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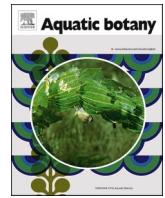
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Dam-induced disruption of hydrochory and macrophyte recovery in the Brisbane River post-flood

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ABSTRACT

Extreme flood events can scour riverbeds and significantly reduce submerged aquatic macrophyte extent in river systems. In regulated systems, large dams disrupt longitudinal connectivity and may constrain post-flood recovery by limiting hydrochorous propagule transport. In 2011, the Brisbane River in south-eastern Queensland Australia experienced a major flood that severely reduced macrophyte abundance across the whole river system. Macrophyte recovery has been slow downstream of a major dam, Wivenhoe Dam, which has not yet recovered to historical abundances. To understand how the dam affects macrophyte recovery downstream following flood events, we quantified hydrochory and the sediment seed banks upstream and downstream of the dam. Propagule drift was measured monthly over 12 months using drift nets at two upstream and two downstream sites, while sediment seed banks were sampled seasonally at three sites both upstream and downstream. The most upstream site yielded an average of 1.15 ± 1 propagules per two-hour sampling period, declining to 0.58 ± 0.23 at the second most upstream site, with no propagules captured downstream of the dam. Seed bank germination found only two species, native macrophytes *Vallisneria nana* and *Myriophyllum verrucosum*, emerging from all upstream samples and no germination from downstream sediment samples. These results indicate that Wivenhoe Dam disrupts hydrochorous dispersal and contributes to limited propagule availability downstream, delaying macrophyte recovery after flood disturbance. Overall, we suggest active restoration strategies are necessary to mitigate the impacts of floods and dams to support macrophyte regeneration post-flood events.

1. Introduction

Macrophytes are a fundamental component of river ecosystems, contributing to habitat complexity, acting as ecosystem engineers by stabilising sediments and moderating flow (Thomaz, 2021). They also provide critical food, refuge, and spawning sites for a wide range of aquatic fauna, supporting increased faunal abundance and diversity (Thomaz, 2021). The distribution and persistence of macrophyte beds are critical to the function of freshwater communities and are strongly influenced by processes of dispersal, colonisation and connectivity.

1.1. Hydrochory

A range of factors influence natural dispersal, settlement, recruitment, and persistence of aquatic macrophytes in rivers (Riis and Sand-Jensen, 2006; Jones et al., 2020). These include hydrological

conditions, substrate availability, propagule traits (e.g. buoyancy, size and morphology) and disturbance regimes, all of which determine how macrophyte populations establish and spread. The most important dispersal mechanism for submerged macrophytes is hydrochory, the process of dispersal by water, that aids in recolonisation of areas affected by disturbances (Boedeltje et al., 2003; Jones et al., 2020; Nilsson et al., 2010). Hydrochory can be associated with hydrological events such as floods (Riis and Biggs, 2003), and is mediated by wildlife foraging (Thomaz, 2025), as well as by anthropogenic disturbances (Baattrup-Pedersen and Riis, 2004). Long-distance hydrochory facilitates connectivity among aquatic macrophyte populations, with downstream flow passively transporting propagules to suitable habitats for establishment (Jones et al., 2020; Nilsson et al., 2010). This dispersal can take place via seeds through sexual reproduction, fragments, rhizomes, or whole plants with distance dependent on biotic (e.g. plant morphology, buoyancy) and abiotic factors (stream morphology) (Riis

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and Biggs, 2003). While seed dispersal is relatively well understood, vegetative propagule dispersal has received less attention, despite its important role in recolonising bare habitats following unpredictable disturbances, such as floods (Barrat-Segretain et al., 1998). In river systems, hydrochory represents the transport phase of a broader multi-stage dispersal process involving propagule release, transport, deposition, and establishment (Rubalcava-Castillo et al., 2025). The success of hydrochory therefore depends not only on transport dynamics, but also on the traits and persistence of the propagules themselves.

Vegetative propagule dispersal plays a key role in recolonizing disturbed habitats, yet macrophyte immigration and growth can be relatively slow and dependent on stable hydrological conditions (Franklin et al., 2008; Riis and Biggs, 2003). At the site scale, natural regeneration of macrophytes following a disturbance can be impeded if all vegetative plant material is removed and seed banks are depleted, as repeated disturbances may mobilise seeds and limit their resupply, potentially leading to poor recovery (Henry et al., 1996; Paice et al., 2017). The loss of aquatic macrophytes can therefore become a self-reinforcing process, with degraded reaches becoming increasingly resistant to natural re-establishment (Riis et al., 2009). However, despite their potential importance, the dynamics of vegetative fragment transport and establishment remains underexplored.

1.2. Impacts of fragmentation on hydrochory

Physical barriers, such as weirs and dams, are known to have a large impact on river connectivity (Jones et al., 2020). Fragmentation of rivers due to in-stream barriers can alter natural flow regimes, sediment transport, and distribution and movement of biota (Brown and Chenoweth, 2008; Jones et al., 2020). Currently, there are an abundance of studies examining the effects of dams on fish movement and populations, however there is a paucity of research investigating the impacts of dams on aquatic macrophyte dispersal (Jones et al., 2020). By disrupting hydrochory, dams and other in-stream barriers can reduce macrophyte abundance, distribution and persistence (Brown and Chenoweth, 2008; Thomaz, 2021). A reduction in propagule dispersal limits recolonisation opportunities following disturbances, potentially limiting habitat availability for aquatic fauna. Barriers may further act as propagule traps, where slow flows and long hydraulic residence times increase propagule sinking and mortality (Jones et al., 2020). Downstream of large barriers, this disruption of hydrochory can lead to severe reductions in macrophyte abundance, richness and diversity (Jones et al., 2020), thereby decreasing the resilience of river ecosystems.

1.3. Impacts of flooding

Extreme flood events, combined with river fragmentation and flow alteration caused by dams and weirs, are major drivers of reductions in macrophyte populations (Jones et al., 2020). Severe flooding can scour the riverbed, erode sediment and uproot macrophytes reducing their abundance and hindering recovery through the loss of seed banks (Lake et al., 2006; Riis and Sand-Jensen, 2006). The intensity and frequency of flooding may determine the success of post-flood recolonisation of riverbeds by macrophytes through hydrochory (Riis and Biggs, 2003). After a disturbance, natural recovery typically occurs through a combination of seed bank germination and vegetative propagules originating from refuges where water velocities were insufficient to break and uproot plant material (Barrat-Segretain et al., 1998; Henry et al., 1996), with seed banks playing an important role in macrophyte recovery downstream of dams (Jones et al., 2020). However, the magnitude and frequency of flooding events can severely impact the sediment seedbank by heavily scouring the riverbed or by deposition of large amounts of sediment resulting in the seedbanks being unviable (Bornette and Puijalon, 2009; Combroux et al., 2001). When large dams are present, flood events can exacerbate downstream impacts by restricting hydrochory

and inhibiting the natural re-establishment of aquatic macrophyte populations.

