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REVIEW

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Impacts of artificial barriers on the connectivity and dispersal of vascular macrophytes in rivers: A critical review

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Abstract

1. Macrophytes play important functional roles in river ecosystems, providing habitat and food, as well as influencing flow, water chemistry, and sediment dynamics. They also represent an important component of river biodiversity.
2. Artificial river barriers have the potential to disrupt macrophyte dispersal, and compromise their distribution and persistence, but little information is available compared to barrier impacts on fish and macroinvertebrates. Here, we review the mechanisms supporting dispersal of river macrophytes in rivers and evaluate the nature of barrier impacts on macrophytes.
3. Hydrochory (dispersal of propagules by water) is the principal mechanism of downstream dispersal, while zoochory (dispersal of propagules by animals) is likely to be the most important vector of upstream dispersal and inter-catchment transport.
4. Most studies have focused on the impact of large structures such as dams, and the findings indicate the impact is highly context dependent. Slow-flowing habitats upstream of dams can act as traps to drifting propagules and thereby interrupt hydrochory. However, the consequences of interrupted hydrochory for downstream populations are unclear. River regulation can result in lower macrophyte diversity, although the lentic habitats associated with reservoirs can also favour an increase in the abundance and richness of macrophyte communities.
5. Instream barriers are unlikely to affect zoochory by birds directly, but barriers are well known to restrict fish movements, so there is considerable potential for barriers to disrupt zoochory by fish, although no empirical study has specifically examined this possibility.
6. There is a paucity of studies examining the impacts of low-head barriers on macrophyte dispersal. Given the influence of macrophytes on river processes, we call for further research into barrier impacts on macrophyte population dynamics in order to gain a better understanding of the consequences of river fragmentation for fluvial communities and ecosystem functioning.

KEYWORDS
aquatic plant, dams, hydrochory, river regulation, zoochory

1 | INTRODUCTION

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

Artificial barriers, such as dams and weirs, can have a pervasive influence on river systems (Ellis & Jones, 2013). However, while barrier impacts on fish populations have received considerable attention (Fullerton et al., 2010; Morita & Yamamoto, 2002; Perkin & Gido, 2012), impacts on aquatic macrophytes remain relatively unexplored. Connectivity is essential for the resilience of freshwater biota and the maintenance of river processes (Fagan, 2002; Pringle, 2001, 2003). Artificial barriers alter river hydrology and create discontinuities in substrate composition, temperature regime, and water chemistry (Mueller, Pander, & Geist, 2011) that could potentially disrupt macrophyte dispersal and population structure. Furthermore, river obstacles affect the distribution and movements of fish (Branco, Amaral, Ferreira, & Santos, 2017; Dehais, Eudeline, Berrebi, & Argillier, 2010; Diebel, Fedora, Cogswell, & O'Hanley, 2015), as well as birds indirectly by affecting habitat availability (Nilsson & Dynesius, 1994; Stevens, Buck, Brown, & Kline, 1997), and these groups can act as important dispersal vectors for riverine macrophytes (Charalambidou & Santamaría, 2002; Horn, 1997; Pollux et al., 2006). There are estimated to be over 16 million barriers in river systems worldwide (Lehner et al., 2011), and recent studies suggest that even this number is likely to be a severe underestimate because the abundance of low-head barriers is not well known (Garcia de Leaniz et al., 2018; Jones et al., 2019). Hence, there is considerable potential for barriers to have wide-reaching effects on macrophyte abundance and distribution.

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

Several studies have examined macrophyte dispersal and settlement dynamics in rivers (Anderson, Nuttle, Saldaña Rojas, Pendergast, & Flecker, 2011; Brochet, Guillemain, Fritz, Gauthier-Clerc, & Green, 2010; Johansson & Nilsson, 1993; Pollux, 2011; Riis, 2008), and the impact of large barriers has been investigated in a number of case studies (Ceschin, Tombolini, Abati, & Zuccarello, 2015; Merritt & Wohl, 2006; Vukov et al., 2018). However, barrier impacts on macrophyte dispersal have not been reviewed. Here, we review the current literature on macrophyte dispersal and settlement, and examine the impacts of anthropogenic barriers on population dynamics.

2 | METHODS

We searched for relevant literature using Google Scholar and Web of Science search engines, utilising different combinations of search terms depending on the subsection of the review (see Table S1 for glossary of terms and Table S2 for search terms and number of hits). No restrictions on year of publication or type of document were imposed. As not all search results were pertinent to the scope of the review, they were systematically reviewed by the lead author. For example, for the section on hydrochory, publications were deemed relevant only if they focussed on aquatic plants, related to fluvial systems, and dispersal by water was the focus of the paper. The use of search term strings sometimes returned very large numbers of hits (see Table S2) so results were ordered in terms of relevance (i.e. records containing highest number of keywords first), and the first 200 records were reviewed for relevance by the lead author. As predefined strings of search terms may not always be effective in returning the most relevant material, key publications highlighted during reading were also added to the reference list. By following the steps detailed above we are confident that we effectively covered the most important literature on the topic.

