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Scale-dependent associations between native freshwater mussels and invasive *Corbicula*

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Abstract

In North America there is conflicting evidence concerning whether the invasive Asian clam, *Corbicula fluminea*, and native mussels (Unionidae), can successfully co-exist. One reason underlying disparate conclusions may be the different spatial scales at which data have been collected. We compared the distribution and abundance of native unionid mussels and *Corbicula* at two spatial scales, stream reaches and 0.25 m² patches, within one biogeographic region, the Ouachita Highlands, of the south central U.S. We found that *Corbicula* abundance was negatively related to native mussel abundance at small spatial scales. While *Corbicula* densities varied widely in patches without native mussels, and in patches where mussels occurred at low abundance, *Corbicula* density was never high in patches where mussels were dense. We hypothesize that the likelihood of successful *Corbicula* invasion decreases with increasing abundance of adult native mussels. Several mechanisms may potentially drive this pattern including lack of space for *Corbicula* to colonize, physical displacement by actively burrowing mussels, and locally reduced food resources in patches where native mussels are feeding. In addition, *Corbicula* may be unable to withstand environmental bottlenecks as readily as unionids. When patch-scale density and biomass information were pooled to represent entire stream reaches, the negative relationship between native mussels and *Corbicula* was no longer as apparent, and there was not a significant relationship between native mussels and *Corbicula*. These results point to the importance of appropriate sample scale in examining potential associations between species.

Introduction

Freshwater ecosystems and the species that inhabit them are highly imperiled on a global level (Allan & Flecker, 1993; Naiman et al., 1995). One of the most highly threatened and rapidly declining groups of freshwater organisms are the pearly mussels (Bivalvia: Unionacea) (Bogan, 1993; Neves et al., 1997). In North America alone, the U.S. Fish and Wildlife Service currently recognizes 12% of the native mussel fauna as extinct and 23% as threatened or endangered, and The Nature Conservancy considers 68% of the U.S. unionid species at risk, compared to only 17% for mammals and

15% for birds (Biggins & Butler, 2000). Historically, these long-lived, large, filter-feeding bivalves dominated the benthic biomass of eastern North American rivers (Parmalee & Bogan, 1998; McMahon & Bogan, 2001; Strayer et al., 2004), especially in undisturbed systems. In recent years, many North American mussel populations have undergone a substantial decline (Bogan, 1993; Neves et al., 1997), with drastic decreases in both species richness and overall mussel abundance (Neves et al., 1997; Vaughn & Taylor, 1999). Recent work has demonstrated that, like their marine bivalve counterparts, unionid mussels can have strong effects in ecosystems in which they are

abundant by filtering algae and seston, excreting and biodepositing nutrients, oxygenating sediments, and providing habitat for other organisms (Kasprzak, 1986; Welker & Walz, 1998; Vaughn et al., 2004). Thus, the overall decline in filter-feeding native mussel biomass may have negative, long-term consequences for the functioning of river ecosystems.

Many factors are believed to have contributed to mussel decline, including changes in land use, habitat destruction, large-scale impoundment and channelization of rivers, over harvesting (first for the shell button industry and more recently for the pearl nuclei industry), pollution, and exotic species introductions (Bogan, 1993; Strayer et al., 2004). Several exotic freshwater bivalves have been introduced into North America over the past century and are believed to have impacted native mussel populations. Most recent research has focused on the zebra mussel, *Dreissena polymorpha*, and negative impacts of this epifaunal bivalve on native mussels are now well documented (Schloesser et al., 1997; Ricciardi et al., 1998; Strayer, 1999; Hart et al., 2001; Nalepa et al., 2001). It has been hypothesized that another exotic bivalve, the infaunal Asian clam *Corbicula fluminea*, also has contributed to mussel declines (Kraemer, 1979; Clarke, 1988), but evidence for impacts of *Corbicula* on native mussels is much weaker than that for zebra mussels (Strayer, 1999).

