

1 **Impacts of artificial barriers on the connectivity and dispersal of vascular**
2 **macrophytes in rivers: a critical review**

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9 Running head: Barrier impacts on macrophytes

10 **Abstract**

- 11 1. Macrophytes play important functional roles in river ecosystems, providing
12 habitat and food, as well as influencing flow, water chemistry and sediment
13 dynamics. They also represent an important component of river biodiversity.
14 2. Artificial river barriers have the potential to disrupt macrophyte dispersal, and
15 compromise their distribution and persistence, but little information is available
16 compared to barrier impacts on fish and macroinvertebrates. Here we review
17 the mechanisms supporting dispersal of river macrophytes in rivers and
18 evaluate the nature of barrier impacts on macrophytes.
19 3. Hydrochory (dispersal of propagules by water) is the principal mechanism of
20 downstream dispersal, while zoochory (dispersal of propagules by animals) is
21 likely to be the most important vector of upstream dispersal and inter-
22 catchment transport.
23 4. Most studies have focused on the impact of large structures such as dams,
24 and the findings indicate the impact is highly context-dependent. Slow-flowing
25 habitats upstream of dams can act as traps to drifting propagules and thereby
26 interrupt hydrochory. However, the consequences of interrupted hydrochory
27 for downstream populations are unclear. River regulation can result in lower
28 macrophyte diversity, although the lentic habitats associated with reservoirs
29 can also favour an increase in the abundance and richness of macrophyte
30 communities.

- 31 5. Instream barriers are unlikely to affect zoochory by birds directly, but barriers
32 are well known to restrict fish movements, so there is considerable potential
33 for barriers to disrupt zoochory by fish, although no empirical study has
34 specifically examined this possibility.
- 35 6. There is a paucity of studies examining the impacts of low-head barriers on
36 macrophyte dispersal. Given the influence of macrophytes on river processes,
37 we call for further research into barrier impacts on macrophyte population
38 dynamics in order to gain a better understanding of the consequences of river
39 fragmentation for fluvial communities and ecosystem functioning.
- 40

41 **1 | INTRODUCTION**

42 Aquatic vascular macrophytes (Tracheophyta) are an important component of river
43 biodiversity, including over 2,600 species from 88 different families globally
44 (Chambers et al., 2008). Apart from their contribution to aquatic biodiversity,
45 macrophytes play important functional roles in river ecosystems: they provide food
46 resources and habitat (Biggs, 1996; Grenouillet et al., 2002), and act as ecosystem
47 engineers by trapping sediments and altering flow dynamics (Carpenter & Lodge,
48 1986; Horvath, 2004; Gurnell et al., 2006). Macrophytes can also regulate water
49 chemistry (Clarke & Wharton, 2001), and are one of the key metrics used to
50 measure the ecological status of river systems under the Water Framework Directive
51 (European Commission, 2000). Hence, maintaining healthy macrophyte communities
52 is essential for river ecosystem function.

53 Artificial barriers, such as dams and weirs, can have a pervasive influence on river
54 systems (Ellis & Jones, 2013). However, while barrier impacts on fish populations
55 have received considerable attention (e.g. Morita & Yamamoto, 2002; Fullerton et
56 al., 2010; Perkin & Gido, 2012), impacts on aquatic macrophytes remain relatively
57 unexplored. Connectivity is essential for the resilience of freshwater biota and the
58 maintenance of river processes (Pringle, 2001, 2003; Fagan, 2002). Artificial barriers
59 alter river hydrology and create discontinuities in substrate composition, temperature
60 regime, and water chemistry (Mueller et al., 2011) that could potentially disrupt
61 macrophyte dispersal and population structure. Furthermore, river obstacles affect
62 the distribution and movements of fish (e.g. Dehais et al., 2010; Diebel et al., 2015;
63 Branco et al., 2017), as well as birds indirectly by affecting habitat availability

64 (Nilsson & Dynesius, 1994; Stevens et al., 1997), and these groups can act as
65 important dispersal vectors for riverine macrophytes (e.g. Horn, 1997;
66 Charalambidou & Santamaría, 2002; Pollux et al., 2006). There are estimated to be
67 over 16 million barriers in river systems worldwide (Lehner *et al.*, 2011), and recent
68 studies suggest even this number is likely to be a severe underestimate because the
69 abundance of low-head barriers is not well known (Garcia de Leaniz et al., 2018;
70 Jones et al., 2019). Hence, there is considerable potential for barriers to have wide-
71 reaching effects on macrophyte abundance and distribution.

72 Invasive species are one of the leading causes of decline in freshwater biodiversity
73 worldwide (Dudgeon et al., 2006; Reid et al., 2019), and the effects of non-native
74 macrophytes can be particularly damaging because they can exclude native species,
75 alter habitat complexity, disrupt food webs, modify sediment dynamics, cause
76 hypoxia, release allelopathic chemicals, and facilitate the establishment of other
77 exotic species (Bunn et al., 1998; Michelan et al., 2010; Schultz & Dibble, 2012;
78 Fleming & Dibble, 2015). Invasive macrophytes generally have higher growth rates,
79 higher plasticity, and disperse more readily than native species (Shultz & Dibble,
80 2012; Umetsu et al., 2012), traits which may make them more suited to
81 establishment in regulated rivers. Hence, it is important to consider the effect of river
82 barriers on invasive macrophytes.

83 Several studies have examined macrophyte dispersal and settlement dynamics in
84 rivers (e.g. Johansson & Nilsson, 1993; Riis, 2008; Brochet et al., 2010; Anderson et
85 al., 2011; Pollux, 2011), and the impact of large barriers has been investigated in a
86 number of case studies (e.g. Merritt & Wohl, 2006; Ceschin et al., 2015; Vukov et al.,
87 2018). However, barrier impacts on macrophyte dispersal have not been reviewed.
88 Here, we review the current literature on macrophyte dispersal and settlement, and
89 examine the impacts of anthropogenic barriers on population dynamics.

90

91 **2 | METHODS**

92 We searched for relevant literature using Google Scholar and Web of Science
93 search engines, utilising different combinations of search terms depending on the
94 subsection of the review (see Table S1 for glossary of terms and Table S2 for search
95 terms and number of hits). No restrictions on year of publication or type of document

96 were imposed. As not all search results were pertinent to the scope of the review,
97 they were systematically reviewed by the lead author. For example, for Section 3.1
98 Hydrochory, publications were deemed relevant only if they focussed on aquatic
99 plants, related to fluvial systems, and dispersal by water was the focus of the paper.
100 The use of search term strings sometimes returned very large numbers of hits (see
101 Table S2) so results were ordered in terms of relevance (i.e. records containing
102 highest number of keywords first), and the first 200 records were reviewed for
103 relevance by the lead author. As predefined strings of search terms may not always
104 be effective in returning the most relevant material, key publications highlighted
105 during reading were also added to the reference list. By following the steps detailed
106 above we are confident that we effectively covered the most important literature on
107 the topic.

