

# Evaluating the influence of land use, drought and reach isolation on the occurrence of freshwater mussel species in the lower Flint River Basin, Georgia (U.S.A.)

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## SUMMARY

1. North American freshwater mussels have been subjected to multiple stressors in recent decades that have contributed to declines in the status and distribution of many species. However, considerable uncertainty exists regarding the relative influence of these factors on observed population declines.

2. We used an occupancy modelling approach to quantify relationships between mussel species occurrence and various site- and catchment-level factors, including land cover, stream size, the occurrence of drought and reach isolation due to impoundment for 21 mussel species native to the lower Flint River Basin, Georgia, U.S.A.

3. Our modelling approach accounted for potential biases associated with both incomplete detection and misidentification of species, which are frequently not accommodated as sources of bias in freshwater mussel studies.

4. Modelling results suggested that mussel species were, on average, four times less likely to be present following severe drought, but the negative effects of drought declined rapidly with increasing stream size. Similarly, mussel species were 15 times less likely to occupy small streams that were isolated from mainstem tributaries by impoundments.

5. This study provides insight into the effects of natural and anthropogenic factors on freshwater mussel species. Our findings add to a growing body of literature aimed at improving understanding of the predominant factors influencing freshwater mussel populations and fostering the development of more informed and effective conservation strategies.

*Keywords:* false-negative errors, false-positive errors, occupancy, unionids, water resource management

## Introduction

Decisions about the management and conservation of water resources must address growing human water demands (Fitzhugh & Richter, 2004) as well as the potential effects of water resource development activities (e.g. expansion of urban and agricultural water infrastructure, construction of impoundments) and conservation activities (e.g. streamflow restoration) on stream-dwelling biota (Richter *et al.*, 2003). In recent decades, freshwater

mussels throughout North America have experienced substantial population declines (Ricciardi & Rasmussen, 1999; Strayer *et al.*, 2004) that have been attributed to a variety of factors, including periodic drought (Golladay *et al.*, 2004; Haag & Warren, 2008), excessive sedimentation (Brim Box & Mossa, 1999), environmental contaminants (Watters, 1999; Augspurger *et al.*, 2003), streamflow alteration (Layzer & Madison, 1995; Peterson *et al.*, 2011) and the construction of impoundments (Watters, 1996; Vaughn & Taylor, 1999). Despite the wide range of attributed

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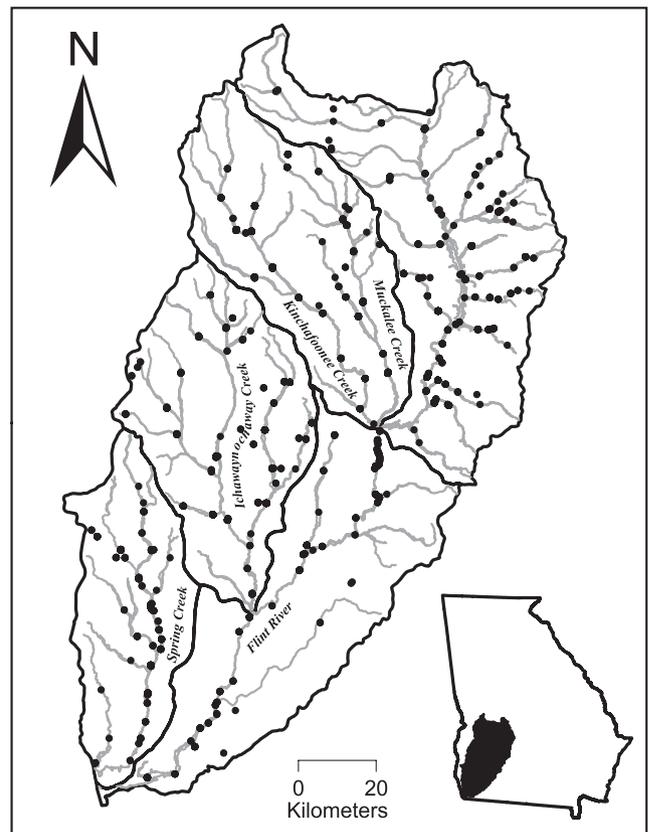
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factors, however, their relative influence on observed mussel population declines remains poorly understood (Downing, Van Meter & Woolnough, 2010). This makes it difficult for managers to identify the primary factors contributing to mussel population declines and may inhibit the development of effective conservation strategies.

Effective conservation and recovery planning for freshwater mussels can be achieved, in part, through the implementation (or continuation) of monitoring programmes. Ecological monitoring data, however, are highly susceptible to potential biases associated with incomplete detection of individuals and species (Williams, Nichols & Conroy, 2002; Tyre *et al.*, 2003). Freshwater mussels can be particularly difficult to sample because of their benthic nature and frequently clumped distributions (Strayer & Smith, 2003). Species misidentification also may bias monitoring data (Royle & Link, 2006), and the risk of misidentification can vary among species and investigators (Fitzpatrick *et al.*, 2009; Miller *et al.*, 2011; Shea *et al.*, 2011). Thus, biases associated with both incomplete detection and misidentification of species may obscure the true ecological patterns that are of primary interest to biologists and managers (Yoccoz, Nichols & Boulinier, 2001). Detection and misidentification biases can be formally accommodated in ongoing monitoring programmes through careful study design and proper training. For historical data sets (i.e. long-term data sets with potentially multiple field crews and sampling protocols), detection and misidentification also can be formally accommodated if details of mussel collections are known, such as sampling method and the identities of field investigators. Formally accounting for the risk of incomplete detection and misidentification may, in turn, improve our understanding of ecological patterns and our ability to develop effective conservation strategies.