Corbicula was purposely introduced to the west coast of North America in the early 1900s and since that time has spread to occupy ponds, lakes, and small to large streams throughout the US except the northernmost plains and New England (Counts, 1986; Isom, 1986) (http://cars.er.usgs.gov). Like unionids, *Corbicula* burrows in the sediment, filter-feeds on suspended matter, and often occurs in dense aggregations (Hakenkamp et al., 2001); however, *Corbicula* differ from unionids in many fundamental characteristics. Unionids are quite large for invertebrates, with adults ranging from less than one to over 30 cm in length. They are slow growing, long-lived (some species can live longer than 100 years), don't reach reproductive maturity until 6–12 years of age, and, although iteroparous, often don't reproduce every year. They have a complex life cycle that includes an obligate ectoparasitic stage (glochidia) on fish, which is the primary method of dispersal (Kat,

1984; McMahon & Bogan, 2001). In contrast, *Corbicula* are smaller than most native species, shorter-lived (1–5 years), grow rapidly, mature earlier, often produce multiple cohorts per year, and disperse both actively and passively throughout their life cycle (Prezant & Chalermwat, 1984; McMahon & Bogan, 2001).

Speculation that *Corbicula* impact native mussels comes primarily from studies reporting non-overlapping spatial distributions, such that native mussels are abundant only where *Corbicula* are rare and vice versa (Kraemer, 1979; Clarke, 1986, 1988; Sickel, 1986). These spatial distribution patterns have been interpreted as evidence that *Corbicula* out-competes and eventually causes the extirpation of native mussels; however, Strayer (1999) points that an equally valid explanation is that *Corbicula* preferentially invade sites where unionid communities are already in decline because of anthropogenic activities or may be able to thrive only in areas where unionids do not occur. In addition, there are numerous examples of dense populations of native mussels and *Corbicula* coexisting (Clarke, 1988; Miller & Payne, 1994; Strayer, 1999).

One underlying reason for the lack of consensus in the literature concerning spatial overlap between populations of native mussels and *Corbicula* may be the spatial scale at which data were collected. Studies comparing distributions of native unionids and *Corbicula* primarily have been conducted at the scale of a stream reach or larger (Sickel, 1973; Gardner et al., 1976; Kraemer, 1979); however, if competition between these organisms is driving distribution patterns, then patterns should be first apparent and strongest at smaller spatial scales where the organisms actually interact (Bengtsson, 1989; Cornell, 1999). To test this prediction, we compared the distribution and abundance of native mussels and *Corbicula* at two spatial scales, stream reaches and 0.25 m^2 quadrats, within one biogeographic region of the U.S.

Materials and methods

Our study was conducted in the Ouachita Highlands of central and western Arkansas and southeastern Oklahoma, U.S. This relatively compact biogeographic area (34° 13′ 52″ N, 95° 37′ 13″ W to

34° 44′ 47″ N, 92° 17′ 23″ W) is a center of speciation for both terrestrial and aquatic organisms (Mayden, 1985), contains a rich native mussel fauna (Gordon, 1980; Vaughn et al., 1996; Vaughn & Spooner, 2004), and streams are relatively unimpacted compared to other areas of North America and Europe (Master et al., 1998; Vaughn & Taylor, 1999). Annual precipitation ranging from 100 to 142 cm combined with steep ''ridge and valley'' topography results in frequent but short-lived spates (Rafferty & Catau, 1991; Matthews et al., 2005). Watershed areas of study streams ranged from 816 to 64,454 km^2 and annual mean discharge ranged from 12 to 843 m^3/s (Matthews et al., 2005). Within this area, we selected 30 stream reaches within 8 rivers as sampling sites (Fig. 1).

We used a hierarchical sampling strategy of quadrats (patches) nested within sites (mussel beds) to allow us to compare information across spatial scales. It has been well demonstrated that *Corbicula* can occur in a broader range of microhabitats than unionids (Strayer, 1999; McMahon & Bogan, 2001). Our objective was to examine the range of *Corbicula* abundance within areas where unionids were known to occur (i.e. mussel beds), and to quantify the effects of variation in mussel abundance on *Corbicula* abundance. Therefore, we purposefully selected sites known to contain mussels but that also encompassed a broad, natural range of mussel abundance and richness (Fig. 2). Sites (mussel beds) ranged in size from 88 to 3,300 m^2, mussel species richness at the sites ranged
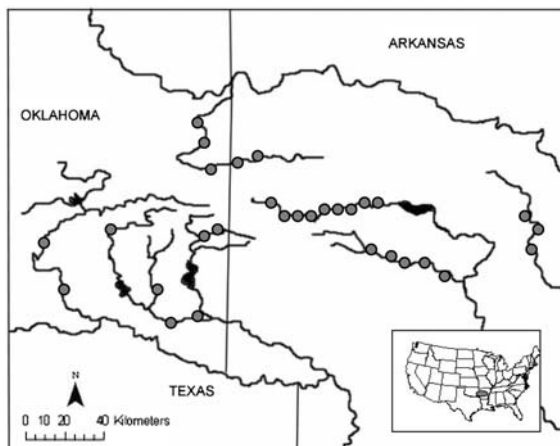
from 1 to 19 species, and mussel average abundance from 1 to 84 individuals/m^2. At each of the 30 sites, we sampled mussel composition and abundance, *Corbicula* abundance, and patch-scale environmental variables, from 10 randomly placed 0.25 m^2 quadrats ($n = 300$ quadrats). Our previous work showed that 10 quadrats provided accurate estimates of the abundance of most mussel species within beds (Vaughn et al., 1997). In addition, we measured reach-scale environmental variables at each site.

