# **BIODIVERSITY RESEARCH**

# Chasing a changing climate: Reproductive and dispersal traits predict how sessile species respond to global warming

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# Abstract

Aim: Studies of species' range shifts have become increasingly relevant for understanding ecology and biogeography in the face of accelerated global change. The combination of limited mobility and imperilled status places some species at a potentially greater risk of range loss, extirpation or extinction due to climate change. To assess the ability of organisms with limited movement and dispersal capabilities to track shifts associated with climate change, we evaluated reproductive and dispersal traits of freshwater mussels (Unionida), sessile invertebrates that require speciesspecific fish for larval dispersal.

Location: North American Atlantic Slope rivers.

Methods: To understand how unionid mussels may cope with and adapt to current and future warming trends, we identified mechanisms that facilitated their colonization of the northern Atlantic Slope river basins in North America after the Last Glacial Maximum. We compiled species occurrence and life history trait information for each of 55 species, and then selected life history traits for which ample data were available (larval brooding duration, host fish specificity, host infection strategy, and body size) and analysed whether the trait state for each was related to mussel distribution in Atlantic Slope rivers.

**Results**: Brooding duration (p < .01) and host fish specificity (p = .02) were significantly related to mussel species distribution. Long-term brooders were more likely than short-term brooders to colonize formerly glaciated rivers, as were host generalists compared to specialists. Body size and host infection strategy were not predictive of movement into formerly glaciated rivers (p > .10).

Main conclusions: Our results are potentially applicable to many species for which life history traits have not been well-documented, because reproductive and dispersal traits in unionid mussels typically follow phylogenetic relationships. These findings may help resource managers prioritize species according to climate change vulnerability and predict which species might become further imperilled with climate warming. Finally, we suggest that similar trait-based decision support frameworks may be applicable for other movement limited taxa.

#### KEYWORDS

adaptive management, climate change, endangered species, freshwater mussels, life history, Unionidae

# 1 | INTRODUCTION

Studies of species' range shifts have become increasingly relevant for understanding ecology and biogeography in the face of accelerated global change, and specifically a warming climate (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Schurr et al., 2012). Although many taxa are able to adapt to global thermal regime changes (Hickling, Roy, Hill, Fox, & Thomas, 2006), the rapid pace of warming is challenging for survival of even some highly mobile animals, such as birds, butterflies and fishes (Devictor, Julliard, Couvet, & Jiguet, 2008; Devictor et al., 2012; Perry, Low, Ellis, & Reynolds, 2005; Warren et al., 2001). For some taxa, the ability to move with climate is hampered by habitat fragmentation (e.g., small and large dams impede movement of freshwater mussels (Watters, 1996) and diadromous fishes (Cooney & Kwak, 2013)), or resource and habitat availability in newly thermally favourable places (e.g., butterflies in Britain; Warren et al., 2001). While studies show that flight has been advantageous for animals tracking climate change (e.g., for birds and butterflies in France), temperature trends are advancing more rapidly than the distributional shifts in these communities (Devictor et al., 2008, 2012). Many taxa are more limited in their movement and dispersal capabilities (e.g., some amphibians, plants, snails and corals); numerous dispersal-limited species are also imperilledfor instance, 41% of amphibians (IUCN, 2016) and 74% of North American freshwater snails (Johnson et al., 2013). This combination of limited mobility and imperilled status places such species at a potentially greater risk of range loss, extirpation or extinction due to climate change.

North American freshwater mussels (Unionida) have an imperilment rate >70%, due to historic overharvesting, habitat destruction and pollution, and are particularly vulnerable to present-day chronic impacts, such as water quality degradation (Cope et al., 2008; Downing, Van Meter, & Woolnough, 2010; Strayer, 2008; Strayer Diversity and Distributions

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et al., 2004; Williams, Warren, Cummings, Harris, & Neves, 1993). Further, mussels are predominantly sessile and represent one extreme among movement limited taxa. Understanding their dynamic distribution in response to climate change is especially important because molluscs are expected to experience increasingly fragmented populations (Inoue & Berg. 2017) and greater loss of suitable habitats than any other freshwater group (Markovic et al., 2014). Similar to plant species that require animal vectors to disperse their seeds, unionid mussels require a host fish for successful development and dispersal of their offspring (Bauer & Wächtler, 2001; Lefevre & Curtis, 1910). Such parasitic and mutualistic species are worthy of attention because they may be more vulnerable to extinction than species that are not symbionts (Dunn, Harris, Colwell, Koh, & Sodhi, 2009). Freshwater mussels are frequently more thermally tolerant than their host fishes, effectively rendering them more vulnerable to a warming environment than they would be without the parasitic life stage (Pandolfo, Kwak, & Cope, 2012). Host fish presence may influence freshwater mussel distributional patterns more than other factors (Pandolfo et al., 2012; Schwalb, Morris, Mandrak, & Cottenie, 2013), and fish movements will no doubt be influenced by future climate scenarios (Comte, Buisson, Daufresne, & Grenouillet, 2013; Lynch et al., 2016; Markovic et al., 2014; Myers et al., 2017). Given the adverse anthropogenic impacts already affecting mussels, climate-driven alterations to aquatic systems, such as modified fish assemblages, drought and altered thermal dynamics, could lead to further imperilment.