The challenges faced by biologists and managers are typified in the Flint River Basin (FRB), Georgia. From its headwaters south of Atlanta, the Flint River flows southwest for 560 km through Piedmont and Coastal Plain physiographic provinces until joining the Chattahoochee River to form the Apalachicola River. The lower Flint River Basin (LFRB) is located completely within the Coastal Plain physiographic province, encompassing 13 952 km<sup>2</sup> in south-western Georgia (Fig. 1). Row-crop agriculture and related infrastructure contribute substantially to the regional economy, making the LFRB one of the most productive agricultural regions in the country (McKissick, 2004). Agricultural activities rely heavily on irrigation water withdrawn from surface and groundwater sources and comprise *c.* 90% of the water used in the

LFRB during the April to September growing season (McDowell, 2006). Approximately 80% of the water used for irrigation in the LFRB is extracted from the Upper Floridan Aquifer, which underlies most of the Coastal Plain province of the south-eastern United States (Hicks, Gill & Longworth, 1987). Surface waters throughout the Coastal Plain are connected heterogeneously to the Upper Floridan Aquifer; thus, the mainstem Flint River and many of its tributaries are in direct connectivity with the Upper Floridan Aquifer (Torak *et al.*, 1996). Agricultural withdrawals from the Upper Floridan Aquifer frequently result in decreased base-flow to springs and streams that are in contact with the aquifer, and peak water withdrawals often coincide with periods of reduced summer flows and high evapotranspiration rates that exacerbate low-flow periods (Torak *et al.*, 1996). The evaluation of long-term data sets from the U.S. Geological Survey (USGS) indicates that 7Q10 (the lowest discharge that occurs over seven consecutive days with a 10-year recurrence interval; Annear *et al.*, 2004) has been lowered



**Fig. 1** Locations within the lower Flint River Basin (LFRB) where freshwater mussel sampling was conducted from 1991 to 2010. The mussel collection data were used to develop predictive models of species occupancy for 21 freshwater mussel species native to the LFRB.

in many LFRB tributaries since the implementation of intensive irrigation in the 1970s (Rugel *et al.*, 2012). Additionally, the LFRB has experienced two severe and prolonged droughts since 1999 (NCDC, 2010). The combined effects of high agricultural intensity, periodic drought and the unique geological and hydrological characteristics of LFRB streams has had the potential to substantially affect aquatic communities in the region.

The LFRB harbours a diverse and imperilled freshwater mussel assemblage. Thirty mussel species are believed to have occurred historically (Clench & Turner, 1956; Williams, Bogan & Garner, 2008), two of which are now presumed extinct or extirpated, five are federally threatened or endangered, and several more are considered species of special concern (Williams *et al.*, 2008). Ongoing monitoring activities in the LFRB have resulted in a long-term data set spanning 1991–2010, which may provide valuable insight into the factors contributing to the present-day status of many LFRB mussel species. However, it is likely that some species remained undetected during historical surveys (false absences). Similarly, some records in the historical data set may represent species misidentifications (false presences; Shea *et al.*, 2011). Thus, we determined that a detailed analysis of historical LFRB mussel collection data required formal accommodation of incomplete detection and misidentification of species.

Our primary goal was to estimate the influence of reach isolation, land use characteristics and severe drought on mussel species occurrence. Our specific objectives were (i) to incorporate methods for correcting historical mussel collection data that were subject to detection and misidentification errors and (ii) to develop predictive models of occurrence for LFRB mussel species in relation to reach isolation, catchment-level land use characteristics and severe drought.

## Methods

### *Mussel collection data*

We investigated the factors influencing the status and distribution of LFRB mussel species using a long-term database comprising mussel collection data spanning 19 years. Samples collected from 1991 to 2010 were conducted by a variety of personnel representing state and federal agencies, university faculty and students and private environmental consulting firms. For the entire time-span, we classified mussel collections into three time periods: pre-2000 (prior to the onset of severe drought in the LFRB in 2000), 2000–2006 (post-severe drought 2000/prior to severe drought 2007) and post-2007 (follow-

ing the onset of severe drought in 2007). These periods were defined because we could not safely assume that the status of mussel species (i.e. the presence or absence of species) remained unchanged following severe drought, thereby violating assumptions of closure necessary for subsequent data analysis (see Multispecies occupancy modelling, below). Additionally, the post-2000 and post-2007 mussel collection data could potentially provide information regarding changes in the status and distribution of mussel species following record low streamflow conditions. Mussel collection data were included only if (i) the sampling date was known, (ii) the site locality was geo-referenced or otherwise recorded (e.g. there was a description of a road crossing), (iii) freshwater mussel species were the primary sampling target, (iv) the sampling method was known and (v) the identity of the field crew that conducted the sample was known. The resulting data set consisted of detection/non-detection data for 21 mussel species collected from 246 stream reaches throughout the LFRB from 1991 to 2010 (Fig. 1). To ensure consistent field identification of species based on differences in naming conventions among the three time periods, we used Williams *et al.* (2008) as the basis for assigning species names. Since the publication of Brim Box & Williams (2000), most name changes for LFRB mussel species in Williams *et al.* (2008) were minor and, we believe, did not contribute to the introduction of false presences or false absences in the data set. We combined data for two species, *Elliptio pullata* (Lea, 1856) and *Elliptio fumata* (Lea, 1857), into *Elliptio sp.* because these species are very difficult to distinguish during field sampling and were usually recorded by field crews as *Elliptio sp.* in all three time periods. Similarly, we combined data for *Pyganodon cataracta* (Say, 1817) and *Pyganodon grandis* (Say, 1829) into *Pyganodon sp.* because these species are indistinguishable in the LFRB without the use of molecular techniques (J. Williams, Florida Museum of Natural History, personal communication) and were usually recorded as *Pyganodon sp.* in all three time periods. Lastly, prior to the publication of Williams *et al.* (2008), some specimens of *Anodontoides radiatus* were incorrectly identified as *Strophitus subvexus*, which does not occur (nor has it ever occurred) in the LFRB; hence, we changed all records of *S. subvexus* to *A. radiatus*. Total sampling effort varied among sites and time periods (Table 1).

### *Mussel sampling protocols*

Each sample occasion was categorised into one of four mussel sampling protocols: timed search surveys, fixed area surveys, longitudinal transect surveys or transverse

**Table 1** Means, standard deviations (SD) and ranges of habitat characteristics for the 246 lower Flint River Basin sample sites used to model mussel species occupancy, and sampling effort for the 74 repeat-visit sites used to model species detection

Characteristics	Mean	SD	Range
Link magnitude	913.50	1510.30	1–4000
Number of isolated sites	17		
Number of post-drought sites	166		
Total number of repeat-visit sites	74		
Number of visits to repeat sites	3.13		2–11
1991–1999 (28 sites)	2.18		2–4
2000–2006 (33 sites)	2.22		2–4
2007–2010 (13 sites)	5.00		2–11
12-Digit HUC land use (% composition)			
Agriculture	36.80	15.90	4–69
Urban	5.60	3.00	2–23
Wetland	15.50	8.90	3–51

transect surveys. For all methods, crews conducted tactile searches of the predominantly sandy-bottomed Coastal Plain streambeds to depths ranging from 0 to *c.* 5 cm below the substrate surface (i.e. quadrat excavations were never conducted). During all surveys, all possible habitats where mussels could occur were searched, including root mats, rock crevices and logs. The relative contribution of various sampling methods (i.e. visual searches, SCUBA, snorkelling, wading) probably varied among surveys, but this information was unknown. Across all three time periods, most (95%) mussel surveys were conducted during spring and summer (March–October).

