



Review

# The Influence of Abiotic Factors on the Distribution of Macrophytes in Small Water Bodies in Temperate Ecosystems

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**Abstract:** Currently, reviews focusing on the distribution of macrophytes focus primarily on large water bodies, regardless of the fact that small water bodies (SWBs), such as ponds, ditches and streams, often support higher levels of gamma macrophyte richness. This review investigates the direction and strength of the relationship between 13 abiotic factors and macrophyte distribution in SWBs. Results demonstrate that there are distinct differences between the effects of abiotic factors on bryophytes and those on vascular macrophytes of different morphological forms. Whilst shading and velocity have a significant ( $p < 0.05$ ) negative relationship with vascular macrophyte richness and a positive relationship with bryophyte richness, the reverse is true for the size of a water body, depth and concentration of nitrogen. Vascular macrophyte richness has a significant ( $p < 0.05$ ) negative relationship with distance to a stream source, isolation, the proportion of surrounding land that is woodland, total phosphorus concentrations and pH. The strength of the influence of substrate size and water body size differs between vascular macrophyte morphologies. Key knowledge gaps include bryophyte distribution and the effect of hydroperiod and surrounding land use on macrophyte communities. In order to conserve all macrophyte morphologies and taxa, it is important to protect SWBs with a diverse set of conditions.



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## 1. Introduction

Macrophytes are plants that either permanently or periodically rely on being completely or partially submerged in water. They provide habitats and a source of food for fish [1], macroinvertebrates [2] and amphibians [3]. They act as oviposition sites [4] and provide refuge from predators and fast flowing currents [5]. They also positively influence biogeochemical cycles within the water by sequestering inorganic nitrogen and phosphorus [6] and function as ecosystem engineers by reducing the speed of water flow and trapping sediments [6]. However, macrophytes are facing unprecedented anthropogenic threats, including those from habitat degradation [7], climate change [8,9], invasive species [10] and eutrophication [11,12]. In order to protect macrophytes, more needs to be understood about their distribution and the factors that influence macrophyte health and community composition.

Small water bodies (SWBs), which refer to ponds, streams and ditches, have been found to support greater levels of gamma macrophyte richness than rivers or lakes [13]. Ditches can be reservoirs of biodiversity, containing rare species that have otherwise disappeared from surrounding agricultural land [14]. Some ditches support larger levels of biodiversity in what would otherwise be a low-biodiversity monoculture cropping system [14]. Similarly, ponds often contain nationally scarce macrophyte species, and

their introduction to agricultural or urban areas is an inexpensive and effective method to enhance local biodiversity [15]. Alongside their importance for regional biodiversity, SWBs face particularly severe impacts from a changing climate as their small size provides a very limited buffering capacity against extreme weather events [16]. They are at particular risk of exposure to agricultural pollutants due to their frequent occurrence on or near agricultural land [16] and their small size, which means that dilution potential is low. As a result of this, SWBs often drive chemical risk assessments. For example, data on pesticide concentrations and associated risks to non-target organisms in ponds, ditches and streams are the foundation of risk assessment for plant protection products [17].

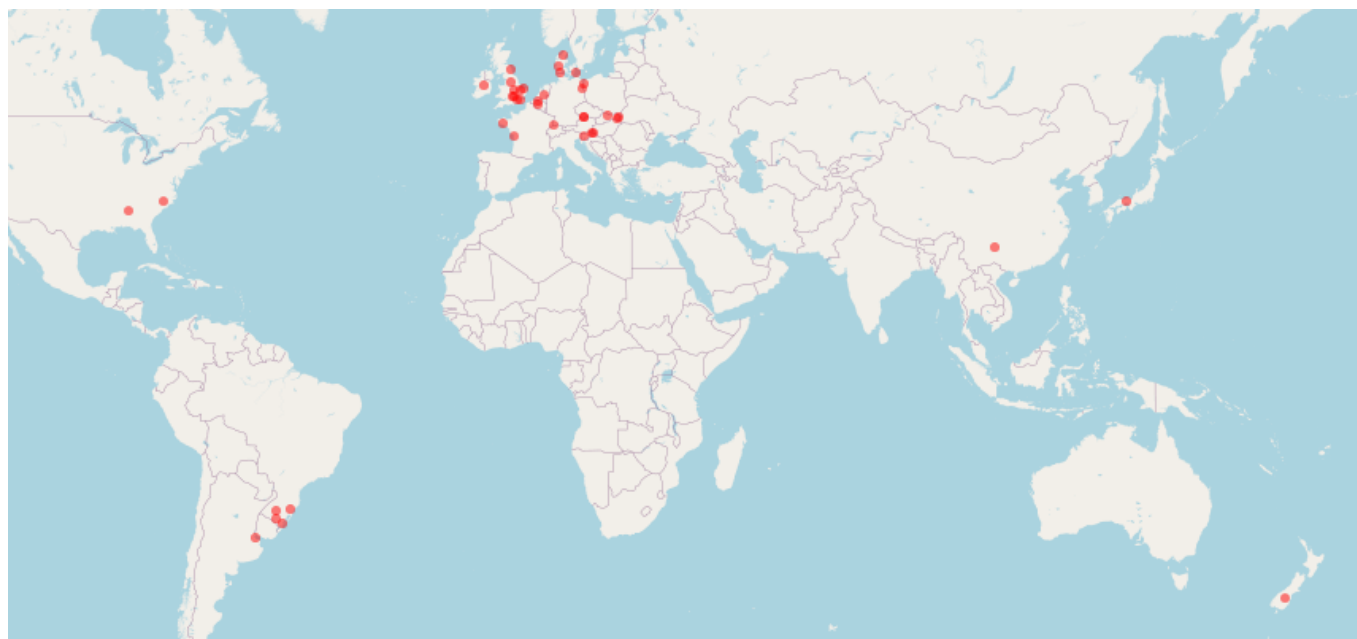
Despite the importance and specific characteristics of SWBs, the small number of reviews that investigate factors that influence macrophyte distribution do not separate SWBs from larger water bodies such as lakes and rivers. As research to date has disproportionately focused on larger water bodies [18], there is a strong potential that some relationships that are specific to SWBs may be masked by those pertaining to lakes and rivers. Bornette and Puijalon [19] undertook a broad comparison of the abiotic factors (including light, water temperature, nutrient content, substrate characteristics, water velocity and flooding) that impact macrophytes in temperate lakes, ponds, wetlands, rivers and streams. Their findings suggest that depth, nitrogen and phosphorus concentrations, recurrence of flooding and velocity most influence macrophyte distribution. Many of these findings were also reported in a previous review by the same authors [20], where they investigated the influence of depth, water temperature, velocity, substrate characteristics, flooding and nutrient availability on macrophytes of different sizes and shapes. They identified that water depth influences macrophyte distribution due to light availability and that optimum nutrient concentrations differ for macrophytes of different sizes [20]. Dar et al. [21] briefly reviewed the literature on both the abiotic and biotic factors that affect the distribution of macrophytes in all water body types. They concluded that light availability and water temperature were the two most influential abiotic factors driving macrophyte distribution. The other abiotic factors studied were nutrient concentrations, water depth and wind and wave exposure.

