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Drivers of ecosystem vulnerability to *Corbicula* invasions in southeastern North America

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Abstract Invasive species introduction is one of the major ongoing ecological global crises. Identifying factors responsible for the success of invasive species is key for the implementation of effective management actions. The invasive filter-feeding bivalve, *Corbicula*, is of particular interest because it has become ubiquitous in many river basins across North America and elsewhere. Here we sampled bivalve assemblages, environmental indicators, and land cover parameters in the Ouachita highlands in southeastern Oklahoma and southwestern Arkansas, and in the Gulf Coastal Plain of Alabama to test three working models (using structural equation modeling, SEM) based on a priori scientific knowledge regarding *Corbicula* invasions. Our models tested three competing hypotheses: (1) Native mussel declines are related to land use changes at the watershed level and subsequent *Corbicula* colonization is a result of an empty niche; (2) *Corbicula* abundance is one of the factors responsible for native mussel declines and has an interactive effect with land use change at the watershed level; (3) Native mussel declines and *Corbicula* success are both related to land use changes at the watershed level. We found no evidence for the first two hypotheses. However, we found that environmental indicators and land cover parameters at the watershed scale were robust predictors of *Corbicula* abundance. In particular, agricultural land cover was positively related with *Corbicula* density. These results suggest that further improvement of conventional agricultural practices including the optimization of fertilizer delivery systems may represent an opportunity to manage this species by limiting nutrient inputs to stream ecosystems. Preservation of extensive floodplain habitats may help buffer these inputs by providing key ecosystem services including sediment and nutrient retention.

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Introduction

One of the major goals of ecologists is to understand the distribution patterns of organisms and their underlying mechanisms. Additionally, researchers are

trying to understand the factors that determine the ability of species to become invasive in novel ecosystems (McMahon 2002; Olsson et al. 2009), the habitats that are conducive to invasion (Havel et al. 2005), and how changes to habitats may influence the success of invasive species (Dukes and Mooney 1999; Weitere et al. 2009). Invasive species are widely accepted as one of the leading direct causes of biodiversity loss (Pimentel et al. 2005) and their establishment may lead to substantial changes in ecosystem function and structure (Crowl et al. 2008). For instance, invasive species can affect ecosystem processes through their resource acquisition, by altering disturbance regimes, or by altering trophic structure and/or food webs of the invaded system (Vitousek 1990).

In freshwater environments, Pearly mussels (Bivalvia; Unionoida, hereafter native mussels) are species-rich and under natural and undisturbed conditions, may represent the major component of the benthic biomass in some systems (Strayer et al. 1999). The first extinctions of native mussels were recorded in the 1970s (Stansbery 1971). Since then, widespread declines in native mussel species have been documented in North America and elsewhere (Williams et al. 1993; Haag 2012; Lopes-Lima et al. 2017). The major causes of this decline are suspected to be a result of the cumulative, long-term effects of dams, land cover modification, and invasive species introductions (Bogan 1993; Haag 2009; Ferreira-Rodríguez and Pardo 2017). For instance, habitat loss, alteration, and fragmentation of river networks by dam construction are the most highly-cited causes of decline in the literature (Bogan 2008; Downing et al. 2010). In addition, land cover modification has been signaled as one of the major contributors to this decline because of increased nutrient loads and water pollution (Poole and Downing 2004). Interactions between these and other factors may account for the decline of mussel populations across broad spatial scales and may have, in turn, led to biologically depauperate environments easily colonized by invasive species in many freshwater ecosystems (Mills et al. 1993; Johnson and Carlton 1996).

