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Long-term macrophyte and snail community responses to population declines of invasive rusty crayfish (*Faxonius rusticus*)

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Abstract

A central focus of invasive species research has been on human efforts to eradicate invaders or reduce their abundance to mitigate the worst of their impacts. In some cases, however, populations of invasive species decline without human intervention, which may inform management responses to these invaders. Such is the case of the invasive rusty crayfish (*Faxonius rusticus*) in northern Wisconsin, USA where systematic population monitoring since 1975 has revealed population declines in approximately half of the lakes surveyed. Population declines of invasive species without human intervention remain understudied, but there is even less research on how communities respond following such declines. Using ten lakes in Vilas County, Wisconsin, we investigated community recovery of habitat (macrophytes) and prey (freshwater snails) of *F. rusticus* following up to 33 years of declines of this invader in some lakes using a dataset with a rare, long-term span over which consistent data were collected (1987, 2002, 2011, and 2020). We compared community responses in lakes where *F. rusticus* populations reached a peak and subsequently declined (boom-bust lakes) and lakes where our dataset only captured the decline of *F. rusticus* (bust lakes) to reference lakes with consistently high or low crayfish abundance over time. We found partial recovery of macrophytes and snails in the bust and boom-bust lakes where *F. rusticus* has declined, with recovery of macrophyte abundance and richness in the boom-bust lakes achieving levels observed in the low-crayfish reference lakes. Snail abundance and richness increased after declines of *F. rusticus*, though not to the level of the low-crayfish reference lakes, suggesting that snail recovery may lag macrophyte recovery because snails are dependent on macrophytes and associated periphyton for habitat. The recovery we document potentially represents long-term ecosystem resilience of lakes to biological invasions. Our results suggest that lake communities may recover without active restoration interventions after invasive crayfish population declines, although identifying which lakes experience these natural declines remains a priority for future research and management.

Keywords: Snail, aquatic macrophyte, boom-bust, alien species, exotic species, gastropod, recovery

Introduction

Invasive species have impacts across levels of the ecological hierarchy, from genes to native populations to communities and ecosystems (Parker et al. 1999, Cucherousset and Olden 2011). To mitigate these effects, considerable research has focused on how to either eradicate invasive species or reduce their abundance through maintenance management (Manchester and Bullock 2000, Zavaleta et al. 2001, Simberloff 2021). In some cases, however, the abundance of invasive species declines naturally without human intervention (Strayer et al. 2017). These “natural” declines are sometimes caused by invasive species themselves, as their impacts on invaded ecosystems harm their own populations through depleted food resources or habitat modification (Tang et al. 2012, Lester and Gruber 2016, Vuorinen et al. 2021). However, natural declines of invasive species are understudied and infrequently documented, leading to uncertainty about their frequency and importance (Simberloff and Gibbons 2004, Aagaard and Lockwood 2016). Similarly, even less is known about the recovery of communities or ecosystems (i.e., post-disturbance resilience) after natural population declines of invasive species (Carpenter et al. 2001, Strayer et al. 2017). A better understanding of the causes and consequences of natural population declines would allow managers to make informed decisions about the necessity of eradication and control during invasion as well as active restoration following invader declines (Simberloff and Gibbons 2004).

As a type of major ecological disturbance, invasive species have inspired much research on the recovery potential of invaded ecosystems (Jones and Schmitz 2009, Prior et al. 2018). However, many studies consider only species that have declined due to human intervention, rather than natural mechanisms (Jones et al. 2016, Kopf et al. 2017), and recovery after natural declines remains uncertain. In a review of ecosystem recovery following anthropogenic disturbances, Jones and Schmitz (2009) found relatively quick (a decade or less) recovery after invasive species removal efforts, which might suggest that some communities and ecosystems could also recover quickly after natural declines of invasive species. Alternatively, invaders that have experienced natural population declines may eventually increase from low abundance as part of a boom-bust cycle, extending their impacts (Strayer et al. 2017, Vuorinen et al. 2021). Even if there is no subsequent recovery in invader abundance, populations of native species may not recover if invader impacts are so severe (e.g., extirpation of native species) that they persist beyond declines, if the invader triggered a shift between alternative stable states, or if a new invasive species arrives (Weber and Brown 2009, Hansen et al. 2013b, Strayer et al. 2017). For example, population declines of the invasive cane toad (*Rhinella marina*) in Australia did not lead to community recovery during the period when *R. marina* was declining, perhaps because their negative effects on top predators persisted past invader decline (Brown and Shine 2019). Further studies are needed to determine if ecosystem recovery is the exception or the rule after natural population declines of invasive species. If communities and ecosystems do not recover after natural declines of invasive species, then more active restoration interventions may be needed (e.g., Hazelton et al. 2018, Kettenring and Tarsa 2020).

The rusty crayfish (*Faxonius rusticus*) is an invasive species in North America that has exhibited natural population declines in some lakes in northern Wisconsin, USA (Larson et al. 2019). Over several decades of intensive study, *F. rusticus* was documented to strongly impact invaded ecosystems, causing declines of native fishes, macroinvertebrates, and macrophytes as its populations grew to hyper-abundance relative to native crayfishes (Olsen et al. 1991, Wilson et al. 2004, McCarthy et al. 2006, Hansen et al. 2013c). This destruction of macrophytes in particular might be responsible for recently observed population declines of *F. rusticus* due to the associated loss of shelter from predators in lakes without other habitat like rock substrate (Kershner and Lodge 1995, Larson et al. 2019), although *F. rusticus* population declines could also be caused by under-studied factors such as pathogen accumulation (Sargent et al. 2014, Stricker et al. 2016) or climate change (Sandström et al. 2014). Irrespective of mechanism, *F. rusticus* population declines in Wisconsin lakes offer an opportunity to investigate community and ecosystem recovery after the natural decline of an invasive species.

Several previous studies in northern Wisconsin lakes have examined whether freshwater communities and ecosystems can recover after either natural or human-caused declines in *F. rusticus* populations. Baldridge and Lodge (2014) found that macrophytes in lakes invaded by *F. rusticus* had only a modest potential for future recovery due to depleted seed banks compared to uninvaded lakes, suggesting that active restoration of lakes might be necessary for recovery of macrophyte communities after *F. rusticus* declines (e.g., Kettenring and Tarsa 2020). Conversely, Hansen et al. (2013a) demonstrated that manual removal of *F. rusticus* from a small lake resulted in substantial recovery of macrophytes, but found no recovery of benthic macroinvertebrates, perhaps because the recovery of fish populations suppressed invertebrate response. Kreps et al. (2012) investigated consequences of natural declines of *F. rusticus* and suggested that recovery of benthic invertebrates, such as freshwater gastropods (snails), may lag the recovery of macrophytes because snails depend on macrophytes for habitat and associated periphyton as food. However, Kreps et al. (2012) was conducted before declines of *F. rusticus* became more pronounced in these study lakes over the following decade; updated monitoring is needed to determine if snail communities have since recovered (Larson et al. 2019). Taxa- or species-specific recovery following declines of invasive species, whether natural or from human intervention, might mean that managers need to target specific organisms with restoration efforts, especially in cases where native community composition has changed since invasion (Sanders et al. 2003, Cucherousset and Olden 2011, Kettenring and Tarsa 2020).