3 | MACROPHYTE DISPERSAL AND SETTLEMENT

Fluvial ecosystems are inherently dynamic environments (Ward & Stanford, 1995), exposed to regular flow disturbances that cause local extirpations of macrophyte communities (Franklin, Dunbar, & Whitehead, 2008; Riis & Biggs, 2003). Aquatic plants have various adaptations that facilitate dispersal, and allow them to recolonise vacant habitat patches (Catford & Jansson, 2014). Longitudinal dispersal in river networks is also important for maintaining genetic diversity of populations (Honnay, Jacquemyn, Nackaerts, Breyne, & Looy, 2010; Horreo et al., 2011; Pollux, Santamaria, & Ouborg, 2005). Dispersal of propagules (including whole plants, vegetative parts, and seeds; Thomaz, Mormul, & Michelan, 2015) can take place via one of four mechanisms (Figure 1): river flow (hydrochory),

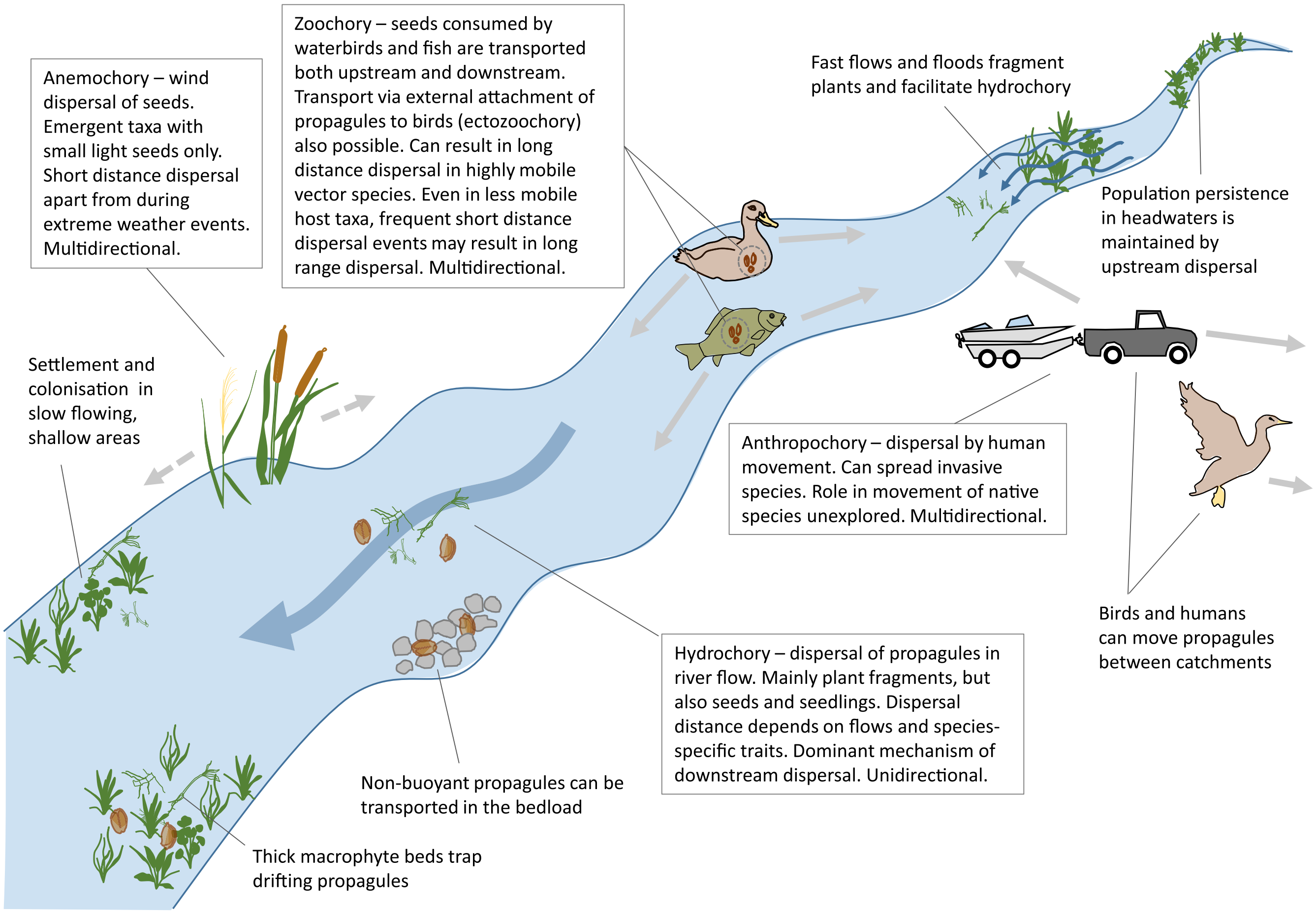


FIGURE 1 The main mechanisms driving dispersal and settlement of macrophytes in rivers

movement by animals (zoochory), by wind (anemochory), or human-mediated dispersal (anthropochory).