Timed search surveys were those for which sample effort was expressed as time spent searching, but for which the area searched was unknown. Timed searches were conducted on at least one sampling occasion for 91 of the 119 sites sampled from 1991 to 1999 and 28 of 130 sites sampled from 2000 to 2006. Most (91) of the timed search surveys were conducted during the summers of 1991 and 1992, during which all mussels were collected by hand using SCUBA, snorkelling or direct observation in shallow areas (Brim Box & Williams, 2000). Total sampling effort for the 1991–1992 surveys varied among sites but averaged 1.9 person-hours per site and ranged from 0.3 to 7.6 person-hours (Brim Box & Williams, 2000). Sampling effort for the remaining qualitative sample sites was unavailable; thus, we assumed that sampling effort was similar to that of the other 91 timed search surveys.

Fixed area surveys were conducted on at least one occasion for all of the 130 sites surveyed from 2000 to 2006. These surveys were conducted by Georgia Department of Natural Resources personnel and private consulting firms who were required to conduct sampling according to protocols developed by the United States

Fish and Wildlife Service (Carlson *et al.*, 2008). Fixed area surveys involved sampling, to the greatest extent possible, the entire wetted stream area 100 and 300 m downstream and upstream, respectively, of potential impact sites (e.g. bridge crossings). Tactile surveys of the streambed were conducted in all available habitats using a variety of methods, including snorkelling, SCUBA and visual searches, as appropriate.

Longitudinal transect surveys were the most labour-intensive sampling method and were conducted on at least one sampling occasion at 47 of 119 study reaches surveyed during the pre-drought period and three of 32 study reaches surveyed during the post-2007 drought period. The protocol for longitudinal transect surveys differed depending on stream size. In small streams (<12 m wide), crews consisting of multiple personnel lined up side-by-side (perpendicular to streamflow) and sampled the surface of the streambed in an upstream direction throughout a 100-m-long study reach (Golladay *et al.*, 2004). In large streams ( $\geq 12$  m wide), longitudinal transect sampling was conducted by crews searching six parallel transects running longitudinally in an upstream direction throughout a 100-m reach (Golladay *et al.*, 2004).

Transverse transect sampling was conducted at 32 study sites from 2007 to 2010 using the following protocol. First, a random start point was selected as the lower end of a 100-m-long study reach. Next, 30 1-m-wide cross-sectional stream transects (perpendicular to streamflow) were randomly assigned to specific locations along the length of the 100-m sample reach. The location of each transect was measured upstream from metre 0 (the downstream-most end of the 100-m reach) and marked with orange flags on both the left and right banks. During sampling, a 1-m-wide band of the streambed corresponding to each randomly selected transect location (0.5 m on either side of each flag) was tactilely searched by a single person.

#### *Site- and catchment-level characteristics*

To evaluate the relationships between land use characteristics and mussel species presence, we used HUC12 subcatchments as the largest sample unit (USGS, 1999). Using existing Geographic Information Systems (GIS) layers, we summarised the land use characteristics of 122 HUC12 subcatchments corresponding to the 246 mussel sample site locations (Table 1). For the land cover data, we used the 2001 National Land Cover Dataset (USGS, 2001a) and calculated the per cent agriculture, forest, urban and wetland coverage (expressed as a percentage of the total HUC12 subcatchment area) for each of the 122 HUC12

subcatchments. Additionally, we defined a stream reach as 'isolated' if it was separated from the mainstem Flint River or any of the five major tributaries (Ichawaynoch-away, Muckalee, Kinchafoonee, Chickasawhatchee and Spring Creeks) by an impoundment. To determine reach isolation, we used the National Inventory of Dams (NID; USACE, 2010) data layer in ARCGIS 9.2 to visually assess the locations of known impoundments in the LFRB. Lastly, we calculated stream size (link magnitude; Shreve, 1966) by manually counting the number of first-order tributaries contributing to each study reach based on 1:24K NHD stream network layers (USGS, 2001b).

### Multispecies occupancy modelling

We used a multispecies occupancy modelling approach (MacKenzie *et al.*, 2006; Royle & Dorazio, 2008) to estimate occupancy and detection probabilities for the 21 mussel species in relation to site- and catchment-level characteristics. Occupancy models produce two types of probability-based estimates: occupancy ( $\Psi$ ) and detection ( $p$ ). Occupancy is defined as the probability that a species is present at a sample location during sampling (MacKenzie *et al.*, 2002). Detection is defined as the probability of detecting a species, given it is present at a study site and available for capture (MacKenzie *et al.*, 2002). Provided replicate surveys are conducted at study locations and assuming the occupancy status of species is constant across replicate surveys, occupancy and detection can be jointly modelled using a binomial likelihood with a zero-inflated class as

$$\begin{aligned} P(Y_{ij} = 1) &= \Psi_{ij} \binom{K}{y_{ijh}} p_{ijh}^{y_{ijh}} (1 - p_{ijh})^{K - y_{ijh}} | P(Y_{ij} = 0) \\ &= \Psi_{ij} (1 - p_{ijh})^K + (1 - \Psi_{ij}), \end{aligned}$$

where  $Y_{ij}$  represents the detection (1) or non-detection (0) of species  $j$  at site  $i$  across  $K$  occasions,  $y_{ijh}$  represents the detection ( $y_{ijh} = 1$ ) or non-detection ( $y_{ijh} = 0$ ) of species  $j$  at site  $i$  during occasion  $h$ ,  $\Psi_{ij}$  represents the probability that site  $i$  was occupied by species  $j$ , and  $p_{ijh}$  represents the probability of detecting species  $j$  at site  $i$  during occasion  $h$ , given the species is present. Using the entire data set, we modelled species detection probability using the detection/non-detection data collected at 74 repeat-visit sample sites (Table 1). We used the predicted detection probabilities (i.e. the average detection probability across all repeat-visit sites) estimated from the repeat-visit sites to model occupancy at the remaining 172 sites that were visited on only a single occasion. For all sample locations, we assumed that the occupancy status of all species did

not change within each time period (pre-2000, post-2000 and post-2007). We believe that this assumption was valid because no widespread, severe disturbances (e.g. severe flood, drought) that we deemed capable of extirpating entire species from study reaches were evident *within* any of the time periods.