We used a long-term dataset (Lodge et al. 1998, Kreps et al. 2012, Baldridge 2013, Larson et al. 2019; this study) to investigate whether habitat (macrophytes) and preferred prey (snails) recover in lakes where *F. rusticus* has experienced natural population declines. The effects of invasive species can vary across invasion stage, and our community sampling at different points within a 33-year timespan (1987, 2002, 2011, and 2020) offers a rare opportunity to study the time dependency of community impacts of invasive species (Blossey 1999, Strayer et al. 2006). In lakes with high relative abundance of *F. rusticus* and no declines, we expected both prey (snails) and habitat (macrophytes) to remain depressed relative to low-crayfish reference lakes over time. We expected that macrophytes might begin to recover in lakes with natural *F. rusticus* population declines, but that prey items like snails may lag this recovery due to their dependence on macrophytes for habitat or because of complex interactions with fish (Brönmark 1989, Turner et al. 1999, Kreps et al. 2012). Community recovery in lakes where *F. rusticus* has naturally declined would constitute long-term ecosystem resilience to the impacts of a major invasive species, and could mean that there are cases where managers do not need to remove or eradicate this species or fund active restoration following its decline.

Methods

Study Region and Species

We sampled macrophytes, snails, and crayfishes in ten *F. rusticus*-invaded and uninvaded lakes (Table 1) between late June and early September of 1987, 2002, 2011, and 2020. Subsets of the 1987, 2002, and 2011 data were previously used in other publications but were never published in a data repository (Olsen 1989, Lodge et al. 1998, Rosenthal 2004, Kreps et al. 2012, Baldridge 2013, Baldridge and Lodge 2014). Data from 2020 are original to this study. Our study lakes are located in Vilas County, Wisconsin, USA, and are part of the Northern Highland Lake District, an intensively studied region with a high density of kettle lakes formed during the last glaciation (Carpenter et al. 2007). Lakes in this region are typically oligotrophic to mesotrophic with undeveloped, forested watersheds (Peterson et al. 2003, Hanson et al. 2007). Our ten study lakes were originally selected because they have high enough calcium concentrations (>5 mg $Ca \cdot L^{-1}$) to support both snails and crayfishes (Lodge et al. 1998). Macrophyte and snail communities within our lakes are relatively diverse, and our dataset includes more than 40 species of macrophytes and 25 species of snails (Appendix S1: Tables S1 and S2). Besides *F. rusticus*, other crayfishes such as the virile crayfish (*Faxonius virilis),* northern clearwater crayfish (*Faxonius propinquus*), and calico crayfish (*Faxonius immunis*) have all been found at low relative abundances in our lakes (Larson et al. 2019).

Faxonius rusticus was introduced to northern Wisconsin during the 1960s and spread between lakes through human vectors such as bait buckets or other intentional release (Capelli and Magnuson 1983, Puth and Allen 2005). Since its initial introduction, *F. rusticus* has become the most common crayfish (by occurrence records) in Wisconsin (Olden et al. 2006), and its impacts have been intensively studied in this region (Olsen et al. 1991, Wilson et al. 2004, McCarthy et al. 2006, Hansen et al. 2013c, Szydlowski et al. 2022a). Crayfishes in eight of our ten study lakes were originally sampled in the 1970s as part of an expansive survey of 67 Vilas County lakes, and the crayfish portion of our community dataset (1987–2020) is an extension of that original sampling (Capelli and Magnuson 1983). This long-term monitoring of *F. rusticus* populations in our study lakes has revealed several different population trajectories, including sustained low relative abundances, increases to a peak before subsequent natural declines, and increases to sustained, high relative abundances (Larson et al. 2019). Of the four lakes where *F. rusticus* has declined (described below), two lakes experienced declines 10-15 years before the others.

Population Monitoring of *F. rusticus*

Between 1975 and 2020, each of our ten study lakes was sampled for crayfishes between nine and 17 times using standard methods for our study system (Table 1; Capelli and Magnuson 1983, Kreps et al. 2012, Baldridge and Lodge 2014, Larson et al. 2019). Wire-mesh Gee minnow traps with two 3.5 cm diameter openings were baited with approximately 120 g of beef liver and set overnight at depths of 1–3 m. Each lake was sampled at either 24 or 36 sites, located at least 100 m apart, to allow for 12 traps per major habitat type present in the lake (cobble, open sand, or macrophyte; Kershner and Lodge 1995, Lodge et al. 1998). Sites were located with marked bathymetric maps in early years of sampling and later with a handheld global positioning system (GPS). Trap numbers were generally consistent between years within lakes, with only minor inter-annual variation due to trap theft or damage. Crayfish species, size, and sex (including reproductive form for males) were recorded for each trap. Because trapping is biased towards adult males, we calculated catch-per-unit effort (CPUE) as male *F. rusticus* per trap, which compares well to other methods of measuring crayfish in our study system such as SCUBA surveys or biomass estimates (Capelli and Magnuson 1983, Olsen et al. 1991). Consequently, all subsequent references to *F. rusticus* relative abundance are male crayfish per trap. Finally, trapping almost always occurred between mid-July and late-August, after *F. rusticus* had molted from its reproductively inactive Form II to its reproductively active or mature Form I (Larson et al. 2019).

Monitoring of Macrophytes and Snails

Macrophytes were sampled during July and August at a subset of crayfish sampling sites (n = 6–14 sites per lake, Table 1) that were selected in 1987 to capture a variety of substrates and both east and west exposure. Sampling depths were randomly assigned to sites during initial sampling in 1987 as either 0.75 m, ½ of Secchi depth, or ¾ of Secchi depth (Kreps et al. 2012), with 1987 depths used for all subsequent sampling years for macrophyte surveys. We followed the line-intercept method to sample macrophytes (Brower et al. 1997), using snorkeling and SCUBA to visually identify and determine the presence or absence of macrophyte species along a 25 m transect set parallel to shore at the pre-determined depth for each sampling site. Transects were marked at 1 m intervals, with the first 10 cm of each interval marked by a band of tape. Divers moved along the transect recording the presence or absence of each macrophyte species crossing the vertical plane of each 10 cm band. The line-intercept method allowed us to obtain a measure of both macrophyte species richness and abundance. Because just presence or absence of macrophyte species was recorded, and only at each 10 cm band, our measurements provide an index for abundance and a minimum estimate for species richness.