Because freshwater mussels must rely on host fishes for both development and transport, we evaluated reproductive and dispersal traits that may allow mussels to track climate change and avoid further endangerment. Using current species distributions, we examined life history traits that facilitated mussel colonization of previously glaciated river basins on the North American Atlantic Slope. The river basins on the North American Atlantic Slope are interesting habitats from a freshwater fauna dispersal perspective, because each drainage



**FIGURE 1** The Last Glacial Maximum covered much of the present-day northern Atlantic mussel faunal province, where mussel diversity is lower compared to the southern Atlantic province (number of species, percentage endemic). Mussel faunal provinces depicted as defined by Haag (2010) (World Basemap and glacial boundary features available via ArcGIS<sup>®</sup> Online; mussel province boundaries created based on the USGS Watershed Boundary Dataset (accessed 19 February 2017)

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empties into the Atlantic Ocean and is effectively isolated from other river basins. Indeed, the theory of island biogeography (MacArthur & Wilson, 1967) was invoked by Sepkoski and Rex (1974) in their study of freshwater mussel distribution in Atlantic Slope rivers, citing steppingstone dispersal among the factors explaining the biogeographic patterns they observed among these disconnected drainages. Although this isolation is common to the entire Atlantic Slope from southern Georgia, USA, to New Brunswick, Canada, mussel species richness differs dramatically in these coastal rivers. The distinction between the species-rich southern Atlantic and the relatively depauperate northern Atlantic drainages has been highlighted in assessments of mussel biogeography, including the most recent evaluation, where Haag (2010) identified a separation of southern and northern Atlantic faunal provinces at the James River Basin, which drains into Chesapeake Bay (Figure 1). The Northern Atlantic province has relatively low mussel richness (20 species) and only one endemic species, whereas the Southern Atlantic faunal province has greater diversity (46 species) and the highest percentage of endemic mussel species (59%) among all North American faunal provinces (Haag, 2010). A likely explanation for the lower species diversity in the Northern Atlantic region is the geologically recent extirpation due to glaciation of the region and subsequent recolonization.

During the Last Glacial Maximum, the Laurentide Ice Sheet covered much of north-central and north-eastern North America, including complete coverage of 10 of the 26 Atlantic Slope river basins that were considered by Haag (2010) (Figure 1, Table 1; coverage determined using ARCGIS® version 10.4.1, Esri, Inc., Redlands, CA, USA). Most ice sheets remained at their maximum extents until about 20,000 years ago, after which deglaciation of the Northern Hemisphere ensued (Clark et al., 2009). Because massive glaciers affected regional climatic conditions well beyond their edges, freshwater mussels already adapted to cooler regimes may have followed climate shifts northwards to ensure their survival. The post-glacial re-expansion of unionid mussels in the dendritically connected Mississippi river basin has been explored (Graf, 1997), and localized colonization-extinction within a drainage on a decadal timescale have been investigated (Vaughn, 2012), but no one has evaluated the post-glacial colonization of unionids in isolated, but geographically proximate, basins like those on the Atlantic Slope of North America. We assess biological traits that influenced mussel distribution in this region, provide insights into how such mechanisms relate to the present-day rapid climate challenge impacts to mussels and offer a climate concern management framework that natural resource professionals may find adaptable to other movement limited taxa.

# 2 | METHODS

# 2.1 | Species occurrence and life history

We used Atlantic region freshwater mussel species occurrence data (compiled and provided by W. R. Haag, personal communication) to evaluate potential differences in life history patterns between **TABLE 1** Twenty-six major rivers comprise the North American Atlantic Slope Basin; 14 rivers occur in the North Atlantic mussel faunal province and 12 occur in the South Atlantic faunal province (Haag, 2010). Rivers are listed in order from north to south; shaded entries were covered in ice during the Last Glacial Maximum (ARCGIS<sup>®</sup> version 10.4.1, Esri, Inc., Redlands, CA, USA)