This review aims to determine the direction and strength of the relationship between a wide range of abiotic factors and macrophyte distribution in SWBs. Thirteen abiotic factors had sufficient published research to include within the review (SWB type and size, substrate size class, water velocity, conductivity, water depth, shading, surrounding land use type, hydroperiod, isolation, distance from the source, nitrogen and phosphorus concentrations, and pH), whilst there was insufficient information to include turbidity, slope, concentration of organic matter, age of water body or altitude. The review separates out the effects of abiotic factors on non-vascular macrophytes (bryophytes) and four categories of vascular macrophytes based on their positioning within a water body (emergent, free-floating, rooted submerged, and submerged with floating leaves). The review extends existing publications through the specific focus on SWBs by considering the role of different macrophyte morphologies and taxa and by incorporating evidence published over the last decade.

## 2. Materials and Methods

This review set out to determine how different abiotic factors influence macrophyte distribution in SWBs and whether the response to abiotic factors varies based on macrophyte taxa and morphology. Web Of Science (Clarivate Analytics) was the only search engine used to source peer-reviewed articles. There was no restriction on the publication date within the searches. All searches were conducted on either 26 January 2023, 9 February 2023 or 5 October 2023, and the same reviewer screened each paper. Papers were removed if the sampling location was not in a temperate, fully humid region (Cfa, Cfb, and Cfc) as defined by the Köppen–Geiger climate classification [22]. The Köppen–Geiger climate classification subdivides the world into thirty categories based on terrestrial climate, taking into account both temperature and precipitation [22]. Therefore, any geographical factors that

could be a potential influence on macrophyte distribution, such as latitude and elevation, are accounted for. Figure 1 shows the sampling locations of all studies used throughout this review. Papers were also removed if the “ponds” studied had surface area larger than 2 ha, following definitions provided by Williams et al. [15]. The screening and selection process involved initially reading the title for relevance and checking for duplicates, then reading the abstract, and lastly, if the paper passed screening, reading the full text (Table 1). Additional peer-reviewed papers were found through citations within the Web of Science sourced papers. Grey literature, such as monitoring datasets and studies that have not been through the peer review process, were sought out via the search engine “Google” on 24 October 2023. Only one suitable item of grey literature was identified, a dataset by “Fens for the Future” [23]. In studies where multiple environmental factors were investigated, single factors were isolated from multivariate analyses where appropriate.



**Figure 1.** Red dots indicate the sampling locations of the studies used throughout this review.

**Table 1.** Web of Science search terms, along with the number of outputs after each screening event.

Web of Science Search Terms	Initial No. of Results	No. of Results After Reading the Title and Removing Duplicates	No. of Results After Reading Abstract	No. of Results After Reading Full Text
ALL = (pond) AND TS = (macrophyte) AND TS = (distribution)	126	17	9	7
ALL = (ditch) AND TS = (macrophyte) AND TS = (distribution)	11	2	2	1
ALL = (stream) AND TS = (macrophyte) AND TS = (distribution)	199	29	15	14
ALL = (temperate) AND TS = (assemblage) AND TI = (macrophyte)	13	4	2	1

Table 1. Cont.

Web of Science Search Terms	Initial No. of Results	No. of Results After Reading the Title and Removing Duplicates	No. of Results After Reading Abstract	No. of Results After Reading Full Text
ALL = (temperate) AND TS = (distribution) AND TI = (macrophyte)	18	1	0	0
ALL = (pond) AND TS = (assemblage) AND TS = (macrophyte)	142	13	10	8
ALL = (ditch) AND TS = (assemblage) AND TS = (macrophyte)	19	4	3	3
ALL = (stream) AND TS = (assemblage) AND TS = (macrophyte)	212	9	8	5
				39

### 3. Results

The review demonstrates that there are distinct differences between the effects of abiotic factors on bryophytes and those on vascular macrophytes of different morphological forms. This is evidenced in Table 2, which summarises the findings of the effects of different abiotic factors on the various classes of aquatic plants. For instance, whilst shading and velocity have a negative relationship with vascular richness and a positive relationship with bryophyte richness, the reverse is true for the size of a water body, depth and concentration of nitrogen (Table 2). Vascular macrophyte richness has a negative relationship with distance to a stream source, isolation, the proportion of surrounding land that is woodland, total phosphorus concentrations and pH (Table 2). The strength of the influence of substrate size, the proportion of surrounding land that is arable and water body size differs between vascular macrophyte morphologies (Table 2). There is not enough research to understand the impact of hydroperiod or conductivity on macrophyte richness, and generally, data are lacking regarding the factors that influence the distribution of bryophytes in SWBs (Table 2).

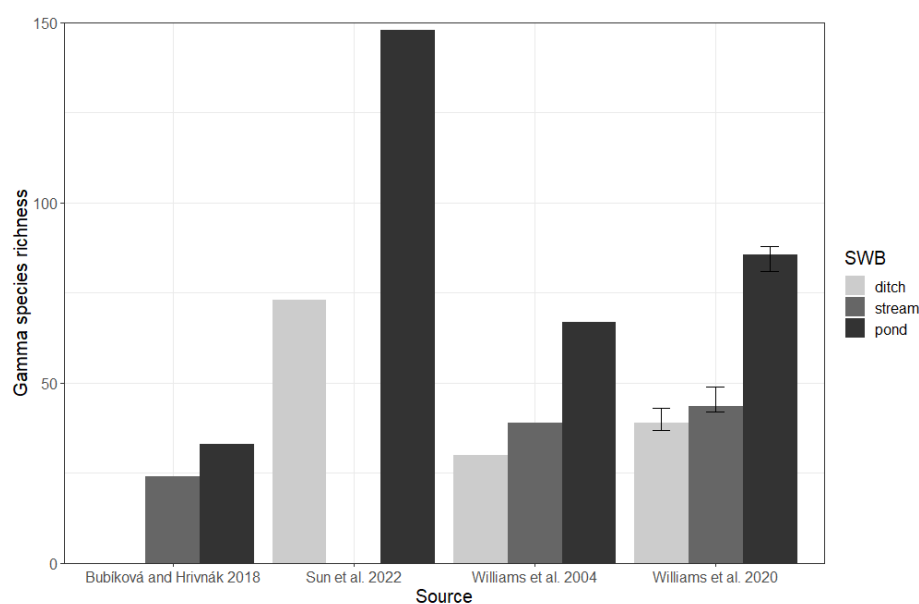
**Table 2.** An overview of the relationship <sup>1</sup> between the abiotic factors investigated in this review and the four different vascular macrophyte morphologies and bryophytes. The number of peer-reviewed papers used for each abiotic factor is also listed.