Freshwater snails were sampled at every crayfish sampling location (n = 24 or 36 sites per lake; see previous section, Table 1) between late June and early August. As with macrophytes, snails were sampled at randomly assigned depths of either 0.75 m, ½ of Secchi depth, or ¾ of Secchi depth. While the same absolute depths were used in 1987 and 2002 based on 1987 Secchi values, depths in 2011 and 2020 were determined using year-specific Secchi values. Most sampling depths in 2011 and 2020 varied only slightly from the 1987 and 2002 values, but in two lakes the change in sampling depth was greater than one meter due to larger shifts in water clarity. The greatest changes in sampling depth (2.7 m in Papoose Lake and 1.5 m in Little John Lake) occurred at the ¾ Secchi depth sites, whereas the ½ Secchi depth sites were less affected by the change in water clarity in these two lakes.

We sampled snails using methods and equipment designed for each habitat type present in our study lakes (soft substrates, macrophytes, and cobble). For soft substrates such as sand and muck (flocculent sediment or sediment rich in organic material), we used a cylindrical polyvinyl chloride (PVC) sediment corer (0.018 m^2) to take a 5 cm sediment core (Appendix S2: Figure S1). For sites with soft substrates where macrophytes were present, we used a modified PVC sampler of the same size but with two hinged PVC halves, and a net made of 1-mm mesh attached to the top (Appendix S2: Figure S1). We carefully closed the two halves of the PVC sampler around macrophytes growing at the surface and zippered the mesh net around taller macrophytes before pushing the corer into the sediment to collect a 5 cm core. Collecting the macrophyte material along with the sediment allowed us to sample any snails on the macrophytes along with those in the sediment. At the water's surface we sieved (with 1 mm mesh) all cores from soft substrates to remove fine sediments and large particles and picked through macrophyte material for snails. Finally, for cobble habitats, we placed a ring (0.1 or 0.5 m^2) on the substrate at each site to define a sampling area. In 1987 and 2002, the 0.1 m^2 ring was used for sites with a high density of snails, and the 0.5 m^2 ring was used for sites with a low density of snails. In 2011 and 2020, we used the 0.5 m^2 ring at all sites. We gently collected the surface layer of rocks within the sampling ring and briefly brought the rocks to the surface, where we scraped attached material into a collection pan and funneled it through a 1 mm mesh sieve to gather snails. We stored snails collected using all sampling methods in 70% ethanol for later identification.

In the lab, we picked snails from all samples and identified them to species or genus (for *Physella sp.*) according to Burch (1989) and Johnson et al. (2013), with revisions for Lymnaeidae (Hubendick 1951) and Planorbidae (Hubendick and Rees 1955). We calculated snail abundance as density to account for differences between the sediment corers and the rings in area sampled. Snail samples from 1987 were lost in a laboratory flood, but specimens from 2002 and 2011 are vouchered at the Notre Dame Museum of Biodiversity in Notre Dame, Indiana, USA. Specimens from 2020 are vouchered at the Illinois Natural History Survey Mollusk Collection at the University of Illinois in Champaign, Illinois, USA.

In 2020, we were not able to sample macrophytes and snails using SCUBA due to limitations from the COVID-19 pandemic. Therefore, we excluded a small portion of deeper sites (approximately 2% of total macrophyte sites and 13% of total snail sites) that could not be sampled accurately and safely while snorkeling. In addition, because of a few lost samples, data from previous sampling years were not always available for each site. Consequently, in our analyses of macrophytes and snails, we only used sites for which we had data in all four sampling years (n = 100 sites/year for macrophytes, n = 208 sites/year for snails; Table 1). In our analyses of snail data, we only included snails which were alive at the time of sampling (i.e., we did not include empty shells).

Statistical Analysis

We classified *F. rusticus* population patterns in our ten study lakes into decline ("bust", "boom-bust") and reference ("high", "low") categories using *F. rusticus* CPUE over the time period for which we have community data (1987–2020; Figure 1). The impacts of *F. rusticus* on macrophytes and snails are minimal below 5 crayfish/trap (Lodge et al. 1998, Vander Zanden et al. 2017), so we classified our lakes based on that threshold. We defined "high" crayfish lakes as those which had *F. rusticus* CPUE above 5 crayfish/trap for more than 85% of crayfish sampling events since 1987, which included three lakes (Papoose Lake, Presque Isle Lake, and Squirrel Lake; Figure 1). Two of these high-crayfish lakes (Papoose Lake and Squirrel Lake) had declining *F. rusticus* CPUE in 2020, but still had *F. rusticus* CPUE well over the 5 crayfish/trap threshold for the majority of sampling years. We defined "low" crayfish lakes as those which had *F. rusticus* CPUE below 5 crayfish/trap for more than 85% of crayfish sampling events since 1987, which included three lakes (Allequash Lake, High Lake, and Wild Rice Lake; Figure 1).

We separated the four decline lakes into two categories because differences in decline timing (10–15 years) might influence whether any recovery has occurred (Figure 1). We classified Spider Lake and Little Star Lake as "bust" crayfish lakes because *F. rusticus* relative abundance in these lakes declined over time from its highest recorded level in 1987 to a current low level (Figure 1). We classified Plum Lake and Little John Lake as "boom-bust" crayfish lakes because *F. rusticus* relative abundance was low in 1987, high in 2002 and 2011 ("boom"), and then low again in 2020 ("bust"; Figure 1).

Faxonius rusticus has previously been shown to have a strong, negative effect on the abundance and richness of macrophytes and snails in our study system (Wilson et al. 2004, Kreps et al. 2012). Consequently, we used abundance and richness (collectively, 'metrics') of macrophytes and snails (collectively, 'community responses') to evaluate recovery after *F. rusticus* declines. We expected abundance and species richness metrics of macrophytes and snails would be depressed in the high-crayfish category relative to the low-crayfish category, which we verified by comparing the high- and low-crayfish categories across all sampling years. We then conducted within-year comparisons between the decline and reference categories to determine if the decline lakes differed significantly from the reference lakes at every time point, allowing us to track community responses to *F. rusticus* over time.

We conducted all analyses at the site-level using generalized linear mixed models (GLMMs) in the *glmmTMB* package in R (Brooks et al. 2017, R Core Team 2020). We conducted site-level, rather than lake-level, analyses because the effects of crayfish on snails are weaker at the whole-lake scale because the abundance of crayfish is far from uniform within lakes, including habitats (e.g., muck) not used by crayfish (Lodge et al. 1998). We controlled for pseudo-replication by including a random effect for lake in all models. We included an effect for year when we compared the high- and low-crayfish reference categories to each other, but we created individual models for each year and decline category when we compared bust and boom-bust categories to high and low reference categories. Both our macrophyte and snail data were zero-inflated. For our macrophyte count data, we consequently used zero-inflation negative binomial GLMMs with a log link. Because we calculated snail abundance as a density, we analyzed snail density and richness using ln(x+1) transformed values in Gaussian GLMMs and an identity link. We selected a log transformation over a log link in this case because it improved model residuals.

