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Ecological interactions of habitat forming emergent vegetation

— With focus on Phragmites australis and Typha sp.

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Abstract

Stands of emergent vegetation such as the common reed (*Phragmites australis*) and members of the genus *Typha* are a key part of many freshwater and brackish shoreline ecosystems. Similar to trees in a forest, these macrophytes provide structural complexity, a source of food, and shelter from harsher abiotic conditions supporting a broad range of flora and fauna. However, in recent years, anthropogenic activities have facilitated these species to dominate their native ecosystems, forming increasingly homogenous reed beds, and furthermore to invade many non native habitats. In this text, I review the ecological interactions of habitat forming emergent vegetation with an emphasis on other macrophytes, fish, birds and invertebrates. Trends in literature highlight both the importance of emergent vegetation to aquatic ecosystems, but also the negative impact they can have when invading, or forming dense homogenous stands. The competitive exclusion of other macrophytes and physical reduction of space within stands of emergent vegetation are the main drivers that negate or reverse most of the beneficial ecological interactions of reed or *Typha* with other organisms. I also detail how various management practices have attempted to address the presented issues, with the most successful methods being those that aim to promote heterogeneity. While progress has been made, future studies should focus on the identification of optimal management practices, to pave the way for more effective conservation applications.

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1. Introduction

Macrophytes are aquatic plants that grow in water, or the transition zone between water and land. They can be categorised by the area of a water body that they grow in, resulting in a generally agreed upon **three** types of macrophytes (Cronk & Fennessy, 2016). **Floating** vegetation, the leaves of which float on the water surface, while the rest of the plant grows beneath the surface. Floating vegetation can either be attached to substrate via the stem, or are free floating, with roots hanging down. **Submerged** vegetation grows attached to the substrate, and entirely underwater. Lastly, **Emergent** vegetation also grows attached to the substrate, however these macrophytes then penetrate the water's surface and continue to grow in the open air.

Much like their terrestrial counterparts, macrophytes add structure and nutrient cycling to aquatic environments, providing the basis for a more diverse ecosystem. They play a crucial role in coastal ecosystems through habitat/shelter provision (Ince *et al.,* 2007, Thomaz, 2021), food provision (Ince *et al.,* 2007), nutrient cycling (Thomaz, 2021) and sediment stabilisation (Madsen *et al.,* 2001). Furthermore, macrophytes may also filter/improve water quality (Dhote & Dixit, 2009) and reduce shoreline erosion (Madsen *et al.,* 2001). These benefits are often not limited to purely aquatic organisms . Many birds (Bibby & Lunn, 1982), invertebrates (Andersen *et al.,* 2021) and mammals (Carter & Bright, 2003) also utilise macrophytes, in particular emergent vegetation. This interaction between emergent vegetation and semi-aquatic organisms can facilitate ecological and biogeochemical interactions between the terrestrial and aquatic realms.

Emergent aquatic species such as the common reed (*Phragmites australis*), hereafter referred to as reed, and *Typha sp.* (also known as "cattail" or "bulrush") are competitively dominant species of macrophytes in many temperate freshwater and brackish coastal habitats (Bansal *et al.,* 2019: Packer *et al.,* 2017). *"Typha"* describes a number of congeners, some native in North America, and others invasive including the hybrid *Typha x glauca* (Bansal *et al.,* 2019), which is most frequently the focal species of *Typha* literature. For the purpose of this review, I will refer to the genus rather than individual species. Reed and *Typha* form dense homogenous "beds" (Figure 2. c) typically spanning across the transition zone from solid dry ground to water saturated substrate, to submerged aquatic substrate (Bansal *et al.,* 2019: Packer *et al.,* 2017). The plants themselves can grow several meters in height, and are physically sturdy, providing structural complexity both above and below water (Bansal *et al.,* 2019: Packer *et al.,* 2017). Emergent vegetation beds can therefore be considered a habitat in their own right. Reed also has a multitude of interactions with humans. It provides a number of ecosystem services such as protecting shorelines against wave exposure (Ostendorp, 1993). It is also often harvested for use in construction (Köbbing *et al.,* 2013), livestock fodder (Köbbing *et al.,* 2013), paper production (Brix *et al.,* 2014: Köbbing *et al.,* 2013), bioenergy (Carson *et al.,* 2018) and is a significant source of international trade (Wichmann & Köbbing 2015). These aforementioned properties mean it naturally has a suite of ecological interactions with organisms in both aquatic and terrestrial ecosystems, and is also subject to various anthropogenic management techniques.

