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

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- 1 Review Paper
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3 Title: Functional traits in macrophyte studies: current trends and future research agenda

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### 13 Abstract

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

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34 Keywords: macrophytes, anthropic pressures, leaf economics, root traits, remote sensing,

35 aquatic environments

### 36 **1. Introduction**

The concept of functional traits is a relatively recent research approach that is rapidly 37 establishing in ecology and is taking the place of purely taxonomic studies because of its high 38 potential in exploring multi-scale environmental issues. Functional traits are defined as any 39 morphological or phenological characteristic that is measurable at the individual level (Díaz et 40 al., 1998; Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), and can mirror the 41 relationships of a species to its habitat conditions, thus revealing the interactions of the plant with 42 the environment (Fu et al., 2015). Moreover, a supplementary advantage of functional trait-based 43 studies is that findings can be compared among different regions, since the different specific 44 community composition does not represent a barrier anymore, thus allowing investigations at 45 wider scales (Schoelynck and Struyf, 2016; Iversen et al., 2019). 46 47 The use of functional traits is of particular interest for aquatic ecosystems, which are 48 environments of major concern when considering the threats posed by anthropic pollution, 49

50 habitat degradation (land use change), and the introduction of non-native species, leading to a

change in the community composition in terms of reduced biodiversity and functional

bomogenization (Bresciani et al., 2012; Phillips et al., 2016; Cantonati et al., 2020; Lindholm et

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,

coinciding with the strongest presence of anthropic activities (Bolpagni et al., 2018; Guareschi etal., 2020).

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

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

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

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

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## 103 2. Research strategy and analysis of articles

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

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

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

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

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

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

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

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## **3. General findings**

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

Besides, considering the number of species studied in each paper, the vast majority of the studies 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

measured in most cases on the aboveground portion of the plant (57.4%) and often also on

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

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

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

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### 252 *4.2 Habitat type*

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

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### 272 *4.3 Macrophyte type*

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

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

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#### 290 *4.4 Study type*

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

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

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#### 317 *4.5 Trait category*

318 We observed that Morphology and Productivity traits are the most investigated among the analyzed papers and show an increasing trend in the last four years (Fig. 4a). Many of these traits 319 are considered "soft traits", relatively cheap and easy to measure in the field, such as leaf area or 320 321 plant height (Cornelissen et al., 2003), which make them a good choice for field studies at the community level, and are also available for many species in online databases. They are often 322 used to compute indices that synthetize functional characteristics within a community, such as 323 324 the "functional trait diversity" index  $(FD_0)$  and functional beta diversity, the "community" weighted means" index (CWM), the SES<sub>MPD</sub>, namely the standardized effect size of abundance-325 weighted mean pairwise distances between species for each trait (Fu et al., 2014a, 2019b; Lukács 326 et al., 2019). These metrics all take into consideration both trait values and species abundance 327 328 within the community. In this sense, researchers are not interested in catching the trait variability at the species level, rather they use traits as an indication of the mean species characteristics, thus 329 330 revealing the function of the species at the community scale: at this scale intraspecific variability is believed to have a negligible influence (e.g., Fu et al., 2014a; García-Girón et al., 2019b). 331 Morphology and Productivity traits often appear together in studies, because they include traits 332 describing the leaf and plant economic spectrum, along with elemental composition (e.g. 333 Specific Leaf Area, Leaf Dry Matter Content, Leaf Nitrogen Content, Specific Root 334 335 Length, Leaf Area Index) (e.g., Pierce et al., 2012; Li et al., 2019a). The economic spectrum is considered explicative of existing trade-offs between, for example, growth and tissue 336 337 construction; its strength may vary along an environmental gradient and in turn it influences the ecosystem functions (Díaz et al., 2004, 2016). These trait categories have been applied to the 338 339 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 like the introduction of invasive species and pollution. For instance, Chmura and Molenda 341 (2012) evaluated the phenology and growth response of three emergent species (Phragmites 342 343 australis, Scirpus sylvaticus, and Typha latifolia) to thermally polluted water, and Thiébaut et al. (2017) used these morphology and productivity traits, along with tissues elemental composition, 344

to assess palatability to gammarid herbivores in two invasive species, *Elodea canadensis* and *E*. 345 nuttallii. Such studies addressing more specific ecological questions often take into consideration 346 347 also the trait plasticity, as mentioned above, in order to understand what are the factors that determine the variability at the species level (e.g., Xie and Yu, 2011b; Glover et al., 2015). 348 Reproduction traits have been widely used to investigate dispersal abilities, how they are affected 349 350 by environmental conditions and how they influence the community structure (Qian et al., 2014). In this context, Chmara et al. (2015) found a strong relationship between traits (including 351 Reproduction and Morphology traits) and the acidity gradient, demonstrating the importance of 352 carbon availability in determining aquatic plants performance. Reproduction and growth-related 353 traits have also been used to detect differences in growth strategies and resource allocation 354 between sexes in the dioecious species Vallisneria spinulosa (Li et al., 2019b). Physiology traits 355 356 are very often measured in what we defined *laboratory* studies, because they are often more expensive and time-consuming to measure directly in the field (e.g., Saha et al., 2016; Tang et 357 358 al., 2018). Besides, physiology-related measurements are very sensitive to changes in environmental conditions, which can be difficult to control when in the field and bias the 359 360 response of plants to defined treatments, e.g., photosynthesis efficiency under different levels of CO<sub>2</sub> (Hyldgaard and Brix, 2012). Again, a widespread purpose for the use of these traits was the 361 362 assessment of effects of pollution and climate change: photosynthetic and enzymatic responses to specific pollutants like cadmium (Huang et al., 2017; Liu et al., 2017), copper (Roubeau Dumont 363 364 et al., 2019), herbicides (Nuttens et al., 2016) and perfluoroalkyl substances (Pietrini et al., 2019) were investigated. *Physiology* traits and especially photosynthesis-related traits and allelopathic 365 366 activity have been used to understand the advantages of invasive species that lead to their successful competition against natives, in the context of increasing temperatures and  $CO_2$ 367 368 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 fluorescence (Kuhlgert et al., 2016; Chen et al., 2019; Gomez-Sanchez et al., 2019) should 370 enable the collection of larger amount of data on some synthetic metric of physiological 371 372 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 palatability of a species: usually these traits include the elemental composition of tissues, the 374 phenolic content, and the Plant Dry Matter Content or Leaf Dry Matter Content, in order to 375

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

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

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

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

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## 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

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

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## 461 *4.8 Connections among topics*

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

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

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

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# 507 5. A research agenda

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

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

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

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

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

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

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

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### 613 Authors' statement

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

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## 619 Supplementary data

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

the 296 papers analysed for the review. The identification number (ID, first column) and the year

- of publication (second column) are used in the summary matrix provided in Table S1. Reviews
- 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 *1to3* 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.