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Functional traits in macrophyte studies: Current trends and future research agenda

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1 **Review Paper**

2

3 **Title: Functional traits in macrophyte studies: current trends and future research agenda**

4

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13 **Abstract**

14 The use of functional traits (FTs) can provide quantitative information to explain macrophyte  
15 ecology more effectively than traditional taxonomic-based methods. This research aims to  
16 elucidate the trait-based approaches used in recent macrophyte studies to outline their  
17 applications, shortcomings, and future challenges. A systematic literature review focused on  
18 macrophytes and FTs was carried out on Scopus database (last accessed May 2020). The latest  
19 520 papers published from 2010 to 2020, which represent 70% of the whole literature selected  
20 since 1969, were carefully screened. Reviewed studies mainly investigated: 1) the role of FTs in  
21 shaping communities; 2) the responses of macrophytes to environmental gradients; 3) the  
22 application of FTs in monitoring anthropic pressures; and 4) the reasons for success of invasive  
23 species. Studied areas were concentrated in Europe (41%) and Asia (32%), overlooking other  
24 important biodiversity hotspots, and only 6.2% of the world macrophytes species were  
25 investigated in dedicated single species studies. The FTs most commonly used include leaf  
26 economic and morphological traits, and we noticed a lack of attention on root traits and in  
27 general on spatial traits patterns, as well as a relatively poor understanding of how FTs mediate  
28 biotic interactions. High-throughput techniques, such as remote sensing, allow to map fine-scale  
29 variability of selected traits within and across systems, helping to clarify multiple links of FTs  
30 with ecological drivers and processes. We advise to promote investigations on root traits, and to  
31 push forward the integration of multiple approaches to better clarify the role of macrophytes at  
32 multiple scales.

33

34 **Keywords:** macrophytes, anthropic pressures, leaf economics, root traits, remote sensing,  
35 aquatic environments

## 36 **1. Introduction**

37 The concept of functional traits is a relatively recent research approach that is rapidly  
38 establishing in ecology and is taking the place of purely taxonomic studies because of its high  
39 potential in exploring multi-scale environmental issues. Functional traits are defined as any  
40 morphological or phenological characteristic that is measurable at the individual level (Díaz et  
41 al., 1998; Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), and can mirror the  
42 relationships of a species to its habitat conditions, thus revealing the interactions of the plant with  
43 the environment (Fu et al., 2015). Moreover, a supplementary advantage of functional trait-based  
44 studies is that findings can be compared among different regions, since the different specific  
45 community composition does not represent a barrier anymore, thus allowing investigations at  
46 wider scales (Schoelynck and Struyf, 2016; Iversen et al., 2019).

47

48 The use of functional traits is of particular interest for aquatic ecosystems, which are  
49 environments of major concern when considering the threats posed by anthropic pollution,  
50 habitat degradation (land use change), and the introduction of non-native species, leading to a  
51 change in the community composition in terms of reduced biodiversity and functional  
52 homogenization (Bresciani et al., 2012; Phillips et al., 2016; Cantonati et al., 2020; Lindholm et  
53 al., 2020). The concern for biodiversity conservation is a critical concern for aquatic plants  
54 (O'Hare et al., 2018), which show a high diversity in sub-tropical to low tropical latitudes  
55 (Murphy et al., 2019), and in lowlands with higher water availability at the regional scale,  
56 coinciding with the strongest presence of anthropic activities (Bolpagni et al., 2018; Guareschi et  
57 al., 2020).

58

59 Aquatic plants are crucial in maintaining water transparency by absorbing nutrients from the  
60 water column and from the sediment, thus competing with phytoplankton for both nutrients and  
61 light (Scheffer, 1999), by releasing allelopathic substances that can inhibit the growth of  
62 phytoplankton (Hilt and Gross, 2008) and by favoring sediment stability and reducing  
63 resuspension (Van Donk and Van de Bund, 2002). Besides, macrophytes can influence  
64 hydrologic features of the water body, especially in lotic systems, by reducing water velocity and  
65 enhancing sedimentation of suspended particles (Rolland et al., 2015). They can also influence  
66 the chemical processes in the rhizosphere by releasing oxygen and other exudates from the roots

67 (Soana and Bartoli, 2013). Moreover, their presence creates structure in the water column and  
68 offer habitat for zooplankton and fish (Schriver et al., 1995; Perrow et al., 1999) and finally,  
69 aquatic plants represent an important food source for a range of different organisms, as  
70 invertebrates, amphibians, fish, birds and mammals (Wood et al., 2017). Because of all these  
71 reasons, the presence of macrophytes promotes complex feedbacks that help maintaining the  
72 ecosystem stability (Bakker et al., 2013), but at the same time they can also trigger dystrophic  
73 events (Bolpagni et al., 2007) As the multiple pivotal roles of macrophytes in influencing the  
74 structure and the dynamics of the ecosystem have been widely recognized in the literature (e.g.,  
75 Ozimek et al., 1990; Scheffer et al., 1993; Van Donk and Van de Bund, 2002), a deeper  
76 understanding in their functionality and interactions with the other components of aquatic  
77 systems should be a prerequisite for developing effective management actions.

78

79 The study of aquatic and terrestrial plants has long been based on a taxonomic approach in order  
80 to detect changes in the community species composition, using indexes like species richness or  
81 beta diversity (McGill, et al., 2006; Lindholm et al., 2020). However, researchers have recently  
82 documented the use of functional traits for investigating important topics like the mechanisms  
83 explaining the structuring of the community (Van Gerven et al., 2015; Eckert et al., 2016;  
84 García-Girón et al., 2019a), the response of species and communities to environmental gradients  
85 (Zhang et al., 2018; Sebilian Wittyngham et al., 2019), the influence of anthropic activities and  
86 climate change (Huang et al., 2017; Yu et al., 2018), the design of effective restoration actions  
87 (Pereira et al., 2017; Pietrini et al., 2019), the spread of invasive species (Thiébaud et al., 2016;  
88 Villa et al., 2017), and the role of traits in determining biotic interactions (Grutters et al., 2016;  
89 Sun et al. 2018). The implementation of trait-based approaches has resulted in an increasingly  
90 abundant literature and in the institution of online databases containing plant functional traits  
91 values accessible to the scientific community (e.g., [www.try-db.org](http://www.try-db.org), [www.leda-traitbase.org](http://www.leda-traitbase.org),  
92 [www.icestes.github.io](http://www.icestes.github.io)). Nevertheless, a systematic and general synthesis on the use of functional  
93 traits in aquatic macrophytes studies is still missing. Given the high interest on these studies and  
94 the wide spectrum of application fields, we intend to answer the need of scrutiny for which  
95 functional traits, species and topics have been investigated so far in the context of aquatic  
96 macrophytes (Pan et al., 2019). We believe that this review has become necessary in order to  
97 evaluate what fields have been exhaustively researched and what other fields deserve further

98 insight and to promote the standardization of procedures so that comparisons among studies are  
99 facilitated. For this reason, we aim to propose a research agenda highlighting the most critical  
100 aspects regarding trait-based approaches tackled so far and indicating what should be the next  
101 steps in this field.

