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1 Article

2 Do habitats show a different invasibility pattern by 3 alien plant species? A test on a wetland protected area

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12 **Abstract:** Biological invasions are deemed as the second most important global driver of
13 biodiversity loss right behind habitat destruction and fragmentation. In this study, we aimed at
14 testing if community invasibility, defined as the vulnerability to invasion of a community, could be
15 associated with the characteristics of a given habitat, as described by the composition and structure
16 of its native species. Based on a probabilistic sampling of the alien flora occurring in the temperate
17 wetland Lake Doberdò (Friuli Venezia Giulia region, NE Italy) and using a null model-based
18 approach, observed occurrence of Invasive Alien Species (IAS) within sampling units were
19 randomized within habitats.

20 While testing the degree of invasibility for each habitat within the wetland, our null hypothesis
21 postulated that habitats are equally invaded by IAS, as IAS can spread homogeneously in the
22 environment thanks to their plasticity in functional traits which make them able to cope with
23 different ecological conditions.

24 The results obtained comparing observed IAS frequencies, abundance and richness to those
25 obtained by the null model randomizations, showed that for all habitats invasion was selective.
26 Specifically a marked preference for habitats with an intermediate disturbance level, a high
27 nutrients level and a medium-high light availability was observed while an avoidance was
28 detected for habitats characterized by lower levels of nutrients and light availability or extreme
29 conditions caused by prolonged submersion.

30 This method allows us to provide useful information using a simple-to-run simulation, for the
31 management of the IAS threat within Protected Areas. Moreover, the method allows us to infer
32 important ecological characteristics leading to habitat invasion without sampling the
33 environmental characteristic of the habitats, which is an expensive operation in terms of time and
34 money.

35 **Keywords:** Alien species, biodiversity, Lake Doberdò, Natura 2000 Network, occurrence
36 probability, randomization, null model.

37 **Abbreviation:** IAS (Invasive Alien Species), PA (Protected Area).

38

39 1. Introduction

40 Biological invasions are deemed as the second most important global driver of biodiversity loss
41 right behind habitat loss and fragmentation [1-3]. Indeed, the introduction and spread of Invasive
42 Alien Species (hereafter IAS) [4,5] have heavy repercussions on ecosystems, leading to negative
43 impacts on native species, habitats, landscape, ecosystem production, naturalistic value, human

44 health and economy [6-9]. For these reasons, research interest on biological invasions has
45 exponentially increased in recent years [10,11].

46 The success of IAS in their non-native ranges is claimed to be an effect of interactions among
47 several mechanisms, divided into three main groups of factors: propagule pressure, habitat
48 invasibility and species invasiveness [12-19]. Propagule pressure represents a composite measure of
49 the number of individuals released into the introduction area [20]: it incorporates estimates of the
50 absolute number of individuals involved in any one release event (propagule size) and the number
51 of discrete release events (propagule number) [21]. Habitat invasibility is a property of recipient
52 ecosystems and depends on the features that may determine their vulnerability to invasion, which,
53 in turns, is potentially determined by the level of disturbance, the competitive abilities of the native
54 species and their resistance to disturbance along with assembly mechanisms of the recipient
55 community [22]. In this context, the rule that determines how the native community is assembled is
56 also related to the occupied and available niche space in a given community [23,24], for example in
57 tropical communities there is low space availability, due to the presence of fast-growing
58 multilayered vegetation that makes them resistant to invasions [25], while deforested mesic habitats
59 with frequent disturbance present a higher rate of invasion because of greater niche availability
60 [26-28]. It is well-known that the success of IAS depends on biotic factors such as competition or
61 predation with native species, features of the native communities, and also on abiotic factors such as
62 availability of nutrients and light, as well as the presence of anthropogenic disturbance and
63 environmental instability, which influence the available niche space [29]. Species invasiveness,
64 namely the features that are consistently associated with the ability of IAS to invade, can be
65 identified from comparative metrics between invasive and non-invasive alien species, such as those
66 related to photosynthetic efficiency, use of water and resources, reproduction and dispersal abilities.
67 In addition species invasiveness is also related to residence time (i.e. the time since the introduction
68 of a taxa to a new area) and taxonomic affiliation (some taxa are more competitive than others due to
69 phylogenetic background) [30]. In the last decade, research efforts have often focused in
70 understanding species functional characteristics that may enhance their invasiveness such as rapid
71 reproduction and growth, high dispersal ability, ecological plasticity [10,15,24,31-33]. Accordingly, it
72 has been postulated that it is more a multiple suites of traits which could explain invasion success in
73 different environments [34-36], rather than a single dominant trait.

74 Even though several studies already investigated how to predict invasion success through the
75 analysis of those factors related to species invasiveness [24,37-39], less attention has been paid on
76 habitat properties underlying community invasibility [40,41]. Invasibility has been studied mainly at
77 a large scale, with data suffering from a reduced accuracy being aggregated from varying sources
78 [42-44] and using rough environmental characteristics [45-47] whereas the smaller (local) scale has
79 been substantially neglected [48,49].

80 To complete the picture, IAS have been largely studied in human-altered and urbanized
81 environments, which are known to be prone to biological invasions [4,5,16,18,50,51] while less
82 information is available for more natural and undisturbed habitat. An increasing number of studies
83 [19,52-54] reported that even Protected Areas (hereafter PAs) can be seriously affected by IAS.
84 Nevertheless, temperate wetland PAs are underrepresented in the invasive plant literature [55].
85 Wetlands are vulnerable ecosystems extremely important for the maintenance of biodiversity, as
86 they are peculiar environments, source of a rich plant and animal diversity. Wetlands are among the
87 most disturbed and exploited ecosystems: they have been continuously subjected to the anthropic
88 pressure, resulting in a dramatic decline during the last decades, especially across Europe, due to
89 extensive habitat destruction and fragmentation [56-58]. This makes them more vulnerable and at
90 greater risk of biological invasion considering that several studies highlight notable gaps for the
91 long-term maintenance of biodiversity in wetland PAs [58,59].