In the regulated mid-Brisbane River, Queensland, Australia, submerged macrophytes provide critical ecosystem services and essential habitat that supports aquatic fauna, including a nationally listed threatened species, the Australian lungfish (*Neoceratodus forsteri*). The Australian lungfish is of considerable cultural and evolutionary significance, and is highly reliant on submerged macrophytes for food, refuge, and spawning (Brooks and Kind, 2002). A common macrophyte species used by Australian lungfish for spawning and juvenile refuge is *Vallisneria nana* R.Br (Brooks and Kind, 2002), a submerged native perennial with a stoloniferous base and ribbon-like leaves that often forms dense clonal beds (Rea et al., 2002). Despite its importance as lungfish spawning and refuge habitat, there is limited research on the ecology of *V. nana* (Duivenvoorden, 2008).

Following the major 2011 flood in the Brisbane River, macrophyte populations downstream of Wivenhoe Dam have shown slow recovery and have not returned to the densities reported in historical surveys conducted two decades earlier by Mackay and Thompson (2000) (Kennard et al., 2021). This was one of the largest floods in modern history of the Brisbane River (Bohensky and Leitch, 2014), resulting in the significant loss of macrophyte habitat across the majority of the catchment. Flooding, compounded by the negative effects of large barriers on hydrochory, can cause major ecological impacts, including the loss of critical habitat and reduced availability of macrophytes for dependent aquatic fauna. In regulated systems, disruption of hydrochory due to large barriers can prolong these effects by preventing effective recolonisation following large floods, as experienced in 2011, resulting in persistent losses of macrophyte habitat and reduced recovery (Jones et al., 2020). Developing effective river management strategies to retain or restore macrophyte populations is essential to mitigate the negative effects of heavily impounded systems and preserve aquatic fauna.

This study aimed to determine the impacts of Wivenhoe Dam on inhibiting post-flood recovery of submerged macrophytes downstream by disrupting hydrochorous dispersal and propagule availability. To address this aim, three complimentary objectives were examined:

(1) assess the impact of Wivenhoe Dam on submerged macrophyte hydrochory; (2) assess the viability of the seed bank upstream and downstream of the dam; and (3) investigate temporal-spatial changes in local dispersal in relation to water depth and velocity. To achieve this, we sampled the sediment seed bank and deployed drift nets to collect propagules upstream and downstream of the dam, hypothesising that limited propagule transport past Wivenhoe Dam and depauperate seed banks contribute to the persistently reduced macrophyte cover and abundance downstream. By determining the impact of the dam on macrophyte hydrochory, our findings can help inform river management practices to enhance or protect macrophyte communities, and thus species dependent on this critical habitat.

2. Methods

2.1. Study area

This research was conducted in the upper and mid-Brisbane River catchment in south-eastern Queensland, Australia (Fig. 1). The region experiences a subtropical climate, with mean maximum monthly temperatures ranging between 21 and 29 °C and total annual rainfall between 900 and 1800 mm, the majority of which falls during the warm summer season (October to February) (Croke et al., 2014). River discharge in the catchment is naturally highly variable both within and between years (Kennard et al., 2007). Although peak flows typically occur during the summer wet season (January–March), variability persists throughout the year, with a minor secondary peak often occurring between April and June (Kennard et al., 2007).

Completed in 1984, Wivenhoe Dam has a full storage capacity of

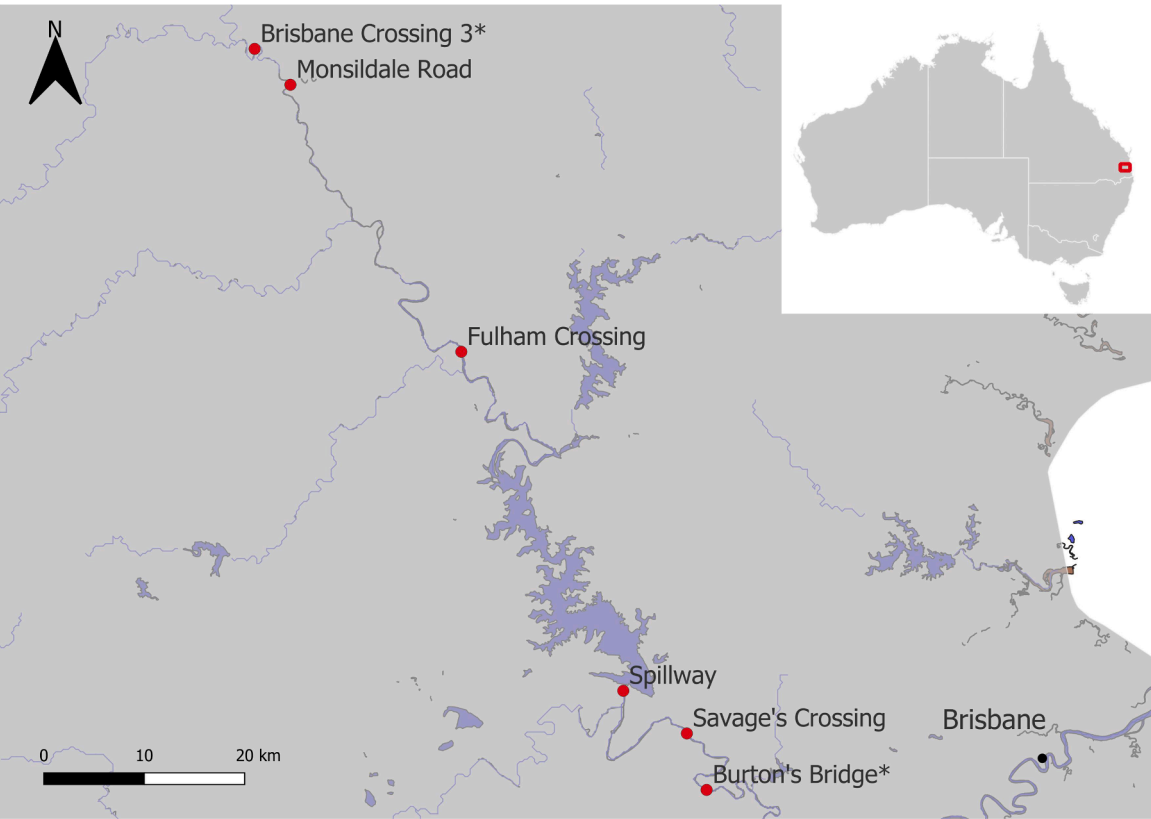


Fig. 1. Location of study sites (red dots) within the upper and mid-Brisbane River. Sites marked with an asterisk (*) indicate additional sampling locations for only seed bank sampling. The red outline indicates the exact spatial extent of the main map panel.

approximately 3.13 million megalitres and serves both as Brisbane’s primary water supply and as a major flood mitigation structure. Wivenhoe Dam dampens flood peaks, reduces seasonal flow variability and stabilizes baseflows. During the 2011 flood, extreme inflows exceeded available flood storage capacity, resulting in spillway releases as part of flood management. Consequently, high-magnitude discharge was experienced downstream of the dam, while upstream reaches experienced catchment wide flooding independent of the dam.

