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PERSPECTIVE

# Enigmatic freshwater mussel declines could be explained by the biodiversity-disease relationship

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## Abstract

1. The biodiversity-disease relationship states that increased species richness leads to lower pathogen pressure (i.e. the dilution effect), an effect that erodes with biodiversity loss. However, whether losses of the dilution effect can trigger extinction cascades remains largely unexplored.
2. To explore this idea, we consider declines in freshwater mussels, on average the most threatened non-marine group of organisms in the world. We argue that anthropogenically stimulated declines in mussel richness amplify pathogens in remaining species. Pathogen amplification triggers further local losses in both mussel abundance and richness, explaining the observed so-called "enigmatic" declines in freshwater mussels.
3. Vulnerable communities could become trapped in cycles of pathogen amplification and host decline. We highlight knowledge gaps and provide key steps to assess the likelihood of this occurring; these key steps are applicable to any host group.
4. *Policy implications*. Our argument constitutes a testable hypothesis that may explain richness or abundance declines in previously intact communities. We provide further impetus for the consideration and preservation of diversity at a local scale and show that effective conservation requires integration of both host and parasite ecology.

**KEYWORDS**
amplification, community ecology, dilution, parasite, pathogen, specialist, unionid

## 1 | INTRODUCTION

The threatened nature of freshwater mussels is well-documented. Over 45% of freshwater mussels are considered near threatened, vulnerable or endangered, a figure which rises to nearly 70% in North America (IUCN, 2022). Many causes of mussel declines are well established, but mussel populations and species are also subject to enigmatic declines: significant reductions in population size, or local extirpations of certain species, that do not have a clear cause. Recent reviews emphasise that significant knowledge gaps still exist in freshwater mussel conservation (Aldridge et al., 2022; Ferreira-Rodríguez et al., 2019; Sousa et al., 2022). Knowledge gaps make addressing these enigmatic declines difficult. If we are to appropriately conserve freshwater mussels, and the vital ecosystem services they

provide (Zieritz et al., 2022), we need to understand all the drivers of mussel declines in order to arrest them (Haag, 2019).

Disease has been suggested as a possible cause of enigmatic declines (Haag, 2019). While others remain sceptical about the role of disease (McElwain, 2019), it appears plausible, given that at many sites where mussels have declined, other fauna (e.g. fish) remain unaffected (Sanchez Gonzalez et al., 2021). Indeed, global richness and diversity of freshwater invertebrates have increased on average, a trend bucked by freshwater mussels (Pilotto et al., 2020). Recent evidence suggests pathogenic viruses and bacteria are highly prevalent and significantly overlooked in freshwater mussels (Brian, Ollard, et al., 2021; Richard et al., 2020). More generally, some aquatic species have exhibited recent rapid declines that appear to be linked to disease, such as certain species of marine mussels (Katsanevakis et al., 2019) and freshwater turtles (Chessman et al., 2020), suggesting that greater consideration of disease is required for the management of threatened populations.

We use the biodiversity-disease relationship to provide a mechanistic hypothesis for disease-driven enigmatic freshwater mussel declines. Haag (2019) draws a distinction between enigmatic declines (affecting the entire mussel community) and mass die-offs (rapid declines that affect one or a few species). We argue that the biodiversity-disease relationship can explain both. The link between mussel declines and the biodiversity-disease relationship has previously been suggested (Brian, 2022, pp. 161–163); here, we provide a more formalised argument. To move forward, the field needs to take a community-level approach to freshwater mussel parasitism and disease, both in terms of mussel host communities, and parasite and pathogen communities. Our hypothesis has relevance not just for freshwater mussels, but for the conservation of any host group.

