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Title: Gene flow simulations demonstrate resistance of long-lived species to genetic erosion of habitat fragmentation

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Abstract

Habitat fragmentation restricts the movement of individuals across a landscape. In terrestrial and aquatic systems, barriers to movement can modify population and community dynamics at local or regional scales. This study contrasted life history traits related to lifespan with habitat fragmentation to determine impacts on species population genetic structure in the Neuse River Basin, USA. For this, we simulated gene flow among evenly-spaced populations in a river network and tracked individual and population genetics for 200 years. The modeled scenarios represent a full cross between five life history strategies and four riverscapes representing varying degrees of fragmentation. The five life history strategies include species (based on freshwater mussels) with average lifespans ranging from 10-50 years and age at maturity from 2-6 years. The movement landscapes included a (1) panmictic, (2) stepping-stone landscape allowing movement to only neighboring populations during each dispersal event, (3) partially-fragmented landscape divided by dams currently in the network, and (4) fully-fragmented landscape. Results suggest species with shorter lifespans have higher population genetic structure in fragmented landscapes than species with longer lifespans. Furthermore, species with shorter lifespans in highly fragmented landscapes may be harboring genetic degradation or decline as allele fixation and loss. Although anthropogenic fragmentation of many river systems is only 100-200 years old, the simulation indicates that species can respond genetically in that period of time. Additionally, the time frame of the simulation suggests that genetic impacts of habitat fragmentation in some species present in the Neuse River Basin may not yet be manifesting and restoration activities could be successful.

1 Introduction

Habitat fragmentation restricts the movement of individuals across a landscape (Fahrig 2003). In a terrestrial system, roads are typical barriers capable of restricting the movement of animals between once-connected populations (Epps et al. 2005). In aquatic systems, dams and other types of barriers (Fuller et al. 2015) limit movement in both the up- and downstream directions (Goodwin et al. 2014). In both terrestrial and aquatic systems, barriers to organism movement can modify population and community dynamics—demographic change of a species and community assembly—at local or regional scales (Campbell Grant et al. 2007).

Movement of individuals is a major life history trait involved in several life history strategies (e.g., life-stage resource partitioning or spawning migration movements (Villegas-Amtmann et al. 2013)) that are directly affected by habitat fragmentation. Some migratory species (e.g., salmon) have life history strategies that require movement to allow individuals at different life stages to be separated in space so as to minimize intraspecific competition or provide distinct life stage-specific resources in different habitats (Rieman and Dunham 2000). Additionally, migration life history stages are sometimes used to track available resources across landscapes and seasons (Winkler et al. 2014). For non-migratory species, rare movements outside of a typical home range, or from natal grounds, is necessary for maintaining metapopulation dynamics (Dunham and Rieman 1999).

Species movement directly influences population genetics through disruption of the balance between gene flow and genetic drift (Hutchison and Templeton 1999). For example, by splitting a population in two and restricting movement (gene flow) between them, the effective population size for each new subpopulation is reduced. Smaller effective population sizes increase the rate of genetic drift in each subpopulation (Lloyd et al. 2013). Then, the increased

rates of genetic drift in each subpopulation will lead to *population genetic structure* — a divergence of subpopulations genetically — in the landscape. Genetic divergence may be observed in varying rates of heterozygosity or allelic richness decline.

In addition to movement, there are other life history traits, particularly lifespan, that affect population genetics. For long-lived species that reproduce annually until death, genetic diversity from past generations is maintained in a population because older individuals continue to supplement the population gene pool (Mock et al. 2013). In contrast, short-lived species are unable to supplement genetic diversity for the population over long time periods because there is decreased generational overlap to pass rare alleles on to new generations (Lloyd et al. 2013). Instead, populations of short-lived species will lose alleles faster and the effects of genetic drift will manifest more quickly. Therefore, the average lifespan of a species is negatively related to the rate of genetic erosion in a population. Consequently, the longer the average lifespan of a species, the more resistant that species should be to the effects of genetic drift. The effect of fragmentation on a particular species is, therefore, dependent on life history traits related to movement and lifespan (Henle et al. 2004; Thiel-Egenter et al. 2009).