The occupancy modelling approach requires that species are identified without error during surveys (i.e. species are not permitted to be detected where they do not exist). However, based on empirical evaluation of misidentification rates for LFRB mussel species (Shea *et al.*, 2011), we determined that the assumption of perfect identification during historical mussel surveys in the LFRB was not valid. Hence, we used a modification of occupancy models following Royle & Link (2006) to account for potential biases associated with false-positive mussel species identification and modelled mussel species occupancy ( $\Psi$ ), detection ( $p_{11}$ ) and misidentification ( $p_{10}$ ) as

$$\begin{aligned} P(Y_{ij} = 1) &= \Psi_{ij} \binom{K}{y_{ijh}} p_{11ijh}^{y_{ijh}} (1 - p_{11ijh})^{K - y_{ijh}} \\ &\quad + (1 - \Psi_{ij}) \binom{K}{y_{ijh}} p_{10ijh}^{y_{ijh}} (1 - p_{10ijh})^{K - y_{ijh}} | \\ P(Y_{ij} = 0) &= \Psi_{ij} (1 - p_{11ijh})^K + (1 - \Psi_{ij}), \end{aligned}$$

where  $Y_{ij}$  represented the detection (1) or non-detection (0) of species  $j$  at site  $i$  across  $K$  occasions,  $y_{ijh}$  represented the detection ( $y_{ijh} = 1$ ) or non-detection ( $y_{ijh} = 0$ ) of species  $j$  at site  $i$  during occasion  $h$ ,  $\Psi_{ij}$  represented the probability that site  $i$  was occupied by species  $j$ ,  $p_{11ijh}$  represented the probability of detecting species  $j$  during occasion  $h$  given it was present at site  $i$ ,  $p_{10ijh}$  represented the probability of falsely identifying species  $j$  given it was detected during occasion  $h$  but did not actually occur at site  $i$ . In practice, joint estimation of species detection ( $p_{11}$ ) and misidentification ( $p_{10}$ ) can be difficult in the absence of strict assumptions of parameters values (e.g. specifying that  $p_{11} > p_{10}$ ; Royle & Link, 2006; Royle & Dorazio, 2008). Alternatively, supplementary data can be used as *a priori* knowledge and incorporated directly into modelling procedures by using informative prior distributions for the misidentification parameter  $p_{10}$  (Royle & Dorazio, 2008). We used informative prior distributions for the misidentification parameter  $p_{10}$  using estimated misidentification rates for LFRB mussel species based on a concurrent study (Shea *et al.*, 2011; Table 2). Based on these estimates, species misidentification rates for the current study ranged from <1 to 31%, depending on specific combinations of species traits (small, medium or large shells) and crew experience (1–16 years; Table 2).

**Table 2** Means and standard deviations (SD) of predicted false-positive error rates for freshwater mussel species collected from 246 sample locations throughout the lower Flint River Basin from 1991 to 2010. For each combination, the mean and SD were used to calculate alpha and beta parameters (via method of moments) for beta prior distributions on mussel species misidentification rates

Combination	Shell size category	Observer experience	Mean	SD
1	Small	1	0.1876	0.0983
2	Small	2	0.1107	0.0719
3	Small	3	0.0651	0.0527
4	Small	4	0.0388	0.0386
5	Small	5	0.0237	0.0284
6	Small	6	0.0148	0.0212
7	Small	7	0.0095	0.0160
8	Small	8	0.0062	0.0123
9	Small	12	0.0014	0.0051
10	Small	13	0.0010	0.0043
11	Small	14	0.0007	0.0036
12	Small	15	0.0005	0.0031
13	Small	16	0.0004	0.0027
14	Medium	1	0.3169	0.0880
15	Medium	2	0.2647	0.0785
16	Medium	3	0.2185	0.0701
17	Medium	4	0.1788	0.0629
18	Medium	5	0.1453	0.0568
19	Medium	6	0.1176	0.0513
20	Medium	7	0.0949	0.0465
21	Medium	8	0.0766	0.0421
22	Medium	12	0.0327	0.0286
23	Medium	13	0.0266	0.0262
24	Medium	14	0.0218	0.0241
25	Medium	15	0.0178	0.0223
26	Medium	16	0.0147	0.0208
27	Large	1	0.1748	0.1015
28	Large	2	0.1421	0.0873
29	Large	3	0.1148	0.0746
30	Large	4	0.0923	0.0635
31	Large	5	0.0740	0.0540
32	Large	6	0.0592	0.0460
33	Large	7	0.0473	0.0393
34	Large	8	0.0379	0.0337
35	Large	12	0.0159	0.0195
36	Large	13	0.0130	0.0174
37	Large	14	0.0106	0.0158
38	Large	15	0.0086	0.0145
39	Large	16	0.0071	0.0135

Predicted error rates are based on the best-fitting hierarchical logistic regression model relating false-positive error rates to species characteristics (maximum adult shell size: small =  $\leq 60$  mm, medium = 61–150 mm, large =  $>150$  mm) and observer experience (years) following Shea *et al.* (2011).