In this study we focus on the Asian clam, genus *Corbicula* Megerle von Mühlfeld, 1811, an invasive bivalve that can be found at very high densities in North America. The taxonomy of *Corbicula* is uncertain and species determination is difficult because of morphological plasticity/variability (Lee et al. 2005; Sousa et al. 2008; Pigneur et al. 2011). The most recent study to examine this question in North America (Haponski and Ó Foighil 2019) revealed evidence of multiple clonal lineages but did not find evidence for multiple taxa. Hence, we will follow Araujo et al. (2020) and refer to North American *Corbicula fluminea* sensu lato (hereafter *Corbicula*) throughout this manuscript. *Corbicula* was probably introduced to North America (West Coast) in the early 1920s. Over the next five decades, the species dispersed to nearly every major watershed in the continent (see McMahon (1982) for a detailed description of *Corbicula* early spread). Although the precise invasion history of *Corbicula* in North America is unknown, evidence suggests that it was concomitant with freshwater mussel declines in many systems. It is commonly assumed that invasive species impact indigenous species and promote their decline through direct competition for space, nutrients or food resources (Dextrase and Mandrak 2006; Hermoso et al. 2011). However, it is not clear whether *Corbicula* introductions have contributed to native mussel declines or whether native mussel declines aided *Corbicula* invasions by the creation of empty niche space.

The habitat use, feeding mechanisms and behaviors of *Corbicula* are similar to those of native mussels. *Corbicula* burrow in the sediment, filter-feed on suspended matter, and often occur in dense (>500 ind./m^2) aggregations in stable substrates (Hakenkamp et al. 2001). There is continued debate about whether native mussels and *Corbicula* compete for space and food, and whether *Corbicula* may be displacing natives via competition or other mechanisms (Strayer 1999; Vaughn and Spooner 2006; Atkinson et al. 2011; Ferreira-Rodríguez et al. 2018a, b; Haag et al. 2021). However, it is possible that the decline of native mussels may also be one of the primary mechanisms contributing to the spread of *Corbicula,* but few prior studies have examined this hypothesis across broad spatial scales (i.e., across multiple drainages and physiographic provinces).

Invasive species theory predicts that diverse communities of native species should confer some degree of ecosystem resistance against invasions (MacArthur 1955; D'Antonio et al. 2001), but other research has also refuted this theory (Holle and Simberloff 2005). Diverse and abundant native mussel faunas may provide ecosystem resistance to *Corbicula* invasions

as a function of their level of mass-specific filtering capacity, their occurrence in high-density, multi-species mussel-beds and their adaptation to local environments [i.e., Elton's (1958) Ecological Resistance Hypothesis; Simberloff 2011]. Vaughn and Spooner first provided observational evidence supporting this theory in 2006. They found that in streams with intact native mussel aggregations, *Corbicula* density was never high in patches where mussels were dense. In contrast, in degraded environments, invasive species may be more successful than more ecologically-sensitive native species (Ruaro et al. 2018). This is perhaps because native species and communities may more effectively use resources (i.e., niche partitioning; Eisenhauer et al. 2013; Byun et al. 2018) in less-impacted habitats, resulting in fewer resources available to invasive species. However, resource availability may co-vary with underlying environmental conditions resulting from changing land cover (Levine and D'Antonio 1999).

There are different mechanisms that may determine *Corbicula* success and we aimed to evaluate three competing hypotheses (Fig. 1) by examining both indirect and direct causal relationships between abiotic factors, land use, habitat alteration, *Corbicula* density and freshwater mussel diversity. We specifically examined whether: (1) native mussel declines are related to changes at the watershed level (i.e., hydromorphological alterations and land cover) and *Corbicula* colonization is facilitated by the creation of empty niches; (2) *Corbicula* colonization is, together with changes at the watershed level, one of the factors responsible for native mussel declines; or (3) native mussels declined for unknown reasons and, together with subsequent changes at the watershed level, their decline is one of the factors responsible for *Corbicula* success. This information may help inform management actions (e.g., habitat restoration and/or native mussel re-introductions) intended to mitigate the impact of *Corbicula* invasions.

