

Research Article

Habitat and landscape variables affecting *Corbicula fluminea* presence in the upper Savannah River drainage (USA)

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Abstract

Aquatic invasive species (AIS) are amongst the greatest threats to native aquatic biodiversity. These introduced species often thrive in human-altered environments and spread through human-mediated pathways to invade new watersheds. *Corbicula fluminea* is a freshwater bivalve native to southeastern Asia first introduced in North America in Seattle, WA, in 1938 and has spread to nearly every major watershed in the southeastern United States. In the present study, we use an information theoretic framework to compare landscape and stream habitat variables associated with *C. fluminea* presence across five HUC10 watersheds in the upper Savannah River basin of South Carolina and Georgia, USA. Predictive models included landscape-level and site-level habitat variables associated with agricultural, developed, and forested landscapes. Models with variables associated with forested and developed landscapes were the top performing models based on AICc values. In top performing models *C. fluminea* presence was positively correlated with increased stream width, but negatively correlated with substrates dominated by cobble. Lower performing models highlight positive correlations with the presence of upstream reservoirs and increased developed landscape surrounding the site. Identification of habitat and landscape correlates with invasive species presence may lead to more efficient introduction monitoring efforts for conservation managers.



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Introduction

Less than 1% of the Earth is covered by freshwater ecosystems, yet these environments contain nearly 10% of all recognized animal species (Balian et al. 2008). These systems are critically important to humans for water supply, recreation and tourism, flood control, and food production. The greatest threat to freshwater ecosystems is habitat degradation, specifically the altering of flow patterns, pollution from runoff, and land-use change (Sala et al. 2000). Habitat degradation may also

affect freshwater ecosystems indirectly through the facilitation of species introductions (Strayer 2010). Consequently, the introduction and proliferation of invasive species may displace native species and can disrupt ecosystem function in the invaded habitat (Strayer 2010). Human activities, specifically land-use changes from agriculture, urbanization, and the creation of reservoirs have led to an increase in habitat fragmentation and spread of invasive species, further endangering freshwater ecosystems (Vörösmarty et al. 2010).

The Basket Clam (*Corbicula fluminea* Müller, 1774) is a freshwater bivalve native to southeast Asia and introduced to North America, South America, Europe, and some countries of North Africa (Clavero et al. 2012; Crespo et al. 2015). In North America, the species first appeared in Seattle, WA in 1938, and quickly expanded across the country. It can now be found in 48 of the 50 United States of America (USGS 2025). Global dispersal is likely facilitated by the building of reservoirs as well as activities related to trade, including global shipping and the construction of shipping canals (Karatayev et al. 2007), the pet trade and use as a food resource (Ferreira-Rodríguez et al. 2019). Once established in a new region *C. fluminea* may spread to new waterbodies through attachment on fishing gear and boat hulls, bait-bucket transfers, as well as passive dispersal (Ferreira-Rodríguez et al. 2019).

Aquatic invasive species (AIS) invade new habitats through vectors such as shipping ballast water (Holeck et al. 2004), aquarium releases, water gardens, deliberate stocking, bait buckets, and horticulture (Keller and Lodge 2007). Certain life history traits improve the likelihood that a species will be a successful AIS, including the following: high reproductive capacity and rates, smaller body size, broad physical habitat tolerances, early maturation, and asexual reproduction or self-fertilization (Kolar and Lodge 2001). *C. fluminea* possess many of the same life history traits as other AIS. *C. fluminea* can reproduce through self-fertilization (Strayer 1999) and can produce 35,000 offspring per breeding season (McMahon 2002), allowing them to establish new populations from only one individual. Outside of human intervention, *C. fluminea* can disperse passively with water current through the release of juveniles, surviving the gut biome of fish, and by attaching to the legs of waterfowl and shorebirds (McMahon 1982). Once released from an adult, larval *C. fluminea* have a short time window (100 hours) where they persist in the water column by “swimming” with an organ called the velum (Mackie and Claudi 2010). This stage allows juveniles to disperse greater distances. During this time juveniles can also attach to human or wildlife vectors, which is most likely the method for short-distance upstream dispersal (Pernecker et al. 2021). Further, *C. fluminea* have a high filtration rate, can feed on a variety of algae, and can efficiently incorporate nutrients into somatic and reproductive growth (McMahon 2002). These dispersal and foraging characteristics of *C. fluminea* likely improve their success when invading new freshwater ecosystems (Pigneur et al. 2012).

