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Habitat morphology and connectivity better predict hydrophyte and wetland plant richness than land-use intensity in overexploited watersheds: evidence from the Po plain (northern Italy)

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1 **Habitat morphology and connectivity better predict hydrophyte and wetland plant richness**
2 **than land-use intensity in overexploited watersheds: Evidence from the Po plain (northern**
3 **Italy)**

4

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15

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18

19 **Abstract**

20 **Context**

21 Preserving hydrophyte and wetland plant diversity is among the most critical environmental issues
22 worldwide. The progressive decline and disappearance of these species led to dramatic
23 consequences on functions and services provided by inland aquatic ecosystems. This is especially
24 relevant for lowlands that are usually disturbance-dominated landscapes, mainly by mechanization
25 in agriculture and land use changes.

26 **Objectives**

27 In these contexts, it is fundamental to understand the key factors affecting the aquatic and wetland
28 plant richness, focusing on relict aquatic habitats, and overcoming a purely trophic-oriented
29 approach.

30 **Methods**

31 To do this, the aquatic and wetland flora of 88 aquatic sites, encompassed in an oversimplified
32 watershed, was explored in terms of the total number of aquatic and wetland plant species,
33 hydrophytes, alien species, and policy species, as well as 18 explanatory variables, including eco-
34 morphological, hydrological, direct human impact, and landscape mosaic drivers.

35 **Results**

36 The results emphasize the key role of site area and hydrological connectivity compared to land-use
37 intensity in explaining hydrophyte and wetland plant richness in overexploited landscapes;
38 conversely, site origin was crucial only for alien species, being more abundant in artificial sites.

39 **Conclusions**

40 This paper offers a new comprehension of the leading contribution of local drivers in explaining
41 macrophyte patterns, suggesting a relevant influence of habitat dynamics in regulating species
42 establishment and developing. The future challenge will be to actively include artificial and/or
43 altered aquatic ecosystems in hydrophyte and wetland plants conservation programs, not forgetting
44 the risks associated with an increasingly spread of alien species.

45

46 **Keywords:** Hydrophytes, alien taxa, lowland floodplains, shallow water bodies, restoration plans,
47 conservation diversity, Po plain, northern Italy

48

49 **Introduction**

50 Worldwide, freshwater environments have been strongly affected by river and lake engineering,
51 pollution, drainage and spread of alien species (Wohl et al. 2017). This is especially true for
52 floodplains that are usually disturbance-prone landscapes (Kadoya et al. 2009). In these contexts,
53 wetlands and aquatic ecosystems under natural conditions have been almost disappeared due to
54 increasing mechanization in agriculture and land use changes (Verhoeven and Setter 2009). This
55 resulted in change of the physical and chemical features of waters and loss of connectivity among
56 them, triggering massive habitat loss and extinction of specialised species (Riis and Sand-Jensen
57 2001; Bolpagni et al. 2013; Bolpagni and Piotti 2015). In particular, wetland and aquatic flora is
58 rapidly declining due to the increased role of external factors that enhance the spread of alien and
59 ruderal species (Januschke et al. 2011; Bolpagni and Piotti 2015), including algae, and exotic plants
60 that are progressively replacing native and sensitive species (Catford et al. 2011; Bolpagni and
61 Piotti 2016).

62
63 Despite this negative trend, at the regional scale relict inland small water ecosystems (SWEs),
64 including ponds, shallow lakes and wetlands, are still playing a key role in the functioning of
65 watersheds (Bolgagni et al. 2019). This is due to their heterogeneous morphology, as well as to the
66 range of physical and chemical features (Oertli et al. 2002; Rosset et al. 2014; Thornhill et al.
67 2017). In this framework, wetland and aquatic macrophytes are relevant actors in regulating
68 services and processes mediated by SWEs (O'Hare et al. 2017). They support and mediate
69 multifaceted ecosystem functions, such as biogeochemical processes, habitat stabilization, and offer
70 multiple resources via provision of food and niches for many organisms (Carpenter and Lodge
71 1986; O'Hare et al. 2017). Macrophytes are thus "*engineering species*" (Bouma et al. 2010;
72 Bolpagni et al. 2015; Ribaud et al. 2018), whose disappearance leads to permanent perturbations in
73 aquatic ecosystems, especially in terms of trophic dynamics (Scheffer et al. 2003). Thus, it is crucial
74 to unravel the trajectories of wetland and aquatic plants in overexploited landscapes in order to find
75 effective adaptive strategies to support the regional biodiversity and enhance the associated
76 ecosystem services.