To maximize our ability to accurately record abundance of unionids and *Corbicula*, all sampling was conducted in mid- to late summer (June–September, 1999–2001) when river water levels and discharge were low. We also wanted to sample when the effects of mussels were strongest; laboratory experiments have predicted that mussels filter and add nutrients to a larger proportion of the water column during periods of
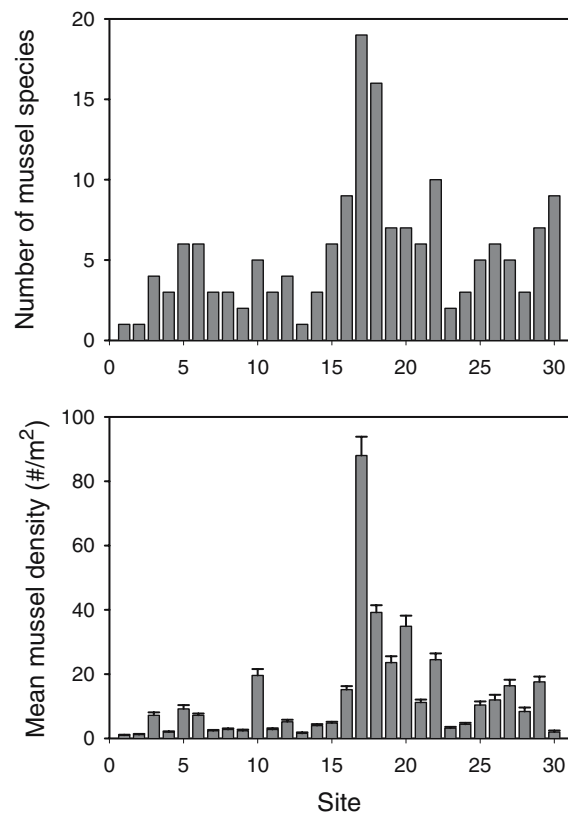

Figure 1. Map showing the 30 sample sites in the Ouachita Uplands.

Figure 2. Range in number of mussel species and average density ($+/- 1$ SE) across the 30 sampling sites.

low discharge (Strayer et al., 1999; Vaughn et al., 2004).

For each sampling site we recorded water temperature, dissolved oxygen, pH, and conductivity from the midpoint of the channel. We took transects across the stream and recorded depth and current velocity at 1 m intervals. Within each quadrat, we estimated the percent cover of filamentous green algae, diatoms, cyanobacteria, detritus and shade at midday (Barbour et al., 1999). Substrate composition was measured as the percentage of six Wentworth size classes (bedrock, boulder, cobble, gravel, sand and silt) (Gordon et al., 1992). We used a Soil Compaction Meter to measure substrate resistance (psi) or penetration. Four measurements of substrate resistance were taken in each quadrat and averaged.

We sampled bivalves in each quadrat last. Quadrats were excavated to a depth of 15 cm and all mussels and *Corbicula* were removed; our method did not allow sampling of individuals less than 5 mm in length. Mussels were identified to species, counted, and their length measured (Vaughn et al., 1997; Vaughn & Spooner, 2004). *Corbicula* were counted; then both groups were returned to the streambed. A subsample of each species of mussel was retained for biomass determination. All soft tissue was removed from the shell, dried, and weighed. We then used species-specific shell length-dry mass regressions to predict biomass for all enumerated mussels.

