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Towards global dominance of invasive alien plants in freshwater ecosystems: the dawn of the Exocene?

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Abstract

The global and seemingly unstoppable spread of invasive alien plants emerges as one of the main topics of current science. This is due to the multiple repercussions of invasive plants on biodiversity and ecosystem functioning, plus huge consequences on human existence. In freshwaters, lots of invaders are extremely competitive by virtue of their idiosyncratic reproductive and adaptive strategies. As "inland islands", freshwaters seem particularly prone to changes when invaded, such as reorganisation of food webs and biotic interactions. Together, these events are self-reinforcing, implying hardly reversible hysteric phenomena. The intention of this paper is to point out: invasion pathways, driving factors, invasion mechanisms, and noticeable effects mediated by plant invaders in freshwaters through an extensive knowledge review. The growing evidence suggests the dawn of a new epochal phase: a globally alien-dominated "bio-historical horizon", tentatively called "Exocene", where invaders play predominant roles that drive freshwaters functioning and successional unexpected stages. In the context of invasion science, Exocene reinforces the need for an ecosystem-based perspective to properly understand the implications of plant invaders in freshwaters. Seven challenging issues emerge to be addressed to better outline the global paths of biodiversity and functioning between biomes when faced with biological invasion.

Introduction

In the last few decades, a growing bulk of literature has been focussed on adverse impacts of invasive alien species (IAS) on ecosystems and humans (Lockwood et al., 2007; Rai & Singh, 2020). IAS have occupied the phylogenetic and functional space within the range formed by native species by bridging existing empty gaps or excluding natives (Loiola et al. 2018; Dalle Fratte et al. 2019). Overall, IAS tend to disrupt the functional links among native species by supporting a progressive multidimensional impoverishment of invaded ecosystems, with various cascading repercussions on their functions and services (Dobson et al., 2006; Gaertner et al., 2014). Therefore, IAS have relevant implications for human existence because they affect agricultural production and also influence health and spiritual well-being (Vaz et al., 2017; Shackleton et al., 2018).

For freshwater ecosystems, IAS-mediated transformations frequently involve water bodies as a whole. This is especially true for small lakes and standing-water ecosystems that are characterised by rather stable environmental conditions and lack internal physical barriers. These characteristics promote the dispersion of plant propagules and the easy complete colonisation of such habitats. Together, river corridors and waterways result among the most invaded ecosystems globally (Hejda et al., 2015). One major cause is the heterogeneous and multiple structures of river ecosystems, characterised by high connectivity rates, the simplicity of propagules transportation, and a variety of micro- and mesohabitats (Tockner & Standford, 2002; Galil et al., 2008; Gurnell et al., 2008). In addition, the high level of anthropogenic disturbance in concert with the intrinsic river flow dynamics significantly increase invasion and colonisation rates by periodically resetting riverine plant assemblages (Čuda et al., 2017 and references therein). At the same time, anthropogenic impacts increase the isolation rates of freshwater ecosystems through the substantial transformation of landscape matrices, mainly in agricultural lands or irrigated plains. These spatial modifications reduce the dispersal capacity of native species and their capability to escape unsuitable conditions (Bickford et al., 2010; Bolpagni et al., 2020a) and may, simultaneously, favour IAS's local success due to the intense use of relict water bodies for recreation activities, which is often associated with the deliberate/accidental release of IAS for ornamental/reinforcing purposes (Brundu, 2015).

Overall, as "inland islands" water bodies are especially prone to external perturbations, and this condition will worsen in the short term due to climate change impacts (Anufriieva & Shadrin, 2018). As recently stated by Dudgeon (2019), climate change will not only affect temperature, but also, and particularly, water availability by influencing flow and inundation patterns, which will have relevant implications for the life cycles of aquatic species that are closely linked with hydrology. This agrees with the findings by Dukes & Mooney (1999), who indicated altered disturbance regimes and increased habitat fragmentation as key drivers of the prevalence of invaders. In line with this, an increasing literature supports the key role of ecological fluctuations in fostering invasions, particularly in disturbed communities or groups that are adapted to only weak variations (Saarinen et al., 2019). Growing disturbances on freshwaters translate into extremely poor plant assemblages, which is one of the fundamental conditions to trigger invasion by invasive alien aquatic plants (IAAP). For instance, marked positive implications of fluctuating resource availability, including water, in fostering the affirmation of IAS have been found for riparian and aquatic plants, such as *Reynoutria japonica* Houtt., *Cabomba furcata* Schult. & Schult.f., or *Veronica anagallis-aquatica* L. (Davis et al., 2000; Matsubara & Sakai, 2018).

Rationale

More than 14,000 plant species, which is about 4% of all existent vascular flora, have been naturalised outside their native ranges (Pyšek et al., 2017, 2020). Of these species, alien aquatics have been largely successful. Aquatic plants can be seen as "natural invasive" plants *sensu* Evernden (1985), mainly due to their multipotential reproductive modes and their "engineering

properties" (Bouma et al., 2010). Therefore, it is not surprising that a major contribution to invasive plant species *sensu* Convention on Biological Diversity (CBD, 2000) takes place by aquatics (Brundu, 2015; Hussner et al., 2017), especially when we consider the most impacting *taxa* (i.e. included on national or international blacklists). In Europe, IAAP constitute around 36% (13 of 36) of alien species of Union concern (the Union list; EU 2016, 2017, last update August 15, 2019) (Table 1). If we also consider six more *taxa* typical from riparian contexts, then 52% of the invasive plants on the Union list are represented by wetland species.

Although aquatic plants constitute only a very low percentage of total plant diversity, not exceeding 2%, they are of prime importance for colonised aquatic habitats as they shape key processes, such as stabilisation of sediment and riparian sectors, provision of food and niches to a plethora of organisms, and release of oxygen to water and sediment to support biogeochemical hotspots (Bouma et al., 2010; O'Hare et al., 2018; Marzocchi et al., 2019). In this context, IAAP's establishment and success can lead to unexpected and not predictable habitat dynamics and functioning (Ribaudo et al., 2018; Salgado et al., 2019). In freshwaters, IAAP can trigger marked abrupt modifications of colonised ecosystems by determining the relevant reorganisation of food webs and internal feedbacks, such as nutrient cycling and competitive interactions (Rejmánková et al., 2018; Strange et al., 2019). These new "alternative equilibria" tend to be self-reinforcing and are largely related to hysteric or "sticky" phenomena, which are often extremely relevant insofar as the return to pristine conditions is almost impossible for perturbed ecosystems (Scheffer et al., 2001; Folke et al., 2004). To a certain extent, this may suggest the affirmation of a new epochal evolutionary phase for freshwater ecosystems: "an alien-dominated "bio-historical horizon", herein provisionally evaluated for IAAP.