108

109 **3 | MACROPHYTE DISPERSAL AND SETTLEMENT**

110 Fluvial ecosystems are inherently dynamic environments (Ward & Stanford, 1995),
111 exposed to regular flow disturbances that cause local extirpations of macrophyte
112 communities (Riis & Biggs, 2003; Franklin et al., 2008). Aquatic plants have various
113 adaptations that facilitate dispersal, and allow them to recolonise vacant habitat
114 patches (Catford & Jansson, 2014). Longitudinal dispersal in river networks is also
115 important for maintaining genetic diversity of populations (Pollux et al., 2005; Honnay
116 et al., 2010; Horreo et al., 2011). Dispersal of propagules (including whole plants,
117 vegetative parts, and seeds; Thomaz et al., 2015) can take place via one of four
118 mechanisms (Figure 1): river flow (hydrochory), movement by animals (zoochory), by
119 wind (anemochory), or human-mediated dispersal (anthropochory).

120 **3.1 | Hydrochory**

121 Hydrochory is considered to be a principal dispersal vector for macrophytes in free-
122 flowing rivers (Dawson, 1988; Merritt & Wohl, 2002). In contrast to terrestrial plants,
123 many macrophytes disperse largely through vegetative parts such as rhizomes,
124 stolons, tubers, turions, stem fragments, and even entire plants (Sand-Jensen et al.,
125 1999; Boedeltje et al., 2004; Umetsu et al., 2012). Aquatic macrophytes often have
126 functional adaptations to facilitate dispersal in flows (Catford & Jansson, 2014),

127 including air-filled structures and hairs which trap air bubbles to increase buoyancy,
128 and therefore expedite drift (Riis & Sand-Jensen, 2006).

129 Production of vegetative fragments occurs either through breakage caused by water
130 currents or animal disturbance (allofragmentation; see Madsen et al., 1988), or via
131 autofragmentation – the release of tissue as a plant reaches peak biomass (Riis et
132 al., 2009). Species with more streamlined morphological adaptations (e.g.
133 *Ranunculus spp.*) are less susceptible to stem breakage and uprooting by flows
134 compared to those with higher hydraulic resistance and weaker rooting strength (e.g.
135 *Rorippa nasturtium aquaticum*; Sand-Jensen, 2003). The structural properties of the
136 vegetative bodies also affect how far they drift. For instance, Riis and Sand-Jensen
137 (2006) found that the majority of denser *Elodea canadensis* fragments settled within
138 0.3 km of the source plant, whereas *Ranunculus peltatus* stems, which were more
139 buoyant, tended to disperse longer distances (up to 5 km). These observations
140 reflect the importance of species-specific traits in determining dispersal distance in
141 river flows (Catford & Jansson, 2014).

142 In emergent taxa and species associated with river margins, seed dispersal can be
143 more important, and experimental evidence suggests that hydrochorous seed
144 dispersal is a major mechanism structuring plant communities along rivers (Nilsson
145 et al., 1991; Pollux et al., 2009). Many species have buoyant seeds to expedite
146 dispersal (Nilsson et al., 2010), with dispersal rates of up to 15 km h⁻¹ recorded in the
147 floating seeds of *Polygonum sp.* (Staniforth & Cavers, 1976). The seeds of some
148 other aquatic plants (e.g. *Juncus spp.*) are negatively buoyant and sink immediately
149 after being liberated, but the young seedlings float and can travel large distances
150 before taking root (Barrat-Segretain, 1996). Even dense seeds can be transported
151 large distances in the bedload of rivers (Markwith & Leigh, 2008, 2012) or on floating
152 debris rafts (Skoglund, 1989).

153 Dispersal and settlement dynamics are highly dependent on hydrology. Many
154 species time the release of propagules to coincide with high flows to facilitate long-
155 distance dispersal (Catford & Jansson, 2014). High water velocities increase drag
156 on drifting plant fragments and, therefore, reduce the likelihood of settlement (Sand-
157 Jensen, 2003). Fast flows also compress plant growth against the stream bed,
158 reducing roughness, and thereby reduce retention rates of drifting propagules (Sand-

159 Jensen, 2003). Hence, high water velocities favour long-distance dispersal, while
160 slow flows, often associated with meanders, are required for propagule settlement.
161 Dispersal distance tends to be positively associated with the width of the stream
162 channel, drift often being higher in large rivers than in smaller streams (Riis & Sand-
163 Jensen, 2006). Stem fragments tend to be more frequently deposited in shallower
164 areas of river channels (Riis & Sand-Jensen, 2006), and in areas with high bed
165 roughness, or where there is thick vegetative growth (Riis, 2008).

166 It is widely accepted that hydrochory is the dominant mode of downstream dispersal
167 in river macrophytes, and results in effective dispersal across scales ranging from
168 hundreds of meters to kilometres (Nilsson et al., 1991; Boedeltje et al., 2003; Riis &
169 Sand-Jensen, 2006). Hence, hydrochorous dispersal is critical to the maintenance of
170 genetic diversity in macrophyte populations. A number of studies have found the
171 unidirectional flow of water results in asymmetrical gene flow (Gornall, 1998; Pollux
172 et al., 2009). For instance, Pollux et al. (2009) found a significant increase in the
173 genetic diversity of *Sparganium emersum* populations with distance downstream,
174 gene flow being approximately 3.5 times higher in a downstream direction than
175 upstream. In the absence of a mechanism for upstream dispersal, the continual
176 downstream drift of propagules via hydrochory would theoretically result in loss of
177 genetic diversity, and eventually population collapse of macrophytes in headwaters
178 (Pollux et al., 2009; Honnay et al., 2010). However, many studies have found no
179 evidence of genetic impoverishment in upstream populations (Tero et al., 2003;
180 Markwith & Scanlon, 2007; Chen et al., 2009; Honnay et al., 2010). It is largely
181 unknown why some populations show evidence of upstream genetic impoverishment
182 while others do not (see Tero et al., 2003; Markwith & Scanlon, 2007; Honnay et al.,
183 2010) but the fact that macrophyte populations can persist in headwaters is good
184 evidence that vectors for upstream dispersal must exist.

185 **3.2 | Zoochory**

186 Zoochory (movement by animals) plays an important role in longitudinal movements
187 of plant propagules along rivers, and has been demonstrated in fish (Pollux et al.,
188 2006), birds (Figuerola & Green, 2002), mammals (Medwecka-Kornaś & Hawro,
189 1993), and reptiles (Padgett et al, 2010). Transport of propagules can either take

190 place inside the gut of animals (endozoochory), or attached to their bodies
191 (ectozoochory).

192 A wide range of fish species are known to consume plant seeds (e.g. García-
193 Berthou, 2001; Nurminen et al., 2003; Correa et al., 2007), which often retain their
194 ability to germinate after passing through fishes' guts (Pollux, 2011). Given that fish
195 are often highly mobile within river catchments (Lucas & Batley, 1996; Makrakis et
196 al., 2007), this offers a potentially important vector for macrophyte dispersal. Some
197 seeds can survive up to 36 hours in the fish gut (Horn, 1997), during which time they
198 could be dispersed over long distances. Evidence of endozoochorous dispersal of
199 seeds by fish has been found in Europe (Pollux et al., 2005; Pollux, 2007), North
200 America (Chick et al., 2003; VonBank et al., 2018a), and South America (Anderson
201 et al., 2009; 2011), suggesting it is a widespread mechanism of upstream dispersal
202 for river macrophytes (see Horn et al., 2011). For example, seeds of *Sparganium*
203 *emersum* have been found to disperse up to 27 km in the gut of the common carp
204 (Pollux et al., 2007), and single dispersal events by fruit-eating fish in the Amazon
205 have been observed to transport seeds over distances greater than 5 km (Anderson
206 et al., 2011) . Fishes differ in their diets (Gerking, 1994) and propensity to move
207 (Lucas & Baras, 2001) so fish-mediated dispersal is likely to be species-specific.