Despite these benefits, excess emergent vegetation can also be problematic. These macrophytes are typically strong competitors, and under certain conditions, they can quickly dominate and then degrade coastal ecosystems. For example, nutrient enrichment (eutrophication) and reduced grazing has likely lead to the expansion and further dominance of reed in the Baltic Sea (Pikkänen *et al.,* 2013) and Chesapeake Bay (Sciance *et al.,* 2016). Furthermore, these strong competitors can easily lead to disruption and eventual degradation of other macrophytes when introduced to a novel habitat, as is the case with some invasive species of *Typha* in the great lakes of North America, which have likewise been facilitated by eutrophication and a lack of grazing (Bansal *et al.,* 2019). Lishawa *et al.,* (2010) also identify climate change induced declines in water level as a stimulant for *Typha* invasion. The primary mechanism for this degrading of habitats is the reduction in macrophyte biodiversity. Emergent vegetation produces large volumes of litter through the accumulation of dead plant parts, which restricts physical space and reduces light penetration to the water surface, preventing the growth of new plants (Vaccaro *et al.,* 2009). Consequently, the reduction in macrophyte biodiversity can then rapidly translate to a reduction in ecosystem biodiversity (Bansal *et al.,* 2019), with some studies identifying possible positive feedback loops in favour of emergent vegetation, further accelerating the rate of decline (Tuchman *et al.,* 2009).

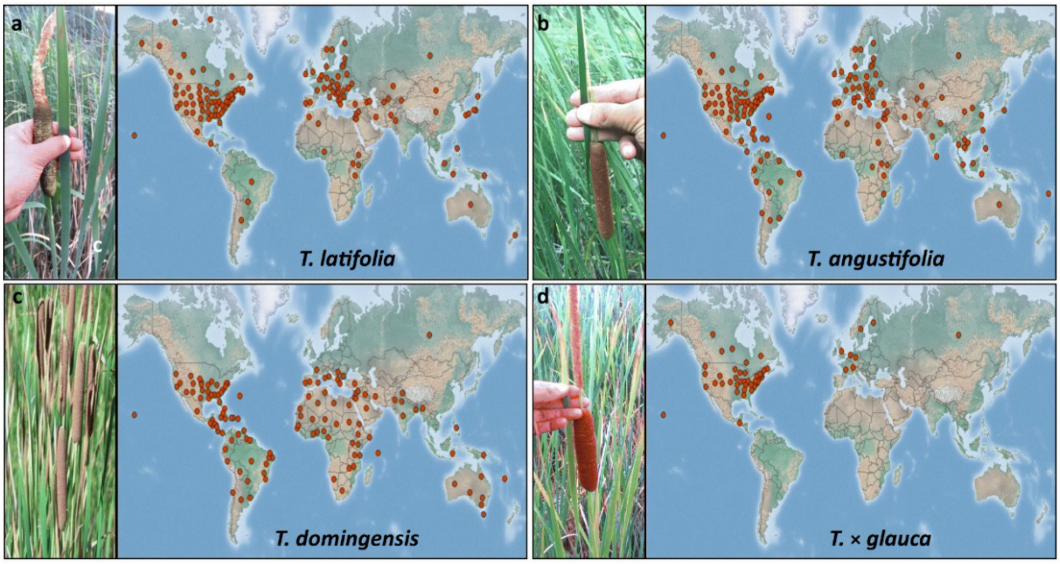

Figure 1. From Bansal et al., 2019, depicting the physical appearance and global distribution of Typha sp. (https://link.springer.com/article/10.1007/s13157-019-01174-7)

Anthropogenic activity has, in some ecosystems, facilitated the expansion of reed and *Typha.* Agricultural run-off increases nutrients in wetland systems and can allow reed to outcompete other macrophytes (Li *et al.,* 2021). Climate change induced declining water levels have also stimulated the invasion of *Typha* in the North American great lakes (Lishawa *et al.,* 2010). These macrophytes could therefore also be considered as the mediating organism for the indirect interactions between humans and all of the aforementioned organisms. This theory has already been proposed to describe long-term declines in aquatic plant diversity (Pitkänen *et al.,* 2013: Silliman & Bertness, 2004). Reed expansion in turn can negatively impact anthropogenic development and activity, for example by degrading pastural land (Bansal *et al.,* 2019). It is therefore important that this emergent vegetation, especially in environments where it is invasive, is effectively managed. Considering the practical applications of harvested reed, there is no reason why such an endeavour should warrant a net cost. In an ideal scenario, reed based Industries will employ well researched management techniques in order to sustainably continue their business while simultaneously contributing to the biodiversity of the ecosystem. A good case study for this can be found in the Liaohe Delta, in China, where reed is harvested to create pulp for paper, in the process creating jobs and benefitting local biodiversity (Brix *et al.,* 2014).

There is a growing body of literature investigating both the potential uses of reed, including biofuel, construction material, animal feed and more as well as management techniques. It is therefore important that researchers conducting these studies, as well as stakeholders who utilise the reed as a resource or manage a reed bed, are aware of the potential ecological implications of their actions. This combined with invasions and increased spread/dominance of emergent vegetation, as well as subsequent positive feedback loops further emphasises the need for knowledge in this area.

