



Review Paper

Functional interactions of non-native aquatic fauna with European freshwater bivalves: implications for management

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Abstract Freshwater bivalves are key faunal elements of aquatic ecosystems. Native species declines are paralleled by increasing distribution and abundances of non-native species. Appropriate management of both groups depends on knowledge of their interactions, which remains limited. Herein, we systematically review the current knowledge status of native and non-native bivalves in Europe, analyzing their functional interactions as well as niche and distribution overlaps between species. We also review existing management tools for non-native species in light of their applicability and sustainability. Strong and multiple interactions as well as niche overlaps between native and non-native bivalves already exist

in Central Europe, especially with regard to *Dreissena* spp., *Corbicula* spp., and *Sinanodonta woodiana*. Direct competition is low with native species that have a high degree of specialization such as *Margaritifera margaritifera*, whereas the greatest niche overlap and competition occurs in generalist species such as *Anadonta anatina*, *Unio pictorum*, and *S. woodiana*. Early detection and preventive measures against undesired species are most successful in limiting their spread. Most methods for managing non-native species are unspecific and thus also include undesired side effects on endangered native species. The conservation and restoration of functionally intact bivalve habitats are the most sustainable and most resilient ways of management.

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Current knowledge status of native and non-native bivalves in Europe

Freshwater bivalves are considered key faunal elements of diverse aquatic habitats, with many native species prioritized in efforts of aquatic conservation and restoration throughout the world (Geist, 2010, 2015; Lopes-Lima et al., 2018; Sousa et al., 2022). Bivalves regulate energy and nutrient dynamics by filtering, storing, and distributing inorganic

and organic matter between the water column and the substrate (Lummer et al., 2016; Vaughn, 2018; Strayer et al., 2019b). They also increase benthic oxygenation by active bioturbation of bed substrates, which has distinct effects on microbiological and macroinvertebrate communities (Boeker et al., 2016; Richter et al., 2016).

The critical services provided by freshwater bivalves are impaired by global declines of native unionid species, which have dramatically eroded both in terms of their distribution and abundances (Haag and Williams, 2014; Walker et al., 2014; Lopes-Lima et al., 2017). Despite the declines in many native species, in particular in unionids, many others (invertebrates and vertebrates) have been reported to increase in density and/or diversity in association with invasive bivalves (see Botts et al., 1996; Stewart et al., 1998; Karatayev et al., 2002; Burlakova et al., 2012; Sylvester & Sardiña, 2015). However, the overall outcome is quite controversial, and likely variable and case-specific. Nevertheless, some factors of decline such as loss or reduction of host fish populations needed for successful development of the so-called glochidia larvae (Modesto et al., 2018) or impaired juvenile habitat conditions due to increased fine sediment loads (Geist & Auerswald, 2007; Hoess & Geist, 2020) have been studied intensively, whereas experimental studies on interactions with non-native species are often limited to specific case studies on single species or descriptive observations (e.g., Ferreira-Rodríguez & Pardo, 2017; Ferreira-Rodríguez et al., 2018; Haag et al., 2021).

A systematic assessment of non-native species is partly complicated by inconsistent use of terminology (e.g., Colautti & MacIsaac, 2004; Essl et al., 2018; Gbedomon et al., 2020; Pereyra, 2020; Fall, 2021). Typically, the terms ‘non-native,’ ‘non-indigenous,’ and ‘alien’ generally refer to species which occur outside their natural distribution range, whereas the term ‘invasive’ is often, yet not totally consistently, used in the context of non-native species whose introduction, colonization, and dispersal cause major ecological, social, or economic impacts. In our paper, we use the term ‘native’/‘non-native’ for species that do/do not naturally occur within European freshwaters, with the exception of *Dreissena* spp., which are of Eastern European origin but have spread throughout Central and Western Europe where they are considered

introduced. We therefore classify both dreissenid species as non-native.

Biological invasions must be routinely tracked (Pergl et al., 2020) to better understand their impacts on native species, their habitats, and ecosystem functions (Geist, 2011). Often, non-native populations move quickly across space and are characterized by boom-bust dynamics (Cerwenka et al., 2014; Strayer et al., 2017), which can result in varying impacts over space and time, including the release of high amounts of nutrients from soft tissue within a very short time (McDowell & Sousa, 2019). Thus, understanding the ecological niches of non-native species in relation to natives, as well as understanding their (potential) habitat overlap, is crucial for defining species-specific management priorities. The co-inhabitation of native and non-native bivalve species in anthropogenic habitats (Sousa et al., 2021) offers several possibilities for active management, which must identify measures that maximize impact on undesired species, while limiting undesired side effects on native unionid species. Given the increased pressures related to global climate change acting in concert with anthropogenic stressors (Mueller et al., 2020), there is a distinct need for an improved systematic understanding of the functional interactions between native and non-native freshwater bivalve species in Europe.

The core objective of this paper is to assess the functional interactions among endangered native unionids and introduced freshwater bivalve species in Europe. Specifically, we focus on identifying the most impacted species and processes by: (i) identifying and characterizing the most important functional interactions between non-native fauna and native freshwater unionids related to trophic effects, habitat competition, reproduction, and predation; (ii) analyzing existing and potential niche and habitat overlap; and (iii) assessing current management options.

Functional interactions between native and some prominent non-native species

Known functional interactions of native unionid species and non-native fauna are summarized in Fig. 1, and can be broadly categorized into direct and indirect effects. While non-native fauna can have both positive and negative effects on native unionids, many studies specifically focus on negative impacts.