Category	Factor	Vascular Macrophytes				Bryophytes	No. of Papers
		Emergent <sup>a</sup>	Free-Floating <sup>b</sup>	Rooted Submerged <sup>c</sup>	Submerged with Floating Leaves <sup>d</sup>		
Water body morphology	Substrate size	--	<b>0</b>	-	+/-	++	8
	Water velocity	--	--	-	+/-	+	9
	Shade	--	--	--	--	++	5
	Depth	<b>++ ≤ ~0.9 m</b> <b>-- &gt; ~0.9 m</b>	<b>++ ≤ ~0.9 m</b> <b>-- &gt; ~0.9 m</b>	+/-	<b>++ ≤ ~0.9 m</b> <b>-- &gt; ~0.9 m</b>	-	9
	Hydroperiod	+/-	+/-	+/-	+/-	No data	4
	Isolation	-	+/-	-	-	No data	7
	Distance from source	--	--	--	--	No data	3
	Size of water body	+	++	++	++	-	11
Surrounding land use	Arable	++	<b>0</b>	+	No data	No data	4
	Urban	+/-	<b>0</b>	+	No data	No data	2
	Woodland	-	-	-	-	No data	3
Water chemistry	Conductivity	+/-	+/-	+/-	+/-	No data	10
	SRP	No data	+	No data	No data	No data	2
	TP	--	--	--	--	No data	3
	Nitrogen	++	+	++	++	-	4
	pH	--	--	--	--	No data	7

<sup>1</sup> “++” and “--” indicate that all studies report a statistically significant (where tested) positive or negative relationship, respectively. “+” and “-” signal that the majority of studies report a statistically significant positive or negative relationship, respectively, but that a small number of studies report a non-significant relationship or that no relationship was present. “0” indicates no relationship. “+/-” indicates that there is no overall consensus, with papers reporting conflicting findings. “No data” refers to combinations where no data were available. Values highlighted in **bold** indicate that there is sufficient research to identify the nature of the relationship. SRP: soluble reactive phosphorus, TP: total phosphorus. <sup>a</sup> Roots are embedded into the substrate, with the leaves and flowers standing vertically out of the water. <sup>b</sup> Either found on the surface of the water or are completely submerged, with the roots unattached to the substrate. <sup>c</sup> A completely submerged plant with roots embedded into the substrate. <sup>d</sup> Roots are embedded into the substrate, but the leaves float on the surface of the water.

### 3.1. Waterbody Type

Although limited research exists, there is a general consensus that ditches, streams and ponds support macrophyte assemblages with different levels of species richness and composition (Figure 2). An intensively monitored, long-term study (75 m<sup>2</sup> of 60 ponds, ditches and streams were surveyed annually for 8 years) investigating macrophyte distribution among SWBs in three catchments in Leicestershire, UK, identified a clear difference in the type of macrophytes present between the three different types of SWB [24]. Ditches exclusively contained emergent plants, whilst streams contained mostly emergent plants with a few submerged species [24]. Ponds, on the other hand, contained a mixture of emergent, submerged and floating macrophyte species [24]. Additionally, the gamma richness significantly ( $p < 0.001$ ) differed between SWB types, with ponds found to have an average of 85.5 species per year, compared to 43.5 species in streams and 38.9 species in ditches [24]. This is supported by an earlier year-long study in Oxfordshire, UK, that surveyed 75 m<sup>2</sup> of 20 ponds, ditches and streams once [15]. Here, they found that there were more macrophyte species located in ponds (67 species) than in streams (39 species) or ditches (30 species; no significance provided) [15]. Similarly, Bubíková and Hrivnák [25] sampled a 100 m<sup>2</sup> section of 25 ponds and 25 streams twice within a year in western Slovakia and found that ponds had a macrophyte gamma richness of 33 species, compared to the 24 recorded in streams, but this was not statistically significant. Ponds were also found to have a significantly ( $p < 0.005$ ) higher gamma richness than ditches in a three-year study by Sun et al. [26] in Southern China. They sampled 225 1 m<sup>2</sup> quadrats across 40 ponds and 90 1 m<sup>2</sup> sampling sites across 26 ditches once [26]. Within ponds, 148 macrophyte species were recorded, compared to only 73 in ditches [26]. However, it is important to note that the water in the ditches surveyed in this study had a high velocity ( $0.85 \pm 0.54$  m/s), faster than the rivers studied. This suggests that the observed pattern may only be true for ditches with fast-moving water, which resemble streams and rivers, and not those with slow-moving water, which resemble ponds and are rarely studied. A potential explanation for this recurring pattern is that ponds are more heterogeneous than streams or ditches, as they are isolated ecosystems [15]. Two adjacent ponds could have extremely different substrates, nutrient levels, depths and/or sizes. Therefore, multiple ponds in close proximity can support a wide variety of macrophyte species, each with its individual niches.



**Figure 2.** Macrophyte gamma species richness of ditches, streams and ponds reported by four studies (see text for detail) [15,24–26]. The average species richness is provided, whilst bars for Williams et al. study from 2020 [15] show the range of annual species richness recorded over eight years of study.

The finding that ponds have a greater gamma richness than streams and ditches is a generality but not an absolute. Mountford and Graham [23] found that the Fens, which is a 4000 km<sup>2</sup>, intensively farmed area in Eastern England, with 2860 km of ditches, contains 217 macrophyte species (79 submerged, 98 emergent, 14 submerged with floating leaves and 26 floating species). The greater species richness could be attributed to the fact that Fenland ditches typically have a constant water level and slow velocity or due to their location, which is on a drained wetland with greater peat abundance. This means that it has remnants of biodiversity and is highly minerotrophic, creating ideal conditions for healthy macrophyte populations.

### 3.2. Substrate

The substrate type influences the richness and composition of macrophytes found in SWBs. Hrivnák et al. [27] found that substrate type alone was shown to account for 5.8% of variance in macrophyte assemblage when sampling 100 m of 39 Slovakian streams once each using a “Plant Mass Estimate” scale. A longer-term study surveying nine Slovenian streams (93 km sampled across four years) reported that substrate type was the most influential driver of macrophyte distribution [28]. Similarly, Svitok et al. [29] sampled 100 m<sup>2</sup> of 40 of each of ponds, ditches and streams in Slovakia twice and determined that the proportion of fine sediment was the best indicator of macrophyte diversity across all SWB types. In ditches, substrate type was the only significant ( $p < 0.05$ ) predictor of macrophyte diversity [29]. This study also found that ditches containing more than 30% sand cover had lower species richness.

The influence of substrate differs depending on the type of macrophyte (Table 2), although inconsistencies in nomenclature make it difficult to draw overall conclusions. Weekes et al. [30] used the River Macrophyte Database, which collates data from a number of sources in Ireland, including the Environmental Protection Agency and PhD theses. They used data on 103 Irish streams and found that non-vascular bryophytes favoured coarser substrates such as gravel (2–16 mm diameter; all grain sizes according to Wentworth [31] (1922); other substrate classifications are converted to this classification throughout), cobble (64–256 mm) and boulder (>256 mm), whereas vascular plants were associated with clay (<0.004 mm), silt (0.004–0.061 mm) and sand (0.061–2 mm). This is supported by Hrivnák et al. [27], who found that some bryophyte species occur exclusively on coarse substrates (no information on grain size provided) and that vascular plants were commonly found in water bodies with the finest substrate types. Baattrup-Pedersen and Riis [32] sampled fourteen Danish streams using 150 25 cm<sup>2</sup> quadrats in each stream. They found that emergent species were associated with finer substrates such as clay, silt and sand (no statistical significance provided), whilst the richness of submerged macrophytes had a significant ( $p < 0.05$ ) positive relationship with the substrate types gravel and pebble [32]. Kuhar et al. [28] found a conflicting influence of the substrate on the abundance of two submerged vascular macrophytes, whereas *Elodea canadensis* Michx. was associated with sand and silt, *Myriophyllum spicatum* L. favoured coarser substrates such as gravel.