208 Endozoochory also occurs through water birds (Smits et al., 1989; Charalambidou &
209 Santamaría, 2002; Brochet et al., 2010). Waterfowl can consume large amounts of
210 seeds which can survive in their guts for periods of hours to days (Figuerola &
211 Green, 2002). A recent study in Brazil showed that whole plants of the *Wolffia* family
212 could survive gut passage intact (Silva et al., 2018). Given that ducks and waders
213 can travel upwards of 50 km h⁻¹ (Welham, 1994), there is considerable potential for
214 long-distance dispersal (Clausen et al., 2002; Van Leeuwen et al., 2012). There is
215 also evidence that piscivorous birds such as cormorants can act as secondary
216 dispersers of plant seeds (Van Leeuwen et al., 2017). Importantly, dispersal by birds
217 is not restricted to river corridors, so inter-catchment transport is possible, and
218 endozoochorous dispersal of seeds in waterfowl is possible over distances up to
219 3,600km (Pollux, 2007). Bird-mediated dispersal is also thought to be responsible for
220 gene flow between lake populations of macrophytes hundreds of kilometres apart
221 within the Yangtze River catchment in China (Chen et al., 2009).

222 A number of studies have suggested ectozoochory is uncommon in waterfowl
223 because macrophytes propagules generally lack adherent properties, and are
224 therefore likely to be carried only short distances (Figuerola & Green, 2002; Brochet
225 et al., 2010; Reynolds & Cumming, 2016). However, recent studies indicate that
226 frequent short-distance dispersal of macrophytes attached to the bodies of birds may
227 be important. 'Stepping-stone' dispersal is possible, whereby plant fragments adhere
228 externally to birds, and are dispersed over short distances as the birds move
229 (Coughlan et al., 2017a,b). Although the plant fragments often tend to be moved only
230 short distances, high frequencies of such events provide the mechanism for long
231 distance dispersal. Ectozoochory is likely to be particularly relevant for small
232 macrophytes such as members of Lemnoideae (Duckweeds; Landolt, 1986;
233 Coughlan et al., 2015). Although not yet experimentally evaluated, it is likely that
234 multiple short dispersal events could also result in eventual long distance
235 endozoochorous dispersal by fish. Irrespective of the precise mechanisms involved, it
236 is widely accepted that zoochory is a principal mechanism for upstream dispersal of
237 macrophytes in rivers (Figuerola & Green, 2002; Pollux *et al.*, 2006; Coughlan et al.,
238 2017a).

239 **3.3 | Anemochory**

240 Dispersal by wind (anemochory) offers an additional mechanism for propagule
241 dispersal. Some authors have suggested this mode of dispersal is rare for aquatic
242 macrophytes as their seeds tend to be relatively heavy, and they generally lack
243 adaptations to promote wind dispersal (e.g. Barrat-Segretain, 1996). For instance,
244 90% of sedge grass (*Carex sp.*) seeds were deposited within 2 m of the source
245 plant, perhaps suggesting anemochory is of limited importance in long distance
246 dispersal (Soomers et al., 2013). However, Soons (2006) showed that 46% of
247 wetland plant species have adaptations to promote anemochory and argued it was of
248 great importance in the dispersal of aquatic plants. Many emergent taxa such as
249 *Phragmites spp.* and *Typha spp.* produce large numbers of small light seeds that are
250 easily dispersed by wind (Shipley et al., 1989; Soons, 2006). Although most wind-
251 blown seeds tend to settle close to the source plant (e.g. >90% of *Phragmites sp.*
252 within 30m, Soomers et al., 2013), it is the small proportion of seeds on the tail of the
253 dispersal curve that are important in long distance dispersal (Nathan et al., 2008),
254 and these seeds can be transported over distances of hundreds of kilometres

255 (Soomers et al., 2013). Wind dispersal is likely to increase substantially during
256 extreme weather events when wind speeds are highest and sampling is problematic
257 (Nathan et al., 2008). Even rare long distance dispersal events are important in
258 facilitating gene flow between populations (Trakhtenbrot *et al.*, 2005). Also, as with
259 zoochory, multiple and frequent short distance dispersal events should theoretically
260 result in long distance dispersal via a 'stepping-stone' effect (Saura et al., 2014), and
261 generate sufficient gene flow to prevent genetic differentiation within
262 metapopulations. At a minimum, anemochory is likely to be an important primary
263 mechanism of dispersal in many plants, whereby dispersal into flowing water creates
264 secondary dispersal opportunities via hydrochory.

265 **3.4 | Anthropochory**

266 Human movements are increasingly spreading plants outside the confines of natural
267 dispersal mechanisms (Hodkinson & Thompson, 1997; Winchmann et al., 2008).
268 This not only allows for long distance longitudinal movement of propagules and
269 genes along rivers (Tero et al., 2003), but also dispersal across catchment
270 boundaries, resulting in dispersal on a global scale (Ciotir & Freeland, 2016).
271 Anthropochory is of particular relevance for the spread of invasive species. For
272 instance, over 400 non-native macrophyte species are traded in Europe, most of
273 which have the potential to become invasive (Hussner, 2008), and the ornamental
274 plant trade is a major pathway for the spread of invasive macrophytes, both via
275 deliberate and accidental introductions (Hussner, 2012). River users can spread
276 plant propagules through recreational activities. For instance, macrophytes can
277 frequently become entangled on recreational boating equipment which can then be
278 transported to other waterbodies (Johnson et al., 2001; Rothlisberger et al., 2010;
279 Kelly et al., 2013). In the UK, 64% of anglers and 78% of canoeists use their
280 equipment in more than one catchment within a fortnight, most without any
281 biosecurity measures (Anderson et al., 2014). Human-mediated dispersal can also
282 result in gene flow between populations of native macrophytes that would otherwise
283 be genetically isolated (Ciotir & Freeland, 2016).

284

285 **4 | BARRIER IMPACTS ON MACROPHYTES**

286 Artificial barriers alter the hydrology (Merritt & Wohl, 2002), temperature (Olden &
287 Naiman, 2010), water chemistry (Byren & Davies, 1989), and sediment dynamics
288 (Williams & Wolman, 1984) of running waters, often creating habitat discontinuities
289 (Ward & Stanford, 1983) that can have profound influences on community
290 assemblages (Parasiewicz et al., 1998). These abiotic and biotic factors can
291 potentially affect aquatic macrophytes in a variety of ways (Table 1; Figure 2).
292 Physical barriers have considerable potential to impact hydrochory and zoochory,
293 and are therefore discussed in separate subsections below. Wind dispersal is
294 unlikely to be significantly affected by the presence of barriers, except perhaps by
295 the largest of dams. We found no papers which covered the effect of barriers on
296 anemochory so this issue was not covered here. There is considerable evidence that
297 barriers influence the distribution of invasive species, so we covered this topic
298 separately (section 4.3) along with human-mediated dispersal.