In this paper, I intend to confer a new semantic attribute to "Exocene", a very recent term coined by Quast (2017) to indicate the necessity of an "Exit-Age" for humankind: "*a consolidated consciousness*" necessary for guaranteeing a future for our species and our planet. Here, Exocene defines a "new functioning era" where IAAP play prominent roles in remodelling quality and the functions of dominated ecosystems. Moreover, this new phase also represents a functioning-oriented implementation of the "Homogocene" concept as imagined by Orians (Rosenzweig, 2001), and it calls for a better understanding of the consequences of the ongoing global redistribution of species. Hence the urgent need to extend knowledge on IAS' incidence on the functioning of ecosystems (Attermeyer et al., 2016; Rejmánková et al., 2018; Pyšek et al., 2020). In fact, the success of IAAP cannot be exclusively related to a progressive homogenisation of plant communities on multiple scales, as they significantly affect, drive and/or change the properties of invaded (or newly created) communities, thus opening new trophic paths (Kumschick et al., 2015; Bolpagni et al., 2020b; Pyšek et al., 2020). The concept of Exocene intends to strengthen the scientific community's interest in the trophic, dynamic and evolutionary repercussions of IAS' presence in ecosystems starting from a systematic review of the multiple implications of IAAP in freshwater ecosystems.

Based on a broad analysis and a functional interpretation of the available literature, this opinion paper wishes to point out: i) key invasion pathways; ii) driving factors (invasion opportunity windows); iii) ecological mechanisms (invasion IAAP features); iv) striking effects of IAAP in freshwater ecosystems; and v) challenges that must be overcome to better understand the current and future implications of IAAP accumulation in freshwaters (Figs. 1 and 2). Differently from the work of Blackburn et al. (2011), which focused on the stages of IAS' invasion process following an individual-population approach (e.g., transport, introduction, establishment, spread), here the Exocene's focus follows an ecosystem-based perspective to better include ecosystem properties in the biological invasion framework.

134 Up to a certain extent, the literature tells us that some of the barriers outlined by Blackburn et al.
135 (2011), which need to be overcome for a species or population to pass on to the next invasion stage,
136 are gradually crumbling or seem to be more permeable than expected, especially in the spread stage
137 and "Boom and Bust" dynamics (Wegner et al., 2019; Crane et al., 2020). Throughout the
138 establishment and spread stages, these barriers are often made up of species, communities or
139 habitats, which complicates our comprehension of invasion processes and suggests a not-negligible
140 role of trophic interactions in regulating the invasion success (Crystal-Ornelas & Lockwood, 2020).
141 This viewpoint is reinforced by the fact that IAAP and freshwaters have relative specificities which
142 make the aquatic invasion process unique, and their synergic interaction (frequently mutually
143 multiplicative) generates extra peculiar conditions that are still difficult to interpret due to the
144 predominant terrestrial-oriented conceptual development and testing in ecology (Thomsen &
145 Wernberg, 2014). Furthermore, freshwater ecosystems and IAAP can serve as an ideal model to
146 better understand the in-progress dynamics of other key alien taxonomic groups (e.g., fish,
147 invertebrates) or invaded biomes (e.g., prairies, forests, savannas), as already happened for other
148 ecological paradigms starting from the "Homage to Santa Rosalia" by Hutchinson (1959) to regime
149 shifts (Scheffer et al., 2001).
150

151 *Alien plants in freshwater ecosystems: invasion pathways*
152 The predominant invasion pathways of IAAP are among the most relevant peculiarities of
153 freshwaters in the biological invasion framework. Based on the Hulme et al. (2008)'s scheme, six
154 are the broad mechanisms controlling the introduction of IAS: escape from captivity, deliberate
155 release, commodity contaminants, stowaways on or in transport vectors, *via* anthropogenic
156 corridors, and unaided spread from other invaded regions. Of these, the first two pathways emerge
157 as the leading ones in freshwaters, with "ornamental trade" largely referred to as the main
158 mechanism of introduction followed by escape from phytoremediation plants (Brundu, 2015) (Fig.
159 1). Indeed, in China 75% of IAAP, which equals 114 species, were introduced through "ornamental
160 trade" (Wang et al., 2016).
161

162 The relevance of the above-mentioned pathways is reinforced by the intrinsic high hydrological
163 connectivity of inland waters. Specifically, rivers and artificial waterways act as ideal dispersal
164 agents, and water infrastructural improvements will further boost the dispersal capacity of the
165 resident IAAP by amplifying their invasive potential. In addition, the role of transport infrastructure
166 in the introduction of species cannot be neglected, considering that alien species are transported as
167 commodities (or as a contaminant of a commodity) and can also arrive in ballast water, cargo and
168 airfreight (Gurnell et al., 2008; Hulme et al., 2008). Indeed, in freshwater networks water flow
169 (hydrochory) emerges as the prominent dispersal driver of macrophyte propagules, in IAAP mainly
170 represented by vegetative fragments (Johansson & Nilsson, 1993; Heidbüchel et al., 2020).
171 Furthermore, IAAP dispersal is also largely supported by zoochory, as noticed first by Darwin
172 (1859). Many animals feed on IAAP and can translocate seeds by defecation, or seeds and
173 propagules can stick to animals (e.g., on feathers, fur, feet) and then be moved to new locations, at
174 distances of even more than hundreds of kilometres from source sites (Sculthorpe, 1967; Van der
175 Pijl, 1972; van Leeuwen et al., 2012).
176

177 *Emerging vectors*
178 The global trade and linked traffic of live organisms are becoming increasingly more relevant
179 among primary IAS pathways (Peres et al., 2018; Reid et al., 2019). Trade of horticultural species
180 and, in particular, e-commerce, is an important driver of IAAP invasions (Humair et al., 2015).
181 Martin & Coetzee (2011) stressed the role of pet traders and aquarists in the spread of IAAP, due to
182 a general lack of knowledge regarding identification and regulation of traded species together with a
183 misinformation about potential dangers. In Germany, Hussner et al. (2010) indicates a sharp
184 increase in IAAP numbers starting from 1980, and a pivotal role of trading in non-indigenous