102

## 103 **2. Research strategy and analysis of articles**

104 The systematic paper research was carried out on the Scopus database ([www.scopus.com](http://www.scopus.com); last  
105 access 15<sup>th</sup> May 2020), addressing the words that identify aquatic plants and confining the  
106 research to functional traits. The string used was: TITLE-ABS-KEY (“aquatic plant\*” OR  
107 macrophyte\* OR hydrophyte\* OR helophyte\* OR pleustophyte\* OR “water plant\*”) AND  
108 TITLE-ABS-KEY (trait\* OR “functional trait\*”). We are aware that by using only the word  
109 “trait” we omitted a number of studies that investigated plant characteristics or attributes, though  
110 not explicitly referred to as “functional traits” (e.g., Fornoff and Gross, 2014; Marzocchi et al.,  
111 2019). However, we intended to delineate our research to studies that refer to a specific and  
112 homogeneous field of research (trait-oriented), adopting a consistent use of terminology. A total  
113 of 738 papers resulted from the research, published from 1969 onwards. Only papers published  
114 between 2010 and 2020 were taken into consideration for this review, in order to focus on recent  
115 developments and current trends on the topic of functional traits applied to macrophytes, for a  
116 total of 520 papers (equal to 70% of the selected papers). The papers were examined to check for  
117 relevance following the “matrix method” approach by Klopper et al. (2007). This method  
118 involves the creation of a matrix that summarizes the information found in the papers using a  
119 series of parameters of interest. The research was open to any macrophyte growth form and  
120 aquatic habitat, including estuarine and marine ecosystems.

121

122 Papers were considered relevant if they included the measurement of functional traits on one or  
123 more macrophyte species (primary studies) or the use of already measured traits from the  
124 literature (secondary studies) in order to address any ecological question. During the elaboration  
125 of results, we made no distinction between these two types of studies. Previous reviews on  
126 specific traits or topics related to macrophyte functional traits were also included, however none  
127 of these offered a wide-ranging overview as the present review. The TRY database list for  
128 functional traits ([www.try-db.org](http://www.try-db.org)) was consulted to check for consistency of the traits considered

129 by the papers. The matrix of revision contained 10 parameters: *Geographic distribution*, *Habitat*  
130 *type*, *Study type*, *Macrophyte type*, *Name of the species*, *Species number*, *Functional trait*  
131 *category*, *Shoot/root functional traits*, *Environmental variables*, and *Main topic*, as listed in  
132 Table 1.

133

134 The first feature *Geographic distribution* is informative of the place where the study was  
135 conducted at the macro-spatial scale (e.g., continent), for both field investigations and/or  
136 laboratory experiments. *Habitat type* refers to where macrophytes were either measured in the  
137 field or collected for further analyses or experiments in the laboratory. Here we distinguished  
138 between i) lentic environments like lakes, ponds, and wetlands, including the small-standing  
139 water ecosystems *sensu* Bolpagni et al. (2019) that are characterized by a larger variability in the  
140 water regime as ephemeral systems, ii) lotic environments, including rivers, streams and canals,  
141 and iii) marine environments. The tag *Any* was assigned to studies not restricted to a single  
142 habitat type and can include more than one habitat where the target macrophyte species were  
143 present and investigated. The parameter *Macrophyte type* includes the three main growth forms,  
144 i.e. submerged, free-floating, and emergent (Fu et al., 2019a; García-Girón et al., 2019b); rooted  
145 emergent (e.g., *Nelumbo nucifera*) and rooted floating leaved (e.g., *Nuphar lutea*, *Nymphaea*  
146 *alba*) were grouped together because often there was no clear distinction in some of the papers  
147 examined. The tag *Any* was given to papers analyzing the whole community including more than  
148 one macrophyte growth form present in the study area. Under *Study type*, *field/lab* refers to  
149 whether traits were measured from samples of plants grown under natural conditions (field) or  
150 grown in manipulated conditions (laboratory). Reviews were listed separately (e.g., Colmer et  
151 al., 2011; Heino et al., 2015). For *Species number* we chose three categories defined based on  
152 preliminary check of the selected papers, in order to distinguish those papers addressing specific  
153 questions to single or very few species (tag *1to3*), papers considering a limited number of species  
154 (*4to6*) and lastly papers studying more than 6 species (tag *>6*), which may be representative of  
155 the whole community.

156

157 The *Functional traits* considered by the papers were classified into 10 categories: *Growth form*,  
158 when this was considered as a variable relevant for the issue investigated; *Morphology*, including  
159 measures of the size and plant structure (e.g., height, stem diameter, root length); *Productivity*,

160 related to fresh and dry weight and biomass allocation, together with growth rates measured on a  
161 biomass basis; *Physiology* includes traits related to physiological processes like photosynthesis,  
162 respiration and enzyme activity (pigment content is also included in this group); *Biochemistry*  
163 refers to the elemental composition of tissues, namely content of C, N, P or other elements; the  
164 traits included in *Reproduction* concern any feature related to vegetative or sexual reproduction  
165 (e.g., number of flowers, seed size, number of vegetative propagules); *Ecological preferences*  
166 take into consideration indexes like the Ellenberg indicator values applied to identify the plant  
167 niche along environmental gradients (Ellenberg et al., 2003); the category *Biomechanical* traits  
168 includes plant features linked to the resistance to mechanical stress, like wind, waves or water  
169 flow velocity. Typical measured traits are flexural rigidity and flexural strain (Łoboda et al.,  
170 2018, 2019). *Biotic interactions* identify traits related to the nutrient uptake strategy facilitated  
171 by other organisms, which may be mycorrhizal fungi or bacteria (see Cornelissen et al., 2003). In  
172 this category we did not include traits that can determine other types of interactions, such as the  
173 elemental composition of tissues or the dry matter content, which are already mentioned in  
174 previous groups. The last category (*Other*) includes all other traits.