3.1 | Hydrochory

Hydrochory is considered to be a principal dispersal vector for macrophytes in free-flowing rivers (Dawson, 1988; Merritt & Wohl, 2002). In contrast to terrestrial plants, many macrophytes disperse largely through vegetative parts such as rhizomes, stolons, tubers, turions, stem fragments, and even entire plants (Boedeltje, Bakker, Brinke, Groenendael, & Soesbergen, 2004; Sand-Jensen, Andersen, & Andersen, 1999; Umetsu et al., 2012). Aquatic macrophytes often have functional adaptations to facilitate dispersal in flows (Catford & Jansson, 2014), including air-filled structures and hairs that trap air bubbles to increase buoyancy, and therefore expedite drift (Riis & Sand-Jensen, 2006).

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

In emergent taxa and species associated with river margins, seed dispersal can be more important, and experimental evidence suggests that hydrochorous seed dispersal is a major mechanism structuring plant communities along rivers (Nilsson, Ekblad, Gardfjell, & Carlberg, 1991; Nilsson, Gardfjell, & Grelsson, 1991; Pollux, Luteijn, Groenendael, & Ouborg, 2009). Many species have buoyant seeds to expedite dispersal (Nilsson, Brown, Jansson, & Merritt, 2010), with dispersal rates of up to 15 km/hr recorded in the floating seeds of *Polygonum* sp. (Staniforth & Cavers, 1976). The seeds of some other aquatic plants (e.g. *Juncus* spp.) are negatively buoyant and sink immediately after being liberated, but the young seedlings float and can travel large distances before taking root (Barrat-Segretain, 1996). Even dense seeds can be transported large distances in the bedload of rivers (Markwith & Leigh, 2008, 2012) or on floating debris rafts (Skoglund, 1989).

Dispersal and settlement dynamics are highly dependent on hydrology. Many species time the release of propagules to coincide with high flows to facilitate long-distance dispersal (Catford & Jansson, 2014). High water velocities increase drag on drifting plant fragments and, therefore, reduce the likelihood of settlement (Sand-Jensen, 2003). Fast flows also compress plant growth against the stream bed, reducing roughness, and thereby reduce retention rates of drifting propagules (Sand-Jensen, 2003). Hence, high water velocities favour long-distance dispersal, while slow flows, often associated with meanders, are required for propagule settlement. Dispersal distance tends to be positively associated with the width of the stream channel, drift often being higher in large rivers than in smaller streams (Riis & Sand-Jensen, 2006). Stem fragments tend to be more frequently deposited in shallower areas of river channels (Riis & Sand-Jensen, 2006), and in areas with high bed roughness, or where there is thick vegetative growth (Riis, 2008).

It is widely accepted that hydrochory is the dominant mode of downstream dispersal in river macrophytes, and results in effective dispersal across scales ranging from hundreds of metres to kilometres (Boedeltje et al., 2004; Nilsson, Ekblad, et al., 1991; Nilsson, Gardfjell, et al., 1991; Riis & Sand-Jensen, 2006). Hence, hydrochorous dispersal is critical to the maintenance of genetic diversity in macrophyte populations. A number of studies have found that the unidirectional flow of water results in asymmetrical gene flow (Gornall, Hollingsworth, & Preston, 1998; Pollux et al., 2009). For instance, Pollux et al. (2009) found a significant increase in the genetic diversity of *Sparganium emersum* populations with distance downstream, gene flow being approximately 3.5 times higher in a downstream direction than upstream. In the absence of a mechanism for upstream dispersal, the continual downstream drift of propagules via hydrochory would theoretically result in loss of genetic diversity, and eventually population collapse of macrophytes in headwaters (Honnay et al., 2010; Pollux et al., 2009). However, many studies have found no evidence of genetic impoverishment in upstream populations (Chen, Li, Yin, Cheng, & Li, 2009; Honnay et al., 2010; Markwith & Scanlon, 2007; Tero, Aspi, Siikamäki, Jäkäläniemi, & Tuomi, 2003). It is largely unknown why some populations show evidence of upstream genetic impoverishment while others do not (see Honnay et al., 2010; Markwith & Scanlon, 2007; Tero et al., 2003) but the fact that macrophyte populations can persist in headwaters is good evidence that vectors for upstream dispersal must exist.

3.2 | Zoochory

Zoochory (movement by animals) plays an important role in longitudinal movements of plant propagules along rivers, and has been demonstrated in fish (Pollux et al., 2006), birds (Figuerola & Green, 2002), mammals (Medwecka-Kornaś & Hawro, 1993), and reptiles (Padgett, Carboni, & Schepis, 2010). Transport of propagules can either take place inside the gut of animals (endozoochory), or attached to their bodies (ectozoochory).