This present text is intended as a review of the ecological interactions emergent vegetation, especially reed and *Typha*, can have with its surrounding biotic and abiotic environment. In this review, I aim to:

- Review changes in abiotic conditions related to presence of dominant emergent vegetation
- Evaluate the influence of emergent vegetation on other macrophytes, fishes, birds and invertebrates
- Discuss how human wetland management practices can alter the relationships between emergent vegetation and the environment
- Identify important areas for future research

Figure 2. a) Typha x glauca (Bobby McCabe, CC BY-SA 4.0, *https://commons.wikimedia.org/wiki/File:Typha_%C3%97_glauca.jpg)*
b) Phragmites australis (R.A. Nonenmacher, CC BY-SA 4.0, *https://commons.wikimedia.org/wiki/File:Phragmites_australis_SCA-3862778.jpg)*
c) A stand of Phragmites australis (photo by W. Ashworth).

2. Environmental influence of emergent vegetation

Studies investigating abiotic changes associated with *Typha* invasion have found several changes in environmental conditions. *Typha* presence correlates with increasing soil organic matter and nutrients (Lishawa *et al.,* 2010: Tuchman *et al.,* 2009), increasing plant litter (Lishawa *et al.,* 2010: Schrank & Lishawa, 2019: Tuchman *et al.,* 2009: Vaccaro *et al.,* 2009) and decreasing dissolved oxygen, water temperature (Lawrence *et al.,* 2016a: Massa & Farrell, 2020: Schrank & Lishawa, 2019) and light penetration (Lawrence *et al.,* 2016b: Lishawa *et al.,* 2015). The increased presence of litter was also associated with decreased light penetration, and decreased water temperature (Larkin *et al.,* 2012). Lawrence *et al.* (2016b) found that herbicide application on *Tyhpa* increased nutrients in the environment, but then subsequent removal of the *Typha* decreased nutrients in the environment.

Kallasvuo *et al.* (2010) measured abiotic conditions at sites with and without reed, finding that reed bed sites had a higher water temperature, higher turbidity and reduced wave exposure. Kallasvuo *et al.* (2010) did not address the potential mechanisms of these results, one plausible explanation could be reduced circulation, as a product of lower wave and wind exposure. The contradictory effects of *Typha* and reed on water temperature may be due to differing points of comparison: Reed vs bare or *Fucus* dominated substrates, *Typha* invaded habitat vs native plant dominated habitat, or differing ecosystems: Reed in the Baltic Sea, *Typha* in the great lakes of North America. Báldi (1999) investigated edge effects of reed beds, finding wind intensity to decline from a peak at the reed bed edge, air temperature to initially decrease before increasing further into the reed, and conversely humidity initially increasing before declining with distance from the reed edge. Similar to wind intensity, light intensity peaked at the edge, before a rapid decline a few meters into the reed bed, followed by a gradual increase from this trough to the end of the studied transect.

Several of these studies however, observed an association between environmental variables and the presence of emergent vegetation (Báldi, 1999: Kallasvuo *et al.,* 2010: Lawrence *et al.,* 2016a: Lishawa *et al.,* 2010: Schrank & Lishawa, 2019: Tuchman *et al.,* 2009: Vaccaro *et al.,* 2009), rather than a resultant change in environmental variable following the management of emergent vegetation (Lawrence *et al.,* 2016b: Lishawa *et al.,* 2015, Massa & Farrell, 2020). It is therefore unclear if the emergent vegetation was the cause of change, or if the change is what allowed the emergent vegetation to inhabit/dominate the studied areas. These reported abiotic conditions should therefore be interpreted with caution.

All of these studies focused on different research questions and took environmental measurements as a part of their methodology. For this reason, most of the reported environmental measures are from the common ‘field season’ meaning very little data is available for the winter months, presenting a gap in the knowledge. Dedicated studies of these environmental variables would not only provide year round environmental data, but could also include several other measurements currently absent from literature such as air temperature, wind speed and chemical analysis. Furthermore, using several points of comparison, e.g. bare substrate, substrate dominated by different macrophyte etc. could improve our understanding of how emergent vegetation actually affects local abiotic conditions.

3. Macrophytes

The effect of dominant stand forming emergent vegetation on other macrophytes is somewhat more straightforward when compared to other groups of organisms, with almost unanimous results in the literature. Studies investigate this topic either by spatial comparison (Pitkänen et al., 2013: Silliman & Bertness 2004: Tuchman et al., 2009: Vaccaro et al., 2009: Von Nummers, 2011), or by observing the removal of the emergent vegetation from an area, and monitoring subsequent changes (Boers et al., 2007: Hall et al., 2008: Lishawa et al., 2015: Lishawa et al., 2019: Lishawa et al., 2020: Neveldine et al., 2019). The main observation being that reed/Typha decrease macrophyte diversity. The mechanisms for this decrease in diversity is the competitive advantage of reed/Typha resulting from their rapid nutrient uptake, growth and expansion, while the litter they produce further reduces the available space and light for other plant species (Larkin et al., 2012: Lishawa et al., 2019: Vaccaro et al., 2009). Reproduction through rhizomes allows reed and Typha to grow and expand despite these poor conditions (Bansal et al., 2019: Packer et al., 2017).