175  
176 *Shoot or root FTs* points out whether the papers dealt with only aboveground or belowground  
177 traits or with both types: belowground traits were those measured specifically on roots or  
178 rhizomes, while aboveground traits were those measured on stems, leaves and reproductive  
179 organs. As for pleustophytes, when biomass was provided, it was considered a shoot trait unless  
180 a distinction between shoot and root biomass was made. Papers were also scanned for *Main*  
181 *environmental variables* that were measured and related to the functional traits. They were in  
182 turn classified into: *Water*, including physical and chemical parameters of the water column like  
183 temperature, pH or nutrient concentration; *Sediment* characteristics such as granulometry or  
184 organic matter content; *Climate*, concerning meteorological variables together with changes in  
185 the atmospheric composition (e.g., increased CO<sub>2</sub>); *Anthropic* refers to the influence of anthropic  
186 activities, for example land use and pollution; the tag *Depth/light* addresses specifically the effect  
187 of a reduction of available radiation both because of shading or increased water depth, while  
188 *Hydrology/topography* includes the information on the hydrologic regime or physical habitat  
189 characteristics. Papers were finally assigned to one or more of the seven *Main topic* categories:  
190 *Environmental gradients* groups papers addressing how community or species traits vary with



191 relation to one or more environmental variable; *Community structure* studies include questions  
192 on the mechanisms that rule the interactions among plant species and how different species  
193 occupy space within the community; *Anthropic pressure* refers to the studies that investigate the  
194 effect of pollution, habitat degradation and climate change on plant traits; the topic *Biotic*  
195 *interactions* explores the effect of plant traits on other organisms both above and belowground,  
196 including phytoplankton, bacteria and fungi, as well as interactions with herbivores; *Invasiveness*  
197 clearly refers to studies investigating relationships between traits and potential invasiveness and  
198 management implications; *Species characteristics* is a broad category that was assigned to  
199 studies investigating relationships among functional traits of single or few species, without the  
200 aim of finding any relation with other variables. The last topic (*Other*) includes all other  
201 questions.

202

### 203 **3. General findings**

204 The first functional trait-based studies on macrophytes were published in the late 1960s and the  
205 trend is so far considerably increasing, with the majority of the papers being published in the last  
206 ten years (520 out of 738, equal to 70% of total publications; Fig. 1). In this review, the papers  
207 published between 2010 and 2020 were screened for relevance. Of these, 296 papers were  
208 considered relevant and included in this study (40% of initial set of papers; Tables S1, S2). Most  
209 of the studies were carried out in Europe (41.4% of the total amount of papers considered) and  
210 Asia (31.5%), followed by North and South America, and only very little attention was given to  
211 this topic in Oceania and Africa (Fig. 2a). As for the habitat type, lakes are the most investigated  
212 (30%), but also lotic environments and wetlands received considerable attention (21.1% and  
213 20%, respectively) (Fig. 2b). Authors dedicated most of their attention specifically to submerged  
214 (39.0%) and emergent macrophytes (29.9%) rather than free-floating ones (8.8%). However,  
215 there is a noticeable number of papers (71 papers, 22.3%), which dealt with all three growth  
216 forms (Fig. 3a). Studies were equally divided into field and lab studies (44% and 42.3%,  
217 respectively) and 16 studies used a combined approach of controlled and field experiments (Fig.  
218 3b). Within the period considered in this study, 24 review papers concerning some delineated  
219 aspects of functional traits were published (ID number highlighted in bold in Table S3).  
220 However, the aim of these papers was not to provide a general framework as in this review.

221 Besides, considering the number of species studied in each paper, the vast majority of the studies  
222 focused on 1 to 3 species (57.3%), and about a third (32.5%) on more than 6 species.

223

224 The most investigated functional traits categories are *Morphology* (27.7% of the papers),  
225 *Productivity* (22.6%), *Reproduction* (13.7%) and *Physiology* (12.2%; Fig. 4a). Traits are  
226 measured in most cases on the aboveground portion of the plant (57.4%) and often also on  
227 belowground organs (38.4%). Only 12 studies focused exclusively on *Root traits*. Among the  
228 environmental variables related to macrophyte traits, *Water* parameters are the most frequently  
229 studied (34.2%), followed by *Depth* and *Light* (17.7%), *Hydrology* and *Topography* parameters  
230 (15.2%) and sediment characteristics (14.1%) (Fig. 4b). As for the main topics, *Environmental*  
231 *gradients* have received by far the greatest attention (30.4%); other importantly explored topics  
232 are related to *Anthropic activities*, namely anthropic pressure (18.2%) and *Invasiveness* (14.7%).

233

#### 234 **4. Analysis of current research trends**

##### 235 *4.1 Geographic distribution*

236 Europe is the continent showing the greatest number of studies on macrophyte functional traits  
237 (Fig. 2a). Research groups are well spread around the countries and we can list examples from all  
238 Europe (e.g., Mermillod-Blondin and Lemoine (2010) in France; Anjum et al. (2013) in  
239 Portugal; Villa et al. (2017) in Italy; Lindholm et al. (2020) in Finland). The same cannot be said  
240 for Asia, the second continent for number of studies, where China accounts for most of the  
241 publications and very few studies have been carried out outside China (e.g., Kato and Kadono  
242 (2011) and Amano et al. (2012) in Japan; Bashir Shah et al. (2014) in India). The other  
243 continents lay far below in the list, but we noted emerging studies in the Brazilian wetlands  
244 present along the Amazon basin (e.g., Delatorre et al., 2019; Catian et al., 2018). Studies  
245 conducted in Oceania mainly concern the topic of invasive species, for example the research on  
246 effective management actions (Eller et al., 2015; Ellawala Kankanamge et al., 2019) or the  
247 impact of disturbance due to anthropic activities on native and invasive species (Mouton et al.,  
248 2019). Similar topics related to invasiveness can be found also in African studies (Venter et al.,  
249 2017), together with studies investigating community assembly rules in South African wetlands  
250 (Sieben and Le Roux, 2017).