92 These environments are usually characterized by marked vegetation zonation, associated with
93 strong environmental gradients, dictated primarily by hydrology [60]. The hydrological regime of
94 wetlands determines the distribution of different communities which are strictly linked to the
95 presence of the water, causing a selective distribution of plant species on the basis of their capacity to

96 tolerate submersion and/or dry periods. This vegetation zonation permits to host numerous species,
 97 including rare and endemic ones, in relative small areas, moreover wetlands act as ecological sinks
 98 accumulating nutrients transported by water, and, for this reason, they can also be more susceptible
 99 to IAS invasion [61,62].

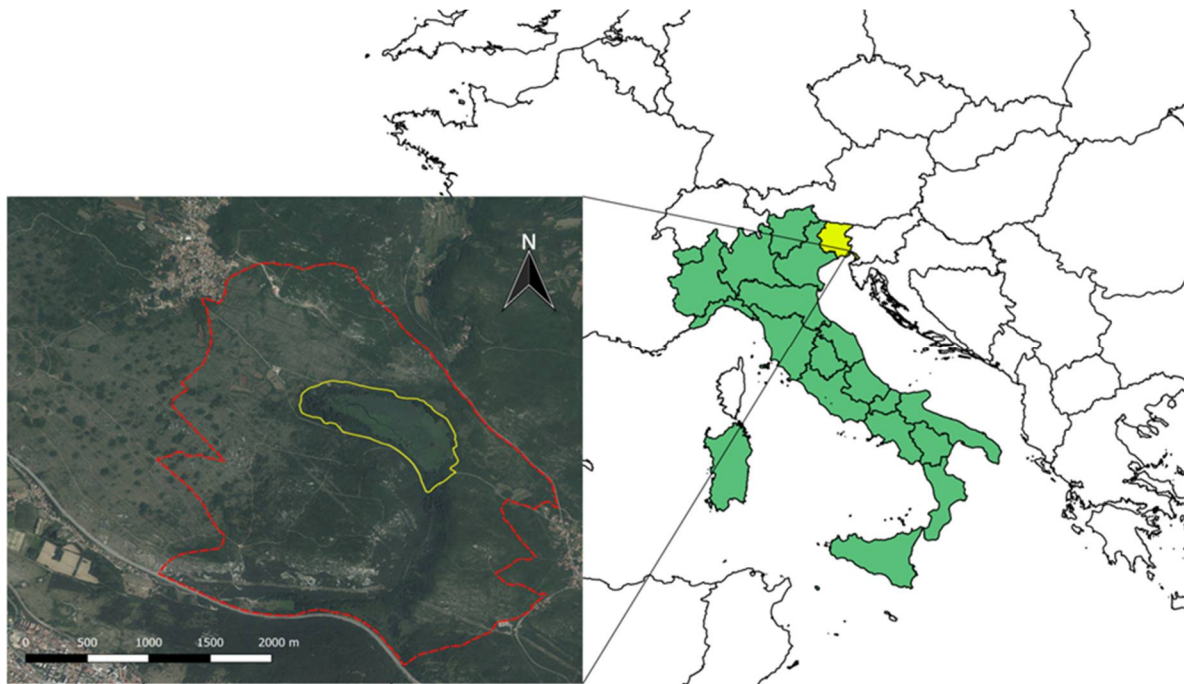
100 In this study, we analyzed the possible effect of habitat features on community invasibility on a
 101 temperate wetland in NE Italy using null models. Specifically, we aimed at estimating the degree of
 102 invasibility for each habitat within the wetland PA. Our null hypothesis postulated that IAS
 103 presented a plasticity able to cope with differences in biological and environmental habitat
 104 characteristics, allowing them to spread without exclusive preferences or, in other words, we expect
 105 them to be randomly spread across the wetland PA.

106 2. Materials and Methods

107 2.1. Study area

108 The study was carried out at Lake Doberdò (Figure 1, Lat. 45.831574, Long. 13.562023), a karstic
 109 lake in north eastern Italy. It is part of the regional natural reserve “Laghi di Doberdò e Pietrarossa”
 110 and is included in the Natura 2000 network (SAC-IT3340006/SPA-IT3341002).

111 The study area (ca. 65 ha) includes the lake and all the surrounding vegetation directly
 112 dependent on the presence of lake water, including the meso-hygrophilous one.



113

114 **Figure 1.** Location of the study area (yellow border) within the Regional Natural Reserve “Laghi di
 115 Doberdò e Pietrarossa” protected area (red dashed border).

116 Bioclimate is temperate with lower meso-temperate thermotype and lower humid ombrotype,
 117 with relatively warm summers and dry and cool winters. Average annual rainfall is around 1200
 118 mm. Mean annual temperature is 15 °C, with an average temperature of 5 °C in January (coldest
 119 month) and 23 °C in July (warmest month) (source <https://www.meteo.fvg.it>, reference period 1999–
 120 2018).

121 The study area is characterized by a complex geomorphology. It consists of a thick succession of
 122 limestone and subordinately dolomitic rocks, dated between the Lower Cretaceous (Aptiano) and
 123 the lower Eocene; the platform deposits are surmounted by turbidite deposits (flysch) [63–65]. The
 124 soils of the study area are classified as “red soils”, e.g., clayey or silty-clayey soils that cover the

125 calcareous or dolomitic substrates with variable thicknesses, filling particular fractures and areas
126 with depressed morphology [66].