North Atlantic Mussel Province	
Petitcodiac River (PET)	
Charles River (CHA)	
St. John River (STJ)	
St. Croix River (STC)	
Penobscot River (PEN)	
Kennebec River (KEN)	
Androscoggin River (AND)	
Merrimac River (MER)	
Connecticut River (CON)	
Hudson River (HUD)	
Delaware River (DEL)	
Susquehanna River (SUS)	
Potomac River (POT)	
Rappahannock River (RAP)	
South Atlantic Mussel Province	
James River (JAM)	
Chowan River (CHO)	
Roanoke River (ROA)	
Tar River (TAR)	
Neuse River (NEU)	
Cape Fear River (CF)	
Waccamaw River (WAC)	
Pee Dee River (PD)	
Santee River (SAN)	
Savannah River (SAV)	
Ogeechee River (OGE)	
Altamaha River (ALT)	

mussel assemblages in unglaciated river basins and those that were previously glaciated. Two of the 57 species that occur in the Atlantic region (*Lasmigona costata* and *Anodontoides ferrusacianus*) were removed from the analyses because they are of Mississippian region origin and would not have colonized previously glaciated rivers via an Atlantic Slope connection. Of the 55 species considered, 40 occur exclusively in unglaciated river basins, 14 occur in both glaciated and unglaciated river basins, and one species occurs exclusively in glaciated river basins (Table 2).

We compiled life history data from several sources, including peer-reviewed publications (Barnhart, Haag, & Roston, 2008; Bertram, Placyk, Williams, & Williams, 2017; Graf & O'Foighil, 2000; Haag & Rypel, 2011; Haag & Warren, 1998; Hanlon & Levine, 2004; Heard & Guckert, 1970; Perkins, Johnson, & Gangloff, 2017; Williams et al., 2017; Zanatta & Murphy, 2006), scholarly volumes (Bauer & Wächtler, 2001; Strayer, 2008), regional identification keys

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nd distribution. Species highlighte	hted in yellow are found only in th	but no occurrence in glaciated rive	'y.com]
ıeir taxonomy, life history traits ar	antic river basins. Species highligh	and Southern Atlantic provinces,	an be viewed at wileyonlinelibrar
e Atlantic Slope faunal region, th	r in glaciated and unglaciated Atl	ed in green span both Northern	ince (Haag, 2010) [Colour table c
ssel species ( $n = 55$ ) found in the	es highlighted in light blue occur	d river basins. Species highlighte	e Southern Atlantic faunal provi
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TABLE 2 Freshwater mu glaciated river basins. Speci province, but not in glaciate in color are found only in th	ussel species (n = 55) foum ies highlighted in light blue id river basins. Species hig ie Southern Atlantic faunal	d in the Atlantic Slo e occur in glaciated ghlighted in green sı Il province (Haag, 20	ipe faunal region, thi and unglaciated Atla pan both Northern a 310) [Colour table <i>c</i> a	eir taxonomy, life histor antic river basins. Specie ind Southern Atlantic pr an be viewed at wileyon	y traits and distributic is highlighted in yellov ovinces, but no occur linelibrary.com]	on. Species highl w are found only rence in glaciate	ighted in dark blue are found only in / in the Northern Atlantic faunal ed river basins. Entries not highlighted
Species <sup>a</sup>	Common name	Tribe	Host specificity <sup>b</sup>	Brooding duration <sup>b</sup>	Infection strategy <sup>b</sup>	Body size <sup>c</sup>	River basins
Pyganodon fragilis	Newfoundland Floater	Anodontini	Generalist	Long	Non		STJ, CHA, PET
Alasmidonta heterodon	Dwarf Wedgemussel	Anodontini	Generalist	Long	Non	Small	NEU, TAR, RAP, POT, DEL, CON, MER
Alasmidonta marginata	Elktoe	Anodontini	Generalist	Long	Non	Large	sus, HUD
Alasmidonta undulata	Triangle Floater	Anodontini	Generalist	Long	Non	Small	All except ALT, SAN, WAC
Alasmidonta varicosa	Brook Floater	Anodontini	Generalist	Long	Non	Small	SAV, SAN, PD, CF, NEU, ROA, JAM, POT, SUS, DEL, HUD, CON, MER, KEN, PEN, STC, STJ, CHA, PET
Elliptio complanata	Eastern Elliptio	Pleurobemini	Specialist	Short	Non	Large	AII
Lampsilis cariosa	Yellow Lampmussel	Lampsilini	Specialist	Long	Attractor	Large	OGE, SAV, PD, WAC, CF, NEU, TAR, CHO, RAP, POT, SUS, DEL, HUD, CON, MER, KEN, PEN
Lampsilis radiata	Eastern Lampmussel	Lampsilini	Specialist	Long	Attractor	Large	PD, WAC, CF, NEU, TAR, POT, SUS, DEL, HUD, CON, MER, AND, KEN, PEN, STC, STJ, CHA, PET
Lasmigona subviridis	Green Floater	Anodontini	Generalist	Long	Non	Small	SAV, CF, NEU, TAR, ROA, JAM, RAP, POT, SUS, HUD
Leptodea ochracea	Tidewater Mucket	Lampsilini	Specialist	Long	Non	Large	SAV, PD, WAC, TAR, ROA, CHO, JAM, RAP, POT, DEL, HUD, CON, AND, KEN, PEN
Ligumia nasuta	Eastern Pondmussel	Lampsilini	Specialist	Long	Attractor	Large	SAV, PD, CF, TAR, CHO, JAM, POT, SUS, DEL, HUD, MER
Margaritifera margaritifera	Freshwater Pearlmussel	N/A	Specialist	Unknown	Non	Large	DEL, HUD, CON, MER, AND, KEN, PEN, STC, STJ, CHA, PET
Pyganodon cataracta	Eastern Floater	Anodontini	Generalist	Long	Non	Large	All except OGE, WAC, RAP
Strophitus undulatus	Creeper	Anodontini	Generalist	Long	Attractor	Large	All except ALT, OGE, WAC
Utterbackiana (Anodonta) implicata	Alewife Floater	Anodontini	Generalist	Long	Non	Large	PD, ROA, CHO, POT, DEL, HUD, CON, MER, AND, KEN, PEN, STC, STJ
Elliptio fisheriana	Northern Lance	Pleurobemini	Specialist	Short	Non		SUS
Lasmigona compressa	<b>Creek Heelsplitter</b>	Anodontini	Generalist	Long	Non		SUS
Elliptio lanceolata	Yellow Lance	Pleurobemini	Specialist	Short	Unknown		NEU, TAR, CHO, JAM, RAP, POT
Fusconaia masoni	Atlantic Pigtoe	Pleurobemini	Specialist	Short	Attractor	Small	OGE, SAV, SAN, PD, CF, NEU, TAR, ROA, CHO, JAM