185 aquatic plants is argued to justify these results. In Brazil, Peres and colleagues (2018) observed that
186 e-commerce offers easy access to many IAAP (mainly as vegetative parts) at low prices (more than
187 80% of plants have costs below US $5).
188
189 ***Alien plants in freshwater ecosystems: driving factors of invasion***
190 Freshwaters are one of the key hotspots for biodiversity, but also one of the most impacted
191 ecosystems worldwide, both by direct human impacts and by climate change (Strayer & Dudgeon,
192 2010; Dudgeon, 2019; Reid et al., 2019). Inland waters act as filters and acceptors for effluents
193 (runoff) and groundwater and are affected by all physical and chemical perturbations exerted and
194 generated on the catchment scale (Ascott et al., 2017; Severini et al., 2020). Moreover, severe
195 conflicts of interest among different stakeholders (e.g., farmers, hydropower companies, industry,
196 drinking water supply) have reduced worldwide the water available for ecosystem purposes (e.g.,
197 environmental flow, natural floods). In such a context, the impairment of energy and matter flows in
198 freshwaters, mainly in the form of resource fluctuations and hydromorphological alterations, is the
199 local main driver keeping open multiple "windows for invasion".
200
201 *Direct human pressures and climate change*
202 Anufriieva & Shadrin (2018) recently reinforced the idea that new destabilised freshwater
203 ecosystems are more susceptible to invasion and, therefore, to host wider non-native diversity. It is
204 generally acknowledged that local repercussions of direct human pressures trigger advantageous
205 settings for non-native species to settle and spread in freshwater ecosystems (Hussner et al., 2014;
206 Fasoli et al., 2018). External perturbations, especially variations in hydrology and temperature (in
207 both water and atmosphere) are likely to open "opportunity windows" for IAAP (Agrawal et al.,
208 2005). As extreme climate and hydrological events are observed more frequently, the probability of
209 generating favourable conditions for IAAP is growing. Indeed, higher temperature and longer
210 growth seasons may contribute to explain today's IAS spread rates by extending their potential
211 suitable habitats (Walther et al., 2009). For example, the spatial distribution of invasive
212 macrophytes *Ludwigia hexapetala* (Hook. & Arn.) Zardini, H.Y. Gu & P.H. Raven and *Ludwigia*
213 *peploides* (Kunth) P.H. Raven is predicted to increase in Europe, especially in northern countries
214 due to the increasing temperatures forecasted for the next decades (Hallstan, 2005; Thouvenot et al.,
215 2013). More recently, Gillard et al. (2017) estimated that *Ludwigia* ssp., *Myriophyllum aquaticum*
216 (Vell.) Verdc., and *Egeria densa* Planch. occupy less than 15% of their suitable habitats globally.
217 Based on climate forecasts, the spatial ranges of these species could expand by spreading upwardly
218 towards higher latitudes than their current ranges.
219
220 Fluctuating resources and eutrophication
221 As previously reported, different anthropogenic impacts also directly affect IAAP distribution.
222 Many papers have explored the positive links between the invasion status of non-native species and
223 the variability and availability of nutrients (David et al., 2000; Funk & Vitousek, 2007; Parepa et
224 al., 2013; Mouton et al., 2019). The anthropogenic-induced eutrophication of freshwaters largely
225 promotes regime shift events which, in turn, directly and largely affect the spatio-temporal patterns
226 of aquatic species, including local extinction dynamics, and the spread of several invasive *taxa,*
227 specifically the free-floating or emergent ones that are able to proliferate even in the presence of
228 turbid waters (Davis et al., 2000; Egertson et al., 2004). Salgado et al. (2019) recently reinforced the
229 driving role of eutrophication to support plant invasion by investigating the long-term
230 (paleolimnological) dynamics of a neotropical shallow lake. These authors highlighted a marked
231 reassembling of aquatic vegetation, including the spread of IAAP, to be attributed to an increase in
232 nutrient availability in concert with relevant shifts in lake water levels. Similarly, carbon cycling
233 strongly influences IAAP dynamics. For example, *Hydrilla verticillata* (L. f.) Royle shows a higher
234 invasive success rate than the native *Egeria najas* Planch., along with increased carbon availability,
235 which is also expected to further increase in the short term due to climate change (Fasoli et al.,

2018). Indeed, the carbon availability strongly controls root production by propagules and
fragments (Hussner et al., 2015). It has been noted that progressive CO_2 depletion lowers the
likelihood of both regeneration and colonisation of aquatic plants. Elodeids display exceptional
metabolic plasticity in using carbon, which probably allows them to overcome critical dissolved
carbon undersaturation levels induced by self-induced CO_2 limitation led by intense weed bed
proliferation (Hussner et al., 2015).

Hydromorphological alterations
Moreover, hydromorphological alterations may profoundly regulate IAAP spatial patterns and
success. Mouton et al. (2019) found compelling evidence about this point after verifying that non-
native plants dominate linear reaches compared to more heterogeneous and sinuous channels. The
progressive simplification and straightening of channels favour the retention of
plant propagules and support the spread of large canopy-forming emergent invasive plants
(Baattrup-Pedersen et al., 2015). In addition, floods amplify this susceptibility by increasing the
probability (in time and space) of diffusing propagules (Gurnell et al., 2008). Furthermore, the
damming of streams and rivers can completely change the functioning of freshwaters, influencing
the species' longitudinal distribution (Ward & Stanford, 1983; Bolpagni et al., 2016).

Alien plants in freshwater ecosystems: invasion mechanisms
Starting with the review by Fleming & Dibble (2014) on macrophytes' ecological invasion
mechanisms, this paragraph deals with contextualising their findings together with some more
recent literature works within the Exocene general framework. Three preeminent classes of invasion
mechanisms can be distinguished as intrinsic key factors that support IAAP's invasive behaviour: i)
genetic traits (i.e., general-purpose genotypes, phenotypic plasticity); ii) clonality and propagule
pressure; and iii) biological interactions (i.e., competition, cooperation) (Fig. 1).

i) Genetic traits
Firstly, IAAP's "natural invasive" behaviour may refer to the frequent occurrence of general-
purpose genotypes in aquatic plants. These genotypes guarantee high success rates over an
extremely variable range of environmental conditions, as well as significant morphological
variations in populations, growing phases, and seasons (Barrett et al., 1993). This exceptional
adaptive plasticity supports a rich suite of compensatory responses that involve morphological,
physiological and phenological traits (Santamaría et al., 2003; Weyl & Coetzee, 2016 and
references therein), which are largely regulated by external physiological stresses (driving factors),
including fluctuating resources, eutrophication and hydromorphological disturbance (Hutchings &
John, 2004; Arshid & Wani, 2013; Rejmánková et al., 2018).