299 **4.1 | Barrier effects on hydrochory**

300 Water velocity is a key parameter determining how far propagules disperse, and
301 hence can have important consequences for plant community composition along
302 rivers (Merritt & Wohl, 2006). Slow flows in impounded reaches can act as barriers
303 for macrophyte dispersal, trapping drifting propagules and resulting in high mortality
304 (Nilsson & Jansson, 1995; Jansson et al., 2000a; Jansson et al., 2000b; Nilsson et
305 al., 2010). Reservoirs can reduce the density of drifting propagules in downstream
306 reaches by as much as 95%, and this effect can extend for several kilometres
307 downstream of large dams (Merritt & Wohl, 2006). Compared to free-flowing rivers,
308 rivers fragmented by large dams tend to show lower richness of drifting propagules,
309 and dispersal rates are also often reduced (Andersson et al., 2000; Jansson et al.,
310 2000a; Merritt & Wohl, 2006), although this is not always the case. For example,
311 Jansson et al. (2005) did not find any evidence to suggest that dams decreased the
312 abundance or diversity of drifting propagules in a comparison of fragmented and
313 free-flowing rivers. However, in this instance, the drifting propagule bank in the
314 fragmented river was derived from local (within-impoundment) sources only
315 (Jansson et al., 2005), suggesting long-distance dispersal via hydrochory was
316 compromised.

317 Floods are important events for hydrochory in free-flowing rivers (Cellot et al., 1998;
318 Franklin et al., 2008; Gurnell et al., 2008), but their intensity and frequency is
319 reduced in many dammed rivers (Magilligan & Nislow, 2005), and this can limit
320 hydrochorous dispersal of propagules (Jansson et al., 2000a). There is evidence that
321 species with different dispersal strategies are affected to different degrees by flow
322 regulation (Jansson et al., 2000a, Jansson et al., 2000b). For example, the reduced
323 frequency of floods in regulated reaches can prevent transport of non-buoyant
324 propagules, whereas those with floating propagules can show higher probability of
325 dispersal (Jansson et al., 2000a; Jansson et al., 2000b).

326 Barrier design can influence the extent to which hydrochory is disrupted. Large dams
327 with big reservoirs are likely to have a greater impact on hydrochory than smaller
328 barriers with negligible impoundments. Through-flow barriers (e.g. culverts) and
329 overflow (e.g. weirs) barriers are likely to intercept less propagules than bottom-
330 release dams. Impoundments with thick vegetative growth should intercept more
331 drifting propagules than sparsely vegetated impoundments (Riss, 2008). Structures
332 with sediment release mechanisms should cause less disruption to transport of
333 seeds in the bedload (Markwith & Leigh, 2008). Hence, the impact of barriers on
334 hydrochory is highly context-dependent (Figure 3).

335 The impact of low-head barriers on macrophytes has been largely unexplored
336 compared to the effects of large dams. Although their impact is likely to be less
337 severe than large dams, smaller barriers such as weirs modify river flows, often
338 creating slow velocity areas (weir pools) immediately upstream. These weir pools
339 tend to stabilise the substrate and increase settlement of fine sediments (Merritt &
340 Wohl, 2006). In trapping river substrates, small barriers likely prevent or at least
341 significantly reduce movement of non-buoyant seeds in the bedload (Markwith &
342 Leigh, 2008, 2012). Stable substrates create opportunities for the establishment of
343 macrophytes that would otherwise have been unable to root (Riis & Biggs, 2003) and
344 can further exacerbate changes by creating a positive feedback loop, whereby the
345 presence of standing macrophytes increases sedimentation rates (Sand-Jensen et
346 al., 1989; Gurnell et al., 2006; Jones et al., 2012) and thereby increases propagule
347 settlement (Gurnell et al., 2008; Riis, 2008). For example, in Norway, weirs are
348 commonly built as part of small-scale hydropower schemes, but weir pools are often
349 associated with increased siltation and subsequent growth of macrophytes, which

350 are regarded as a nuisance (Rorslett & Johansen, 1996). However, other studies
351 have found little evidence that weirs affected macrophyte diversity or abundance
352 (Mueller et al., 2011). The variation in the response of macrophytes is likely to
353 depend on the nature of hydrological alteration: i.e. where weirs stabilise flows and
354 substrate macrophyte cover tends to increase, whereas barriers with negligible
355 effects on hydrology and substrate movement tend to have little effect on
356 macrophytes.

357 The potential link between disrupted hydrochory and community structure
358 downstream is unclear. Although dams can significantly reduce hydrochorous
359 dispersal, the abundance and diversity of plant populations downstream of dams
360 may in some cases remain the same as upstream (Merritt & Wohl, 2006).
361 Discontinuities in community composition have been associated with dams, with
362 assemblages exhibiting a shift from a composition similar to the drifting
363 hydrochorous propagule bank upstream, to communities derived from local seed-
364 bearing plants downstream (Andersson et al., 2000; Jansson et al., 2000a).
365 Decreases in macrophyte diversity and abundance have been reported downstream
366 of dams (Casado et al., 1989; García de Jalon et al., 1994), while in other cases an
367 increase in macrophyte abundance has been reported (Goes, 2002; Abati et al.,
368 2016; Tena et al., 2017), although in these studies, changes in macrophyte
369 population structure were not directly linked to disruptions of hydrochory, and
370 probably related to differences in hydrological regime. However, other studies have
371 found evidence that the richness of riverine plant communities was linked to
372 hydrochorous seed input, with free-flowing rivers showing higher richness (Nilsson et
373 al., 1991; Merritt et al., 2010).

374 Many of the observed changes in macrophyte community have been associated with
375 the hydrological effects of dams, rather than their role in disrupting hydrochory.
376 Stable flow conditions often found downstream of dams can increase aquatic plant
377 cover in affected reaches (Goes, 2002; Ibáñez et al., 2012; Abati et al., 2016).
378 Moderate disturbance caused by hydropeaking (frequent, short duration, artificial
379 flow events) can also lead to increased macrophyte richness and abundance,
380 compared to unregulated rivers (Bernez et al., 2002; Bernez et al., 2004). Where
381 hydrological disturbance is more severe, macrophyte communities tend to show low

382 diversity and be less abundant (Casado et al., 1989; García de Jalon et al., 1994;
383 Merritt et al., 2010).

384 Impoundments upstream of dams are characterised by slow flows, reduced
385 turbulence and more uniform habitats, increasing sedimentation rates and creating
386 conditions that resemble lentic systems (Anderson et al., 2015; Vukov et al., 2018).
387 Dissolved concentrations of critical nutrients such as phosphorous and nitrate are
388 often higher in these impounded reaches, leading to increased plant growth
389 (Benítez-Mora & Camargo, 2014). As a result of these changes, slow flowing
390 habitats immediately upstream of dams often support high macrophyte biomass,
391 albeit generally with communities more representative of lacustrine habitats
392 (Tombolini et al., 2014; Ceschin et al., 2015; Vukov et al., 2018). Some authors have
393 described these changes as 'favourable' due to locally increased macrophyte
394 diversity (Ceschin et al., 2015). However, the establishment of largely lacustrine
395 macrophyte species likely occurs to the detriment of riverine flora and fauna within
396 impounded areas.

397 **4.2 | Barrier effects on zoochory**

398 Given the importance of ichthyochory (movement of seeds by fish) for upstream
399 dispersal (Pollux et al., 2006; Anderson et al., 2011; Horn et al., 2011), impediment
400 of fish movements by barriers (e.g. Lucas & Batley, 1996; Winter & Van Densen,
401 2001; Garcia de Leaniz, 2008) could potentially impact macrophyte dispersal and
402 population connectivity. To date, no study has specifically assessed how the
403 presence of barriers may affect endozoochorous dispersal of seeds by fish, although
404 it has been raised as an issue of concern (e.g. Correa et al., 2007; Horn et al., 2011).
405 The group of fish in which seed dispersal has been identified tend to be weaker-
406 swimming members of river fish communities such as cyprinids, characids, and
407 ictalurids (e.g. Chick et al., 2003; Anderson et al., 2009; VonBank et al., 2018a).
408 These species are more likely affected by barriers because they lack the swimming
409 speed and leaping ability to overcome many obstacles (Beecham, 2004; Tudorache
410 et al., 2008; Langerhans & Reznick, 2010).