(Continues)

Species <sup>a</sup>	Common name	Tribe	Host specificity <sup>b</sup>	Brooding duration <sup>b</sup>	Infection strategy <sup>b</sup>	Body size <sup>c</sup>	River basins	
Alasmidonta arcula	Altamaha Arcmussel	Anodontini	Generalist	Long	Non		ALT, OGE	
Alasmidonta robusta	Carolina Elktoe	Anodontini	Generalist	Long	Non	Small	SAN	
Elliptio angustata	Carolina Lance	Pleurobemini	Specialist	Short	Non		SAN, PD, WAC, CF, ROA, CHO	
Elliptio arctata	Delicate Spike	Pleurobemini	Specialist	Short	Non		ALT, OGE, SAV, SAN, PD, WAC, CF	
Elliptio cistellaeformis	Box Spike	Pleurobemini	Specialist	Short	Non		SAN, PD, CF, NEU, TAR	
Elliptio congarea	Carolina Elephantear	Pleurobemini	Specialist	Short	Non		OGE, SAV, PD, CF, NEU, TAR	
Elliptio dariensis	Georgia Elephantear	Pleurobemini	Specialist	Short	Non		ALT	
Elliptio errans (syn. icterina)	Oval Elliptio	Pleurobemini	Specialist	Short	Non		ALT, SAV	
Elliptio folliculata	Pod Lance	Pleurobemini	Specialist	Short	Non		OGE, SAV, SAN, PD, WAC, CF	
Elliptio hepatica (syn. icterina)	Brown Elliptio	Pleurobemini	Specialist	Short	Non		SAV	
Elliptio hopetonensis	Altamaha Slabshell	Pleurobemini	Specialist	Short	Non		ALT, OGE	
Elliptio icterina	Variable Spike	Pleurobemini	Specialist	Short	Non		All South Atlantic province rivers (11)	
Elliptio judithae (syn. roanokensis)	Plicate Spike	Pleurobemini	Specialist	Short	Non	Large	NEU	
Elliptio lugubris (syn. icterina)	Sad Elliptio	Pleurobemini	Specialist	Short	Non		ALT, OGE, SAV, SAN	
Elliptio marsupiobesa	Cape Fear Spike	Pleurobemini	Specialist	Short	Non	Large	PD, CF, NEU	
Elliptio producta	Atlantic Spike	Pleurobemini	Specialist	Short	Non	Large	OGE, SAV, SAN, PD, WAC, CF	
Elliptio raveneli (syn. icterina)	Carolina Spike	Pleurobemini	Specialist	Short	Non		PD, WAC, CF, NEU, TAR, CHO	
Elliptio roanokensis	Roanoke Slabshell	Pleurobemini	Specialist	Unknown	Non	Large	SAV, PD, CF, NEU, TAR, ROA, CHO	
Elliptio shepardiana	Altamaha Lance	Pleurobemini	Specialist	Short	Non		ALT	
Elliptio spinosa	Altamaha Spinymussel	Pleurobemini	Specialist	Short	Non		ALT	
					Non			
Elliptio waccamawensis (syn. congeraea)	Waccamaw Spike	Pleurobemini	Specialist	Short	Non		PD, WAC	
Lampsilis dolabraeformis	Altamaha Pocketbook	Lampsilini	Specialist	Long	Attractor		ALT	
Lampsilis fullerkati (syn. radiata)	Waccamaw Fatmucket	Lampsilini	Specialist	Long	Attractor	Small	WAC	
Lampsilis splendida	Rayed Pink Fatmucket	Lampsilini	Specialist	Long	Attractor	Large	ALT, OGE, SAV, PD, WAC, CF	
Lasmigona decorata	Carolina Heelsplitter	Anodontini	Generalist	Long	Non	Large	SAV, SAN, PD	
Parvaspina (Pleurobema) collina	James Spinymussel	Pleurobemini	Specialist	Short	Attractor	Large	ROA, JAM	
							(Continues)	