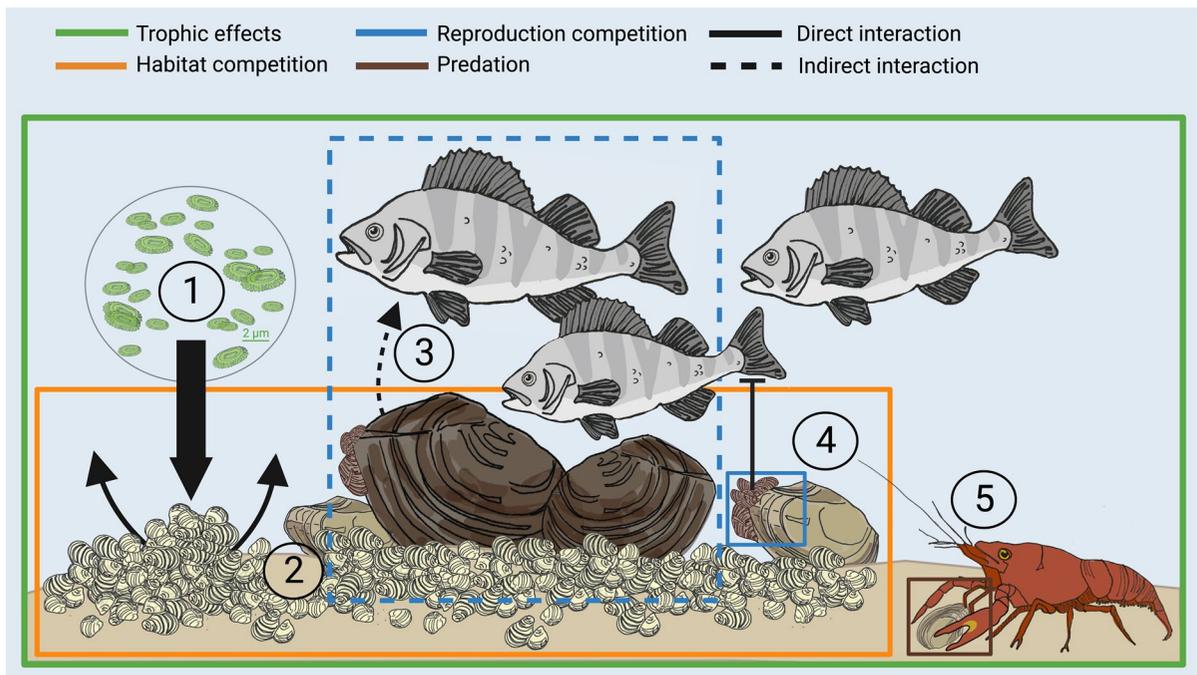


Fig. 1 Functional interactions between native and non-native species: (1) Filtering by invasive bivalves results in trophic competition with native unionids and host fish. (2) Competition for space occurs between dense assemblages of invasive bivalves and native unionids. (3) Competition for host fish, e.g., by infestation with high rates and volumes of non-native

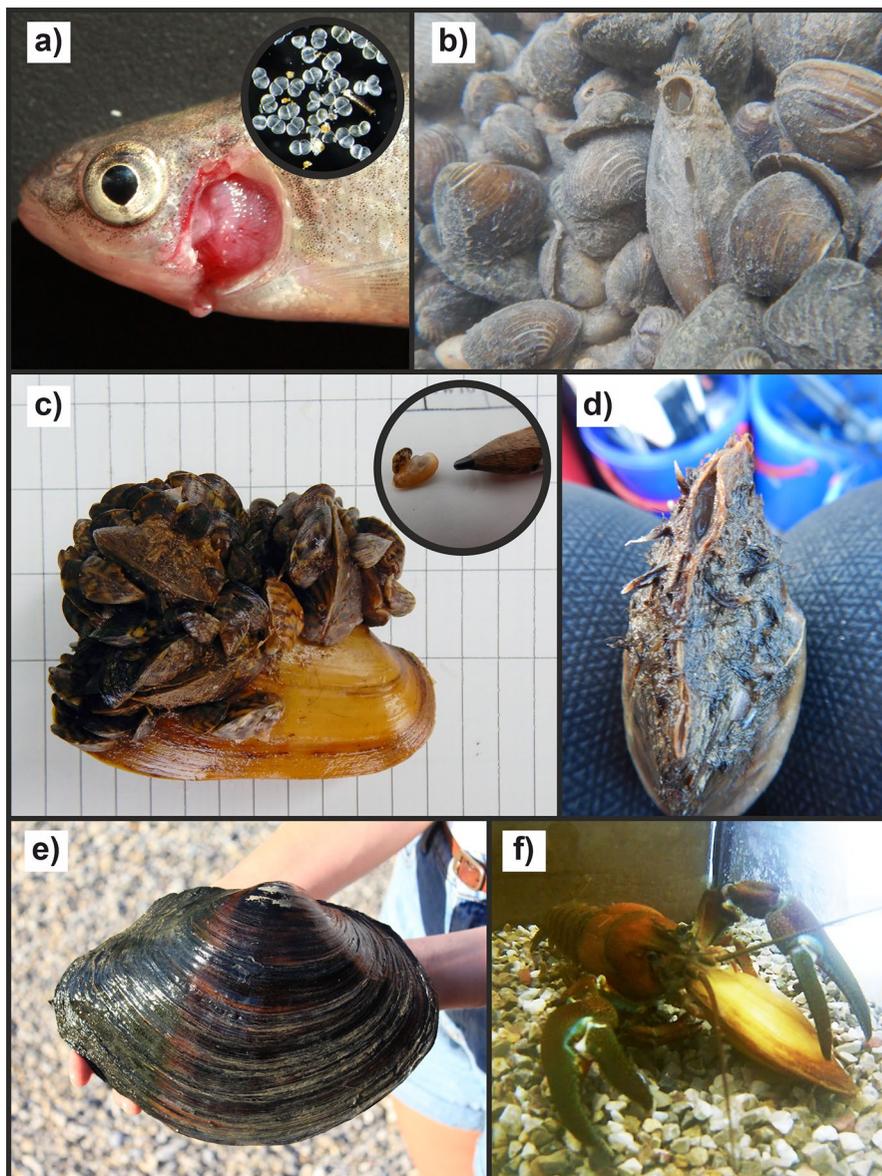
glochidia can indirectly lead to cross-resistance to native glochidia. (4) Physical fouling by non-native bivalves limits reproduction, movement, and filter activity of native mussels. (5) Predation by non-native fauna upon native mussels occurs at higher rates

Direct competition for food and habitat has been characterized for many species and habitat types. Large assemblages of non-native *Corbicula* and *Dreissena* spp. filter water at high rates and limit plankton availability for native species. A prominent and probably one of the few long-term studies on such effects is from the Hudson River in New York, where filter feeding of *Dreissena polymorpha* significantly decreased turbidity, and declines of native species were reported in parallel (Strayer & Smith, 1996; Strayer et al., 2011, 2014, 2019a, 2019c; Strayer & Malcom, 2014). However, there are many examples in the literature where invasive species have been shown to directly or indirectly favor native fishes and bivalves. For instance, invasive fishes can feed on and therefore reduce the abundance of non-native bivalves (Brandner et al., 2012), and there are also examples of non-native bivalves and fishes favoring populations of native fishes including endangered ones (Dietrich et al., 2006; Peterson et al., 2007; Madenijan et al., 2010; Weber et al., 2011; Crane & Einhouse, 2016;

Jacobs et al., 2017; Pothoven et al., 2017; Bruestle et al., 2019; González-Bergonzoni et al., 2020). Following the dreissenid invasion of the Hudson River, open-water fishes declined while littoral fishes were observed to increase (Strayer et al., 2004). Effects of invasive bivalves on native fauna can even extend beyond the water body itself as demonstrated by the use of *D. polymorpha* as a food source for waterfowl (Werner et al., 2005).