We fitted multispecies occupancy models relating mussel species presence to site and catchment-level characteristics and drought to evaluate the influence of these factors on LFRB mussel species occupancy. However, this approach cannot account for dependence (i.e. autocorre-

lation) among repeated samples, and we suspected that repeated observations on mussel species at locations throughout the LFRB were dependent (i.e. spatial autocorrelation; Royle & Dorazio, 2008). To account for dependence among species and locations, we fitted hierarchical occupancy models to the mussel species data. Hierarchical occupancy models differ from more familiar occupancy modelling techniques in that dependence among observations collected at lower-level units (here, detection/non-detection data for multiple species across multiple study locations) within upper-level units (here, sites and species) is incorporated by including random effects for the lower-level intercept and slopes (Royle & Dorazio, 2008). The species-level random effects were assumed to be normally distributed with a grand mean (intercept or slope) and random effect-specific variance (Bryk & Raudenbush, 2002). The site-level random effect was assumed to be normally distributed with a mean 0 and random effect-specific variance. The random components represented unique effects associated with sites and species that were unexplained by covariates included in the model. To accommodate this complex model structure, we used Markov chain Monte Carlo (MCMC) as implemented in WINBUGS software, version 1.4 (Spiegelhalter, Thomas & Best, 2006) to fit candidate hierarchical multispecies occupancy models. The number of iterations was determined by fitting the global model running three parallel chains and testing for convergence using the Gelman–Rubin diagnostic (Gelman & Rubin, 1992). All models were fitted using 200 000 iterations and 75 000 iteration burn-in (i.e. the first 75 000 MCMC iterations were dropped). We used diffuse priors for all parameters, with the exception of the misidentification parameter  $p_{10}$ , for which informative priors were specified using a beta distribution with parameters alpha and beta. The alpha and beta parameters that defined the prior distributions were calculated via method of moments using the mean and standard deviation of predicted misidentification rates for specific combinations of experience and species characteristics (Table 2).

Prior to fitting candidate models, we evaluated the relative fit of 10 different variance structures for the hierarchical multispecies occupancy model random effects using the global (all predictors) model. The 10 variance structures contained different combinations of fixed effect and random effects associated with species, sites, a single site-level predictor (link magnitude) and covariance between the various random effects (Table 3). The variance structure associated with the best-approximating model was then used in all candidate hierarchical multispecies occupancy models.

**Table 3** Alternative variance structures evaluated for fitting candidate multispecies occupancy models

Parameter	Error structure									
	A	B	C	D	E	F	G	H	I	J
Random intercept (species)	X	X		X	X		X	X		
Random intercept (site)	X		X	X		X	X		X	
Random slope (link magnitude × species)	X	X	X	X	X	X				
Covariance (site intercept and link magnitude)	X		X							
Covariance (species intercept and link magnitude)	X	X								
Covariance (both intercepts and link magnitude)	X									

Parameters included in each scenario are denoted by X. The best-fitting error structure (D) was used to fit subsequent candidate multispecies occupancy models.

**Table 4** List of variables included in candidate multispecies occupancy models for freshwater mussels in the lower Flint River Basin, Georgia, with corresponding ecological interpretation

Parameter	Interpretation/hypothesis
Per cent agriculture	Agricultural land use negatively influences mussel species by decreasing water quality, increasing sedimentation and increasing water use
Per cent urban	Urban land use negatively influences mussel species by altering stream flows and decreasing water quality
Per cent wetland	Wetland coverage negatively influences mussel species occurrence by reducing host fish availability and water quality (extreme DO and temperature)
Link magnitude	Stream size influences mussel species occurrence, but the relationship varies substantially among species
2000–2002 drought	Mussel assemblages were negatively affected by severe drought during 2000–2002
2007–2008 drought	Mussel assemblages were negatively affected by severe drought during 2007–2008
Agriculture × link magnitude	The effect of agricultural land use decreases with increasing stream size
Urban × link magnitude	The effect of urban land use decreases with increasing stream size
Wetland × link magnitude	The effect of wetland coverage decreases with increasing stream size
2000–2002 drought × agriculture	The effect of severe drought increases with increasing amount of agricultural land use
2000–2002 drought × urban	The effect of severe drought increases with increasing amounts of urban land use
2000–2002 drought × wetland	The effect of severe drought increases with increasing amounts of wetland coverage
2000–2002 drought × link magnitude	The effect of severe drought decreases with increasing stream size
Reach isolation	Mussels are negatively influenced by the downstream presence of impoundments due to the elimination of potential colonists

Our primary objective was to evaluate the relative influence of site characteristics, catchment-level characteristics and drought on mussel species occupancy. Secondly, we sought to identify the factors influencing mussel species detection probability and to account for false-positive errors associated with species misidentification. We used an information-theoretic approach (Burnham & Anderson, 2002) to evaluate the relative support for hypothesised relationships between drought, site characteristics, catchment-level characteristics and mussel species occupancy and detection (Table 4). To facilitate model-fitting, we standardised all continuous predictor variables (link magnitude, per cent agricultural land use, per cent urban land use and per cent wetland coverage) with mean zero and standard deviation of one. The

drought predictors included post-2000 drought and post-2007 drought and were binary coded as '1' for any sample that was conducted during or following the onset of severe drought (2000–2006 and 2007–2010). We distinguished between the post-2000 and post-2007 droughts to evaluate the relative influence of the two distinct droughts that were separated by a period of normal flow conditions on LFRB mussel assemblages. The global model contained the following predictors: link magnitude, reach isolation, per cent agriculture, per cent urban and per cent wetland land cover, post-2000 drought and post-2007 drought. The global model also contained 2-way interactions between link magnitude and post-2000 drought, per cent agriculture, per cent urban and per cent wetland. The global detection probability model contained link magnitude

and covariates corresponding to occasion-specific sampling methods (timed search, fixed area, longitudinal transect and transverse transect) and drought. The sampling methods were binary coded as '1' if a method was used on a given sampling occasion, with fixed area searches serving as the statistical baseline. We then developed additional candidate models by systematically excluding variables, for a total of 32 candidate models.

### Model selection

We evaluated the relative plausibility of each candidate model by calculating Akaike's Information Criteria (AIC; Akaike, 1973) with the small-sample bias adjustment (AIC<sub>c</sub>; Hurvich & Tsai, 1989). Akaike's Information Criterion is an entropy-based measure used to compare candidate models, with lower AIC values indicating better predicting models (Burnham & Anderson, 2002). To count model parameters, we counted fixed effects as 1 parameter and random coefficients as 1 parameter. To facilitate comparisons among models, we calculated Akaike weights that range from zero to one with the best-approximating candidate model having the highest weight (Burnham & Anderson, 2002). The ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham & Anderson, 2002). For example, a model with an Akaike weight of 0.5 is 10 times more likely to be the best predicting model compared to a model with an Akaike weight of 0.05. We considered the most plausible models to be those with Akaike weights that were at least 10% of the best-approximating model, which is similar to Royall's general rule-of-thumb of 1/8 or 12% for evaluating strength of evidence (Royall, 1997).