411 The presence of river barriers is unlikely to affect the movements of birds directly,
412 but changes in the distribution of riverine habitats brought about by flow regulation
413 can alter the composition and distribution of waterfowl communities (Nilsson &

414 Dynesius, 1994). For example, the accumulation of fish at barriers can also lead to
415 local increases in piscivorous birds (Stevens et al., 1997, Baumgartner et al., 2008)
416 and still waters within impoundments provide habitat for many waterfowl (Nilsson &
417 Dynesius, 1994). Because birds can act as important agents of propagule dispersal
418 (Figuerola & Green, 2002; Charalambidou & Santamaría, 2002; Coughlan et al.,
419 2015), changes in their distribution have the potential to influence aquatic plant
420 dispersal, although this has not yet been examined. Further research is required to
421 elucidate the impacts of barriers for zoochorous dispersal of seeds by animals.

422 **4.3 | Barrier effects on invasive macrophytes**

423 Hydrochory has been highlighted as an important mechanism for the spread of
424 aquatic invasive plants (Thébaud & Debussche, 1991; Okada et al., 2009; Aronson
425 et al., 2017). The trapping of drifting propagules by large barriers such as dams can
426 inhibit or prevent the spread of invasive species that rely on hydrochory for dispersal
427 (Rood et al., 2010). However, any such effect is also likely to impact population
428 connectivity of native macrophytes (Merritt & Wohl, 2006; Nilsson et al., 2010).

429 Invasive species tend to be most successful where naturally occurring communities
430 are stressed by anthropogenic disturbance (Byers et al., 2002; Johnson et al., 2008;
431 Strayer, 2010), including damming (Johnson et al, 2008; Greet et al., 2013).

432 Hydrological modifications associated with river barriers can result in changes in
433 community composition, as native macrophytes may be unable to cope with modified
434 conditions (Catford & Jansson, 2014), creating opportunities for invasive
435 macrophytes to establish. For example, damming of the river Guadiana in Spain has
436 led to increased spread of the invasive water hyacinth (*Eichhornia crassipes*; Téllez
437 et al., 2008). A recent study has also shown that thick mats of water hyacinth can
438 themselves trap and disrupt downstream transport of hydrochorous seeds (Vonbank
439 et al., 2018b). Artificial reservoirs in North America tend to support more invasive
440 species than natural lakes, likely because native species have less of a stronghold in
441 artificial systems (Johnson et al., 2008). Flow regulation in the River Rhine has
442 favoured the spread of invasive *Elodea nuttallii*, which has become dominant in
443 many altered reaches (Van Geest et al., 2005) and modified flow regimes
444 downstream of dams have also favoured the invasion of non-native macrophytes in
445 riverine wetlands within the Murray River, Australia (Catford et al., 2011). However, a

446 reduction in flood disturbance due to river regulation in a Californian river system
447 resulted in reduced propagule dispersal in the invasive aquatic macrophyte *Ludwigia*
448 *hexapetala* (Thomason et al., 2018). These contrasting findings indicate that the
449 outcomes of hydrological modification depend on the flow regimes imposed and the
450 dispersal traits of the invasive plants present.

451 Reservoirs often receive higher numbers of boat users and anglers than free-flowing
452 sections of rivers (Havel et al., 2005; Cooper, 2006), and impounded areas can be
453 sites of high introduction risk within catchments (Johnson et al., 2008; Jacobs &
454 Macisaac, 2009; Tamayo & Olden, 2014). For instance, artificial reservoirs in South
455 Africa were highlighted as high risk areas for invasion of *Hydrilla venticillata* due to
456 high boat traffic (Coetzee et al., 2009). Recreational disturbance (e.g. kayaking,
457 boaters, fishermen etc.) in impounded reaches can also result in the fragmentation of
458 invasive plants, resulting in higher hydrochorous dispersal (Thomason et al., 2018).
459 Outreach efforts to increase public awareness, biosecurity campaigns, and
460 promotion of rigorous cleaning protocols can be highly effective in reducing
461 anthropogenic dispersal of invasive macrophytes (Rothlisberger et al., 2010).

462

463 **5 | CONCLUSIONS**

464 Macrophytes are an essential component of healthy rivers and barriers have the
465 potential for impacting them in subtle, insidious ways (Pringle, 2001; 2003), and yet,
466 the effects of anthropogenic barriers on river macrophytes have received little
467 attention compared to fish and other riverine biota. For instance, while we found 333
468 articles in Web of Science dealing with barrier impacts on fish, and 30 on
469 macroinvertebrates, only 19 investigated effects on macrophytes (see Table S3 for
470 search strings). This is perhaps due to the assumption that macrophyte populations
471 are sedentary, and therefore relatively unaffected by barriers. However, there is
472 strong evidence that macrophytes can disperse over relatively long distances, both
473 drifting with the river flow and transported via animal movement, and this dispersal is
474 crucial for maintaining population connectivity and persistence.

475 The empirical evidence indicates large barriers such as dams have substantial
476 impacts on macrophyte dispersal (e.g. Jansson et al., 2000b; Nilsson et al., 2010),
477 acting as traps to drifting propagules, and thereby starving downstream reaches of

478 hydrochorous input (Andersson et al., 2000; Merritt & Wohl, 2006). However, the
479 abundance and diversity of the drifting propagule bank is not always affected
480 downstream of dams (Jansson et al., 2005), and the consequences of disrupted
481 hydrochory for community dynamics are unclear. The existing literature has
482 overwhelmingly focussed on large dams only, despite the fact that small weirs and
483 low-head structures are much more abundant (Januchowski-Hartley et al., 2013;
484 Garcia de Leaniz et al., 2018; Jones et al., 2019), and may also impact on
485 macrophytes (Rorslett & Johansen, 1996). The potential for small barriers to
486 intercept hydrochoric drift has not been adequately explored (Table 2).

487 Most studies assessing barrier effects on macrophyte dispersal have focussed on
488 their influence on hydrochory. However, upstream dispersal is equally critical to
489 maintaining macrophyte abundance and distribution, and the role of barriers in
490 disrupting potentially important mechanisms such as ichthyochory needs to be
491 examined (Table 2). This will likely require knowledge of the spatial scale of
492 zoochory, the precise dispersal mechanisms involved (e.g. stepping stone effects),
493 and the extent to which barriers effect the movements and distributions of the
494 specific taxa which act as dispersal vectors (Table 2).

495 There is contradictory evidence regarding damming effects on the macrophyte
496 standing crop in affected reaches, with some studies reporting a negative impact on
497 macrophyte populations (e.g. Casado et al., 1989; Nilsson et al., 1991), while others
498 indicate increases in abundance and diversity in regulated reaches (e.g. Ceschin et
499 al., 2016; Vukov et al., 2018). Hence, the effect of dams on macrophytes is complex
500 and appears to be very much context-dependent. The local factors influencing the
501 impact of barriers on macrophytes require further investigation (Table 2). Some
502 studies indicate small barriers such as weirs can cause shifts in macrophyte
503 distribution and abundance (Rorslett & Johansen, 1996) while others report non-
504 significant effects (Mueller et al., 2011), and these contrasting outcomes may depend
505 on the nature of hydrological alterations. However, the impact of small barriers on
506 macrophyte population dynamics requires further attention (Table 2). Also, flow
507 regulation appears to favour the establishment of invasive macrophytes, but the
508 mechanisms involved are not well understood, and need evaluation (Table 2).