Throughout the US, declines of native bivalve species have been suspected to be linked with the spread of non-native *Corbicula* spp., which have been shown to assimilate a wider range of food sources than their native counterparts (Atkinson et al., 2010; Haag et al., 2021). However, competitive trophic effects are expected to be the strongest if non-native bivalves directly attach to the shells of natives as is the case with *D. polymorpha* and *Dreissena rostriformis* (Stepien et al., 2014), where the biomass of the unionid host is often exceeded by the biomass of the attached dreissenids (Fig. 2c). Such attachment can

Fig. 2 Prominent examples of interactions between non-native and native freshwater bivalves/species including **a** reproduction (glochidia of the non-native *Sinanodonta woodiana* occupying the natural host fish, *Squalius cephalus*, of native freshwater unionids), **b** habitat (competition for space between native *Unio crassus* and non-native *Corbicula fluminea*), **c**, **d** physical impairment (non-native *Dreissena spec.* fouling on native *Unio pictorum*, which may result in physical deformation of the shell), **e** growth (fast growing and large non-native *S. woodiana*) as well as **f** predation effects (invasive *Pacifastacus leniusculus* feeding on native *U. pictorum*)



result in impaired growth and deformations (Fig. 2d) as well as complete immobility or even toppling of the native host unionid, which decreases the filtering and reproductive abilities and increases the overall mortality risk of such specimens (Ozgo et al., 2020). There is evidence from pristine lake-stream transition zones that intact habitats which contain a great bivalve diversity seem to provide a greater level of resistance against such hitchhiking effects (Ozgo et al., 2021). Growth rate and size also play a role in the impact of non-native species. Faster and larger growing species such as *Sinanodonta woodiana*,

which can reach a size of more than 1.5 kg within a few years (Fig. 2e; Dobler et al., 2022), can potentially outcompete slow-growing species for nutrients or habitat.

More subtle direct interactions can be observed in predation by crayfishes on bivalves (Fig. 2f). Native and non-native crayfish species can co-occur and interact with native and non-native bivalves (Schmidt & Vandr , 2012; Meira et al., 2019; Dobler & Geist, 2022). Cross-exposure experiments identified a greater resistance of the non-native bivalve *S. woodiana* against predation by the native crayfish *Astacus*

astacus and non-native crayfish *Pacifastacus leniusculus* compared to native unionids of the same size (Dobler & Geist, 2022). Crayfish and other crustaceans have also been observed to actively consume *D. polymorpha* (Piesik, 1983; Karatayev et al., 1994; Molloy et al., 1994, 1997).

Non-native species can also compete with native bivalves indirectly. With regard to host fish use, glochidia larvae of *S. woodiana* remain viable for longer periods of time and can tolerate a wider range of temperatures than the glochidia of native *Unio crassus*, resulting in a competitive advantage already at an early life stage (Benedict & Geist, 2021). It has also been shown that *S. woodiana* uses a broader host fish spectrum than native *Anodonta* species, which also includes several European fish species (Douda et al., 2012, 2017a; Huber & Geist, 2019b). In addition, previous infestations of fish hosts with glochidia of *S. woodiana* can reduce host suitability in subsequent infestations of glochidia from native unionid species (Donrovich et al., 2017) and a high infestation density of *S. woodiana* glochidia can impair fish physiology and condition (Douda et al., 2017b).

On the other hand, native *Anodonta* species were also found to use non-native fishes as hosts (Huber & Geist, 2017, 2019a), but at least in the case of *A. anatina*, non-native fish are significantly worse hosts and their entry into water bodies dilutes native fish host resources with negative effects on native mussel diversity (Douda et al., 2013).

Non-native species might also function as vectors for pathogens and parasites (Cichy et al., 2016). This is most likely if adult specimens drive the invasion, such as in the case of *S. woodiana* from aquarium or pond trade. *Sinanodonta woodiana* individuals have shown high infestation rates by parasites (Taskinen et al., 2021) and may therefore induce spread to co-occurring native mollusk species (Yurishinets, 2010). On the other hand, introduced species may be less susceptible to native diseases, as they have not developed a co-evolutionary relationship to native parasites and pathogens, which gives them an advantage over their native counterparts (Prior et al., 2014).

Another aspect that has been poorly examined is the potential hybridization of bivalve species (Sousa et al., 2014). Although hybridization has been used to introduce desired traits in marine bivalve aquaculture (Guo, 2009), it is primarily considered a threat to the genetic integrity of wild bivalve populations, as

outbreeding and genetic swamping can reduce the fitness of highly adapted native species (e.g., Todesco et al., 2016; Adavoudi & Pilot, 2021). This interaction would be most likely between more closely related bivalves such as *Sinanodonta* and *Anodonta* species.

Finally, habitats invaded by *D. polymorpha* are often subsequently colonized by other Ponto-Caspian species, such as *D. rostriformis* (Hetherington et al., 2019; Haltiner et al., 2022), potentially resulting in invasional meltdown (Simberloff & von Holle, 1999). Such meltdown events can also include introductions of other invertebrate species as demonstrated in the North American Great Lakes (Ricciardi, 2001), the Danube (Brandner et al., 2012; Beggel et al., 2016; Pander et al., 2022) and Great Britain (Gallardo et al., 2015).

Most prominent non-native species and their niche/habitat overlap with native species

Due to their broad ecological niche, non-native species can spread easily from their original introduction sites in often highly modified waterbodies to natural waterbodies inhabited by native, generalist bivalve fauna. In systems which exhibit habitat and niche overlaps between native and non-native species, non-natives are often able to outcompete their native counterparts. Non-natives benefit from their tolerance to high temperatures, their extended breeding period, short generation time, early maturation, faster growth rates, and efficient larval dispersal (Sousa et al., 2014; Taskinen et al., 2021), which allow rapid colonization and establishment in new habitats. Due to these numerous and distinct competitive advantages, the occurrence of non-native bivalves does not exclusively depend on their habitat preferences and tolerances, but also on their invasion status and current distribution.