127 Lake Doberdò is a karst lake with a typical peculiar hydrology: it has no superficial inflow or
128 outflow; the superficial runoff is near zero and the water feed mainly comes from the underground
129 waters [67]. The water fills the lake emerging through karst springs located on the north-western
130 side and disappears through the swallow holes on the eastern side of the lake. The lake feeding is
131 mainly due to the underground flows of the Isonzo river and the precipitations, recharging the karst
132 groundwater [65,68,69]. The water level of the lake is extremely variable throughout the year,
133 leading to a significant change in the extension of the lake surface area, from 200 m² during dry
134 periods to 400000 m² during wet periods [70].

135 The vegetation of the lake is characterized, starting from the center of the lake and going
136 outwards, by aquatic communities (dominated by submerged and floating-leaved rooted plants
137 such as *Potamogeton* spp., *Myriophyllum* spp. and *Nuphar lutea*), by helophytic marsh vegetation
138 dominated by tall sedges (*Carex elata*) and common reeds (*Phragmites australis*); behind these, a thin
139 strip of mud soil along the lake shore hosts hygro-nitrophilous herbaceous communities. The
140 zonation is completed toward the lake shores and landwards by hygrophilous willow shrubs and
141 woods (with *Salix cinerea*, *Salix alba*), and a meso-hygrophilous woodland with the field elm (*Ulmus*
142 *minor*), black poplar (*Populus nigra*) and narrowed-leaved ash (*Fraxinus angustifolia* subsp. *oxycarpa*),
143 with its mantle with *Ulmus minor* and *Paliurus spina-christi*.

144 2.2. Sampling design and data collection

145 The identification of the habitats occurring in the study area was based on the phytosociological
146 analysis of plant communities, following the approach adopted in modern European habitat
147 classifications [71-74]. According to a preliminary vegetation survey of the area, carried out in 2015, 33
148 plant communities were classified according to the phytosociological approach [75-77]. Due to the
149 scarce extension of some communities (<1000 m²) or to the small-scale heterogeneity in communities
150 spatial arrangements in some areas (where complex vegetation mosaics were present), only 20
151 vegetation types were effectively mapped (Figure S1) and considered in this study as different habitat
152 units (Table 1).

153 IAS occurrences within the 20 vegetation types were sampled by means of a probabilistic
154 sampling approach. Specifically, a stratified random approach was adopted using vegetation types as
155 homogeneous strata. For each vegetation type identified, squared sampling units (hereafter plots) of 1
156 m² were randomly selected, with their number proportional to the total area occupied by the
157 vegetation type, precisely the number of plots was selected proportionally to the area of the
158 communities as follows: 4 plots for all the communities with an extension up to 1.5 ha and 1 plot was
159 then added every 0.7 ha up to a total extension of 5 ha; for communities bigger than 5 ha, the
160 proportion 1 plot/ha was used. This sampling design was chosen to ensure the best compromise for
161 representing small communities without oversampling the larger ones, thus maintaining a good
162 compromise between statistical robustness and sampling effort. A total of 123 plots were sampled
163 within the whole study area. We used such a small plot size (1 m²) in order to reduce the margin effect
164 due to the scarce extension and jagged shape of some vegetation types.

165 The plots were materialized in the field and only IAS abundance was recorded within each plot,
166 measured as percent cover based on visual estimation. Data were collected during the late
167 summer-autumn 2015. Nomenclature, taxonomy and classification of invasion status of naturalized
168 and invasive alien plant species follow Galasso et al. [78], syntaxonomic nomenclature of the plant
169 communities up to the level of alliance follows Biondi et al. [79]. All alien species have been included
170 in the null model analysis irrespective of their invasion status. Alien plants occurring in only 1 plot
171 were excluded from further analyses.

172 2.3. Statistical analyses

173 Considering the limited dimension as well as the similar ecological value of certain vegetation
174 types, we merged, for the following statistical analyses, the 20 vegetation types in 7 main habitats that

175 reflect the hierarchical phytosociology classification to the class level. In particular the following
 176 habitats were obtained (Table 1): aquatic vegetation (*Lemnetea minoris* and *Potametea pectinati*),
 177 helophytic marsh vegetation (*Phragmito australis-Magnocaricetea elatae*), lake shore hygro-nitrophilous
 178 herbaceous vegetation (*Agrostietea stoloniferae* and *Bidentetea tripartitae*), hygrophilous willow
 179 shrublands and woodlands (*Alnetea glutinosae* and *Salicetea purpureae*), meso-hygrophilous shrublands
 180 and forests (*Rhamno catharticae-Prunetea spinosae* and *Salici purpureae-Populetea nigrae*), anthropogenic
 181 neophytic nitrophilous forests (*Robinietea*) and plantations (hybrid poplars).

182 **Table 1.** Description, extent and number of sampled plots referring to the vegetation types of the
 183 wetland PA included in the main habitats.