A few studies found that a heterogeneous substrate promotes the most species-rich macrophyte communities. Baattrup-Pedersen and Riis [32] showed that as substrate heterogeneity increased, so did macrophyte coverage and diversity ( $p < 0.01$ ). Here, substrate type ranged from coarse stone to fine sand and substrate heterogeneity was measured using an index of similarity between the substrate type of two neighbouring quadrats in a stream. A stream with an average substrate heterogeneity of 0.51 (0.37–0.66) had a species richness of 62, whilst another with a substrate heterogeneity of 0.38 (0.24–0.53) had a species richness of 52 macrophytes [32]. A different study, which surveyed the 785 km length of 39 Slovenian streams, found that *Elodea canadensis* was associated with heterogeneous substrates containing a mixture of gravel, sand and silt [33]. Rolon et al. [34] also found that macrophyte richness in Southern Brazil (four surveys were carried out over a year, each covering the entirety of 15 wetlands) was positively correlated with habitat diversity,



which in their study referred to a combination of substrate heterogeneity and varying water depth (no statistical analysis provided).

There are a variety of reasons why the substrate type may impact the distribution of macrophytes within a SWB. Firstly, it could control how readily a macrophyte will dislodge, with macrophytes potentially being more vulnerable to dislodging in coarser substrates such as pebbles, cobbles and boulders. This would be particularly problematic for rooted submerged and emergent macrophytes, whose roots penetrate the substrate and may explain why many studies found that rooted macrophytes were not associated with coarser substrates [27,28,30,32]. In contrast, bryophytes have rhizoids instead of roots [35], and these are able to attach to the surface of coarse substrates, allowing them to thrive under these conditions. Additionally, Li et al. [36] undertook laboratory experiments that showed a positive association between substrate porosity and both the height and biomass of *Vallisneria spiralis* L. The authors suggested that increased substrate porosity may enhance how readily the macrophyte can acquire nutrients from the substrate. This will not impact free-floating macrophytes, which acquire nutrients directly from the water.

### 3.3. Water Velocity

Water velocity is one of the most influential drivers of macrophyte distribution in SWBs with lotic water [26,37]. Zelnik et al. [38] found that velocity accounted for up to 4% of the variance in macrophyte biotype when sampling 100 m stretches of 33 Slovenian streams over a five-year period. Moreover, Kuhar et al. [28] identified it as the parameter that best explains macrophyte assemblages. Vaughn and Davis [39] investigated the occurrence of the emergent vascular macrophyte *Justicia americana* (L.) Vahl in streams within the Cahaba River Watershed, USA, using one aerial photograph of each of the 24 sites, and found that water velocity (ranging from 0 to 0.55 m/s) was a good predictor ( $p < 0.01$ ) of the occurrence of *J. americana*. The same study used models to predict the probability of *J. americana* occurring under different velocities and found that for a velocity of 0.064 m/s, there was a 95% chance of it occurring, whereas, at 0.56 m/s, it was <1% [39]. Riis and Biggs [40] investigated 50 m of 15 New Zealand streams on a single occasion and detected a notable reduction in macrophyte abundance at velocities > 0.4 m/s. The submerged vascular macrophyte, *Myriophyllum triphyllum* Orchard, was not observed at all at velocities above 0.4 m/s, whilst the vascular macrophyte *Ranunculus trichophyllum* Chaix (rooted with floating leaves) was found at velocities up to and including 0.75 m/s [40]. Weekes et al. [30] determined that rooted macrophytes were sensitive to high velocities (defined there as velocities > 0.5 m/s) because high water velocity dislodges them from the substrate. Westwood et al. [41] surveyed the entire length of six streams once only within the Thames basin, UK, and found that the occurrence of the vascular macrophyte, *Ranunculus peltatus* Schrank (rooted with floating leaves), was significantly ( $p < 0.05$ ) positively correlated with velocity (no range provided).

In contrast to vascular macrophytes, bryophytes, which have no true roots and so do not experience dislodging, have been shown to survive in SWBs with high (>0.5 m/s) velocities (no statistical analysis provided) [30]. Another reason that bryophytes may favour faster-flowing waters is that they can only acquire carbon dioxide and nutrients from the water, so they require a constant replenishment of fresh water, which is provided under high velocities [35].

The variation in water velocity was shown to impact macrophyte distribution in 44 Danish streams, where 100 m of each stream was surveyed just once [42]. This study found that the greatest species richness and diversity was located in streams with low flow variability as well as long periods of low flow (no statistical analysis provided). Here, flow variability was calculated using a number of different indexes, including the consistency of velocity over a year, the difference between flow in two consecutive days and a measure of the spread of velocity over time.



### 3.4. Conductivity

Research suggests that there is a positive relationship between conductivity and macrophyte richness within SWBs. Conductivity describes the water's potential to conduct electricity via dissolved salts and inorganic materials, meaning that SWBs with a greater conductivity have greater concentrations of dissolved salts. A significant ( $p < 0.05$ ) positive correlation between conductivity (ranging from 8 to 945  $\mu\text{S}/\text{cm}$ ) and macrophyte richness was found by Kochjarová et al. [43], who sampled 24 Slovakian ponds once. Sun et al. [26] also found that conductivity was significantly ( $p < 0.005$ ) positively correlated with macrophyte richness in SWBs. Here, conductivity levels ranged from 45 to 483  $\mu\text{S}/\text{cm}$  in ponds and 127 to 562  $\mu\text{S}/\text{cm}$  in ditches [26]. Rolon et al. [44] reported a significant ( $p < 0.001$ ) positive correlation between conductivity and macrophyte richness in ten ponds in Southern Brazil (each pond was sampled eight times over a two-year period) when acting in conjunction with the variable hydroperiod (a measure of the length of time a waterbody contains water). Similarly, Mauchamp et al. [45] detected a significant ( $p < 0.05$ ) positive correlation between macrophyte richness and conductivity (ranging from 487 to 3985  $\mu\text{S}/\text{cm}$ ) in 11 drainage ditches. These ditches were sampled annually over a four-year period in Western France, using 25 0.5-m<sup>2</sup> quadrats along a 125 m transect in each ditch. Another study, which sampled 1 km of 41 streams in Central Argentina three times, found a positive correlation between conductivity and macrophyte richness for floating species, but there was a negative correlation (no statistical analysis for conductivity provided) for emergent macrophytes found on the margins of SWBs [46]. The mean conductivity measured within each season in that study ranged from 1225 to 6012  $\mu\text{S}/\text{cm}$  [46], larger than the conductivity levels reported in most other studies.