This study area includes the upper and mid-Brisbane River reaches. Two upstream and two downstream sites located at varying distances from Wivenhoe Dam were used to assess propagule transport dynamics (Fig. 1; Table 1). No instream barriers exist, between the upstream sites and Wivenhoe Dam where flow connectivity is continuous, and no barriers occur downstream from Wivenhoe Dam within the study reach that will affect hydrochorous transport. Few macrophyte beds were present within the downstream section of the study reach, and none were observed immediately upstream of the dam wall (Table 1). A single 10 m² bed located 1.9 km upstream of Savages Crossing corresponded to the same bed recorded for Burton’s Bridge and was used to assess potential propagule dispersal (Table 1). For the seed bank experiment, an

additional upstream and downstream site were sampled, resulting in three sites upstream and three downstream of Wivenhoe Dam seed bank (Fig. 1). The upstream sites experienced predominantly natural base-flow conditions throughout the study period from November 2022 to December 2023 (Supplementary Figure 1A), while downstream sites are subjected to regulated discharge, typically reflecting stable low flows below 10 m³ s⁻¹ (Supplementary Figure 1B). However, downstream flows peaked at 38.2 m³ s⁻¹ at the beginning of the study period, reflecting the range of hydrological variability under current water management regimes (Supplementary Figure 1B).

Sites to assess propagule transport dynamics were chosen based on proximity of the dam and spatially separated enough to reflect local processes. A flood event occurred in February 2022 prior to sampling, however macrophyte recovery downstream of the dam was limited prior to this event. Upstream, Monsildale Road was chosen as a site where an extensive *Vallisneria nana* macrophyte bed persisted after the major 2011 flood and through the 2022 flood, to investigate local propagule dispersal, while Fulham Crossing was the closest accessible sampling point upstream of Wivenhoe Dam. Downstream, the Spillway was included immediately below Wivenhoe Dam to assess hydrochory

Table 1
Location of study sites within the upper and mid-Brisbane River in relation to Wivenhoe Dam (km). Sites marked with an asterisk (*) indicate additional sampling locations for seed bank sampling. Distances are measured along the river channel.

	Site	Latitude	Longitude	Distance from Wivenhoe Dam (km)	Distance from nearest upstream macrophyte bed (km)	Area of nearest upstream macrophyte bed (m ²)
Upstream	Brisbane Crossing 3*	-26.7522	152.2341	112	0	50
	Monsildale Road	-26.7884	152.2701	104	0.05	>100
	Fulham Crossing	-27.0577	152.4424	53	1	10
	Spillway	-27.3997	152.6056	0.5	-	-
Downstream	Savages Crossing	-27.4427	152.6697	20	1.9	10
	Burton's Bridge*	-27.4997	152.6897	32	13.9	10

immediately downstream of the dam wall, and Savages Crossing provided a more distal site to capture spatial variation in propagule transport along the river. Rapid 100 m surveys were undertaken upstream of each site to confirm the presence of existing macrophyte beds.

2.2. Hydrochory sampling

Hydrochorous macrophyte propagules and non-propagating material (e.g. *V. nana* leaves) were sampled monthly from December 2022 to November 2023 using drift nets at two sites upstream and two sites downstream of Wivenhoe Dam (Fig. 2). Non-propagating vegetative fragments were collected and quantified as indicators of macrophyte dispersal and downstream transport, thereby increasing the likelihood of detecting downstream macrophyte dispersal through the system, particularly where macrophyte beds are limited. Although these fragments do not represent viable propagules capable of establishment, their presence reflects mechanical breakage and downstream transport of macrophyte material from upstream beds, thereby providing evidence of hydrochorous movement through the system. Ramets and non-propagating fragments were quantified as counts rather than biomass or volume because drift material consisted of small, highly variable pieces (e.g. whole or partial leaves and stem fragments). Counts therefore provided a consistent metric of transported macrophyte material and relative hydrochorous transport through the system. Each net was deployed for 120 min before retrieval and collection of aquatic macrophyte material, a duration consistent within literature (Brown and Chenoweth, 2008; Moggridge et al., 2009).

Sites were selected to represent functional contrasts in propagule supply and regulation. At Monsildale Road, three drift nets were positioned 5, 7, and 10 m downstream of a large *Vallisneria nana* bed to capture propagules released directly from the bed and to assess

immediate downstream transport (Supplementary Figure 2). The remaining five nets were placed 50 – 90 m downstream, at 10 m intervals, to determine whether propagules were transported over longer distances and to evaluate the potential for hydrochory beyond the immediate vicinity of the source bed. At Fulham Crossing and all sites downstream of Wivenhoe Dam, there were no *V. nana* beds present within 100 m of the site. At these sites, drift nets were spaced at 10 m intervals across transects to maximise the likelihood of detecting propagules in transport (Supplementary Figure 2). Net locations were fixed throughout the study period and did not change between sampling occasions, except where minor adjustments were required in response to changes in wetted width associated with flow variation. At each site, nets were distributed across the full wetted channel width, with some positioned within the main flow path (thalweg) and others in marginal or lower-velocity zones to ensure representative sampling of hydraulic variability. Drift nets were secured using star pickets and raised to the surface of the water level if exceeding the nets opening depth to focus on positively buoyant long-distance dispersal propagules. Drift nets were cube-shaped with a 50 cm × 50 cm × 50 cm frame (10 mm diameter plastic pipe) encompassed by 500 µm mesh net open at one end. A sample collection cup (10 cm height × 5 cm diameter) was attached to the downstream end of the net. While the nets were deployed, we avoided stirring up sediment, algae and macrophytes that could bias the sample. After the drift nets were removed, microhabitat characteristics (woody debris, filamentous algae) and macrophyte cover were visually assessed at each net location.

At each net location, water depth (cm) and velocity (m s^{-1}) were measured to determine the volume of water transferred through the nets. A calibrated YSI ProDSS (YSI Inc., USA) was used to measure water physiochemistry at each site including water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg l^{-1}), turbidity (NTU), conductivity ($\mu\text{S cm}^{-1}$), and pH



Fig. 2. Propagule dispersal nets deployed at different depths and flow velocities across the river channel.

were measured at each sampling occasion. Mean daily discharge ($\text{m}^3 \text{s}^{-1}$) and water level (m) were obtained from the closest gauging stations 143007 A and 143001 C (Queensland Government) upstream and downstream, respectively.

2.3. Vegetative sample processing

Vegetative matter from each trap was collected into individual labelled bags, and chilled to be sorted later inside the laboratory. Samples were refrigerated for no more than 5 days before processing to prevent decay. Each sample was individually sorted into species, then non-propagating matter (e.g. leaves, sexual reproductive structures) and viable propagules including ramets (clonal propagules), whole plants, and seeds. Leaf material was classified as non-propagating because *Vallisneria nana*, the main focal species, does not reproduce vegetatively via detached leaves without an attached stolon (Li et al., 2018). Native macrophyte species co-occurring within the upper and mid-Brisbane River study reach, including *Myriophyllum verrucosum* Lindl., *Hydrilla verticillata* (L.f.) Royle, and *Potamogeton crispus* L., are capable of vegetative propagation from stem fragments; therefore, a conservative approach was adopted by excluding branched stem fragments from propagule counts unless roots were visible. This approach increased the likelihood that propagules were viable and capable of immediate settlement. Species were identified as per Sainty et al., (1994).

