 2014). In particular, Giordani et al. (2014) showed that the percentage of
319 macrolichens was the most reliable indicator, since 56.7% of its variation could be explained by
320 nitrogen deposition. Moreover, both narrowly lobed and broadly lobed foliose lichens were
321 negatively affected by acidic deposition, while narrowly lobed species were also negatively
322 influenced by increasing concentrations of SO_4^{2-} (Giordani et al. 2012). Under high eutrophication
323 levels, differences in tree-related factors were not related to significant differences in epiphytic
324 lichen communities composition (Giordani & Malaspina 2016). In fact, different epiphytic lichen
325 functional groups with different nitrogen tolerances responded to several atmospheric pollutants,
326 which had both independent and joint effects, whereas they did not show significant differences
327 depending on bark pH.

328

329 **3.3. Secondary grasslands, grazing and land-use change**

330 Changes in grazing intensity produced significant changes in species and functional traits
331 composition in montane grasslands (Catorci et al. 2016; Giarrizzo et al. 2017). The increase in
332 grazing pressure produced an increase in species showing traits associated with frequent disturbance
333 (Giarrizzo et al. 2017), usually poorly palatable and characterized by strong grazing avoidance
334 strategies (Catorci et al. 2016). In lichens, Giordani et al. (2014a) found a similar shift, with a
335 significant increase in the similarity of the oligotrophic component of lichen communities due to
336 nitrogen accumulation. Grazing cessation leads to an overall reduction of functional diversity
337 together with an increase in productivity through a shift from functional strategies devoted to
338 grazing avoidance and tolerance to those devoted to competition for light and resource acquisition
339 (Tardella & Catorci 2015). In fact, in abandoned grasslands several studies assessed how the
340 dominance of some grasses (e.g. *Brachypodium genuense*, Tardella et al. 2017; *Sesleria nitida*,
341 Wellstein et al. 2014) influence community composition by competitive exclusion of subordinate
342 species. Such dominance proved to be context-dependent and related to functional traits. For
343 instance, in central Apennines, *Brachypodium genuense* populations showed different strategies
344 under different conditions (mesic vs xeric), with a fast-growing strategy and high competitive
345 ability (high SLA and plant height) in productive environments (Tardella et al. 2017). Even
346 subordinate species, which often are highly palatable for wild herbivores (Corazza et al. 2016),
347 showed different context-dependent trait-based strategies to coexist and to cope with the dominant
348 species. Here, flowering, whole plant, seed, clonal and belowground traits played a key role
349 (Halassy et al. 2005; Catorci et al. 2012b; Wellstein et al. 2014; Corazza et al. 2016). However, the
350 impact of grazing on functional composition of grasslands may vary with climate, productivity,

351 dominant life forms and may not be functionally related to direct herbivore damage (McIntyre et al.
352 1999, and references therein).

353

354 **3.4. CSR plant strategy theory**

355 Competitor, stress-tolerator, ruderal (CSR) plant strategy theory was conceived by Grime (1974,
356 1977, 2001) as a trade-off between three extreme adaptive trait syndromes that have evolved in
357 response to competition (biotic limitations to biomass production), stress (abiotic limitations to
358 productivity) and disturbance (biomass destruction). In Grime's most modern definition (Grime &
359 Pierce 2012) these trait syndromes are supposed to facilitate the survival of genes via: "(C) the
360 survival of the individual using traits that maximise resource acquisition and resource control in
361 consistently productive niches, (S) individual survival via maintenance of metabolic performance in
362 variable and unproductive niches, or (R) rapid gene propagation via rapid completion of the
363 lifecycle and regeneration in niches where events are frequently lethal to the individual". This
364 formulation has the advantage of being the only trait-based ecological strategy theory with
365 empirical support across major taxonomic groups (Grime & Pierce 2012).

366 In terms of traits, the fundamental characters that can universally link CSR strategies in all
367 organisms are the proportions of essential elements (especially carbon, nitrogen and phosphorus)
368 "invested in traits involved in resource acquisition, maintenance or regeneration". Thus, the
369 quantity of biomass produced is related to the amount of carbon acquired by the organism, and
370 tissue density to the way in which essential elements are deployed for primary metabolism or
371 reproduction. In a practical sense, plant traits that are measured include size traits such as leaf area
372 or canopy height, resource-use and tissue density traits such as SLA and LDMC, respectively, or
373 reproductive traits, particularly those involved in flowering and fruiting phenology (Hodgson et al.
374 1999; Pierce et al. 2013, 2017). These trait relationships have been confirmed to reflect fundamental
375 underlying trade-offs throughout vascular plants (Díaz et al. 2016). Crucially, it is important to
376 avoid the misconception that each trait is measured to represent either C, S, or R: CSR values
377 represent the balance between traits and thus the three-way trade-off. For example, the degree of
378 'C-selection' is never calculated from a single trait, but is weighted by all of the traits measured
379 (Pierce et al. 2017).