Early detection and prevention of invasive species are more cost-effective solutions than removal or sustained management (Coughlan et al. 2020). Surveillance of aquatic environments for invasive species often lags behind the establishment of new populations (Beric and MacIsaac 2015), but could be improved through a better understanding of habitat suitability of the invader. Across their range, *C. fluminea* are considered habitat generalists, occurring in a wide range of lentic and lotic conditions (Karatayev et al. 2005), and across various substrate classes (Karatayev et al. 2003; Schmidlin and Baur 2007; Kelley et al. 2022). In the southeastern United States, greater *C. fluminea* densities have been linked to agricultural land use, including the amount of agriculture in the watershed, increased water temperature, and increased nitrogen pollution (Ferreira-Rodríguez et al. 2022).

Our objective in this study is to understand the habitat and landscape variables that affect *C. fluminea* dispersal and presence in the upper Savannah River watershed in Georgia and South Carolina. Based on previous literature, we expect *C. fluminea* presence to be positively associated with the amount of agricultural land cover (Ferreira-Rodríguez et al. 2022) and the presence of reservoirs upstream. *C. fluminea* have been associated with reservoirs receiving recreational pressure and seen in higher abundances downstream of dams; therefore, we expect to see the same association in our study (Karatayev et al. 2005; Robb-Chavez et al. 2022). Understanding the habitat and landscape variables that affect *C. fluminea* dispersal may allow more effective monitoring and prioritization of habitats for preventative measures.

Methods

Study area

The upper Savannah River basin begins in the Blue Ridge region of North Carolina, South Carolina, and Georgia. The Savannah River forms at the convergence of the Seneca and Tugaloo rivers. This portion of the Savannah River drainage is home to five of the largest reservoirs in South Carolina, including Lake Hartwell (227 km²) and Lake Keowee (75 km²) (Wachob et al. 2009). The study area spanned five Hydrologic Unit Code 10 (HUC10) watersheds in the upper Savannah River drainage: the Chattooga, Chauga, Coneross, Lower Tugaloo, and Little River watersheds (Fig. 1). Hydrologic Unit Codes serve as a numerical classification system to delineate hydrologic features in the United States ranging from regions (2-digit) to subwatersheds (12-digit). The north-western portion of the study area is dominated by forested land cover of the Chattahoochee-Oconee National Forest in Georgia, and the Francis Marion and Sumter National Forests in South Carolina. In the south-eastern portion of the study area near the Hartwell and Keowee reservoirs, higher densities of agricultural land cover and development are present (Fig. 1).

Site surveys

We selected study sites and conducted biotic and habitat surveys using the methods of the Brook Floater Rapid Assessment Protocol (Sterrett et al. 2018), originally designed for site selection and survey of native freshwater mussels (*Bivalvia*: *Unionida*). Ten sites were sampled in each of five HUC10 watersheds. Briefly, 50 sites were randomly selected from a pool of all possible bridge crossings within a HUC10 watershed using the primary roads layer in the U.S. Census Bureau's Transportation dataset (USCB 2023) and the United States Geological Survey National Hydrography Dataset (USGS 2023). Within each of the 5 watersheds, 40 bridge crossings were randomly chosen, and randomly split into 20 priority sites and 20 replacement sites. Our goal was to sample 10 priority sites; if there were not enough suitable priority sites to reach the goal of 10, then replacement sites were randomly chosen to sample until 10 sampled sites was achieved. We considered sites suitable for sampling if they met criteria of the rapid assessment protocol (Sterrett et al. 2018), including < 1 m in mean depth and ≥ 3 m in mean width, legally and safely accessible from the bridge, and safe to traverse. Sites that did not meet suitability criteria were replaced with a randomly chosen replacement site that did meet the survey criteria. Upon arrival at a site, 100 meters were measured in the upstream direction from the road crossing, then another randomly chosen