We used nested analysis of variance (Zar, 1999; Magnusson & Mourao, 2004), with quadrats nested within sites, to test for the effects of mussel presence or absence in a quadrat on *Corbicula* density in a quadrat. Because different species of unionid can vary greatly in adult size (Parmalee & Bogan, 1998) equal densities of adult mussels could occupy differential amounts of streambed depending on species composition, and thus might have different impacts on *Corbicula*. To account for this in our analyses, we examined both unionid density and biomass. We used correlation to examine the relationship between unionid density and biomass and *Corbicula* density in quadrats, and between mean unionid density and biomass and mean *Corbicula* density for sites. Densities and biomass were square-root transformed to achieve normality (Sokal & Rohlf, 1981).

Stepwise multiple regression ($p < 0.15$ for variable inclusion) was used to estimate which combination of variables best predicted *Corbicula* density at both the quadrat and site scales. Variables used in the model at the quadrat scale were native mussel species richness, square-root transformed mussel density, square-root transformed mussel biomass, mean substrate resistance, coefficient of variation (CV) of substrate resistance, % boulder, % cobble, % sand, % silt, % filamentous green algae, and % detritus. Mean values of these variables were used in the site-scale model. In addition, the site-scale model included depth and flow variables that were measured at the site scale but not at the quadrat scale: maximum, mean, minimum and CV of depth and maximum, mean and CV of current velocity.

Results

Quadrat scale

Corbicula densities were significantly higher in quadrats without mussels ($n = 130$) than in quadrats containing mussels ($n = 170$) ($F = 12.67$, $p < 0.001$). At the quadrat scale, *Corbicula* density and mussel density and *Corbicula* density and mussel biomass (Fig. 3a) were negatively correlated; this relationship was marginally significant for mussel biomass ($r = -0.11, p = 0.06$) and nonsignificant for mussel density ($r = -0.07, p = 0.22$). However, the relationships produced triangular scatter patterns such that quadrats with low mussel density and/or biomass encompassed a wide range of *Corbicula* densities, but quadrats with high mussel density and/or biomass never had high *Corbicula* densities. Multiple regression produced a significant model to predict *Corbicula* density in quadrats based on three variables: native mussel biomass, % boulder, and % filamentous green algae (Table 1).

Site scale

At the site scale, there were no significant correlations between mean *Corbicula* density and mean mussel density ($r = 0.012$, $p = 0.95$) or mean mussel biomass ($r = -0.056$, $p = 0.76$) (Fig. 3b).
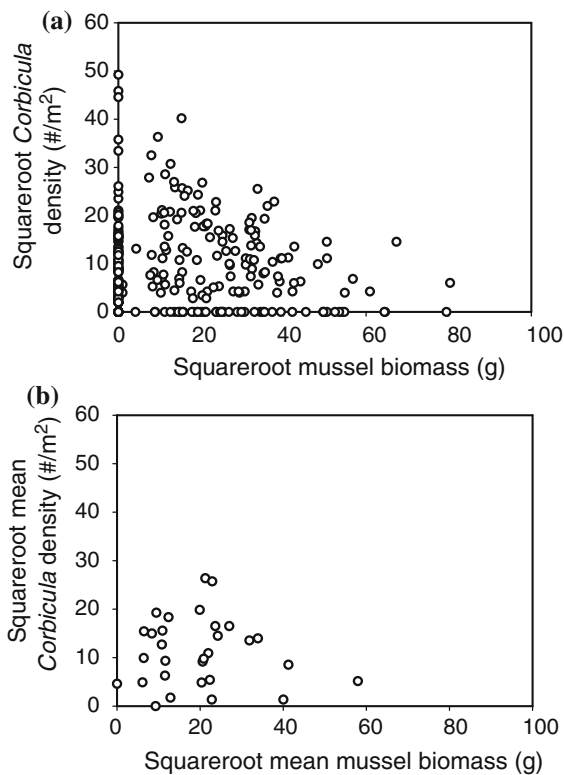
Figure 3. The relationship between mussel biomass and Corbicula density for the 300 quadrats (a) and mean mussel biomass and mean Corbicula density across the 30 sites (b).

Table 1. Results of stepwise multiple regression analyses for the effects of native mussels (density, richness and biomass) and habitat variables on Corbicula density at two spatial scales

Model	Variable	T	p
Quadrat-scale	Native mussel biomass	−2.18	0.03
$R^2 = 0.48$	Boulder (%)	−3.2	0.004
$F_{(3,223)} = 7.98$	Filamentous green	3.96	0.001
$p < 0.001$	algae (%)		
Site-scale	Maximum flow	−1.96	0.063
$R^2 = 0.789$	Boulder (%)	−3.46	0.002
$F_{(9,20)} = 8.34$	Cobble (%)	−3.34	0.003
$p < 0.001$	Gravel (%)	−1.68	0.107
	Detritus (%)	1.86	0.078
	Filamentous green	3.89	< 0.001
	algae (%)		
	Mean substrate resistance	−2.69	0.01
	CV substrate resistance	−3.74	0.001

Only variables retained by the models are shown.