We assessed the precision of parameter estimates for each model by calculating 95% Bayesian credible intervals (Congdon, 2001), which are analogous to 95% confidence intervals. To facilitate interpretation, we calculated odds ratios (OR) for each fixed-effect parameter estimate (Hosmer & Lemeshow, 2000). The OR for all continuous predictors were interpreted as a change in odds associated with a 1 SD change in the value of a predictor variable. We assessed MCMC convergence for each model in the confidence set using the diagnostics detailed by Gelman & Rubin (1992).

## Results

### Mussel collections

From 1991 to 2010, 246 individual stream reaches were sampled on at least one occasion (Fig. 1). Across all

sampling locations and occasions, 21 species were detected during both the pre-2000 and post-2000 periods. Only 20 species were detected during the post-2007 period. The single species that was undetected during the post-2007 period, *Villosa villosa* (Wright, 1898), was generally uncommon in the LFRB and tended to inhabit small, spring-fed streams and backwater sloughs and impoundments (Williams *et al.*, 2008). The most commonly collected species during the pre-2000 period were *Elliptio fumata/pullata* (64% of study locations), *Villosa vibex* (Conrad, 1834; 50%), *Villosa lienosa* (Conrad, 1834; 43%) and *Quadrula infucata* (Conrad, 1834; 42%). The most commonly collected species during the post-2000 and post-2007 periods were *Elliptio pullata/fumata* (59%), *Villosa lienosa* (40%), *Villosa vibex* (38%), *Toxolasma paulum* (Lea, 1840; 31%) and *Unio merus columbensis* (Lea, 1857; 28%). During the pre-2000 period, surveyors failed to detect any mussel species at 7% (8/119) of sample locations, whereas surveyors failed to detect any mussel species at 27% (43/162) of sample locations during the post-2000 and post-2007 drought periods.

### Multispecies occupancy models

The best-approximating variance structure for the multispecies occupancy models included random effects associated with the species-level occupancy intercept and the occupancy slope associated with stream size, and a site-level random effect, with no covariance between the random effects (Table 3). The best-approximating model of species detection probability included longitudinal transect sampling, link magnitude, timed search sampling and drought. Thus, all candidate models included these random effects in the occupancy models and these covariates in the detection probability model. The best-approximating multispecies occupancy model relating mussel species presence to site- and catchment-level characteristics contained link magnitude, per cent agricultural land use, post-2000 drought, post-2007 drought, reach isolation and three 2-way interactions: link magnitude  $\times$  post-2000 drought, link magnitude  $\times$  agriculture and agriculture  $\times$  post-2000 drought (Table 5). Based on Akaike weights, the best-approximating model was 33 $\times$  more plausible than the next best-approximating model that included urban, agriculture, link magnitude, post-2000 drought, post-2007 drought, reach isolation and five 2-way interactions: link magnitude  $\times$  post-2000 drought, urban  $\times$  link magnitude, agriculture  $\times$  link magnitude, urban  $\times$  post-2000 drought and agriculture  $\times$  post-2000 drought (Table 5). There was very little support for any of the remaining candidate models; hence, we report

**Table 5** Akaike's Information Criterion (AIC<sub>c</sub>), number of parameters (Np),  $\Delta$ AIC<sub>c</sub> and Akaike weights ( $w_i$ ) for the confidence set of models ( $i$ ) estimating mussel species occupancy ( $\Psi$ ) and detection probability ( $p$ ) in the lower Flint River Basin, Georgia

Candidate model	AIC <sub>c</sub>	Np	$\Delta$ AIC <sub>c</sub>	$w_i$
$\Psi$ (link magnitude, agriculture, post-2000 drought, post-2007 drought, isolation, link magnitude $\times$ agriculture, link magnitude $\times$ post-2000 drought, agriculture $\times$ post-2000 drought), $p$ (longitudinal transect, timed search, link magnitude, post-drought)	4297.116	15	0.000	0.971
$\Psi$ (link magnitude, agriculture, urban, post-2000 drought, post-2007 drought, isolation, link magnitude $\times$ agriculture, link magnitude $\times$ urban, link magnitude $\times$ post-2000 drought, agriculture $\times$ post-2000 drought, urban $\times$ post-2000 drought), $p$ (longitudinal transect, timed search, link magnitude, post-drought)	4304.157	18	7.040	0.029

Only models with an Akaike weights  $>0.01$  are included.

**Table 6** Parameter estimates, standard deviations (in parentheses), upper and lower 95% credibility intervals (CI) and odds ratios (OR) for the best-approximating multispecies occupancy ( $\Psi$ ) and conditional detection probability ( $p$ ) models

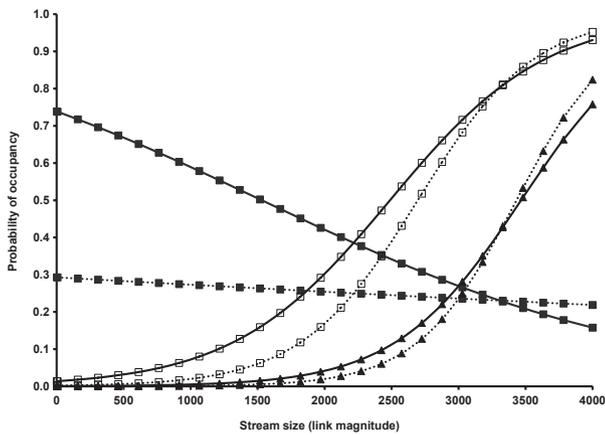
Parameter	Estimate	95% CI		OR
		Lower	Upper	
<i>Occupancy (<math>\Psi</math>)</i>				
Fixed effects				
Intercept	-2.729 (0.277)	-3.778	-1.062	
Link magnitude	-0.570 (0.596)	-1.753	0.604	0.566
Per cent agriculture	0.039 (0.201)	-0.350	0.436	1.039
Link magnitude $\times$ agriculture	0.392 (0.164)	0.075	0.721	1.480
Post-2000 drought	-1.390 (0.277)	-1.940	-0.850	0.249
Post-2000 drought $\times$ agriculture	0.203 (0.234)	-0.261	0.659	1.226
Post-2000 drought $\times$ link magnitude	0.877 (0.291)	0.300	1.447	2.403
Post-2007 drought	-0.497 (0.300)	-1.093	0.085	0.608
Reach isolation	-2.710 (0.705)	-4.144	-1.384	0.067
Random effects				
Intercept (species)	2.402 (0.423)	1.791	3.330	
Intercept (site)	1.844 (0.131)	1.576	2.105	
Link magnitude (species)	2.285 (0.445)	1.583	3.340	
<i>Detection (<math>p</math>)</i>				
Fixed effects				
Intercept	1.099 (0.214)	0.689	1.530	
Link magnitude	0.237 (0.154)	-0.044	0.559	
Longitudinal transect	1.103 (0.297)	0.569	1.733	
Timed search	-0.741 (0.239)	-1.204	-0.272	
Post-2000 and 2007 drought	0.533 (0.219)	0.099	0.959	