2.4. Seed bank sampling

Seed bank sampling was conducted in February and September 2024 during the austral summer and spring periods. Ninety-six samples were collected at each sampling event, comprised of 16 sediment core samples (7.5 cm diameter $\times$ 10 cm depth) at each of three sites upstream and three sites downstream of Wivenhoe Dam, respectively. Cores were taken randomly across the river channel, including within and outside macrophyte beds, in zones associated with sediment transport and deposition, and across a range of local conditions (e.g. depth and velocity). In areas where no macrophyte beds were present, samples were taken from where macrophyte beds were historically located from prior surveys (Kennard et al., 2021). Visible roots, tubers, rhizomes, aquatic invertebrates, large stones, and various other debris were removed during the washing process.

The seedling emergence method (Boedeltje et al., 2003) was used to assess the potential retention of viable seeds within the collected samples. To aid in breaking any seed dormancy, promote germination, and render any remaining root material nonviable, samples were completely air dried over four weeks. Salter et al. (2010) reported that seeds of *Vallisneria australis*, a species that occupies habitats comparable to those of *V. nana*, exhibited twice the germination rate after prolonged drying compared with continuous waterlogged conditions. Although *V. australis* was not used in the present experiment, its ecological similarity to *V. nana* provided a rationale for applying the same drying treatment in our experimental design. Previous studies have also shown that drying can enhance germination in species adapted to environments with unpredictable flooding regimes (Casanova and Brock, 2000; Porter et al., 2007).

The collected material was placed outdoors in 1 L containers, waterlogged with rainfall when available, or with tap water during periods of low precipitation, and maintained with at least 3 cm of standing water above the substrate. Germination was monitored daily to identify emerging species and record the number of seeds germinated. Shade cloth was used to allow sufficient light for growth while preventing the establishment of terrestrial seeds, and germination was monitored for a period of 12 weeks. A minimum of 4 weeks without germination was used as confirmation that germination had concluded. The 12-week monitoring period therefore ensured that late germination events were unlikely to have been missed and is consistent with durations commonly used in freshwater macrophyte seedling-emergence experiments

(Kimber et al., 1995; McFarland and Shafer, 2011).

2.5. Data analysis

Data collected from propagule drift nets were summarized graphically. Downstream sites exhibited uniformly zero propagule and non-propagating fragment counts across all nets and sampling occasions, resulting in complete separation between upstream and downstream observations and no within-group variance. As maximum likelihood estimation is unreliable under these conditions, downstream sites were excluded from statistical analysis and are presented descriptively only. Statistical analyses were restricted to upstream sites where sufficient variation existed. Due to overdispersion in the response data, negative binomial general linear models (GLMs) with a log link were used to model upstream counts of ramets (no other propagules were detected during sampling) and non-propagating fragments, utilising the MASS package (Ripley et al., 2013). Counts of drifting vegetative fragments were used to summarise temporal patterns in macrophyte transport and were presented descriptively to illustrate relative differences in fragment abundance between upstream and downstream sites. An offset for $\log(\text{sampled water volume})$ was included in all models to account for variation in water volume filtered among nets. Initial models included site, river discharge (m sec^{-1}), depth (m) and day of year. Sampled water volume was calculated as net mouth area multiplied by mean water velocity at each net and deployment duration. Covariates were centred and scaled prior to analysis with collinearity among predictors assessed using variance inflation factors. Model selection was based on AIC and likelihood ratio tests, with final models retaining ecologically meaningful predictors. Final model adequacy was assessed using residual diagnostics, including inspection of residual plots and checks for overdispersion. McFadden's pseudo R^2 were used to assess goodness-of-fit during model selection. Pseudo R^2 values are not directly comparable to linear R^2 values and are typically lower in magnitude (Smith and McKenna, 2013).

To examine drivers of local-scale propagule transport where a substantial upstream macrophyte source was present, an additional negative binomial GLM was fitted for Monsildale Road only. The response variable was total vegetative fragments including propagules and non-propagating fragments. This model included local hydraulic variables (water velocity (m sec^{-1}) and depth (m)) and distance downstream from the macrophyte bed (m) as predictors, with an offset for $\log(\text{sampled water volume})$. Interaction terms among hydraulic variables and distance were initially explored but were not retained in final models due to lack of support based on AIC and likelihood ratio tests. Final model adequacy was assessed using residual diagnostics as described above. Model predictions and partial effects were generated using the ggeffects package for visualisation (Lüdtke, 2018). No statistical analyses were conducted on the seed bank data due to insufficient sample sizes. All data analyses were performed using R version 4.2.2 (R Core Team, 2022).

3. Results

3.1. Hydrochory sampling

Physical characteristics and water quality conditions across the four sampling sites during the hydrochory sampling period fell within ranges considered suitable for macrophyte establishment and growth (Supplementary Table 1). Aquatic vegetation fragments and propagules were collected in drift nets at the two upstream sites which were sampled, but no vegetation or propagules were collected at the two downstream sites on any sampling occasion (Fig. 3A), and no seeds were detected at any sites. Of the upstream sites, significantly more non-propagating vegetative material was collected at Monsildale Road, the most upstream site, compared with Fulham Crossing, located further downstream ($p < 0.001$, Table 2). Monsildale Road samples contained