Multiple regression produced a significant model to predict mean Corbicula density at a site based on eight habitat variables: maximum flow, % boulder, % cobble, % gravel, % detritus, % filamentous green algae, and mean and CV of substrate resistance (Table 1). No variables used to quantify mussel communities (richness, density, biomass) were predictive of Corbicula density at the site scale.

Discussion

In this study, Corbicula abundance was negatively related to native mussel abundance at small spatial scales. While Corbicula densities varied widely in patches without native mussels, and in patches where mussels occurred at low biomass, Corbicula density was never high in patches where mussel biomass was high. When patch-scale density and biomass information were pooled to represent entire stream reaches, the negative relationship between native mussels and Corbicula was no longer as apparent, and there was not a significant relationship between native mussels and Corbicula. It is important to point out that our site-scale results are biased because we did not purposefully sample stream reaches that contained Corbicula but not native mussels. In addition, because we used a nested design, our sample size is by definition larger for quadrats (300) than for sites (30). Nonetheless, these results point to the importance of sample scale in examining potential associations between species, and lend insight into the untested prediction that Corbicula invasions decrease the health of native mussel populations. If we had only examined site-scale distributional patterns we would not have concluded that there were any associations, negative or positive, between native mussels and Corbicula. Thus, differences in sample scale may help explain some of the disparate results obtained by researchers examining this question.

Based on our results, we hypothesize that the likelihood of successful Corbicula invasion decreases with increasing biomass of adult native mussels. Several mechanisms may potentially drive this pattern including lack of space for Corbicula to colonize, physical displacement by actively burrowing mussels, and locally reduced food resources in patches where native mussels are feeding. This hypothesis is supported by multiple

field observations of other researchers that *Corbicula* preferentially invade sites where native mussel communities are already in decline because of anthropogenic activities (Strayer, 1999).

The term 'adult' is critical to the above hypothesis, as the relationship between adult native mussels and *Corbicula*, and juvenile native mussels and *Corbicula*, is quite different. Juvenile mussels occur most commonly in the sediment interstitial zone, and often in areas separated from patches of adults (Yeager, 1994; McMahon & Bogan, 2001). Under these conditions, *Corbicula* has been demonstrated to affect the survival and growth of newly metamorphosed juvenile mussels through both competition for food and by disturbing the sediment and displacing juvenile mussels downstream (Fuller & Richardson, 1977; Strayer, 1999; Yeager et al., 2000). There also is evidence that *Corbicula* may incidentally siphon newly metamorphosed juvenile mussels and glochidia (larvae) (Yeager et al., 2000). In addition, ammonia released by decomposing *Corbicula* has been shown to exceed the acute tolerance levels of juvenile mussels (Cherry et al., 2005; Cooper et al., 2005). None of these interactions have been satisfactorily demonstrated between *Corbicula* and adult mussels.

Non-overlapping distributions of native mussels and *Corbicula* commonly have been attributed to either habitat differences or the perceived superior competitive abilities of *Corbicula* through competition for food. Our sampling was restricted to mussel beds, thus by definition our sampling was carried out in very similar habitats. At the scale of entire mussel beds, *Corbicula* was most common in beds with lower flows and finer substrates; this observation is consistent with the literature (Leff et al., 1990; Hakenkamp et al., 2001). At the scale of patches within mussel beds, only three of our measured variables significantly predicted *Corbicula* densities. *Corbicula* were not present in patches with boulders (nor were unionids), they displayed an affinity for high abundance of filamentous green algae (see discussion below), and they were negatively associated with unionid biomass. Although *Corbicula* have been stated to prefer "sandier" substrate that unionids (McMahon & Bogan, 2001), our patch-scale results do not support this conclusion.