509 Even common plant species can be susceptible to genetic impoverishment due to
510 habitat fragmentation (Honnay & Jacquemyn, 2007). River fragmentation is an
511 ongoing process (Grill et al., 2015; Couto & Olden, 2018), so increasing isolation of
512 populations could potentially leave many macrophyte species vulnerable to genetic
513 erosion. In terrestrial plants, low levels of gene flow (1 seed per generation) are
514 sufficient to prevent genetic differentiation between populations (Wright, 1931;
515 Honnay et al., 2005). However, there is a need to identify the frequency of dispersal
516 events over dams that would be required in order to avoid genetic divergence and
517 population decline in river macrophytes (Table 2). This would likely require
518 metabarcoding to examine rates of gene flow under different frequencies of
519 hydrochoric immigration, including multi-generational studies to assess rates of
520 genetic divergence under different dispersal scenarios. Such studies would need to
521 be undertaken both at catchment and sub-catchment scales. There is also little
522 knowledge of what modifications might be made to dam and reservoirs in order to
523 improve dispersal of macrophyte propagules (Table 2). Due to the different dispersal
524 characteristics of distinct taxa (e.g. buoyant and sinking propagules), a variety of
525 alterations would likely be required to provide for uninterrupted dispersal of diverse
526 macrophyte communities.

527

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535

536 **CONFLICTS OF INTEREST**

537 The authors declare no conflict of interest.

538

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1031 **TABLE 1** Summary of barrier impacts on macrophyte dispersal and population structure

Attribute	Effect	Mechanism	Reference
Dispersal	Reservoirs trap hydrochorous propagules	Slow flow in impounded reach	Nilsson & Jansson (1995) Andersson et al. (2000) Jansson et al. (2000b) Merritt & Wohl (2006) Nilsson et al. (2010)
	Reduced abundance and richness of hydrochorous seeds downstream	Slow flow in impounded reach Reduced frequency and intensity of floods	Andersson et al. (2000) Jansson et al. (2000a) Merritt & Wohl (2006) Jansson et al. (2000a) Jansson et al. (2000b) Jansson et al. (2005)
	No effect of dams on abundance or diversity of drifting propagules downstream	Local (within-impoundment) sources contributed similar abundance and diversity of hydrochorous propagules to upstream	
	Lower species richness downstream	Reduced hydrochory	Nilsson et al., (1991) Merritt et al. (2010)
Population structure	Higher species richness downstream	Increased nutrients Intermediate disturbance caused by moderate hydropeaking	Benitez-Mora & Camargo (2014) Bernez et al. (2002) Bernez et al. (2004)
	No effect of barriers on species richness	Local seed sources downstream from dams contributed similar diversity to upstream Species richness was highly variable between sites limiting ability to identify weir effects	Merrit & Wohl (2006) Mueller et al. (2011)
	Discontinuities in community composition	Reduced hydrochory	Merritt & Wohl (2006) Andersson et al. (2000) Jansson et al. (2000a)
	Increased biomass in impounded area	Creation of lentic habitat Reduced flow velocity Increased sedimentation	Ceschin et al. (2015) Tombolini et al. (2014) Vukov et al. (2018) Rorslett & Johansen (1996)

			Vukov et al. (2018)
	Increased biomass downstream	Stable flows	Goes (2002)
			Ibáñez et al. (2012)
		Increased nutrients	Abati et al. (2016)
			Tena et al. (2017)
	Decreased biomass downstream	Higher turbidity	Benitez-Mora & Camargo (2014)
		Stable flows	García de Jalon et al. (1994)
Invasiveness	Increased spread of invasive species	Modified flow regimes	Casado et al. (1989)
			Tellez et al. (2014)
			Van Geest et al. (2005)
	Reduced spread of invasive species	Increased anthropochory	Coetzee et al. (2009)
		Interrupted hydrochory	Thomason et al. (2018)
			Rood et al. (2010)

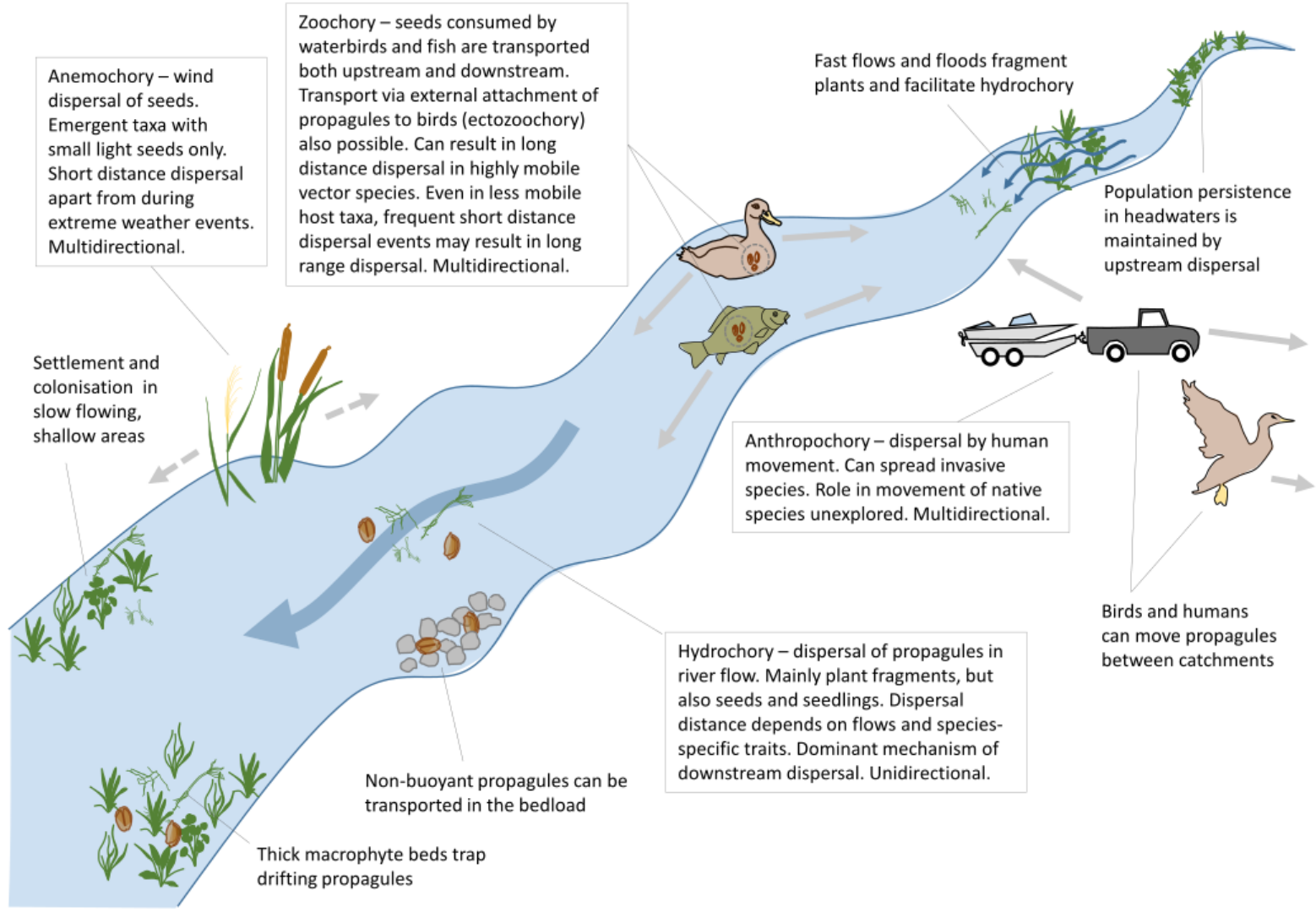
1032 Dams are defined as a large barriers (generally >5m) that create large impoundments (reservoirs) upstream. Weirs are defined as
 1033 smaller (<5m) barriers with overtopping flow.