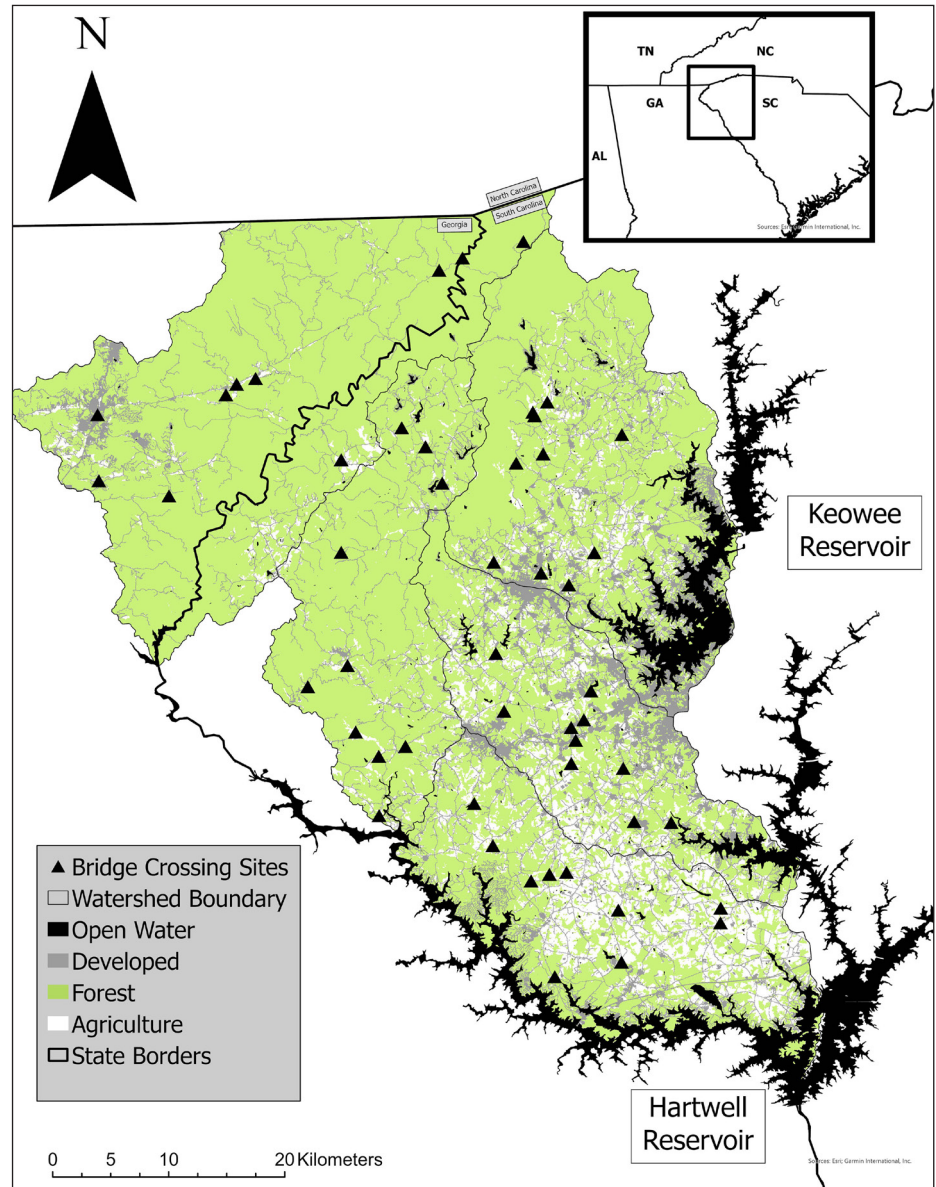


Figure 1. Study area detailing the boundaries of the five Hydrologic Unit Code 10 (HUC10) watersheds and land use classification. The northern region of the study area is dominated by forest, while the southern regions contain more of an agricultural and developed landscape. Inset map shows location of study area within southeastern United States.

distance (using a random number generator) between 0–100 meters was measured to mark the start of the survey site. This protocol was designed to avoid scour pools or other habitat bias associated with bridge crossings (Sterrett et al. 2018).

Visual and tactile surveys were conducted along longitudinal transects (i.e., lanes) running the length of the stream reach. The number of lanes was equal to the number of observers ($n \geq 3$). The width of each lane was equal to the stream width divided by the number of observers, where lane width was a minimum of 1 meter and a maximum of 3 meters. Surveys were standardized to a total of 2-person hours, and surveyors were trained to maintain a survey search rate of approximately 10 m² per minute. Surveyors initiated the search at the downstream origin of the transect and moved in the upstream direction searching the benthos of their lane until the 2-person hours limit was reached, at which point the surveyors would be at the end (upstream) of the transect. Each observer used

snorkeling or view buckets to scan the stream substrate within their lane and documented the presence of either shell or live *C. fluminea*. Due to the density of *C. fluminea* at sites where they were present, it was not practical to enumerate shells/individuals, but rather to only record presence/absence. Evidence supports snorkeling as a more effective method for detecting freshwater mussels (Nuri et al. 2022), but many sites in our study area were small and shallow, making clear-bottom view buckets the only feasible method. For that reason, observers used snorkeling whenever stream conditions allowed.

Habitat variables at each site were assessed as means of lane-specific habitat characteristics, or data collected at the reach level. Stream depth variation at a site was a measure of the coefficient of variation between all measurements of depth at a site. Depth measurements were taken from five locations in each lane (start, 25%, 50%, 75%, end). Similarly, the dominant substrate was measured at the same five locations along each lane. Surveyors classified the substrate into a substrate size class (ranging from fine silt [≤ 0.06 mm] to bedrock [> 4 m]) as characterized by the National Rivers and Streams Assessment 2013–2014 (USEPA 2013). Large woody debris was quantified as the number of wood pieces >10 cm in diameter and > 1.5 m long within each lane. If a lane contained large wood in the form of snags, log jams, or root wads, they were counted as one large wood. Large wood was measured by a surveyor once per lane and averaged for the site. Canopy cover was estimated using a modified spherical densiometer counting the number of 17 intersections covered by canopy vegetation. This measurement was taken at the middle of the reach along both banks and was the average of readings in upstream, downstream, river-right, and river-left directions taken at each bank. Mesohabitat composition was estimated as the approximate percentage of riffle, run, or pool within the study reach. Lane level habitat values were averaged across lanes, except for substrate classes, where we calculated the frequency of occurrence of each substrate type as the dominant substrate.