Dreissena polymorpha

One of the most widespread and well-known aquatic invasive species is the zebra mussel *D. polymorpha*, which dispersed from its native Ponto-Caspian range first into Europe in the 1880s and later into North America in the 1980s, where it continues to spread in high densities and at all scales (Pollux et al., 2010). Although it is frequently mentioned as a flagship

example for harmful invasive species, *D. polymorpha* is not listed as a species of “Union Concern” in the EU as it is of European origin (Scalera et al., 2020). However, due to its high dispersal ability and strong ecological and economic impacts, it is classified as an “invasive alien species” in several legislative documents (e.g., European Commission, 2008) and therefore its legal status is “alien, of member state (MS) concern” in the European Alien Species Information Network (EASIN, 2022; Table 1). The bivalve’s invasion success is largely attributed to its successful ‘hitchhiking’ ability, where adult specimens are actively transported over long distances along shipping and boating routes (De Ventura et al., 2016), as well as its high reproductive capacity, in which free-living veliger larvae produced in mass spawning events are transported great distances by water currents (Mackie, 1991). Juvenile and adult specimens of *D. polymorpha* tend to be found in shallow to deep littoral zones of most lakes and large river systems (Table 1), where they attach by strong byssal threads to solid substrates such as rocks and pipes, as well as to spherical clusters or dense beds of their own shells, or to the shells of native unionids, which allows them to move into softer substrates over time (Nalepa et al., 1996; Strayer & Malcom, 2006). In systems with overlaps of *D. polymorpha* and native unionids, *D. polymorpha* directly outcompetes natives for food and space due to their high filter rate and rapid regeneration times (Borcherding, 1991; Baker & Hornbach, 1997). These competitive effects are magnified when *D. polymorpha* physically attaches to native unionids. Pilotto et al. (2016) found that dreissenids which attached to native unionid shells exhibited higher biomass and glycogen content in comparison to those which attached to non-living control substrates. Attached dreissenids may also indirectly affect native unionid survival by inhibiting their movement and interfering with larval release (Schwalb et al., 2021), which limits the ability of native unionids to relocate and reproduce in more suitable environments. In large scale dreissenid invasions, dense assemblages of *D. polymorpha* become the most dominant biomass of entire systems and filter water at extreme rates (Strayer & Smith, 1996; Karatayev et al., 1997). Such invasions may facilitate the collapse of entire native unionid populations, either directly via bivalve-to-bivalve competition for food and space, or indirectly by altering the trophic ranges of fish hosts for native

unionid species. Further spread of *D. polymorpha* is likely to occur within its already established range, as it is believed that the bivalve may be close to filling its entire ecological niche in the northern hemisphere (Quinn et al., 2014; Alix et al., 2016).

Dreissena rostriformis

The quagga mussel *D. rostriformis* has largely traced the invasion routes of *D. polymorpha* of the same Ponto-Caspian origin throughout Europe (similar legal status as *D. polymorpha*), Canada, and the US, but their exact distribution is unclear, as it is slower to establish, less visible, and in some cases difficult to distinguish from *D. polymorpha* (Beggel et al., 2015), with which it often co-occurs. *Dreissena rostriformis* is generally found in soft substrates of deep, cold regions of large lakes and river systems, most notably in the North American Great Lakes and in the Rhine, Danube, and Meuse Rivers in western Europe (Matthews et al., 2014; Quinn et al., 2014). From depths > 30 m, *D. rostriformis* filters water at rates 40% faster than *D. polymorpha* and is thus able to access nutrients unavailable to *D. polymorpha*, which is distributionally limited to shallow zones (Diggins, 2001; Nalepa et al., 2009). In waterbodies with overlaps of both dreissenid species, *D. rostriformis* has begun to replace *D. polymorpha* as the most dominant dreissenid (Hetherington et al., 2019), and weaker infestations of native unionids by *D. polymorpha* have been recorded in parallel (Burlakova et al., 2014). These results suggest that *D. rostriformis* may act indirectly and sub-additively (i.e., “invasional interference”) in systems previously invaded by *D. polymorpha* and may therefore have more varied impacts on native unionid diversity. Direct interactions between *D. rostriformis* and native unionids are difficult to detect, as *D. polymorpha* tends to invade water bodies before *D. rostriformis*, and interacts more directly with native unionids such that subsequent effects by *D. rostriformis* are largely masked. More recently, *D. rostriformis* has expanded into shallow areas previously occupied exclusively by *D. polymorpha* and have also been reported in warmer waters in the southwestern US (Berkman et al., 2000; Nalepa, 2010). This may indicate that *D. rostriformis* may not have reached, or is not fully documented within, the full limits of its geographical range.

Table 1 Species life history strategy (after Lopes-Lima et al. (2017) for species native to Europe and various sources for non-native species), host fish use of native and non-native unionid species, as well as legal state (conservation state after

IUCN European Red list of Species (2011) for native unionids, invasion state after European Alien Species Information Network (EASIN, 2022) for non-native species) as well as temperature range, habitat type, and trophic state of potential habitats

Species	Species life history strategy	Host fish use	Legal status	Temperature range	Habitat type	Trophic state
Native						
<i>A. anatina</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Least concern	cool range, warm range	ULT, LLR, PND, TRD, SLR, SSR, URS, MTR, CAN	MT, ET
<i>A. cygnea</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Near threatened	cool range, warm range	LLR, PND, SLR, SSR, CAN	MT, ET
<i>M. bonellii</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Vulnerable	warm range	LLR, SLR, SSR, MTR, CAN	OT
<i>M. margaritifera</i>	Long-lived, late maturation, slow growing	Host specialist	Critically endangered	cool range	ULT, LLR, SLR, SSR, URS, CAN	OT
<i>P. auricularia</i>	Long-lived, late maturation, slow growing	Host specialist	Critically endangered	warm range	SLR, CAN	OT
<i>P. complanata</i> ,	Medium long-lived, medium early maturation, medium growing	Host generalist	Near threatened	cool range	ULT, LLR, PND, SLR, SSR,	OT, MT
<i>P. littoralis</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Endangered	warm range	LLR, SLR, SSR, MTR, CAN	OT
<i>U. crassus</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Endangered	cool range	LLR, P, TRD, SLR, SSR, URS, CAN	OT, MT
<i>U. delphinus</i>	Short-lived, early maturation, fast growing	Host generalist	Near threatened	warm range	LLR, SLR, SSR, URS, MTR	OT, MT
<i>U. mancus</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Near threatened	warm range	LLR, TRD, SLR, SSR, MTR, CAN	OT, MT
<i>U. cf. elongatulus</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Near threatened	warm range	ULT, LLR, PND, TRD, SLR, SSR, URS, CAN	OT, MT
<i>U. pictorum</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Least concern	warm range	LLR, PND, TRD, SLR, SSR, URS, CAN	MT, ET
<i>U. ravoisieri</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Near threatened	warm range	LLR, SSR, MTR	MT, ET