A wide range of fish species are known to consume plant seeds (Correa, Winemiller, Lopez-Fernandez, & Galetti, 2007; García-Berthou, 2001; Nurminen, Horppila, Lappalainen, & Malinen, 2003), which often retain their ability to germinate after passing through fishes' guts (Pollux, 2011). Given that fish are often highly mobile within river catchments (Lucas & Batley, 1996; Makrakis et al., 2007), this offers a potentially important vector for macrophyte dispersal. Some seeds can survive up to 36 hr in the fish gut (Horn, 1997), during which time they could be dispersed over long distances. Evidence of endozoochorus dispersal of seeds by fish has been found in Europe (Pollux, 2007; Pollux et al., 2005), North America (Chick, Cosgriff, & Gittinger, 2003; VonBank, DeBoer, Casper, & Hagy, 2018), and South America (Anderson et al., 2011; Anderson, Rojas, & Flecker, 2009), suggesting it is a widespread mechanism of upstream dispersal for river macrophytes (see Horn et al., 2011). For example, seeds of *S. emersum* have been found to disperse up to 27 km in the gut of the common carp (Pollux, Ouborg, Groenendael, & Klaassen, 2007), and single dispersal events by fruit-eating fish in the Amazon have been observed to transport seeds over distances greater than 5 km (Anderson et al., 2011). Fishes differ in their diets (Gerking, 1994) and propensity to move (Lucas & Baras, 2001) so fish-mediated dispersal is likely to be species-specific.

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

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

3.3 | Anemochory

Dispersal by wind (anemochory) offers an additional mechanism for propagule dispersal. Some authors have suggested this mode of dispersal is rare for aquatic macrophytes as their seeds tend to be relatively heavy, and they generally lack adaptations to promote wind dispersal (Barrat-Segretain, 1996). For instance, 90% of sedge grass (*Carex* sp.) seeds were deposited within 2 m of the source plant, perhaps suggesting anemochory is of limited importance in long-distance dispersal (Soomers et al., 2013). However, Soons (2006) showed that 46% of wetland plant species have adaptations to promote anemochory and argued it was of great importance in the dispersal of aquatic plants. Many emergent taxa such as *Phragmites* spp. and *Typha* spp. produce large numbers of small light seeds that are easily dispersed by wind (Shipley, Keddy, Moore, & Lemky, 1989; Soons, 2006). Although most wind-blown seeds tend to settle close to the source plant (e.g. >90% of *Phragmites* sp. within 30 m, Soomers et al., 2013), it is the small proportion of seeds on the tail of the dispersal curve that are important in long-distance dispersal (Nathan et al., 2008), and these seeds can be transported over distances of hundreds of kilometres (Soomers et al., 2013). Wind dispersal is likely to increase substantially during extreme weather events when wind speeds are highest and sampling is problematic (Nathan et al., 2008). Even rare long-distance dispersal events are important in facilitating gene flow between populations (Trakhtenbrot, Nathan, Perry, & Richardson, 2005). Also, as with zoochory, multiple and frequent short-distance dispersal events should theoretically result in long-distance dispersal via a *stepping-stone* effect (Saura, Bodin, & Fortin, 2014), and generate sufficient gene flow to prevent genetic differentiation within metapopulations. At a minimum, anemochory is likely to be an important primary mechanism of dispersal in many plants, whereby dispersal into flowing water creates secondary dispersal opportunities via hydrochory.