77
78 Studies carried out to evaluate the main drivers of wetland and aquatic plant distribution in highly
79 impacted SWEs were mainly trophic-oriented (Menetrey et al. 2005; Rosset et al. 2014). However,
80 James et al. (2005) found that most of the physical-chemical and biological variables investigated
81 failed to explain macrophyte patterns, with winter nitrogen (N) resulting the only significant factor,
82 in conjunction with the "vegetative rest" period of aquatic plants. Furthermore, Rosset et al. (2014)

83 stressed the scarce predictability of the trophic status of lowland waterbodies in structuring
84 macrophyte communities, suggesting a not-negligible role of landscape structure as driver of small
85 waterbodies biodiversity (Cheruvilil and Soranno 2008; Akasaka et al. 2010; Jog et al. 2017).
86 Specifically, focusing on the surrounds of SWEs, Declerck et al. (2006) found a negative effect of
87 trampling and coverage by crop land on the vegetation complexity of a series of ponds at the local
88 scale (<200 m radius), and Pedersen et al. (2006) confirmed that agricultural uses in buffer zones
89 were strongly linked to the local vanishing of a threatened isoetid species (*Littorella uniflora*).
90 For SWEs placed in agro-ecosystems, the functional concept of connectivity is mainly related to
91 water availability. Recently, Toyama and Akasaka (2017) stressed the role of water depletion as
92 compared to the cessation of anthropogenic disturbance on plant successional changes. Also, Brose
93 (2001) emphasized the stronger effect of spatial heterogeneity of hydro-periods on plant richness in
94 temporary wetlands compared to biogeography. Similarly, Bolpagni and Piotti (2015, 2016)
95 highlighted the influence of water level variations on both wetland vegetation diversity and its
96 spatial distribution. Additionally, Bolpagni et al. (2013) stressed the importance of site origin
97 (natural vs man-made) and structural heterogeneity for amphibian and aquatic plant diversity.

98

99 In this study, we aimed to assess the key factors affecting the aquatic and wetland plant richness in
100 an overexploited landscape, overcoming a purely trophic-oriented approach. The study focuses on
101 relict aquatic habitats in an extremely human-transformed landscape of northern Italy, in the Brescia
102 province (Frattoni 2008; Soana et al. 2011), where we expect that floristic richness would decrease
103 with increasing human disturbance and connectivity loss, as well as with decreasing of habitat
104 amount (hypothesis 1). Additionally, the number of alien species is expected to increase in the most
105 impacted water bodies, while an opposite trend is predictable for species of conservation concern
106 (hypothesis 2).

107

108 **Material and methods**

109 *Study area*

110 The survey was performed in the Northern-East part of the Po plain (northern Italy), that largely
111 falls within the lower Oglio River basin (Fig. 1), covering an area of more than 2,000 km². Climate
112 is temperate (Type C, Köppen-Geiger climate classification system), with a mean annual
113 temperature of 13–14 °C, and an average annual precipitation of ~700 mm, mainly concentrated
114 during autumn and spring (Peel et al. 2007). The area includes two main geomorphological sectors:
115 the lowland one, including the Oglio riverscape and the lower plain of the Brescia province, and a
116 hilly sector, corresponding to the morainic hills of the Garda and Iseo lakes (Fig. 1). The former is a

117 typical overexploited lowland of Central and Southern Europe, mainly used for poplar plantations,
118 annual crops, and livestock (mostly cows and pigs) farming. In this context, natural or semi-natural
119 land uses account for less than 5% of the area (Bolpagni and Piotti 2015, 2016). As a result, for the
120 lower Oglio River, an agricultural-dominated catchment, it has been estimated that the average
121 nitrogen surplus in agricultural land is $\sim 180 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Soana et al. 2011), among the highest
122 values reported for European watersheds (Viaroli et al. 2018). This strong positive nitrogen balance
123 is a major driver of ecosystem processes and critically affects the conservation status of the aquatic
124 habitats and groundwater.

125

126 The hilly sector (with an average height between 100 and 250 m a.s.l.) embraces the southern
127 shores of the Garda and Iseo lakes, and originates by subsequent phases of expansion and retreat
128 respectively of the Sarca and Oglio glaciers. Scattered forest patches, slight slopes in alternation to
129 flat plains, small wetlands and water sources, vineyards and olive groves, characterize this sector. In
130 general, agricultural activities are less intensive than in the lowland sector, resulting in a lower
131 impact on aquatic habitats and groundwater (Soana et al. 2011; Pinardi et al. 2018).

132

133 *Site selection and field plant survey*

134 The aquatic and wetland sites considered in this study were those investigated by Frattini (2008).
135 All of them had an area larger than 0.1 ha and did not show evident recent direct human
136 perturbations (e.g. vegetation or plant cutting, sediment excavation, shoreline armouring). They
137 were identified thanks to the support of local municipalities, private owners, stakeholders, and
138 citizens, through a specific analysis form developed to collect preliminary information about the
139 spatial distribution and the main features of aquatic habitats (Frattini 2008). Based on an extensive
140 three-year field survey (2003–2005), starting from a preliminary set of 515 sites, a final group of 88
141 aquatic sites was selected (Fig. 1; Frattini 2008). 30 sites belong to the Garda hilly sector (n. 15–48;
142 see Supplementary material 1), 14 belong to the Iseo hilly sector (n. 1–14; see Supplementary
143 material 1), and the rest to Oglio River watershed (n. 49–88, see Supplementary material 1). Data
144 about the flora were collected within each selected site, during the 2006 growing season (from May
145 to September) by extensively searching the entire aquatic and wetland habitats of each site (Frattini
146 2008).

147

148 All hydrophytes and wetland plants were considered, being defined as those plant species with an
149 Ellenberg's moisture value $F \geq 8$ (Bolpagni et al. 2018). In this group we included all the species
150 that are strongly ecologically linked to “wet and aquatic” habitats characterized by saturated

151 substrates and therefore influenced by the periodical submersion and/or by a constant saturation of
152 colonized sediments (Pignatti et al. 2005). Species nomenclature and designation of alien species
153 follow Galasso et al. (2018).