Beyond the aforementioned competition for nutrients, light and space, several studies have also identified positive feedback loops, emphasising the ability of these macrophytes to dominate a wetland ecosystem. Tuchman et al. (2009) suggest that the litter production and soil enrichment resulting from Typha invasion may create a positive feedback loop, which further facilitates the invasion. Monks et al. (2019) highlight that Typha facilitates the invasion of another invasive species in North America, the European frogbit, Hydrocharis morsus-ranae. The frogbit is a floating macrophyte and is therefore uninhibited by the reduction in space caused by litter and so outcompetes many native submerged species (Monks et al., 2019). This may cause yet another positive feedback mechanism, where the frogbit expansion is functionally similar to litter accumulation, eventually blocking space and light for submerged species, see Figure 3.

Figure 3. European Frogbit, Hydrocharis morsus-ranae, forming a dense layer on the water's surface surrounding some ermergent vegetation. (Krzysztof Ziarnek, CC BY-SA 4.0, https://commons.wikimedia.org/wiki/File:Hydrocharis_morsus-ranae_kz10.jpg)

Frieswyk & Zedler (2006) not only observed a concurring degradation of other wetland vegetation from *Typha* invasions, but also the deterioration of the wetlands' seedbank, thus impeding the environments resilience to *Typha* invasion, possibly causing yet another positive feedback loop (Figure 4). The influence of reed invasion on seedbank composition has also been studied (Hazelton *et al.,* 2018), producing less clear results. Hazelton *et al.* (2018) compared seedbank characteristics between plots dominated by invasive reed, plots dominated by native flora, and manged plots formerly dominated by invasive reed. The results suggested that the individual abiotic conditions of each plot explained variation in seedbank characteristics rather than the presence, or former presence of invasive reed. Contrary to Frieswyk & Zedler (2006) however, Hazelton *et al.* (2018) report diverse seedbanks to be present within reed monocultures, allowing native flora to regrow following the removal of reed. One notable difference between these two studies which may help explain the contrasting results are the study sites, with Frieswyk & Zedler (2006) investigating *Typha* invasion in the freshwater great lakes of America, and Hazelton *et al.* (2018) investigating reed invasion in the brackish coastline of Chesapeake Bay.

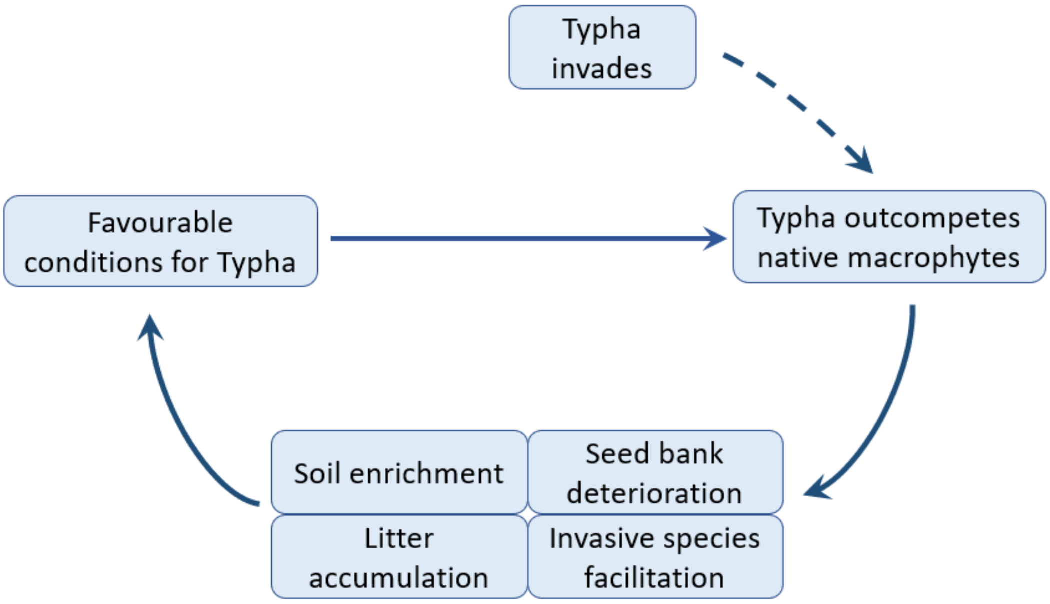

Figure 4. Possible positive feedback mechanisms based on Frieswyk & Zedler (2006), Tuchman et al. (2009), Monks et al. (2019), Vaccaro et al. (2009).

While it is established that reed have a competitive advantage over many other macrophyte species, there is further environmental conditions which tip the scales even further in favour of the reed. Li *et al.* (2021) observed reed to be more competitive when nitrogen levels are high, likely meaning that coastal environments exposed to anthropogenic nutrient inputs such as agricultural run-off may afford reed an even greater competitive advantage over other macrophytes. Vasquez *et al.* (2005) noted that reed grows faster and copes better with high salinity than many other "freshwater" species, allowing reed to dominate many estuarine, salt lake, and low salinity coastal sea environments.