251

## 252 4.2 Habitat type

253 Lakes result as the most studied habitat, which in part mirrors the wide number of studies  
254 conducted in Chinese lakes (e.g., Xing et al., 2016; Wang et al., 2017; Fu et al., 2018; Su et al.,  
255 2019; Fig. 2b). Here, shallow lakes have been chosen to investigate the effect of water depth on  
256 macrophyte population stability and traits intraspecific variability (Fu et al., 2018; Zhou et al.,  
257 2019) and wind disturbance combined with eutrophication effects on traits (Zhu et al., 2018a), or  
258 the drivers influencing functional diversity in different macrophyte communities (Fu et al.,  
259 2019a,b). After lakes, lotic environments and wetlands are roughly equally studied. In both  
260 environments, aspects related to the hydrologic regime are particularly investigated, namely the  
261 effects of water level changes and water flow disturbance on biomechanical or life history traits  
262 (e.g., Colmer et al., 2011; Miler et al., 2014) or the relationship between sediment properties and  
263 plant performance (Sutton-Grier and Megonigal, 2011). Papers belonging to the category *Any*  
264 *habitat* include some reviews (e.g., the review by Schultz and Dibble, 2012), focusing on how  
265 invasive macrophytes may influence fish and macroinvertebrates communities, the paper by  
266 Eckert et al. (2016) on the consequences of clonal and sexual reproduction for aquatic plants, or  
267 the review by Schoelynck and Struyf (2016) exploring the role of silicon as a trait for aquatic  
268 vegetation, and many studies on single species, in which samples are collected for trait  
269 measurements in several environments where the species of interest was found (e.g., Efremov et  
270 al., 2015; Kwong et al., 2017).

271

## 272 4.3 Macrophyte type

273 All macrophyte growth forms (e.g., Korol and Ahn, 2016; Dong et al., 2017; Huang et al., 2018)  
274 have been well represented in the trait-based studies we analyzed, except for a lower number of  
275 studies regarding free floating species, a result that could be expected due to the relatively lower  
276 number of species included in this group (Chambers et al., 2008; Fig. 3a). These species have  
277 mainly been used to investigate responses to water contamination and possible uses of these  
278 plants in phytoremediation (Mesa et al., 2017; Pietrini et al., 2019) or aspects related to the  
279 dispersal and proliferation of highly invasive species like *Eichhornia crassipes* or *Pistia*  
280 *stratiotes* (Gao et al., 2012; Fan et al., 2013; Venter et al., 2017). On the other hand, submerged  
281 macrophytes represent the most studied growth form. They have been investigated for a variety  
282 of purposes, and in particular they were selected to investigate the responses to and effects on

283 sediment properties (Lemoine et al., 2012; Zhu et al., 2012), or to explore the use of different  
284 forms of inorganic carbon to support underwater photosynthesis (Hussner and Jahns, 2014; Eller  
285 et al., 2015). Emergent macrophytes have also been widely explored, especially with a focus on  
286 trait plasticity in relation to water parameters and water level fluctuation (Demetrio et al., 2014;  
287 Stander et al., 2018) and responses to disturbance by wind or water flow (Cao et al., 2016; Wang  
288 et al., 2010).

289

#### 290 4.4 Study type

291 Studies carried out under natural conditions or under controlled conditions (*field* and *laboratory*  
292 studies) are equally abundant in this research, however laboratory studies include almost  
293 exclusively papers considering only few species (Fig. 3b), and often try to explain the adaptation  
294 (i.e., intraspecific trait variability) of a species trait to changes in a certain environmental  
295 condition determined by biotic or abiotic factors (Nuttens et al., 2016; Silveira and Thiébaud,  
296 2017; Thouvenot et al., 2017). Field studies tend to bypass intraspecific variability, and more  
297 often aim at detecting changes in the community trait composition, thus determined by a  
298 different species composition and relative abundance rather than due to variability at the species  
299 level (Fu et al., 2014a; Lindholm et al., 2020). 16 studies have used a dual approach to compare  
300 results obtained in the two experimental conditions or combine information from different kinds  
301 of experiments. For example, Kordyum et al. (2017) compared the aerenchyma formation and  
302 enzyme biosynthesis in two emergent species (*Sium latifolium* and *S. sisaroides*), under natural  
303 and experimental conditions, and Paz et al. (2019) analyzed palatability traits to herbivores for  
304 three macrophyte species (*Egeria densa*, *Gymnocoronis spilanthoides*, *Ludwigia peploides*) in  
305 the laboratory, and later transplanted them in the field to assess actual consumption under natural  
306 conditions. Among the 24 reviews scrutinized, the topic of invasive species is very common:  
307 traits were used to explain the effects of invasive species on the ecosystem and on interactions  
308 among the components (Strayer, 2010) or for the redaction of risk assessments based on  
309 functional traits (Gordon et al., 2012; Azan et al., 2015). Other topics debated in these reviews  
310 are linked to specific questions such as the response of aquatic vegetation to abiotic factors  
311 (Bornette and Puijalon 2011), the role of silica in aquatic plants (Schoelynck and Struyf, 2016)  
312 or effects of water level fluctuations (Carmignani and Roy, 2017). Root functional traits were  
313 taken into consideration in 11 out of 24 review papers: Fusconi and Mucciarelli (2017) explored

314 arbuscular mycorrhiza, while the most extensive review we found on root functional traits is by  
315 Ali et al. (2019), focusing on nutrients and heavy metal abatement.

316

#### 317 *4.5 Trait category*

318 We observed that *Morphology* and *Productivity* traits are the most investigated among the  
319 analyzed papers and show an increasing trend in the last four years (Fig. 4a). Many of these traits  
320 are considered “soft traits”, relatively cheap and easy to measure in the field, such as leaf area or  
321 plant height (Cornelissen et al., 2003), which make them a good choice for field studies at the  
322 community level, and are also available for many species in online databases. They are often  
323 used to compute indices that synthesize functional characteristics within a community, such as  
324 the “functional trait diversity” index (FD<sub>Q</sub>) and functional beta diversity, the “community  
325 weighted means” index (CWM), the SES<sub>MPD</sub>, namely the standardized effect size of abundance-  
326 weighted mean pairwise distances between species for each trait (Fu et al., 2014a, 2019b; Lukács  
327 et al., 2019). These metrics all take into consideration both trait values and species abundance  
328 within the community. In this sense, researchers are not interested in catching the trait variability  
329 at the species level, rather they use traits as an indication of the mean species characteristics, thus  
330 revealing the function of the species at the community scale: at this scale intraspecific variability  
331 is believed to have a negligible influence (e.g., Fu et al., 2014a; García-Girón et al., 2019b).