154

155 *Explanatory variables' characterization*

156 For each site, we recorded 18 explanatory variables, divided into 4 groups: (a) eco-morphological;
157 (b) hydrological; (c) direct human impact; and (d) landscape mosaic drivers (Table 1;
158 Supplementary material 1). Explanatory variables WBar (waterbody area), WBpe (waterbody
159 perimeter), RIco (river connectivity), WBco (waterbody connectivity), WBls (landscape sector),
160 WBaa (impact of agriculture areas), WBsm (impact of semi-natural, natural areas), WBua (impact
161 of urban areas), and WBAq (impact of waterbodies) were retrieved from spatial data sources QGIS
162 ver. 2.8.9 (Wien; <http://qgis.org/de/site/>). WBpa was calculated by WBar and WBpe data; WBnl,
163 WBpl, and WBsl were based upon nutrient budgeting approach in agricultural land, as detailed later
164 in the text. The Lombardy Regional Topographical Database, the field evidences and the
165 information by landowners were used to derive the type of water body origin (WBor), hydroperiod
166 (WBhy), superficial water supply (WBws), as well as the utilization of water bodies as basin for
167 irrigation (WBbu), and their management level (WBml).

168

169 Specifically, aquatic habitats proximity (RIco, and WBco) and waterbodies vulnerability to land use
170 impacts (WBls, WBaa, WBsm, WBua, and WBAq) were quantified on a 500 m buffer around each
171 site (Cheruvilil and Soranno 2008; Gleason and Rooney 2017). This threshold was selected based
172 upon results from previously studies that investigated the relationships between macrophytes and
173 landscape features (Declerck et al. 2006; Pedersen et al. 2006; Cheruvilil and Soranno 2008;
174 Akasaka et al. 2010; Jog et al. 2017). These authors used different buffer zones as a proxy for
175 topographic catchment areas, in the range 50–3200 m, finding that macrophytes richness is best
176 explained by land use at the local scale, within up to 500 m buffer around each site (Declerck et al.
177 2006; Akasaka et al. 2010). The land use/land cover type was derived from Lombardy Region
178 database (<http://www.geoportale.regione.lombardia.it/>), both considering a historical layer (referred
179 to the 1954, Gruppo Aeronautico Italiano planimetric flight) and a contemporary layer to the
180 floristic records (Land Cover Map 2007; DUSAF 2.1, Regione Lombardia 2008).

181

182 As a proxy for anthropogenic pressures, diffuse loads of N, P, and Si (WBnl, WBpl, and WBsl)
183 were calculated integrating farming census data in a nutrient budgeting approach previously applied
184 to the Po River system (Viaroli et al. 2018) and to some of its most human-impacted sub-basins

185 (Soana et al. 2011; Castaldelli et al. 2013; Pinardi et al. 2018). Briefly, nutrient budgets were
186 estimated as the net difference between inputs (livestock manure, synthetic fertilizers, atmospheric
187 deposition, and, limited to N budget, biological fixation) and outputs (crop harvest and, limited to N
188 budget, ammonia volatilization and denitrification in soils) across the utilized agricultural area
189 (UAA). Nutrient budgets were calculated for each municipality where the relict waterbodies are
190 located, and expressed in term of annual fluxes per unit of utilized agricultural area ($\text{kg ha}^{-1} \text{UAA}$
191 yr^{-1} ; details about calculations and data sources are reported by Pinardi et al. 2018).

192

193 As response variables, we quantified the total number of aquatic and wetland plant species (species
194 richness), the total number of hydrophytes and computed the percentage of alien species, and the
195 policy species. This latter includes plants of EU, national and regional conservation interest, based
196 on regional regulations on rare and threatened species (Regional Law n. 10 of 2008; Regional
197 Council Deliberation n. 11102 of 2010). Hydrophytes were selected based on the Ellenberg's
198 moisture value (considering values of 11 and 12, therefore aquatic plants rooted in waterlogged
199 sediments or submerged plants), and the Raunkiaer's classification of life-forms (considering
200 hydrophytes; Raunkiaer 1934).

201

202 *Statistical analysis*

203 A stepwise Variance Inflation Factor (VIF) procedure was performed to remove collinear
204 predictors. VIF has been calculated from the square of the multiple correlation coefficient that
205 results from regressing a predictor variable against all other predictor variables. A value of $\text{VIF}=2$
206 was used as threshold for the selection (Zuur et al. 2010) and the function *vifstep* of the R package
207 *usdm* was used (Naimi et al. 2014). Twelve variables were selected by VIF procedure and used as
208 predictors to investigate the diversity facet patterns (see Table 1).