Table 1 (continued)

Species	Species life history strategy	Host fish use	Legal status	Temperature range	Habitat type	Trophic state
<i>U. tumidiformis</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Vulnerable	warm range	SSR, MTR	MT, ET
<i>U. tumidus</i>	Medium long-lived, medium early maturation, medium growing	Host generalist	Least concern	warm range	LLR, PND, TRD, SLR, SSR, CAN	OT
Non-native						
<i>C. fluminea</i>	Short-lived, early maturation, fast growing	No host	Alien, of MS concern	warm range	LLR, PND, TRD, SLR, SSR, MTR, CAN	MT, ET
<i>C. fluminalis</i>	Short-lived, early maturation, fast growing	No host	Alien, of MS concern	warm range	LLR, PND, TRD, SLR, SSR, MTR, CAN	MT, ET
<i>D. polymorpha</i>	Short-lived, early maturation, fast growing	No host	Alien, of MS concern	warm range	ULT, LLR, SLR, SSR, CAN	MT, ET
<i>D. rostriformis</i>	Short-lived, early maturation, fast growing	No host	Alien, of MS concern	warm range	ULT, LLR, SLR, SSR, CAN	MT, ET
<i>S. woodiana</i>	Short-lived, early maturation, fast growing	Host generalist	Alien, of MS concern	cool range, warm range	ULT, LLR, PND, TRD, SLR, SSR, URS, MTR, CAN	MT, ET

The classification of habitat types (“ULT”=Upland lakes/tarns, “SLR”=large, slow-flowing lowland rivers, “LLR”=lowland lakes and reservoirs, “TRD”=trickles and ditches, “URS”=upland rivers and streams, “SSR”=streams and small flowing rivers, “PND”=ponds, “TMR”=mediterranean temporary rivers, “CAN”=canals) and trophic state (“OT”=oligotrophic, “MT”=mesotrophic, “ET”=eutrophic) is based on Lopes-Lima et al. (2017), Killeen et al. (2004) and others, including personal observation; for detailed information on species temperature requirements and on life history parameters as life span, maturation, growth and breeding, as well as supporting literature, see Supplementary Data S1 and S2

Corbicula fluminea

C. fluminea is considered one of the most widespread and successful aquatic invaders both in Europe and on a global scale (Nentwig et al., 2017; Guareschi & Wood, 2020), classified as “of MS concern” within the EU (Table 1). It was introduced to Europe in the 1970s most likely via ballast water containing their free-ranging pediveliger larvae (Karatayev et al., 2007; Sousa et al., 2008). Their high fecundity, ability to self-fertilize, fast growth and early maturation (3 to 6 months, Sousa et al., 2008), together with the high mobility of the pediveliger and juveniles facilitates a rapid dispersal from the original introduction site. Due to their ability to burrow into the substrate, *C. fluminea* larvae are able to colonize faster flowing streams than dreissenids (Karatayev et al., 2005).

The species’ current European distribution includes most of the large European river basins from Portugal (e.g., Tua river), Spain, France (e.g., Seine), Germany (e.g., Rhine), to Serbia (e.g., Danube) and Moldova as well as Great Britain and Ireland (e.g., Shannon river, Lucy et al., 2012) where it is reported, often in high densities, along populations of native *A. anatina*, *Potomida littoralis*, and *Unio delphinus* (Ferreira-Rodríguez et al., 2018; Modesto et al., 2021) or native *A. anatina*, *U. pictorum*, and *U. tumidus* as well as non-native *S. woodiana*, *D. polymorpha*, and *C. fluminalis* (Labecka et al., 2005). The species prefers fine sand and silt and warm temperatures between 2.0 and 36.0–37.0°C (Mouthon, 2001; Karatayev et al., 2005), while it is intolerant to hypoxic conditions as well as low levels of calcium (Sousa et al., 2008). Where these conditions are met, *C. fluminea* can

be found in a high variety of habitats ranging from small to large streams over lakes to canals (Table 1; Lucy et al., 2012). High numbers of *C. fluminea* have been suggested to negatively impact native bivalve communities in North America and Europe (Sousa et al., 2008, 2014; Ferreira-Rodríguez et al., 2018; Haag et al., 2019) as it alters environmental conditions due to its burrowing and bioturbation activities with the potential to displace native juveniles and an overall competition for suitable habitat space. Their high filtration rates together with their ability to pedal feed lead to a reduction of available food for native unionids and their juveniles (Haag et al., 2021). Furthermore, the transfer of suspended organic matter from the water column to the substrate through the deposition of feces or pseudofeces may degrade juvenile habitat quality of native unionids (Sousa et al., 2008; Ferreira-Rodríguez et al., 2018). *C. fluminea* may modulate C:N differently and at larger scales than native bivalves and thus alter nutrient dynamics in entire systems (Atkinson et al., 2010). It further poses the threat of ingesting large amounts of sperm or larvae of native unionids, therefore further reducing their reproduction potential (Sousa et al., 2008). Sudden fluctuations in abiotic conditions, such as a decrease in oxygen conditions during the summer months, often lead to massive die-offs of large *C. fluminea* populations, causing ammonia toxicity harmful to native bivalves (Cherry et al., 2005; Cooper et al., 2005). While *C. fluminea* populations usually recover quickly from such events, native unionid populations recover more slowly due to their lower growth and reproduction rates. In addition, higher water temperatures were shown to increase floating behavior in *C. fluminea*, increasing the dispersal potential by drift. Therefore, climate change as well as changes in temperature regimes following dam construction could enhance a further spread of the species (Rosa et al., 2012). Gama et al. (2016) used an ensemble of niche-based distribution models to predict potential habitats of *C. fluminea* and found waterbodies that seem suitable but are not yet occupied by the species all over Europe, as well as in Africa and Australia, showing the high potential of a further spread. Lucy et al. (2012) predicted a rapid spread of *C. fluminea* throughout the island of Ireland due to the high number of waterbodies with suitable habitat conditions as well as high connectivity and proximity of river

basins, which is also the case of many European water inland waters.