TABLE 2 (Continued)

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Species <sup>a</sup>	Common name	Tribe	Host specificity <sup>b</sup>	Brooding duration <sup>b</sup>	Infection strategy <sup>b</sup>	Body size <sup>c</sup>	River basins
Parvaspina (Elliptio) steinstansana	Tar River Spinymussel	Pleurobemini	Specialist	Short	Attractor	Small	TAR, ROA, CHO
Pyganodon gibbosa	Inflated Floater	Anodontini	Generalist	Long	Non		ALT
Toxolasma pullus	Savannah Lilliput	Lampsilini	Specialist	Long	Attractor		ALT, OGE, SAV, PD, WAC, CF, NEU, ROA
Uniomerus carolinianus	Eastern Pondhorn	Pleurobemini	Specialist	Short	Non	Large	ALT, OGE, SAV, SAN, PD, WAC, CF, TAR
Utterbackia imbecillis	Paper Pondshell	Anodontini	Generalist	Long	Non	Large	ALT, OGE, SAV, SAN, PD, CF, NEU, TAR, ROA, CHO
Utterbackiana (Anodonta) couperiana	Barrel Floater	Anodontini	Generalist	Long	Non	Large	ALT, SAV, CF
Villosa constricta	Notched Rainbow	Lampsilini	Specialist	Long	Attractor	Small	SAN, PD, CF, NEU, TAR, CHO, JAM
Villosa delumbis	Eastern Creekshell	Lampsilini	Specialist	Long	Attractor	Small	ALT, OGE, SAV, SAN, PD, WAC, CF
Villosa vaughaniana	Carolina Creekshell	Lampsilini	Specialist	Long	Attractor	Small	SAN, PD, CF, ROA, CHO
Villosa vibex	Southern Rainbow	Lampsilini	Specialist	Long	Attractor	Small	ALT, OGE, SAV, PD, CF, ROA, CHO
<sup>a</sup> Newly recognized genera arr that revisions within <i>Elliptio</i> a <sup>b</sup> Traits that were known in tl specificity).	e used, with previous gener re provisional. All species a ne literature for a species	a listed in parenthese re presented with pre are marked in bold;	es; newly assigned sy evious and revised na plain text indicates a	nonymy ("syn.") for speci ames to facilitate referen a trait assumption based	es is listed in parenthes ce to earlier literature. on genus (for host inf	ies (Williams et al ection strategy a	., 2017). Williams et al. (2017) emphasize ind brooding duration) or tribe (for host

specificity). <sup>c</sup>Categorized as small (<75 mm) or large (≥75 mm) based on data from the literature; however, we recognize such categorization is somewhat arbitrary (e.g., *Parvaspina collina* length was on the cusp at 75.2 mm; disagreement between Lampsilis radiata and L. fullerkati, now in synonymy with L. radiata). **EY** 

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(Bogan, 2017; Bogan & Alderman, 2008), endangered species recovery plans (US Fish & Wildlife Service, 1990) and other publicly available outlets (NatureServe, 2018; NCWRC, 2018; Watters & Cummings, 2011). We gathered available data on several parameters related to mussel reproduction and dispersal, including the following: age at maturity, life span, body size (as maximum length), primary host fish group, host infection strategy, host specificity, fecundity, larval brooding duration and larval viability.

Despite the apparent wealth of resources, many details about the basic life history of most freshwater mussels remain unknown. For example, some sources reported on age at maturity and fecundity, but no specific information was available for the Atlantic Slope species of interest. Based on abundance and completeness of data, we selected four candidate life history traits to evaluate as potential mechanisms allowing mussels to track a warming climate: host infection strategy, host specificity, brooding duration and body size. Trait data were not available for every species, but several traits appear well correlated with phylogeny (Barnhart et al., 2008), and this relationship facilitated formation of reasonable assumptions explained below.