209 Generalized linear models (GLM) were used to identify the contribution of each explanatory
210 variable to species richness, as well as the number of hydrophytes, alien plant species (AS), and
211 policy plants (AS) species. A GLM model with a quasi-Poisson error distribution was used for
212 species richness, while a Poisson error distribution was used for the other dependent variables.
213 Outliers were removed when necessary and model residuals were tested for spatial autocorrelation.
214 alien plant species richness

215

216 **Results**

217 *Taxonomic synopsis*

218 A total of 101 species were recorded, mainly represented by wetland species (68). Indeed, the most
219 common species – present in more than the 60.0% of sites – are exclusively non-aquatic taxa (11).
220 Among these, the most widespread species were *Carex acutiformis* (recorded in 75 sites out of 88;
221 85.2%), *Bidens frondosus* (70; 79.5%), *Lycopus europaeus* (65; 73.9%), *Typha latifolia* (63;
222 71.6%), and *Phragmites australis* (62; 70.5%). Most of the species were locally rare: 81 occurred in
223 less than the 30.0% of sites (≤ 26), and more than a third of these rare species were hydrophytes
224 (HY). Only *Sparganium erectum*, *Alisma plantago-aquatica*, and *Lemna minor* were rather
225 widespread hydrophytes, recorded at 56, 46 and 44 sites, respectively. Fifteen species were
226 recorded at one site as in the case of the red-listed *Utricularia vulgaris* and *Utricularia minor*, and
227 the invasive *Eichhornia crassipes* and *Egeria densa* (Supplementary material 2). Indeed, the
228 wetland plant assemblages are species poor and characterized by a marked skewed pattern in
229 species abundance, with species showing quite unequal abundances (Fig. 2).

230

231 The number of species per site ranged across one order of magnitude, from 5 to 51, and averaged
232 17.8 ± 8.1 (mean $\pm$ standard deviation, Fig. 3); whereas the number of alien species ranged up to 4
233 species per site (mean: 1.1), with a total richness of 14 species. The number of policy species
234 showed a large variability across sites, ranging from 0 to 14, with a mean value of 2.7 and a total
235 richness of 29 (Fig. 3; Supplementary material 2).

236

237 *Explanatory variables of plant species richness*

238 Habitat amount (WBar) was the strongest predictor for all the four different plant richness facets in
239 analysis (Table 2). Similarly, the RIco variable – expressing the isolation gradient of aquatic
240 habitats – was statistically significant for species richness, policy species, and hydrophytes, but not
241 for alien ones. Also relevant but less significant were WBua07 (i.e. surfaces occupied by urban
242 areas in the surrounding area of each aquatic habitat at 2007) for species richness and policy
243 species, WBpa (perimeter/area ratio) for policy species, WBor (wetland origin) for alien species,
244 and WBhy (hydroperiod) for hydrophytes (Table 2).

245

246 Specifically, the total richness increased with increasing area of aquatic habitats ($P(>\chi) < 0.001$),
247 decreasing isolation (0.002), and increasing of urban areas in the surrounding area (0.033).
248 Additionally, species richness also increased with decreasing of perimeter/area ratio but with an
249 almost statistically significant level (0.053). Alien species richness increased with increasing area of
250 aquatic habitats (< 0.006), and in habitats with an artificial origin (0.046). The richness of policy
251 species were positively related to habitat area (< 0.001), perimeter/area ratio (0.003), and increasing

of urban areas in the surrounding area (0.002) and negatively related to increasing isolation (0.004). In addition, policy species increased at sites characterized by greater hydrological stability (WBhy; 0.076). Lastly, the richness of hydrophytes was positively related to area (<0.001), and to permanent aquatic habitats (<0.001), and negatively to isolation (0.011). Moreover, WBml (management level) and WBws (existence of a superficial water supply) had a minor, positive effect on hydrophytes, but only with an almost statistically significant level (0.057, and 0.076, respectively). Non-managed sites with a direct connection to the superficial hydro-system showed higher richness of hydrophytes (Tables 1, and 2).

Discussion

Our findings emphasize the higher importance of eco-morphology (in particular site area) and hydrological connectivity as compared to land-use intensity (exemplified by land uses and nutrient loads) in determining plant richness in aquatic habitats in overexploited watersheds (Rolon et al. 2008). A counterintuitive result indicates that the policy species are enhanced by an increasing urbanization in the landscape. Site origin was crucial only for alien species, being more abundant in artificial sites.

Habitat size is a well-known driver of species richness (Mac Arthur and Wilson, 1967), also for small habitats as in the case of relict lowland wetlands, ponds, or in more general terms, SWEs (Hill et al. 2019; Oertli and Parris 2019). In our study, all the response variables (total species, alien and policy species, and hydrophytes richness) were influenced by site size, confirming its importance in determining wetland plant richness in overexploited landscapes. Recently, Guareschi et al. (2019) confirmed the relevance of wetland dimensional features in explaining the biodiversity they host. However, for a similar geographical context to that investigated by the present study, these authors highlighted the preeminent role of the physical heterogeneity of sites compared to the dimension *tout court*. In all likelihood, for small marginal areas, such as SWEs, the size per se is a fundamental descriptor to explain specific richness, while for larger systems (for example wetlands) the heterogeneity of habitats acts as a prominent driver in diversifying ecological niches and therefore the plant diversity harboured. This is in line with the observations by Shi et al. (2010) for a series of Chinese wetlands and their vascular plant species richness, and with the results by Báldi (2008) for invertebrate richness in Hungarian protected areas.