1034

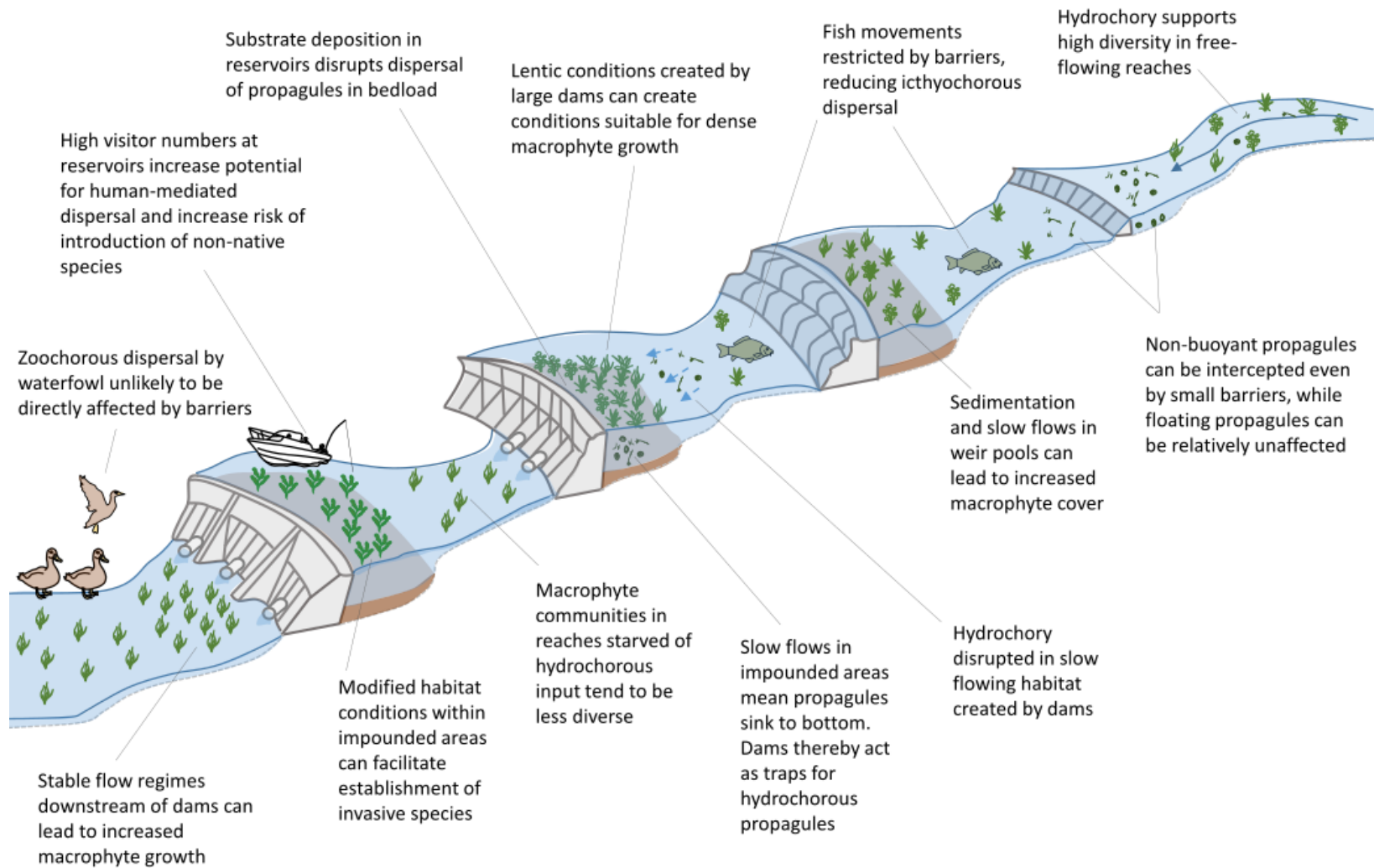
1035 **TABLE 2** Knowledge gaps identified during this review

Suggested future research directions	Relevant studies
The dominant role of hydrochory in downstream dispersal is well established, but further research is required to identify mechanisms supporting upstream dispersal, and their relative importance	Pollux et al. (2009); Markwith & Scanlon (2007); Pollux et al. (2005); Charalambidou & Santamaría (2002)
There is contradictory evidence regarding the consequences of interrupted hydrochory for the composition of macrophyte communities within rivers. Little is known about the site-specific factors influencing barrier effects on macrophyte population dynamics	Merritt & Wohl (2002, 2006); Jansson et al. (2005); Andersson et al. (2000); Nilsson et al. (2010)
Many animal species can disperse macrophytes, particularly birds and fish, but the prevalence of animal dispersal is uncertain	Pollux et al. (2005, 2006); Figuerola, & Green (2002); Charalambidou & Santamaría (2002)
Given the well documented effects that river barriers have on fish movements, their impact on ichthyochory requires evaluation	Pollux et al. (2005, 2006); Correa et al. (2007); Horn et al. (2011)
'Stepping-stone' dispersal is likely to be of great importance in supporting long distance dispersal by both zoochory and anemochory, and these processes require further investigation	Coughlan et al. (2015; 2017a,b); Saura et al. (2014)
There is good evidence that the presence of barriers can result in the establishment of invasive macrophytes, but the mechanisms facilitating colonisation are not well understood and need evaluation	Johnson et al. (2008); Rood et al. (2010); Catford et al. (2011)
Most studies examining barrier effects on macrophytes have focussed on large dams and reservoirs, but low-head barriers are much more numerous, and their cumulative impact could be considerable and requires assessment	Rorslett & Johansen (1996); Markwith & Leigh (2008); Mueller et al. (2011)
Mitigation solutions for reducing the impact of river barriers on macrophyte populations are unavailable and require investigation.	N/A