Models were fitted using standardised data for the continuous predictor variables; hence, parameter estimates and ORs should be interpreted for a one standard deviation change in the predictor variable.

parameter estimates for only the best-approximating model (Table 6).

Parameter estimates based on the best-approximating model indicated that mussel species presence was strongly and negatively related to the 2000 drought and to reach isolation (Table 6; Fig. 2). Odds ratios indicated that mussel species were, on average, 4.02 $\times$  less likely to be present following the 2000 drought. Odds ratios also indicated that mussel species were 15.03 $\times$  less likely to be

present in stream reaches that were isolated by an impoundment from major tributaries or the mainstem Flint River (Table 6). Parameter estimates for two interaction terms, link magnitude  $\times$  post-2000 drought and link magnitude  $\times$  agriculture, indicated that the negative relationships between mussel species occupancy and the 2000 drought and per cent agriculture decreased with increasing stream size (Table 6). The parameter estimate for the remaining interaction term, drought  $\times$  agriculture,



**Fig. 2** Predicted occupancy during pre-drought (solid lines) and post-drought (broken lines) conditions for three representative lower Flint River Basin (LFRB) mussel species: *Villosa vibex* (filled squares), *Elliptio crassidens* (open squares) and *Elliptioideus sloatianus* (filled triangles). *Villosa vibex* represents LFRB mussel species that primarily inhabit small to medium-sized tributaries. *Elliptio crassidens* represents LFRB mussel species that primarily inhabit medium- and large-sized tributaries but occasionally inhabit small tributaries. *Elliptioideus sloatianus* represents LFRB species that are generally restricted to large tributaries and almost never inhabit small tributaries.

indicated that the negative relationship between occupancy and drought decreased with increasing agricultural land use; however, the parameter estimate was imprecise (Table 6). Parameter estimates also suggested that mussel species occupancy was weakly and positively related to per cent agricultural land use and negatively related to the post-2007 drought, but the estimates were generally imprecise (Table 6). Lastly, species-level random effects indicated substantial heterogeneity remained among mussel species regarding overall occupancy (i.e. intercept) and the relationship (i.e. slope) between stream size and occupancy (Table 6).

## Discussion

Numerous factors have been implicated in recent population declines of North American freshwater mussel species. Previous studies have demonstrated relationships between mussel population declines and reach isolation (Watters, 1996; Vaughn & Taylor, 1999), land use (Poole & Downing, 2004) and drought (Golladay *et al.*, 2004; Haag & Warren, 2008). However, few studies have directly estimated the influence of these factors on mussel species occurrence, and we are unaware of any published studies that have accounted for potential biases in survey data associated with both incomplete detection and misidentification of mussel species. We found that the occurrence of freshwater mussels in the LFRB was strongly influ-

enced by drought, reach isolation and stream size. We also found that the strong negative influence of drought was less severe with increasing stream size, suggesting that management and conservation efforts should focus on recovering mussel species and populations that occur in small to mid-order LFRB streams, as well as protecting populations in higher-order tributaries because they may serve as important refugia for many mussel species.

Mussel assemblages in the LFRB appear to have experienced substantial reductions in species richness since the onset of severe drought in 2000. Various reaches of many small and mid-order LFRB streams were reported dry during the 2000–2002 drought (Golladay *et al.*, 2004; McCargo & Peterson, 2010). During extreme low-flow periods, mussel mortality can be severe due to prolonged emersion, thermal stress and dissolved oxygen extremes (Holland, 1991; Bartsch *et al.*, 2000; Golladay *et al.*, 2004). Reduced streamflows during the 2000 drought may have resulted in poor water quality and inhospitable conditions that reduced mussel survival. Haag & Warren (2008) reported that several species that were rare prior to the onset of severe drought were not detected in study reaches following severe drought. Several species in the LFRB appear to be both rare and restricted to small to mid-order tributaries, including imperilled species such as *Anodontoides radiatus* (Conrad, 1834), *Elliptio purpurella* (Lea, 1857), *Hamiota subangulata* (Lea, 1840), *Medionidus penicillatus* (Lea, 1857) and *Pleurobema pyriforme* (Lea, 1857). Rare species that occur primarily in small to mid-order LFRB tributaries may be exceptionally prone to reduced survival and possibly local extirpation (i.e. extirpation from a stream reach) in response to severe drought.

Despite being equally or perhaps more severe and prolonged, the 2007–2008 LFRB drought appears to have affected mussel assemblages to a lesser extent than the drought that occurred during 2000–2002. Although this was counter to our expectations, some possible explanations exist. Prior to 2000, the most recent severe drought in the LFRB occurred during 1954–1955 (Cook *et al.*, 1999), whereas the LFRB has experienced two severe and prolonged droughts since 1999. Hence, LFRB mussel populations appear to have experienced a long period (c. 50 years) over which they could potentially recover from the presumably negative effects of the 1954–1955 drought. Mussel populations in the LFRB have had comparatively little time to recover from the 2000 drought, as another severe drought began in 2007. Additionally, successful recruitment from local and neighbouring populations may also be impeded by the temporary loss of host fish species from drought-affected

reaches (McCargo & Peterson, 2010). Thus, we hypothesise that LFRB mussel species in drought-affected stream reaches have been slow to fully recover from the effects of the 2000–2002 drought because of drought-induced reductions in survival and recruitment.