Material and methods

Study areas

We examined associations between *Corbicula* and native mussels in two distinct biogeographic regions of North America; the Ouachita Highlands in southeastern Oklahoma and southwestern Arkansas, and the Gulf Coastal Plain of west-central Alabama (Fig. 2). These two regions support diverse
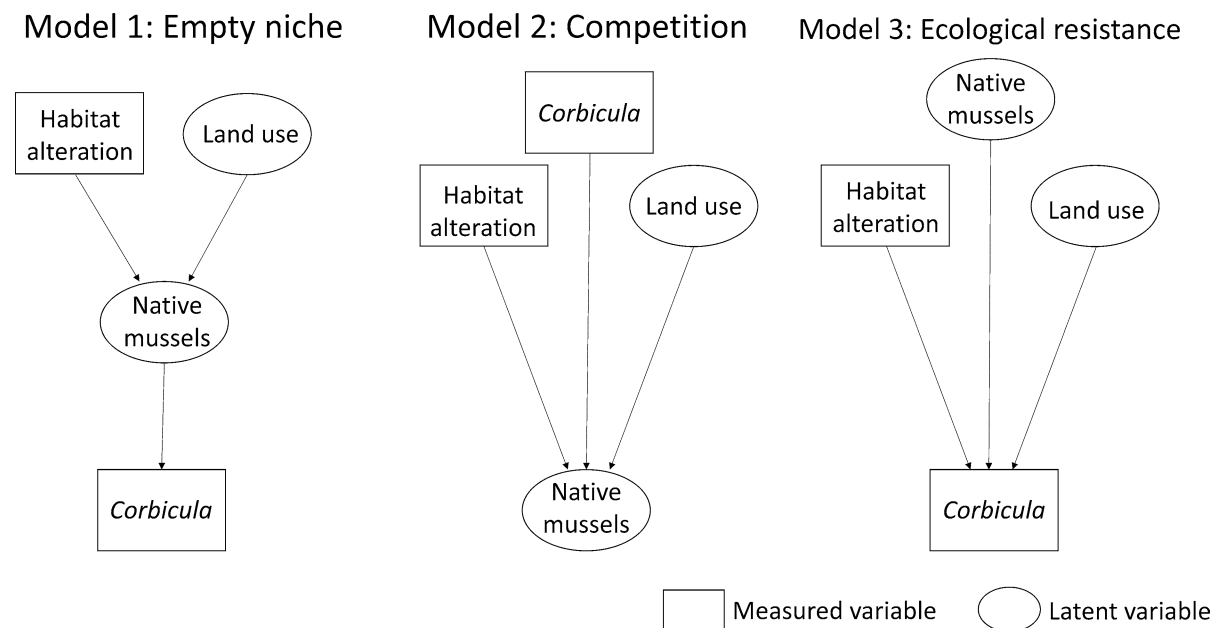

Fig. 1 Models tested in the SEM analysis. Three models were designed to explain *Corbicula* success based on empty niche creation (Model 1), competition theory (Model 2), and the ecological resistance hypothesis (Model 3)
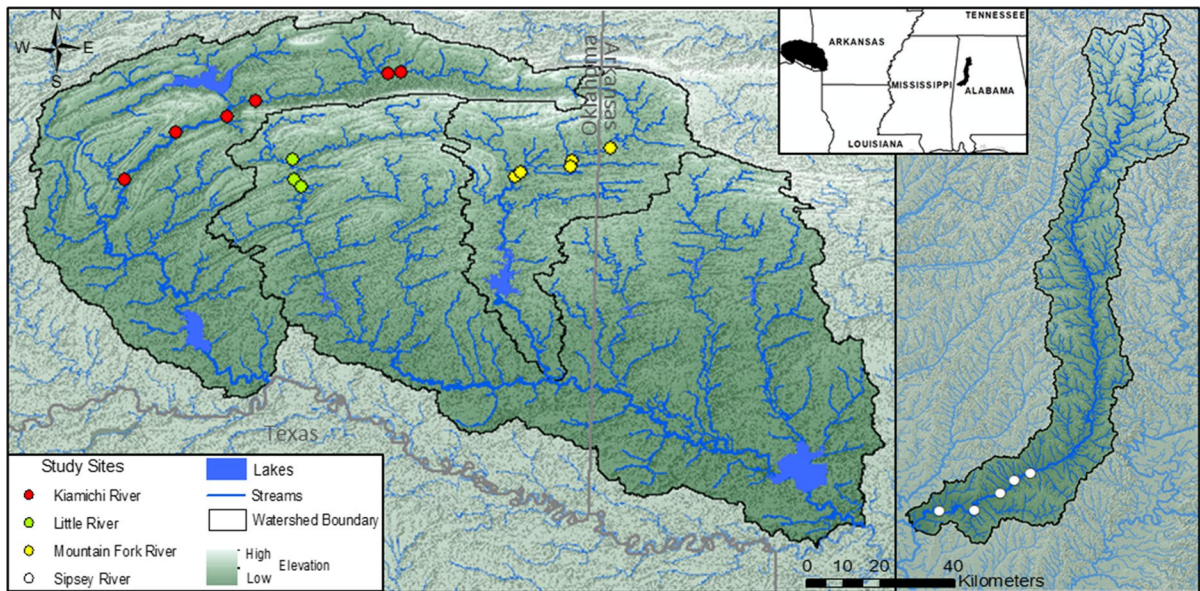
Fig. 2 Sampling locations, streams and man-made lakes (dams) in Oklahoma (Kiamichi, Little, and Mountain Fork Rivers; Red River watershed) and Alabama (Sipsey River; Tombigbee River watershed). Green color gradient shows elevation