In contrast to the numerous reports of a positive relationship between conductivity and macrophyte richness, Maltchik et al. [47] found that conductivity was significantly ( $p < 0.05$ ) negatively correlated with macrophyte richness in ditches running through rice fields in Southern Brazil when combined with the effect of water temperature. This study used three 0.25 m<sup>2</sup> sampling sites in each of the four ditches, which were each surveyed once. This is supported by Van Onsem and Triest [48], who also found that conductivity (ranging from 374 to 942  $\mu\text{S}/\text{cm}$ ) had a significant ( $p < 0.05$ ) negative correlation with macrophyte community composition in 16 ponds in Belgium. In this study, each pond was sampled using three transects in two consecutive summers, and conductivity was the only abiotic factor found to impact macrophyte composition (other abiotic factors included within the study were pH, nitrogen and phosphorus concentrations, and depth). Francová et al. [49] is the only study in temperate SWBs to find that conductivity (ranging from 407 to 974  $\mu\text{S}/\text{cm}$ ) had no influence over the macrophytes present. Here, they sampled twenty fishponds using between three and five transects in each (depending on pond size), twice in the Czech Republic.

There is little research into whether water conductivity influences the growth of macrophytes, meaning it is difficult to understand why conductivity impacts macrophytes at population levels. Coldsnow et al. [50] conducted a lab study on the impact of salinity on *Elodea canadensis*. They found that the greater levels of conductivity (2950–3197  $\mu\text{S}/\text{cm}$ ) caused by increased salinity resulted in a significant ( $p < 0.05$ ) decrease in gross primary productivity. Simmons [51] undertook a laboratory study to understand how conductivity caused by different ions impacted macrophyte health. They found that 50% inhibition of growth of *Lemna minor* L. resulted from exposure to 26,000 or 6000  $\mu\text{S}/\text{cm}$  when ions were present in the form of either potassium sulphate or sodium sulphate, respectively. This highlights potential complexities in the relationship between conductivity and macrophyte health, and the presence of different ions may explain some of the apparent contradictions in the data (Table 2).

### 3.5. Shade

Shading impacts the richness and composition of macrophyte communities in SWB (Table 2), with Hrivnák et al. [27] reporting that variation in shading accounted for 3.5%

of the variation in community composition ( $p < 0.001$ ). Shading is typically caused by riparian vegetation, such as trees, shrubs and bushes on the SWB edge. The presence of vascular macrophytes has been shown to decrease with increased shade cover, and in some situations, no macrophytes were present if more than a third of the SWB was shaded [52]. That study collated macrophyte data from over 600 sampling sites in Belgian streams from the Research Institute for Nature and Forest and the Flemish Environment Agency [52]. Shaw et al. [53] surveyed a 10-metre stretch of 175 ditches once in Oxfordshire, UK. They reported that as the percentage of shade increased (range 0 to 95%), both the taxonomic richness and coverage of macrophytes decreased, but this was not statistically significant [53]. Sayer et al. [54] identified a significant ( $p < 0.05$ ) negative relationship between macrophyte diversity and percent shade (ranging from 0 to 90%) when surveying 28 ponds in Norfolk, UK. This study used historical survey data, meaning that some ponds were surveyed only once, whereas others were surveyed multiple times over a seven-year period. Everitt and Burkholder [55] investigated macrophyte distribution in 10 streams in North Carolina, USA, surveying an area of between 12 and 156 m<sup>2</sup> biweekly over a three-year period. They found a significant ( $p < 0.05$ ) positive relationship between the percent cover of macrophytes and the levels of photosynthetic active radiation (PAR) reaching an SWB. PAR values per stream ranged from an average of  $29 \pm 3\%$  to  $93 \pm 2\%$  of values in open locations.

Bryophytes tend to dominate shaded SWBs as they require less light for photosynthesis compared to vascular plants [56] and their spores are sensitive to high levels of ultraviolet radiation [57]. Everitt and Burkholder [55] concluded that shading increased the abundance of the bryophyte *Fontinalis*. Similarly, Hrivnák et al. [27] found that shading promoted bryophyte populations in Slovakian streams, whilst Haury [58] determined that the bryophyte *Scapania undulata* L. dominated shaded sites of Kernec Brook in Northwestern France (the study stream was subdivided into 196 50-metre stretches that were surveyed monthly over a three-year period).

### 3.6. Depth

Depth and shade are intrinsically linked, as both shaded and deep SWBs have restricted light availability. Even though SWBs are rarely associated with extreme ranges in depth, this factor is still known to influence macrophyte composition and richness [37,59]. A positive relationship was found between an increased area of depth  $> 0.6$  m and species richness in 50 ponds in Northumberland, UK when sampling the entirety of each pond once using an abundance scale (no significance values provided) [60]. Similarly, a positive relationship (no significance values provided) was observed between taxonomic richness and water depth (average depth ranged from 0 to 0.57 m) by Shaw et al. [53]. Mauchamp et al. [45] also found that higher water levels (absolute range 0.18 to 0.87 m) significantly ( $p < 0.05$ ) increased macrophyte richness. These findings may be due to the fact that deeper waters are less sensitive to changes in temperature [53] or because greater depth increases SWB microtopography, providing more niches for different species and increasing species richness [60].

The three papers detailed above, which found a positive correlation between macrophyte richness and depth, all had deepest depths of  $< 0.9$  metres. Studies that investigate SWBs deeper than this start to find a negative correlation between the two variables. For instance, a significant ( $p = 0.001$ ) negative correlation was found between water depth, which ranged from 0.2 to 1.4 m, and the presence of the emergent vascular macrophyte *Justicia americana* [39]. Their study predicted that at a depth of 0.3 m, there was a 95% probability of *Justicia americana* presence and that this fell to 21% at a depth of 0.9 m [39]. Svitok et al. [29] also found that shallower ponds (depths ranging from 0.07 to 2.85 metres) supported significantly ( $p < 0.05$ ) higher levels of macrophyte diversity. Similarly, Akasaka et al. [61] found that water depth negatively influenced the presence of emergent and floating macrophytes in 55 Japanese ponds, which were each sampled entirely just once with depths ranging from 0.9 to 5.4 m; however, water depth had less impact on the

presence of submerged macrophytes (no statistics provided). This is potentially due to the fact that as depth increases, less light is able to reach macrophytes. Additionally, in deep waters, emergent macrophytes require longer stems to reach the water's surface.

Hrivnák et al. [27] also found a significant ( $p < 0.001$ ) relationship between water depth ( $0.31 \pm 0.25$  m) and macrophyte assemblages and determined that bryophytes were associated with shallower waters, whereas vascular plants were found in medium to deep waters (no measurements provided; Table 2). Unlike vascular macrophytes, bryophytes thrive in shallow waters as they are typically smaller and require a constant replenishment of carbon dioxide directly from the water, which is often provided in shallow water bodies [35].

It is important to note that SWBs with varying depths may have the greatest species richness because multiple niches will be provided for differing types of macrophytes [34]. Interestingly, Sun et al. [26] attributed their significantly ( $p < 0.005$ ) different species composition at varying depths to the function of the SWB. For instance, ditches less than 1 m in depth in this particular study were used for flood control and sewage disposal, whereas ditches with depths greater than 1 m were used for irrigation [26].