Phenotypic plasticity also emerges as a preeminent mechanism involved in IAAP's dissemination
strategy. Floating species (i.e., *Eichhornia crassipes* (Mart.) Solms and *Pistia stratiotes* L.) can
change their complex root systems in response to variations in water nutrient availability (Huang et
al., 2019) by developing peculiar root branching arrangements. Concurrently, the populations of
three of the most aggressive aquatic invaders in New Zealand, namely *Lagarosiphon major* (Ridl.)
Moss, *E. densa* and *Elodea canadensis* Michx., exhibit an almost general lack of genetic variability,
probably due to their recent introduction into the country (about 60-140 years) (Riis et al., 2010).
This translates into a marked lability of their interpopulation morphological variability. Under
controlled growing conditions, these elodeids tend to lose the differences found across wild
populations (Riis et al., 2010). As for pleustophytes, these findings suggest a significant role of
local nutrient conditions in regulating elodeids' adaptive responses. However, a minor genetic
variation has been found, which could be the basis for future local adaptations, generally needing a
relatively diverse gene pool to trigger natural selection (Ward et al., 2008). Along these lines,

286 Lambertini et al. (2010) suggested that the evolutionary changes observed for the *E. canadensis* and
287 *L. major* populations in New Zealand are attributable to post-dispersal somatic mutations despite
288 their narrow genetic variation, which sheds new light on post-invasion population dynamics in
289 aquatic invaders. However, epigenetic processes could also play an active role in these changes,
290 which suggests the need for conducting further research work in this area to examine these aspects
291 in-depth. Conversely in South Africa, *Myriophyllum spicatum* L. turned out to be extremely
292 variable in morphological terms. Divergent morphologies were observed to be an effect of specific
293 local adaptations during a long evolutionary history in the region (Weyl & Coetzee, 2016).
294 However, when the experimental growing conditions were changed, different *M. spicatum*
295 populations displayed a similar behaviour, especially under lower nutrient conditions. This confirms
296 the possible evolution of specific local adaptations for aquatic plants (Barrett et al., 1993;
297 Santamaría et al., 2003), which reinforces their invasive behaviour and the appearance of local
298 bottleneck effects supported by a limited gene flow (Weyl & Coetzee, 2016).

ii) Clonality and propagule pressure
301 Clonality governs dispersal processes on the landscape scale by influencing metapopulation
302 patterns, especially throughout higher competition in early establishment stages of a few dispersal
303 clonal propagules. Thus, by investigating the genetic diversity of *H. verticillata* in Brazil, Lucio et
304 al. (2019) described the presence of only a single genotype founder. All the individuals collected in
305 the Upper Parana River basin (within a spatial range of 600 km) showed pistillate flowers, which
306 indicate the presence of only deciduous female ramets that are unable to sexually reproduce (Sousa,
307 2011). A similar mechanism has also been reported for *E. canadensis* in boreal lakes (Tattersdill et
308 al., 2017), where the species is competitive given ramets' tendency to fragment, plus their capability
309 to grow in Autumn and to regrow early in spring with water temperatures lower than 5 ºC. Actually,
310 the propagule pressure mechanism is closely related to not only the number of release events, but
311 also to the number of released individuals (Simberloff, 2009; van Kleunen et al., 2018). In a sense,
312 therefore, it is under controlled by invaders' reproductive capability. Aquatic plants have peculiar
313 reproductive strategies with mixed combinations (sexual vs. asexual) based on clonal regeneration
314 modes (Sculthorpe, 1967). These regeneration modes have a pivotal influence on both mating
315 processes and genetic dispersal mechanisms by, for example increasing the capability to establish
316 new persistent populations outside native ranges. Generally, all submerged plant organs are
317 totipotent, which makes them potential propagules, and individuals overpass critical seasons as
318 dormant clonal propagules as a dispersal mode in time (Eckert et al., 2016).

320 The spreading potential of aquatic invasive plants via fragments has recently been investigated in
321 detail by exploring *in situ* fragmentation rates and the influence of stream flows on facilitating
322 propagule dispersal (Heidbüchel & Hussner, 2020), species-specificity during the fragmentation
323 process (Heidbüchel et al., 2019), and the regeneration and colonisation abilities of fragments
324 (Heidbüchel & Hussner, 2019). The main results reported by Heidbüchel & Hussner (2020) confirm
325 the key role of hydrology as a regulator of fragmentation and, in turn, of vegetative spreading
326 potential and invasion success of *M. spicatum, Potamogeton crispus* L*., E. canadensis and Elodea*
327 *nuttallii* (Planch.) H. St.John. Indeed, a large portion of aquatic plants regenerates thanks to very
328 small fragments (only a single node; Kuntz et al., 2014), which stresses the considerable
329 contribution of drift duration in boosting propagule pressure (Riis, 2008).

iii) Biological interactions
332 The last invasion mechanism is represented by biological interactions: competitive – in particular
333 resource acquisition ability, population abundance, enemy release and novel weapons – and "non-
334 competitive" ones as such as invasional meltdown, based on cooperative interactions. These
335 interactions, which are intimately associated with invasion driving factors (Fleming & Dibble,
336 2014), cover a very wide spectrum of modalities and are also often difficult to be disentangled from

invasion impacts. Here the "invasion mechanism" character of biological interactions is privileged in relation to the relevance of their "invasion effects" (discussed in the next paragraph).

If competitive ability in resource acquisition is reckoned among prevalent invasive traits (see Paolacci et al., 2016), it emerges as a leading invasion driver in the presence of non-limiting nutrient availability (i.e., eutrophication, increased water carbon concentration), as clearly stated by Hussner et al. (2015), Mouton et al. (2019) and Salgado et al. (2019). However, invasive competition does not operate only in response to nutrient availability but is actually regulated also by IAAP density and biomass. To explore this issue, a series of experiments was carried out by Michelan et al. (2018) and Silveira et al. (2018), who found that the success of *H. verticillata* and *Urochloa arrecta* (Hack. ex T.Durand & Schinz) Morrone & Zuloaga against native *taxa* was extremely density- and biomass-dependent. Increased IAAP density and biomass significantly lowered the growing rates of native species and their recolonisation success. However, competition acts in concert with a complex series of interrelated processes that cannot be separately evaluated. These include the absence of natural enemies, such as predators, parasites, and pathogens, in new colonised areas (enemy release hypothesis). Although this hypothesis seems reasonable, it is often debated and the literature highlights lack of consistency across *taxa* (Hofstra et al., 2020).

Furthermore, competition is also strictly related to the "novel weapon hypothesis" based on IAAP's allelopathic abilities (Callaway & Ridenour, 2004). These aspects have been investigated in detail by several authors (see Grutters et al., 2017 and references therein) as a direct (resisting pathogens, deterring herbivores) or indirect (reducing competitors' vitality, interfering with decomposition) mechanism. Along these lines, Thiébaut et al. (2019) observed a positive role of allelopathy in favouring the spread of alien species: *L. hexapetala* seems to be able to sustain its invasiveness via autoallelopathy, and more interestingly, the leachates released by *M. aquaticum* and *L. peploides* (two other companion invaders) have a positive effect on the physiological and morphological traits of *L. hexapetala*. Conversely, Adomako et al. (2019) added insights on the potential role played by allelopathy in regulating plant community invasibility. These authors obtained positive feedback between species-rich and dense plant communities and increasing allelopathy as a major mechanism of biotic resistance. This confirms the weak predictive value of IAAP's origin in explaining the strength of plant secondary compounds, which is apparently related to the phylogeny (i.e., eudicots) and growth (i.e., emergent, or floating) strategy (Grutters et al., 2017).