and endemic native freshwater mussel assemblages (40 + extant species in each region) with relatively few species in common (Haag 2009, 2012). In the Ouachita Highlands, three rivers (Kiamichi, Little, and Mountain Fork rivers; Red River watershed) were surveyed in 2012. In the Gulf Coastal Plain, the Sipsey River (Tombigbee River watershed) was surveyed in 2016.

All three focal rivers in the Red River Watershed are blocked by major dams constructed in 1969 (Pine Creek Lake, Little River), 1970 (Broken Bow Lake, Mountain Fork River) and 1974 (Hugo Lake, Kiamichi River). In addition, three sampling points at the Kiamichi River are downstream from an impoundment, Sardis Lake (Fig. 2). This reservoir, constructed between 1977 and 1982, may affect downstream water quality in terms of flow and thermal conditions and other environmental factors (Kędra and Wiejaczka 2018; and references therein). There are no major impoundments on the Sipsey River. However, fish and mollusk migration is impeded downstream in the Tombigbee River by two dam complexes constructed in 1954 (Demopolis Lock and Dam) and 1972 (Howell Heflin Lock and Dam).

Sampling strategy

In the Ouachita Highlands, 15 sites across the 3 rivers were selected. Each site was subdivided into three reaches and, in each reach, one 100-m transect was selected. In the Gulf Coastal Plain, 6 sites in the Sipsey River were selected. Each site was subdivided into three reaches, and each reach into twelve 80-m transects. In order to characterize bivalve abundance and assemblage composition we followed the methodology proposed by Villella and Smith (2005). This method relies on a two-phase sampling design that yields precise estimates of mussel densities and does not require further efforts to determine when all species present are detected. First, qualitative samples (one 30-min timed visual/tactile search per reach) were done to locate mussel beds and to establish native mussel species composition. Second, between five and eighteen 0.25 m^2 quadrats—including cobble, sand and muddy sediments—were excavated (to a depth of ~ 10 cm) and sieved (through 6 mm mesh) in each transect. Richness (number of taxa) and density (number ind./m^2) were computed by species at the quadrat scale.

Physicochemical parameters

Temperature, pH, conductivity (μS/cm), and dissolved oxygen (mg/L) were measured with a DO meter (accuracy ± 0.2–0.3 mg/L, resolution 0.01 mg/L) and a conductivity-pH meter (pH accuracy ± 0.1–0.2, resolution 0.01 unit; conductivity accuracy ± 0.5 μS/cm, resolution 01–1 μS/cm). Also, samples for total dissolved nitrogen and phosphorus were collected, field-filtered, acidified, and analyzed (following persulfate digestion) within 28 days of collection using a flow injection analyzer. All habitat variables were measured under summer or fall base flow conditions, typically during or immediately following mussel surveys.