Fragmentation is particularly profound for aquatic species in river networks (Fagan 2002). The linearity of each river segment makes its fragmentation for a species more difficult (and usually impossible) to circumvent than a terrestrial fragmentation agent where alternative routes may be possible (Fuller et al. 2015). The dendritic structure of river networks already interacts with species movement patterns (Campbell Grant et al. 2007), so fragmentation of those networks has additional consequences for population growth and community composition (Fagan 2002). Therefore, species with life history traits or strategies that are sensitive to restricted movement of individuals and are short-lived should be particularly vulnerable to habitat

47 fragmentation in river networks. The vulnerability of these species can manifest in population
48 demographic impacts (e.g., reduced population growth rate (Samia et al. 2015)) or population
49 genetic impacts (e.g., genetic erosion and diversity loss (Bijlsma and Loeschcke 2012)).
50 To better understand the contrasting influences of life history and fragmentation on
51 population genetics, ideal study organisms would have similar movement capabilities, but
52 contrasting longevities. Freshwater mussels (Unionidae) show a diverse set of life histories that
53 range in both movement ability and lifespan (Haag 2012). Most long-distance movements for
54 freshwater mussels are achieved during their parasitic larval stage as glochidia (Kappes and
55 Haase 2012). During this period, each glochidium attaches to the gills or fins of a fish host where
56 it develops (on average for 2-4 weeks, but can range from 1 to 14 weeks depending on the
57 species) into a small juvenile mussel (Haag 2012). The distance travelled by the host fish until
58 the juvenile mussel drops from its host will determine the major movement phase of an
59 individual freshwater mussel. Known fish hosts for just one species of mussel can have very
60 different movement patterns and abilities (Lellis et al. 2013). For *Elliptio complanata*, hosts
61 range from the migratory American eel (*Anguilla rostrata*) that are capable of traveling hundreds
62 of kilometers in just a few days (Haro 2003) to benthic mottled sculpins (*Cottus bairdii*) with
63 annual movement ranges of less than 100 m (Breen et al. 2009). Consequently, freshwater
64 mussels are a good study organism to evaluate the impacts of habitat fragmentation because they
65 are capable of long-distance dispersal, but can also persist in isolation if the proper resident fish
66 hosts are available.
67 In addition to mobility dichotomies for freshwater mussels, life history strategies can
68 diverge along lifespan. Different phylogenetic groups within the order Unionoida have mean
69 lifespans ranging from 11 to 50 years, but for some mussel species (e.g., *Margaritifera*

margaritifera) individuals living 100+ years is not uncommon (Haag and Rypel 2011). Most mussel species have size-specific fecundity and reproduce annually until death (Haag and Staton 2003), which makes species with long-lived life history strategies capable of contributing alleles to the reproductive population for many consecutive years. Subsequently, these long-lived individuals act as genetic memory banks in the population, helping to resist the deleterious impacts of genetic drift or erosion for the species relative to a life history strategy that emphasizes shorter generation times and earlier age at maturity.

The goal of this study was to contrast the life history trait of lifespan with anthropogenic habitat fragmentation to determine the impacts on species population genetic structure. This contrast was made by simulating gene flow among populations in a river network (Neuse River Basin, North Carolina, USA) and tracking the genetics of individuals and populations for 200 years. The modeled scenarios represent a full cross between five life history strategies—longevities—and four riverscapes representing varying degrees of fragmentation (Table 1). The five life history strategies include theoretical mussel species with average lifespans ranging from 10 to 50 years. The movement landscapes ranged from fully fragmented to panmictic with a stepping-stone landscape allowing movement to only neighboring subpopulations for each dispersal event and a fragmented landscape divided by the dams currently standing in the river basin. It was expected that scenarios with more restricted movement would exhibit greater population genetic structure, lower observed heterozygosity, and lower allelic richness at the end of the 200 year simulation. Furthermore, scenarios simulating species with short average lifespans should have greater population genetic structure than species with long lifespans. The simulation results are discussed relative to species currently inhabiting the Neuse River Basin.