In the present study, we focused on abundance and richness metrics previously shown in this system to be negatively impacted by *F. rusticus* (Wilson et al. 2004, Kreps et al. 2012), but community composition can also shift after biological invasions (Sanders et al. 2003, Cucherousset and Olden 2011). Quantitative analyses on community composition were outside the intended scope of our study, but we qualitatively assessed macrophyte and snail community change over time through nonmetric multidimensional scaling (NMDS) using abundance data for each lake-year combination and a Bray-Curtis dissimilarity matrix. We interpreted only the first two NMDS axes for clarity. We excluded unknown species and those which occurred at only one lake during one sampling event, as well as lake-year sampling events during which no species were found. Although our NMDS analyses included all lakes, we focused our interpretation on boom-bust lakes (Little John Lake and Plum Lake) because they have a less impacted reference year (1987) that bust lakes lack. We anticipated that macrophyte and snail communities would diverge from pre-boom conditions at the peak of *F. rusticus* abundance (2002, 2011), but community recovery would be supported after *F. rusticus* declines if 2020 communities resemble those in 1987 (e.g., Bogan and Lytle 2011). We did not visualize boom-bust lakes by NMDS in comparison to low- and high-crayfish reference lakes because these lakes differ by macrophyte and snail communities irrespective of crayfish population status – crayfish affect abundance and richness metrics of prey and habitat, but our preliminary analyses revealed that community composition differs between lakes for factors distinct from invasion status (Appendix S3: Figures S1 and S2). All NMDS were run using the vegan package in R (Oksanen et al. 2020, R Core Team 2020).

Results

Over time, macrophyte and snail metrics were elevated in the low-crayfish reference category relative to the high-crayfish reference category, and the two categories were significantly different for all four metrics (all $p < 0.05$). There was no significant effect of year on either macrophyte metric (all $p > 0.05$), but there was a significant negative effect of year on the snail metrics (all $p < 0.05$). In particular, snail abundance declined over time in the low-crayfish reference lakes (Figure 2). However, because all macrophyte and snail metrics in the high- and low-crayfish categories were significantly different from one another, we were able to use them as references in our within-year comparisons to the bust and boom-bust categories (Figure 2).

As we predicted, macrophyte metrics in the bust category increased over time as *F. rusticus* abundance decreased (Table 2; Figure 2). Both macrophyte abundance and richness in the bust lakes were lower than in the low-crayfish lakes in 1987, 2002, and 2011 (all $p < 0.05$), and were not significantly different from the high-crayfish lakes in the same years (all $p > 0.05$; Table 2; Figure 2). In 2020, macrophyte metrics increased once again and were significantly different (for the first time) from both the low- and high-crayfish categories ($p < 0.05$; Table 2; Figure 2). This increase in macrophytes in the bust category to a current state that is between the two reference categories is consistent with our expectation of macrophyte recovery where *F. rusticus* has declined.

In the boom-bust category, macrophyte metrics were elevated in 1987 (when *F. rusticus* abundance was low) relative to the peak of invasion in 2002 and 2011, when macrophytes decreased and were no longer significantly different from the high-crayfish reference category ($p < 0.05$; Table 2; Figure 2). Both macrophyte abundance and richness in the boom-bust category then increased in 2020, after declines of *F. rusticus*, and were not significantly different from the low-crayfish reference category ($p < 0.05$; Table 2; Figure 2). The increase in macrophytes in the boom-bust category to a state that is not significantly different from the low-crayfish reference category is consistent with a stronger recovery of macrophytes in the boom-bust lakes than in the bust lakes, where macrophytes only recovered to a state between the reference categories.

Similar to the results for macrophytes, snail metrics increased in the bust category over time as *F. rusticus* abundance declined. In 1987, snail abundance and richness in the bust category were depressed below the level of the high-crayfish category (all $p < 0.05$; Table 2; Figure 2), consistent with an even stronger response of snails in these lakes to *F. rusticus* than in the high-crayfish lakes. In the following sampling years (2002, 2011), there were slight increases in snail abundance and richness over time in the bust category relative to 1987, and the snail metrics remained significantly different from the low-crayfish category (all $p < 0.05$) while increasing to a point not significantly different from the high-crayfish category (all $p > 0.05$; Table 2; Figure 2). Finally, snail metrics increased in 2020 to a state between the two reference categories (all $p > 0.05$) for the first time, consistent with the expectation of some recovery (Table 2; Figure 2).

In the boom-bust category, snail metrics in 1987 were not significantly different from the low-crayfish reference category (all $p > 0.05$) before subsequently declining in 2002 and 2011 to a state not significantly different from the high-crayfish reference category as *F. rusticus* abundance increased (all $p > 0.05$; Table 2; Figure 2). In 2020, after *F. rusticus* abundance decreased, snail metrics were significantly below the low-crayfish reference category but significantly above the high-crayfish reference (all $p < 0.05$), consistent with the expectation of some recovery of snails in the boom-bust category (Table 2; Figure 2). While there was some recovery of snails in both the bust and boom-bust categories, our snail metrics remained significantly different from the low-crayfish reference lakes. Detailed results for all model comparisons can be found in Appendix S4.

The NMDS analysis of macrophyte community composition was consistent with an impact of *F. rusticus* followed by some recovery after invasive crayfish population declines in our boom-bust lakes. Macrophyte communities in both Little John Lake and Plum Lake moved away from 1987 composition when *F. rusticus* was highly abundant in 2002 and 2011, but then recovered in 2020 once *F. rusticus* declined (stress = 0.152; Figure 3). In Plum Lake, for example, the most abundant species after *F. rusticus* declined in 2020 (*Vallisneria americana* and *Najas flexilis*) were also the most abundant species in 1987 before invasion, even though the most abundant species during invasion in 2002 (*Potamogeton amplifolius* and *V. americana*) and 2011 (*N. flexilis* and *Myriophyllum sibiricum*) had changed. In Little John Lake, *Ceratophyllum demersum* and *Elodea canadensis* were the most abundant macrophytes across all four years. However, the third- and fourth-most abundant macrophytes changed from 1987 (*N. flexilis* and *M. sibiricum*) to 2002 (*Potamogeton zosteriformis* and *Potamogeton robbinsii*), to 2011 when only *C. demersum* and *E. canadensis* were recorded, to 2020 (*P. zosteriformis* and *N. flexilis*). *Myriophyllum sibiricum,* the fourth-most common macrophyte found in Little John Lake in 1987, was not found in 2020, but *N. flexilis*, the third-most common in 1987, appears to have made some recovery.

Similar patterns of community recovery are apparent for snails in Little John Lake, but are less clear in Plum Lake (stress = 0.127; Figure 3). In Little John Lake, the two most abundant species of snails in 2020 (*Physa spp.* and *Amnicola limosa*) were the same as in 1987, before invasion. This recovery followed a shift in the most abundant species in Little John Lake during the height of *F. rusticus* invasion in 2002 (*Lyogyrus walkeri* and *Marstonia lustrica*) and 2011 (*A. limosa* and *M. lustrica*). In Plum Lake, the most abundant species of snails were variable across sampling events, but were generally hydrobiids. The most abundant species in 1987 were *M. lustrica* and *A. limosa,* while the most abundant in 2020, after *F. rusticus* declines, were *Gyraulus deflectus* and *A. limosa*. The most abundant snail in Plum Lake during the peak of invasion in 2002 was *M. lustrica,* while the most abundant in 2011 were *A. limosa* and *M. lustrica*.