Habitat type	Vegetation type	Area (ha)	N. Plot
Aquatic vegetation (<i>Lemnetea minoris</i> and <i>Potametea pectinati</i>)	Submerged communities in standing water in small channels (<i>Lemnion trisulcae</i> , <i>Potamion pectinati</i>)	0.15	4
	Submerged communities in flowing water (<i>Potamion pectinati</i> , <i>Batrachion fluitantis</i>)	0.80	4
	Submerged and floating-leaved communities in pools (<i>Nymphaeion albae</i> , <i>Potamion pectinati</i> , <i>Ceratophyllion demersi</i>)	1.51	5
Marsh vegetation (<i>Phragmito australis-Magnocaricetea elatae</i>)	Community dominated by <i>Schoenoplectus lacustris</i> (<i>Scirpetum lacustris</i>)	1.33	4
	<i>Phragmites australis</i> reedbed (<i>Phragmitetum australis</i>)	9.99	10
	Community dominated by <i>Eleocharis palustris</i> (<i>Eleocharitetum palustris</i>)	0.13	4
	Community dominated by <i>Persicaria amphibia</i> and <i>Persicaria hydropiper</i> (<i>Polygonetum hydropiperis</i>)	1.03	4
	<i>Carex elata</i> sedge beds (<i>Caricetum elatae</i>)	12.40	13
	<i>Carex vesicaria</i> sedge beds (<i>Caricetum vesicariae</i>)	0.74	4
	Helophyte mosaic (<i>Phragmitetalia</i> , <i>Magno-Caricetalia</i>)	0.63	4
Lake shore herbaceous vegetation (<i>Agrostietea stoloniferae</i> and <i>Bidentetea tripartitae</i>)	Community dominated by <i>Sparganium erectum</i> (<i>Glycerio-Sparganietum neglecti</i>)	0.18	4
	Communities dominated by <i>Agrostis stolonifera</i> and <i>Rorippa sylvestris</i> , community dominated by <i>Bidens tripartita</i> and <i>Persicaria hydropiper</i> (<i>Potentillion anserinae</i> , <i>Bidention tripartitae</i>)	2.97	7
Willow shrublands and woodlands (<i>Alnetea glutinosae</i> and <i>Salicetea purpureae</i>)	Community dominated by <i>Salix cinerea</i> (<i>Frangulo alni-Salicetum cinereae</i>)	1.13	4
	Community dominated by <i>Salix alba</i> (<i>Salicetea purpureae</i>)	2.53	6
Meso-hygrophilous shrublands and forests (<i>Rhamno catharticae-Prunetea spinosae</i> and <i>Salici purpureae-Populetea nigrae</i>)	Shrub community with <i>Ulmus minor</i> and <i>Paliurus spina-christi</i> (<i>Berberidion vulgaris</i>)	3.63	8
	Meso-hygrophilous forest dominated by <i>Ulmus minor</i> and <i>Populus nigra</i> (<i>Salici purpureae-Populetea nigrae</i>)	14.35	15
	Meso-hygrophilous forest dominated by <i>Ulmus minor</i> and <i>Fraxinus angustifolia</i> subsp. <i>oxycarpa</i> (<i>Salici purpureae-Populetea nigrae</i>)	4.42	9
Nitrophilous forests (<i>Robinietea</i>)	<i>Robinia pseudoacacia</i> forest with <i>Lamium orvalae</i> (<i>Lamio orvalae-Sambucetum nigrae</i>)	0.71	4
	<i>Robinia pseudoacacia</i> forest (<i>Bryonio dioicae-Sambucetum nigrae</i>)	2.12	5
Plantations	Hybrid poplar plantations	1.56	5

184 To determine if the distribution, abundance and richness of IAS in the main habitats were
 185 significantly different from random expectation, we used a simulation approach based on Monte Carlo
 186 randomization [80]. The randomization is designed to produce a pattern that would be expected in the
 187 absence of a particular ecological mechanism [81]. To the best of our knowledge, this is the first

188 attempt to use null models to test IAS distribution in relation to habitat invasibility, thus reducing
189 drastically the amount of data required to test null hypothesis, compared for example to correlative
190 studies.

191 A similar approach was used by Bajocco & Ricotta [82] to identify land-cover types where fire
192 incidence was higher (preferred) or lower (avoided) than expected from a random null model. This
193 method was originally designed to study resource selection by animals [83,84]. Bajocco & Ricotta [82]
194 considered fire as an “herbivore” with variable preferences for different resources (i.e. land-cover
195 types); we considered in the same way IAS and habitats. The effect of the method is that the random
196 frequencies are only dependent on the habitat extension, i.e. larger areas have higher probability to
197 have a IAS.

198 Observed occurrences for each IAS in the sampled plots were randomly reassigned to the 7
199 habitats by the simulation, so that the probability of the species to be assigned to a given habitat was
200 proportional to the area of that habitat itself. The null hypothesis was that IAS were randomly
201 distributed in the study area while the alternative hypothesis was that IAS were clustered (or absent)
202 according to the habitat type. Comparing the result of 9999 randomizations to the observed occurrence
203 data, we evaluated the probability (pseudo P-value) that observed occurrences were significantly
204 different from those of the simulations. For each habitat, P-values (two-tailed test, $\alpha=0.05$) were
205 calculated as the proportion of Monte Carlo derived values that were as low or lower (or as high or
206 higher) than the real ones. The same method was applied also for the randomization of IAS
207 abundances.

208 On the basis of the IAS frequencies resulting from the null model simulations, we calculated also
209 the IAS random richness for every habitat, reshuffling 9999 times the matrix assembled with the
210 random frequencies of each IAS per habitat (keeping the IAS probability resulting from the null model
211 fixed). In this case the null hypothesis was that the observed IAS richness per habitat was not different
212 from the one resulting from the simulated one.

213 3. Results

214 3.1. Description of the collected floristic data

215 A total of 12 alien species in the 123 plots were sampled. Among them, 11 are invasive
216 (*Ailanthus altissima* (present only in 1 plot, discarded from the null model simulations), *Ambrosia*
217 *artemisiifolia*, *Amorpha fruticosa*, *Bidens frondosa*, *Cuscuta campestris*, *Elodea nuttallii*, *Oxalis stricta*,
218 *Parthenocissus quinquefolia*, *Robinia pseudoacacia*, *Vitis ×ruggerii*, *Xanthium italicum*) and 1 naturalized
219 (*Bidens vulgata*).