380 The CSR approach proved to be suitable outside its original area of development (Britain), and to
381 be consistent with traits variation in a broad sample of Italian species (including aquatic plants,
382 Pierce et al. 2012) of the continental, sub-alpine and alpine bioclimatic zones (Cerabolini et al.
383 2010b), but also in coastal habitats (Ciccarelli 2015). Specifically, high elevation species were
384 predominantly stress-tolerators but included some competitive-ruderals and ruderals (Fig. 2a;
385 Caccianiga et al. 2006; Pierce et al. 2007a,b; Gentili et al. 2013). Here, both abiotic stress resulting

386 from a scarcity of resources and physical disturbance limited plant growth. Several studies
387 conducted along transects in glacier forelands demonstrated a functional shift from broadly ruderal
388 pioneers towards stress tolerance in late succession (Caccianiga et al. 2006; Gobbi et al. 2010). This
389 shift was also reflected in phylogenetic changes, indicating that species sorting by environmental
390 filtering tends to favor the co-occurrence of phylogenetically related species (Ricotta et al. 2015).
391 Additionally, the progressive substitution of ruderal species by stress tolerators was accompanied by
392 a constant and significant decrease in community-level functional diversity and uniqueness,
393 meaning that the increased uniformity of vegetation structure over time goes together with an
394 increase in functional redundancy (Ricotta et al. 2016). Till deposited at the retreating glacier
395 terminus provides a substrate that can support faster growing species (with high foliar N contents),
396 but is only tenable to those that can avoid physical disturbance via rapid phenological development
397 (i.e. ruderals), while stress-tolerance (and lower N contents) in late succession suggested selection
398 for efficient nutrient use (Caccianiga et al. 2006; Gobbi et al. 2010). Interestingly, such functional
399 shifts (from R-strategists to S-strategist) have been confirmed also in coastal dune primary
400 successions (Ciccarelli 2015), suggesting that during primary successions there is a shift from
401 ruderality to stress-tolerance across ecosystems (Fig. 2b).

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

410

411 **3.5. Plant functional traits and ecological processes in coastal ecosystems**

412 Plant functional traits gave useful insights into the temporal trends and into the conservation status
413 of sandy coastal systems. Prisco et al. (2016) showed that a general increase in natural vegetation
414 cover occurred in recent years in coastal protected areas, although this increase was mainly in the
415 wooded dune habitats. Here, late-successional, tall-growing and large-seeded species showed the
416 clearest signs of cover expansion. However, this expansion occurred in part at the expense of
417 coastal dune grasslands, which thrive under the natural disturbance regimes of healthy coastal dune
418 systems, and have declined since the 1960s. In fact, the total cover of therophytes and species with
419 high LDMC values has tended to decrease (Prisco et al. 2016). Then, by analyzing temporal trends
420 in functional traits, Prisco et al. (2016) were able to determine which type of species were favoured