Discussion

As expected, we found at least partial recovery of macrophytes and snails in all of our study lakes where *F. rusticus* naturally declined. At the onset of sampling in 1987, *F. rusticus* relative abundance in the bust lakes was at its highest recorded point (Larson et al. 2019), and metrics of macrophytes and snails were low like the high-crayfish reference lakes. Even as *F. rusticus* started to decline in these bust lakes, our community response metrics remained depressed until 2020, when we observed an increase and partial recovery of macrophyte and snail metrics to a state between our two reference categories. In the boom-bust category, *F. rusticus* abundance was low at the start of sampling in 1987 and our community response metrics were similar to the low-crayfish reference lakes. As *F. rusticus* abundance increased to a peak and started to decline, our community response metrics decreased, becoming similar to the high-crayfish reference lakes in both 2002 and 2011. After *F. rusticus* population declines became more pronounced, macrophyte metrics in 2020 in the boom-bust category increased and were comparable to the low-crayfish reference category for the first time since 1987. In contrast, snail abundance and richness in 2020 did not resemble the low-crayfish reference lakes in either of the decline categories, providing some support for our hypothesis that the recovery of snails may lag that of macrophytes. Although continued monitoring is needed to determine whether *F. rusticus* populations oscillate back to a high abundance state in the future, our findings suggest these lakes may not need active, manual restoration measures following declines of this major invasive species.

Recovery in our lakes might have been expected based on results following invader removal studies (Jones and Schmitz 2009, Hansen et al. 2013a), but community or ecosystem recovery has not been universally observed in other cases of natural declines of invasive species. For example, there was no recovery of native species on a short timescale (27 months) following declines of *R. marina* in Australia, perhaps because top predators, already at low abundances, could be killed by the consumption of even a single poisonous toad (Brown and Shine 2019). Conversely, a longer 10-year study of New Zealand mudsnail (*Potamopyrgus antipodarumin*) declines in a California stream found recovery of native macroinvertebrate grazer abundance (Moore et al. 2012), and a survey of sites impacted by invasive giant hogweed (*Heracleum mantegazzianum*) between 11 and 48 years after invasion found recovery of native plant richness and productivity approximately three decades after invader declines (Dostál et al. 2013). Similarly, our study offers one of the longest temporal contexts of any study on recovery following natural invasive species declines, including up to 33 years of *F. rusticus* declines in the bust lakes. Longer timescales can reveal disturbance-recovery dynamics that are missed by shorter datasets. Macrophytes and snails in the bust lakes, for example, had a lesser degree of recovery than the boom-bust lakes, which might be attributable to a longer period of time when *F. rusticus* abundance was elevated and acting as a press disturbance in the bust lakes (e.g., Bogan and Lytle 2011). More long-term studies like ours are needed to reveal whether community or ecosystem recovery is common after natural declines of invasive species and if the length of these press disturbances dictates the degree or timing of recovery. These studies may also need to include more community members or ecosystem processes than we considered, as *F. rusticus* population declines could have complex, indirect effects on native crayfishes, fish populations, or water quality (Maezono et al. 2005, but see Szydlowski et al. 2022a). However, if ecosystem recovery following natural invader declines is common, then the effects of some invasive species may be alleviated over long periods of time regardless of the duration of high invader abundance (Dostál et al. 2013, Strayer et al. 2017).

The post-disturbance recovery of individual species may be affected by selective herbivory by crayfish (Olsen et al. 1991) and natural history traits such as seed dispersal distance or dispersal speed (e.g., Kirkman et al. 2004, Gatto and Trexler 2020). Many of the macrophytes in our study lakes rely on vegetative propagation, rather than seeds, to spread (Kautsky 1988), and snails can move between habitats on seasonal time scales in response to *F. rusticus* (Lewis 2001). Based on these traits alone, we might have expected snails to recover before macrophytes because their greater mobility could allow them to spread more quickly within a lake to sites where they were previously excluded by crayfish. Instead, we observed a delayed recovery of snails relative to macrophytes, which provides support for our hypothesis that snail recovery would be slowed due to their dependence on macrophytes for habitat, protection from predation by fishes, and food resource availability (Brönmark 1989, Turner et al. 1999, Kreps et al. 2012).

Recovery that depends on coevolutionary relationships and secondary interactions like those we suggest here has been well-documented following other disturbances or eradication of invasive species (Zavaleta et al. 2001, Ripple and Beschta 2012). In restoration efforts, both bottom-up and top-down processes, along with food web and coevolutionary relationships, are important considerations (Block et al. 2001, Memmott 2009, M'Gonigle et al. 2015). Future studies could focus on potential bottom-up recovery processes after declines of invasive species to further investigate differences in recovery timing between prey and habitat like those we document here.

We also observed a decline in snail abundance in the low-crayfish reference category over time that was unexpected because *F. rusticus* was either absent or at low abundance in these lakes (Lodge et al. 1998, Vander Zanden et al. 2017). Observed snail declines might be caused by increased predation by other crayfish species such as *F. virilis* or *F. propinquus*, though these crayfishes did not exceed 1 crayfish/trap in any of our monitoring years since 1987 (Larson et al. 2019). Predation by fish may also drive snail declines if fish species impacted by *F. rusticus* recover (Lodge et al. 1987, Hansen et al. 2013a), but fish predation trends in our study lakes are unknown over time. Alternatively, snail declines may be influenced by sampling bias and the timing of snail reproduction. Approximately 75% of snails in 1987 were alive at the time of sampling, in contrast to 60% in 2011 and 43% in 2020 (Szydlowski et al. 2022b). Many of the snails in our study lakes, such as hydrobiids, are semelparous and die after reproduction (Osenberg 1989), and the difference in the proportion of living snails between years could indicate that our results were influenced by variation in either sampling or reproductive timing. For example, sampling in 2011 and 2020 occurred approximately 2-3 weeks after sampling in 1987 and 2002. Consistent with this explanation, snail declines in the low-crayfish reference lakes seem to be driven by loss of hydrobiids, indicating that later sampling in more recent years may have occurred after their reproduction and die-off (Szydlowski et al. 2022b). Regardless of cause, declines in snails in lakes with low *F. rusticus* relative abundance support the need for reference ecosystems to account for shifting baselines while assessing post-disturbance recovery (Higgs et al. 2014, Soga and Gaston 2018).