Corbicula fluminalis

Clear taxonomic differentiation between *C. fluminea* and *C. fluminalis* remains uncertain (Pigneur et al., 2011) and therefore the use of classification terms varies between studies and institutions. While the IUCN and the EASIN list them as two separate species, the Global Invasive Species Database (GISD) lists them as synonymous (Gama et al., 2016). In many studies, they are therefore considered as different morphotypes, and not different species (e.g., Paunović et al., 2007). However, due to this fact, it is difficult to be sure how and if the species were differentiated when reported in the literature, which makes it difficult to distinguish their ecological niches and potential interactions with native unionid species. Nonetheless, when both species were identified, it appears that *C. fluminalis* occurred at fewer sites than *C. fluminea* (e.g., in Italy: Ciutti & Cappelletti, 2009; Belgium: Nguyen & De Pauw, 2002; Serbia: Paunović et al., 2007) and its abundance is lower in habitats, where both species co-occur. It remains unclear if they occupy slightly different ecological niches or if other mechanisms such as secondary introduction or lower reproductive potential of *C. fluminalis* underlie these patterns.

Sinanodonta woodiana

The Chinese pond mussel *S. woodiana* spread rapidly from its native Yangtze and Amur River Basin ranges in the 1970s and 1980s throughout Europe, Asia, and the Americas, where it is largely considered either 'introduced' or 'non-native' (e.g., Munju, 2008; Bogan et al., 2011; Bolotov et al., 2016; Zieritz et al., 2016, 2018; Bepalaya et al., 2018; Kondakov et al., 2018; Konecny et al., 2018; Urbańska & Andrzejewski, 2019; Urbańska et al., 2021). In Europe, this unionid was initially detected in modified water bodies such as fish ponds and thermally heated reservoirs (Urbańska et al., 2012), but has since rapidly spread into natural water bodies such as lakes, rivers, and slow moving streams (Table 1; Labecka & Domagala, 2019; Dobler et al., 2022). Within these systems, *S. woodiana* can establish in a wide range of habitats, in

	native														non-native					Habitat type overlap
	<i>M. margaritifera</i>	<i>P. auricularia</i>	<i>A. anatina</i>	<i>A. cygnea</i>	<i>P. complanata</i>	<i>U. crassus</i>	<i>U. tumidiformis</i>	<i>U. pictorum</i>	<i>U. delphinus</i>	<i>U. ravoisieri</i>	<i>U. cf. elongatulus</i>	<i>U. mancus</i>	<i>U. tumidus</i>	<i>P. littoralis</i>	<i>M. bonellii</i>	<i>S. woodiana</i>	<i>C. fluminea</i>	<i>C. fluminalis</i>	<i>D. polymorpha</i>	
<i>M. margaritifera</i>		0	0	0	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. auricularia</i>			0	0	0	0	0	0	1	0	2	2	2	2	2	0	0	0	0	0
<i>A. anatina</i>	X			20	4	7	4	14	5	5	8	6	3	1	1	33	14	14	9	9
<i>A. cygnea</i>	X	X	X		4	6	2	11	4	3	5	5	3	2	2	20	10	10	9	8
<i>P. complanata</i>	X		X	X		8	0	0	0	0	0	0	0	0	0	4	0	0	0	0
<i>U. crassus</i>			X	X	X		0	1	1	0	0	1	1	1	1	7	0	0	1	0
<i>U. tumidiformis</i>			X	X				2	2	4	1	2	0	0	0	4	4	4	2	2
<i>U. pictorum</i>	X		X	X	X	X			5	3	7	6	4	2	2	14	12	12	9	8
<i>U. delphinus</i>	X		X	X	X		X	X		3	7	7	4	5	5	5	4	4	4	3
<i>U. ravoisieri</i>			X	X					X		2	3	1	1	1	5	5	5	3	3
<i>U. cf. elongatulus</i>		X	X	X		X	X	X		X		9	8	4	4	8	6	6	4	4
<i>U. mancus</i>		X	X	X		X	X	X		X			7	5	5	6	6	6	5	4
<i>U. tumidus</i>	X		X	X	X	X		X	X		X	X		5	5	3	3	3	2	1
<i>P. littoralis</i>	X		X	X	X	X	X	X	X				X		6	1	1	1	2	1
<i>M. bonellii</i>	unknown host															1	1	1	2	1
<i>S. woodiana</i>			X	X	X	X		X		X	X	X	X				14	14	8	8
<i>C. fluminea</i>	no host																	14	8	8
<i>C. fluminalis</i>	no host																		8	8
<i>D. polymorpha</i>	no host																			9
<i>D. rostriformis</i>	no host																			

Host fish overlap

Fig. 3 Pairwise comparison of potential distribution and host fish overlap of native and invasive freshwater bivalve species. The upper right triangle represents the number of overlapping habitats, indicating a potential distribution overlap, based on the habitat type, trophic state and temperature range of the species summarized in Table 1; color gradient represents number

of habitat overlaps from light= few to dark= many. The lower left triangle represents host fish overlap which is represented by "x" and is based on Lopes-Lima et al. (2017) for native unionid species and on Donrovich et al. (2017), Douda et al. (2012), Huber and Geist (2019b), Pou-Rovira et al. (2009) for non-native *S. woodiana*

temperatures ranging from 5 to 25°C, in muddy and silty to coarse gravel substrates, although it is most commonly found in shallow softer sediments with other native unionids (Urbańska et al., 2019, 2021; Benedict and Geist, 2021; Poznanska-Kakareko et al., 2021; Dobler et al., 2022). Because *S. woodiana* is a generalist unionid bivalve, many of its life requirements overlap with those of European native unionid species (Fig. 3), which makes it particularly unique and urgent case in the study and management of native/non-native niche overlaps.

Sinanodonta woodiana grows at fast rates and may be able to partition food sources more efficiently than native bivalves (Sárkány-Kiss et al., 2000; Douda & Čadková, 2018). Its host fish spectrum overlaps with nine of the 15 native species (Fig. 3) and it produces multiple larvae broods per year in high numbers (Labecka & Domagala, 2018; Labecka & Czarnoleski, 2021). Consequently, it may infest host fishes at higher rates and likely increase host immunity toward infection with native glochidia. This has already been demonstrated for

A. anatina (Donrovich et al., 2017), therefore limiting native reproduction (Sárkány-Kiss et al., 2000; Wächtler et al., 2001; Huber & Geist, 2019b). In disturbed systems affected by climate- and/or human-mediated drought, it is likely that *S. woodiana* can outcompete natives over space and time, as it has been observed to burrow 20 cm into the substrate and move up to 10 m in one day (Urbańska et al., 2021). Further occurrence of the species may be enhanced by carp aquaculture and by the common practice of selling and distributing the species in pond and aquarium trade, as well as the limited management tools that exist for this species, which has yet to be given an invasive status in many European countries (Dobler et al., 2022).