421 and which were not, and why. Similarly, the functional approach was better than focusing solely on
422 taxonomic diversity, for capturing the response of plant communities to spatial and temporal
423 landscape patterns in coastal sand dunes. In fact, while taxonomic diversity seemed to be only
424 moderately affected by landscape processes, this was not the case for functional diversity (Malavasi
425 et al. 2016). In addition, Jucker et al. (2013) also found a negative association of both the
426 taxonomical and the functional diversity of coastal dune communities with the level of invasion by
427 a highly invasive alien species from South Africa (*Carpobrotus* spp.). By examining trait patterns,
428 the authors hypothesized that this is likely the result of the selective exclusion of specific functional
429 groups from the native community by this highly competitive alien plant, through a combination of
430 niche- and fitness-related processes. Moreover, Stanisci et al. (2010) using a functional approach
431 including belowground traits, pinpointed the characteristics of the most successful invaders among
432 alien taxa in coastal sand dunes: large leaf area, biennial/annual life cycle and thick and long roots.
433 Plant functional traits have also been useful to infer assembly rules in plant communities
434 particularly along natural stress gradients, which have been extensively studied in coastal sand
435 dunes. Specifically, by allowing the quantification of species' ecological niches, functional traits can
436 be used to test the predominance of certain ecological filters along gradients, thereby allowing to
437 make inferences on the processes behind the co-existence of species under different levels of abiotic
438 stress. For example, coastal habitats closer to the sea (higher levels of environmental stress) were
439 found to have higher proportions of specialized species. On the contrary, sheltered backdune
440 habitats, at the other end of the gradient, were mostly dominated by generalists (Carboni et al.
441 2016). Recently, Conti et al. (2017) suggested that in order to assess the assembly processes
442 underlying community patterns, it is revealing to analyze jointly the functional and the spatial
443 patterns of species co-occurrences, as they can convey complementary information, while also
444 accounting for the so-far overlooked role of micro-environmental heterogeneity. For example, in
445 Central Italian coastal dunes, spatial segregation of species within communities was more common
446 farther from the sea, suggesting the dominance of competitive processes in the least stressed
447 communities. But in addition, whether the species coexisting within communities shared similar or
448 highly divergent functional traits (i.e. plant height, seed mass, SLA), depended not only on the
449 average stress level along the gradient, but also on the environmental heterogeneity within the
450 community. Finally, functional patterns in coastal plant communities were also partly linked to
451 phylogeny. At the overall species pool level, there was evidence of a phylogenetic signal in species
452 traits (i.e. closely related species shared similar traits). However, while functional diversity among
453 communities was closely mirrored by their phylogenetic variability, this was not the case for the
454 communities' functional composition (Carboni et al. 2013). In conclusion, functional trait patterns
455 have been shown to be useful to gain insights into the processes of both plant community assembly

456 and invasion in coastal dune systems.

457

458 **3.6. Plant functional traits and intraspecific variability**

459 Most of the studies included species of montane primary and secondary grasslands (Wellstein et al.
460 2013; Catorci et al. 2014c; Gratani et al. 2012, 2014; Puglielli et al. 2015a), with *Sesleria nitida*
461 (Wellstein et al. 2013; Gratani et al. 2014; Puglielli et al. 2015a), an endemic grass of the montane
462 belt of the Apennines, being the most represented. Such species showed significant intraspecific
463 differences in trait attributes. In detail, leaf traits (mainly SLA or its inverse LMA, leaf tissue
464 density, LTD, and leaf thickness, LT) of *S. nitida* were highly responsive to light availability
465 (Puglielli et al. 2015a) and elevation (as proxy of temperature, Gratani et al. 2014), with mean
466 plasticity index (PI, *sensu* Valladares et al. 2000) ranging from 0.05 to 0.32 (for SLA plasticity see
467 Fig. 3). However, Wellstein et al. (2013) showed a relatively low plasticity of leaf traits and plant
468 height in two contrasting grasslands (mesic vs xeric), while clonal traits demonstrated to be highly
469 plastic. The investigated clonal traits were related to space occupancy and multiplication frequency
470 and were regulated by soil nutrient and moisture availability.

471 Different studies focused on species of Mediterranean ecosystems using field observations
472 (Crescente et al. 2002; Puglielli et al. 2017a; Gratani et al. 2018) and common garden approaches
473 (Gratani et al. 2003; Catoni and Gratani 2013; Puglielli et al. 2017b). In particular, Crescente et al.
474 (2002), Gratani et al. (2003) and Peguero-Pina et al. (2017) revealed significant levels of
475 phenotypic plasticity for plant and leaf traits in *Quercus ilex* ecotypes. For example, PI for plant
476 height was 0.50 for *Q. ilex* individuals growing at a climax area and at the northern distribution
477 limit of the species in Italy (Crescente et al. 2002). At the leaf level, PI values for SLA and LTD
478 ranged between 0.15-0.27 and 0.15-0.32, respectively, in *Q. ilex* plants grown from acorns sampled
479 along an aridity gradient (Gratani et al. 2003). A remarkable leaf morphological plasticity of SLA
480 and LT was also found in the widespread Mediterranean shrub *Cistus salvifolius* in response to a
481 reduced light environment (Puglielli et al. 2017a). Moreover, SLA changes were also mostly related
482 to changes in physiological and biochemical leaf traits revealing a long-term acclimation process of
483 *C. salvifolius* to a low light environment. Also, within species inter-annual variability in anatomical
484 components of LMA has been demonstrated to reduce net photosynthesis (on area basis)
485 responsiveness to air temperature changes (Gratani et al. 2018). However, such relationship held
486 only for evergreen sclerophyllous species compared to semi-deciduous ones, highlighting that inter-
487 annual leaf plasticity patterns in response to temperature (and their relationship with
488 photosynthesis) depend on leaf habitus within Mediterranean communities. At the within individual
489 level, Puglielli et al. (2017b) demonstrated that different leaf cohorts of *Cistus* spp. are
490 characterized by differences in leaf trait coordination patterns. Such strategy allows species to