220 Concerning life forms, there is a prevalence of perennial species (7 species) while annual species
221 are 5. Species mainly originated from North America (10).

222 The most abundant IAS was *B. frondosa*, collected in 48.78% of the total sampled plots (60 out of
223 123), followed by *B. vulgata* and *X. italicum*, both collected in 16.26% of total sampled plots (20 out of
224 123). Overall, the average number of IAS per plot was 1.20 ± 1.29 (mean \pm SD) while the average
225 number of IAS per plot within each habitat was: 0.69 ± 0.48 for aquatic vegetation, 1.13 ± 1.06 for
226 marsh vegetation, 4.29 ± 0.95 for lake shore herbaceous vegetation, 1.4 ± 1.07 for willow shrublands
227 and woodlands, 0.78 ± 1.01 for meso-hygrophilous shrublands and forests, 0.67 ± 0.87 for
228 nitrophilous forests and 2.2 ± 0.45 for plantations.

229 3.2. Null model simulations

230 Null models' results are shown in Table 2 and Table 3.

231 The number of occurrences was higher than expected from a random null model for *E. nuttallii*
232 in aquatic vegetation, *X. italicum* in marsh vegetation, *A. artemisiifolia*, *B. vulgata*, *C. campestris* and *X.*
233 *italicum* in lake shore herbaceous vegetation, *B. vulgata* in willow shrublands and woodlands, *O.*
234 *stricta* in meso-hygrophilous shrublands and forests, *R. pseudoacacia* in nitrophilous forests and *A.*
235 *fruticosa* in plantations; while the frequencies were lower than expected from a random null model

236 for *B. frondosa* in aquatic vegetation, *R. pseudoacacia* in marsh vegetation and *B. vulgata* and *X. italicum*
 237 in meso-hygrophilous shrublands and forests.

238 **Table 2.** For each habitat type, the observed frequencies (expressed as %) of the IAS are shown with
 239 the 95% confidence intervals (C.I.) obtained from 9999 Monte Carlo simulations. In bold and with
 240 asterisks the observed IAS frequencies significantly different than expected (** $p < 0.001$; ** $p < 0.01$; *
 241 $p < 0.05$).

Habitat type		<i>Ambrosia artemisiifolia</i>	<i>Amorpha fruticosa</i>	<i>Bidens frondosa</i>	<i>Bidens vulgata</i>	<i>Cuscuta campestris</i>	<i>Elodea nuttallii</i>	<i>Oxalis stricta</i>	<i>Parthenocissus quinquefolia</i>	<i>Robinia pseudoacacia</i>	<i>Vitis ×ruggerii</i>	<i>Xanthium italicum</i>
Aquatic vegetation	%Freq.	0	0	7.7*	0	0	61.5***	0	0	0	0	0
	%C.I.	0-23.1	0-30.8	15.4-84.6	0-38.5	0-23.1	0-23.1	0-15.4	0-7.7	0-23.1	0-7.7	0-38.5
Marsh vegetation	%Freq.	6.4	4.2	48.9	17	6.4	2.1	0	0	0*	0	27.7*
	%C.I.	0-10.6	2.1-17	34-66	8.5-25.5	2.1-12.8	2.1-12.8	0-10.6	0-4.2	2.1-12.8	0-4.2	8.5-25.5
Lake shore herbaceous vegetation	%Freq.	42.9**	0	100	100***	85.7***	0	0	0	0	14.3	85.7***
	%C.I.	0-28.6	0-42.9	0-100	0-42.9	0-28.6	0-28.6	0-28.6	0-14.3	0-28.6	0-14.3	0-42.9
Willow shrublands and woodlands	%Freq.	0	10	70	50*	0	0	0	0	0	0	10
	%C.I.	0-20	0-30	10-90	0-40	0-30	0-30	0-20	0-10	0-30	0-10	0-40
Meso-hygrophilous shrublands and forests	%Freq.	0	12.5	40.6	0**	0	0	15.6**	6.2	0	3.1	0**
	%C.I.	0-12.5	0-18.7	28.1-68.7	6.2-28.1	0-15.6	0-15.6	0-12.5	0-6.2	0-15.6	0-6.2	6.2-28.1
Nitrophilous forests	%Freq.	0	0	44.4	0	0	0	11.1	0	100***	0	0
	%C.I.	0-22.2	0-33.3	11.1-88.8	0-44.4	0-22.2	0-22.2	0-22.2	0-11.1	0-22.2	0-11.1	0-44.4
Plantations	%Freq.	20	100***	100	0	0	0	0	0	0	0	0
	%C.I.	0-40	0-40	0-100	0-60	0-40	0-40	0-20	0-20	0-40	0-20	0-60

242 Where frequencies were significantly higher (or lower) than null models, the cover of IAS
 243 within the plots followed the same trend (Table 3), or rather, IAS that had higher frequencies had
 244 also higher abundances and vice versa, except for *B. frondosa* in lake shore herbaceous vegetation
 245 where its frequency was not significant but its abundance was higher than random, *B. vulgata* in
 246 willow shrublands and woodlands where its frequency was significantly higher but its abundance
 247 was not, *B. frondosa* and *O. stricta* in meso-hygrophilous shrublands and forests habitats, where the
 248 former had a significantly lower abundance and the latter had a significantly higher frequency. The
 249 species that did not differ by the random expectation, both in terms of frequencies and abundances,
 250 were *P. quinquefolia* and *V. ×ruggerii*. Overall, considering the results provided by Tables 2 and 3,
 251 there were 11 preferences and 5 avoidances for habitats by IAS.

252 The results of IAS richness per habitat analysis (Table 4) showed that IAS richness in aquatic
 253 vegetation, marsh vegetation and meso-hygrophilous shrublands and forests was significantly
 254 lower than random richness resulting from the null models.