2 Methods

To evaluate how life history strategies interact with habitat fragmentation, species with lifespans ranging from short to long were contrasted with riverscapes ranging from completely fragmented to completely connected. The contrast between five lifespan life history strategies and four riverscapes varying in their resistance to movement produced 20 modeling scenarios (Table 1). For each scenario, the population genetic structure of a theoretical aquatic species (loosely based on freshwater mussels) was measured to demonstrate the genetic consequences of the interaction between habitat fragmentation and life history strategy.

2.1 Simulation scenarios

Twenty modeling scenarios were compared in the simulations (Table 1). These scenarios come from the cross between five life history strategies and four landscapes with varying resistance to movement. The lifespan life history trait included two components (maximum age and age at maturity) that varied among lifespan scenarios. Lifespan ranged from 10-50 years at 10-year intervals and age at maturity ranged from 2-6 years for each of the five lifespan longevities respectively (Table 1). These life histories were roughly based on freshwater mussels whose communities include species that have a similar range of mean lifespan and age at maturity (Haag and Staton 2003; Haag and Rypel 2011; Haag 2012). Once mature, adult individuals in the simulation reproduced until death, which is also a common trait among freshwater mussel species (Haag 2012).

For each life history strategy, four different landscapes were presented to the species that ranged in their resistance to individual movement (Table 1). At one end of the movement spectrum, movement mimicked a panmictic population (P10-P50 scenarios) where individuals could move to any other subpopulation in the river network (Figure 1). At the other end of the

spectrum, fragmentation by theoretical barriers (F10-F50 scenarios) completely restricted movement (no migration) so individuals only mate within their natal subpopulation. Between these two extremes was a stepping-stone landscape (S10-S50 scenarios), where individuals were restricted to moving only to the neighboring up- or downstream subpopulations in the river network. Finally, the dams landscape (D10-D50) represented the current habitat fragmentation by dams in the simulation landscape (Neuse River network; see Section 2.2). Dams functioned as complete barriers to movement of individuals, so individuals could only move to other subpopulations with no intervening dams along the river network.

2.2 Simulation landscape

All simulations operated across a representation of the Neuse River network in North Carolina, USA (Figure 2). Species subpopulations were distributed evenly through the river basin with a habitat patch and associated subpopulation in each HUC-12 sub-watershed (i.e., each HUC-12 had one subpopulation). This subdivision of the Neuse River network produced 145 subpopulations.

The dam scenarios simulate the effect of the ubiquitous dams in the Neuse River basin, of which there are over 600 (Figure 1) (Hoenke et al. 2014). The fragmented scenarios simulate a maximally-fragmented river network with barriers between each subpopulation so individuals remain within their natal population for the duration of their lives. The stepping-stone scenarios assume that individuals may be able to overcome small numbers of barriers, but barriers remain restrictive to movement within the network (only short distance dispersal to neighboring populations possible). Because the majority of dams are low-head, run-of-river dams in the Neuse River basin, the stepping-stone scenario may be thought of as representing the partial permeability of these types of dams as boundaries (*sensu* Strayer et al. (2003)).

2.3 The gene flow model

The simulation of freshwater mussel gene flow was conducted in CDPOP (Landguth and Cushman 2010). CDPOP is an individual-based model that tracks genetic exchange among individuals in time and space. The landscape the model operates across is a user-defined landscape grid with each individual occupying a cell within that rasterized environment. Movement among individuals is mediated using cost-distance matrices for each pair-wise distance between individuals. This framework for movement allows the user to control where individuals move in the landscape for dispersal events at each time step. For this study, pair-wise river distances between all 145 subpopulations were measured along river segments of the Neuse River network to generate the cost-distance matrix used in the simulations. Cost-distances between individuals within a subpopulation were set at 0 such that movement within a subpopulation was unrestricted for mating. Cost-distances between individuals in other subpopulations were assigned based on the river distance separating their subpopulations. This river distance cost-distance matrix was used for the Fragmented, Stepping-stone, and Panmictic scenarios. For the Dams scenarios, a cost-distance matrix was generated by tallying the number of dams that separated each pair-wise combination of subpopulations. This cost-distance matrix allowed the simulations to identify when dams were present and therefore restricting movement between subpopulations for this scenario.