Land cover parameters

We used ArcGIS (Version 10.0, ESRI, Redlands, California) to obtain landscape-scale habitat and land cover classification data at the 21 sites at a spatial resolution of 30 m. We measured upstream catchment area (km^2), rank and link magnitude (the number of upstream first order tributaries) and percentage of surface cover comprising 11 land cover classes (open water, wetland, high-intensity urban, low-intensity urban, grassland, pasture, row-crop agriculture, evergreen, deciduous and mixed forest, and barren ground). Based on a priori scientific knowledge, our objective was to assess the effect of land cover rather than the effects of different vegetation classes. Hence, we combined several land cover classes to compute coarse scale land cover parameters. Specifically, we combined the percentage of open water and wetland classes into water; high-intensity and low-intensity urban into urban; pasture, row-crop agriculture, grassland into agriculture; and deciduous, evergreen, and mixed forest into forest. Finally, following Allen et al. (2018) we identified study sites located downstream of dams and calculated the potential influence of a dam on that site as the height of the dam divided by the distance a site is downstream of the dam.

Statistical analysis

We used a structural equation modeling (SEM) approach to assess whether the data support any of the three working models (Fig. 1) developed based on a priori scientific knowledge. In SEM, there is no requirement for predictor variables to be parametric. However, because dependent variables did not fit a multivariate normal distribution (Shapiro-Wilks test, $P < 0.001$), the robust Satorra and Bentler (2001) method was applied to adjust for deviation from normality. Because the Satorra and Bentler method is only valid for matrices with no missing data, a final matrix of 333 quadrats covering 16 sites with complete information (i.e., physicochemical and land cover information) was used. Data were clustered to test our working hypotheses at the individual watershed, river and site scale.

Three latent factors (i.e., biodiversity, abiotic factors, and land use) were calculated. First, because the number of species, as well as the number of individuals of each species, are common constituents of diversity indexes, biodiversity, as latent factor, was measured by two observed factors: native mussel richness and total native mussel density. Second, temperature, water pH, conductivity, DO and total N were combined as abiotic factors. In addition, covariance between temperature and DO and between DO and total N was modeled. Third, anthropogenic land uses (i.e., urban and agriculture cover) were combined as land use. Finally, because SEMs can handle both single-indicator and latent (i.e., multiple-indicator) factors, habitat alteration, as measured by the potential influence of (i.e., distance to) a dam, was included in the model. Links between native mussel diversity and *Corbicula* density were investigated throughout three paths. In the first (Empty Niche) model, abiotic factors, land use and habitat alteration influence native mussel diversity, and diversity can predict *Corbicula* density. In the second (Competition) model, abiotic factors, land use, habitat alteration and *Corbicula* density influence native mussel diversity. In the third (Ecological Resistance) model, abiotic factors, land use, habitat alteration and native mussel diversity predict *Corbicula* density.

Based on Hu and Bentler's (1999) Two-Index Presentation Strategy for evaluating model fit, we used the standardized root mean squared residual (SRMR) as an absolute fit index, and the Comparative Fit Index (CFI) as an incremental fit index. Both are robust to violations of normality and are useful for small sample sizes (Hu and Bentler 1999). The SRMR should be ≤ 0.08 and the minimum value for CFI should be ~ 0.9 to indicate adequate fit of the model to the data. The model needs to meet both SRMR and CFI

cutoff criteria to be considered acceptable. All SEMs were evaluated using the *lavaan* package (version 0.5-22; Rosseel 2012) in R (version 3.3.1, R Core Team 2018).

Results

We collected 8490 freshwater mussels in 1073 quadrats from 20 of the 21 sites in four rivers within the two river basins. Pooling all collections, at the quadrat scale, mussel density ranged from 0 to 448 ind./m^2 (mean $\pm$ SE: 31.65 $\pm$ 1.37 ind./m^2). Quadrat-level species richness ranged from 0 to 11 (mean $\pm$ SE: 2.67 $\pm$ 0.07 spp./m^2), with the greatest density and richness occurring in the Sipsey River. In total, 4126 individuals of *Corbicula* were collected. *Corbicula*

density ranged from 0 to 348 ind./m^2 (mean $\pm$ SE: 15.38 $\pm$ 1.07 ind./m^2), with the greatest density occurring in the Mountain Fork River (Fig. 3).