Spatial data

We classified land cover data for each site at a spatial resolution of 10 m using two metrics, the landcover within a 3 km buffer of the site and the landcover within the delineated catchment of a site. Analysis was conducted using the U.S. Geological Survey (USGS) National Land Cover Database (USGS 2021). We calculated the percentage of land use of four land cover classes: water (combining open water, woody wetlands, and emergent herbaceous wetlands), agriculture (combining pasture/hay, cultivated crops, and grassland/herbaceous), forest (combining deciduous forest, evergreen forest, and mixed forest) and developed landscape (combining developed open space, developed low intensity, developed medium intensity, developed high intensity, and barren land). We then calculated the percentage of each land cover class within a site's catchment and the land cover percentage in a 3 km buffer surrounding each site.

We used the USGS National Hydrography Dataset (NHD; USGS 2023) to measure each site's relationship to reservoirs within the HUC10 watershed using two metrics: the distance to the nearest reservoir (river km) and a binary indicator denoting whether there were any reservoirs present upstream. To be considered in the analysis, reservoirs must have been larger than 0.05 km². Karatayev et al. (2005) evaluated reservoirs across Texas and found that *C. fluminea* were uncommon in reservoirs smaller than 0.10 km². However, the majority of reservoirs within our study system were smaller than this. Because of the smaller average size of the reservoirs in our study area, a lower threshold value was chosen to exclude

the smallest reservoirs in our study area. All spatial analyses were conducted in ArcGIS Pro (Version 3.0.3, ESRI, Redlands, California). In total, we had 20 descriptor variables, that included the watershed where the site was located, seven landscape-level variables from GIS layers, 10 site-level variables measured directly in the sampling sites during May-September of 2023, and two that were based on a site’s position in the watershed relative to reservoirs (Suppl. material 1: table S1).

Statistical analysis

We used binomial logistic regression models to evaluate the effects that site specific habitat and landscape variables have on the presence of *C. fluminea*. We developed multiple competing models for each landscape category (i.e., agricultural, forested, developed), each containing variables shown to be affected by these land use patterns (Jacobson et al. 2001) (Suppl. material 1: table S2). For example, % agricultural and % developed landscapes in a watershed increases fine sediment in streams. Therefore, we included the proportion of sand or fine sediments as a predictor variable in models explaining *C. fluminea* presence during agricultural or developed land use dominant cases, but not forested land use. From this, a set of 10 candidate models was constructed using *a priori* hypotheses associated with agricultural, forested, or developed landscapes (Table 1). A Pearson correlation coefficient of $r = 0.6$ was used as a threshold to limit the inclusion of two correlated variables in any single model; when two variables were highly correlated, the more biological meaningful variable was retained (Suppl. material 1: fig. S1). In the case of categorical variables, the generalized variance inflation factor (GVIF) was calculated when considering which variables to include. Stream width is not characteristic of any dominant landscape type (Suppl. material 1: fig S1); therefore, we included the variable into subsets of models from each category. All models were ranked using Akaike’s Information Criterion (Burnham and Anderson 2004) values corrected for small sample size (AICc) to determine which model and characteristics most influenced *C. fluminea* presence at a site. We chose to only interpret models with a cumulative AIC weight of 95%. A Hosmer-Lemeshow Goodness-of-fit test was used to assess the fit of the interpreted models. An alpha level of 0.05 was used as the level of significance in all statistical tests, which were performed in the R statistical programming language (R Core Team 2024).

Table 1. *A priori* models used to predict *C. fluminea* site presence by combining habitat and landscape variables.

Model	Model predictors
Agriculture 1	% agriculture catchment + sand + variation in depth + run
Agriculture 2	% agriculture surrounding + sand + fine gravel + canopy cover + stream width
Agriculture 3	sand + fine gravel + stream width
Forest 1	% forest catchment + cobble + riffle + pool
Forest 2	% forest surrounding + riffle + canopy cover + LWD + stream width
Forest 3	cobble + riffle + stream width
Develop 1	% developed surrounding + upstream reservoir presence + sand + stream width
Develop 2	% developed catchment + upstream reservoir presence + reservoir distance
Develop 3	upstream reservoir presence + sand + stream width
Develop 4	canopy cover + sand + variation in depth

Results

Watershed characteristics

We found *C. fluminea* at 20 of the 50 sites sampled (Table 2). The Chattooga watershed was characterized by nearly 90% forest cover and the lowest agricultural (2.6%) and developed (6.9%) land cover. This watershed also had the fewest reservoirs, with only one site being associated with an upstream reservoir, and was the only watershed where *C. fluminea* was absent. In contrast, the Coneross watershed had the highest proportion of developed land cover (22%) due to the towns of Seneca, Westminster, and Walhalla. It also contained the greatest number of sites with reservoirs present upstream (eight) and the most number of sites with *C. fluminea* present (eight). A summary of land cover, reservoir presence, and prevalence of *C. fluminea* for each watershed can be found in Table 2.