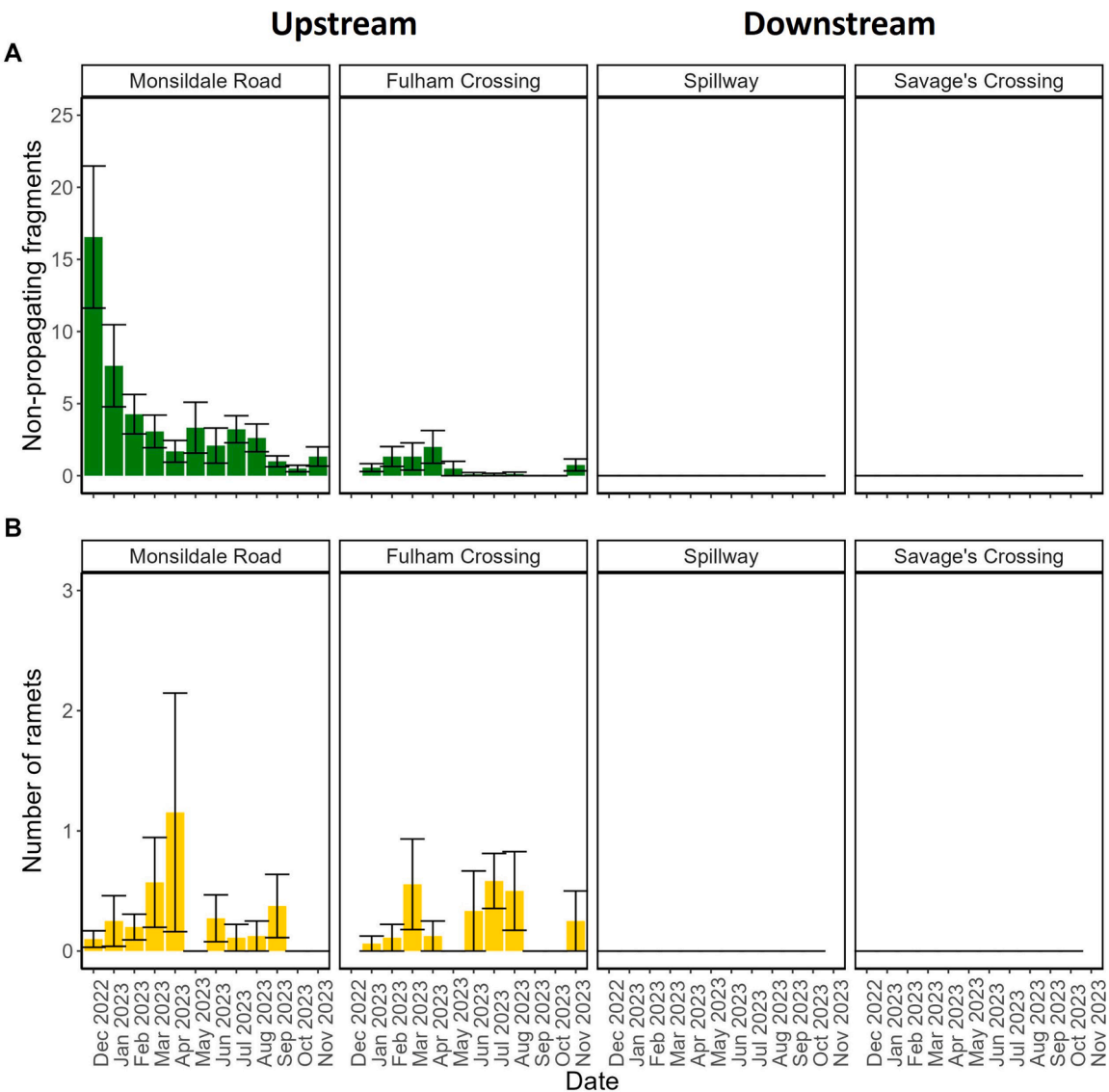


Fig. 3. Mean number $\pm$ standard error of non-propagating vegetative fragments (A) and mean number of ramets (B) captured in propagule drift nets across sampling sites throughout the study period.

Table 2
Parameter estimates ($\pm$ SE) from negative binomial GLMs assessing the effects of site and discharge on vegetative fragment and ramet abundance at upstream sampling locations. Coefficients are reported on the log link scale. Models included an offset for log(sampled water volume) to account for variation in sampled water volume among nets. McFadden's pseudo R^2 is shown for each model.

Fixed effects	Response variables					
	Fragments			Ramets		
	Estimate $\pm$ SE	z	P	Estimate $\pm$ SE	z	P
Intercept	3.41 $\pm$ 0.22	15	<0.001	1.93 $\pm$ 0.41	4.7	<0.001
Site	1.78 $\pm$ 0.26	6.9	<0.001	0.57 $\pm$ 0.47	1.2	0.229
Discharge (m sec ⁻¹)	-	-	-	-1.46 $\pm$ 0.38	-3.9	<0.001
McFadden's pseudo R^2	0.14			0.06		

mostly non-propagating vegetative material over the year of sampling,

with a small proportion of ramets. At the upstream sites, propagule abundance was relatively low with maximum mean 1.15 ± 1 propagules at Monsildale Road and 0.6 ± 0.2 propagules at Fulham Crossing (Fig. 3B). The majority of fragments across all upstream sites and sampling periods were detached leaves, while viable ramets occurred in much lower numbers without ever exceeding 2 ramets per sampling period at upstream sites. Non-propagating fragment abundance was highest at Monsildale Road in the early sampling months, with a peak mean of 16.6 ± 4.9 fragments in December 2022. Fragment abundance declined sharply after February 2023 and remained consistently below a mean of 5 vegetative fragments at Monsildale Road (Fig. 3A). Estimates from the negative binomial GLMs indicated that fragment density was strongly site-dependent after standardising for sampled water volume ($p < 0.001$, Table 2), while in contrast, ramets did not differ significantly between upstream sites but declined significantly with increasing river discharge ($p < 0.001$, Table 2).

Five species of submerged macrophytes were captured in drift nets at upstream sites (mean $\pm$ SE). At Monsildale Road, *Vallisneria nana* was the most abundant species (9.3 ± 1.6 fragments per sampling occasion including both non-propagating fragments and ramets), followed by *Myriophyllum verrucosum* (2.9 ± 1.4), *Potamogeton crispus* (1.4 ± 0.2),

Potamogeton tricarlinatus F.Muell. & A. Benn. (1.4 ± 0.3), and *Hydrilla verticillata* (1.0 ± 0). Monsildale Road exhibited the greatest species richness, with five species detected. At Fulham Crossing, only two species were detected. *Potamogeton crispus* was the most frequently captured (3.2 ± 0.5), followed by *V. nana* (1.8 ± 0.4). Across the sampling period, Fulham Crossing, despite not having a macrophyte bed in close proximity upstream, collected a total of eight ramets of *P. crispus* and five of *V. nana* were collected.

3.2. Local scale variations downstream of a Vallisneria nana bed

At Monsildale Road, drift nets were deployed at incremental distances downstream of a *V. nana* bed: three nets at 5, 7, and 10 m, and a single net placed at 10 m intervals between 50 – 90 m downstream (Supplementary Figure 2). Vegetative fragments were captured at multiple positions both longitudinally downstream of the source bed and laterally across the channel, including along the banks and within the thalweg. Negative binomial modelling restricted to Monsildale Road indicated that vegetative macrophyte material declined significantly with increasing distance from the macrophyte bed ($p < 0.001$; Fig. 4A), water depth ($p < 0.05$; Fig. 4B), and water velocity ($p < 0.05$; Fig. 4C) after standardising for sampled water volume (Supplementary Table 2).

3.3. Soil seed bank

No seed germination occurred in samples from any of the downstream sites. Only 22 seeds germinated from upstream sites across the 192 cores sampled (Table 3). The site with the highest number of seeds germinating was Monsildale Road, where both *V. nana* and *M. verrucosum* germinated, followed by Fulham Crossing (Table 3) and Brisbane Crossing 3 with only 4. In total 10 of the 96 upstream samples produced germinated plants during the first sampling period, and no seedlings emerged in the second sampling conducted in September 2024.

Table 3
Total germinated plants from soil seed bank samples upstream and downstream of Wivenhoe Dam, QLD.