## 2 | THE BIODIVERSITY-DISEASE RELATIONSHIP

Most species are infected with a variety of parasites and pathogens (henceforth 'pathogens'). Freshwater mussels are no exception (Brian & Aldridge, 2019). While some pathogens are generalists and able to infect a variety of different host species, most pathogens are specialists: they can only infect a very limited range of species (Carlson et al., 2019). This specialisation is characteristic of host–parasite networks due to reciprocal selection dynamics and co-evolution (Blasco-Costa et al., 2021). Therefore, as the number of host species increases, the number of pathogen species also increases (Figure 1a; Brian & Aldridge, 2022). However, high host richness means that most of the individuals in a community will be unsuitable for a given pathogen species, which can only succeed in a small number of host species. Therefore, the prevalence or abundance of any one pathogen should *decrease* with host richness (Figure 1b). This negative relationship is caused by 'wasted' infections, with the pathogen dying or unable to reproduce in hosts that it does not specialise on (Garrido et al., 2021). This relationship may not hold at very low host richness, as abundant hosts (which are more likely to be observed in species-poor host communities) tend to host parasites at higher prevalences and have more parasite individuals per host (Figure 1c; McCaffrey & Johnson, 2017). However, at local spatial

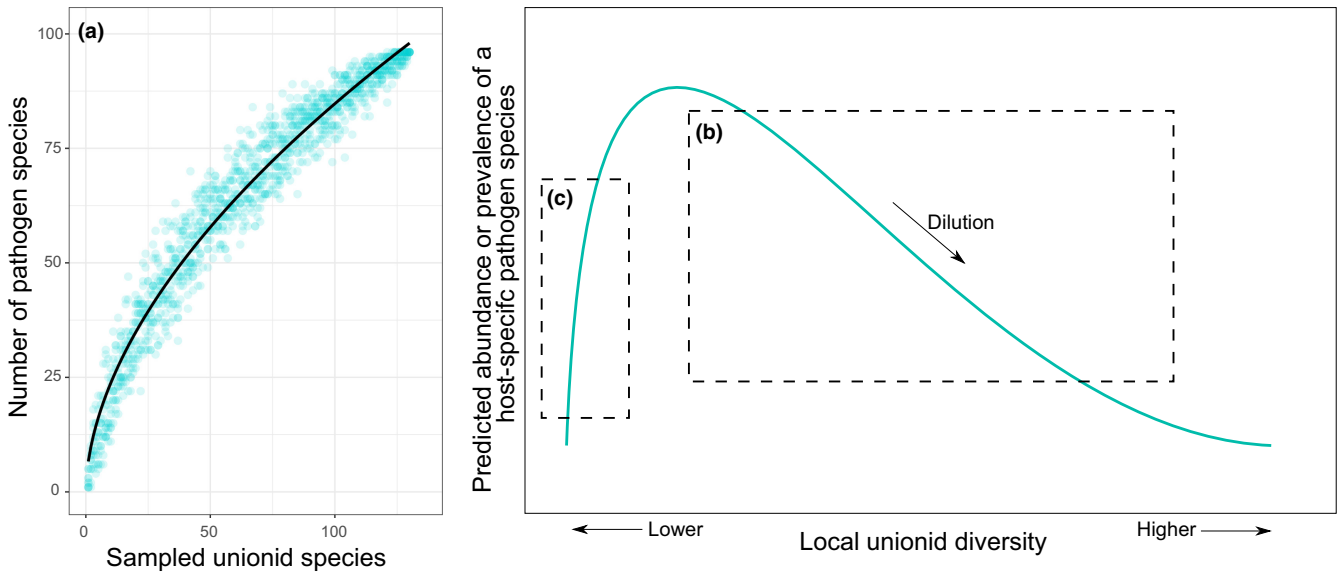


FIGURE 1 The biodiversity-disease relationship. (a) Pathogen richness increases with host richness. The lack of asymptote suggests that pathogen diversity in unionid mussels remains severely undescribed. Curve made using 10 random samples for each number of host species and calculating the current number of pathogens observed in those host species. Data from Brian & Aldridge et al. (2022). (b) High unionid diversities should encourage lower prevalence and abundance of any given pathogen species, through the dilution effect. (c) When unionid diversity is low, the dilution effect cannot apply, and pathogen prevalence or abundance is promoted. Figure 1b,c adapted with permission from Halliday and Rohr (2019).

scales, the biodiversity-disease relationship (Figure 1b,c) tends to be strongly right-skewed, meaning that with higher host richness comes a reduced risk of pathogen-induced morbidity or mortality (Halliday & Rohr, 2019; Rohr et al., 2020), a phenomenon known as the dilution effect (Figure 1b).