491 modulate resource-acquisition and -use strategies with varying environmental conditions,
492 highlighting another level of phenotypic plasticity. Relevant levels of phenotypic plasticity in
493 leaf traits have been found also in *Fagus sylvatica*, *Picea excelsa* and *Populus nigra* along
494 biogeographical gradients in studies conducted at continental scale, including Italy (Bauer et al.
495 1997; Kang et al. 2011; Guet et al. 2015).

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

505

506 **3.7. Aquatic environments and plant growth: evidence from river and shallow inland** 507 **ecosystems**

508 River stretches, wetlands and eutrophic shallow lakes of the continental biogeographic region in
509 northern Italy were the most studied environments. Several papers were focused on single species.
510 Studies related to growth form and performance of *Phragmites australis* found significant
511 differences in attributes according to site-specific ecological status. Flooded stands or sites with
512 permanent submersion were characterized by high rates of clumping habit and dead apical bud, and
513 lower culm diameters, showing clear signs of plants dieback (Lastrucci et al. 2016, 2017). Other
514 studies addressed the growth response of a rare fern, *Marsilea quadrifolia*, and a widespread
515 opportunistic species, *Vallisneria spiralis*, respectively to sediment trophic level and physico-
516 chemical water features, demonstrating a certain capacity of both species to grow under varying
517 levels of nutrients in water and sediment (Bolpagni & Pino 2017; Bolpagni et al. 2015). Finally, two
518 studies focusing on plant-mediated gas exchange of *Trapa natans* clarified its pivotal role in
519 inducing persistent hypoxia and anoxia in the colonized water bodies, and in conditioning CO₂ and
520 CH₄ stand fluxes at the water-atmosphere interface (Bolpagni et al. 2007; Pierobon et al. 2010).

521 At community level, Oglio river wetlands (northern Italy) were studied in order to assess the effect
522 of wetland origin (natural vs artificial) and hydrology (lotic vs lentic) in shaping growth forms
523 composition of riverine wetland vegetation. In general, data revealed the predominance of terrestrial
524 herbaceous species and the deterioration of the obligate aquatic plant contingent and the helophyte
525 representativeness in such ecosystems (Bolpagni et al. 2013; Bolpagni & Piotti 2015, 2016).

526 Wetlands origin and their structural complexity rather than hydrological features seemed to
527 condition community composition in terms of growth forms (Bolpagni et al. 2013; Bolpagni &
528 Piotti 2016).

529 Furthermore, some studies coupled the remote sensing approaches with field sampling in order to
530 assess macrophyte growth forms distribution at different spatial scales along time or water feature
531 gradients in lakes (Bolpagni et al. 2014; Villa et al. 2015, 2017). This constitutes a step forward for
532 macrophyte traits mapping going beyond the local scale, and can be used for supporting regional to
533 continental monitoring of spatial and temporal dynamics of primary producers in freshwater
534 ecosystems (Villa et al. 2015, 2017).

535 Only one study was related to lichens (Nascimbene et al. 2009), evaluating the effectiveness and
536 life-strategies of freshwater lichens in colonizing newly constructed stone structures in low-
537 elevation streams. Size of thalli, morphological and ontogenetic traits of the species were influenced
538 by the age of restored habitats.

539

540 **4. CONCLUSIONS AND FUTURE RESEARCH PERSPECTIVES**

541 Our review represents the first comprehensive overview of the main findings in studies linking plant
542 functional traits to environmental and human drivers in Italy. It can be a stepping stone to develop
543 functional quantitative analyses of plant communities based on plant traits, especially in ecosystem
544 services evaluations, and it can be a starting point to extend this comprehensive perspective beyond
545 the national scale, to tie more firmly Italian researchers to international scientific networks on plant
546 traits.