	Site	Species	
		<i>Vallisneria nana</i>	<i>Myriophyllum verrucosum</i>
Upstream	Brisbane Crossing 3	4	0
	Monsildale Road	6	4
	Fulham Crossing	8	0
Downstream	Spillway	0	0
	Savages Crossing	0	0
	Burton's Bridge	0	0

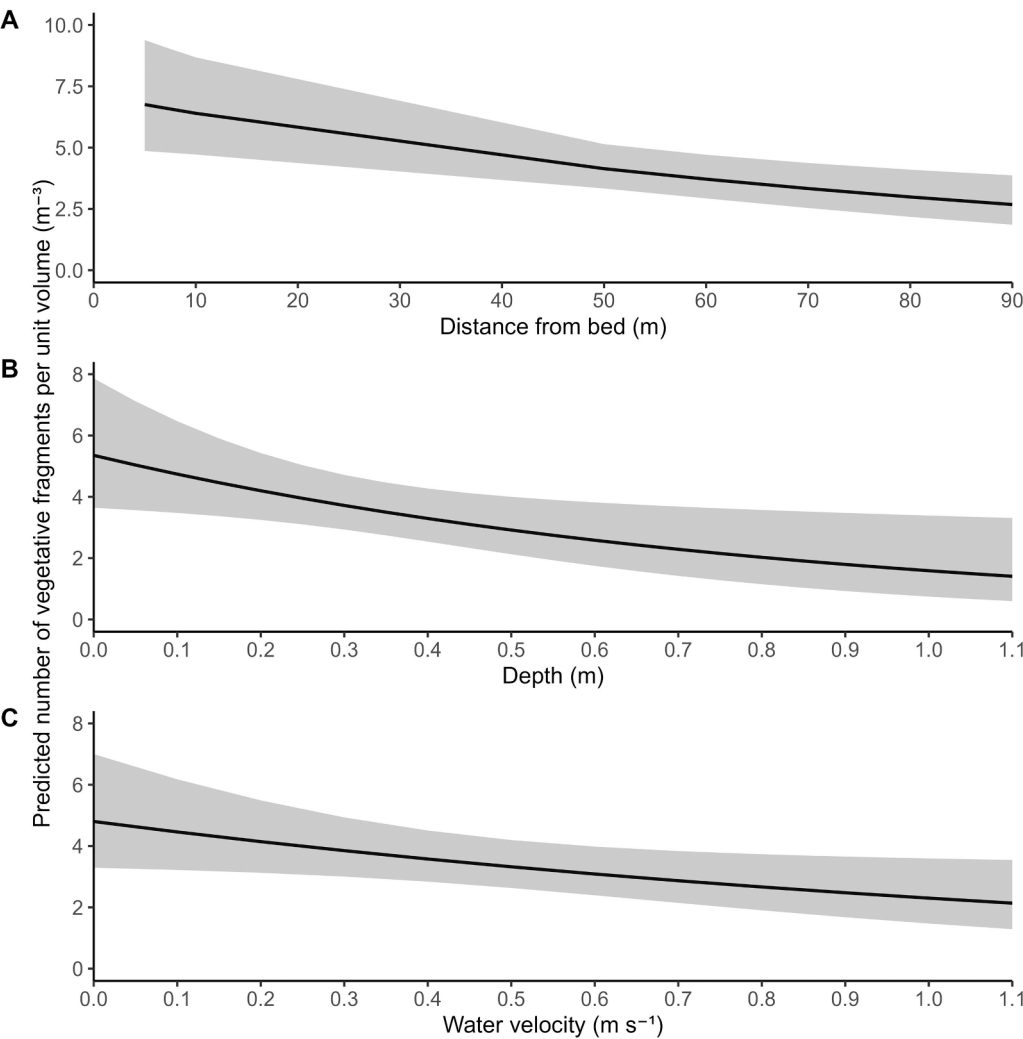


Fig. 4. Partial effects of distance from the source bed (m) (A), depth (m) (B), and water velocity (m s⁻¹) (C) on predicted number of vegetative fragments per unit volume (m⁻³) at Monsildale Road. Lines represent fitted values from negative binomial models and shaded areas indicate 95% confidence intervals, with predictions standardised by sampled water volume.

4. Discussion

4.1. Broad-scale propagule transport and barrier effects of the dam

Our study supports the hypothesis that Wivenhoe Dam may be reducing macrophyte hydrochory under base-flow conditions. Propagules were absent both immediately below the dam (Spillway; ~500 m downstream) and at a broader downstream site (Savages Crossing), suggesting a reach-scale limitation within the regulated section rather than a simple distance-dependent decline. This limitation could be a significant factor in the delayed recovery of critical macrophyte habitat downstream of the dam post disturbance. This is consistent with findings from other dammed rivers (Brown and Chenoweth, 2008; Merritt and Wohl, 2006) where large dams reduced rates of hydrochory by up to 95%. Although sites were not arranged along a continuous gradient of distance from the dam wall, they were selected to represent functional contrasts between upstream free-flowing reaches and the regulated downstream reach, allowing assessment of connectivity at the reach scale.

At the upstream site closest to Wivenhoe Dam impoundment, Fulham Crossing, vegetative material was collected including viable *P. crispus* and *V. nana* propagules. This indicates that macrophyte hydrochory is occurring in the river directly upstream of the dam and would likely contribute to macrophyte recovery post-floods upstream of the dam. Previous research reported that the water residence time in Lake Wivenhoe can be as long as 20 years under base-flow conditions (Burford et al., 2007). High water retention time and low water velocities within the reservoir, causes the reservoir to act as a sink by trapping propagules and preventing downstream dispersal, at least during non-flood periods. While the absence of propagules and viable seed banks downstream is consistent with disruption of hydrochory by the dam, alternative explanations cannot be excluded. Broader post-flood source depletion across the catchment or limited local macrophyte beds downstream of the dam may also contribute to the observed pattern.

Transport rates of macrophyte vegetative material varied significantly among upstream sites over the study period. Upstream of the dam, relatively few vegetative propagules were transported, and no seeds were detected. The propagule drift rates were lower than expected and low compared to other studies (Brown and Chenoweth, 2008; Merritt and Wohl, 2006). However, the low but detectable upstream drift (e.g. <1 ramet per sampling occasion) contrasts with the complete absence of propagules downstream of the dam. While low upstream drift likely reflects limited propagule release under base-flows, the lack of propagules observed downstream indicates a structural barrier to dispersal rather than merely reduced propagule supply. This distinction suggests that even infrequent upstream propagule movement represents functional connectivity, whereas the absence of downstream hydrochory reflects effective dispersal disconnection under non-flood conditions. This study was conducted only ten months after the major flood disturbance in early 2022, when discharge at Savages Crossing exceeded $4563 \text{ m}^3 \text{ s}^{-1}$, followed by a smaller but still significant event in November 2022. These high-flow events likely scoured existing macrophyte beds, substantially reducing available source material for propagule dispersal. Differences in the abundance of macrophyte material captured between upstream sites may be driven by hydraulic variations influencing propagule dispersal. Although this present study measured propagule transport at base-flow, it is likely that large flood events would mobilise more propagules, particularly if discharge is sufficient to disturb the substrate (Riis and Biggs, 2003).