3.4 | Anthropochory

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

4 | BARRIER IMPACTS ON MACROPHYTES

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

4.1 | Barrier effects on hydrochory

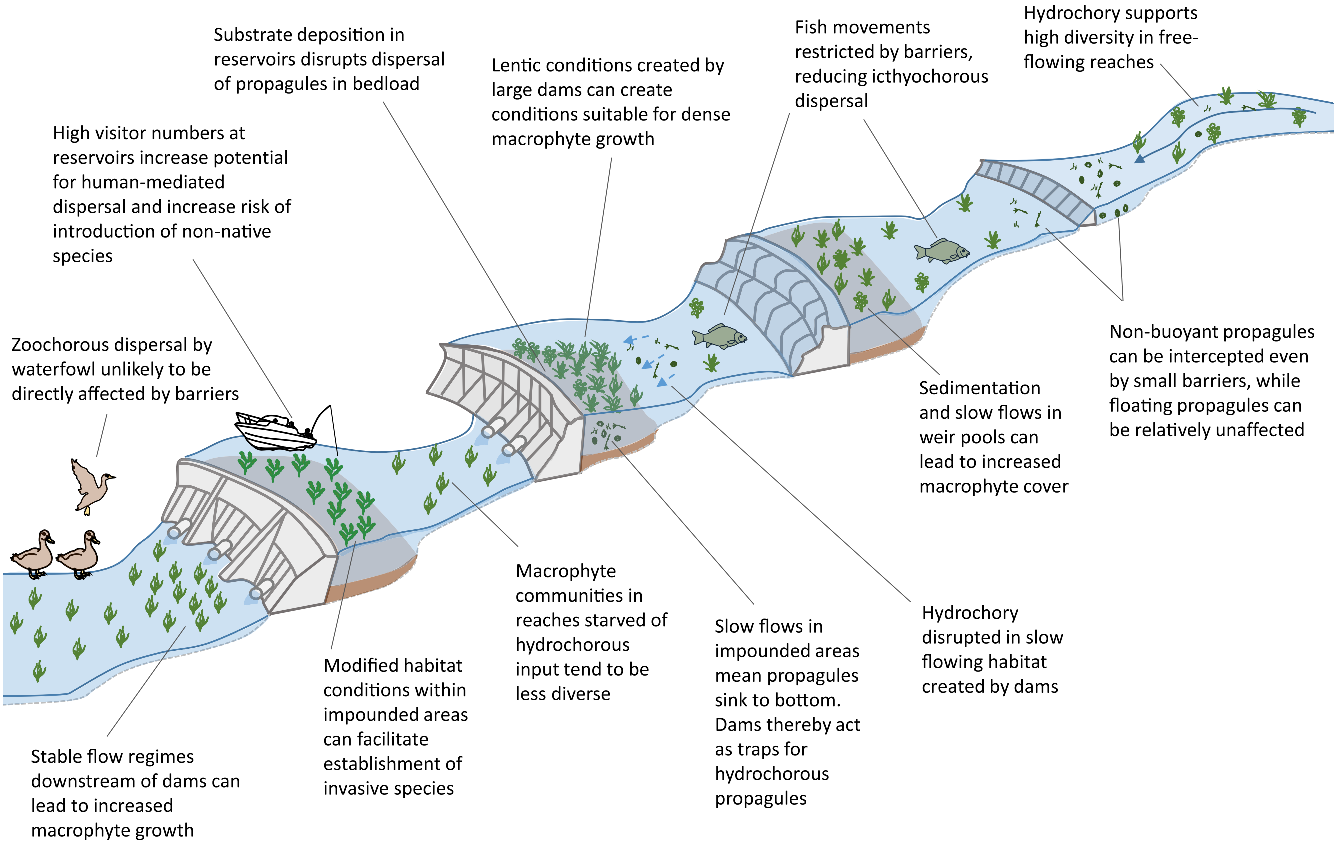
Water velocity is a key parameter determining how far propagules disperse, and hence can have important consequences for plant community composition along rivers (Merritt & Wohl, 2006). Slow flows in impounded reaches can act as barriers for macrophyte dispersal, trapping drifting propagules, and resulting in high mortality (Jansson, Nilsson, Dynesius, & Andersson, 2000; Jansson, Nilsson, & Renöfält, 2000; Nilsson et al., 2010; Nilsson & Jansson, 1995). Reservoirs can reduce the density of drifting propagules in downstream reaches by

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

Attribute	Effect	Mechanism	References
Dispersal	Reservoirs trap hydrochorous propagules	Slow flow in impounded reach	Nilsson and Jansson (1995) Andersson et al. (2000) Jansson, Nilsson, and Renöfält (2000) Merritt and Wohl (2006) Nilsson et al. (2010)
	Reduced abundance and richness of hydrochorous seeds downstream	Slow flow in impounded reach	Andersson et al. (2000) Jansson, Nilsson, Dynesius, et al. (2000) Merritt and Wohl (2006)
		Reduced frequency and intensity of floods	Jansson, Nilsson, Dynesius, et al. (2000) Jansson, Nilsson, and Renöfält (2000)
	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	Jansson et al. (2005)
Population structure	Lower species richness downstream	Reduced hydrochory	Nilsson, Ekblad, et al. (1991) and Nilsson, Gardfjell, et al. (1991) Merritt et al. (2010)
	Higher species richness downstream	Increased nutrients Intermediate disturbance caused by moderate hydropeaking	Benítez-Mora and 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	Merritt and Wohl (2006)
		Species richness was highly variable between sites limiting ability to identify weir effects	Mueller et al. (2011)
	Discontinuities in community composition	Reduced hydrochory	Merritt and Wohl (2006) Andersson et al. (2000) Jansson, Nilsson, Dynesius, et al. (2000)
	Increased biomass in impounded area	Creation of lentic habitat	Ceschin et al. (2015) Tombolini et al. (2014)
		Reduced flow velocity	Vukov et al. (2018)
		Increased sedimentation	Rorslett and Johansen (1996) Vukov et al. (2018)
	Increased biomass downstream	Stable flows	Goes (2002) Ibáñez et al. (2012) Abati et al. (2016)
		Increased nutrients	Tena et al. (2017) Benítez-Mora and Camargo (2014)
	Decreased biomass downstream	Higher turbidity	García de Jalon et al. (1994)
		Stable flows	Casado et al. (1989)
Invasiveness	Increased spread of invasive species	Modified flow regimes	Greet, Cousens, & Webb, 2013 Van Geest et al. (2005)
		Increased anthropochory	Coetzee et al. (2009)
	Reduced spread of invasive species	Interrupted hydrochory	Thomason et al. (2018) Rood et al. (2010)

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

as much as 95%, and this effect can extend for several kilometres downstream of large dams (Merritt & Wohl, 2006). Compared to free-flowing rivers, rivers fragmented by large dams tend to show lower richness of drifting propagules, and dispersal rates are also often reduced (Andersson, Nilsson, & Johansson, 2000; Jansson, Nilsson, Dynesius, et al., 2000; Merritt & Wohl, 2006), although this is not always the case. For example, Jansson, Zinko, Merritt, and Nilsson (2005) did not find any evidence to suggest that dams decreased the abundance or diversity of drifting propagules in a comparison of fragmented and free-flowing rivers. However, in this instance, the drifting propagule bank in the fragmented river was derived from local (within-impoundment) sources only (Jansson et al., 2005), suggesting that long-distance dispersal via hydrochory was compromised.