The adverse effect of the 2000–2002 drought on LFRB mussels was much less severe in larger streams. Haag & Warren (2008) reported similar findings in that mussel abundance and assemblage composition changed little in larger streams following extreme drought. Additionally, Golladay *et al.* (2004) reported that larger stream reaches in the LFRB generally maintained adequate stream flows during the 2000 drought. Previous work in the LFRB also has determined that although stream-reach-level meso-habitat availability (i.e. total volume of run, pool, riffle and edgewater habitats) was reduced during drought conditions, reductions in habitat availability were less pronounced as stream size increased (Peterson *et al.*, 2009). Consequently, fish assemblages in higher-order stream reaches were less affected by drought conditions (i.e. fewer species were lost) compared to those inhabiting small to mid-order streams (McCargo & Peterson, 2010). Mussel assemblages in higher-order stream reaches may be similarly resilient to the direct effects of drought, as well as secondary effects such as increased water temperature and decreased water quality. The greater resiliency of large-river mussel assemblages also suggests that demographic support from populations in the mainstem Flint River and major tributaries (if present) may be critical to the persistence of some mussel species in smaller tributaries. A metapopulation structure has been postulated for freshwater mussels (Vaughn, 1997; Strayer, 2008); however, metapopulation dynamics in the context of freshwater mussels are currently poorly understood (Newton, Woolnough & Strayer, 2008).

Mussel species occurrence was negatively influenced by the presence of impoundments. These results were consistent with previous studies (Watters, 1996; Vaughn & Taylor, 1999) that demonstrated the adverse effects of impoundments on freshwater mussel assemblages. Low-head dams in small tributaries are known to prevent the movement of potential host fish species into upstream reaches (Watters, 1996). Many fish species in the LFRB have been shown to respond to reach isolation in a similar manner (McCargo & Peterson, 2010). Moreover, widespread disturbances, such as severe drought, may eliminate some mussel and host fish species from affected reaches, and natural re-colonisation through host fish dispersal may be inhibited by the presence of impoundments. This suggests that the combined effects of drought and reach isolation may cause many LFRB mussel

populations to become increasingly fragmented and potentially more vulnerable to local extinction. The removal of existing impoundments in the basin may benefit stream-dwelling organisms, including freshwater mussels (Poff & Hart, 2002). However, such activities should be carefully evaluated, as dam removal may cause increased sediment loads in downstream reaches (Sethi *et al.*, 2004). Moreover, some small impoundments have been shown to positively influence the persistence of downstream mussel populations, and removal of these structures may increase the risk local extinction for some populations (Singer & Gangloff, 2011). It is important to note that many small impoundments are not included in the NID database, which was used to identify the locations of impoundments in the LFRB for this study. Thus, the extent to which impoundments have contributed to the isolation and fragmentation of mussel populations may be more widespread in the LFRB and other river basins than is currently recognised.

The composition of mussel species assemblages in the LFRB appears to vary substantially among streams of different sizes. Although many mussel species are known to have an affinity for streams of particular sizes (Strayer, 1993), the mechanisms responsible for these affinities are not well understood. Presumably, some mussel species require particular host fish species that inhabit certain types of streams (e.g. large rivers, small headwater wetlands). In contrast, other mussel species may have more generalised host fish requirements, or they may utilise a narrow range of widely distributed host fishes. Mussel species also may differ in their ability to persist in particular environmental conditions. For example, some species may be better adapted to slow-flowing headwater tributaries that exhibit substantial variability in dissolved oxygen, temperature and stream discharge, whereas others may be better adapted to more stable habitat conditions found in higher-order stream reaches. Several LFRB mussel species appear to be largely restricted to higher-order tributaries and the mainstem Flint River, including *Elliptio crassidens* (Lamarck, 1819), *Elliptioideus sloatianus* (Lea, 1840), *Lampsilis floridensis* (Lea, 1852), *Megalonais nervosa* (Rafinesque, 1820) and *Quadrula infucata*. However, the majority of LFRB mussel species, including several imperilled species (*Anodontoides radiatus*, *Elliptio purpurella*, *Hamiota subangulata*, *Pleurobema pyriforme* and *Medionidus penicillatus*), are more likely to inhabit small to mid-order tributaries. Populations of most LFRB mussel species in small to mid-order tributaries may therefore be highly susceptible to local population declines and possibly local extinction in the event of large-scale disturbances, such as severe drought.

When compared to the long-term climate history in Georgia (1600s to present), the middle 1950s through to the 1990s encompassed an unusually wet period characterised by relatively infrequent and short-duration droughts (Cook *et al.*, 1999). In contrast, the two severe droughts that have occurred in the LFRB since 1999 appear to be more indicative of long-term climatic conditions in Georgia (Cook *et al.*, 1999). Perhaps more importantly, contemporary droughts are compounded by the effects of agricultural water withdrawals (Rugel *et al.*, 2012). Indeed, recent work in a small Chattahoochee River tributary indicated that increased levels of water use may contribute to an increased risk of population extinction for three imperilled freshwater mussel species (Peterson *et al.*, 2011). Ongoing management and conservation activities in the LFRB must therefore contend with the combined effects of severe drought and water use on freshwater mussel populations. Our study suggests that such activities should focus on strategies that (i) contribute to the recovery of mussel populations in small and mid-order tributaries and (ii) protect existing populations in higher-order tributaries that may serve as important refugia for many LFRB mussel species.

### Acknowledgments

This project was funded by a grant from the United States Fish and Wildlife Service and the Georgia Department of Natural Resources. Sandy Abbott, Paul Benton, Ben Carswell, Justin Dycus, Jason Emmel, Andrea Fritts, Ryan Harrell, Greg Moyer, Katie Owers, Will Pruitt, Brittany Trushel and Deb Weiler assisted with field collections. Earlier drafts of the manuscript were improved by suggestions from Brett Albanese, Mary Freeman, Megan Hagler, David Strayer and an anonymous referee. The use of trade, product, industry or firm names or products is for informative purposes only and does not constitute an endorsement by the US Government or the US Geological Survey. The Georgia Cooperative Fish and Wildlife Research Unit is jointly sponsored by the US Geological Survey, the US Fish and Wildlife Service, the Georgia Department of Natural Resources, the University of Georgia and the Wildlife Management Institute.

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(Manuscript accepted 29 October 2012)