We checked alternative models at different scales (results not shown), but model support was strongest clustering the data at the individual watershed (hydrologic unit code: HUC-8; available at https://water.usgs.gov/GIS/huc.html) scale. Based on the cutoff criteria for SRMR (< 0.08) and CFI (> 0.9) indexes, only the third model met both criteria of acceptability (i.e., Ecological Resistance Model; SRMR $= 0.049$, CFI $= 1.000$; Table 1). In contrast, the Empty Niche Model and the Competition Model met the CFI cutoff criterion but did not meet the SRMR cutoff criterion (SRMR $= 0.106$ and CFI $= 1.000$, and SRMR $= 0.118$ and CFI $= 0.985$, respectively).

Abiotic factors and land use had significant regression weights in the Ecological Resistance Model

Fig. 3 Patterns of native mussel a density (number ind./m^2) and b richness (number of taxa), and c *Corbicula* density (number ind./m^2) by river. The boxes indicate the 1st and 3rd quartiles, and the dark lines indicate the median. Points more than 1.5 times the inter-quartile range away from the box are shown with hollow circles
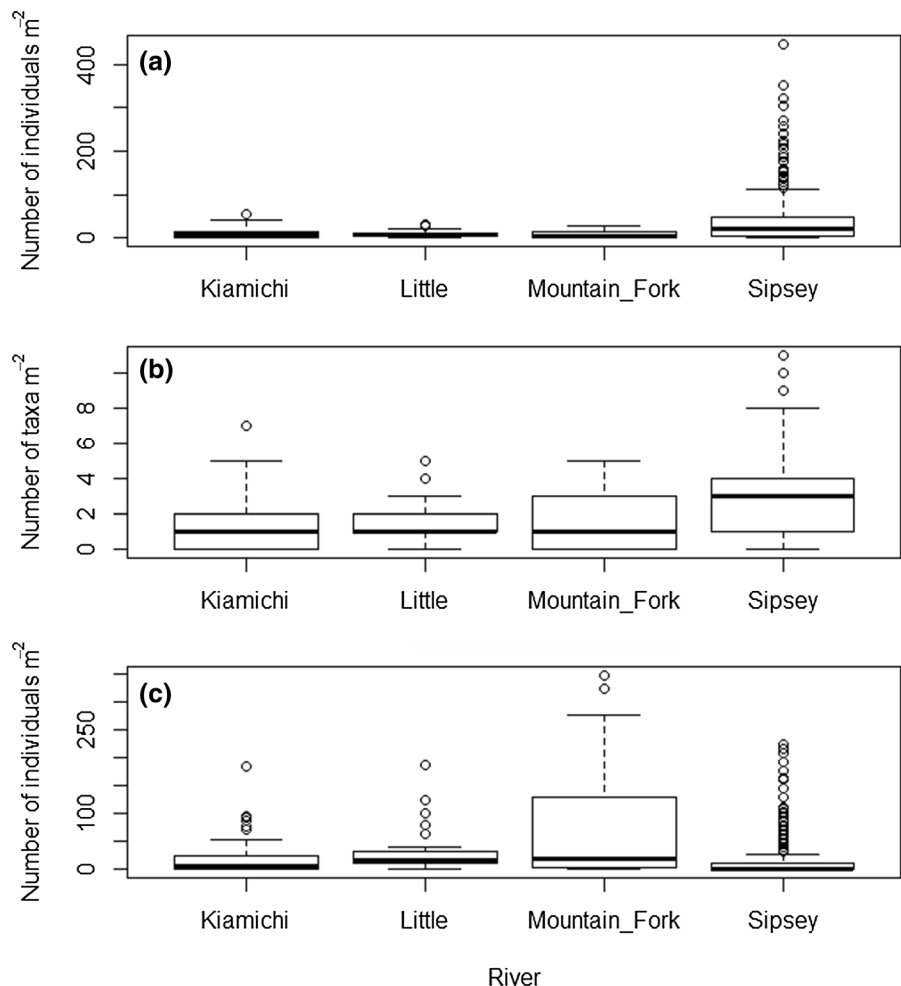
Table 1 Model fits for the three suggested pathways explaining native mussel decline and *Corbicula* success in southern North America. The cutoff criteria were set as < 0.08 for mean squared residual (SRMR) and as > 0.9 for the Comparative Fit Index (CFI)