The dilution effect is an important benefit of biodiversity that prevents pathogen outbreaks (Keesing et al., 2006). While the ubiquity of the dilution effect is debated (Rohr et al., 2020), recent work suggests it is observable particularly where there has been biodiversity loss (i.e. local species extirpations, Halliday et al., 2020). Natural biodiversity gradients show little trend in terms of pathogen severity, perhaps because these local communities have evolved to reach equilibrium conditions over long periods of time. However, communities where there have been observed or experimentally induced richness reductions show strong increases in pathogen prevalence and abundance (Halliday et al., 2020) because community disassembly tends to favour the most competent hosts (Johnson et al., 2013). Therefore, communities that have undergone recent biodiversity reductions, such as freshwater mussels, may be particularly vulnerable to pathogen amplification in the remaining species. This underlying framework provides a plausible mechanism for freshwater mussel declines.

## 3 | DECLINES IN MUSSEL BIODIVERSITY AMPLIFY PATHOGENS IN REMAINING SPECIES

Intact freshwater mussel communities are highly speciose, especially in North America. Therefore, we also expect a high number of pathogens to exist in these communities (Brian & Aldridge, 2022; Figure 1a). Though pathogens remain severely understudied (Brian & Aldridge, 2019), a wide variety of potentially pathogenic bacteria and viruses are being described from freshwater mussels (Bojko, 2022; Chittick et al., 2001; Goldberg et al., 2019; Richard et al., 2020, 2021, 2022; Starliper et al., 2011). Fungi have also been occasionally observed inside freshwater mussels but are largely overlooked (Popova & Biochino, 2001); given their role in devastating amphibian declines, fungi may warrant future attention. In addition, macroparasites such as trematodes and mites can also lead to population-level declines (Brian, Dunne, et al., 2021). Trematodes often lead to castration and thus recruitment failure (Taskinen et al., 1997), a characteristic of some enigmatic declines (Haag, 2019).

Mussels have undergone severe recent declines, through a variety of known causes. By causing local extirpations or large reductions in density of certain species, we suggest that declines have eroded the beneficial dilution effect of high mussel biodiversity, thus promoting pathogen abundance in their remaining target species. Pathogen amplification then traps mussels in a cycle which promotes further biodiversity losses (Figure 2). Importantly, there may be a time lag from previous impacts until the effects of pathogen accumulation are observed, leading to declines in the apparent absence of other drivers.