Model selection and parameter estimation

Models associated with forest and developed environments ranked as the top two models with a cumulative AICc weight of 0.949 (Table 3), with the top model (Forest 3) having an AICc weight of 0.906. Stream width was a positive predictor of *C. fluminea* site presence in every model in which it appeared (Table 4, Suppl. material 1: table S3, Fig. 2). In almost all cases, the models that contained stream width within a landscape hypothesis type outperformed other models that did not contain the predictor. The inclusion of watershed as a predictor resulted in high GVIF scores (> 5), indicating a high degree of collinearity with other model predictors and was therefore not included in our final analysis.

Habitat variables related to substrate composition and mesohabitat descriptions appeared as positive and negative predictors of *C. fluminea* site presence. The amount of site composed of cobble was a significant negative predictor of *C. fluminea* site presence in the top model (Table 4, Fig. 2), while sand, fine gravel, and riffle were significantly affecting *C. fluminea* presence in lower ranked models (Suppl. material 1: table S3).

The presence of a reservoir upstream of a site was a significant variable in one of the top models (Develop 1, Table 4) while also appearing significant in lower ranked models (Suppl. material 1: table S3) and represented an approximate 3-fold increase in probability of *C. fluminea* presence at a site (Fig. 3). The density of landscape characteristics was a significant predictor of *C. fluminea* presence when measured in 3km buffers around sites, but never when measured within a site's catchment in our models. Land cover attributes related to agricultural density did not appear significant in any of our models.

Table 2. Attributes of 5 HUC10 watersheds surveyed for *C. fluminea*. Ten survey sites were selected within each HUC10 watershed.

Watershed	# of sites w/ <i>C. fluminea</i> present	% Developed	% Forest	% Agriculture	# Sites w/ Reservoir Upstream	# Reservoirs \geq 0.05km ²
Chauga	4	7.5	86.7	5.1	6	6
Little	5	15.5	67.2	8.3	3	6
Coneross	8	21.9	53.0	21.9	8	5
Chattooga	0	6.9	89.8	2.6	1	2
Lower Tugaloo	3	13.1	47.6	29.4	3	5

Table 3. Results from logistic regression models to predict *C. fluminea* presence at a site. Models were created using a specific set of habitat and landscape variables (see Table 1) that represented characteristics of a specific habitat type. AICc = Akaike information criterion corrected for small sample size, K = the number of parameters in a model, LogLik = Log likelihood for a given model, Δ AICc, AICc weight (AICcWT), and cumulative weight (Cum.Wt) are also shown.

Model	K	LogLik	AICc	Δ AICc	AICcWT	Cum.Wt
Forest 3	4	-18.657	46.203	0.000	0.906	0.906
Develop 1	5	-20.463	52.289	6.086	0.043	0.949
Forest 2	6	-19.590	53.132	6.929	0.028	0.977
Develop 3	4	-23.309	55.506	9.303	0.009	0.986
Develop 2	4	-23.631	56.152	9.949	0.006	0.992
Agriculture 3	4	-24.021	56.930	10.727	0.004	0.996
Agriculture 2	6	-21.809	57.572	11.369	0.003	0.999
Forest 1	5	-25.437	62.238	16.035	< 0.001	0.999
Develop 4	4	-30.009	68.906	22.703	< 0.001	0.999
Agriculture 1	5	-29.344	70.053	23.850	< 0.001	1.000

Table 4. Best fitting models, model statistics, and parameter estimates for logistic regression models of habitat and landscape variables affecting *C. fluminea* presence. Parameter estimates provided on the scale of the model using the logit link. AICc = Akaike information criterion corrected for small sample size, LogLik = Log likelihood for a given model. K = the number of parameters in a model. AICc weight (AICcWT) is also shown.