Life history strategies for short and long lifespans were simulated by creating five separate population demographic inputs for the model. The population demographic parameters that varied among life history scenarios included the maximum lifespan of a mussel, and the age at maturity (Table 2). Other population demographic parameters (e.g., subpopulation size and sex

ratio) were held constant across all simulation scenarios (Table 2). The maximum subpopulation size was set at 100 individuals due to computational restrictions. The sex ratio was kept near 50:50 across all simulation years and represents a common sex ratio among mussel species (Haag 2012). For each scenario, the model was run for 200 years, and each simulation scenario run 10 separate times to generate an estimate of variability in output for each scenario to accommodate the stochasticity in the model.

Stochasticity exists in the model at several points during each time step. During mating events, individuals within their subpopulation are paired randomly. Additionally, genetic recombination between mating individuals also occurs randomly as each allele for a given locus in the offspring is selected randomly from each parent. Furthermore, alleles for each locus are selected randomly for each individual when the model is initialized. This is equivalent to the simulation starting from a panmictic population. Movement to new locations also occurs randomly (within the allowable dispersal range based on the cost distance among subpopulations) for a migrating individual. The panmictic scenarios allow movement of individuals selected to migrate to any other subpopulation in the network regardless of its distance from the origin/natal patch. Therefore, selection of the destination patch during migration is made randomly for all scenarios that allow migration.

The age structure of a population also has stochasticity built into the simulation. Individuals all die (100% mortality) when they reach the maximum age for the given life history strategy. However, random mortality also exists in the model for younger individuals. Individuals in their first year have a 50% mortality rate, 10% mortality rate in year 2, 5% mortality rate in year 3, and a 1% mortality rate for the remaining years until they reach the

maximum age of their life history strategy. This allows the population to maintain some older individuals, but also allows new recruits in the population at each time step.

2.4 Population genetic analysis

Twenty-five loci with two alleles each were used in each individual to trace gene flow during the simulation. This marker set was based on the historic use of 20 or fewer microsatellite markers in previous landscape genetic studies (Storfer et al. 2010) and assumed to be sufficient for quantifying population genetic structure from the model output where there is perfect knowledge of each genotype.

To evaluate population genetic structure among the scenarios, three different genetic statistics were used to characterize the population genetics of the simulation output. First, the population divergence statistic F_{ST} (Weir and Cockerham 1984) was calculated globally for each simulation replicate. This F_{ST} value compares the genetic variation among all subpopulations with the genetic variation across all 145 pooled subpopulations (entire set of individuals in the landscape). Consequently, the statistic is a quantitative value describing the population genetic structure across the entire simulation landscape (all subpopulations). The initiation state (year 1) of each simulation set F_{ST} to approximately 0, but the analysis following the simulation came from the final time step (year 200 of the simulation). A two-way analysis of variance (ANOVA) was then used to compare means and variance of the F_{ST} values from each of the 20 scenarios and their 10-independent replicate runs using lifespan and movement as the predictors. This assessed whether short- and long-lived species responded differently to habitat fragmentation genetically. Tukey's HSD post-hoc tests determined which pairwise contrasts between scenarios contributed to any significant global two-way ANOVA test.

Second, observed heterozygosity at year 200 for all individuals in the landscape was used to compare scenarios (year 1 H_o approximately 0.5 for each scenario). The observed heterozygosity was evaluated statistically using the same two-way ANOVA and Tukey's HSD tests with observed heterozygosity predicted by life history strategy and movement scenario. Third, allelic richness at the subpopulation level (total number of alleles in a subpopulation) was used to identify the impact of genetic isolation and drift (Greenbaum et al. 2014). Each simulation scenario was initiated with all 50 alleles represented in each population across the landscape. The number of alleles in each subpopulation at year 200 was averaged across all subpopulations for each scenario replicate. The mean allelic richness for each scenario was then, also, evaluated using a two-way ANOVA followed by Tukey's HSD tests. All analyses on simulation output, were conducted in the statistical software R (R Core Team 2016) using the packages "adegenet" (Jombart et al. 2008, 2010; Jombart and Ahmed 2011), "ape" (Paradis et al. 2004; Popescu et al. 2012), "hierfstat" (Goudet 2005), "pegas" (Paradis 2010), and "poppr" (Kamvar et al. 2014, 2015) .