In addition to our analysis of abundance and richness, we also qualitatively assessed macrophyte and snail community composition over time in boom-bust lakes, revealing a strong recovery of macrophyte communities and a weak, lagging, or new target for recovery of snail communities (Figure 3). The delayed recovery of snail community composition could be related to coevolutionary processes (Block et al. 2001, Memmott 2009, M'Gonigle et al. 2015), or, like snail declines, it could be attributable to later sampling dates in 2011 and 2020 and a decline in hydrobiids. Future work might follow-up on this study by focusing more on species traits rather than taxonomy. For example, we observed recovery of *N. flexilis,* which readily produces seeds, in both of the boom-bust lakes, possibly indicating that seed production may be an important driver of macrophyte recovery (Rosenthal et al. 2006, Baldridge and Lodge 2014, Hansen et al. 2013a). We might also have expected that species less impacted by *F. rusticus* would recover first, as they would presumably have had a higher abundance from which to recover. This is consistent with the recovery of *V. americana* and disappearance of *M. sibiricum* that we observed in the boom-bust lakes because invasive crayfishes have a greater effect on single-stemmed, delicate or branching macrophytes (such as *Myriophyllum* spp.) than basal rosette species such as *V. americana* (Lodge and Lorman 1987, Cronin et al. 2002). Similarly, we might have expected operculate snails with tougher shells, such as *Campeloma decisum* or *Viviparus georgianus* to recover first because they are more protected against predation (Kreps et al. 2012, Hansen et al. 2013a), though such changes are difficult to assess because of the lagging recovery of snails. Future trait-based analyses might be able to more definitively assess macrophyte and snail community composition before, during, and after the peak of *F. rusticus* invasion.

Efforts to reduce or eradicate invasive crayfish are routinely unsuccessful despite substantial investments of time and resources (Gherardi et al. 2011). For example, removal efforts in one lake in our study region failed to entirely eradicate *F. rusticus* even after seven years of work, and *F. rusticus* declines in this lake may have been partially driven by drought rather than human effort (Hansen et al. 2013a, Hansen et al. 2013b, Perales et al. 2021). Conversely, some invasive crayfish seem to experience natural population declines following invasion in this and other study systems (Sandström et al. 2014, Jussila et al. 2016, Larson et al. 2019). If post-invasion declines of invasive crayfish are common and ecosystems recover to a pre-invasion state, then managers may decide not to invest money and time on removal or eradication of crayfish invaders (Lodge et al. 2016). However, such choices depend on the magnitude of damages during the period of high abundance of the invader. For example, an estimated $1.5 million in fishing opportunities were lost annually during the first thirty years of *F. rusticus* invasions in Vilas County, which would have been avoided by policies to discourage the introduction, establishment, and spread of this invasive species (Keller et al. 2008).

Given high damages from some invaders and the uncertainty of bust dynamics, the prevention of invasions altogether should remain a high priority for managers and policymakers (Lodge et al. 2012, Lodge et al. 2016). Any management plan or policy that assumes that natural declines of invasive species will occur will be vulnerable to the high context dependence and unpredictability of natural declines. For example, *F. rusticus* has not declined in all of our study lakes, and managers would benefit from knowing which lakes are most likely to experience declines of this invader and subsequent recovery in order to best allocate monitoring resources relative to magnitude and duration of invader impacts (Vander Zanden et al. 2017). Habitat quality might predict *F. rusticus* declines if crayfish expose themselves to predation by destroying macrophytes in lakes without enough suitable rock habitat for their protection (Larson et al. 2019). If habitat is an important factor driving *F. rusticus* population declines, then managers might be able to predict boom-bust dynamics based on related characteristics such as lake morphometry or underlying geology (e.g., Riera et al. 2000). However, *F. rusticus* numbers may eventually increase if the recovery of macrophytes we documented provides crayfish renewed protection from fish predators, reversing one hypothesized cause of *F. rusticus* decline (Hansen et al. 2013b, Larson et al. 2019). *Faxonius rusticus* abundance may otherwise remain low if fishes (*Lepomis* spp.) recover after crayfish declines and prey upon juvenile crayfish (Roth et al. 2007, Perales et al. 2021), if diseases persist among *F. rusticus* populations (Sargent et al. 2014), or due to genomic and phenotypic change from factors like the "founder effect" and genetic drift (Jackson et al. 2017, Strayer et al. 2017, Lang et al. 2021). Ongoing monitoring in this and other systems will inform whether declines are predictable and what mechanisms are driving them, with implications for management responses (Strayer et al. 2017, Vuorinen et al. 2021).

Despite these caveats, our study does offer encouragement for the possibility of community and ecosystem recovery in cases of either natural or management-driven declines of invasive species (Simberloff 2021). In particular, our results are largely consistent with community recovery following an intensive *F. rusticus* removal project in a small lake located in our study region (Hansen et al. 2013a). Such eradication or maintenance management efforts are often impractical at larger or landscape scales for common invaders like *F. rusticus* (Gherardi et al. 2011), but emerging approaches may be more effective at controlling or eradicating invaders in the future. For example, genetic management or biological control agents like crayfish-specific pathogens could be used to lower invasive crayfish abundance (Lodge et al. 2012, Simberloff 2021). Past work in our study system, which found macrophyte seed banks depleted after *F. rusticus* invasions, might suggest that invasive crayfish declines are not enough for ecosystem recovery, which would instead require active restoration by managers (Baldridge and Lodge 2014). The strong recovery of macrophytes we document refutes this conclusion and suggests that active restoration of macrophytes is unnecessary following *F. rusticus* declines, though ongoing monitoring is needed to determine whether snails will eventually recover to the level of our low-crayfish reference lakes. Continued monitoring by managers is also needed to determine if *F. rusticus* abundance will eventually increase in our bust and boom-bust lakes, but we demonstrate that some lakes may be resilient over long timescales to the impacts of this major freshwater invasive species.

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Conflicts of Interest

All authors declare they have no conflicts of interest.

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Tables and Figures

Table 1. Summary of characteristics for our ten study lakes, including geographic coordinates (latitude, longitude), surface area (km^2), and maximum depth (m), number of times sampled for crayfish (1975–present), the number of sites in each lake that we sampled for either macrophytes (macr.) or snails in all four sampling years, and category based on *F. rusticus* population trajectory. Lake surface area and depth are from the Wisconsin Department of Natural Resource's "Find a Lake" service (https://dnr.wi.gov/lakes/lakepages/).