Model	AICc	LogLik	AICcWT	K
Forest 3	46.203	-18.657	0.906	4
Parameter	Estimate	Standard error	z value	p value
Intercept	-1.815	1.184	-1.534	0.125
Cobble	-0.181	0.070	-2.589	0.009
Riffle	-0.056	0.031	-1.818	0.069
Stream width	0.512	0.197	2.603	0.009
Develop 1	52.289	-20.463	0.043	5
Parameter	Estimate	Standard error	z value	p value
Intercept	-5.155	1.551	-3.324	<0.001
Upstream reservoir presence	1.677	0.837	2.002	0.045
% developed surrounding	0.107	0.050	2.143	0.032
Sand	0.022	0.015	1.397	0.112
Stream width	0.200	0.106	1.891	0.058

Discussion

Corbicula fluminea are an AIS currently found throughout most major watersheds in the United States (Karatayev et al. 2007, USGS 2025), and whose effects on native biota are not fully understood (Haag et al. 2021). Often considered a habitat generalist (Kelley et al. 2022), *C. fluminea* may be associated with varying habitat correlates depending on the system they are invading. Nevertheless, understanding relationships with habitat and spatial variables could aid in targeted management or monitoring prior to the establishment of new populations. To better understand the distribution of *C. fluminea* in the upper Savannah River watershed of South Carolina and Georgia (USA), we used an information theoretic approach to evaluate multiple competing hypotheses of landscape use (agricultural, forest, developed) and site level habitat to best predict *C. fluminea* presence. We found

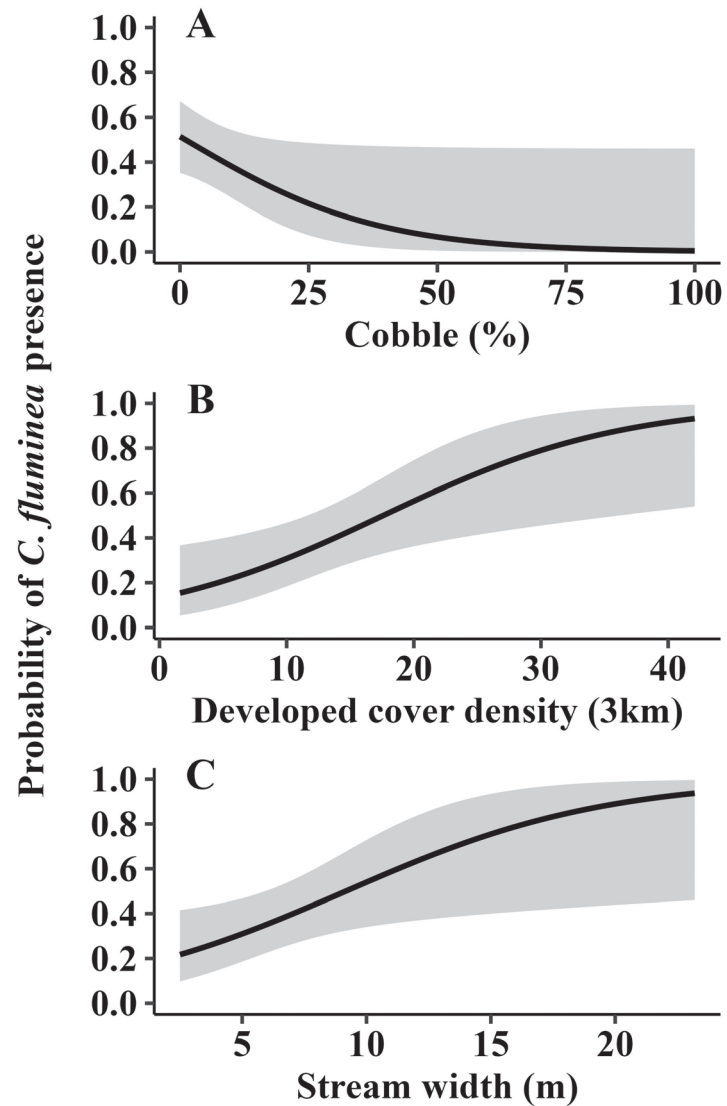


Figure 2. Generalized linear model (GLM) predictions of the probability of *C. fluminea* presence across various habitat and landscape variables. Each subplot represents the relationship between *C. fluminea* presence (binary response) and a specific predictor variable from the best fitting model containing that predictor: (a) cobble substrate composition, (b) developed land within a 3 km radius (%), (c) stream width (meters). The y-axis displays the predicted probability of *C. fluminea* presence, with 95% confidence intervals indicated by the shaded bands. Variables were selected based on their ecological relevance to *C. fluminea* habitat preferences.

C. fluminea presence was predicted best by increasing stream width, and negatively associated with an increase in cobble as the dominant substrate.