Model	Definition	Dependent	Explanatory	SRMR	CFI
1	Empty niche	*Corbicula*	Biodiversity	0.106	1
2	Competition	Biodiversity*	Abiotic factors, Land Use, Habitat alteration, *Corbicula*	0.118	0.985
3	Ecological resistance	*Corbicula*	Abiotic factors, Land Use, Habitat alteration, Biodiversity	0.049	1

*Biodiversity: latent factor measured by native mussel richness and total native mussels' density

($p < 0.05$). Urban land cover was negatively related to land use (path weight = −0.52) whereas agriculture land cover was positively related to land use (path weight = 4.44), suggesting an indirect positive effect of agriculture cover on *Corbicula* density. Abiotic factors were related with temperature (path weight = 0.121), pH (path weight = 0.228), conductivity (path weight = −0.599), DO (path weight = 0.053) and total N (path weight = 0.674). In addition, total N had a negative relationship with DO (path weight = −0.03). However, neither native mussel diversity nor habitat alteration were statistically significant predictors of *Corbicula* density ($p < 0.05$) (Table 2).

Discussion

We examined the direct and indirect causal relationships between abiotic factors, land use, habitat alteration, *Corbicula* density and native mussel diversity. Specifically, we examined the likelihood of three scenarios: (1) Native mussel declines were related to land use changes at the watershed level and subsequent *Corbicula* colonization was a result of an empty niche. (2) *Corbicula* abundance is one of the factors responsible for native mussel declines. (3) *Corbicula* invasions act in concert with land use

change to drive native mussel declines at the watershed level. Our results show that *Corbicula* density was partially explained by a sub-set of commonly measured land cover and stream physicochemical parameters. In particular, *Corbicula* density at the watershed scale was positively related to agricultural land cover and negatively related to urban land cover. Similarly, *Corbicula* density was negatively related to abiotic factors, which were characterized by higher temperatures, pH, DO, total N and lower conductivity levels. Among our environmental indicators, total N—which most strongly links abiotic factors to agricultural land cover—is an important latent indicator of *Corbicula* density. Understanding how these land use and habitat conditions synergistically interact to explain *Corbicula* density and distribution at the local and watershed scale, may be important for managing *Corbicula* invasions. It should be noted, however, that all habitat variables were measured under summer or fall base flow conditions, which may not account for seasonal differences. Despite this, measuring water chemistry parameters under summer or early fall base flow conditions in this region may provide the best measure of conditions that may limit the distribution or population size of native and invasive bivalves.

Environmental parameters have been previously linked with *Corbicula* density at different organizational levels, ranging from internal metabolic

Table 2 Regression statistics produced from the SEM analysis

Latent Factor	Indicator	B	SE	Z	p-value	Beta
Corbicula	Abiotic factors	−15.951	1.009	−15.817	0.000	−0.358
Corbicula	Land Use	38.086	9.927	3.837	0.000	0.856
Corbicula	Habitat alteration	−7.222	4.441	− 1.626	0.104	−0.162
Corbicula	Biodiversity	3.904	5.950	0.656	0.512	0.088

processes to population dynamics (Vidal et al. 2002; Sousa et al. 2008; Ferreira-Rodríguez and Pardo 2014). For instance, temperature may be related to extreme climatic events that have drastically reduced *Corbicula* population densities in invaded regions globally (Werner and Rothhaupt 2008; Ilarri et al. 2011; McDowell et al. 2017). Stream pH appears to influence the vulnerability of *Corbicula* to other ecological stressors as changes to stream acidity affect the ability of bivalves to detoxify metabolic wastes and increases their sensitivity to chemical pollutants from urban and industrial activities (Vidal et al. 2002; Fournier et al. 2004). Conversely, increased concentrations of dissolved ions including Ca^{2+} (a key component of bivalve shells and metabolic processes) buffer many fresh waters in this region against acidification but high-conductivity waters also support higher *Corbicula* density and population growth rates (Ferreira-Rodríguez et al. 2017). The negative relationships observed between *Corbicula* density and DO may be related to the ability of *Corbicula* to modify local physicochemical conditions through organic matter accumulation and decomposition, or to DO directly controlling *Corbicula* populations (Hakenkamp and Palmer 1999; Ferreira-Rodríguez et al. 2019).