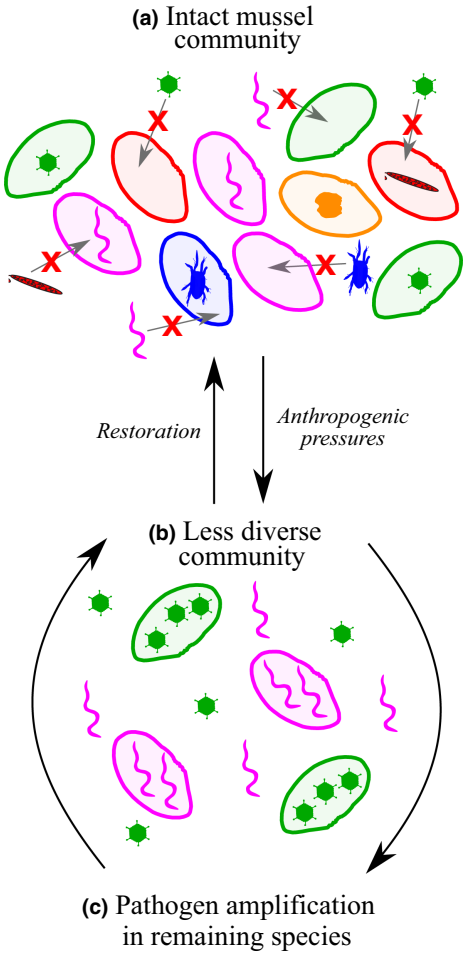


FIGURE 2 A hypothesis for enigmatic declines in freshwater mussels. Different mussel species are different colours, each with their own specialist pathogen of matching colours. (a) An intact, diverse mussel community should have high pathogen richness but all at low prevalence due to 'wasted' infections in non-suitable hosts (red crosses). (b) Anthropogenically stimulated losses reduce the effectiveness of the dilution effect, by reducing the proportion of hosts that are non-competent for pathogens of the remaining species. (c) Losses amplify the pathogens of those remaining species (as a greater proportion of hosts are competent for that given parasite), reinforcing the diversity loss/amplification cycle. Restoration action could rebuild the strength of the dilution effect.

As an example, Richard et al. (2020) documented a mass die-off in *Actinonaias pectorosa* (pheasantshell) in the Clinch River, USA, which was strongly correlated with the prevalence of a previously unreported densovirus. This die-off appeared limited to *A. pectorosa* and did not affect the other 46 mussel species in the river, which was striking as *A. pectorosa* was previously one of the most common species in the community (Jones et al., 2014). However, this species-specific effect is entirely consistent with the biodiversity-disease relationship. Host-specific viruses of *A. pectorosa* may have previously been diluted by non-competent mussel species. With local losses of some of these rarer species due to pollution and other factors in this river (Ahlstedt et al., 2016), the dilution effect was eroded, with the consequence being virally

induced mass mortality in the focal host (Richard et al., 2020). Haag (2019) also highlights that enigmatic declines in the Little Tennessee River were most pronounced in *Alasmidonta* spp., the most common species in the river. We note that the dilution effect is not limited to common species, and would be expected to be observed for all remaining species in the community. Erosion of the dilution effect is thus consistent with the ubiquitous declines across all species that often characterise enigmatic declines (Haag, 2019). However, this erosion will be most visible in common species because they will have the highest densities to sustain their specialist pathogens, and it cleanly explains the increasingly frequent observation of species-specific mass die-offs in previously dominant mussel species. One of the reasons Haag (2019) leans away from disease as a possible cause of declines is because a given pathogen would need to be highly virulent to *all* freshwater mussels, which he considers unlikely. However, the biodiversity-disease relationship highlights that this need not be the case: if previous stressors have led to reductions in mussel abundance or richness (and thus reductions in dilution), every species-specific pathogen of remaining mussels may be amplified, and thus lead to ubiquitous reductions.

The biodiversity-disease relationship is not a 'smoking gun'—with the diversity of threats facing mussels and the diversity of habitats they occupy, it is unlikely that any one factor fully explains declines. However, we argue that the biodiversity-disease relationship and the loss of dilution successfully integrates anthropogenically stimulated mussel losses with more enigmatic declines. Most importantly, it constitutes a testable hypothesis. Many long-term surveys exist of mussel populations and communities in multiple locations, which likely represent a gradient of biodiversity losses over time (some sites will have undergone limited biodiversity changes, others will have lost many species). Using recently developed techniques, which can include non-destructive sampling (Brian & Aldridge, 2021b; Richard et al., 2020), these communities should be sampled for pathogen load. We predict that those communities that have experienced higher diversity loss will have corresponding higher pathogen loads. This mechanism may hold even in lower-diversity rivers or basins such as in Europe, as biodiversity loss rather than underlying low richness is the key mechanism disrupting dilution (Halliday et al., 2020). Any losses, even from sites with low starting diversity, may reduce benefits of the dilution effect.

If correct, our hypothesis would be a major step forward in understanding enigmatic declines and provide additional impetus for conserving freshwater mussel biodiversity. It raises the possibility of translocations of non-competent species to at-risk rivers to dilute the pathogen risk for remaining host species (Stanicka et al., 2022). We note that the biodiversity-disease relationship is most likely to be observed for passively dispersed pathogens, such as bacteria and viruses. Other pathogens such as mites (and possibly trematodes) are able to actively select hosts, and so will still be able to effectively target their specific host species even at low density (e.g. Downes, 1991).