Lake	**Lat, Long**	**Surface Area (km^2)**	**Max Depth (m)**	**Crayfish Surveys (n)**	**Macr. Sites (n)**	**Snail Sites (n)**	**Category**
Allequash	46.039, -89.623	1.10	7.3	10	9	20	low
High	46.155, -89.548	3.00	11.0	16	10	18	low
Wild Rice	46.065, -89.797	1.55	7.9	12	10	24	low
Papoose	46.184, -89.802	1.71	19.8	18	12	16	high
Presque Isle	46.222, -89.780	4.71	31.4	15	10	18	high
Squirrel	45.868, -89.895	5.30	14	9	11	18	high
Little Star	46.115, -89.861	1.05	20.4	14	8	16	bust
Spider	46.121, -89.823	1.13	13.1	14	10	21	bust
Little John	46.014, -89.645	0.61	5.8	17	6	31	boom-bust
Plum	46.003, -89.519	4.28	17.4	14	14	26	boom-bust

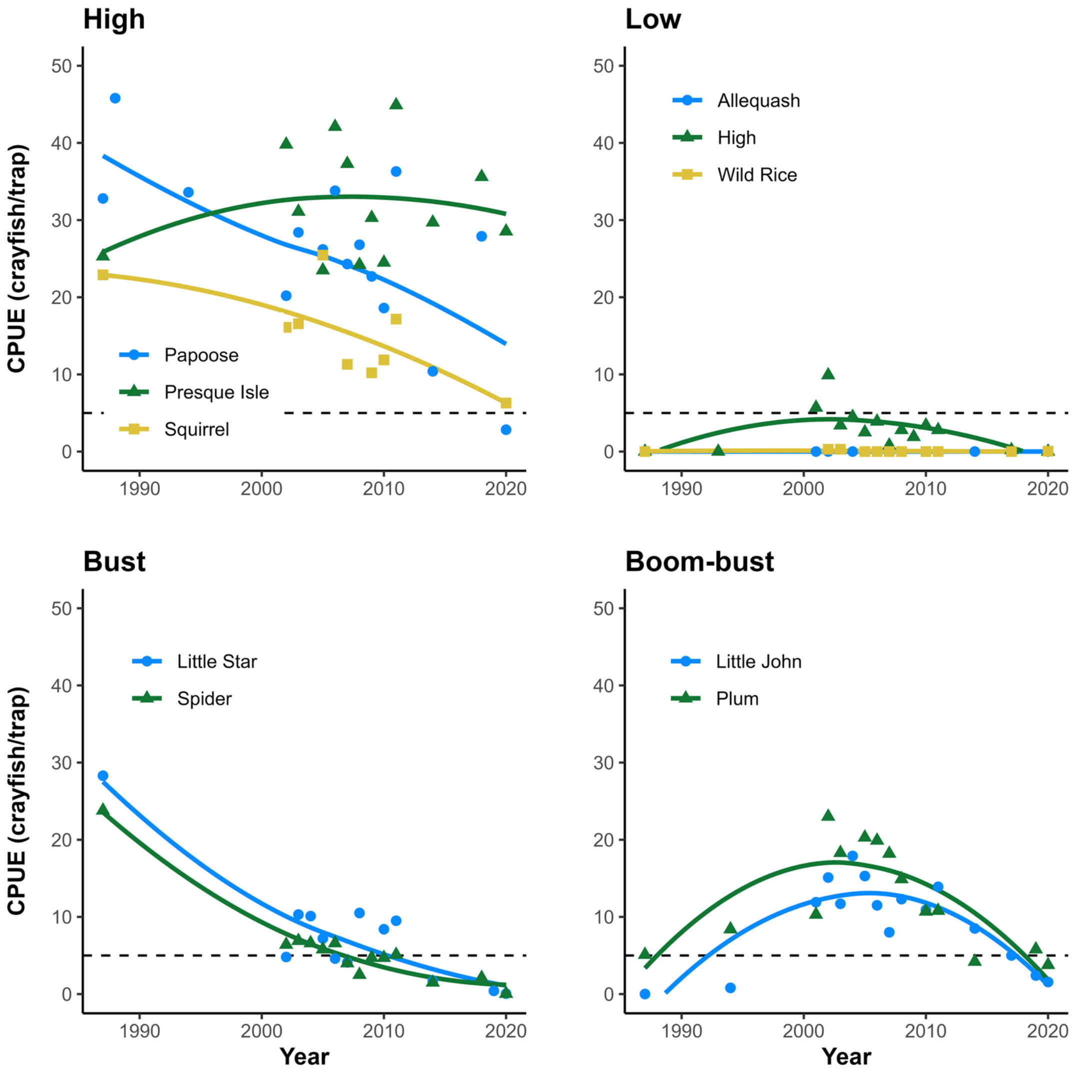
Table 2. Results from GLMM comparisons between the decline and reference categories, organized by community metric and year. 'H*' represents metrics that were significantly different ($p < 0.05$) from the low-crayfish category but not significantly different ($p > 0.05$) from the high-crayfish category. '*L' represents metrics that were significantly different ($p < 0.05$) from the high-crayfish category but not significantly different ($p > 0.05$) from the low-crayfish category. '**' represents metrics that were significantly different ($p < 0.05$) from both the high-crayfish category and the low-crayfish category. In 1987, categories with '**' had community metrics depressed to a level below our high-crayfish reference lakes, but categories with '**' in 2020 had intermediate recovery to a level between our two reference categories. Detailed results for all model comparisons can be found in Appendix S4.

Decline category	**Metric**	**1987**	**2002**	**2011**	**2020**
Bust	macrophyte abundance	H*	H*	H*	**
	macrophyte richness	H*	H*	H*	**
Boom-bust	macrophyte abundance	*L	H*	H*	*L
	macrophyte richness	*L	H*	H*	*L
Bust	Snail abundance	**	H*	H*	**
	Snail richness	**	H*	H*	**
Boom-bust	Snail abundance	*L	H*	H*	**
	Snail richness	*L	H*	H*	**

Figure 1. *Faxonius rusticus* catch-per-unit effort (CPUE, male crayfish/trap) between 1987 and 2020 for each lake within our four crayfish population categories (high, low, bust, boom-bust). A 5 crayfish/trap threshold for impacts of this invader is represented with a dashed horizontal line (Lodge et al. 1998, Vander Zanden et al. 2017). Trends are shown using locally estimated scatterplot smoothing included in the *ggplot2* package in R (Wickham 2016, R Core Team 2020).

Figure 2. Model-estimated means and 95% confidence intervals for macrophyte abundance, macrophyte richness, snail abundance, and snail richness for 1987, 2002, 2011, and 2020 in each crayfish population category. Means for the low and high lake categories are taken from the bust models, but the presented results only vary slightly from the boom-bust models. Means for snail abundance and richness are back-transformed from model estimates. Refer to Table 2 for a summary of GLMM comparisons between the decline and reference categories. Means of raw data for each category with 95% confidence intervals are provided in Appendix S5.

Figure 3. Plots from non-metric multidimensional scaling analysis for macrophyte (top) and snail (bottom) communities. Plots on the left show lake-year community composition for both Little John Lake (LJ) and Plum Lake (PL) in all four study years (1987, 2002, 2011, 2020). Arrows are drawn to show direction of change over time. Plots on the right show species vectors for the two lakes. For ease of interpretation, we only show the two lakes in the boom-bust category and the 15 most common species of macrophytes and snails across both lakes, even though analyses were run using community data from all lakes and all known species.