For host infection strategy, mussels can be categorized generally as host attractors or non-attractors. Attractors entice hosts with elaborate fishing lures composed of extra mantle tissue or external sacs (conglutinates) that contain larvae and are disguised as prey, such as an aquatic insect, fly larva or minnow. As the host fish is tricked into biting the prey mimic, larvae are expelled from the sacs or mussel's marsupium hidden between her mantle flaps and attach to the fish's gills or fins (Barnhart et al., 2008). Non-attractors freely broadcast their larvae directly into the water and contact fishes in the water column or on the stream bed. Patterns of host infection strategies are grouped based on taxonomic subfamilies and tribes, and specific strategies are known for many species and genera (Barnhart et al., 2008). The strategy of 17 species considered here were identified (Barnhart et al., 2008; Bauer & Wächtler, 2001; Haag, 2012; Perkins et al., 2017; Zanatta & Murphy, 2006). For those species whose host infection strategy was not available in the literature, we assigned a strategy based on the known trait of congeners (n = 37, 20 of which are Elliptio).

Host fish specificity is generally discussed as a dichotomous trait: mussels are either generalists, able to metamorphose on several families of fishes, or specialists, targeting a select few species or a particular group (Barnhart et al., 2008). Haag and Warren (1998) reported that host specificity patterns were apparent in subfamilies and listed many genera (including 10 of 16 genera in this study) for which the host generalist or specialist trait state has been confirmed (Table 2). In addition, Barnhart et al. (2008) described *Margaritifera margaritifera* and *Fusconaia* as host specialists, as did Bertram et al. (2017) for *Fusconaia* spp., and Perkins et al. (2017) noted that *Parvaspina* spp. specifically target cyprinid fishes. For the two species in our dataset lacking a genus-level designation from the literature (*Leptodea ochracea* and *Uniomerus carolinianus*), we assigned host specificity according to taxonomic tribe.

Freshwater mussels have two strategies for brooding their larvae. Short-term brooders typically breed in spring, hold their eggs until the larvae develop and then release them shortly thereafter. Long-term brooders breed in late summer or autumn, and females hold their brood through the winter months before releasing them the following spring (Graf & O'Foighil, 2000). Brooding strategy was available for 30 species, and patterns within genera and tribes were apparent (Bogan, 2017; Bogan & Alderman, 2008; Graf & O'Foighil, 2000; Hanlon & Levine, 2004; Heard & Guckert, 1970; NatureServe, 2018; NCWRC, 2018). For species whose brooding duration was unknown, we determined that an assignment of consistency with congeners was appropriate, based on previous literature (Barnhart et al., 2008; Graf & O'Foighil, 2000) and agreement among species within common genera. Two species in our dataset (Roanoke Slabshell (Elliptio roanokensis) and Freshwater Pearlmussel (Margaritifera margaritifera)) either had no information known for congeners or had information potentially contrary to the consistency assumption. The Freshwater Pearlmussel has been reported as a short-term brooder (Barnhart et al., 2008), but also as a facultative long-term brooder (Graf & O'Foighil, 2000), and two sources list the breeding period of the Roanoke Slabshell as unknown (Bogan, 2017; NCWRC 2018). No assumption was made for these species, and they were removed from the brooding duration analysis.

Maximum length data were available for 34 of the 55 species analysed (Bogan, 2017; Bogan & Alderman, 2008; Haag & Rypel, 2011). Because length data varied widely within genera, no assumptions were made regarding length and only 34 species were used in this comparison.

#### 2.2 | Statistical analysis

Each life history parameter was categorized into two complementary trait states, similar to categories used in previous mussel trait research (Graf, 1997; Vaughn, 2012): host infection strategy = attractor or non-attractor; host specificity = specialist or generalist; brooding duration = short-term or long-term; and body size = small (maximum length <75 mm) or large (maximum length  $\geq$ 75 mm). Each trait was then tallied for mussel species in glaciated and unglaciated river basins and analysed to determine whether a relationship existed between the trait state and its distribution. Significant relationships were determined using a chi-square test statistic (Microsoft Office Excel 2013), with statistical significance ( $\alpha$ ) determined by a probability (p) <.05.

### 3 | RESULTS

Several trends and statistically significant relationships were detected in comparisons between mussel distribution and biological species traits. Host specificity and brooding duration each had a significant relationship with mussel distribution in glaciated and unglaciated rivers ( $\chi^2(1) = 5.37$ , p = .02 for host specificity and  $\chi^2(1) = 7.74$ ,



**FIGURE 2** The distribution of host fish generalists to specialists in glaciated river systems was significantly different from those in unglaciated river systems. The greater percentage compared to source (i.e., unglaciated) river basins indicates host generalists were more successful in colonizing previously glaciated river basins

p < .01 for brooding duration). The proportion of host generalists was slightly larger in previously glaciated rivers than host specialists. Generalists comprised 60% of the fauna (n = 9) in glaciated rivers, compared to 40% specialists (n = 6). Fauna in unglaciated rivers showed trait dominance in the opposite direction, with 28% being generalists (n = 15) and 72% specialists (n = 39) (Figure 2). Long-term brooders were more prevalent in glaciated rivers than short-term brooders. For mussels in glaciated rivers, 93% of the fauna were long-term brooders (n = 13 long term and 1 short term). This trait was evenly distributed in unglaciated rivers, where long-term brooders for the fauna (n = 27 long-term and 25 short-term) (Figure 3).