Although *Corbicula* is much smaller than native mussels, it typically occurs at higher densities and has much higher mass-specific filtration rates (Kraemer, 1979; McMahon & Bogan, 2001). This results in community filtration rates that can exceed those of native bivalve assemblages (Strayer et al., 1999), and potentially limit the availability of suspended food for adult mussels (Strayer, 1999; Vaughn & Hakenkamp, 2001). In support of this view, declines in suspended phytoplankton have been documented in areas where *Corbicula* are very dense (Cohen et al., 1984; Lauritsen, 1986; Leff et al., 1990; Phelps, 1994); however, Strayer (1999) has pointed out that the 'winner' of resource competition between native mussels and *Corbicula* should not necessarily be the organism with the highest feeding rate, but rather the organism that can survive and reproduce at the lowest food concentration. Although *Corbicula* has documented higher filtration rates than native mussels, it also has higher metabolic and growth rates, and thus greater energetic demands (Williams & McMahon, 1985; McMahon & Bogan, 2001). In addition, recent work has shown that riverine mussels can feed on re-suspended detrital material (Nichols & Garling, 2000; Raikow & Hamilton, 2000) and may not be dependent on phytoplankton as a food resource. Thus, if food is limiting in dense mussel patches, slow-growing mussels may have a long-term competitive advantage over rapidly growing *Corbicula*.

An alternative hypothesis for the lack of *Corbicula* in dense mussel patches may be that adult mussels can typically withstand harsher environmental conditions, and for longer periods of time, than *Corbicula* (Williams & McMahon, 1985, 1989; McMahon & Bogan, 2001). *Corbicula* populations are notorious for undergoing rapid die-offs, particularly in response to summer low flows and high water temperatures (Cherry et al., 2005), typical summer conditions in the southern U.S. (Matthews et al., 2005). In contrast, adult mussels are less sensitive and more drought tolerant. Periodic drought events in the Ouachita Highlands result in isolated pools and long reaches of dry streambed (Spooner & Vaughn, 2000) that may expose mussel individuals to temperatures over 40°C, well beyond the documented critical thermal maximum for *Corbicula* (McMahon & Bogan, 2001), but within or on the periphery of tolerance for most native mussels from the region

(Spooner & Vaughn, 2005). In addition, higher water temperatures and no-flow conditions in pools lead to decreased dissolved oxygen concentrations. Under hypoxic conditions, unionids have the ability to regulate oxygen consumption and decrease metabolic activity (McMahon & Bogan, 2001). In contrast, *Corbicula* are non-regulators of oxygen consumption that often fail to meet their metabolic demand under periods of hypoxia resulting in high mortality rates (McMahon, 2002). Emersion tolerance may be the best evidence of the disparity in drought tolerance between the bivalve groups. McMahon documented an emersion tolerance of 36 days at 20 °C for *Corbicula*, while mussels could sustain emersion up to 572 days at 15 °C (McMahon, 2002). Thus, even if *Corbicula* successfully invade dense patches of native mussels, they may not survive the first summer 'bottleneck' of low flow and high temperature. The environmental bottleneck hypothesis is indirectly supported by our observations that *Corbicula* preferred areas with higher filamentous green algal abundance at both spatial scales (Table 1). In our study area, areas that supported high densities of filamentous green algae were typically rapidly flowing, well-oxygenated runs that did not dry up during periods of drought. The mussel biomass and environmental bottleneck hypotheses should not be considered mutually exclusive; it is likely that both mechanisms are operating.

While impacts of *Corbicula* on juvenile mussels have been demonstrated, there is no conclusive evidence that this invasive species has impacted mussel populations, either negatively or positively (Strayer, 1999). We suggest that one reason effects have not conclusively demonstrated is the scale of observation, and suggest that researchers search for interactions at the small spatial scales at which native mussels and *Corbicula* are likely to interact. In addition, it may be that *Corbicula* has become a 'naturalized' member of the bivalve assemblage in North American rivers (Williamson, 1996; Mack et al., 2000). Riverine mussels have always occurred as multi-species assemblages, and denser, more species-rich assemblages are typically healthier (Vaughn, 1997; Vaughn & Hakenkamp, 2001). *Corbicula* are taxonomically and functionally very similar to unionid mussels (Vaughn & Hakenkamp, 2001). Several researchers have hypothesized that a large proportion of the

variation in the impact of an invasive species on a community could be explained by the community's prior experience with species functionally similar to the invader (Diamond & Case, 1986; Moyle & Light, 1996; Ricciardi & Atkinson, 2004). If this is true, then introducing *Corbicula* to a mussel assemblage may be little different than introducing an additional unionid species to a mussel assemblage.

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