2.5 Simulation assumptions and limitations

The simulations in this study hold population size stable across the landscape to focus primarily on changes to population genetics. Each subpopulation contained 100 individuals and this size limit was necessary due to limits on computational resources. Because this key demographic was held constant, this modeling effort is able to focus on the life history and fragmentation variation explicitly identified in the modeling framework. However, it is necessary to acknowledge that the population size dynamics of a species can also affect change in its population genetic structure.

3 Results

3.1 Population genetic structure

Population genetic structure (as F_{ST} values) ranged from 0 to 0.28 across all movement and lifespan scenarios (Figure 3). Both lifespan and movement were significant predictors of F_{ST} (two-way ANOVA; Table 3). The fragmented network scenario with no movement of individuals among populations demonstrated the greatest population genetic structure among the lifespan scenarios (Figure 3). Furthermore, it had significantly greater population genetic structure than the three other movement scenarios (Tukey's HSD test: $p<<0.001$; Figure 3). There was no difference in population genetic structure between the stepping-stone or panmictic scenarios (Tukey's HSD test: $p>0.05$), but the dams scenario had significantly greater population genetic structure than the stepping-stone and panmictic scenarios (Tukey's HSD test: $p<<0.001$; Figure 3). The shortest lifespan scenario (10-year lifespan) demonstrated significantly greater population genetic structure than all other lifespans (Tukey's HSD test: $p<<0.001$; Figure 3). The 20-year lifespan scenario had significantly greater population genetic structure than lifespan scenarios with terminal ages of 30, 40, and 50 years (Figure 3). No significant differences in population genetic structure existed among scenarios with lifespans of 30, 40 and 50 years (Tukey's HSD test: $p>0.05$).

3.2 Observed heterozygosity

Observed heterozygosity was significantly predicted by both lifespan and movement (two-way ANOVA: Table 3) (Figure 4). The fragmented movement scenario had significantly lower observed heterozygosity than the other three scenarios, while the dams scenario had significantly lower observed heterozygosity than the stepping-stone and panmictic scenarios (Tukey's HSD

test: $p<<0.001$; Figure 4). There was no difference in the observed heterozygosity between the stepping-stone and panmictic scenarios. The shortest lifespan scenario had significantly lower observed heterozygosity than all other lifespan scenarios at the end of the simulation (Tukey's HSD test: $p<<0.001$; Figure 4). The lifespan scenario with a 20-year terminal age was significantly lower than the 30-, 40-, and 50-year lifespan scenarios (Tukey's HSD test: $p<<0.001$; Figure 4). There was no significant difference in the observed heterozygosity among 30-, 40- and 50- year lifespan scenarios (Tukey's HSD test: $p>0.05$).

3.3 Allelic richness

Allelic richness was predicted by both lifespan and movement (two-way ANOVA: Table 3) (Figure 5). The fragmented movement scenario had significantly lower allelic richness than the other three movement scenarios (Tukey's HSD test: $p<<0.001$), while dams, stepping-stone, and panmictic scenarios were not statistically different from each other (Tukey's HSD test: $p>0.05$; Figure 5). The shortest lifespan scenario had significantly lower allelic richness than all other lifespan scenarios at the end of the simulation (Tukey's HSD test: $p>0.05$), but no other significant differences were noted between lifespan scenarios (Tukey's HSD test: $p>0.05$; Figure 4). The decrease in magnitude of allelic richness from 50 to 49 alleles during the 200-year simulation for the 10-year lifespan scenario represents an average fixation of one of 25 marker loci (or 4% of the neutral, biallelic genetic markers) per population in the simulation.