Host infection strategy was unrelated to mussel distribution in Atlantic Slope river basins (p > .10). Both glaciated and unglaciated rivers were dominated by non-attractors (73% in glaciated and 72% in unglaciated basins). Glaciated rivers contained four host attractors and 11 non-attractors, and unglaciated rivers had 15 host attractors and 38 non-attractors. Body size was also unrelated to species distribution (p > .10). Both glaciated and unglaciated river basins were dominated by species categorized as large (71% in glaciated and 62% in unglaciated river basins). Glaciated rivers had four small and 10 large species, and unglaciated rivers had 13 small and 21 large species.

# 4 | DISCUSSION

Surviving current trends in climate change may depend on the ability of freshwater mussels to emigrate northward once again. Emigration through the oceanic barrier up the Atlantic Coast may be increasingly important now, compared to post-glacial colonization, because the prevalence of dams and resulting reservoirs will likely impede an alternative option of upstream migration towards cooler headwaters without human management intervention (Strayer et al., 2004; Watters, 1996). Moreover, river basins in the South Atlantic province are predicted to lose more mussel species due to host fish loss and habitat reduction through climate change, especially among



**FIGURE 3** The distribution of long-term to short-term brooders in glaciated river systems was significantly different from those in unglaciated river systems. The greater percentage occurrence of long-term brooders, compared to source (i.e., unglaciated) river basins, indicates they were more successful in colonizing previously glaciated river basins

host specialists (Spooner, Xenopolous, Schneider, & Woolnough, 2011). Based on the results of our study, host specificity and brooding duration traits of freshwater mussels may have influenced the success of their post-glacial northward emigration along the Atlantic Slope; otherwise, assemblages in previously glaciated rivers would be expected to have the same trait state distributions as those of the source populations in unglaciated river basins. In fact, we observed significantly different distributions between the glaciated and unglaciated river basins for both host specificity and brooding duration. Previously, Vaughn (2012) found that host specificity was an important trait influencing mussel colonization of new habitats on a local scale. The trend of greater success with increased host generalism is supported across taxonomic scales among mutualist/ parasitic species (e.g., mite/bird and insect/host plant relationships; Dunn et al., 2009).

The proportion of host generalists in glaciated rivers (60%) is notably different from the source mussel assemblages in unglaciated rivers (28%; Figure 2). Characteristics of the host fishes are another important consideration because mussels using hosts with short movement distances (e.g., darters (Percidae)) are more likely to be critically imperilled (Schwalb, Cottenie, Poos, & Ackerman, 2011). Likewise, the thermal tolerances of host fishes may influence mussel persistence and dispersal (Pandolfo et al., 2012). The disparity in the distribution of host specificity along the Atlantic Slope is especially remarkable when the host characteristics of the glacially distributed specialists are considered. Three specialist species (Lampsilis cariosa, Leptodea ochracea and Margaritifera margaritifera) use anadromous host fishes, including salmonids (Salmonidae), alewife, herring (both Clupeidae) and silversides (Atherinidae) (Barnhart et al., 2008; Bogan, 2002; Bogan & Alderman, 2008; Watters & Cummings, 2011). Anadromous hosts migrate between rivers and the ocean for their own spawning and offer a potential advantage for dispersal into new river systems along the disconnected Atlantic Slope. The remaining glacially distributed host specialists (Elliptio complanata, Lampsilis radiata and Ligumia nasuta) use fishes that inhabit brackish waters **ILEY** Diversity and Distributions

or have extensive native and introduced ranges (i.e., *Perca flavescens, Fundulus diaphanus* and sunfishes (Centrarchidae); Bogan, 2017; Barnhart et al., 2008; Bogan & Alderman, 2008; Watters & Cummings, 2011), which also would provide an advantage for mussel movement.

The proportion of long-term brooders in glaciated rivers (93%) is substantially higher than the source mussel assemblages in unglaciated rivers (52%; Figure 3). Long-term brooders hold larvae through the winter and release them the following spring when water temperature, host fish availability and food resources become optimal. Conversely, short-term brooders have a narrow window of time to accomplish sperm acquisition, larval development and release, host fish infection, metamorphosis, and juvenile drop-off and settling (Graf & O'Foighil, 2000). All of these processes typically occur in a short time frame between spring and fall, leaving little time for juvenile growth before winter. Such a strategy is likely less advantageous for colonizing cooler habitats. Long-term brooding species potentially capitalized on resources more effectively than short-term brooders during the brief summers and cool meltwater conditions of glacial retreat by releasing their larvae at the onset of warming. Indeed, Graf (1997) reported the same pattern of long-term brooder dominance in previously glaciated rivers of the Mississippian region and cited cold meltwater conditions as a plausible factor giving long-term brooders an advantage. Brooding duration is also an important trait governing local population dynamics, but for extinction rather than colonization (Vaughn, 2012).