Connectivity is among the most relevant drivers of biodiversity, especially in inland aquatic ecosystems (Hamer and McDonnell 2008; Schöpke et al. 2019). This is due to the hydrological

286 disturbance exerted by floods via offsetting competition by a continuous regeneration of niches
287 (Bornette et al. 1998) and propagules (Keruzoré et al. 2013). Specifically, Reid et al. (2016) found
288 that the hydrological connection triggers wetland plant germination via water delivery and by
289 modifying hydraulic habitat, but it does not seem to govern wetland vegetation by propagules
290 exchange between habitats (rivers vs oxbow lakes). Our results are consistent with these findings,
291 reinforcing the view of an intimate relationship between connectivity and hydroperiod (i.e. water
292 level variations; Bolpagni and Piotti 2015, 2016). Water depletion is able to drive plant successional
293 changes favouring the ingression of terrestrial species in wetland areas, whereas differentiated
294 hydroperiods may expand the niches available for colonization by aquatic and wetland species
295 (Brose 2001; Toyama and Akasaka 2017).

296

297 Anthropogenic land uses in the surrounding of wetlands negatively affect their biodiversity
298 (Declerck et al. 2006; Cheruvilil and Soranno 2008; Akasaka et al. 2010; Jog et al. 2017), as
299 verified for aquatic insects or amphibians (Hamer and McDonnell 2008). However, here a positive
300 influence of urban area in the landscape on total species and policy species richness were recorded,
301 although the percentage of urbanized areas in the surrounds of the investigated sites (mainly
302 represented by farmhouses and accessory buildings) never exceeds 1%. This may be explained by
303 an active role of landowners in maintaining aquatic habitats for multiple purposes, like fishing or
304 water storage. The active management of SWEs can periodically renew the ecological niches
305 available for aquatic plants, for example by removing sediments or cutting riparian strips.
306 Additionally, Gallego et al. (2015) found that artificial farm ponds are characterized by a higher
307 diversity of aquatic pioneer species compared to natural counterparts, suggesting a non-negligible
308 role of human intervention in regulating macrophytes filtering into assemblages.

309

310 Finally, our results corroborate the view that trophic determinants can be considered only weak
311 drivers for aquatic and wetland plant richness in overexploited watersheds, as stressed for
312 hydrophytes by James et al. (2005) in shallow lakes, and by Rosset et al. (2014) in ponds. Here, we
313 used diffuse nutrient loads as a proxy for anthropization, and the lack of a significant effect, despite
314 the wide ranges recognized (from 23.8 to 279.8 kg N ha⁻¹ yr⁻¹ for nitrogen, for example), could be
315 due to the oversimplification of the landscape matrix, as well as to the limitation of using data
316 estimated at municipality level. To investigate trophic determinants, we followed this “land use
317 oriented” approach, rather than acquiring data relating to physical and chemical features of waters
318 or sediments of habitats, since it is generally acknowledged that these parameters are widely
319 susceptible to intra-day or intra-seasonal variability. In addition, the presence of dense macrophyte

320 beds is able to deeply modify the physical and chemical conditions of colonized habitats, especially
321 at the peaks of growing seasons, making it difficult to disentangle the role of the physical
322 environment from those mediated by plants (Tall et al. 2011; Marzocchi et al. 2019).

324 *Implications for plants conservation in overexploited watersheds*

325 Based on our evidence, site size emerges as the preeminent driver of aquatic and wetland plant
326 richness in marginal, isolated water bodies, suggesting the need to keep the surfaces of aquatic
327 domains, and wherever possible increase them. Additionally, the creation, maintenance and the
328 ecological recovery of dispersal corridors (i.e. favouring and strengthening the reconnection among
329 habitats) as well as of potential new colonisable habitats (i.e. expanding the areas suitable for
330 further colonisations) may enhance the preservation of plant richness in agricultural landscapes
331 (Chester and Robson 2013; Schöpke et al. 2019). This is true despite the general scarce water and
332 sediment quality of artificial and semi-natural hydro-systems in lowlands.

333 Additionally, the development of specific strategies aimed at reconstructing and managing more
334 naturally intra-annual hydroperiods is probably one of the few interventions that can ensure the
335 survival of a large number of hydrophytes, irrespective of the hydro-morphological recovery of
336 riverscape dynamicity as a whole (Brose 2001; Bolpagni and Piotti 2015, 2016; Toyama and
337 Akasaka 2017). In this regard, also newly created aquatic habitats can provide fundamental roles in
338 order to guarantee a sufficiently large network of ecological connections (Oertli and Parris 2019 and
339 references therein). Thus, Gallego et al. (2015) have stressed the key contribution of artificial farm
340 ponds in conserving the regional aquatic plant richness in a Mediterranean context. They found a
341 relevant, positive role of management actions in guaranteeing continuously new and suitable
342 habitats for pioneer plants. Further, also aquatic habitat area strongly depends on water body uses
343 reinforcing the active role of artificial aquatic habitats in harbouring a relevant proportion of
344 biodiversity in agricultural landscapes (Chester and Robson 2013). However, our data confirm the
345 direct link between artificial sites and alien plant richness (Bolpagni and Piotti 2015, 2016; Gallego
346 et al. 2015) suggesting the inherent high associated risks with the progressive replacement of
347 natural aquatic habitats with artificial ones. This is a critical issue and challenge for biodiversity
348 conservation in highly modified landscapes as overexploited watersheds. Future actions will have to
349 try to minimize the impact and invasiveness of alien species in newly created aquatic habitats, as
350 well as to promote the establishment and spread of native plants and vegetation. In this regard,
351 another option can be represented by the active recovery of lost aquatic habitats due to agricultural
352 intensification (i.e. by drainage or infilling) (Bolpagni, 2020). To this regard, Alderton et al. (2017)
353 have recently strengthened the role of buried seed-banks in supporting macrophyte diversity in

354 SWEs. Working on *ghost ponds*, these authors have shown the high potential of buried propagules
355 to remain viable on a centennial-scale, representing a potential for future recolonization in modern
356 agricultural landscapes.