At the same time, the role of "non-competitive" interactions in regulating IAAP spread is generally recognised, especially in relation to the invasional "meltdown" hypothesis (Braga et al., 2020), as showed in the work of Thiébaut et al. (2019) reported above, where "positive interactions" were observed between *L. hexapetala* and *L. peploides* and *M. aquaticum*. This hypothesis was originally proposed considering the general lack of reciprocal interference between introduced species, capable of preventing later invasions, and the evidence of synergistic effects between invaders able to boost impacts on native ecosystems (Simberloff & Van Holle, 1999). Recently, Wegner and colleagues (2019) explored these processes by focusing on the dynamics of two mass invaders, *E. nuttallii* and the quagga mussel *Dreissena rostriformis bugensis* (Andrusov, 1897), in a temperate shallow lake over a 20-year period. These authors confirmed the existence of mutual facilitation in these species' early establishment stages, followed by fierce competition for space, which thus provides a theoretical base for explaining the typical boom-bust dynamics of the *Elodea* populations. These findings were reinforced by Crane et al. (2020) when they tested the competitive and facilitative interactions of three widespread and often co-occurring aquatic invaders: *Dreissena polymorpha* (Pallas, 1771)*, E. canadensis* and *E. nuttallii*. Crane et al. (2020) found that *D. polymorpha* significantly promotes the growth of *E. nuttallii* and the two species predominate *E. canadensis* when they co-occur. These interactions seem to be associated with the huge shifts in water nutrient concentrations triggered by zebra mussels. However, Braga et al. (2020) found only

additive effects for different combination of invaders *H. verticillata*, *Limnoperna fortunei* (Dunker, 1857), and *Astronotus crassipinnis* (Heckel, 1840) in mesocosm experiments. However, these invasive species did not show any sign of mutual antagonistic effects, and the amount of impacts increased along with the number of invasive species tested.

Alien plants in freshwater ecosystems: invasion effects

The effects of IAAP invasion have been intensively investigated across continents, particularly in Europe (Gallardo et al., 2016), where many large water bodies are dominated entirely by IAAP, which impact biomass dynamics and, concurrently, the diversity of submerged aquatic vegetation (Bolpagni et al., 2017). In the 16 largest subalpine lakes in northern Italy, together representing 56% of all Italian surface water resources, *L. major* and *E. nuttallii* emerge as the dominant submerged *taxa* with fresh biomass frequently exceeding 10 kg *per* square metre (Idro Lake; Bolpagni, unpublished data). Overall, these two elodeids are present in more than two thirds of the investigated plots (2,560 of 3,873 plots) (Bolpagni et al., 2017). For emergent macrophytes, a plethora of papers describe the effects mediated by IAAP, starting with the small floating Lemnaceae species (as for *Lemna minuta* Kunth; Ceschin et al., 2018, 2020) to larger species like water primroses (*Ludwigia* ssp.) and *Nelumbo nucifera* Gaertn. (Tóth et al., 2019).

By focusing on the IAAP of European "Union concern" (Table 1), and to better comprehend their effects on freshwater ecosystems, an exploratory review on Scopus was carried out using the following search string: "scientific name" OR "common name" AND alien OR exotic OR weed* OR "non-native" OR "non-indigenous" OR introduced OR invasive OR invading OR allochthonous OR invader AND effect* OR impact* (topic; last accessed 13 November 2020). For "*Ludwigia grandiflora*" (Michx.) Greuter & Burdet and "*Salvinia molesta*" D.S. Mitch., the synonyms "*Ludwigia hexapetala*" and "*Salvinia adnata*" Desv. were also included as selection criteria for the present review. As it is difficult to disentangle the invasion interactions from their drivers, at the same time also the effects mediated by invaders and their adaptative responses to environmental drivers largely overlap. In the following sections, I will focus on the effects rather than adaptations.

Queries returned numerous papers that potentially deal with the effects of target species (equalling 1,167 hits), and most papers focussed on four species: *E. crassipes* (519), *Alternanthera philoxeroides* (Mart.) Griseb. (262), *Salvinia molesta/adnata* (87); *M. aquaticum* (64). Given this large number of hits, only the 2018-2020 period (304 papers) was carefully checked to explore the preeminent invasion effects of the targeted IAAP. The results indicated that just under a quarter of these papers (72) had investigated the effects of IAAP, which can be sorted into the following macro-categories: i) biological interactions (62), including mainly competition and biological interactions (as already introduced in the previous paragraph); ii) metabolic and eco-physiological processes or adaptations that refer mainly to nutrient cycling and chemical and physical impact on ecosystem (17); and iii) biodiversity-related issues, primarily focused on diversity and floristic issues (16) (Table 1, Appendix 1).

i) Biological interactions

The papers describing biological interactions mediated by IAAP are mainly focused on competition. Silveira & Thiébaut (2020) proved that the growth of submerged IAAP (i.e., *E. canadensis, E. densa* and *L. major*) is largely influenced by the presence, identity and relative densities of neighbouring species, and that the interactions between IAAP with a similar morphology were distinctly asymmetrical. When comparing the responses of mixed native communities to the establishment of *L. major*, Petruzzella et al. (2018) observed growing biotic resistance with increasing native species' dominance. Both experiments suggest plant functional group identity to be an important factor in regulating IAAP's invasion repercussions. Biological interactions turn out to be also very closely associated with plant phenological dynamics, which increasingly emerge as

439 key factors in explaining IAAP's invasive behaviour in freshwater ecosystems. This was recently
440 observed by Tóth and colleagues (2019), whose investigated the spread of *L. hexapetala* and *N.*
441 *nucifera* in a series of temperate fluvial lakes. They found a significantly longer growing season for
442 exotic species than for native ones (*Nuphar lutea* (L.) Sm.*, Nymphaea alba* L.*, Trapa natans* L.),
443 especially in Autumn months, which is associated with higher chlorophyll *a* and *b* and carotenoid
444 content in both exotic *taxa*.
445