4 Discussion

The results of this study indicate that the population genetic response to habitat fragmentation is related to the lifespan of a species. Species using life history strategies with long lifespans benefit from generational overlap that insulates their population from the genetic

impacts of habitat fragmentation more than species with shorter-lifespan life history strategies. This divergence in population genetic structure for species with contrasting longevities has been observed for two freshwater mussel species that co-occurred across the Pacific Northwest, USA (Mock et al. 2013). The two species of freshwater mussel had overlapping distributions, but diverging life history traits related to average lifespan and host-fish movement ability. Similar to the simulation results of this study, the species of mussel with a longer lifespan and more mobile fish hosts demonstrated less population genetic structure than the species with poorly dispersing fish hosts and a shorter lifespan (Mock et al. 2013).

The actual population genetic structure in river networks for mussels will be derived from the combined effects of each species' life history and movement patterns. Empirical studies have demonstrated limited population genetic structure for some species of freshwater mussels (Small et al. 2012; Abernethy et al. 2013; Mock et al. 2013). Abernethy et al. (2013) showed that mussel subpopulation genetics were similar upstream and downstream of several dams that were more than 175 years old. Simulation results from this study would suggest that only species with lifespans shorter than 20 years and small effective populations (≤100 individuals) would have exhibited genetic divergence over that period of fragmentation. The two species they sampled (*Elliptio arca* and *Elliptio complanata*) have average lifespans greater than 35 years, so the sampled subpopulations would have required extremely small effective population sizes or passed through a genetic bottleneck in order to have diverged genetically. Similarly, little population genetic structure was noted in three mussel species across a larger spatial extent in the Altamaha River (Small et al. 2012). One of these species of mussel (*Elliptio icterina*/*complanata* complex) has lifespans potentially greater than 90 years (Strayer and Malcom 2012). The

293 simulation results in this study, regardless of any habitat fragmentation effects, suggest that
294 observing population genetic structure would be unlikely in this landscape for this species.
295 In addition to lifespan playing a key role in reducing population genetic structure across a
296 landscape, even small dispersal events may be sufficient for reducing the impacts of habitat
297 fragmentation if the barriers are not complete (as they are generally assumed to be), but slightly
298 permeable. The simulation results demonstrate that the stepping-stone model had significantly
299 less population genetic structure than the fully fragmented landscape. This suggests only
300 moderate gene flow to adjacent subpopulations is required across a system as large as the Neuse
301 River basin (drainage area: ~14,600 km^2, mainstem length: ~440 km) to maintain genetic
302 diversity. There are mechanisms for some of the Neuse River basin mussel species to overcome
303 barriers and these mechanisms can produce very large dispersal events. For example, the
304 American eel (*Anguilla rostrata*) is a capable climber that has the ability to surpass dams less
305 than 2m tall, while several species of goby (Gobiidae) are capable of surpassing dams up to 30m
306 tall (Cooney and Kwak 2013). Similarly, the fragmentation agent itself could have windows of
307 time when the barrier is ineffective (e.g., large floods that create moderate overland-flow in the
308 floodplain surrounding a dam for movement past a barrier).
309 Population genetic structure is only one metric used to measure the impacts of habitat
310 fragmentation on the genetics of a species. Allelic richness is another and it is directly related to
311 the evolutionary adaptive potential of a species (El Mousadik and Petit 1996). Since genetic drift
312 drives random allele fixation more rapidly in small populations, a species whose range has been
313 split into two or more smaller subpopulations is the most susceptible to the impacts of genetic
314 drift (Honnay and Jacquemyn 2007). Even though the allelic diversity remained high for most
315 scenarios in this study (Figure 5), the decline in allelic richness for short lifespan species

observed in the fragmented scenario is important to consider when evaluating species in systems like the Neuse River network where barriers are prevalent. Fragmentation in similar river networks may push species to a point where their genetic adaptability to disturbance is diminished, making them genetically vulnerable. The rate of fixation for neutral genetic markers observed in simulations of this study was as high as 4%. If the fixation rate for coding segments of the genome (especially those that are not currently under selection) is anywhere near the neutral marker rate, evolutionary adaptive potential for species could decline rapidly. Furthermore, while genetic diversity and evolutionary adaptive potential may be declining in isolated populations, its demographics might be stable, which sets up a "genetic extinction debt" similar to the species extinction debt described first by Tilman et al. (1994).