357

358 **Conclusions**

359 Our findings open new perspectives concerning the aquatic and wetland plants responses in
360 overexploited watersheds, reinforcing the preeminent contribution of local drivers in explaining
361 macrophyte patterns (Alahuhta 2015; Bolpagni and Piotti 2016). Here, plant diversity responds
362 mainly to variations in habitat amount and connectivity loss. At the same time, alien species were
363 also directly influenced by the origin of colonized aquatic habitats, suggesting a non-marginal
364 contribution of habitat dynamics in regulating their susceptibility and response to invasion
365 (Bolpagni and Piotti 2016). Typically, the emergence of barriers to species and individuals
366 dispersion has relevant effects on competition outcomes, with cascading consequences for the
367 maintenance of biodiversity facets at local and regional scale (Harvey and MacDougall 2018).
368 Based on this, future challenges would include a thorough understanding of the spatio-temporal
369 processes shaping aquatic and wetland plant diversity in artificial and/or altered ecosystems, also –
370 for example – by remote sensing techniques that may offer exceptional information for measuring
371 aquatic ecosystem dynamics at multiple temporal and spatial scales (Ghirardi et al. 2019). This is a
372 forced path in order to strengthen the effectiveness of biodiversity conservation programs in
373 floodplains beyond the risks associated with the increasingly spread of alien species.

374

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377 not-for-profit sectors.

378

379 **Electronic supplementary material**

380 **Supplementary material 1:** List of the explanatory variables: for each site we reported the
381 geographical coordinates (Long., Lat.; Gauss-Boaga projection), the variable's values (for
382 abbreviations see Tab. 1), and the total plant species richness (SR), the total alien plant richness
383 (AS), and the total policy plant richness (PS). Data were taken from Frattini (2008);

384 **Supplementary material 2:** List of the sampled hydrophytes and wetland plants: for each site we
385 reported the site number (Site; as reported in Supplementary material 1), the name of species, the
386 life form (G = geophyte; H = hemicryptophyte; He = helophyte; Hy = hydrophyte; P =
387 phanerophyte; T = therophyte), and their presence (1) at site level; additionally, we reported the

388 alien (AS; 1) and policy (PS; 1) species. The authors are solely responsible for the content and
389 functionality of these materials. Queries (other than absence of the material) should be directed to
390 the corresponding author.

391

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569 **Table 1.** Explanatory variables with their abbreviations (Ab), in bold are highlighted the variables
570 selected by the stepwise Variance Inflation Factor (VIF) procedure.

Ab	Parameter	Description, methods for quantification	Range	Type
Eco-Morphological				
WBar	Waterbody area	In m², calculated in GIS environment	1000–257'000	C
WBpe	Waterbody perimeter	In m, calculated in GIS environment	118–3'181	C
WBpa	Perimeter/area ratio	Ratio between perimeter and area	0.012–0.192	C
WBor	Origin	Wetland originated by natural processes (1) not (2), or mixed (both natural and artificial, 3)	1–3^a	CO
Hydrological				
RIco	River connectivity	In m, mean distance from waterbody's margin to the nearest five rivers, calculated in GIS environment	800–11'090	C
WBco	Waterbody connectivity	In m, mean distance from waterbody's margin to the nearest five waterbodies, calculated in GIS environment	1'259–8'131	C
WBhy	Hydroperiod	Duration and intensity (spatial) of drought events; based upon survey' evidences and information from land owners	1–3^b	CO
WBws	Superficial water supply	Known complete or not complete isolation of water bodies from superficial waters: presence (1) or absence (0) of a connection with superficial hydro system)		B
Direct Human impacts				
WBbu	Water body used as water source	Water bodies used (1) for watering fields, etc., or not (0)		B
WBml	Water body management level	Known active (high or moderate; H or M) management or not (complete natural evolution; N); based upon information from land owners	1–3^c	CO
Landscape mosaic				
WBls	Landscape sector	Position filled by each waterbodies into landscape sectors based on altitude (m a.s.l.)	35–305	C
WBaa	Impact of land use: agriculture areas	In %, estimated superficies occupied by crops in the surrounding area of each waterbody (within a buffer strip of 500 m), calculated in GIS environment for the years 1954 and 2007	0.00–0.55	C
WBsm	Impact of land use: semi-natural, natural areas	In %, estimated superficies occupied by natural habitats in the surrounding area of each waterbody (within a buffer strip of 500 m), calculated in GIS environment for the years 1954 and 2007	0.23–0.99	C
WBua	Impact of land use: urban areas	In %, estimated superficies occupied by urban areas in the surrounding area of each waterbody (within a buffer strip of 500 m), calculated by use of GIS map for the years 1954 (54) and 2007 (07)	0.00–0.77	C
WBAq	Impact of land use: waterbodies	In %, estimated superficies occupied by open waters (waterbodies) in the surrounding area of each waterbody (within a buffer strip of 500 m), calculated by use of GIS map for the years 1954 (54) and 2007 (07)	0.00–0.15	C