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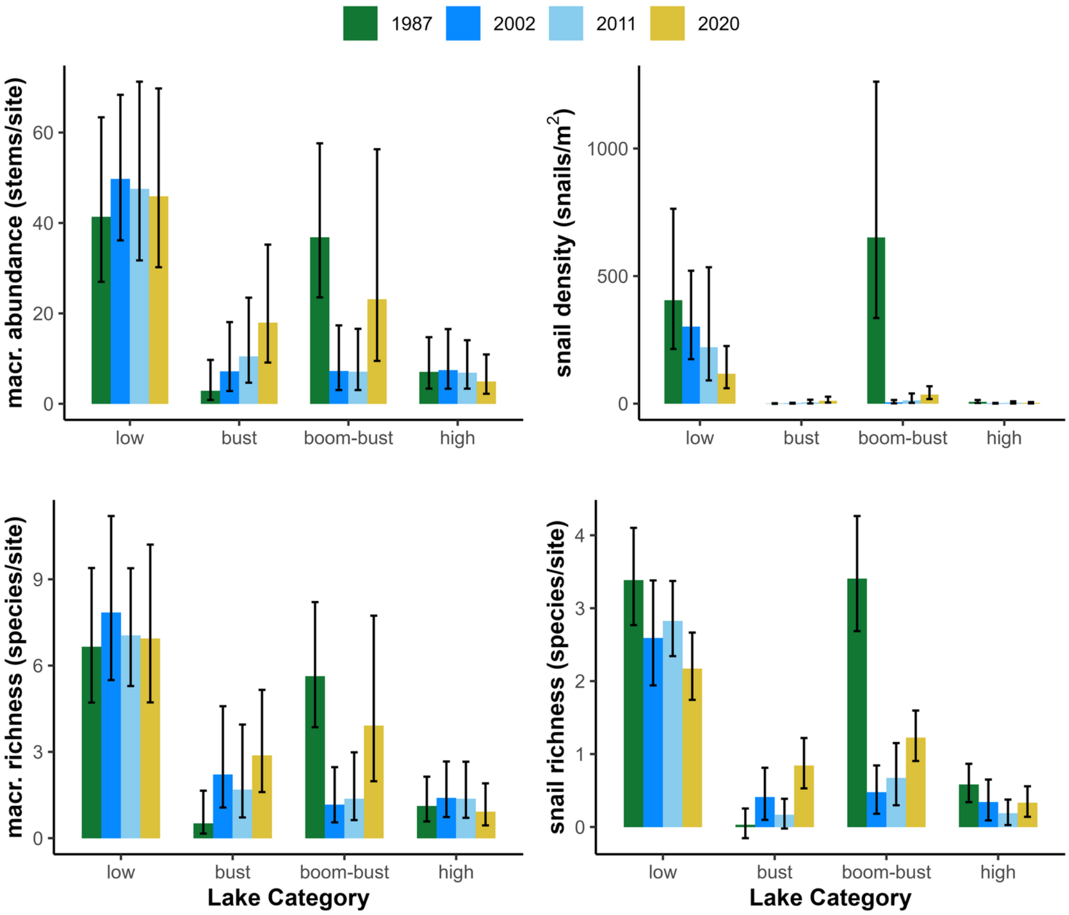

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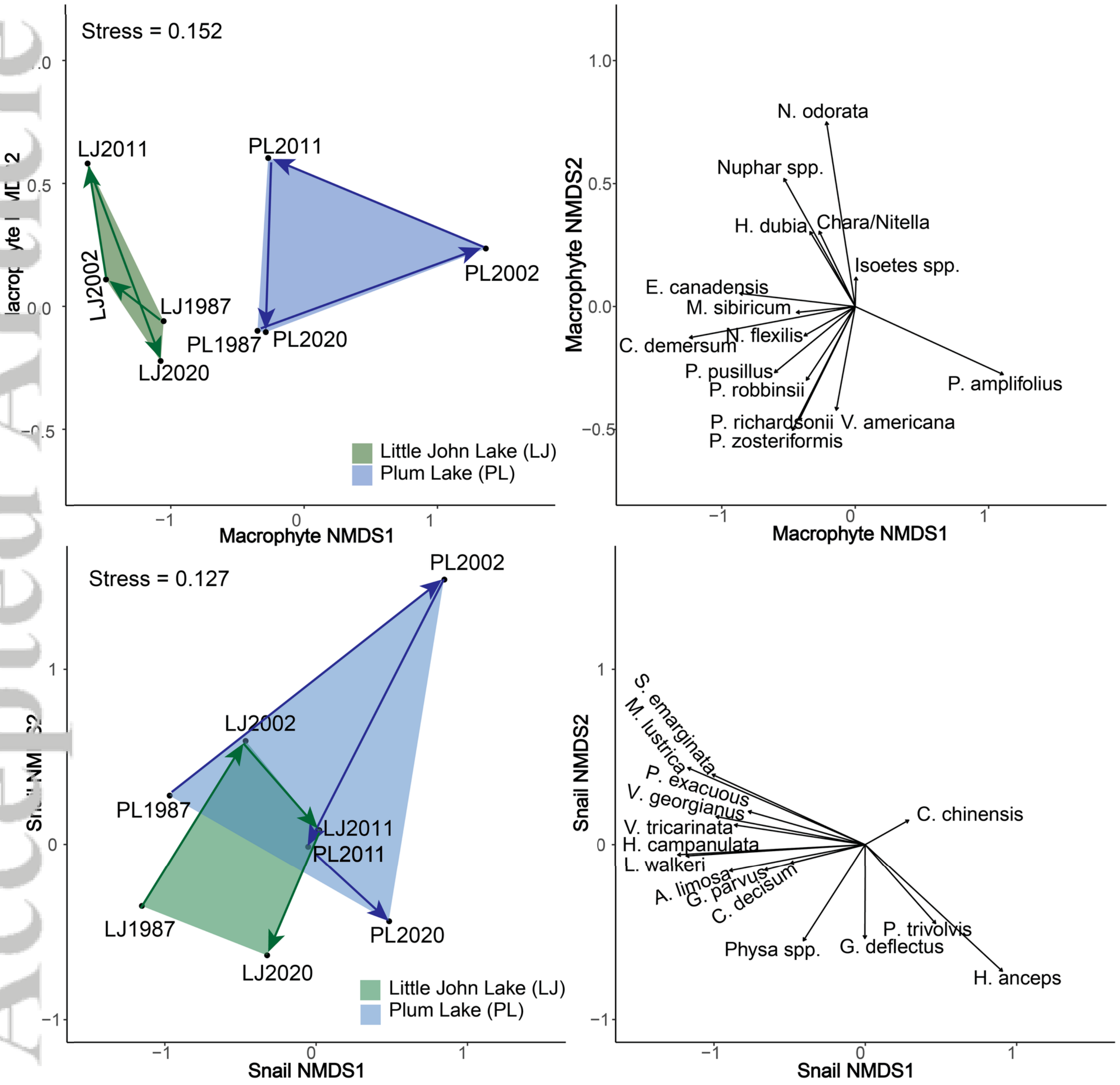

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