At Monsildale Road, elevated discharges in December 2022 (Supplementary Figure 1A) coincided with an increase in the number of vegetative fragments collected, although this did not lead to a greater number of propagules collected. Higher counts of vegetative fragments were also observed during periods of decreasing river discharge, which may reflect the delayed release of material previously retained on in-

stream structures. In contrast, ramets declined significantly with increasing discharge, suggesting that elevated flows may reduce the transport or retention of intact propagules. This delayed release during lower flow conditions could facilitate settlement and establishment, as high-flow periods are less conducive to successful colonisation by uprooted plants.

Low drift rates of submerged macrophyte material may primarily reflect hydraulic and structural processes that favour propagule retention over downstream export. During low flows, water velocity within dense macrophyte beds is greatly reduced compared to open channels, creating conditions that promote local retention rather than dispersal. Well-established vegetation can therefore act as a trap, retaining propagules within beds more effectively than non-vegetated reaches (McKendrick et al., 2024; O'Briain et al., 2022). Additionally, certain hydrologic conditions may need to exceed a threshold to disturb sediments and increase long-distance dispersal of propagules downstream. Although increased discharge may exceed disturbance thresholds capable of remobilising sediments and uprooting plant material, such events are often episodic and may not consistently facilitate successful downstream establishment. Instead, disturbance may fragment beds locally without increasing effective dispersal at broader spatial scales.

While such hydrologic thresholds may enable episodic long-distance dispersal, low drift rates may also reflect reproductive strategies favouring localised clonal growth over sexual recruitment. All five species captured are capable of clonal reproduction, and following disturbance, macrophytes may shift toward vegetative expansion of existing beds rather than producing dispersive propagules. Rhizomes of *V. nana* likely aid in persisting in highly disturbed environments, anchoring plants and providing a mechanism for local regrowth (Rea et al., 2002; Townsend et al., 2017). However, large floods that uproot entire plants and remobilise sediments can hinder regeneration of macrophyte beds from these structures (Riis and Sand-Jensen, 2006). Large stands of clonal propagules may allow macrophyte populations to persist in unfavourable ecological conditions (Barrett, 2015). Similar patterns have been reported in the Rhône River, where *Chara vulgaris* recovered primarily through vegetative propagules after flood-induced scouring (Combroux et al., 2001). Local population genetics may also play a role in productivity of sexual and asexual reproduction. In other systems, for example, populations of seagrass, *Zostera japonica*, exhibited genetic differentiation that influenced their relative capacity for clonal versus seed-based reproduction (Zhang et al., 2020). Clonally dominant aquatic plants often exhibit reduced genetic diversity, particularly in disturbed environments where persistent clones limit opportunities for sexual recruitment (Zhang et al., 2020). Local genetic variation and recruitment strategies of macrophytes may strongly influence recovery trajectories, highlighting the need for future research into population genetics and the balance between sexual and vegetative reproduction in freshwater macrophytes.

4.2. Local propagule transport and role of hydraulic conditions

At Monsildale Road, the most upstream site situated near an existing macrophyte bed, propagules were dispersed both longitudinally, at varying distances downstream and laterally across the full width of the river channel. The highest number of vegetative fragments was recorded within 7 m of the macrophyte bed. However, vegetative material significantly declined with increasing water velocity and distance downstream, indicating that proximity to the source bed and low-velocity conditions were primary drivers of fragment abundance. These findings are consistent with McKendrick et al. (2024) who reported that 56% more macrophyte propagules were trapped within aquatic vegetation compared to open river channels. This pattern may reflect the influence of local hydrodynamics and in-stream retention structures resulting in a delayed release of fragments from microhabitats. For example, the monitoring site 50 m downstream of the macrophyte bed was the deepest and slowest section of the transect,

representing a low-flow depositional pool zone where propagules may temporarily accumulate before being remobilised under changing flow conditions.

Along the transect, propagule abundance generally reflected local hydraulic variability, with higher retention observed in low-velocity sections and lower counts in faster riffle zones. The slight increase in vegetative fragments at the 70 m monitoring site may therefore reflect local hydraulic conditions rather than a greater presence of physical obstacles. The 70 m section corresponded to the beginning of a shallow riffle with concentrated flow, potentially altering local transport pathways and fragment dispersal. Physical obstacles such as woody debris and rocks can also contribute to temporary retention of fragments under higher flow velocities, increasing the likelihood of settlement and subsequent colonisation (Riis, 2008). However, receding water levels can cause exposed macrophytes to dry out, limiting hydrochorous transport and reducing the supply of propagules for downstream dispersal (Duivenvoorden, 2008).

Vegetative material was still captured 90 m downstream, although at reduced abundance with increasing distance, suggesting that hydrochory at Monsildale Road facilitates not only local dispersal but may also contribute to long-distance transport. This established bed is potentially providing propagules for recolonisation and recovery after flooding in the upstream reaches. Macrophyte fragments were also collected at Fulham Crossing, where the nearest macrophyte bed (10 m²; Table 1) was located approximately 1 km upstream, supporting the idea that even small remnant beds can serve as sources for long-distance propagule dispersal. The dispersal of vegetative propagules depends on traits such as density, buoyancy duration, and size (Boedeltje et al., 2003). In this study, drift nets were positioned near the surface (down to 50 cm depth), targeting floating propagules. These findings underscore the need for further investigation into the propagule dynamics of different macrophyte species and how this varies across different flow regimes.

4.3. Seed bank availability

All germinated seeds originated from the February 2024 seed bank sampling, approximately two growing seasons after the 2022 flood disturbance, and yielded 22 seedlings in total. Germination was limited to *Myriophyllum verrucosum* and *Vallisneria nana* in upstream sediments, with no germination observed from downstream samples. The low germination count could be due to *V. nana* seeds likely not being a major contributor to recolonisation post-disturbances, consistent with previous work in the Daly River, northern Australia (Rea et al., 2002), indicating limited reliance on sexual reproduction unless specific environmental conditions for flowering are met. This is common across many *Vallisneria* species which primarily spread vegetatively through ramets (Rea et al., 2002). Additionally, the seed banks of the upstream sites, Brisbane Crossing 3 and Monsildale Road, may have been depleted following the large disturbance event of the 2022 floods. The low germination numbers observed may indicate that insufficient time has passed for sediment seed banks to recover after this event. Additionally, the plants may channel more energetic resources into ramet production rather than seed production to more rapidly expand and recover from large disturbances (Ma et al., 2021). Low germination may also reflect flood-driven river scouring, which can remove sediment seed banks, thereby reducing the availability of viable seeds for future recruitment and recovery.