WBnl	Diffuse load of N (kg N UAA ⁻¹ y ⁻¹)	In kg, estimated annual load of nitrogen released at municipality-scale per hectare of utilized agricultural area	23.8–279.8	C
WBpl	Diffuse load of P (kg P ha UAA ⁻¹ y ⁻¹)	In kg, estimated annual load of phosphorous released at municipality-scale per hectare of utilized agricultural area	-13.7–90.2	C
WBsl	Diffuse load of Si (kg Si ha UAA ⁻¹ y ⁻¹)	In kg, estimated annual load of silica released at municipality-scale per hectare of utilized agricultural area	-29.8–77.0	C

571

572 C, continuous; CO, categorical and ordered parameter. ^aCoded as follows: 1, natural origin; 2, artificial
573 origin; 3, mixed origin. ^bCoded as follows: 1, permanent water bodies; 2, semi-permanent water bodies, with
574 wet/flooded area greater than the 20% of potential maximum area of the water body; 3, temporary water
575 bodies, with at least 15 days of complete drought. ^cCoded as follows: 1, high level of water levels
576 management; 2, moderate level of water levels management; 3, no actions. B: binary.

577 **Table 2.** Summaries of the ANOVA results for the effect of the explanatory variables selected by the VIP procedure for SR (total plant species
578 richness), AS (total alien plant species richness), PS (total policy plant species) and HY (hydrophytes); significance: in bold the statistically
579 significant variables [$P(>\chi) \leq 0.05$]; highlighted in pale grey the almost statistically significant variables [$0.05 < P(>\chi) < 0.1$]; $P(>\chi)$ is chi-square
580 statistic.

581

582

Parameter	df	SR					AS					PS					HY				
		Estimate	R.df	Dev.	R.Dev.	$P(>\chi)$	Estimate	R.df	Dev.	R.Dev.	$P(>\chi)$	Estimate	R.df	Dev.	R.Dev.	$P(>\chi)$	Estimate	R.df	Dev.	R.Dev.	$P(>\chi)$
Intercept (Null)			84		270.30			87		57.282			85		135.122			84		157.331	
WBar	1	0.235	83	103.881	166.42	<0.001	0.124	86	7.5137	49.768	0.006	0.149	84	13.2005	121.921	<0.001	0.385	83	29.0442	128.287	<0.001
WBpa	1	-0.066	82	6.373	160.05	0.053	-0.100	85	0.3124	49.455	0.576	-0.213	83	8.5674	113.354	0.003	0.040	82	0.0187	128.268	0.891
WBor	1	-0.065	81	3.563	156.48	0.147	0.176	84	3.9764	45.479	0.046	-0.116	82	0.4350	112.919	0.510	-0.110	81	0.9127	127.355	0.339
RIco	1	-0.089	80	16.411	140.07	0.002	-0.003	83	0.0027	45.476	0.958	-0.195	81	8.2112	104.708	0.004	-0.153	80	6.5139	120.841	0.011
WBhy	1	-0.045	79	0.948	139.12	0.455	-0.048	82	0.0589	45.417	0.808	-0.115	80	3.1564	101.551	0.076	-0.186	79	14.5880	106.287	<0.001
WBws	1	0.011	78	0.040	139.09	0.878	-0.126	81	0.5231	44.894	0.470	0.059	79	0.0046	101.546	0.946	0.130	78	3.1463	103.107	0.076
WBbu	1	-0.013	77	0.029	139.06	0.896	0.036	80	0.1400	44.754	0.708	0.018	78	0.8831	100.663	0.347	0.058	77	0.0942	103.013	0.759
WBml	1	0.040	76	2.453	136.60	0.229	-0.064	79	0.7958	43.959	0.372	0.016	77	0.0011	100.662	0.973	0.134	76	3.6223	99.390	0.057
WBaa	1	0.046	73	2.113	125.42	0.264	-0.058	76	0.1962	42.076	0.658	0.070	74	0.5232	88.870	0.469	-0.024	73	0.0898	97.489	0.764
WBua07	1	-0.066	75	7.718	128.88	0.033	-0.013	78	0.1372	43.821	0.711	0.224	76	9.8338	90.828	0.002	0.078	75	1.7964	97.594	0.180
WBaq07	1	-0.063	74	1.355	127.53	0.371	0.122	77	1.5496	42.272	0.213	0.035	75	1.4352	89.393	0.231	-0.013	74	0.0153	97.579	0.902
WBSl	1	-0.020	70	0.414	119.44	0.621	-0.009	73	0.0051	41.670	0.943	0.049	71	0.3570	86.124	0.550	-0.054	70	0.5027	96.604	0.478
WBua	1	-0.025	72	2.834	122.58	0.196	0.059	75	0.2596	41.816	0.610	0.039	73	0.0395	88.831	0.843	-0.015	72	0.1615	97.327	0.688
WBaq	1	-0.065	71	2.732	119.85	0.204	-0.037	74	0.1408	41.675	0.708	-0.116	72	2.3497	86.481	0.125	-0.036	71	0.2205	97.107	0.639

583 **Figure legends**

584 **Fig. 1.** Study area: the sampling aquatic sites are marked as black dots, as the Garda hilly sector,
585 including the clusters of sites 1–14 (Iseo hilly surrounds), and 15–48 (Garda hilly surrounds); also
586 the hydrosystem is reported in pale grey, as the two main lakes in the area: Iseo and Garda.