Since several non-native species do not seem to have reached their full dispersal potential yet (e.g., Sousa et al., 2014; Guareschi & Wood 2020; Urbańska et al., 2021; Dobler et al., 2022), in particular under ongoing climate change, a further expansion of their range poses an increasing threat on native unionid species. To evaluate their impact on different native species, identification of potential habitat overlap is an important prerequisite to identify species at risk and take mitigation measures in time. Generally, since one of the main characteristics of invasive species is their broad ecological niche, specialized species as *Margaritifera margaritifera* or *U. crassus* that are adapted to oligotrophic conditions have a low risk of encountering native and non-native generalist species (Fig. 3) and being affected by functional interactions. In contrast, native generalists such as *Anodonta* spp. have a greater risk of being affected by non-native species due to the overlapping habitats and ecological niches. Highest potential habitat overlap can be observed between *S. woodiana* and *A. anatina*, *A. cygnea*, and *U. pictorum* that seem also highly susceptible to interacting with *Corbicula* spp. and dreissenids. Moreover, occurrence of one non-native species might hinder the colonization of additional non-natives due to the same interaction mechanisms, most probably the competition for food and space. For instance, the reduction of the trophic state of many Irish lakes by the filtering activity of dreissenids has lowered the potential for colonization with *C. fluminea* due to food competition (Lucy et al., 2012). The observed replacement of *D. polymorpha* by *D. rostriformis* is another example for an ongoing invasion progress.

Due to the already known but also potential habitat and niche overlaps, the pressure of non-native species' interactions on native unionids is likely to increase in future which requires appropriate management measures for mitigation.

Management of invasive freshwater bivalve species

Non-native species can exhibit different life history strategies, habitat requirements, invasion states, and legal statuses, which complicates the implementation of comprehensive programs for their management. In Europe, non-native bivalves such as *Dreissena* spp., *Corbicula* spp., and *S. woodiana* share similar habitat requirements but differ greatly in their life history strategies and invasion states, so that their interactions with native species may also differ (Table 2; Robertson et al., 2020). Other aspects, such as effectiveness and sustainability of the management measure, condition, and suitability of the target water, undesired side effects on other species, as well as legal constraints must always be considered when choosing the most appropriate measure.

Pre-border pathway management tools such as ballast water treatment are applied as a precautionary measure to prevent the transport of any non-native species from point to point (Tsolaki & Diamadopoulos, 2010). To achieve desired management success and to prevent the release of toxic and carcinogenic byproducts generated by this method, continuous control is crucial (Werschkun et al., 2014). If non-native species are already in transit between systems, management measures must be taken at designated target locations. Recreational watercrafts are prominent vectors for the spread of *Dreissena* and *Corbicula* spp. in the US, and likely also in Europe. A common and essential interception method is the inspection and decontamination of vessels prior to their launching (Zook & Phillips, 2009). Following specific protocols, both larval and adult bivalves are neutralized (Comeau et al., 2011).

In the case of *S. woodiana*, breeding and sale is a hardly recognized yet important vector for the bivalve's spread in Europe (Dobler et al., 2022). Trade bans and further legal regulations ("secure keeping"), as they exist in Poland, for example, could be an appropriate mitigation measure to secure at least adult specimens in captivity (Urbańska et al.,

Table 2 A selection of measures for the management of invasive bivalve species

Management type	Management tool	Required effort	Target species	State of invasion	Undesired effects	Example of application	References
Pre-Boarder Management	Ballast water management	Continuous control	Dreissenids, <i>Corbicula</i> spp.	NR, IT	Byproducts harm other species	International Ballast Water Management Convention	Jessen et al. (2006), Werschkun et al. (2014)
	Import and trade bans	Continuous control	<i>S. woodiana</i> , <i>Corbicula</i> spp.	NR, IT	Economic effects	Poland	Polish national law, i.e., Art. 120 para. 1 of the Act of 16 April 2004 on Nature Conservation
Interception	Watercraft inspection and decontamination	Continuous control	Dreissenids	IT	Economic effects	Lake Mead, NE (USA), Lake George, NY (USA)	Comeau et al. (2011), and Zook and Phillips (2009)
Limits to keep	Legal regulations	Continuous control	<i>S. woodiana</i> , <i>Corbicula</i> spp.	IT, CC	Economic effects	Poland	Polish national law, i.e., Art. 120 para. 1 of the Act of 16 April 2004 on Nature Conservation
Eradication	Bacterial toxin/Zequanox® (<i>Pseudomonas fluorescens</i>) (industry)	Few treatments needed	Dreissenids	SU, RW, SW, WS	Low Toxicity to other Organisms	Lake Carlos, MI (USA)	Luoma et al. (2015), Luoma et al. (2019), and Molloy et al. (2013)
	Biobullets® (industry/open waters)	Protection of native unionid population	Dreissenids, <i>Corbicula</i> spp.	SU, RW, SW, WS	more species-specific	Spanish irrigation system	Aldridge et al. (2006) and BioBullets Ltd. (2012)
	Copper sulfates (open waters)	Protection of native unionid population, restoration of aquatic fauna	Dreissenids	SU, RW, SW, WS	Lethal to other aquatic species	Lake Offutt, NE (USA)	Kennedy et al. (2006) and URS Group Inc. (2009)
	(Winter) Water drawdowns (regulated waters)	Protection of native unionid population, habitat restoration	All	SU, RW, SW, WS	Lethal to many species	River Nederrijn (NL), Lake Zorinsky, NE (USA), Lake Rothsee (GER),	Hargrave and Jensen (2012), Leuven et al. (2011), personal observation
Complete reproductive removal	Manual removal (open waters)	Continuous process	All, Juveniles, Adults	SU, RW, SW, WS	Spatially defined impact range	Lake George, NY (USA)	Wimbush et al. (2009)

Table 2 (continued)

Management type	Management tool	Required effort	Target species	State of invasion	Undesired effects	Example of application	References
Containment	Benthic mats (open waters)	Continuous treatment	Dreissenids, <i>Corbicula</i> spp.	SU, RW, SW, WS	Spatially defined impact range, affects other species	Lake Tahoe CA, NV (USA)	Wittmann et al. (2012)
Suppression	Biological control/ predation (open waters)	Control of predatory species	Dreissenids	SU, RW, SW, WS	May affect other species	Redear sunfish <i>Lepomis microlophus</i> , SW (USA)	Molloy et al. (1997), Prejs et al. (1990), and Wong et al. (2013)
Impact adaption	Feed/Food source	Further processing	All	WS	Economic effects	Feed supplement for poultry	McLaughlan et al. (2014)
Restoration	Creation of near natural habitats	Restoration measures	Dreissenids, <i>Corbicula</i> spp.	NR, IT	Economic, ecological effects		Sousa et al. (2021)

The classification by management type and states of invasion ("NR" = No Risk, "IT" = In Transit, "CC" = In Captivity / Cultivation, "SU" = Surviving in the Wild, "RW" = Reproducing in the Wild, "SW" = Spreading in the Wild, "WS" = Wide spread) are based on those of Robertson et al. (2020). Methods must not be exclusively assigned to the specified types of management

2019). In order to prevent an invasional progress to further stages, legal regulations to limit the keeping of this species are necessary.