255
256
257
258

Table 3. For each habitat type, the observed mean abundance (expressed as % cover of the plot) of the IAS are shown with the 95% confidence intervals (C.I.) obtained from 9999 Monte Carlo simulations. In bold and with asterisks the IAS mean abundance significantly different than expected (** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$).

Habitat type		<i>Ambrosia artemisiifolia</i>	<i>Amorpha fruticosa</i>	<i>Bidens frondosa</i>	<i>Bidens vulgata</i>	<i>Cuscuta campestris</i>	<i>Elodea nuttallii</i>	<i>Oxalis stricta</i>	<i>Parthenocissus quinquefolia</i>	<i>Robinia pseudoacacia</i>	<i>Vitis ruggerii</i>	<i>Xanthium italicum</i>
Aquatic vegetation	%Abund.	0	0	0.1**	0	0	24.2***	0	0	0	0	0
	%C.I.	0-12.8	0-13.1	1.3-15.8	0-4.9	0-2.7	0-12.1	0-1.9	0-0.5	0-23.1	0-0.8	0-10.9
Marsh vegetation	%Abund.	3.3	0.6	6.7	0.6	0.3	1.8	0	0	0**	0	7.4**
	%C.I.	0-6.1	0.3-6.3	3.7-10	0.4-2.7	0.1-1.4	0.4-6.6	0-0.8	0-0.1	2.1-12.8	0-0.2	1.4-6.7
Lake shore herbaceous vegetation	%Abund.	27**	0	43***	20***	10***	0	0	0	0	1.4	23**
	%C.I.	0-14.3	0-16	0.3-20.1	0-7	0-3.9	0-14.4	0-3.4	0-0.9	0-28.6	0-1.4	0-14.9
Willow shrublands and woodlands	%Abund.	0	3.7	8	2	0	0	0	0	0	0	0.1
	%C.I.	0-15.3	0-13	0.7-16.5	0-5.6	0-2.7	0-14	0-2.5	0-0.6	0-30	0-1	0-12.5
Meso-hygrophilous shrublands and forests	%Abund.	0	0.4	1.5**	0**	0	0	0.6	0.2	0	0.1	0***
	%C.I.	0-7.6	0-7.8	2.6-10.9	0.2-3.2	0-1.8	0-7.8	0-1.2	0-0.2	0-15.6	0-0.4	0.8-7.9
Nitrophilous forests	%Abund.	0	0	1.3	0	0	0	2.7	0	100***	0	0
	%C.I.	0-15.8	0-17.5	0.7-17.8	0-6.6	0-2.9	0-15.6	0-2.7	0-0.7	0-22.2	0-1.1	0-13.7
Plantations	%Abund.	0.4	64***	10.6	0	0	0	0	0	0	0	0
	%C.I.	0-20	0-18	0-24.4	0-8	0-5.2	0-18	0-4.8	0-1.2	0-40	0-2	0-17.2

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Table 4. For each habitat type the observed IAS richness values are shown with the 95% confidence intervals of the random IAS richness and the p-values (two-tailed test) obtained reshuffling 9999 times the matrix assembled with the random frequencies of each IAS per habitat (keeping the IAS probability resulting from the first null model simulations fixed). In bold the p-values significantly lower than expected.

Habitat type	Observed IAS richness	Random IAS richness C. I.	p-value
Aquatic vegetation	2	4-9	0.0008
Marsh vegetation	7	9-11	0.0008
Lake shore herbaceous vegetation	6	2-8	0.3482
Willow shrublands and woodlands	4	3-9	0.1438
Meso-hygrophilous shrublands and forests	5	7-11	0.0004
Nitrophilous forests	3	3-8	0.0611
Plantations	3	1-7	0.3837

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266 4. Discussion

267 In this study, we used a null model simulation to test the association between alien species and
268 different habitats in a wetland PA, taking into account only the habitat as a possible determinant for
269 the observed resulting distribution. A first analysis of the alien floristic data shows that a third of the
270 sampled IAS belongs to the *Asteraceae* family, confirming it as a successful invader taxon [85-88]:
271 among them, in particular, *Bidens frondosa* invaded indistinctly almost every habitat in the study
272 area, except for the aquatic vegetation. Moreover, our results pointed out that IAS frequency,
273 abundance and richness were not randomly distributed within habitats and that some types of
274 habitat were more prone to invasion by IAS (see Tables 2, 3, 4).

275 The differences we observed in IAS distribution across habitats might be indirectly inferred by
276 considering both habitat features and IAS functional traits, and referring to IAS autoecology
277 described in other studies [13,19,41,89]. Analyzing one habitat at a time and both the IAS frequencies
278 and abundances significantly higher (or lower) than expected by chance, starting from the aquatic
279 vegetation, we observed that the only successful invader here was *Elodea nuttallii*, a perennial
280 submerged rooted hydrophyte native to North America. This species was detected for the first time
281 in Lake Doberdò in 2011 [90] and seems to have completely replaced another IAS, *Elodea canadensis*,
282 which was previously reported in the area [91]. *E. nuttallii* asexual propagation is reported to be
283 improved by nutrient rich sediments [92] and its regeneration and colonization abilities are slightly
284 higher than *E. canadensis*, but these characteristics alone, seem insufficient to explain the
285 displacement of *E. canadensis* by *E. nuttallii* in the area [93]. However, the replacement of *E. canadensis*
286 by *E. nuttallii* has been observed in many European areas [94-96]. Conversely, *B. frondosa* occurrence
287 and abundance in this habitat resulted significantly lower than random expectation, a feature easily
288 explainable taking in account that the species cannot live submerged for long periods. In this case it
289 was pretty obvious that the only successful IAS would have been a plant adapted to live in the water
290 but, although trivial, this result served to verify the null model efficiency.