587 **Fig. 2.** Hydrophytes and wetland species occurrence-probability.

588 **Fig. 3.** Box plots of the numbers of plant species richness (SR), the totals of alien species (AS) and
589 policy species (PS) (upper panel); and the numbers of Raunkiaer's life-forms (Raunkiaer, 1934):
590 HY (hydrophytes), G (geophytes), H (hemicryptophytes), He (Helophytes), P (phanerophytes), and
591 T (therophytes).

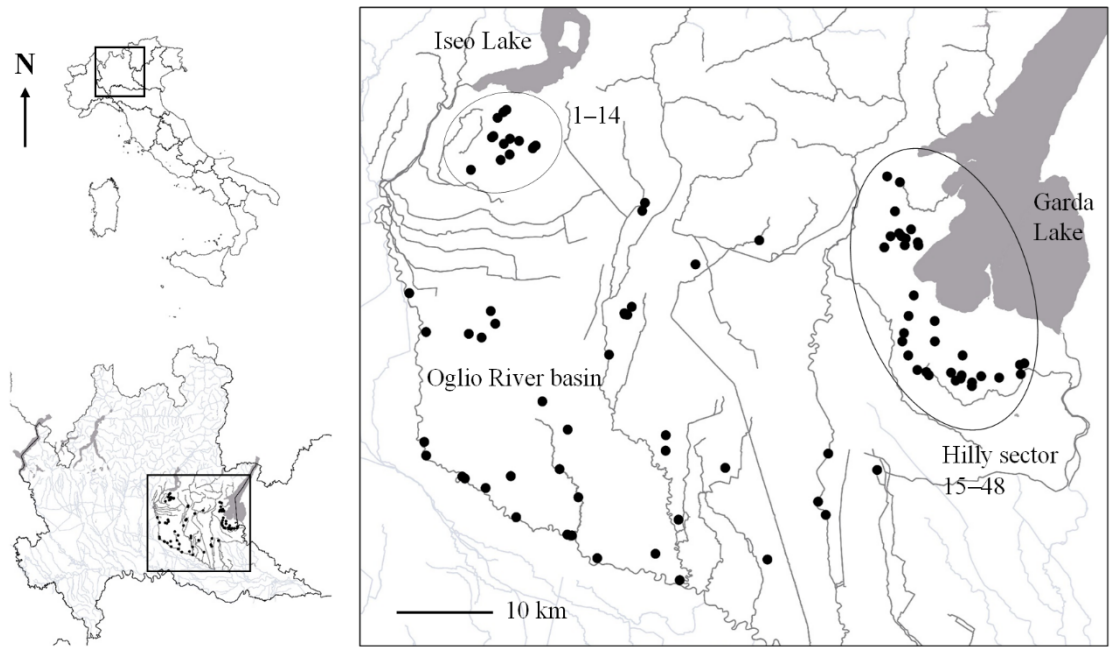
592

593 Fig. 1

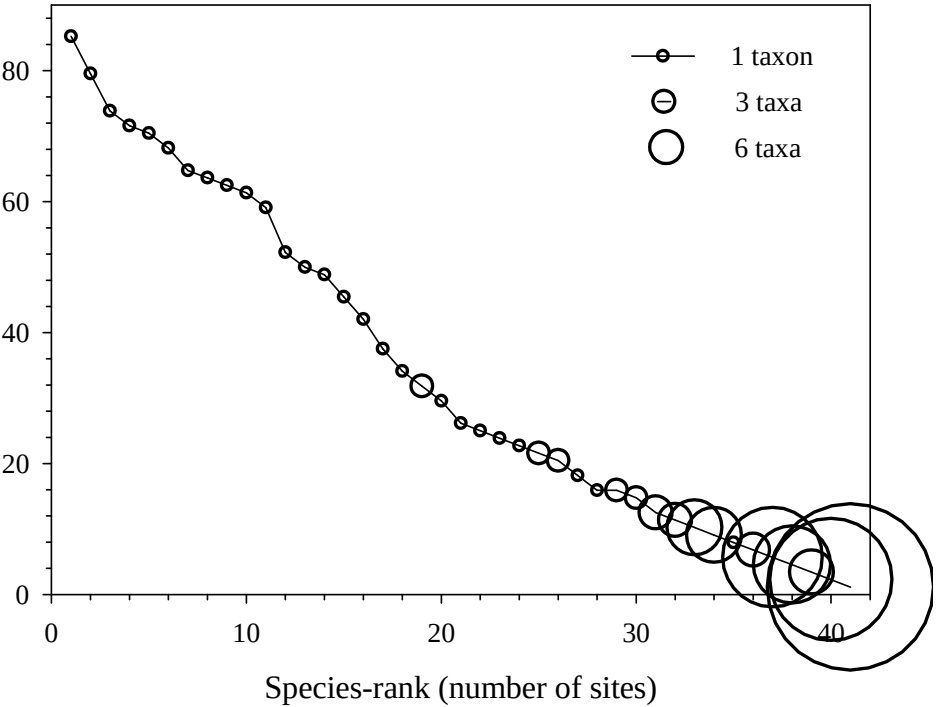
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597 Fig. 2



614 Fig. 3

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