547 We took note of species encountered while working at this review (looking at the considered papers
548 and related supplementary materials), which traits have been studied at least once on a population
549 located in Italy; we supply the species list in Appendix 2. We found a surprisingly high number of
550 traits available for 1080 vascular plants (of which only 3.2% endemics), mainly related to whole-
551 plant, leaf, seed, phenology and flowering traits. On the contrary, we registered a lack of traits
552 measurements for bryophytes and lichens. We also observed that functional traits of belowground
553 organs (root and clonal traits) have been often neglected, despite the fact that these traits are
554 extremely informative on resource acquisition strategies and other key functions, such as space
555 occupancy, recovery after damage (Lambers et al. 2006; Laliberté 2017; Ottaviani et al. 2017) as
556 well as other fundamental mechanisms such as plant-plant, plant-soil and plant-climate interactions.
557 Also the availability of wood traits measured in Italy, which include a time factor since they can be
558 dated within tree-ring series (Baas et al. 2016; Beeckman 2016), could represent a valuable step
559 forward in plant functional analysis at local scale. In the meantime wood traits are available in TRY
560 database (Kattge et al. 2011), or could be easily obtained from other sources (see Beeckman 2016).

561 We explored the TRY database (a global archive of plant traits, Kattge et al. 2011) found trait values
562 for about 900 species deriving from Italian datasets (i.e. contributors with traits measurements
563 carried out in Italy). They were mainly related to leaf traits (Pierce et al. 2007a,b, 2012, 2013,
564 2014b; Cerabolini et al. 2010a,b; Campetella et al. 2011; Ciccarelli 2015; Burrascano et al. 2015;
565 Giarrizzo et al. 2017). Combining the above mentioned information and the data collected in this
566 review (Appendix 2), we gathered information on plant traits measured on Italian populations for an
567 overall total of 1418 taxa, which represent almost the 20% of the entire Italian vascular flora
568 (Bartolucci et al. 2018). Most of this information is shared in TRY database, but not all (Figure 4).
569 About 500 species whose traits measurements have been published in papers considered in this
570 review are not available in TRY. Moreover, 113 species among these (8% of the 1418 taxa) are
571 totally missing in TRY database. Additionally, we explored the correspondence between the
572 functional trait database for Mediterranean Basin plants (BROT 2.0, Tavşanoğlu & Pausas (2018))
573 and our data related to the Mediterranean biogeographic region (Appendix 2, 126 taxa), assessing
574 that 32 species (25% of the 126 taxa) are totally missing in BROT 2.0 database. It is therefore
575 evident that Italian researchers can easily give a more effective contribution to TRY and BROT 2.0
576 databases and to global research, by sharing their own already published trait measurements. This
577 could lead to an improving of the spatial coverage of the global and regional archives of plant traits
578 and give a crucial contribution regarding plant communities still poorly investigated such as those
579 of the Mediterranean region.

580

581 The plant traits approach holds promises in disentangling several issues still controversial in plant
582 ecology. For example, the assessment of determinants responsible for the invasion potential of alien
583 species is crucial in the light of the ongoing climate change. Recently, Petruzzellis et al. (2018)
584 compared several functional and mechanistic (sensu Brodribb et al. 2017) traits in a native and in an
585 alien species in sites under different light regimes, and suggested that a trade-off between hydraulic
586 safety and resource acquisition and use efficiency could promote invasion by alien species. Plant-
587 animal interactions in pollination and dispersal, which influence the maintenance of plant
588 populations and communities (Fantinato et al. 2018a; Morales & Traveset 2008) have been scarcely
589 investigated by means of plant traits. Recently floral traits, such as flowering phenology, floral
590 morphology and anther position, have been proved to influence the co-existence of co-flowering
591 species in species-rich communities (Fantinato et al. 2018b). Further investigations of trait-driven
592 interactions might open new perspectives on plant-plant co-existence (Pauw 2018).

593 Intraspecific Trait Variability, which has a strong effect on the sampling size and effort (Petruzzellis
594 et al. 2017), is still scarcely considered at population and community level, while intraspecific
595 variability is often considered in ecophysiological studies. Moreover, we underline the need of

596 approaches evaluating trait-environment relationships at broad spatial and temporal scales, possibly
597 resulting from the collaboration of several research groups at national level, as well as analysis of
598 traits variations along ecological gradients, in order to make predictions about land use and climate
599 change impacts.

600 Italy could be a good regional model to explore emerging research fields in plant ecology, like those
601 related to ecosystem services and functional biogeography. There is a growing evidence that plant
602 traits considered at community level have strong effects on ecosystem processes underlying
603 important ecosystem services (Suding & Goldstein 2008; Lavorel et al. 2010; Lavorel & Grigulis
604 2011). Also functional biogeography (i.e. the study of the geographic distribution of trait diversity
605 across organizational levels; Violle et al. 2014) could find a fertile ground in Italy, given its broad
606 biogeographical range.