332 *Morphology* and *Productivity* traits often appear together in studies, because they include traits  
333 describing the leaf and plant economic spectrum, along with elemental composition (e.g.  
334 Specific Leaf Area, Leaf Area, Leaf Dry Matter Content, Leaf Nitrogen Content, Specific Root  
335 Length, Leaf Area Index) (e.g., Pierce et al., 2012; Li et al., 2019a). The economic spectrum is  
336 considered explicative of existing trade-offs between, for example, growth and tissue  
337 construction; its strength may vary along an environmental gradient and in turn it influences the  
338 ecosystem functions (Díaz et al., 2004, 2016). These trait categories have been applied to the  
339 most disparate research purposes other than the insight into community assembly rules and  
340 community responses to environmental conditions, such as in the response to anthropic activities  
341 like the introduction of invasive species and pollution. For instance, Chmura and Molenda  
342 (2012) evaluated the phenology and growth response of three emergent species (*Phragmites*  
343 *australis*, *Scirpus sylvaticus*, and *Typha latifolia*) to thermally polluted water, and Thiébaud et al.  
344 (2017) used these morphology and productivity traits, along with tissues elemental composition,

345 to assess palatability to gammarid herbivores in two invasive species, *Elodea canadensis* and *E.*  
346 *nuttallii*. Such studies addressing more specific ecological questions often take into consideration  
347 also the trait plasticity, as mentioned above, in order to understand what are the factors that  
348 determine the variability at the species level (e.g., Xie and Yu, 2011b; Glover et al., 2015).  
349 *Reproduction* traits have been widely used to investigate dispersal abilities, how they are affected  
350 by environmental conditions and how they influence the community structure (Qian et al., 2014).  
351 In this context, Chmara et al. (2015) found a strong relationship between traits (including  
352 *Reproduction* and *Morphology* traits) and the acidity gradient, demonstrating the importance of  
353 carbon availability in determining aquatic plants performance. *Reproduction* and growth-related  
354 traits have also been used to detect differences in growth strategies and resource allocation  
355 between sexes in the dioecious species *Vallisneria spirulosa* (Li et al., 2019b). *Physiology* traits  
356 are very often measured in what we defined *laboratory* studies, because they are often more  
357 expensive and time-consuming to measure **directly** in the field (e.g., Saha et al., 2016; Tang et  
358 al., 2018). Besides, physiology-related measurements are very sensitive to changes in  
359 environmental conditions, which can be difficult to control when in the field and bias the  
360 response of plants to defined treatments, e.g., photosynthesis efficiency under different levels of  
361 CO<sub>2</sub> (Hyldgaard and Brix, 2012). Again, a widespread purpose for the use of these traits was the  
362 assessment of effects of pollution and climate change: photosynthetic and enzymatic responses to  
363 specific pollutants like cadmium (Huang et al., 2017; Liu et al., 2017), copper (Roubeau Dumont  
364 et al., 2019), herbicides (Nuttens et al., 2016) and perfluoroalkyl substances (Pietrini et al., 2019)  
365 were investigated. *Physiology* traits and especially photosynthesis-related traits and allelopathic  
366 activity have been used to understand the advantages of invasive species that lead to their  
367 successful competition against natives, in the context of increasing temperatures and CO<sub>2</sub>  
368 availability (Thouvenot et al., 2015; Gillard et al., 2017). To this regard, the recent development  
369 of innovative instruments (i.e., more portable and less expensive) for measuring chlorophyll  
370 fluorescence (Kuhlgert et al., 2016; Chen et al., 2019; Gomez-Sanchez et al., 2019) should  
371 enable the collection of larger amount of data on some synthetic metric of physiological  
372 performance (e.g., photosynthetic yield) allowing for the extent of physiology traits studies.  
373 Interactions with herbivores were often studied using a combination of traits that describe the  
374 palatability of a species: usually these traits include the elemental composition of tissues, the  
375 phenolic content, and the Plant Dry Matter Content or Leaf Dry Matter Content, in order to

376 detect differences in the response to herbivores between native and invasive species and outline a  
377 possible management solution against invasive species, and understand the reasons for their  
378 successful competition (Grutters et al., 2016; Thiébaud et al., 2017), or to determine the effects of  
379 the introduction of invasive herbivores, so that the choice of poorly palatable species in  
380 restoration action can prevent the spread of herbivores (Yam et al., 2016). Similarly, relations  
381 with herbivores and palatability traits are used to identify the most suitable (e.g., less palatable)  
382 species to introduce in constructed wetlands and other restoration actions (Paz et al., 2019). On  
383 the other hand, the least investigated traits directly describing *Biotic interactions* in terms of  
384 relations with bacteria and fungi as an uptake strategy. We found only four papers focusing on  
385 this subject, of which three are reviews that discuss the role and importance of traits describing  
386 the interactions with bacteria (Bornette and Puijalón, 2011) or mycorrhiza (Fusconi and  
387 Mucciarelli, 2018; Ali et al., 2019). The only study we found that experimentally measured  
388 bacterial associations is by Rejmánková et al. (2011), who attempted to explore plant strategies  
389 for phosphorus uptake and related phosphatase activity to bacteria associated to roots. In general,  
390 as we mentioned above, root traits have been quite understudied. Within our research there are  
391 several papers (n = 111) that deal with combined shoot and root traits, however, most of the time  
392 they principally concern root biomass, to calculate the root-shoot ratio (e.g., Fu et al., 2013;  
393 Hussner and Jahns, 2014; Dong et al., 2017).