In summary, literature is almost entirely in agreement that dominant monotypic stands of emergent vegetation decrease macrophyte biodiversity. This is a result of the rapid nutrient uptake, growth and expansion capabilities of emergent vegetation combined with the reduction in light and space for other macrophytes caused by litter accumulation. Furthermore, a series of positive feedback mechanisms further facilitate the dominance of emergent vegetation under favourable conditions.

4. Fishes

The relationship between reed and fishes is complex. Underneath the water, the reed provide structural complexity and a habitat to several fish species. For example, pike, *Esox lucius*, utilise the coverage of the reed to conceal themselves while they wait to ambush prey (Pauwels *et al.,* 2017). The reed structure is also utilised when spawning by pike (Lappalainen *et al.,* 2008: Nilsson *et al.,* 2014: Niemi *et al.,* 2023), perch, *Perca fluviatilis,* (Snickars *et al.,* 2010), roach, *Rutilus rutilus*, (Härmä *et al.,* 2008) and several more species (Kallasvuo *et al.,* 2011). While this could suggest that the expansion of reed is therefore universally beneficial to many fish species, in some scenarios at least, reed has expanded into environments which are above the reproductive salinity tolerance of these freshwater species (Härmä *et al.,* 2008: Lappalainen *et al.,* 2008), and hence have a reduced benefit, as they can only be utilised for foraging, and not for spawning.

Many studies suggest the primary function of the reed for the fishes is as refuge to avoid predation. Biomass of juvenile fishes has also been recorded as greater within reed (Okun & Mehner, 2005) and within littoral zones (Okun *et al.,* 2005) than in open water. Kallasvuo *et al.* (2010) only observed juvenile pike to be present in environments with reed, while being absent from bladder wrack, *Fucus vesiculosus*, dominated and bare/baron shores. Skov *et al.* (2002) found young of the year pike to prefer more complex habitats over simple habitats designed to represent emergent vegetation in clear water, with no preference in turbid water, presumably meaning the preference for complex structure is due to visual obstruction of potential predators. Okun & Mehner (2005) theorise that roach and perch prefer reed habitats during the day exists to avoid avian predators. Hawkins *et al.,* (2003) also observed an initial preference for reed in juvenile pike in a mesocosm study without predators, however this strength of preference reduced over time. This implies that the juvenile pike may have left the safety of the reed once they realised no predators were present.

Conversely, numerous studies from North America have found *Typha* to be generally detrimental to most fish species. The *Typha* dominated low macrophyte biodiversity landscape offers reduced cover and food availability (Bansal *et al.,* 2019). This difference may again be a result of the fact that *Typha is* invasive in

North America. Schrank & Lishawa (2019) observed a reduction in fish diversity and abundance in association with the *Typha*, likely due to the decrease in dissolved oxygen. This change in abiotic condition did however favour the hypoxia tolerant mudminnow, *Umbra limi*, which thrived in *Typha* dominated areas. This complements the suggestion from Monks *et al.,* (2019), that the autumn die off of the *Typha* facilitates European frogbit and leads to hypoxic conditions.

Several studies have also identified *Typha* to be specifically detrimental to pike reproduction/juvenile pike (Farrell 2001: Farrell *et al.,* 2006: Massa & Farrell, 2020: Neveldine *et al.,* 2019). Two of these studies (Massa & Farrell, 2020: Neveldine *et al.,* 2019) further highlight the need to excavate channels within dense *Typha* stands to provide access for pike to sedge meadows, favoured spawning grounds that are otherwise inaccessible. Casselman & Lewis (1996) conducted an investigation to identify ideal habitats for pike reproduction, differentiating pike spawning habitats from pike nursery habitats. They found the presence of *Typha* to often form low quality spawning habitats, whereas emergent vegetation appeared to be beneficial as a nursery habitat for juveniles. This contrast in benefit to adults and juveniles, may well be present but undetected in other contexts, where studies have investigated the influence of emergent vegetation on a single life history stage of a fish species, or indeed, any organism

While the native reed are utilised as spawning and nursery grounds by many species, and likely have a net positive influence on fish diversity and abundance, it seems plausible that some other mechanisms may limit the benefit of the reed. Supporting this, Skov & Berg (1999) found that juvenile pike preferred more structurally complex habitats to those offered by reed and *Typha*, hypothesising that pike graduate to less complex habitats once they are larger. As foraging returns are significantly lower in complex habitats (Werner *et al.,* 1983), habitat selection may logically be determined by a relationship between the likelihood of encountering a predator compared to the likelihood of encountering viable prey, which is naturally defined by a size threshold. Eklöv (1997) further affirms this hypothesis, as he also observed larger pike and perch to prefer less complex habitats, whereas smaller fish preferred habitats that are more complex.