Environmental conditions have changed in North American fresh waters since the establishment of the first human settlements in pre-colonial times (Stinchcomb et al. 2011). Nevertheless, it was in colonial and pre-industrial times that intensive land use change (e.g., forest clearing, plowing, and mining; James 2011) had the most profound influence on hydrological systems. Between 1850 and 1950, thanks to improved mechanization, synthetic fertilizers, and improved varieties of seed, agricultural development greatly expanded spatially and dramatically increased total crop yields and the productivity of land under cultivation (USDA 2012). Watershed denudation following the loss of native forest cover and its subsequent conversion into agricultural or timber lands has reduced water retention capacity, increasing runoff, erosion, and sediment load across much of eastern and southeastern North America (Troendle and Olsen 1994; Zhang et al. 2017). In addition, much of North America experienced a substantial increase in the use of nitrogen fertilizers linked to agriculture during the twentieth century (Power and Schepers 1989). In both ground and surface waters, chronic nutrient

enrichment after decades of intensive fertilization has altered stream productivity and energetic pathways, and has had dramatic effects on aquatic biota (David et al. 2010; Pascal et al. 2013; Stelzer et al. 2020). Increased stream productivity associated with agricultural enrichment may be especially relevant for *Corbicula* as these bivalves apparently require a high quantity of food resources during the exponential phase of population growth and range expansion (Burke and Grime 1996; Petter et al. 2014). In this sense, the relationships between *Corbicula* and agricultural land cover found within our model may at least partially explain its successful establishment in most temperate and subtropical North American watersheds. However, in the second half of the 20th Century, total land devoted to agricultural production decreased, leading to a drastic reduction in total nitrogen and phosphorous loads (David et al. 2010; and references therein). Hence, it is possible that these changes may have to some degree moderated *Corbicula* productivity and standing crops across its naturalized range in North America. Unfortunately, *Corbicula* densities are rarely quantified by biologists in long term monitoring programs so it is difficult to assess changes in abundance or even occupancy (Sanchez Gonzalez et al. 2021).

Although environmental conditions may have improved in recent decades, *Corbicula* has already become widely established across North America. As a result, complete eradication is unlikely to be feasible. However, there are a few management options that may help reduce *Corbicula* productivity (sensu Robertson et al. 2020). First, monitoring environmental conditions in order to assess the role of habitat suitability (e.g., warm streams with high N and DO levels) and using models of land use and water chemistry to predict which habitats can support the establishment of large populations of *Corbicula* may help reduce the size and productivity of potential sources of further invasion. In regulated streams it may be possible to alter some environmental parameters and create conditions that are unfavorable to *Corbicula* (e.g., manipulate water temperatures or oxygen concentrations that are beyond the tolerances of *Corbicula* but not native bivalves) and reduce population size. Second, further improvement of conventional agricultural practices through upland and riparian zone forest protection along with use of precision farming at the watershed scale and the

implementation of more efficient fertilizer delivery systems could help reduce nutrient levels in surface and groundwaters (sensu Diacono et al. 2013). Ultimately, broad-scale efforts to reduce nutrient loading and in-stream productivity appear to have the greatest potential to limit the further establishment of dense *Corbicula* populations while probably also benefitting native bivalve faunas.

Conclusion

The success of *Corbicula* across North American watersheds appears to be explained partially by the extent of in-stream nutrient enrichment and food availability linked to agricultural development. Hence, we suggest that implementing invasive species management practices at the watershed scale and focusing on both aquatic and terrestrial environments is critical. In particular, we suggest that nutrient management is needed to reduce riverine nutrient inputs. This causal link requires further investigation, but could represent the basis for designing management plans aimed to limit the spread and productivity of *Corbicula*. Although our model is robust, we cannot exclude the possibility that observed *Corbicula* densities may be related to other sources of habitat degradation not considered in this study. Our results may help invasive species managers achieve successful outcomes while minimizing costs and impacts to sensitive native biota, including native mussels. It remains difficult, however, to draw conclusions from observational data about causal links between *Corbicula* invasions and the decline of native mussels in North America. In this regard, manipulative experiments are needed to explore further how changes related to agricultural development may affect competition.

Declarations

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