394

#### 395 *4.6 Multi-scale trait patterns*

396 Exploring plant functional variability at different scales in both spatial (from community to  
397 ecosystem, up to landscape) and temporal (from daily to seasonal dynamics, up to long-term  
398 changes) dimensions requires an approach that is at the same time effective and feasible  
399 (Abelleira Martínez et al., 2016; Anderson, 2018). Remote sensing provides high-throughput  
400 data and techniques that can be translated into quantitative metrics related to vegetation features  
401 and overcome logistic and economic constraints of directly measuring most of the plant species  
402 inhabiting all biomes (Jetz et al., 2016; Gamon et al., 2019). Remote sensing applications to trait-  
403 based vegetation studies have shown an increasing trend during the last couple of decades  
404 (Homolová et al., 2013; Wang and Gamon, 2019), with a particular focus on terrestrial plant  
405 communities, especially in forest and grassland ecosystems (e.g., Asner et al., 2015; Schneider et

406 al., 2017; Schweiger et al., 2018), but some studies on aquatic plants have recently emerged,  
407 implementing and extending *in situ* measurements (Villa et al., 2014, 2017).  
408 In our research, we found 9 papers applying remote sensing techniques to macrophyte studies,  
409 focusing in particular on floating and emergent growth forms. Interactions between light and  
410 plant canopy elements, in particular reflectance and transmittance due to leaves, shape vegetation  
411 spectral response; these interactions result in a strong link between anatomical and biochemical  
412 properties (Leaf Pigments Content, Specific Leaf Area, Leaf Tissue Density) and optical  
413 properties (Klančnik et al., 2014; Klančnik and Gaberščik, 2016), which in turn can be exploited  
414 to model the performance and productivity of macrophytes stands (Liu et al., 2011). For  
415 example, Wang et al. (2012) used indices obtained from multispectral remote sensing data  
416 (Normalized Difference Vegetation Index and Vegetation-Water Index) to classify vegetation  
417 functional types in relation to water level dynamics. An approach based on remote sensing has  
418 found application also in the determination of traits favoring invasion success: Santos et al.  
419 (2012) used airborne imaging data to compare pigments and light use efficiency of native and  
420 non-native submerged species, and Tóth et al. (2019) characterized morphological and  
421 physiological traits with leaf reflectance for autochthonous and allochthonous emergent species.  
422 The contribution of remote sensing data in this context allows for a larger scale sampling and a  
423 prompter evaluation of seasonal variability of the macrophytes stands (Tóth et al., 2019).  
424 Reflectance and transmittance spectra of floating-leaved species were also measured as specific  
425 traits that influence light availability in the water column and then alter the environmental  
426 conditions underneath the water surface, and these properties can be explained by species  
427 exhibiting different morphological and biochemical leaf traits (Klančnik et al., 2018).

428

#### 429 *4.7 Species covered*

430 The papers included in our review have applied functional traits to a total amount of 1124  
431 aquatic *taxa*, which were in most cases identified to the species level, but for few studies the  
432 identification reached only the genus level (e.g., Molnár et al., 2015; Cao et al., 2016;  
433 Cornacchia et al., 2019). Some papers included also terrestrial species (Zhang et al., 2017; Dalle  
434 Fratte et al., 2019), but they were not considered in the evaluation of the diversity of species  
435 studied in this review. The world macrophyte species diversity has been estimated to count on  
436 3457 species (Murphy et al., 2019), so our study revealed that in the last ten years about one



437 third of the total macrophyte diversity has been explored in terms of functional traits. However,  
438 if we consider only the two categories of papers that focused on up to six species, the *taxa*  
439 investigated are only 213. This suggests that specific ecological questions have been asked only  
440 on a very limited portion of the total macrophyte diversity, while most of the diversity is  
441 explored in the context of vast community studies (e.g., Monção et al., 2012; Török et al., 2013),  
442 in which mainly “soft traits” are used (e.g., morphology traits), even if it is “hard traits” (e.g.,  
443 physiology traits) that could be more explicative of plant functionality (*sensu* Hodgson et al.,  
444 1999; Cornelissen et al., 2003), although more difficult and expensive to measure. According to  
445 our results, the ten most studied species are: *Myriophyllum spicatum* (63 papers), *Ceratophyllum*  
446 *demersum* (52 papers), *Potamogeton crispus* (41 papers), *Stuckenia pectinata* (40 papers), *P.*  
447 *australis* (39 papers), *E. canadensis* (35 papers), *Potamogeton perfoliatus* (31 papers), *Lemna*  
448 *minor* (30 papers), *Hydrilla verticillata* (28 papers) and *Persicaria amphibia* (28 papers).  
449 Common applications of traits for these species include the research of features determining  
450 plant palatability, physiological adaptations in response to eutrophication and the presence of  
451 contaminants, and plant adaptations to hydrological stress (Table 1, Table S4). Most of these  
452 species were well represented both in community studies and in specialized experimental studies:  
453 for *M. spicatum* see Thouvenot et al. (2019) and Fu et al. (2020); for *C. demersum* see Fu et al.  
454 (2017) and Sun et al. (2018); for *P. australis* see Yam et al. (2016) and Sikorska et al. (2017).  
455 However, species belonging to the genus *Potamogeton*, including *S. pectinata*, although widely  
456 spread across aquatic plant communities, were very poorly represented in the latter category of  
457 studies (3, 2, and 1 papers, respectively; Amano et al., 2012; Gillard et al., 2017; Riis et al.,  
458 2018; Zhu et al., 2018a; Zhang et al., 2019; Pätzig et al., 2020), indicating a need for further  
459 examination of their functionality.

460

#### 461 4.8 Connections among topics

462 If we consider how papers are connected with each other in terms of the examined categories and  
463 topics, it is quite difficult to observe distinct clusters of narrative trends: most subjects are quite  
464 evenly linked with each other (Fig. 5). However, it is still possible to detect at least one strong  
465 narrative trend, which, to some extent, had already emerged in the above discussed paragraphs:  
466 studies that investigate the topic of environmental gradients mainly use morphology and  
467 productivity traits measured in field, with a notable portion of laboratory studies on submerged