607

608 **Authors contributions**

609 S.Ch., M.Ma., and E.Ba. promoted and coordinated the review; A.Pe., G.Pu., and C.We. contributed
610 to write the structure of the entire manuscript; A.Ac., E.Ba., R.Bo., L.Br, G.Ca., A.Ch., L.Co.,
611 M.Ma., J.Na., S.Or., S.Pi., C.Ri., and F.Ta. organized the workshop "Plant traits 2.0" and/or revised
612 single chapters according to their expertise; B.Ce., S.Ch., M.Ma. and E.Ba. led the writing of the
613 conclusions; all the authors collected papers and revised the final version of the manuscript.

614

615 **Supplementary material**

616 **Appendix 1.** List of papers included in the review.

617 **Appendix 2.** List of species (vascular plants and bryophytes) for which there is the availability of
618 attributes measured in the field.

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1179 **Table 1.** Application fields of the most used plant functional traits in Italy with indications of the
 1180 number of papers and biogeographic region (A: Alpine; C: Continental; M: Mediterranean;
 1181 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

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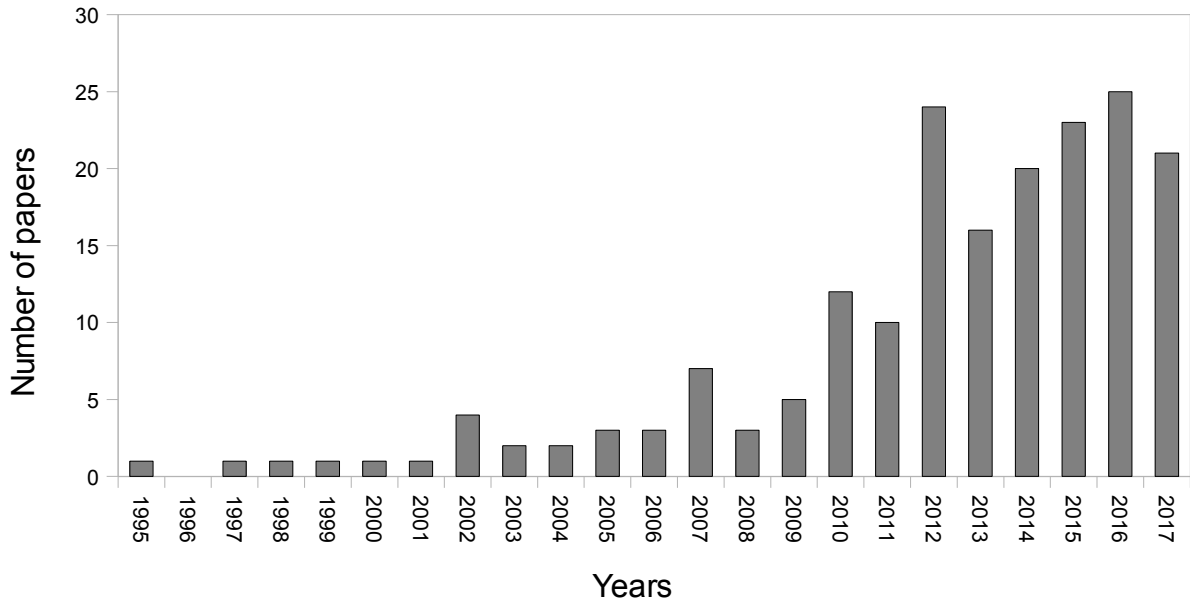
1195 **Table 2.** Main topics and related papers for each section.

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; Carbognani 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
	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
3.2. Response of functional traits to forest management and eutrophication	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