When undesired non-native species are already established within a system, measures must be carried out directly within the area of interest. To avoid further spread, a complete reproductive removal would be the most appropriate management tool (Robertson et al., 2020). In Lake George (NY, USA) the removal of *D. polymorpha* by SCUBA divers succeeded in reducing the population to such an extent that further reproduction was no longer successful, which may also have been favored by the lake's naturally low calcium content, which is not suitable for *D. polymorpha* (Wimbush et al., 2009; Nierzwicki-Bauer & Frischer, 2018). To achieve such a success, early detection of invasion and a rapid management response are crucial (Wimbush et al., 2009). To prevent both initial establishment as well as continued reproduction of any existing invasive populations, larval settlement inhibitors are commonly used in industrial infrastructure (Sousa et al., 2014; Pucherelli, 2020). This can be achieved for example by physically induced pressure due to low frequency sounds (Donskoy et al., 1996), plasma pulse technology (Ge et al., 2019; Miller, 2000), or chemical treatments (Mackie & Claudi, 2010). These measures are not applicable in open waters without reservations due to the feasibility of the physical measures and the environmental impacts of the chemical treatments (Passamanek, 2018).

For water treatment in industrial infrastructure, a wide range of chemical treatments are usually applied for eradication and removal of undesired species. Due to its efficiency and cost effectiveness, chlorination is the most common and effective method in dreissenid control (Mackie & Claudi, 2010). However, its toxicity to other aquatic organisms and its potential to form carcinogenic trihalomethanes in combination with dissolved organic compounds renders it unsuitable for use in open waters.

Treatment selectivity is a crucial factor to determine appropriate mitigation measures in open waters. In one example of an open-water chemical eradication measure for *D. polymorpha* in Lake Offutt, USA, the application of two treatments of copper sulfate resulted in approximately 41,500 pounds of dead fish (URS Group Inc., 2009). On the other hand, winter drawdown treatments may be applicable in artificially regulated open waters such as dams and reservoirs

(Passamaneck, 2018). In most cases, this treatment is chosen to mitigate fouling by dreissenids (Leuven et al., 2014), but could also be used to manage *S. woodiana* populations. Since this measure also impacts non-target organisms, appropriate accompanying measures should be provided. Depending on the scale of the operation, native bivalves should be collected and either returned to the residual water or temporarily maintained in suitable waters. In this context, cleaning native bivalves from dreissenids and physically removing *S. woodiana* individuals would be a possible additional (yet work-intensive) eradication method.

The problem of selectivity could also be addressed by use of the BioBullet®, which has been used largely for open-water management of dreissenids (Aldridge et al., 2006). The BioBullet® is a microscopic biocide which is encapsulated in an edible material uptaken by target species (Aldridge et al., 2006). Since the BioBullet® does not hinder the bivalves' natural uptake of particles via filtration, a faster and more effective accumulation of the toxin is possible, which allows for a substantial reduction of the toxin dosage (Aldridge et al., 2006). The selectivity could be increased by additional coating as well as size modifications for a more species-specific impact (Costa et al., 2011).

Methods of containment or suppression, which limit the further spread or reduce the distribution of undesired species within the area of interest (Robertson et al., 2020), can serve as additional management techniques when the target invasive species is already successfully reproducing. In Lake Tahoe (CA, NV, USA), the use of benthic mats proves to be an effective control measure for *C. fluminea* (Wittmann et al., 2012), where areas settled by *C. fluminea* were covered by gas impermeable tarps so that dissolved oxygen was rapidly limited. A treatment like this, of course, affects the entire benthic fauna. Success and feasibility of this treatment also depend on the existing conditions of the benthic zone.

In addition, the biotic resistance of the native bivalve community against the invasion of non-native species could be conserved or increased following the restoration of degraded habitats. This was shown in a long-term study of the undisturbed Szeszupa River in Poland, where *D. polymorpha* is present at low densities and its abundance and distribution remained stable over the last 35 years (Ozgo et al., 2021).

A rather large number of applied control measures address *Dreissena* and *Corbicula spp.* in the industrial framework, where habitat overlap with native bivalves is typically not a problem. In context of conservation of native bivalve populations threatened by non-native / invasive bivalves, most of these measures are not applicable. Management programs for *S. woodiana* are still in their infancy since this species is not relevant in the industrial context, although its distribution strongly overlaps with native bivalves (Fig. 3).

In general, management measures that have a direct negative impact on the system cannot be regarded as protective measures in the first place. A harm-benefit assessment, which also considers the harm caused by the target invasive species, must be conducted before choosing an appropriate treatment. Costs and efforts of eradication measures and habitat restoration increase. Accordingly, one may assume that preventive measures to avoid or interrupt the invasion process at an early stage, prior to the infestation of the target water body, are considered desirable. This does not seem to hold true since more resources are invested primarily to control existing invaders rather than to prevent new invasions (Finnoff et al., 2007).

As intact freshwater systems seem to have a greater resilience against biological invasions compared to anthropogenically altered ones (Ozgo et al., 2021), the conservation and restoration of such habitats are the most sustainable management option. As a rule of thumb, the conservation of intact habitats tends to be the preferred solution over restoration, also from an economic point of view (Geist, 2015).

Conclusions

As evident from the niche overlaps as well as the strong and multiple interactions of non-native fauna with native bivalve species in Europe, management of endangered bivalve populations must also include monitoring and management of non-native species. As evident from successful invasions of undesired species such as *Dreissena spp.*, *Corbicula spp.*, and *S. woodiana* within European lake and river systems, early detection and prevention of their introduction are essential. Generalist species tend to be mostly affected by competitive interaction, whereas highly

specialized native species have a lower risk of niche overlap and competition with non-native species. The conservation of intact and restoration of disturbed habitats for native bivalves is a more resilient and sustainable management measure compared to direct eradication attempts for non-native species which typically also have undesired side effects. Some fast-spreading species in Central Europe, especially *S. woodiana*, are currently poorly monitored and largely unaffected by most management measures, therefore deserving increased attention.

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