At Fulham Crossing, a site without a macrophyte bed within 1 km of the site, *V. nana* seeds successfully germinated, indicating the presence of a seed bank despite the absence of established vegetation. This suggests that either hydrochorous dispersal has occurred from upstream macrophyte beds in the past, or dormant seeds have persisted within the sediment. Although germination numbers were low, the presence of viable seeds indicates potential for recolonisation following disturbance. However, successful recruitment of *V. nana* in the field likely depends on suitable light availability, stable sediments, and flow conditions that

permit seedling anchorage and growth. Frequent sediment disturbance and burial during elevated flows may limit seedling establishment even when viable seeds are present. Similar challenges in detecting viable seed banks have been reported in other systems, for example, in a eutrophic lake in China, only nine seedlings germinated from the soil seed bank and all died before species identification was possible (Lu et al., 2012). Although only a few seeds germinated, their presence indicates potential for recolonisation after flood events, as shown by *V. nana* successfully germinating Fulham Crossing, with no macrophyte bed within a kilometre. Seed production within river systems that experience frequent flooding require further exploration in their role in recolonisation post disturbance.

The limited germination observed across all sites may reflect both a scarcity of viable propagules in upstream reaches and restricted downstream transport due to the presence of the dam. Frequent intense flooding can scour the sediment, redistributing or burying seed banks limiting both seed persistence and seedling establishment (Lake et al., 2006). In the Brisbane River, severe flooding in early 2022 scoured much of the river resulting in large amounts of sediment being remobilised and deposited, potentially burying potential seed banks. A similar process likely occurred during the 2011 flood event as well, contributing to the limited macrophyte presence observed downstream (Kennard et al., 2021). Large impoundments and dams can act as propagule traps, preventing the downstream transport of propagules. When combined with repeated large flood events that cause scouring and sediment mobilisation, this likely limits the natural replenishment of propagules required for macrophyte recovery following disturbances. However, large impoundments can reduce peak flood flows downstream, leading to extended periods of hydrological stability (Jones et al., 2020). The stable conditions may promote macrophyte growth and protect established beds and sediment seed bank from disturbances.

This study was designed to contrast the upstream unregulated reach with the regulated downstream reach under base-flow conditions, providing insight into reach-scale patterns of propagule availability. While the number of sampling sites was limited, sites were selected to represent functional contrasts in propagule supply and regulation. Proximity to upstream macrophyte beds differed among sites and may influence propagule detection; however, this reflects natural variation in source availability within the system. As water levels were higher earlier in the study period, it is possible that some semi-buoyant or negatively buoyant fragments transported near the riverbed were not collected, as we targeted floating propagules. For example, Riis and Sand-Jensen (2006) found in Danish streams that *Elodea canadensis* Michx. stem fragments tended to drift under the water surface, which resulted in being retained in deeper water and obstacles. These considerations define the scope of inference but do not alter the consistent absence of propagules observed downstream during the study period.

4.4. Management recommendations

Our findings indicate that long-distance hydrochorous dispersal is occurring in the Brisbane River upstream of a major dam, although at a relatively slow rate within the first year following the 2022 flood. The low water velocities typical of large reservoirs likely results in propagules sinking before they can reach the dam wall (Jones et al., 2020). This highlights how physical barriers can reduce hydrochory processes essential for macrophyte recovery after disturbance events. While dam removal has been promoted as a solution to restore hydrological connectivity and has shown increased macrophyte hydrochorous transport (Brown and Chenoweth, 2008), it is not a viable option in many cases, especially where the dam serves as the primary water supply and provides flood mitigation for a major city.

Active restoration of macrophytes following disturbance events may provide an alternative strategy to overcome dispersal limitation and promote recovery. Trials of active restoration of macrophytes in the mid-Brisbane River below Wivenhoe Dam have been completed with some

short term success, however, this approach faces significant logistical challenges (Burke et al., 2024). For example, the establishment of 360 m² of *V. nana* beds within protected fenced plots were rapidly grazed to near zero coverage by herbivorous aquatic fauna, such as the Australian lungfish and a range of other macrophyte consuming aquatic species, that depend on macrophyte beds for food, habitat and spawning (Burke et al., 2024). Additionally, any large flood events in the months – years following planting will dislodge newly establishing macrophyte beds, causing substantial losses limiting the time available for natural seed bank replenishment. These challenges underscore the need for carefully designed and sustained restoration strategies in regulated river systems.

A novel method of active restoration is ‘managed hydrochory’, a concept proposed by Nilsson et al., (2010) to enhance propagule dispersal. This involves reintroducing macrophytes by utilising hydrochory to distribute new propagules to areas devoid of natural propagules. Managed hydrochory involves the deliberate manual release of propagules into river systems to mimic natural dispersal processes and overcome dispersal limitation, thereby promoting recolonisation and recovery of downstream reaches with reduced macrophyte coverage following a disturbance. The aim is to support the recovery of downstream sections of river with minimal macrophyte coverage present after a disturbance event. Managed hydrochory may be combined with other active management interventions, such as increasing channel structural complexity (e.g. logs, boulders, stakes) to aid higher rates of retention of propagules further supporting propagule establishment (Nilsson et al., 2010).

The differences in abundance of macrophyte propagules captured in this study between upstream and downstream sites are likely due to the presence of the Wivenhoe Dam creating a barrier for hydrochory. Historical data (1996 – 1997) indicates that the mid-Brisbane River downstream of Wivenhoe Dam had extensive submerged macrophyte beds with similar species diversity as upstream reaches (Mackay and Thompson, 2000). Perhaps counter-intuitively, the early development of extensive macrophyte beds was likely facilitated by the construction of Wivenhoe Dam in 1985, which in effect stabilised flows, with no major hydrological disturbances occurring until 2011 (Mackay et al., 2014). However, surveys following the 2011 flood event revealed that macrophyte recovery has been notably slow with lower species diversity and abundance (Kennard et al., 2021). These findings highlight the potential impacts of dams on macrophyte dispersal and the need to consider hydrochory in the assessment and management of dam impacted river systems. Active restoration may therefore be a required management intervention to mitigate the negative effects of dams on hydrochory and support the recovery of macrophytes and macrophyte dependant species like the threatened Australian lungfish. More research is needed to establish if managed hydrochory is a viable method to overcome negative impacts of barriers on rivers potentially facilitating recovery after major flood events.

4.5. Conclusion

The absence of propagules and a seed bank downstream of Wivenhoe Dam is consistent with reduced downstream propagule transport within the regulated reach. Our findings suggest that the dam may limit hydrochorous connectivity by acting as a physical barrier that traps propagules before they can disperse downstream. Together, these findings highlight how the combined effects of large dams and intense flood events may disrupt key ecological processes, including hydrochorous propagule transport and seed bank replenishment, thereby constraining the recovery of macrophyte assemblages downstream of impoundments.

CRediT authorship contribution statement

Burke Colin Lee: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mark J.**

Kennard: Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Franklin Hannah M:** Writing – review & editing, Supervision, Methodology, Conceptualization. **David T. Roberts:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Luke Carpenter-Bundhoo:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2026.104025.

Data availability

Data will be made available on request.

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