5. Birds

Emergent vegetation functions as a breeding habitat and foraging area for a plethora of birds, including waterfowl, rails, herons, waders, passerines. Reed beds form ideal conditions for many waterfowl to build their nests. Dense live reed can provide sturdy platforms for nest building, and effectively conceals animals from any potential predators, while dead read fragments may provide optimal nest building materials.

The influence of reed and *Typha* beds on birds is complex, and cannot be generalised. Even within more specific phylogenetic scales, studies have found contrasting results. A number of studies have identified a positive influence of stand forming macrophytes on multiple bird species through the provision of breeding and foraging sites, including: diving ducks (Broyer & Calenge, 2010), reed parrotbills, *Paradoxornis heudei*, (Boulord *et al.,* 2011), blackbirds, *Icteridae*, (Linz *et al.,* 2003) and tentatively the eastern grass owl, *Tyto longimembris*, (Beranek, 2020). Bibby & Lunn (1982) also note that reed provide important habitats for several rare species in the UK. Broyer & Curtet (2012) further highlight a possible link between reed bed area and bird species richness. Conveying a similar result, other studies have reported a detrimental impact of reed removal management on passerines (Schmidt *et al.,* 2005: Valkama *et al.,* 2008). Conversely Kačergytė *et al.,* (2022) found no effect of reed removal management on eight groups of birds typically associated with wetlands. Lishawa *et al.,* (2020) even observed an increase in bird biodiversity when *Typha* was removed. Several studies identified the cutting of reed to benefit some passerine species, and negatively affect others (Graveland 1999: Poulin & Lefebrve, 2002: Vadász *et al.,* 2008: Yang *et al.,* 2021). Broyer & Calenge (2010) theorise that in fertilized ponds, large reed beds could facilitate carp, *Cyprinus carpio*, increasing competition with the diving ducks for invertebrate prey, possibly as the carp have more cover from predators. Under these circumstances, the positive effect of reed would then be reversed, becoming detrimental to diving ducks (Figure 5.). Ultimately, the interaction between emergent vegetation and birds varies between species and contexts and therefore cannot be generalised.

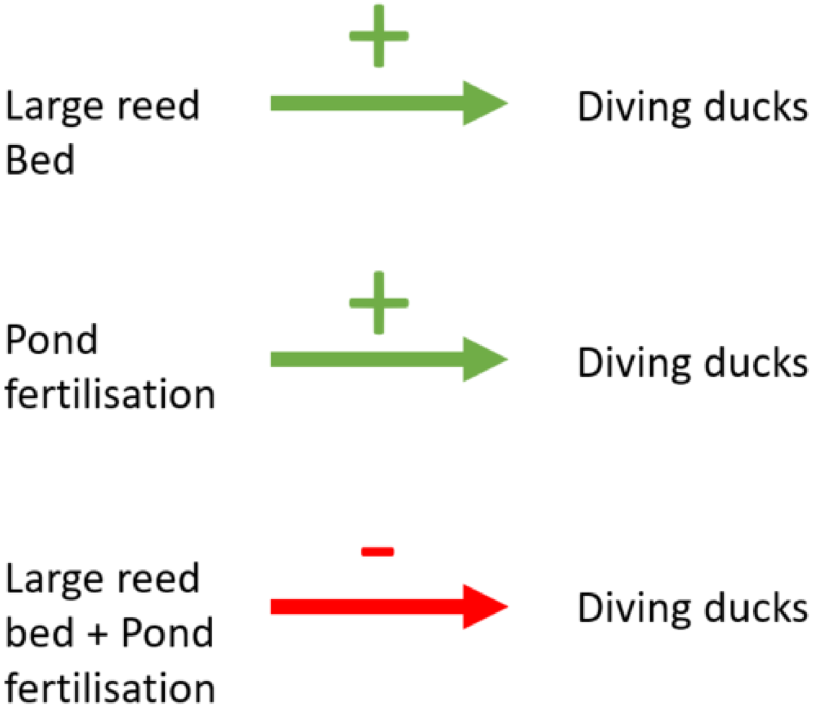

Figure 5. Influence of large reed bed presence and fertilisation on diving duck pair abundance as described in Broyer & Calenge (2010).

Despite contrasting results, Boulord *et al.* (2011) and Lishawa *et al.* (2020) highlight a conforming mechanism in which reed and *Typha* can be detrimental to bird populations, through the accumulation of litter. If not removed, the stems of these plants remain decaying within the live reed and *Typha*. This prevents many other macrophytes from growing, which are important high energy food for many birds (Lishawa *et al,* 2020). Both Boulord *et al.* (2011) and Lishawa *et al.* (2020) suggest the same solution, to harvest the respective reed/*Typha*, to overcome this problem. Although Boulord *et al.* (2011) recommend less frequent harvesting. Despite these similarities, the two studies still describe the stand forming macrophytes as good or bad for birds. Boulord *et al.* (2011) observed the vegetation in harvested areas to be too low for the focal reed parrotbill to nest, whereas Lishawa *et al.* (2020) identified an increase in bird biodiversity in harvested areas, hypothesised to arise indirectly from an increase in macrophytes commonly consumed by birds. This difference may arise due to the scope of birds investigated, as Boulord *et al.* (2011) investigated a single (passerine) species, whereas Lishawa *et al.* (2020) discussed general bird diversity. This again would illustrate that the influence of reed/*Typha* is dependent on the species of bird. An alternative explanation however, could be that the *Typha* is invasive, whereas the reed is native in the respective study countries. Despite their dominance, habitats defined by native emergent vegetation can support a high biodiversity (Morganti *et al.,* 2019).