## 4 | FACTORS INFLUENCING LOSS OF DILUTION AS AN EXPLANATION FOR ENIGMATIC DECLINES

Many factors could influence the likelihood or strength of the dilution effect. First, freshwater fish are also important to consider. Freshwater mussels are themselves parasitic and often host-specialists, with glochidia (juvenile mussels) attaching to the gills and fins of certain species of freshwater fish (Aldridge et al., 2023). While host fish losses are a recognised cause of mussel declines, less explored is the relationship between host fish community composition and mussel success. If fish communities change so that the preferred host of a given mussel species is outcompeted, that specific mussel population will decline (as most of its glochidia end up on non-viable hosts). This decline would also be consistent with observed enigmatic declines and is caused by the dilution effect occurring from the perspective of the fish community. Further, fish could amplify or ameliorate parasite burdens. The presence of many predatory fish at high trophic levels could reduce parasite exposure and burden by stimulating mussel valve closure (Cornelius et al., 2023), but these same fish can act as the final host for trematode parasites (Brian, 2022), and so their presence could increase trematode burden in mussels. A multi-trophic perspective on parasite community ecology is ultimately required to comprehensively understand the role of diversity losses in the erosion of the dilution effect.

Second, rapidly spreading invasive mussels (such as zebra and quagga mussels) require careful consideration. If they are competent hosts for native pathogens, they provide an additional viable (reservoir) host and could thus drive further pathogen amplification, even when native hosts are at very low density (Kelly et al., 2009). If they are non-competent they could potentially contribute to dilution and provide a cryptic benefit to natives, something recently shown to benefit native snails (Stanicka et al., 2023). Invasive mussels could also potentially consume pathogen infective stages, particularly those of trematodes (Koprivnikar et al., 2023). However, invasive mussels host their own parasites, which could spill over to native mussels: introduction of a new pathogen to naïve native mussels could devastate populations and would also be consistent with rapid declines, independent of the dilution effect (Brian, Ollard, et al., 2021). Competence and spillover could be tested in a hypothesis-driven fashion; for example, phylogenetically similar invaders (such as *Sinanodonta woodiana* to native *Anodonta* species) may be able to host the same pathogens (Cichy et al., 2016), while phylogenetically more distinct invaders such as *Dreissena* spp. may not (Brian & Aldridge, 2019). The assessment of these issues requires integration of native and invasive mussel community ecology with disease ecology.

Third, successful pathogen transmission relies on sufficient host density. Richness or abundance losses lead to potentially less dense remaining populations, and so pathogen transmission would also decrease as more transmissible stages are lost to the environment (i.e. wasted in the environment as opposed to being wasted

in non-competent hosts). However, smaller populations often aggregate and so maintain or even increase their density, promoting pathogen transmission (Marcogliese, 2023); this supports our proposed mechanism for enigmatic declines. Further, mussels are prodigious filter feeders and so may actively accumulate passive transmissible stages of pathogens.

Finally, there are facets of enigmatic declines that the dilution effect cannot explain—for example, the patchy spatial nature of declines (Haag, 2019), especially mass die-offs. However, biogeographic patchiness of disease outbreaks is extremely common (Dallas et al., 2019). It may be that mass die-off events (as opposed to more general declines) are caused by the interaction of pathogens with other stressors. For example, digenean trematodes castrate their hosts but also cause elevated death rates in anoxic conditions (Jokela et al., 2005). Climate change therefore potentially exacerbates existing pathogenicity, which should be investigated further. In addition, some enigmatic declines have been observed to progress in an upstream direction (Haag, 2019). Upstream progression would not be expected if disease was a driver, as pathogen dispersal is most likely passive and should largely progress downstream. However, we argue that loss of the dilution effect remains a plausible hypothesis to explain many declines and should be tested.