450 *ii) Metabolic and eco-physiological processes*
451 Concerning the metabolic and eco-physiological processes regulated by IAAP, the spread of *T.*
452 *natans,* capable of creating dense free-floating stands, is strictly associated with significant
453 variations in water dissolved oxygen concentrations, which can negatively influence aquatic fauna
454 (Hummel & Findlay, 2006). Under *T. natans* meadows, a low oxygen concentration was recorded
455 with an increasing hypoxia risk (Bolpagni et al., 2007). This condition pushes small fish towards
456 the edges of macrophyte beds and exposes them to a higher predation risk, which ultimately
457 determines fish community simplification. In addition, dense mats and spiny nuts discourage the
458 recreational use of colonised water bodies and make boating difficult (Caraco & Cole, 2002).
459 Similar evidence has been found for a series of oligo-mesotrophic shallow lakes in SW France,
460 where the spread of *E. densa* and *L. major* has dramatically altered local biogeochemical conditions
461 by inducing relevant metabolic and functional shifts between seasons (Ribaudo et al., 2018). Here
462 the IAAP affirmation resulted in recurring hypoxia events and intense nutrient regeneration by
463 sediments (Ribaudo et al., 2018). Recently, Zhang et al. (2019) observed that the establishment of
464 dense free-floating plant mats may also have extraordinarily strong effects on riparian leaf litter
465 decomposition: floating species like *E. crassipes* can preventively intercept the leaves of riparian
466 plants, and negatively influence the carbon and mass loss rates thus altering the ecosystem
467 metabolism globally.
468

469 *iii) Biodiversity*
470 Focusing on biodiversity-related effects, and by making a special reference to plant-plant
471 interactions, in South China extremely high invasiveness rates have been found for the
472 invasive Alligator weed (*A. philoxeroides*). This behaviour seems to be controlled by precipitation
473 rates, whose increase favours the spread of this species across aquatic and terrestrial habitats and
474 determines a marked decrease in pristine aquatic plant richness (Wu et al., 2017). Additionally, *A.*
475 *philoxeroides* has been found to aggravate its invasive behaviour in laboratory experiments, where
476 increased nutrient availability resulted in stimulating its competitive dominance over native
477 counterparts (*Oenanthe javanica* (Blume) DC., and *Iris pseudacorus* L.) (Zhang et al., 2017).
478 Similar results have been recently obtained by Lolis et al. (2020) while investigating the impacts of
479 *E. crassipes* on biodiversity by comparing its native communities (Brazil) to those in introduced
480 ranges (China). These authors found a significant decrease in the cumulative number of species and
481 beta (β) diversity in invaded communities compared to native ones, along with an increase in *E.*
482 *crassipes* biomass. They also observed vast changes in species composition in dominated *vs.* non-
483 dominated plots, and exclusively within the introduced range. Overall, the work of Lolis and
484 colleagues (2020) provides new perspectives on the mechanisms involved in regulating IAAP
485 impacts on biodiversity. Firstly, the availability of data from both native and invasion ranges will
486 enable us to better quantify the potential impacts associated with the invasion process. Secondly,
487 these authors indicate the engineering ability of *E. crassipes* as the leading invasion driver.
488 Similarly, invaded lakes in Minnesota are much more similar to one another than non-invaded ones,
489 and they are all generally becoming progressively more similar over time because common species
490 become more frequent and rare species sporadic. IAAP seem able to influence native species
491 dynamisms by shaping the community structure by actively contributing to their biotic
492 homogenisation (Olden & Rooney, 2006). In other words, IAAP influence not only diversity on the
493 community scale (α), but also on the regional one (γ), with potential negative feedback about the

future resilience of freshwater ecosystems to disturbance. Indeed, the progressive spread of IAAP leads to a compositional uniformity of communities (Muthukrishnan & Larkin, 2020).

As previously mentioned, the spread and establishment of IAAP may also cause adverse impacts on other aquatic biological communities. Recently, Stiers & Trient (2017) investigated the effects of three aquatic non-native invasive species (*Hydrocotyle ranunculoides* L.f., *L. grandiflora* and *M. aquaticum*) on phytoplankton and zooplankton abundance. Their main results indicated that these species' cover had strongly, and negatively impacted zooplankton density as high plant cover rates determined the disappearance of large cladocerans and littoral *taxa*. Similarly, these species modulate the under-water light environment by changing the spatial and temporal responses of phytoplankton functional groups.

Future challenges for freshwater invaders science

New scientific awareness is affirming the behavioural distinctness of freshwater ecosystems both in itself, and towards biological invasions (Capers et al., 2007; Fleming et al., 2015; van Rees et al., 2020), as reinforced by the idiosyncratic behaviour of IAAP *in primis*, and as explicitly suggested by their invasion mechanisms based mainly on multiple genetic and reproductive modes (Sculthorpe, 1967). A lot of work in this direction has been done, but a number of key questions remain open despite the eight years that have passed since Strayer's position paper was published "about invasions and ecosystem functioning" (Strayer, 2012). By comparing the Exocene's conceptual basis with current knowledge, and particularly with the special recommendations outlined by van Rees et al. (2020) to guide the planning agenda for the new global biodiversity framework, seven issues emerge as those of priority interest in developing freshwater invasion science (Fig. 2). These issues complement van Rees et al. (2020) and offer new ideas for action, placing the increasingly relevant, multiple roles of IAAP into the heart of freshwater challenges.

1. Substantiate the invasion specificity of freshwaters

The presumed aquatic "invasion distinctiveness" seems to be partially supported by the recent cumulative meta-analysis carried out by Crystal-Ornelas & Lockwood (2020), which pointed out the close interrelations between invasions and trophic cascades. In this regard, Smith et al. (2014) found that the spread of aquatic invaders (algae) was able to induce a significant decrease in native species richness, and exclusively at specific trophic levels. Lack of real awareness about the crucial importance of resource-supply variation and how invaders can change the trophic picture of invaded communities and ecosystems have reduced our capability to deeply understand freshwater biodiversity dynamics so far. Indeed Gallardo et al. (2016) emphasised for the first time the strong implications of trophic frameworks as fundamental interpretative keys for capturing structure and functionality changes in aquatic ecosystems following biological invasions. The links between trophic positions and invasions need to be paid more attention in the future to extend to freshwaters the reasoning raised by Chapin et al. (1996) on species' functioning role in terrestrial habitats. Indeed, this is in keeping with the first special recommendation by van Rees et al. (2020) which establishes the uniqueness of freshwaters as a true ecological "third realm".