1036

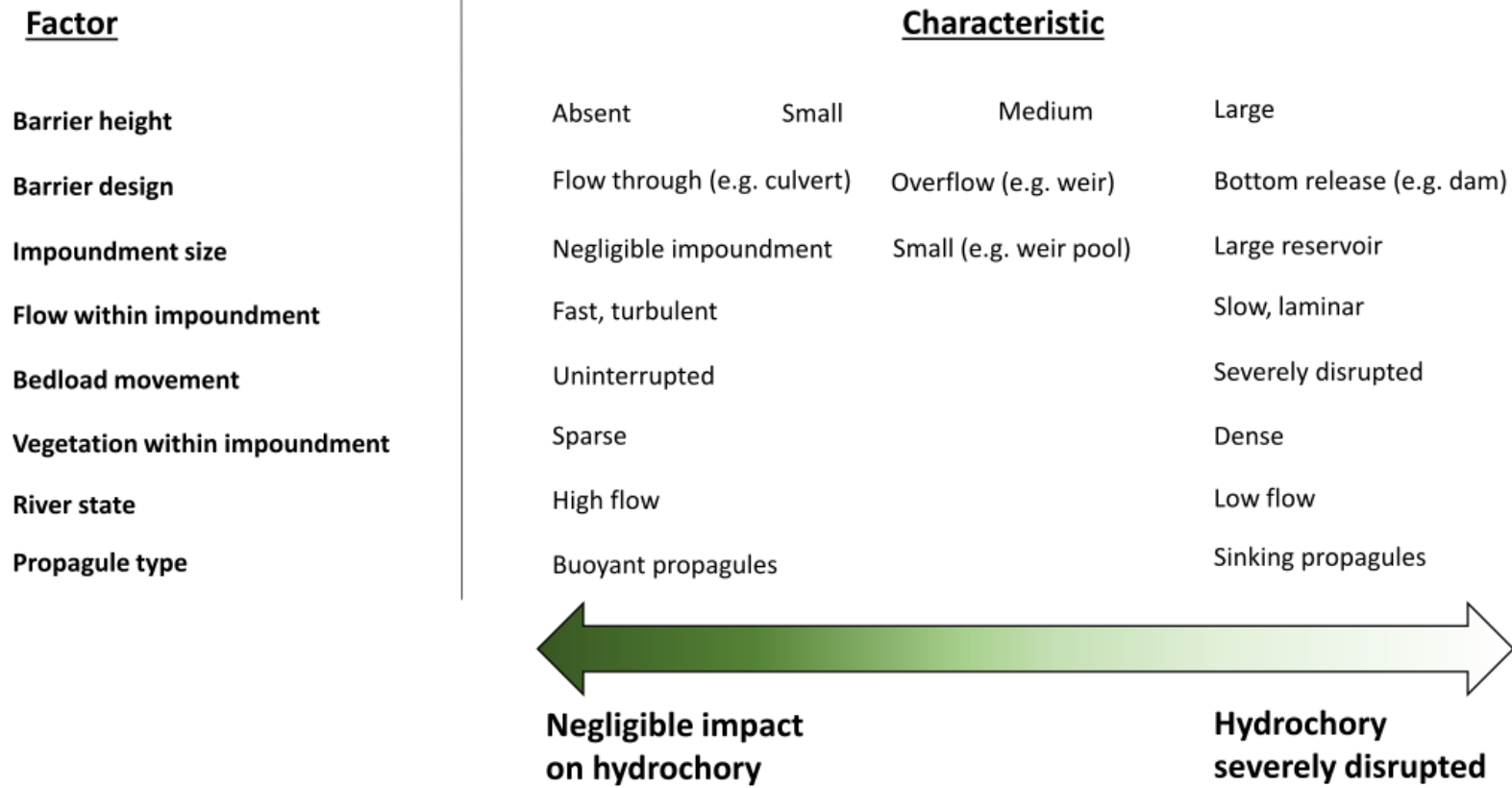


1037
 1038 **FIGURE 1** The main mechanisms driving dispersal and settlement of macrophytes in rivers
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1041 **FIGURE 2** Potential impacts of barriers on macrophyte dispersal and population structure



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1043 **FIGURE 3** The influence of various context-dependent factors on the impact of barriers on hydrochory

1044 **Table S1** Glossary of technical terms used in manuscript

Term	Definition	
Allofragmentation	Release of vegetative fragments due to physical disturbance	1045
Anemochory	Dispersal of propagules by wind	1046
Anthropochory	Dispersal of propagules by humans	1047
Autofragmentation	Release of vegetative fragments when a plant reaches peak biomass	
Ectozoochory	Transport of plant propagules attached to the external surface of animals	1048
Endozoochory	Transport of plant propagules (generally seeds) within the gut of animals	
Hydrochory	Dispersal of propagules by water	
Ichthyochory	Transport of seeds in the gut of fish	
Macrophyte	Aquatic vascular plants of the division tracheophyta that are large enough to be seen with the naked eye, i.e. excludes bryophytes, macroalgae, and microalgae.	
Propagule	Any plant material that functions in propagation, i.e. includes seeds, vegetative parts (e.g. rhizomes, turions, stolons, tubers, or plant fragments) and whole plants	
Zoochory	Dispersal of propagules by animals	

1049 **Table S2** Search strings utilised in selecting literature for the review and the number of results produced in Google Scholar and
 1050 Web of Science (WOS)

Subsection	Topic	Search string	Number of results	
			Google Scholar	WOS
Section 3.1	Hydrochory	(macrophytes OR aquatic plant OR propagule OR plant fragment OR seed) AND (dispersal OR drift OR hydrochory OR asymmetric OR bidirectional OR flow OR unidirectional OR gene flow) AND (river OR fluvial OR freshwater OR lotic OR stream)	174,000	1,497
Section 3.2	Zoochory	(macrophytes OR aquatic plant OR propagule OR plant fragment OR seed) AND (dispersal OR zoochory OR endozoochory OR ectozoochory OR epizoochory OR gene flow) AND (river OR fluvial OR freshwater OR lotic OR stream)	68,500	1,188
Section 3.3	Anemochory	(macrophytes OR aquatic plant OR propagule OR plant fragment OR seed) AND (wind dispersal OR anemochory OR gene flow) AND (river OR fluvial OR freshwater OR lotic OR stream)	42,000	127
Section 3.4	Anthropochory	(macrophytes OR aquatic plant OR propagule OR plant fragment OR seed) AND (human-mediated dispersal OR anthropochory OR gene flow) AND (river OR fluvial OR freshwater OR lotic OR stream)	3,260	16
Section 4.1	Barrier effects on hydrochory	(macrophytes OR aquatic plant) AND (barrier OR dam OR weir OR obstacle OR river regulation OR impoundment) AND (hydrochory) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (impact OR fragmentation OR connectivity OR effect)	820	5
Section 4.2	Barrier effects on zoochory	(macrophytes OR aquatic plant) AND (barrier OR dam OR weir OR obstacle OR river regulation OR impoundment) AND (zoochory) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (impact OR fragmentation OR connectivity OR effect)	345	0
Section 4.3	Barrier effects on invasive macrophytes	(macrophytes OR aquatic plant) AND (barrier OR dam OR weir OR obstacle OR river regulation OR impoundment) AND (invasive species OR alien OR non-native) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (hydrochory OR impact OR fragmentation OR connectivity OR effect)	60,600	28

1052 **Table S3** Search strings used to assess the number of articles examining the impact of river barriers on fish, invertebrates and
1053 macrophytes in Web of Science.

Topic	Search string	Results
Impact on fish	(fish) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (barrier OR dam OR regulation OR weir OR obstacle) AND (fragmentation OR connectivity) AND (impact)	333
Impact on invertebrates	(invertebrate) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (barrier OR dam OR regulation OR weir OR obstacle) AND (fragmentation OR connectivity) AND (impact)	30
Impact on macrophytes	(macrophyte OR aquatic plant) AND (river OR fluvial OR freshwater OR lotic OR stream) AND (barrier OR dam OR regulation OR weir OR obstacle) AND (fragmentation OR connectivity) AND (impact)	19

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