When invasive however, studies tend to observe a decreased biodiversity. Particularly well studied in *Typha* invasion of the great lakes of North America (Lishawa *et al.,* 2020). This may be a result of differing co-evolutionary time scales. In native habitats, many species have adapted to benefit from dense emergent vegetation (Bibby & Lunn, 1982). Such adaptations are likely absent from environments where the emergent vegetation is invasive. Over an evolutionary time period, invasive plant shaped habitats could reach biodiversity levels similar to that of the native habitat, once the ecosystem has time to evolve. Benoit & Askins (1999) compliment this theory, identifying invasive reed beds to support fewer species of bird, although some species were more abundant in these invaded reed-dominated areas. From a management perspective however, improvements in biodiversity are usually desired sooner than would be possible over an evolutionary time scale, and so harvesting of emergent vegetation would appear to be the best course of action to improve bird biodiversity on a shorter timescale.

6. Invertebrates

6.1 Macroinvertebrates

The reed forms a vital habitat for diverse insect and arachnid communities. Andersen *et al.,* (2021) found old reed beds to support a high richness of terrestrial invertebrates, while managed beds supported a high biomass. While this suggests that specific management practices can optimise the trade-off between biomass and richness (Andersen *et al,* 2021), it is clear that the reed form an important habitat for terrestrial invertebrates. Schmidt et al., (2005) identified variation in communities between cut and uncut reed areas, but could not conclude that one supported a higher biodiversity than the other. Cut area assemblages however may miss some key invertebrate prey species for insectivorous birds. Hardman *et al.,* (2012) concluded that a diverse habitat would support the highest richness of macroinvertebrates. Valkama *et al.,* (2008) found intense management to be detrimental to macroinvertebrate biodiversity, however, they also identify an intermediate management strategy as potentially optimal to benefit invertebrate communities. Together these studies suggests that intermediate management practices would promote the most diverse community of terrestrial macroinvertebrates.

Lawrence *et al.,* (2016a) report *Typha* invaded areas to support lower aquatic macroinvertebrate biomasses, suggesting the mechanism for this was the homogenization of habitats caused by *Typha* formed monocultures. This also supports the interpretation that heterogeneous emergent vegetation stands benefit not only terrestrial, but also aquatic macroinvertebrates. Additionally, Holomuzki & Klarer (2010) concluded a lack of negative effects, and even by some metrics improvements of aquatic macroinvertebrate biodiversity, as a result of reed invasion. Bushaw-Newton *et al.,* (2008) further found no functional difference between dissolved organic matter derived from invasive reed compared to native *Spartina* when ingested by the filter feeding ribbed mussel, *Geukensia demissa* in North America. Continuing the comparison between *Spartina* and reed, Able & Hagan (2000) found some decapod crustaceans to be more abundant in *Spartina,* and others more so in reed. Considering that *Spartina* is also an emergent species of vegetation, this also points in favour of habitat heterogeneity benefitting decapod crustaceans.

Pawlikowski & Kornijów (2022) observed the highest density, biomass and biodiversity of benthic macroinvertebrates in the middle of reed stands, suggesting large reed beds are important for these communities. Okun *et al.,* (2005) also found greater benthos biomasses within reed beds, compared to open water. Similar to the literature studying terrestrial invertebrates, the influence of emergent vegetation on aquatic macroinvertebrates appears to vary, with some studies again highlighting that a diverse habitat will support the greatest biodiversity. Ultimately, macroinvertebrates represent a significantly wider functional diversity, than the other taxa previously discussed, and so a high habitat heterogeneity is likely to support the greatest diversity.

6.2 Zooplankton

Okun *et al.* (2005) found a greater biomass of zooplankton in open water, when compared to the reed associated littoral zone. Kallasvuo *et al.* (2010) however, found a higher density of zooplankton in association with reed. While it may initially appear that this contradicts Okun *et al.,* (2005), the contrasting methodologies of these two studies, may explain the differences. Okun *et al.* (2005) compared zooplankton at different distances from a reed bed (littoral zone vs open water), whereas Kallasvuo *et al.* (2010) compared zooplankton in areas of shoreline with vs without reed. Together, these studies may suggest, that while zooplankton densities are greater in open water than closer to the reed, the presence of reed in the environment is still beneficial to the zooplankton living in the open water.