It is important to note that our study only evaluated presence of *C. fluminea*, but not abundance or density. We believe that presence only data can be helpful in defining suitable habitat for an invader, but may be improved upon to evaluate optimal habitat through the inclusion of quantitative estimates of density or abundance. We also did not evaluate detection probability in our study, and therefore cannot be certain that a recorded absence of *C. fluminea* is representative of true absence or imperfect detection. We used a rapid assessment protocol to maximize the number of sites that can be surveyed within a day, using a search rate of 10 m² per minute (Sterrett et al. 2018). Others have proposed that an effective search rate for freshwater bivalves in low densities is closer to 1–2 m² per minute

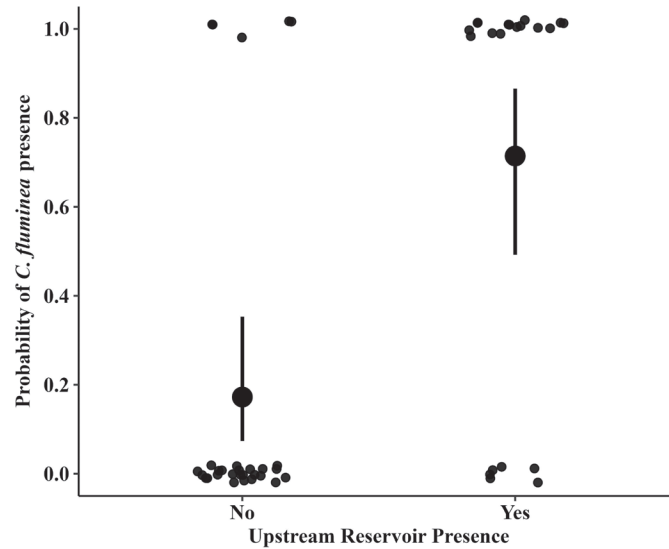


Figure 3. Probability of *C. fluminea* presence and the relationship with upstream reservoir presence. The points represent the observed site occurrences in a corresponding upstream reservoir scenario. The lines with black points indicate the predicted probabilities from a logistic regression model ($\pm 95\%$ confidence intervals).

(Strayer and Smith 2003; Smith 2006). While it is possible that the rapid search rate may have added false negatives at sites, *C. fluminea* often reach very high densities (e.g., 1.7–132 clams/m²; Kelley et al. 2022) and thus the likelihood of detecting at least one individual at these densities is high.

Our findings suggest that stream size was the most important factor associated with the presence of *C. fluminea*. As stream size increased, the probability of *C. fluminea* presence also increased (Fig. 2). The distribution and abundance of aquatic species is often related to increased stream size due to a greater diversity of habitat and available resources found in larger rivers or streams (Schlosser 1982; Vaughn and Taylor 2000). But in this case, the relationship could be more complex. Stream size was also highly correlated with larger catchment areas (Pearson $r = 0.9$, Suppl. material 1: fig S1). As catchments increase in size, there may be a greater number of accidental or deliberate introductions of invasive species through human activity simply due to greater area (Kolar and Lodge 2001). Once established, *C. fluminea* disperses downstream (Pernecker et al. 2021), aided by its free-swimming juvenile stage that lasts for approximately 100 hours (Mackie and Claudi 2010), sufficient time for larvae to reach the outflow of reservoirs and be carried further downstream. Therefore, it is possible that the stream width relationship in our study indicates a greater probability of *C. fluminea* being introduced higher in the watershed.

In our best explanatory model, we found a negative association between *C. fluminea* presence and increasing proportion of cobble as the dominant substrate (Fig. 2), which may be indicative of smaller, headwater streams in forested watersheds. Successful aquatic invaders may tolerate a wide range of habitats, and *C. fluminea* can withstand a range of flow conditions and substrate types in lentic and lotic systems. Previous studies have indicated increased presence and abundance in slow-moving sandy rivers (Schmidlin and Baur 2007), rivers with larger substrate (Kelley et al. 2022), and in reservoirs (Karatayev et al. 2003; Patrick et al. 2017). In a behavioral habitat preference experiment, Schmidlin and Baur (2007) found *C. fluminea* preferred fine sediments including sand and fine gravel. The behavioral preference corroborated observations of higher natural densities in fine sediments in the Rhine River (Schmidlin and Baur 2007). In our study, proportion

of sandy substrates was also a significant and positive predictor of presence, but only in lower performing models (Agriculture 3, AICc = 56.930, AICcWT = 0.004; Suppl. material 1: table S3). The lack of a strong positive relationship between presence and substrate may be indicative of *C. fluminea*'s ability to colonize multiple substrate types, but it is also difficult to compare our presence data with abundance data reported from other studies.