### 3.7. Nutrient Content

#### 3.7.1. Phosphorus

Macrophyte assemblage composition, diversity and richness can be impacted by nutrient concentrations within SWBs (Table 2). Phosphorus is an important nutrient for macrophytes, supporting plant growth and structure and facilitating a number of important biochemical processes. Plants are only able to acquire phosphorus when it is in the form of “soluble reactive phosphorus” (SRP) and are unable to use most forms of phosphorus included in a measure of “total phosphorus” (TP) [62]. Feijoó and Lombardo [46] illustrated that floating macrophytes were associated with SWBs with high concentrations of SRP (no statistical analysis provided), with mean seasonal values ranging from 0.05 to 0.43 mg/L. van Zuidam and Peeters [63] studied 50 ditches in the Netherlands by sampling an entire 25 m length of each ditch twice and determined that free-floating macrophytes were found at significantly ( $p < 0.001$ ) higher phosphorus concentrations (0.42–0.73 mg/L) compared to submerged macrophytes (0.10–0.22 mg/L). High phosphorus concentrations may have a stronger influence on free-floating macrophytes than on rooted submerged macrophytes because the former acquire all nutrients directly from the water.

Francová et al. [49] reported that high concentrations of TP (ranging from 21 to 860  $\mu\text{g/L}$ ) had a negative impact on macrophyte communities. This is supported by Leyssen et al. [52], who found a significant ( $p < 0.05$ ) negative relationship between TP (ranging from 132 to 973  $\mu\text{g/L}$ ) and the presence of the vascular macrophyte *Ranuncion fluitantis* Lam (submerged with floating leaves). Similarly, Johnson and Angeler [64] found a significant negative relationship between TP (no range provided) and macrophyte richness ( $p < 0.001$ ), abundance ( $p < 0.01$ ) and diversity ( $p < 0.001$ ) in 35 streams located in Northern Germany, Denmark and Southern Sweden. Here, a 100 m length of each stream was surveyed once. This pattern is potentially due to elevated TP concentrations promoting eutrophication, which reduces the amount of sunlight reaching macrophytes [65].

#### 3.7.2. Nitrogen

The impact that nitrogen has on macrophyte communities can vary based on taxonomic groups and morphology (Table 2). Nitrogen plays a crucial role in plant photosynthesis, as it is a major component of chlorophyll [66]. Vascular plants outcompete bryophytes in nitrogen-rich environments by utilising nitrogen to promote growth [67]. Arts et al. [68] found that the total shoot length of the vascular macrophyte *Myriophyllum spicatum* had a significant ( $p < 0.05$ ) positive relationship with nitrate-nitrogen concentrations in experimental ditches in the Netherlands. Feijoó and Lombardo [46] found that floating macrophyte species were associated with low to medium nitrate concentrations, whilst emergent species preferred medium to high nitrate concentrations (no statistical analysis provided, no definitions provided for “low”, “medium”, or “high” concentrations). In

this study, average seasonal nitrate concentrations ranged from 0.13 to 3.08 mg/l [46]. Hrivnák et al. [27] investigated the influence of nitrite, nitrate and ammonium, which had concentrations of  $0.3 \pm 1.3$  mg/L,  $1.5 \pm 1.6$  mg/L and  $0.5 \pm 2.4$  mg/L, respectively, on macrophyte distribution. They found that neither nitrate nor ammonium concentrations had a significant impact on macrophyte distribution. However, vascular plants were associated with higher nitrite concentrations, and bryophytes were significantly ( $p < 0.05$ ) associated with SWBs with low nitrite content. Bryophytes are slow-growing and require far less nitrogen than vascular plants [69], so they can thrive in nitrogen-poor waters where vascular plants cannot survive.

### 3.8. Land Use

The type of land surrounding a SWB influences the macrophytes present (Table 2). Akasaka et al. [61] found that the diversity of submerged macrophytes was best explained by the type of land within 10 m of the SWB, whereas for floating leaves and emergent macrophytes, it was land use within 500 and 1000 m, respectively. The same study found that the proportion of farmland surrounding the SWB was positively correlated with emergent macrophyte richness, whilst there was a negative relationship between macrophyte diversity and the proportion of urban land surrounding the SWB (no statistical significance provided) [61]. Pereira et al. [70] surveyed 40 ponds in Southern Brazil and found that the proportion of surrounding land that was either agricultural or urban significantly ( $p < 0.05$ ) positively influenced the richness of emergent macrophytes, whilst the proportion of surrounding land that was urban significantly ( $p < 0.001$ ) positively impacted submerged macrophyte richness. Neither the proportion of urban nor agricultural land use influenced the richness of floating macrophytes [70]. This study used a 3 min non-linear transect, with sampling ending once two transects found no new species. This meant the number of transects in each pond ranged from 5 to 34. Kuhar et al. [33] surveyed 39 streams (785 km in total) in Slovenia and determined that the occurrence of the submerged vascular macrophyte *Elodea canadensis* was significantly ( $p < 0.001$ ) impacted by the surrounding land use type and was more abundant in SWBs surrounded by agricultural land (no statistical analysis provided).

In a study investigating the impact of land use on macrophyte richness in 36 ditches in Eastern England, the ditches surrounded by arable land supported a gamma richness of 8 macrophyte species, whereas those running through pasture sites supported 21 species [71]. The same study conducted a transplant experiment and found that submerged macrophytes thrived in ditches surrounded by pasture, whilst ditches in arable land were associated with emergent macrophytes and were less species diverse [71]. Arable ditches also had a smaller total macrophyte biomass, potentially because these ditches experienced eutrophication from fertiliser exposure and had a lower sediment organic matter content than pasture ditches [71].

Notably, a significant ( $p < 0.05$ ) negative relationship was found between the proportion of surrounding woodland and macrophyte richness [45], potentially due to the shading from riparian vegetation in woodland areas. The presence of the submerged with floating leaves species *Ranunculus peltatus* had a significant ( $p < 0.05$ ) positive correlation with the proportion of semi-natural grassland [41]. Francová et al. [72] found that the greatest species diversity was located in SWBs surrounded by a “mosaic” of arable land, grassland and forest.

Leysen et al. [52] is the only study found that reported no relationship between surrounding land use and macrophyte distribution. They used multiple buffer sizes (50, 100 and 250 m) to investigate the impact of surrounding land use type on macrophyte distribution. This study also investigated the impact of land use intensity (measured by using three arbitrary categories of “low”, “medium” and “high”) in conjunction with land use type, which also yielded no significant relationship. However, this may be because of other factors that are associated with land use and that can lead to either positive or negative effects on macrophyte richness. For instance, even though arable land is likely to

result in less shading from riparian vegetation than woodland, there will be a counteracting potential for pollution from agricultural chemicals.