7. Management

Several management techniques for emergent vegetation are available. Bansal *et al.,* (2019) provide a summary of these techniques, listing: water-level manipulation, herbicide management, burning, physical disturbance, biomass harvest, herbivory/grazing, re-vegetation of macrophyte diversity, and nutrient management. Many studies highlight the benefits that management can have on birds (Boulord *et al.,* 2011: Schmidt *et al.,* 2005: Yang *et al.,* 2021), fishes (Massa & Farrell 202, Neveldine *et al.,* 2019, Olson *et al.,* 1998), and macrophytes (Hall *et al.,* 2008: Keyport et al., 2018: Neveldine *et al.,* 2019). While this evidence is convincingly in support of macrophyte management, further literature emphasises that some important steps must be adhered to, in order for the management to be effective. For example, Lishawa *et al.,* (2019) tested the influence of multiple *Typha* management techniques on macrophyte diversity, and concluded that management is only effective if the *Typha* and litter is removed from the environment, rather than just cutting and removing the live vegetation. In contrast to studies highlighting the benefits of management, some studies have shown a neutral or negative effect of management on macrophytes (Kostecke *et al.,* 2004) and fishes (Nilsson *et al.,* 2014), further emphasising that management practices should be well understood and well refined before being put into broader use. Boulord *et al.,* (2011) also highlight the potential detriment of reed harvesting, but suggest that harvesting every four years would provide optimal vegetation for reed parrotbills. Harvesting an entire ecosystem annually results in vegetation that is too low for the parrotbills to utilise, however a complete lack of harvesting, as previously mentioned, allows litter to build up (Boulord *et al.,* 2011) which is also detrimental to parrotbills. The suggested solution is therefore to harvest an entire ecosystem over four years, with different sub areas harvested each year (Boulord *et al.,* 2011). A similar solution was identified by Andersen *et al.* (2021) and Schmidt *et al.* (2005) while studying invertebrate taxa. Schmidt *et al.* (2005) further highlight that this benefit to invertebrates would also indirectly benefits insectivorous passerines.

Synthesising the results from these studies, I conclude the highest biodiversity in emergent vegetation habitats is found in locations that are heterogenous and managed with non-intensive practices, but still maintain a large proportion of emergent vegetation coverage. The habitat forming reed beds provide many important beneficial functions for other species in the ecosystems they are embedded in, however, these interactions may be overshadowed, reduced or even negated when reed is allowed to become completely dominant in an ecosystem. Effective management techniques should therefore be employed to keep reed beds below the threshold of competitive dominance, but also allow the reed to remain abundant enough to continue supporting diverse wetland communities, and provide us with ecosystem services. In scenarios where reed are managed as a resource, management techniques may be more intensive, and so particular attention should be paid to the ecological interactions.

As previously eluded to, for many species, and therefore the overall biodiversity of coastal ecosystems, the optimal management technique appears to be a less intensive rotational practice, resulting in areas of varying successional states and an increased environmental heterogeneity.

8. Conclusion

In this text, I outline studies observing a plethora of interactions between emergent habitat forming vegetation and aquatic ecosystems, exploring the abiotic environment, macrophytes, fishes, birds, and invertebrates. The overall trend illustrates the importance of emergent vegetation to the ecosystems they naturally inhabit, while also highlighting that when invading and or becoming overwhelmingly dominant, they can instead have adverse effects. As a result, several studies have also reported, whether emergent vegetation is beneficial in their focal context, and that management of the emergent vegetation is beneficial to the species they interact with.

Key knowledge gaps that future research should address include comprehensive investigation of how emergent vegetation influences the abiotic environment, identification of the optimal management practices, and a general increase in the variation of emergent vegetation species and ecosystems studied, beyond reed and *Typha* in North American and Europe. Furthermore, comprehensive studies are limited mainly to invertebrates and macrophytes, leaving a gap when it comes to comprehensive studies of vertebrate taxa at a class level including birds and fishes. With the minor exception of the bird insect predator prey dynamic, few studies investigate multiple taxa in the same field experiment or survey, potentially neglecting community ecology contexts.

Furthermore, the vast majority of studies focus on the presence and absence of emergent vegetation, leaving substantial knowledge gaps in how differences in qualitative metrics e.g., average stem height, thickness, or density can influence the surrounding ecosystem. Likewise, the influence of landscape factors such as patch size, edge effects or connectivity on emergent vegetation habitats also presents another avenue for future research.

While there is a substantial foundation of existing literature, it is clear there are still many novel questions to explore, which once answered will hopefully contribute to the effective management and sustainable exploitation of our emergent vegetation ecosystems.

Some of these questions I aim to address in my PhD project. Primarily, I will conduct a study in which communities of macrophytes, fishes and birds are compared between an area where reed is harvested and a reference location. By monitoring all of these taxa within the same community, we can study more complex ecological interactions than the two species interactions which dominate current literature, particularly studies focused on fishes and birds. We hope that by taking a more comprehensive approach when investigating the response of biodiversity to a reed management technique, we can address a substantial knowledge gap in existing literature.

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