Substrate deposition in reservoirs disrupts dispersal of propagules in bedload

Lentic conditions created by large dams can create conditions suitable for dense macrophyte growth

Fish movements restricted by barriers, reducing icthyochorous dispersal

Hydrochory supports high diversity in free-flowing reaches

High visitor numbers at reservoirs increase potential for human-mediated dispersal and increase risk of introduction of non-native species

Zoochorous dispersal by waterfowl unlikely to be directly affected by barriers

Non-buoyant propagules can be intercepted even by small barriers, while floating propagules can be relatively unaffected

Sedimentation and slow flows in weir pools can lead to increased macrophyte cover

Macrophyte communities in reaches starved of hydrochorous input tend to be less diverse

Slow flows in impounded areas mean propagules sink to bottom. Dams thereby act as traps for hydrochorous propagules

Hydrochory disrupted in slow flowing habitat created by dams

Modified habitat conditions within impounded areas can facilitate establishment of invasive species

Stable flow regimes downstream of dams can lead to increased macrophyte growth

FIGURE 2 Potential impacts of barriers on macrophyte dispersal and population structure

Floods are important events for hydrochory in free-flowing rivers (Cellot, Mouillot, & Henry, 1998; Franklin et al., 2008; Gurnell, Thompson, Goodson, & Moggridge, 2008), but their intensity and frequency is reduced in many dammed rivers (Magilligan & Nislow, 2005), and this can limit hydrochorous dispersal of propagules (Jansson, Nilsson, Dynesius, et al., 2000). There is evidence that species with different dispersal strategies are affected to different degrees by flow regulation (Jansson, Nilsson, Dynesius, et al., 2000; Jansson, Nilsson, & Renöfält, 2000). For example, the reduced frequency of floods in regulated reaches can prevent transport of non-buoyant propagules, whereas those with floating propagules can show higher probability of dispersal (Jansson, Nilsson, Dynesius, et al., 2000; Jansson, Nilsson, & Renöfält, 2000).

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

The impact of low-head barriers on macrophytes has been largely unexplored compared to the effects of large dams. Although their impact is likely to be less severe than large dams, smaller barriers such as weirs modify river flows, often creating slow velocity areas (weir pools) immediately upstream. These weir pools tend to stabilise the substrate and increase settlement of fine sediments (Merritt & Wohl, 2006). In trapping river substrates, small barriers probably prevent or at least significantly reduce movement of non-buoyant seeds in the bedload (Markwith & Leigh, 2008, 2012). Stable substrates create opportunities for the establishment of macrophytes that would otherwise have been unable to root (Riis & Biggs, 2003) and can further exacerbate changes by creating a positive feedback loop, whereby the presence of standing macrophytes increases sedimentation rates (Gurnell et al., 2006; Jones, Collins, Naden, & Sear, 2012; Sand-Jensen et al., 1989) and thus increases propagule settlement (Gurnell et al., 2008; Riis, 2008). For example, in Norway, weirs are commonly built as part of small-scale hydropower schemes, but weir pools are often associated with increased siltation and subsequent growth of macrophytes, which are regarded as a nuisance (Rorslett & Johansen, 1996). However, other studies have found little evidence that weirs affected macrophyte diversity or abundance (Mueller et al., 2011). The variation in the response of macrophytes is likely to depend on the nature of hydrological alteration: i.e. where weirs stabilise flows and substrate macrophyte cover tends to increase, whereas barriers with negligible effects on hydrology and substrate movement tend to have little effect on macrophytes.

The potential link between disrupted hydrochory and community structure downstream is unclear. Although dams can significantly