2. Outline the geographical patterns of IAAP

The increase in global numbers of alien species does not show any sign of saturation to date (Seebens et al., 2017). An ever-increasing spread of invasive aquatics is expected in future climate scenarios (Rodríguez-Merino et al., 2018; Fasoli et al., 2018). Also, the expansion of both legal and illegal e-commerce will likely affect this trend (Peres et al., 2018). This has been recently reiterated by Pyšek et al. (2020) by evaluating the global extent of invasions. In the last few decades, a growing amount of data on IAS' spatial patterns has become available thanks to international collaborations and the development of new analysis tools (e.g., IUCN SSC, DAISIE, NOBANIS, CABI). However, an updated picture on current IAAP distribution is still lacking. In the same way

545 as recently done for the global diversity of aquatic plants by Murphy et al. (2019), we urgently need
546 a twin spatial analysis on IAAP to prioritise as soon as possible the areas at high invasion potential,
547 the diversity hotspots of IAAP and their geographical ranges (at macro- and micro-scale). For
548 instance in the Central Alps, *E. nuttallii* has shown its ability to live at altitudes of up to 2,000 m
549 a.s.l., which suggests that almost all water bodies in Italy can be colonised by IAAP (R. Bolpagni,
550 pers. observ.).
551
552 *3. Promote a unified functional trait-based framework for IAAP investigation*
553 Functional traits are becoming increasingly important for studying key aspects of freshwaters,
554 including structural drivers of communities, their responses to environmental gradients and biotic
555 interactions (García-Girón et al., 2019; Wittyngham et al., 2019; Dalla Vecchia et al., 2020). The
556 use of functional traits may improve our capacity to explore IAAP/IAS dynamics and pressures
557 more than traditional taxonomic-based methods. However, when analysing the literature, a
558 generalised lack of data on functional traits of macrophytes and, in particular, IAAP is evident
559 (Dalla Vecchia et al., 2020). In this context, the topic of invasiveness has been related mainly to
560 anthropogenic pressure and water parameters, with the key intent to explore the implications of
561 morphology and productivity traits in driving IAAP success. Conversely, the main existing
562 knowledge gaps relate to the spatial patterns of traits and root traits, aspects that are primarily
563 involved in biological invasions. Therefore, it is of primary importance to stimulate wide and
564 immediate collaboration initiatives in this field by particularly paying attention to the root traits and
565 regions hosting the highest macrophyte diversity (Dalla Vecchia et al., 2020).
566
567 *4. Deepen the aquatic biodiversity-IAAP interrelations*
568 It is generally acknowledged that diversified plant communities turn out to be more stable and
569 exhibit higher functional diversity: as diversity in species increases, the functional ability to use
570 resources and space increases, as well as biotic resistance (Dostál, 2011; Henriksson et al., 2016).
571 However, contrasting reports on the role of biodiversity in regulating invasiveness also exist.
572 Muthukrishnan et al. (2018) verified that (shallow) lakes with very high plant richness are more
573 likely to be invaded. At the same time, biotic interactions do not offer resistance to invasion, but
574 lessen local-scale diversity via competitive exclusion. Salgado et al. (2019) found that the
575 establishment of *E. crassipes* and *E. densa* does not determine native macrophyte species loss,
576 rather a substantial lake habitats modification by increasing local habitat heterogeneity. These
577 findings contribute to advancements in the larger debate about the effective role of invasive species
578 in the more general biodiversity decline process (Didham et al., 2005 and references therein).
579 Accordingly, the spatial research scale emerges as a fundamental factor for the analysis of invasive
580 species effects. Prevalent negative correlations between invasion success and native richness are
581 measured on small/neighbourhood scales, where interspecific interactions take place. Conversely, a
582 positive contribution of invasive species to species richness is often found on larger spatial scales
583 (Lolis et al., 2020 and references therein). All this calls for us to look at this topic in-depth,
584 especially by considering the disproportionate biological diversity harboured by freshwaters and the
585 dramatic scenarios for its fate.
586
587 *5. Improve knowledge of IAAP eco-evolutionary processes*
588 Given the relevance of genetic traits to support the invasive behaviour of IAAP, as well as the
589 growing evidence that rapid evolutionary changes can occur in non-native *taxa* during
590 invasions (Sultan et al., 2013; Bock et al., 2015), it turns out to be crucial to further investigate the
591 mutual ecological and evolutionary processes involved in IAAP dynamics. Since the publication
592 of *Genetics of Colonizing Species* about 50 years ago (Baker & Stebbins, 1965), evolutionary
593 studies have made considerable progress in understanding the speed of adaptation, the effect of
594 bottleneck events in invasions, and the distinctiveness of invaders (Bock et al., 2015). However,
595 numerous unknowns persist, mainly regarding: i) the source of genetic variation, ii) the "expansion

load", and iii) the role of propagule pressures in shaping the genetic diversity supporting the successful establishment of invaders (Bock et al., 2015). In this respect, IAAP may represent optimal model species for evolution and evolutionary ecology sciences. Unfortunately, only very scarce data on their phylogeographic patters are available so far (Hyldgaard et al., 2017; Rüegg et al., 2017). This kind of information is essential to define, among other things, the origin of invaders, the hypothetical occurrence of multiple introductions, the occurrence of cryptic invasions, and, ultimately, assess adaptation and evolutionary trajectories in the invaded ecosystems. Future genetic research needs to make the most of opportunities afforded by IAAP, also considering the ease with which it is possible to set up manipulative experiments with aquatic plants, a key advantage to achieve an all-round knowledge of freshwaters invasion.

6. Pursue an unbiased ecosystem-oriented evaluation of invader functions in freshwaters
The analysis of invaders' needs to extend beyond the conventional negative sign of IAAP effects. Ewel & Putz (2004) were among the first authors to postulate a possible positive role of alien *taxa* in ecosystems by denouncing the undesirable implications of the one-way negative consideration of invasive species in ecology restoration. Likewise, Dunwiddie & Rogers (2017) suggested to carefully weight the risks alongside the benefits associated with the establishment of invasive alien species in natural areas before taking specific management measures. They also stressed the necessity to stimulate field studies and to collect robust data about invaders' biology. Indeed, a disproportionate resort of expert judgment is still being used and is very often the only available tool to assess the impacts of alien species on habitats (Lazzaro et al., 2020). This reasoning does not imply the direct use or voluntary introduction of non-native species outside their native ranges but advocates for a more pragmatic and non-ideological approach to consider IAAP/IAS in ecosystems. More recently, Rejmánková et al. (2018) placed further emphasis on this concept by underlying lack of awareness about the potential benefits provided by IAAP and the general underestimation of their positive repercussions on ecosystems (Sax et al., 2007; Havel et al., 2015; Hussner et al., 2017). However, the progressive global erosion of reference/pristine ecosystems mainly due to climate change and biological invasions will make it increasingly difficult to understand the effective roles of IAS since "experimental control sites" are missing. This is an issue that will quite likely and strongly affect future research lines and questions about biological invasions.