Host specificity and brooding trait states frequently co-occurred; long-term brooders tended to be host generalists, while short-term brooding was associated with host specialists (Table 2). Because life history data are sparse, such a correlation, along with reasonable phylogenetic assumptions, may prove helpful in future assessments of mussel biogeographic dynamics. Malacologists should be aware of updates as new data become available and phylogenies are refined through more frequent genetic studies. For example, the most recent update to unionid taxonomy reassigned four of our species to different genera and placed seven in synonymy with others (Williams et al., 2017; Table 2). Genus reassignments and accompanying references provided by Williams et al. (2017) were helpful in confirming trait assignments. We also had to consider the potential impact of species that were placed in synonymy. Because they did not affect the findings of our study (p = .02 for brooding duration and p = .05for host specificity when accounting for synonymy) and Williams et al. (2017) emphasized that the changes to Elliptio (six of the seven synonymous assignments here) were provisional and hypothesized, we retained species as listed by Haag (2010). However, such updates could be important in future studies considering phylogenetic traits as variables.

Although we did not detect a link between host infection strategy or body size and mussel distribution in this study, these and other traits may be worthy of consideration in future studies. For example, more data or different categories of body size may be insightful. Vaughn (2012) also reported that size did not predict mussel colonization (or extinction); however, she did find that host infection strategy was a dominant factor explaining colonization in that local-scale analysis. Several of the other traits considered for analysis here were excluded due to the paucity of data available. Our study and Vaughn's (2012) further support the need for more basic research on freshwater mussel life history traits and phylogeny to fully understand their biogeographic evolution and to guide decisions in conservation and management applications, such as population augmentation and translocation (Barnhart et al., 2008; Spooner & Vaughn, 2008).

Incorporating evolutionary ecology is prudent for a more holistically informed approach to conservation. Resource managers can use known traits of species and reasonable assumptions of traits that follow phylogeny to aid conservation decisions, especially in the absence of species-specific information. Reproductive and dispersal traits may then be combined with information typically used in conservation decision-making, such as species distribution patterns or ecological requirements, to categorize mussels on a scale of most to least concern for climate change impacts. For example, host specialists that occur in few river basins may be of greatest climate concern, while host generalists that occur in many river basins may be considered a lower climate-impact priority (Figure 4). Species that have many hosts coupled with a narrow range (e.g., Alasmidonta heterodon) might be categorized as moderate climate concern, and mussels with few hosts and an expansive range (e.g., Lampsilis radiata) may vary from moderate to some climate concern, depending on the range of their hosts (Figure 4). Similar climate concern and conservation priority frameworks may also apply to other movement limited or symbiotic taxa (e.g., plant range/abiotic constraint and seed dispersal syndrome (Riibak, Ronk, Kattge, & Pärtel, 2017), gastropod distribution and relevant life history traits (Johnson et al., 2013)).



**FIGURE 4** Proposed climate concern framework for freshwater mussels based on life history traits, such as host specificity (shown as number of host fishes), and ecological or population data (e.g., current mussel species distribution, represented here as number of river basins occupied)

The climate concern framework may also prove useful to guide conservation of more mobile taxa. Warren et al. (2001) highlighted the differing responses of butterflies that were habitat generalists or specialists when faced with climate change and habitat challenges simultaneously; generalists fared better in conditions with limited habitat and changing climate. Perry et al. (2005) and Lynch et al. (2016) have already elucidated some life history traits of fishes that were important predictors of climate-related range shifts that could be incorporated into such a framework (i.e., maximum length, age and length at maturity, and thermal preference). While the management and conservation of freshwater mussels (and other taxa) must be considered in the context of conservation status, habitat affinity and conditions (e.g., fragmentation (Watters, 1996; Strayer, 2008)), and climate-related characteristics like thermal ecology and thermal compatibility with their hosts (Archambault, Cope, & Kwak, 2013, 2014a,b; Ganser, Newton, & Haro, 2015; Pandolfo et al., 2010, 2012; Spooner & Vaughn, 2008), this climate concern framework recognizes the importance of life history traits as response mechanisms, and may help to incorporate the degree of climate concern and conservation priority into assessments for species in need of conservation and management actions. A better understanding of how life history traits and species interactions influence climate vulnerability may also aid conservation and management agencies in wise allocation of limited resources. We encourage natural resource professionals who study other climate vulnerable taxa to consider adapting and incorporating our decision support framework in prioritizing action for species in conservation need.

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# DATA ACCESSIBILITY

Data used in analyses are available from the corresponding author upon request.

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# BIOSKETCHES

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