### 3.9. Hydroperiod

The majority of research supports the idea that the hydroperiod (the length of time that a SWB contains water) influences macrophyte assemblages in SWBs; however, there is currently no consensus as to the direction of the relationship (Table 2). Francová et al. [72] found that fishponds that were drained annually so had a shorter hydroperiod and had a significantly ( $p < 0.05$ ) greater macrophyte cover than fishponds which did not undergo regular drainage. Similarly, ditches in Western France that underwent frequent dry periods had a significantly ( $p < 0.05$ ) higher species richness than those with a longer hydroperiod [45]. The same study found that ditches can experience 144 days with no water without any negative effects on the macrophyte community [45]. On the other hand, Rolon et al. [44] established that hydroperiod significantly ( $p < 0.001$ ) impacted species composition and had a significant ( $p < 0.001$ ) positive relationship with macrophyte richness, indicating that the less time a SWB spends dry, the more macrophyte species were present. This study measured the “hydroperiod” by recording how many out of the eight samples taken were with or without water, thus giving no indication as to the length of time the SWBs had actually been dry. Pätzig et al. [73] collated data from a number of different pond monitoring studies between 1993 and 2008 in Northeastern Germany and found a significant ( $p < 0.05$ ) positive relationship between hydroperiod and species richness. Notably, this study found a negative relationship (no significance provided) between the number of Red List species and hydroperiod [73].

### 3.10. Isolation

MacArthur and Wilson’s [74] island biogeography theory can be applied to the relationship between pond isolation and macrophyte communities, with species richness having an inverse relationship with pond isolation (Table 2). Bosiacka and Pieńkowski [75] found a negative relationship (not statistically significant) between isolation and species richness in 50 Polish ponds (the outer boundary of each pond was surveyed once). Similarly, Biggs et al. [76] used data from the UK National Pond Survey (which sampled 150 ponds) and found a significant ( $p < 0.001$ ) negative relationship between the distance to other ponds and species richness of emergent macrophytes. Rolon et al. [34] also identified a significant ( $p < 0.01$ ) negative relationship between species richness and the average distance to the nearest three ponds, as well as a significant ( $p < 0.05$ ) relationship between macrophyte composition and isolation. Jeffries [77] found a positive relationship (no statistical significance provided) between species dissimilarity and isolation in 30 ponds in Northumberland. This study used 81 1 m<sup>2</sup> quadrats to survey each pond once only. Sun et al. [26] found that SWBs within a 4 km radius had similar macrophyte compositions. Interestingly, this study also found that isolation impacted macrophyte diversity in ponds more than in ditches [26]. It is thought that isolation reduces macrophyte richness as well as species similarity because vascular plants produce seeds, which require wind or animal dispersal [34].

In contrast to other findings in the literature, Pereira et al. [70] found that pond isolation (measured by the number of other SWBs present in a 500 m radius) and species richness had a significant ( $p < 0.01$ ) positive correlation. They suggest that this observed pattern is due to the fact that many of the macrophyte species they studied, specifically the floating species, reproduce asexually. Asexual fragments can be transported long distances by birds into geographically distant ponds, making these distant ponds functionally connected [70]. This may explain a lack of correlation between isolation and species richness, but the reasons for the observed positive correlation are not known.



### 3.11. Distance from Source

Whilst isolation influences macrophyte assemblages in ponds, the distance of a stream section from the source of the stream is known to have a strong influence on macrophyte communities within streams (Table 2). Zelnik et al. [38] attributed 15% of variability in macrophyte biotype to distance from the source. Rolon et al. [34] determined that there was a significant ( $p < 0.005$ ) negative relationship between the distance to the source (which ranged from 7 to 23 km) and emergent macrophyte richness. This is supported by Zelnik et al. [38], who found a significant ( $p < 0.001$ ) negative correlation between distance from the source and the number of taxa and abundance of macrophytes. This pattern is potentially due to the fact that water quality tends to decrease further downstream [78]. Westwood et al. [41] found that macrophytes were associated with downstream (distance from the source ranged from 0.73 to 20.52 km) conditions (no statistical significance provided) due to the fact that upstream reaches experience more variable flow regimes.

### 3.12. Size of Water Body

There is a general consensus that the surface area of a SWB impacts macrophyte richness, with Bosiacka and Pieńkowski [75] claiming that pond size explained 28% of the total variation in species richness of Polish ponds. Similarly, Møller and Rørdam [79], who surveyed 27 Danish ponds, each for exactly two hours twice, reported that pond area (ranging from 0.02 to 0.14 ha) was the best predictor of species richness due to the fact that a larger area provides a greater chance of the pond receiving a migrating propagule. Pereira et al. [70] concluded that pond size (average size was  $0.61 \pm 0.51$  ha) was significantly ( $p < 0.05$ ) related to species composition of emergent species and that there was a significant ( $p < 0.01$ ) positive correlation between pond size and the richness of floating macrophyte species. Similarly, Jeffries [60] found a positive correlation between the richness of emergent taxa and pond size (ranging from 0.01 to 0.15 ha; no statistical analysis was provided). Biggs et al. [76] reported a significant ( $p < 0.001$ ) positive relationship between species richness and pond area (range was not provided). Akasaka et al. [61] found that the species richness of macrophytes increased with pond size up to 0.5 ha but decreased for ponds larger than 0.5 ha (no statistical analysis provided). This may be due to the fact that wind stress will be severe in larger SWBs, meaning there is greater potential for damage to macrophytes. Rolon et al. [34] did not find a relationship between pond area (range 0.01–0.24 ha) and species richness. They suggested that this may have been due to the small size of their ponds; however, other studies (such as Jeffries [60]) found relationships when studying smaller ponds.

The impact of stream width varies for different types of macrophytes (Table 2). Hrivnák et al. [27] found a non-significant relationship, whereby narrower streams tended to contain species-poor bryophyte assemblages, whilst larger streams were associated with more species-rich vascular plant communities (the average stream width was  $4.1 \pm 3.4$  m). This is potentially due to the fact that narrower streams tend to have a higher water velocity [80], which promotes species-poor bryophyte populations. Westwood et al. [41] found that the presence of the vascular macrophyte *Ranunculus peltatus* was significantly ( $p < 0.05$ ) positively correlated with stream width. Similarly, Leyssen et al. [52] detected a positive correlation between stream width and the abundance of submerged vascular macrophytes (no significance values provided). However, it is important to note that even though Baattrup-Pedersen and Riis [32] also found a positive relationship between stream width (ranging from 3.3 to 8.5 m) and submerged macrophyte richness, they detected a significant ( $p < 0.05$ ) negative association between emergent macrophytes and stream width. This finding might be attributable to wider streams having increased wind stress, which will impact emergent macrophytes more so than submerged ones. An alternative possibility is that wider streams tend to also be deeper, and depth has been shown to impact macrophyte populations. For instance, Baattrup-Pedersen and Riis [32] sampled streams with a width of between 3.3 and 8.5 m and depth of 0.29 to 0.82 m, whilst Leyssen et al. [52]



studied streams with a width of 1.72–9.94 m and a depth of 0.29 to 1.3 m. This suggests that wider streams tend to be deeper.