Freshwater ecosystems are often affected by changing land use (Sala et al. 2000), and land cover in the catchment of a site may affect in-stream habitat parameters (Jacobson et al. 2001). Land use can influence water flow and sediment loads, which in turn may impact benthic organisms, and critical habitat along and within the streams (Allan 2004). Ferreira-Rodríguez et al. (2022) found *C. fluminea* densities were positively associated with the amount of agricultural land cover in a watershed. We did not see any relationship between agricultural land use and *C. fluminea* presence, but it is possible that agricultural land use is a better predictor of abundance than of presence only. Conversely, we did see a significant negative relationship with the % forest, and a significant positive relationship with % developed land within a 3km buffer around a site. However, these relationships were reported in lesser performing models representing 3% (Forest 2) and 4% (Develop 1, Fig. 2) of AICcWT (Suppl. material 1: table S3). The association of *C. fluminea* presence with surrounding land cover may indicate that habitat degradation promotes establishment and proliferation of AIS. For example, increased developed land use, and conversely declining forested land use adjacent to a stream may result in declining habitat quality (Allan et al. 1997), reduced native biodiversity (Strayer et al. 2003), and thereby foster an invasion. It is also feasible that increased developed landscape (or decreased forested landscape) may indicate increased introduction and propagule pressure from human aided dispersal. Rodríguez-Rey et al. (2023) found that anthropogenic variables related to dispersal (e.g., road density, distance to ports or boat ramps, and human population density) provide greater relative importance in predicting the presence of AIS in the United Kingdom. It is possible that the gradient response of forested vs. developed land use in our study represents a gradient of anthropogenic activity aiding in *C. fluminea* dispersal in the upper Savannah River basin.

Human activity within and between reservoirs also serves as a potential mechanism of overland dispersal for aquatic hitch-hikers. Reservoirs have been shown to act as stepping stones for AIS invasions by providing accessible environments for human activities serving as introduction vectors (Johnson and Carlton 1996; Johnson et al. 2008). As relatively new habitats, reservoirs generally have lower species biodiversity than their original lotic systems, resulting in open niches that invasive species can exploit (Wetzel 1990; Havel et al. 2015). Karatayev et al. (2005) related *C. fluminea* presence to landscape characteristics throughout the state of Texas, USA. The authors found that *C. fluminea* were disproportionately present in larger reservoirs compared to smaller ones due to the amount of human activity that these reservoirs received. We found a positive relationship between the presence of upstream reservoirs and the presence of *C. fluminea* (Fig. 3), though this was in a lesser performing model (Develop 1). The initial introduction of *C. fluminea* may have been facilitated by human recreational activities, including boating, swimming, and fishing, and may have spread to nearby reservoirs in the same manner (Havel et al. 2015), or through passive transport on the feet and feathers of aquatic birds (McMahon 2002). We did not, however, assess presence of *C. fluminea* in upstream reservoirs and we acknowledge that this pathway is speculative, yet a plausible explanation given support from the literature. The potential of reservoirs as stepping-stones of passive dispersal by *C. fluminea* warrants continued investigation.

Our findings suggest that some landscape variables related to forest and developed environments may play a role in determining *C. fluminea* presence; however, site level habitat characteristics including substrate and stream width showed clearer relationships to *C. fluminea* absence or presence. Differences in our results from those previously published may simply be a result of differences in habitat and landscape processes that predict presence vs. abundance. Whereas habitat and landscape correlates of abundance or density are more indicative of optimal or quality habitat, presence data may be helpful in identifying suitable habitat where an invasion may initially occur. Given support in the literature, future research on *C. fluminea* may benefit from further evaluation of upstream reservoirs and developed landscapes on clam presence and abundance.

Author contribution

ZS: research conceptualization, sample design & methodology, investigation and data collection, data analysis and interpretation, writing – original draft, writing – revisions; MB: research conceptualization, sample design & methodology, investigation and data collection, data analysis and interpretation, writing – revisions; MH: data analysis and interpretation, writing – revisions; BI: data analysis and interpretation, writing – revisions; PH: research conceptualization, sample design & methodology, investigation and data collection, data analysis and interpretation, writing – revisions, funding.

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Ethical statement

All sampling activities were permitted by SCDNR under permit number F – 23 – 058, as well as written permission for stream access from private landowners and the United States Forest Service Francis Marion and Sumter National Forest.

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary material.

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Supplementary material 1

Additional information

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Data type: docx

Explanation note: **table S1.** Summary table describing all potential predictor variables analyzed to find their effect on *C. fluminea* site presence. **table S2.** Hypothesized pathways for how major land-use types could experience different factors that cause changes in stream habitat and result in decreases (-) or increases (+) of several potential predictor variables used in the candidate model set for predicting the probability of *C. fluminea* site presence. **table S3.** Additional models, model statistics, and parameter estimates for logistic regression models of habitat and landscape variables affecting *C. fluminea* presence. **fig. S1.** Correlation matrix of all predictor variables that we considered using in final models for *C. fluminea* presence. A correlation level of 0.6 was chosen to eliminate redundancy within models. Predictor variables with a value of 0.6 or greater were not used in the same model.

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