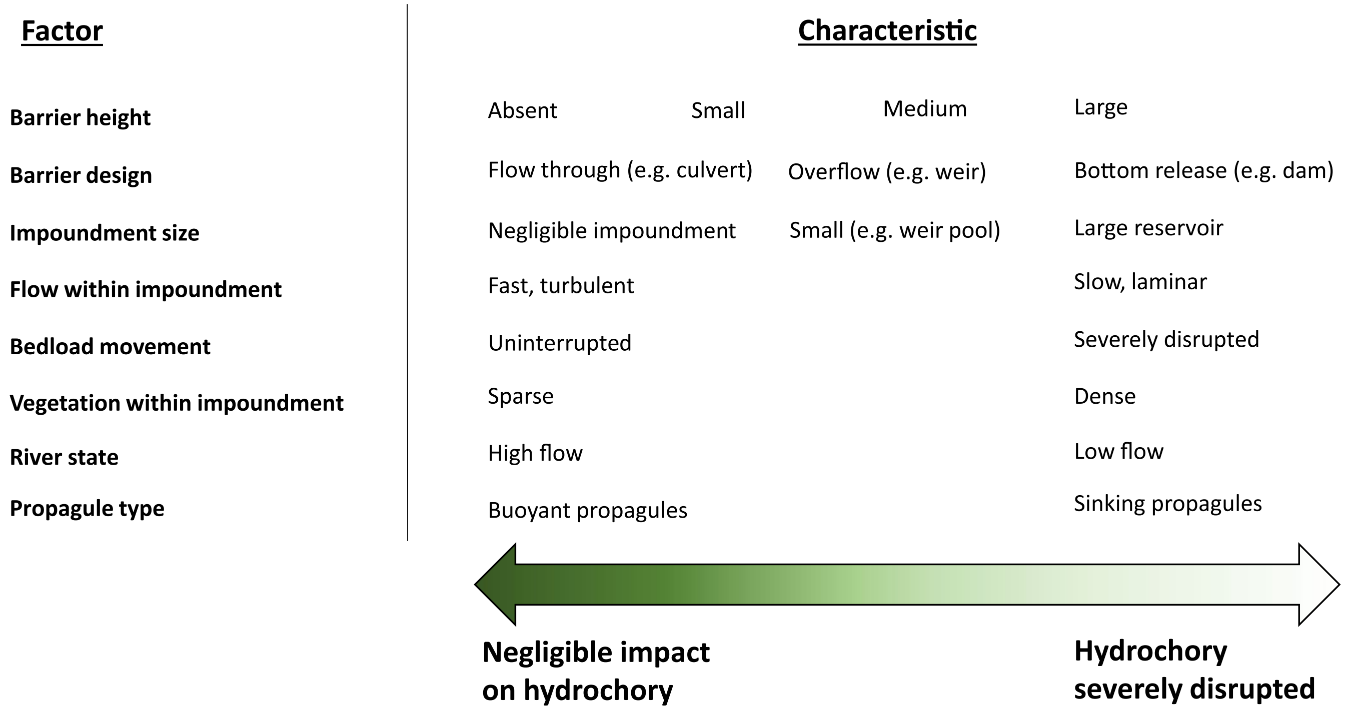


FIGURE 3 The influence of various context-dependent factors on the impact of barriers on hydrochory

reduce hydrochorous dispersal, the abundance and diversity of plant populations downstream of dams may in some cases remain the same as upstream (Merritt & Wohl, 2006). Discontinuities in community composition have been associated with dams, with assemblages exhibiting a shift from a composition similar to the drifting hydrochorous propagule bank upstream, to communities derived from local seed-bearing plants downstream (Andersson et al., 2000; Jansson, Nilsson, Dynesius, et al., 2000). Decreases in macrophyte diversity and abundance have been reported downstream of dams (Casado, García de Jalon, Delolmo, Barcelo, & Menes, 1989; García de Jalon, Sanchez, & Camargo, 1994), while in other cases an increase in macrophyte abundance has been reported (Abati, Minciardi, Ciadamidaro, Fattorini, & Ceschin, 2016; Goes, 2002; Tena, Vericat, Gonzalo, & Batalla, 2017), although in these studies, changes in macrophyte population structure were not directly linked to disruptions of hydrochory, and probably related to differences in hydrological regime. However, other studies have found evidence that the richness of riverine plant communities was linked to hydrochorous seed input, with free-flowing rivers showing higher richness (Merritt, Nilsson, & Jansson, 2010; Nilsson, Ekblad, et al., 1991; Nilsson, Gardfjell, et al., 1991).

Many of the observed changes in macrophyte community have been associated with the hydrological effects of dams, rather than their role in disrupting hydrochory. Stable flow conditions often found downstream of dams can increase aquatic plant cover in affected reaches (Abati et al., 2016; Goes, 2002; Ibáñez, Caiola, Rovira, & Real, 2012). Moderate disturbance caused by hydropeaking (frequent, short duration, artificial flow events) can also lead to increased macrophyte richness and abundance, compared to unregulated rivers (Bernez, Daniel, Haury, & Ferreira, 2004; Bernez, Haury, & Ferreira, 2002). Where hydrological disturbance is more severe, macrophyte communities tend to show low diversity and be less abundant (Casado et al., 1989; García de Jalon et al., 1994; Merritt et al., 2010).

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

4.2 | Barrier effects on zoochory

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

The presence of river barriers is unlikely to affect the movements of birds directly, but changes in the distribution of riverine habitats brought about by flow regulation can alter the composition and distribution of waterfowl communities (Nilsson & Dynesius, 1994). For example, the accumulation of fish at barriers can also lead to local increases in piscivorous birds (Baumgartner, Stuart, & Zampatti, 2008; Stevens et al., 1997) and still waters within impoundments provide habitat for many waterfowl (Nilsson & Dynesius, 1994). Because birds can act as important agents of propagule dispersal (Charalambidou & Santamaría, 2002; Coughlan et al., 2015; Figuerola & Green, 2002), changes in their distribution have the potential to influence aquatic plant dispersal, although this has not yet been examined. Further research is required to elucidate the impacts of barriers for zoochorous dispersal of seeds by animals.