### 3.13. pH

Water pH has been shown to impact macrophyte richness and diversity. There is a negative relationship between dissolved CO<sub>2</sub> and pH [81], meaning that in waters with a high pH, there is less CO<sub>2</sub> available for photosynthesis. For instance, James et al. [82] found that water with a pH of 7.6 had 230% more CO<sub>2</sub> available to plants than water with a pH of 8.1. Some macrophytes exclusively require carbon dioxide as their carbon source, whereas others can also use bicarbonate, so they will be less impacted by high pH levels [29]. Van Onsem and Triest [48] found that pH was one of the only (the other being conductivity) abiotic factors that impacted macrophyte composition and abundance (they also studied TP, SRP, nitrogen concentrations and water depth). Svitok et al. [29] found that waterbodies with a pH > 8.4 had significantly ( $p < 0.05$ ) lower macrophyte richness than those with a lower pH (pH ranged from 6.1 to 9.4). Similarly, Pätzig et al. [73] found a significant ( $p < 0.05$ ) negative relationship between water pH and macrophyte richness, with pH explaining 3.8% of the variation in macrophyte distribution. Hardion et al. [83] investigated the distribution of *Potamogeton coloratus* Hornem in 30 streams in Southwestern France (100 m of each stream was surveyed once) and identified that percent cover of the submerged macrophyte had a significant ( $p < 0.01$ ) negative correlation with pH ( $7.5 \pm 0.4$ ). Conversely, both Jeffries [60] and Biggs et al. [76] found that macrophyte richness and pH (no range provided for either study) had a significant ( $p < 0.001$ ) positive relationship in British ponds. Kochjarová et al. [43] also found a significant ( $p < 0.05$ ) positive relationship between species richness and pH (4.8–8.7) in Slovakian ponds. There are no studies detailing the influence of pH on bryophyte richness in SWBs (Table 2).

## 4. Discussion

### 4.1. Key Findings

This review demonstrates that macrophytes with varying morphologies and taxa favour SWBs with differing abiotic factors (Table 2). In order to conserve the full spectrum of macrophytes in temperate ecosystems, it is essential to protect SWBs with diverse conditions. For example, restoring and creating only unshaded SWBs with a fine substrate may promote vascular macrophytes but will not support bryophyte richness. It is important not to neglect SWBs associated with lower levels of macrophyte richness. For instance, whilst ponds were shown to support the highest levels of macrophyte richness compared to other SWB types (Figure 2), it is important to conserve macrophyte communities in all types of SWBs, as ditches and streams can contain healthy macrophyte populations in an otherwise low-biodiversity landscape.

### 4.2. Knowledge Gaps

Several of the factors where there is currently a lack of knowledge (Table 2) will be subject to modification by climate change. For instance, climate change will result in shorter hydroperiods in many areas [84,85], whilst warmer surface waters [86] will increase conductivity [87]. The impact of these on macrophyte communities is unknown due to a lack of relevant research (Table 2). Future research should focus on the abiotic factors that are both underrepresented in the literature and likely to change over time. This review also identifies an overall lack of research focusing on the distribution of bryophytes in SWBs (Table 2). Bryophytes play an important role in preventing sediment erosion [88], supporting invertebrate biodiversity [89] and cycling of nitrogen [90].

### 4.3. Importance of This Review

A number of physical SWB properties, which were completely excluded from previous reviews on all freshwater bodies (such as surrounding land use type, water body size and

isolation), were shown to significantly influence the distribution of macrophytes (Table 2). Discrepancies in findings between this review and previous reviews encompassing research on all freshwater bodies highlight that a review focusing specifically on SWBs was needed. For instance, Bornette and Puijalon [20] reported that bryophytes occupy deeper waters than vascular plants; however, they only considered one study, which sampled lakes > 28 m [91]. SWBs typically do not reach such depths, and this review concluded the opposite outcome.

#### 4.4. Challenges

Throughout this review, challenges arose due to inconsistent use of terminology. Here, a pond was defined as being between 25 m<sup>2</sup> and 2 ha in area [15], but many studies used different thresholds to distinguish ponds from lakes. Studies that investigated “ponds” larger than 2 ha in area were excluded from the review. Moreover, there is no quantitative definition of a stream [92], meaning that distinguishing a stream from a river is currently subjective. Many papers did not report the size of the water bodies that were investigated, so the review has included all research that the authors attributed to “streams”. Given the importance of SWBs for landscape biodiversity, the adoption of a consistent set of definitions for SWBs would benefit conservation efforts as well as academic research.

Attempting to disentangle the influence of individual abiotic factors on macrophyte distribution is challenging. For example, it was determined that ponds have the greatest species richness of all SWB types, with Williams et al. [15] attributing this to large heterogeneity between ponds. However, considering a negative relationship was detected between water velocity and species richness, the greater species richness in ponds may be attributable to a lack of significant flow as well as heterogeneity. Similarly, surrounding land use impacts both shading and nutrient content. SWBs in arable land will often have less shade from riparian vegetation; however, there are likely to be higher inputs of nitrogen and phosphorus from fertiliser runoff. Both low levels of shading and high nitrogen concentrations promote vascular macrophytes, whereas high concentrations of total phosphorus have a negative impact on the richness of vascular macrophytes. Bae et al. [93] investigated the relationships between different abiotic factors in three South Korean streams. They found that the distance from the source significantly positively correlated with conductivity, pH and stream width and the proportion of surrounding land that was urban significantly positively correlated with total phosphorus and nitrogen concentrations, conductivity and the proportion of sandy substrate [93]. Aside from total phosphorus concentrations, all these abiotic factors have been shown to positively influence rooted submerged macrophyte communities. Water velocity was shown to significantly positively correlate with gravel, cobble and boulder substrates [93], which all provide ideal habitats for bryophyte populations. Given the diversity of research approaches across the literature, this review investigated each abiotic factor as a separate entity, but this ignores cross-correlation between factors and may overlook relationships masked by the influence of confounding variables.

#### 4.5. Macrophyte Management Strategies

The 39 peer-reviewed studies used throughout this review were predominantly observational, even though SWBs provide an ideal opportunity for manipulative experiments due to their size and frequent lack of connectivity. These attributes also make SWBs an ideal candidate to implement low-effort, effective management strategies to conserve macrophyte populations. For instance, it is often possible to completely isolate ponds and headwater streams from anthropogenic influences but much less so for larger water bodies. Additionally, we can halt the removal of ponds and even restore ghost ponds, reducing pond isolation, which has risen over the last century [94]. This would promote healthier populations of vascular macrophytes (Table 2). Some conservation policies aimed at promoting biodiversity may, in fact, adversely impact macrophyte communities if not implemented with care. For instance, the EU aims to plant three billion trees by 2030 [95].

Without careful consideration and management strategies, such as leaving an unshaded buffer around the SWB, this could negatively impact the macrophyte richness of SWBs situated in the newly forested areas (Table 2).

## 5. Conclusions

For the first time, findings on the relationship between thirteen abiotic factors and macrophyte distribution in SWBs have been succinctly summarised. Results indicate that the influence of abiotic factors varies based on macrophyte morphology and taxa. The results provide important information regarding how to manage and protect macrophyte populations in an anthropogenically changing world. Throughout this review, challenges arose due to both an inconsistency in nomenclature as well as difficulty in disentangling the influence of individual abiotic factors. Topics, including specific macrophyte taxa and certain abiotic factors, which are lacking sufficient research, have been identified.

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