468 species (and less frequently on emergent ones), and relate these traits to water parameters  
469 especially in lakes, covering sites located in Asia and Europe. This pattern is consistent with the  
470 most studied features observed for each category (Figs. 2 to 4). The works of a group of  
471 scientists of the Chinese Academy of Sciences from Wuhan and Beijing are emblematic of this  
472 trend (e.g., Fu et al., 2013; Zhu et al., 2018a,b; Su et al., 2019). For example, Su et al. (2019)  
473 investigated how plant size and biomass of submerged species could establish feedbacks  
474 determining water transparency in subtropical shallow lakes. In this case, they found that small,  
475 bottom dwelling macrophytes were more effective in maintaining water transparency because  
476 they impeded more efficiently sediment resuspension, and released more oxygen to the water  
477 column, thus probably contributing to phosphorus immobilization. Overall, the pattern of  
478 connections among features shows that the topic of environmental gradients has been  
479 exhaustively explored and linked to nearly all the subjects we considered in this review (Fig. 5).  
480 Other topics do not show the same amount of coverage: for instance, “anthropic pressure” and  
481 “invasiveness” are strongly linked only to water parameters, among all environmental variables.  
482 Nevertheless, sediment or hydrology characteristics, have been demonstrated to be fundamental  
483 in determining the variability of root (Ali et al., 2019) and shoot traits (Zhu et al., 2018a), and  
484 therefore plant function in the ecosystem, especially in the context of invasive species (Venter et  
485 al., 2017). On the other hand, we mentioned root traits received far less attention than shoot  
486 traits, and we therefore suggest implementing the integration between root traits and sediment  
487 characteristics in future studies. At the same time, the topic of invasiveness has been studied  
488 mainly from the point of view of morphology and productivity traits, setting aside reproduction  
489 traits. Although vegetative propagation seems to be the main mechanism of spreading of aquatic  
490 invasive species (Bashir Shah et al., 2014; Urban and Dwyer, 2016), sexual reproduction may  
491 also be important in spreading dynamics. This could either lead to loss of genetic diversity, due  
492 to hybridization with native species, or higher vigor to hybrids in case of hybridization with non-  
493 natives, as observed for *Ludwigia* spp. in Brazil (Thouvenot et al., 2013b). Moreover, Kwong et  
494 al. (2017) found that fruit weight and fruit number in *Sagittaria platyphylla* was higher in  
495 introduced ranges than in native habitats, due to the absence of specialist herbivores. This work  
496 suggests the importance of evaluating the effects of biotic interactions on various traits  
497 categories and not only on biochemistry and productivity, as in most papers analyzed here (e.g.,  
498 Grutters et al., 2016; Jiménez-Ramos et al., 2018). Reproduction traits resulted the third most

499 studied trait category, however it does not keep the same position as for number of links, being  
500 related mainly only to the topics of environmental gradients and anthropic pressure (Fig. 5).  
501 Finally, we observed that the two continents that count the highest number of papers are not  
502 equally connected to all the subjects considered in this review: on one side Asian studies mostly  
503 stick to the most common pattern of lake studies on plant responses to water parameters, and on  
504 the other European studies basically encompass all the other subjects; the rest of continents are  
505 extremely underrepresented.

506

## 507 **5. A research agenda**

508 What emerges from this systematic review is that the use of functional traits in aquatic botany  
509 studies enormously increased in recent years (almost doubling in the last 5 years compared to the  
510 period 1969-2014). Indeed, researchers have long been dealing with macrophytes functional  
511 characteristics: see for example the works on the macrophyte productivity by Hogeland and  
512 Killingbeck (1985) or plant strategies by Murphy et al. (1990). However, only recently this  
513 research field has benefited from a standardization of measurements and a sharing of the  
514 information collected in online databases. Although so far, studies have been very heterogeneous  
515 in their purposes and methods, highlighting the vast range of the research fields that can be  
516 investigated using a functional trait approach, here we tried to offer a unified perspective. This  
517 allows researchers to identify a few aspects that can be represent a starting point for future  
518 developments in studying traits applied to macrophytes:

519

- 520 i. In the papers examined in this review, sediment characteristics have been associated to  
521 traits almost as often as other parameters like hydrology or water depth and light  
522 availability, confirming the importance of substrate type influencing plant traits (Xie and  
523 Yu, 2011a; Anjum et al., 2015) and performance (Bolpagni and Pino, 2017). Roots of  
524 aquatic plants colonize the sediment and so they represent the plant interface between the  
525 water column and the rhizosphere, and although aquatic plants are able to absorb  
526 nutrients from shoots as well, roots are not only passive organs in charge of ensuring  
527 anchorage to the substrate, but they have an active role in determining plant performance  
528 (Huang et al., 2018; Moe et al., 2019). However, we noticed a consistent lack of interest  
529 towards root traits, except for root biomass and number (e.g., Glover et al., 2015; Silveira

530 and Thiébaud, 2017), whereas much less attention has been given to anatomy and  
531 physiology traits such as root lacunal volume and different tissues proportions, elemental  
532 composition, exudates and uptake strategies, which could reveal crucial implications for a  
533 deeper understanding of macrophytes functions (Kordyum et al., 2017; Ali et al., 2019).  
534 Again, we believe that traits related to root biotic interactions (we refer to bacterial and  
535 mycorrhizal associations) should receive further attention, because of their potential in  
536 influencing plant functioning (Rejmánková et al., 2011; Fusconi and Mucciarelli, 2019).  
537 It has been demonstrated that structural and physiological root traits play an important  
538 role in influencing other levels of biotic interactions, so their collection should be  
539 implemented: for example, root density was related to plant ability to regrow after  
540 herbivores damage (Wood et al., 2018). Therefore, we would like to stress the need of  
541 further collection and processing of macrophytes root traits and the study of the  
542 relationships with sediment characteristics, in view of a change of perspectives, which  
543 will see plant roots as major actors of life dynamics and not only as shoot subordinates.

544  
545 ii. A main goal for future studies in this field will be to effectively capture the complexity  
546 that is intrinsic in natural systems dynamics, especially in aquatic ecosystems. The  
547 environmental heterogeneity characterizing macrophytes habitat, connected with their  
548 high phenotypic plasticity (Vivian-Smith, 1997), results in fine-scale patchiness of  
549 aquatic plant communities, and disentangling trait variability among and within species in  
550 more than few ecosystems would require an amount of data impossible to collect in the  
551 field using traditional data collection techniques. Integrating remote sensing into the  
552 functional measurements and monitoring pipeline can enable the effective upscaling of  
553 some relevant community traits (Anderson, 2018), especially for emergent or floating-  
554 leaved species, thus helping to study the spatial variability of functional traits across  
555 systems, and its links with ecological processes (Funk et al., 2017). Furthermore, for  
556 submerged macrophytes acoustic systems (i.e., side-scan sonar, echo sounders, and  
557 multibeam sonar) can expand the range of application of optical methods providing high-  
558 resolution, 3D data to delineate the underwater patterns of macrophytes (Bučas et al.,  
559 2016; Mizuno et al., 2018). The multiple roles of macrophytes are well known and they  
560 state that macrophytes, as primary producers, do not live in isolation but they constantly

561 interact with the other biotic and abiotic components (O’Hare et al., 2018). It will be  
562 essential to deepen our understanding of these interactions by applying traits-oriented  
563 frameworks, e.g., the Biodiversity-Ecosystem Functioning approach (Tilman and  
564 Dowing, 1994), in order to have a more complete view of ecosystems functioning,  
565 avoiding separating different compartments during the assessment.