4.3 | Barrier effects on invasive macrophytes

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

Invasive species tend to be most successful where naturally occurring communities are stressed by anthropogenic disturbance (Byers et al., 2002; Johnson, Olden, & Vander Zanden, 2008; Strayer, 2010), including damming (Greet et al., 2013; Johnson et al., 2008). Hydrological modifications associated with river barriers can result in changes in community composition, as native macrophytes may be unable to cope with modified conditions (Catford & Jansson, 2014), creating opportunities for invasive macrophytes to establish. For example, damming of the river Guadiana in Spain has led to increased spread of the invasive water hyacinth (*Eichhornia crassipes*; Téllez et al., 2008). A recent study has also shown that thick mats of water hyacinth can themselves trap and disrupt downstream transport of hydrochorous seeds (Vonbank, Casper, Pendleton, & Hagy, 2018). Artificial reservoirs in North America tend to support more invasive species than natural lakes, probably because native species have less of a stronghold in artificial systems (Johnson et al., 2008). Flow regulation in the River Rhine has favoured the spread of invasive *Elodea nuttallii*, which has become dominant in many altered reaches (Van Geest, Coops, Roijackers, Buijse, & Scheffer, 2005) and modified flow regimes downstream of dams have also favoured the invasion of non-native macrophytes in riverine wetlands within the Murray River, Australia (Catford, Downes, Gippel, & Vesk, 2011). However, a reduction in flood disturbance due to river regulation in a Californian river system resulted in reduced propagule dispersal in the invasive aquatic macrophyte *Ludwigia hexapetala* (Thomason, McCort, Netherland, & Grewell, 2018). These contrasting findings indicate that the outcomes of hydrological modification depend on the flow regimes imposed and the dispersal traits of the invasive plants present.

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

5 | CONCLUSIONS

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

The empirical evidence indicates large barriers such as dams have substantial impacts on macrophyte dispersal (Jansson, Nilsson, & Renöfält, 2000; Nilsson et al., 2010), acting as traps to drifting propagules, and thereby starving downstream reaches of hydrochorous input (Andersson et al., 2000; Merritt & Wohl, 2006). However, the abundance and diversity of the drifting propagule bank are not always affected downstream of dams (Jansson et al., 2005), and the consequences of disrupted hydrochory for community dynamics are unclear. The existing literature has overwhelmingly focussed on large dams only, despite the fact that small weirs and low-head

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	Charalambidou and Santamaría (2002), Markwith and Scanlon (2007), Pollux et al. (2009), and Pollux et al. (2005),
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	Andersson et al. (2000), Jansson et al. (2005), Merritt and Wohl (2002, 2006), and Nilsson et al. (2010)
Many animal species can disperse macrophytes, particularly birds and fish, but the prevalence of animal dispersal is uncertain	Charalambidou and Santamaría (2002), Figuerola and Green (2002), Pollux et al. (2006), and Pollux et al. (2005)
Given the well documented effects that river barriers have on fish movements, their impact on icthyochory requires evaluation	Correa et al. (2007), Horn et al. (2011), Pollux et al. (2006), and Pollux et al. (2005)
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, Kelly, Davenport, et al. (2017), Coughlan et al. (2015), Coughlan, Kelly, and Jansen (2017), and 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	Catford et al. (2011), Johnson et al. (2008), and Rood et al. (2010)
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	Mueller et al. (2011), Markwith and Leigh (2008), and Rorslett and Johansen (1996)
Mitigation solutions for reducing the impact of river barriers on macrophyte populations are unavailable and require investigation	N/A

structures are much more abundant (Garcia de Leaniz et al., 2018; Januchowski-Hartley et al., 2013; Jones et al., 2019), and may also impact on macrophytes (Rorslett & Johansen, 1996). The potential for small barriers to intercept hydrochloric drift has not been adequately explored (Table 2).

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

There is contradictory evidence regarding damming effects on the macrophyte standing crop in affected reaches, with some studies reporting a negative impact on macrophyte populations (Casado et al., 1989; Nilsson, Ekblad, et al., 1991; Nilsson, Gardfjell, et al., 1991), while others indicate increases in abundance and diversity in regulated reaches (Ceschin et al., 2015; Vukov et al., 2018). Hence, the effect of dams on macrophytes is complex and appears to be very much context-dependent. The local factors influencing the impact of barriers on macrophytes require further investigation (Table 2). Some studies indicate small barriers such as weirs can cause shifts in macrophyte distribution and abundance (Rorslett & Johansen, 1996) while others report non-significant effects (Mueller et al., 2011), and these contrasting outcomes may depend on the nature of hydrological alterations. However, the impact of small barriers on macrophyte population dynamics requires further attention (Table 2). Also, flow regulation appears to favour the establishment of invasive macrophytes, but the mechanisms involved are not well understood, and need evaluation (Table 2).

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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