## 5 | A COMMUNITY APPROACH TO BIODIVERSITY AND DISEASE

Current knowledge on freshwater mussel parasites and pathogens is inadequate. The field has relied on a small group of researchers, who typically study one type of pathogen (for example, trematodes, mites or viruses). If we are to fully understand the ecology of freshwater mussels, and therefore their die-offs and declines, greater investment is required into the study of host–parasite community ecology.

First, pathogen-mussel relationships need to be understood from the perspective of the host community, particularly regarding host competency. The degree of pathogen diversity, specialism and generalism in freshwater mussels are fundamental knowledge gaps, caused by a severe lack of sampling. To understand possible pathogen dilution and amplification, we need to be able to definitively state which host species a pathogen is *absent* from, as well as present in. Much closer attention needs to be paid to the relationship between host and pathogen richness, the vast majority of which remains yet to be described (Brian & Aldridge, 2022). As well as increasing knowledge on pathogen-mediated declines, this has additional practical importance. First, pathogens can significantly alter the ecosystem services provided by the wider mussel community (Brian et al., 2022), something which cannot be predicted without understanding parasite diversity and distributions. Second, if certain mussel species are found to be reliably non-competent for disease-causing pathogens, they could be introduced into vulnerable locations to restore the benefit of the dilution effect (Stanicka et al., 2022; Figure 2). However, such restoration action relies on comprehensive knowledge of pathogens' host ranges and competency, information known for very few freshwater or invertebrate taxa.

Second, interactions within the pathogen community may influence pathogen distributions, and thus their effect on freshwater mussels. Parasite competition is commonly reported in snail hosts and has the potential to alter parasite distributions (e.g. Hechinger et al., 2011). In two recent freshwater mussel studies, both positive and negative interactions were recorded between pathogens, including some which appeared to exclude certain parasites from individual mussels (Brian & Aldridge, 2021a, 2023). To our knowledge, these are the only studies to date that considers the community ecology of freshwater mussel parasites, in terms of assembly and interactions. However, these studies only looked at macroparasites. There needs to be increased investigation into microparasites (e.g. bacteria, viruses) and their interaction with macroparasites. Incidental evidence suggests a link between trematode presence and viral load (J. Richard, personal communication).

Host competency, host–parasite and parasite–parasite interactions need to be considered beyond native freshwater mussels: invasive species and other members of freshwater communities such as fish also require close assessment. Using network approaches and incorporating host phylogeny has been successful in predicting mammal and fish parasites (e.g. Dallas et al., 2017; Dallas & Becker, 2021); such an approach could also be useful in predicting the parasite landscape of freshwater systems, and how changes in community richness or composition could affect parasite burden, in freshwater mussels and beyond.

## 6 | CONCLUSION

Biodiversity losses have been shown to reduce the effectiveness of dilution and thus enhance pathogen and parasite risk. Using freshwater mussels as an example, we have hypothesised that these losses enhance the risk of local or global extinction, and explain so-called 'enigmatic' declines in vulnerable or endangered fauna, something also observed in other freshwater taxa (e.g. Chessman et al., 2020). Given parasites are severely understudied, the relationship between diversity, parasitism and species loss requires much greater attention. If correct, our hypothesis provides further impetus for the consideration and protection of biodiversity on local as well as global scales.

### AUTHOR CONTRIBUTIONS

Joshua I. Brian conceived the idea. Joshua I. Brian and David C. Aldridge discussed the idea, and Joshua I. Brian drafted the manuscript, with contributions from David C. Aldridge. *Statement on inclusion*: Our perspective did not include local data collection. However, our hypotheses are based on data and observations from Europe and North America, where both authors work. We recognise there are highly diverse freshwater mussel communities in South America, Asia and Africa; to our knowledge, there is almost no information

regarding the community ecology of their parasites or pathogens. Engaging with local scientists to fill this knowledge gap is a high priority of our future research.

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## CONFLICT OF INTEREST STATEMENT

The authors confirm no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.ngf1vhj0k (Brian, 2023).

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