291 In the marsh vegetation, the observed occurrence and abundance of *Xanthium italicum* was
292 higher than expected while the occurrence and abundance of *Robinia pseudoacacia* was lower than
293 random expectation. *X. italicum* was mostly found in those communities occupying the dryer parts
294 of the marsh vegetation, and in particular in the areas where nutrients accumulate [97]. For Lake
295 Doberdò, these situations occur in the marginal areas of the lake, which dry out during the summer
296 and are subject to the deposition of nutrients due to the direction of the flowing water. *X. italicum*
297 fruits are easily dispersed by clinging to the fur of animals and its seeds can tolerate prolonged
298 submersion without showing significant effects on final germination during the dry season [98] and
299 for these reasons it is particularly competitive in this environment. Concerning the distribution of *R.*
300 *pseudoacacia* in marsh vegetation, its lower observed occurrence and abundance is related to the
301 species avoidance strategy to protracted submersion [99], a characteristic in common with most of
302 trees with the exception for those adapted to wet conditions (e.g. *Salix* spp.).

303 The lake shore herbaceous vegetation is distinctly the most invaded habitat as shown both in
304 terms of IAS significant occurrences and abundances (Tables 2, 3). Indeed, this habitat type showed
305 highly significant frequencies for 4 species: *Ambrosia artemisiifolia*, *Bidens vulgata*, *Cuscuta campestris*
306 and *X. italicum*, and highly significant abundances for all the previous ones plus *B. frondosa*. Its high
307 indiscriminate invasibility is probably related to three characteristics of the habitat such as recurrent
308 disturbs linked to the peculiar hydrological regime (water level oscillations, duration and
309 seasonality of floods), high availability of nutrients transported by water flow especially in spring
310 period [100] and high solar energy availability. These characteristics are also confirmed by the
311 observed poorly structured herbaceous native communities, which showed high dynamism in their
312 structure during the year, shifting from the predominance of associations of the *Agrostietea*
313 *stoloniferae* class in spring to that of associations of the *Bidentetea tripartitae* class in the late summer,
314 which leads to an environment more susceptible to invasion [29]. We could detect the invasion
315 success of *A. artemisiifolia*, an annual plant native to North America, as related to both high solar
316 radiation (due to the available spaces in these plant communities) and nutrients level in the habitat
317 [101]. *B. vulgata* and *B. frondosa* were facilitated by the high dynamism in the resident plant

318 communities, in which the native *B. tripartita* was replaced by both *B. vulgata* and *B. frondosa*. The
319 latter is known to be more competitive than its native congener for many characteristics such as a
320 higher competitiveness where nutrients level is high, a high plasticity of the vegetative phase length,
321 that allows it to grow taller than *B. tripartita* and to foster seed production and, finally, cause of the
322 greater resistance to drought during summer [102-104]. Similar characteristics are probably present
323 also in *B. vulgata*, that is often reported in co-occurrence with *B. frondosa* [105,106]. Furthermore,
324 *Bidens* seeds are easily dispersed by animals and humans for tens of km, explaining their wide
325 distribution in the study area. For the last two species, *X. italicum* and *C. campestris*, which are
326 strongly related because the latter grows often as parasite on the former, they have been found as
327 strongly associated to the lake shore herbaceous vegetation, both IAS finding a suitable habitat
328 because the first is a nitrophilous species, as stated before, and the second normally grows as a
329 parasite by twisting around the stems of species of *Polygonum*, *Xanthium* and several other
330 psammophilous plants [107].

331 As regards the willow shrublands and woodlands habitat, we observed an occurrence higher
332 than expected for *B. vulgata* but its abundance was not significantly different than random. Its
333 frequency suggests a certain degree of affinity for this habitat, due to nutrients accumulation,
334 although lower than in the lake shore herbaceous vegetation. However, the not significant
335 abundance could indicate the presence of limiting factors, for example a lower light availability due
336 to higher shading.

337 In the meso-hygrophilous shrublands and forests habitat, both frequency and abundance of *B.*
338 *vulgata* and *X. italicum* were lower than expected, while only the abundance of *B. frondosa* was
339 significantly lower than random expectation. Conversely, *Oxalis stricta* occurrence was here
340 significantly higher. *O. stricta* is a perennial herbaceous plant with overwintering buds at ground
341 level, native to North America. It prefers moist soils, both in sunny and partially shaded areas [108].
342 Its occurrence was here favored by two reasons: the low or absent competition with the sparse
343 herbaceous vegetation [30] and the high coverage of native shrubs that precludes potential invasions
344 by other IAS. This is confirmed by the low frequencies and abundances of the other IAS. The habitat
345 resistance to invasion is also favored by the slope that let water washing away nutrients from the soil
346 after the lake floods.

347 *R. pseudoacacia* resulted highly associated to the nitrophilous forests habitat where it is known to
348 add or replace the native *Sambucus nigra* [109] showing high cover values also due to asexual
349 reproduction through root suckering. Here, other IAS were limited in their spreading (see Tables 2,
350 3) due to shading conditions and to competition with highly abundant *R. pseudoacacia*.