1197 **FIGURES**

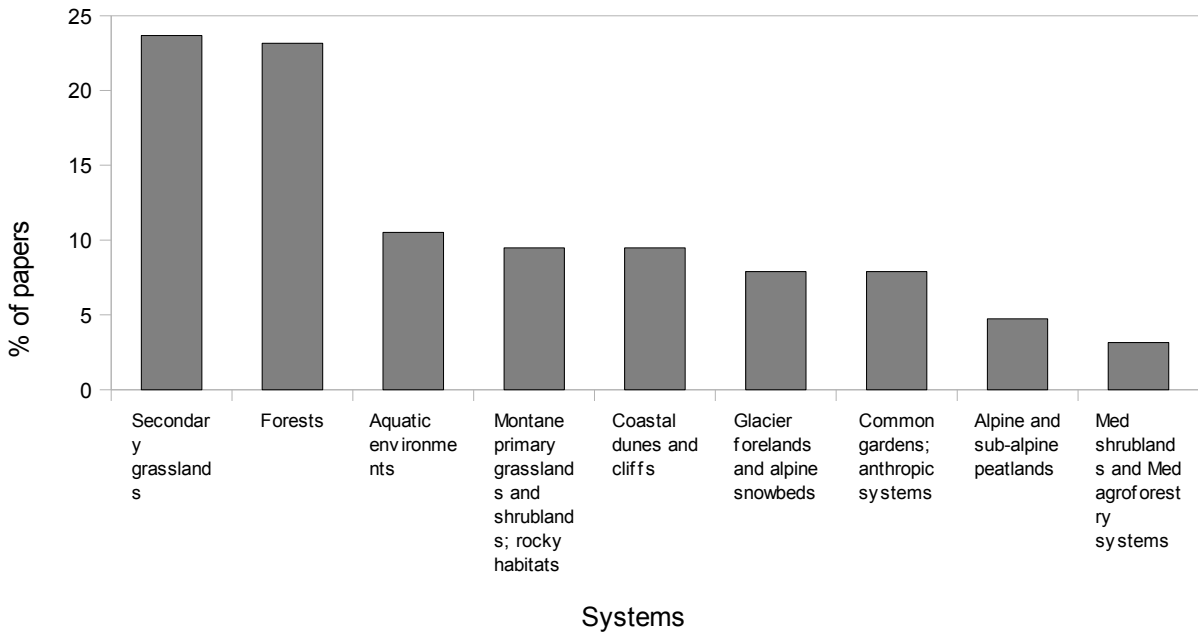
1198 **Figure 1.** Italian studies on functional traits in relation to environmental variables/gradients: (a)
1199 temporal trend in the number of papers published per year; (b) distribution of the collected
1200 papers regarding studied ecosystems; (c) number of vascular plant species accounted for the
1201 most frequently investigated functional traits.