566

567 iii. Invasive species represent one of the main threats to biodiversity and ecosystem  
568 functioning that aquatic habitats are facing in recent years (Strayer, 2010; Bolpagni et al.,  
569 2015; Rumlerová et al., 2016). Biological invasions correspond indeed to one of the most  
570 investigated topics among the papers we analyzed; however, we noticed some research  
571 gaps in this field, related to the type of traits studied and the environmental parameters  
572 associated. We promote the extension of these studies to other functional traits besides  
573 morphology, productivity and elemental composition, since there is evidence that also  
574 physiological and reproduction traits play an important role in non-native species  
575 establishment and colonization success (Kwong et al., 2017; Tóth et al., 2019). Moreover,  
576 the role of traits in invasive species has seldom been associated to environmental  
577 variables other than water chemical and physical parameters, although other parameters  
578 have been demonstrated relevant effects, such as light availability, in driving competition  
579 with native species, especially in the first phases of establishment (Ellawala Kankanamge  
580 et al., 2019), and hydrology parameters, in determining important consequences in  
581 propagule dispersion and plant resistance to variable water regimes (Urban and Dwyer,  
582 2016; Zhang et al., 2016). Remotely sensed data, allowing quantitative, standardized  
583 measures of specific traits (Tóth et al., 2019), can make the allochthonous *vs.*  
584 autochthonous species comparison feasible across scales and sites, thus facilitating the  
585 assessment of environmental drivers for invasiveness (Rocchini et al., 2015; Niphadkar  
586 and Nagendra, 2016), at least for floating and emergent plants. We also encourage the  
587 investigation of invasive species and their biotic interactions, focusing in detail on the  
588 effects of specialist herbivores rather than generalists and on their foraging strategy (e.g.,  
589 foraging on meristems and flowering organs rather than on mature leaves), which could  
590 be more effective in the control of invasive alien aquatic plants (Grutters et al., 2016).

591

592 iv. One of the main purposes of trait-based studies should be to allow for comparisons at  
593 multiple scales, as wide as possible. However, our review highlights how most of the  
594 recent research in the context of aquatic macrophytes has been carried out in Europe and  
595 China, while entire continents like Africa and Oceania have been almost neglected.  
596 Besides, very little attention has been given to some important hotspots of macrophyte  
597 biodiversity, like Brazil, which alone hosts more than one fifth of the global macrophyte  
598 species pool (Murphy et al., 2019). The same study from Murphy et al. (2019) divided the  
599 globe into squares of 10x10° latitude x longitude in order to evaluate global macrophyte  
600 diversity, and it states the urgency of not neglecting any part of the world, since all the  
601 squares contained at least 55 different species. It is then clear how global research on  
602 macrophyte functional traits is omitting some of the regions hosting the highest diversity.  
603 In this context, collaboration within the scientific community is essential in order to share  
604 the expertise and reach a faster advance in macrophyte functional traits research. The  
605 pledge of favoring a wider and immediate collaboration has already been launched in the  
606 context of carbon emissions from inland aquatic habitats (Marcé et al., 2019), and we  
607 believe that this concept is particularly fitting our field as well. Moreover, mapping data  
608 retrieved from remote sensing can increase the resolution of current knowledge we have  
609 on plant diversity, by improving the spatial scale of analysis where trait data available are  
610 already abundant, and providing a mean to fill gaps where species or traits data are scarce  
611 (Jetz et al., 2016).

612

#### 613 **Authors' statement**

614 ADV and RB conceptualized the study. Literature inspection was carried out by ADV. All  
615 authors discussed the results. ADV led the writing of the original draft. All authors contributed  
616 critically to the drafts and gave final approval for publication. Alice Dalla Vecchia (ADV), Paolo  
617 Villa (PV), Rossano Bolpagni (RB)

618

#### 619 **Supplementary data**

620 Table S1 – Summary analysis data matrix of the 296 reviewed papers. Table S2 – Revision  
621 matrix summarizing the information obtained from the 296 papers analysed. The absolute and  
622 relative representativeness of each category within each feature is presented. Table S3 - List of

623 the 296 papers analysed for the review. The identification number (ID, first column) and the year  
624 of publication (second column) are used in the summary matrix provided in Table S1. Reviews  
625 IDs are highlighted in bold. Table S4 – Extension of Table 1 showing the functional traits and  
626 applications for the ten most studied species, including references. On the same line, traits and  
627 corresponding ecological questions addressed are marked. Only paper studying *Ito3* species  
628 were included in this table.

629

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639

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1338 **Figures**

1339 **Figure legends**

1340

1341 **Figure 1.** Publication trend of the 738 macrophyte trait-based studies.

1342

1343 **Figure 2.** The number of papers conducted in different continents (*Geographic distribution*, A),  
1344 South America (SAm), North America (NAm), and Global Studies (Global), and *Habitat type*  
1345 (B). Stacked bars show the repartition in years of publication.

1346

1347 **Figure 3.** The number of papers focusing on different macrophyte *Growth forms* (A) and *Study*  
1348 *type* (B). Study types include field studies (*field*), controlled-conditions experiments (*lab*),  
1349 combined approaches (*lab and field*) and reviews.

1350

1351 **Figure 4.** Categories of functional traits that have been measured by the authors or acquired from  
1352 the literature and used to reach the aim of the study (A) and main topics investigated (B). The  
1353 categories of functional traits are: *Morphology* (Mor), *Productivity* (Pro), *Reproduction* (Rep),  
1354 *Physiology* (Phys), *Biochemistry* (BioC), *Growth form* (GroF), *Ecological preferences* (EcoP),  
1355 *Biomechanical* traits (Mec), *Other* (OthFT) and *Biotic interactions* (Bint). Main topics are:  
1356 *Environmental gradients* (EnvG), *Anthropic pressure* (AntPr), *Invasiveness* (Inv), *Community*  
1357 *structure* (ComS), *Biotic interactions* (BioI), *Specific characteristics* (SpCh) and *Other topics*  
1358 (OthTop).

1359

1360 **Figure 5.** Diagram illustrating the major links among the features considered in this review. Arc  
1361 width is representative of the strength of the link between two nodes, i.e., the number of papers  
1362 including both nodes in the study, and circle size is proportional to how many connections the  
1363 node installs with other nodes. For clarity links weaker than 15 (less than 15 studies showing that  
1364 connection) are omitted, just as nodes not showing links of this strength.