351 For what concerned the poplar plantations, we observed the significant occurrence and
352 abundance of *Amorpha fruticosa*, a woody shrub native to North America. *A. fruticosa* can tolerate dry
353 soils, but it is most abundant along river or lake banks and at the edges of flooded forests. The plant
354 grows well in medium to wet, well-drained, soils in full sun to light shade and is tolerant of
355 occasional flooding, lasting less than 30 days [110-114]. This explains its observed high frequency in
356 the habitat, which is more favorable to the species because of the moist soil, the light shade and the
357 occasional flooding events. Its high potential invasive behavior is due not only to its high tolerance
358 of various environmental conditions but also to its reproduction strategies through self-seeding and
359 suckers to form thickets [110]. *A. fruticosa* usually colonizes degraded wet habitats but also invades
360 natural plant communities where it competes with native vegetation leading to a decrease in species
361 diversity [115]. For this reason, it represents a serious threat for the diversity conservation, especially
362 in wetlands.

363 Comparing observed and simulated IAS richness (Table 4) we can highlight that some habitats
364 were less prone to a non-selective IAS invasion than others. While this may result quite obvious for
365 aquatic vegetation, where only one of the sampled IAS was a hydrophyte, this is quite surprising for
366 marsh vegetation and meso-hygrophilous shrublands and forests habitats. Although both habitats
367 presented a relatively high number of sampled IAS, respectively 7 and 5, they represented together
368 the 77% of the study area and for the species richness-area relation [116] we could have expected to
369 spot a higher IAS richness. These habitats resulted to be less prone to invasion, in case of the marsh

370 vegetation because of extreme conditions caused by periodical and long lasting floods which require
371 special adaptations for survival of plants, and in that of meso-hygrophilous shrublands and forests
372 because of a medium-low nutrients level and low light availability, which do not favor the spread of
373 IAS, which are generally nutrient/light-demanding species.

374 In general what we observed in the study area was that invasion was promoted in the habitats
375 where one or more of the following conditions were satisfied: an intermediate disturbance level,
376 caused by the water fluctuation or by high dynamism of the communities within a habitat, a high
377 level of nutrients and a medium to high light availability. These factors favored IAS invasion as they
378 are known to be more competitive than natives both in a condition of intermediate disturbance [117]
379 and when resources are easily available [30,41,89,118]. On the contrary, invasion by terrestrial IAS
380 was avoided in the habitats where the communities presented a stable structure during the year,
381 without seasonal changes, a medium nutrients level, moderate to low light availability or extreme
382 conditions caused by long lasting floods. Such different conditions in the small Lake Doberdò area
383 were reflected as well by the native communities, represented by 33 different associations adapted to
384 those peculiar environments. However, the high resource availability and the advantageous biotic
385 interaction observed for some habitats may become a key driver along the subsequent stages of the
386 invasion, leading to a loss in native diversity [19,41,89,119]. This is even more serious considering
387 that the habitats are part of a wetland PA, in a global scenario of a dramatic decline in wetland areas
388 due to extensive habitat degradation and fragmentation driven by human activities [56-58]. An early
389 warning and eradication of IAS may impede new invasions and/or halt the ongoing ones: this would
390 be particularly urgent in wetland PAs if we want to preserve their biodiversity, their conservation
391 purpose and prevent the degeneration of native communities.

392 Regarding the possible weakness of the null model simulations, in some cases, they were not
393 capable of highlighting the actual distribution pattern of species: e.g. *E. nuttallii* is a hydrophyte and
394 its distribution across the non-aquatic habitats was never significantly lower than random, as we
395 expected to observe. In particular IAS avoidances may have been masked by confidence intervals in
396 some cases (see Tables 2, 3) as the confidence intervals have almost always the lower limit equal to 0.
397 This probably happened because the random reassemble of the matrix was only weighted by the
398 habitat area. Moreover, the null model suffered also for the low frequencies of certain species (e.g. *P.*
399 *quinquefolia* and *V. ×ruggerii*) even though, overall, it provided useful results. In fact, we were not
400 completely focused on highlighting the actual distribution of all IAS within the wetland, but rather
401 on pointing out those IAS that were particularly threatening for the different habitats of the PA.

402 We have also to stress that the adopted sampling design was originally planned to evaluate the
403 occurrence of alien species in different habitats in a rather complex area and to assess the
404 conservation status of the native communities. A multi-scale approach should have been adopted
405 considering that the pattern of variation in the alien/native species are strongly scale dependent [19].
406 The adopted plot size, then, somehow questionable for the characterization of plant community
407 structure, can represent a limitation of this study and future analyses will take in account a
408 multi-scale approach.

409 Nonetheless, the method tested in this study provides useful information to monitor and
410 manage the IAS threat within PAs. By inferring important ecological property leading to habitat
411 invasion without sampling the environmental characteristics of the habitats (an expensive and
412 time-consuming operation in the field), we suggest to use the applied method as a complementary
413 tool in the analysis of biological invasions.

414 5. Conclusions

415 The results highlight an interesting linkage between IAS and invaded habitats, confirming that
416 some habitats are more prone to biological invasion than others, and that environmental conditions
417 can promote or avoid invasion depending also on the specific IAS ecology and biology. The study
418 clearly shows the role of habitats in filtering the invasion depending on the species, besides the role
419 of natural intermediate disturbance resulting on one side in an environment rich of biodiversity, on
420 the other side advantaging IAS colonization of the area [117].

421 Concerning the method, it allowed to derive useful information, proving to be a low-cost
 422 analysis to integrate routinely PAs management activities. In particular it may help to detect highly
 423 endangered habitats and to invest more efficiently time and money to control IAS, and, when
 424 possible, also to prevent IAS colonization.

425 **Supplementary Materials:** The following are available online at www.mdpi.com/xxx/s1, Figure S1: Habitat
 426 map based on vegetation types of the study area (Lake Doberdò).

427 **Author Contributions:** Conceptualization and methodology all authors; description and attribution of plant
 428 communities M.C., L.P.; data collection F.L., M.C., A.A.; formal analysis and data curation F.L., M.C., E.T.;
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