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1204 **(b)**

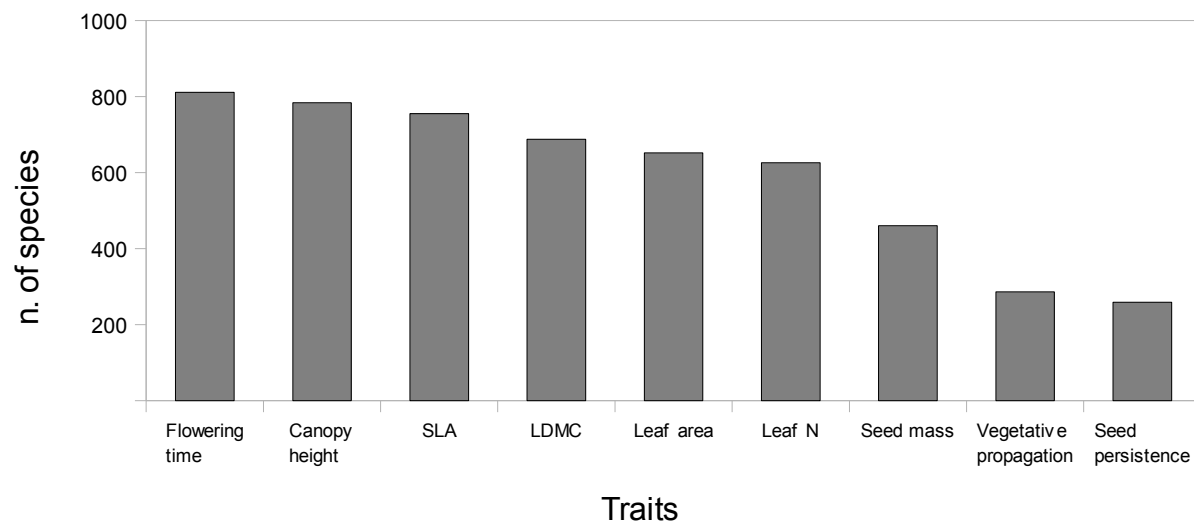


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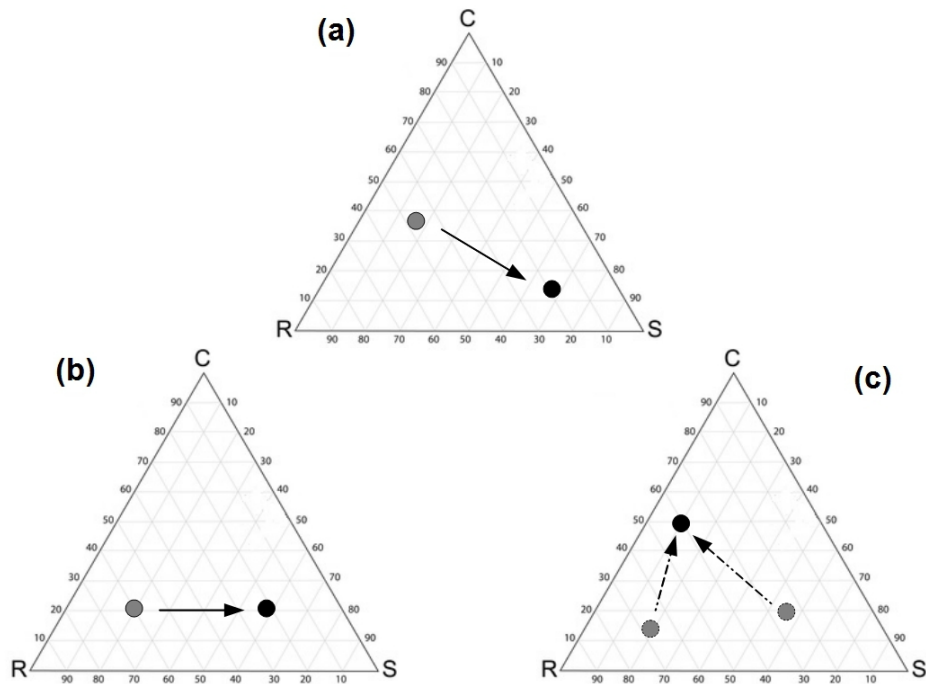
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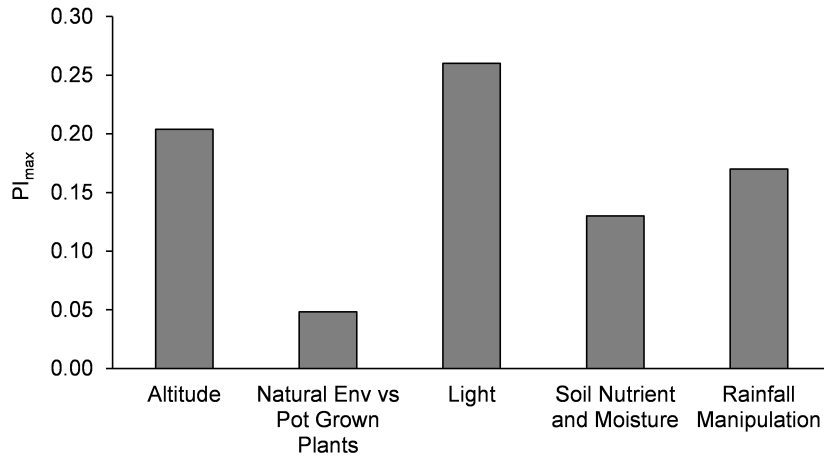
1211 **Figure 2.** CSR triangles synthesizing general mean strategies and shifts of vegetation along
1212 gradients of (a) increasing elevation (based on Caccianiga et al. 2006; Pierce et al. 2007a,b;
1213 Gentili et al. 2013), (b) primary successions, including glacier forelands and coastal dunes (based
1214 on Caccianiga et al. 2006; Gobbi et al. 2010; Ciccarelli 2015), and (c) grazing abandonment
1215 (based on Pierce et al. 2007a; Cerabolini et al. 2010a).
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1219 **Figure 3.** Maximum values of plasticity index (PI, sensu Valladares et al. 2000) of Specific Leaf
1220 Area for the endemic *Sesleria nitida* in different environments or along gradients (altitude,
1221 Gratani et al. 2014; natural environment vs. pot grown plants, Puglielli et al. 2015b; Light,
1222 Puglielli et al. 2015a; soil nutrient and moisture, Wellstein et al. 2013; rainfall manipulation,
1223 Wellstein et al. 2017).

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1229 **Figure 4.** Gathered information on plant traits of Italian populations deriving from our review
1230 (Appendix 2) and the Italian contributors to TRY, for an overall total of 1418 taxa, almost the
1231 20% of the entire Italian vascular flora (Bartolucci et al. 2018). Traits measurements of about
1232 900 species (65% of the 1418 taxa) are already shared in TRY database (i.e. species found both
1233 in the reviewed papers and in the Italian datasets contributing to TRY, or species found only in
1234 the Italian datasets contributing to TRY), while trait values for 502 species (35% of the 1418
1235 taxa) recorded by this review are not available in TRY; among these latter, 113 species (8% of
1236 the 1418 taxa) are totally missing in TRY.
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