7. Put invaders in the strategies context to conserve aquatic biodiversity-ecosystem functioning
The idea that aquatic invaders can play not exclusively negative roles does not come into conflict with recent global reviews that highlight threats and conservation challenges for freshwater biodiversity, as discussed by Bolpagni et al. (2019), Cantonati et al. (2020), and Tickner et al. (2020). On the contrary, this opinion paper substantiates the need to develop sound knowledge on the preconditions (pathways and driving factors) and impacts of IAAP/IAS invasion at current and future spread and establishment rates. This is a key prerequisite for implementing an adaptive awareness framework into the ongoing global species redistribution (Didham et al., 2005). In this direction, Tickner et al. (2020) have also reaffirmed the importance of identifying the major introduction pathways of invasive aquatics (e.g., living organisms' trade, ballast-water transfer, undesired releases of plants and animals) as a first grasp strategy to their spread. However, the global capability to regulate the introduction of invasive species outside their native ranges seems far from satisfactory, as previously discussed at large. This is due to the overall lack of social awareness about the actual effects of invasive species, together with lack of a keen supranational policy action to counteract their diffusion (Early et al., 2016). Control and management inadequacies are reinforced by the inherent difficulties to detect alien species in new ecosystems. Generally, a delay in identifying alien *taxa* is also expected, which will reduce our capability to set early response actions to limit the establishment of invaders. This is especially true for freshwaters, which are highly dynamic, difficult to monitor and subjected to severe impacts. In this regard,

646 several emerging methods, such as environmental DNA, proteomics, and nontraditional data
647 repositories, can offer effectives tools to detect invasion events in a timely manner.
648

Synthesis and Conclusions
650 The main features of aquatic plants, including genetic, reproductive, physio-, morpho-, and
651 phenological traits, contribute to explain their "natural invasive" potential (Evernden, 1985). This
652 attitude is considerably enhanced by anthropogenic impacts on freshwater ecosystems (Dukes &
653 Mooney, 1999). Indeed IAAP establishment is based on complex synergic mechanisms that involve
654 the presence of specific invasion pathways and driving factors (climate change, human direct
655 impacts, reclaimed land, dispersal vectors, e-commerce) that substantially allow IAAP to spread
656 and establish outside native ranges. Subsequently, all the above-mentioned factors largely promote
657 IAAP's success *via* mechanisms that seem consistent with the "passenger model" by MacDougall &
658 Turkington (2005), who stressed the key role of non-interactive factors in invasive species'
659 establishment and spread.

661 In current spread scenarios, IAAP will contribute to more and more actively shape and drive the
662 successional trajectories of the colonised physical environment (Stiers & Triest, 2017; Rejmánková
663 et al., 2018; Ribaudo et al., 2018), which will give rise to novel ecosystems (Hobbs et al., 2006).
664 Invasive aquatics are definitely the actors of novel "functional states" for colonised environments
665 (Gallardo et al., 2016), and this overview strongly corroborates the hypothesis that a new "alien
666 dominated" functioning and evolutionary phase for freshwater ecosystems is globally boosting.
667 Thus, Exocene might represent the first step towards a new paradigm to better comprehend the
668 multiple complexity of IAS success since scientific evidence seems to suggest that an irreversible
669 "bio-historical horizon" is ongoing and not exclusively for aquatic plants and freshwater
670 ecosystems. By analysing mutualistic seed-dispersal interactions, Fricke & Svenning (2020) were
671 able to quantitatively understand the effects of introduced IAS on ecological networks for the first
672 time. They found that IAS have eroded the identity of biogeographical realms across the global
673 plant-frugivore meta-network.

675 Hence a systematic change of perspective in the ecosystem roles played by aquatic invaders in
676 freshwaters is essential, as Strayer (2012) originally warned when discussing that some knowledge
677 about invasions and ecosystem functioning is lacking. For instance, further research on IAAP's
678 behaviour and effects are urgently needed to fully understand the extent and magnitude of
679 evolutionary trajectories of freshwater systems at global level (see previous paragraph). In 2014,
680 Evangelista and colleagues (2014) already verified the existence of a significant lack of knowledge
681 on tropical ecosystems, the interactions between alien species and fish or microorganisms and, in
682 general, the absence of multi-*taxa* studies. These gaps significantly reduce our ability to understand
683 IAAP's roles in ecosystems, and massively limit the effectiveness of conservation plans and
684 actions. This is also one of the research priorities suggested recently by Pyšek et al. (2020), and I
685 totally agree with the need «*to improve our ability to predict new invasions and their impacts*».
686 However, I also consider that understanding habitats' responses to invasion is central for depicting
687 their future trajectories. Even in the presence of effective eradications it is, for example, impossible
688 to exclude the persistence of "legacy effects", which modulate the structure and functioning of
689 ecosystems, triggered by eradicated invaders. Secondary habitats or unexpected habitat paths are
690 continuously created by the presence of IAS and, as stated by the regime shift theory, in most cases
691 it is not possible to go back to pre-invasion conditions or the "pristine equilibrium" (Scheffer &
692 Carpenter, 2003).

694 More attention must be paid to the trophic interactions and functional effects of IAAP by resorting
695 to a holistic perception, one including both biodiversity issues and functional and trophic aspects
696 (Fricke & Svenning, 2020). To do so, relevant keys to understand could be offered by the

15

Biodiversity-Ecosystem Functioning approach (BEF, Tilman & Dowing, 1994) and the new tri-trophic interactions theory (TTIs; Abdala-Roberts et al., 2019). Both these approaches need to be more widely applied to freshwaters to disentangle the processes mediated by IAAP across organisation scales and levels. Furthermore, BEF and TTIs approaches need to also be applied and tested, but without neglecting the ecosystem-oriented theoretical advances in invasion science, such as the PAB hypothesis and "invasion syndromes" (Catford et al., 2009; Kueffer et al., 2013). Expected outputs would allow us to better link biodiversity decline (homogenisation) with the functional changes of ecosystems (Exocene, Fig. 1) by shedding light on the multiple implications and feedbacks of IAAP accumulation.

Supplementary materials
Appendix 1. List of the recent papers (2018-2020) that focus on the biological interactions (*Bio_int*), metabolic and eco-physiological processes (*Met_pro*) and biodiversity-related issues (*Bio_iss*) mediated by the invasive alien aquatic species of Union concern, as defined in Table 1.

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Fig. 1. Exocene loops: invasion pathways (in blue palette), driving factors (invasion opportunity windows; in yellow palette), ecological mechanisms (preeminent invasion classes; in green palette), and effects (in red palette) mediated by invasive alien aquatic plants in freshwater ecosystems. Only key elements and preeminent links among factors are reported (whose size is directly proportional to their intensity).

Fig. 2. Matrix diagram illustrating where the seven "IAAP challenging issues" agree with the Special Recommendations (SRs) for future strategies to safeguard freshwater biodiversity by van Rees et al. (2020). Filled circles indicate full concordance, whilst open circles indicate where the "IAAP challenging issues" need further development within the context of the new global freshwater biodiversity conservation framework, as detailed in the text.