In North Carolina, eight species of freshwater mussel are federally listed as endangered species and two of these species (*Alasmidonta heterodon* and *Elliptio steinstansana*) exist in the simulated river network (Neuse River) (Bogan 2002). Both species have short lifespans and, while it is unknown if genetic diversity loss is contributing to their population decline, this study demonstrates the potential for their populations to harbor the genetic impacts of isolation due to the highly-fragmented river networks they occupy. These endangered species may be responding to the last 200 years of fragmentation in different ways than other members of the Neuse River mussel community. The decline of one species versus another could be related to the genetic erosion (Bijlsma and Loeschcke 2012) that has accumulated for short-lived species while longer-lived species remain in presumably more stable condition.

While lifespan is an important life history trait for maintaining genetic diversity in a population (Landguth et al. 2010), this insulation to genetic change comes with a tradeoff. The maintenance of allelic diversity also restricts a species from adapting quickly to environmental

change and allowing allele frequencies to fluctuate (Slatkin 1987). Short-lived species, then, are better suited to respond to rapid environmental change because adaptive allele frequencies can more rapidly adjust to the new environment (Storfer 1999). Modern landscapes are characterized by both frequent disturbances and high fragmentation. This study demonstrates that the genetic response to these habitat changes diverges for species with contrasting life history strategies. To maintain biodiversity, life history strategies of species will be an important indicator of survival in a contemporary environment. So, in modern river systems, which are both fragmented and rapidly changing, long-lived species may suffer because they cannot adapt rapidly to change, while short-lived species may be subject to rapid genetic erosion. This leads to a sort of a squeeze where only species whose life histories fall in a sweet spot can survive. In extreme cases, this sweet spot may be squeezed out of existence.

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Tables

Table 1: Alpha numeric names of scenarios contrasting species movement and lifespan. "Lifespan" scenarios offer the values for maximum age and age at maturity (years). "Movement" scenarios indicate the extent to which individuals can move between subpopulations during each time step of the simulation (see Figure 1 for movement scenario descriptions).

Lifespan		**Movement**			
Maximum	*Maturity*	*Fragmented*	*Dams*	*Stepping-stone*	*Panmictic*
10	2	F10	D10	S10	P10
20	3	F20	D20	S20	P20
30	4	F30	D30	S30	P30
40	5	F40	D40	S40	P40
50	6	F50	D50	S50	P50

Table 2: Model demographic parameter values/ranges and citations supporting their use assuming theoretical mussel species.

Model Parameter	**Value**	**Citations supporting value**
Sex ratio	1:1	(Haag and Staton 2003; Haag 2012)
Maximum age (years)	10-50*	(Haag and Rypel 2011)
Age at maturity (years)	2-6*	(Haag and Staton 2003)
Population size	100	*computation limited*
Time steps (years)	200	

* See Table 1 for specific values used within these ranges.

Table 3: Two-way ANOVA table results using lifespan and movement scenario as independent variables predicting population genetic structure (F_{ST}), observed heterozygosity (H_o), and allelic richness.

Dependent	Independent	df	Sum Sq	Mean Sq	F-value	p-value
F_{ST}	Lifespan	4	0.1473	0.03682	40.7	<<0.0001
	Movement	3	0.5749	0.19162	212.0	<<0.0001
	Residuals	191	0.1727	0.0009		
H_o	Lifespan	4	0.03811	0.00953	41.5	<<0.0001
	Movement	3	0.11746	0.03915	170.6	<<0.0001
	Residuals	191	0.04384	0.00023		
Allelic Richness	Lifespan	4	2.78	0.6951	28.6	<<0.0001
	Movement	3	1.35	0.4501	18.5	<<0.0001
	Residuals	191	4.649	0.0243	0	

Figures

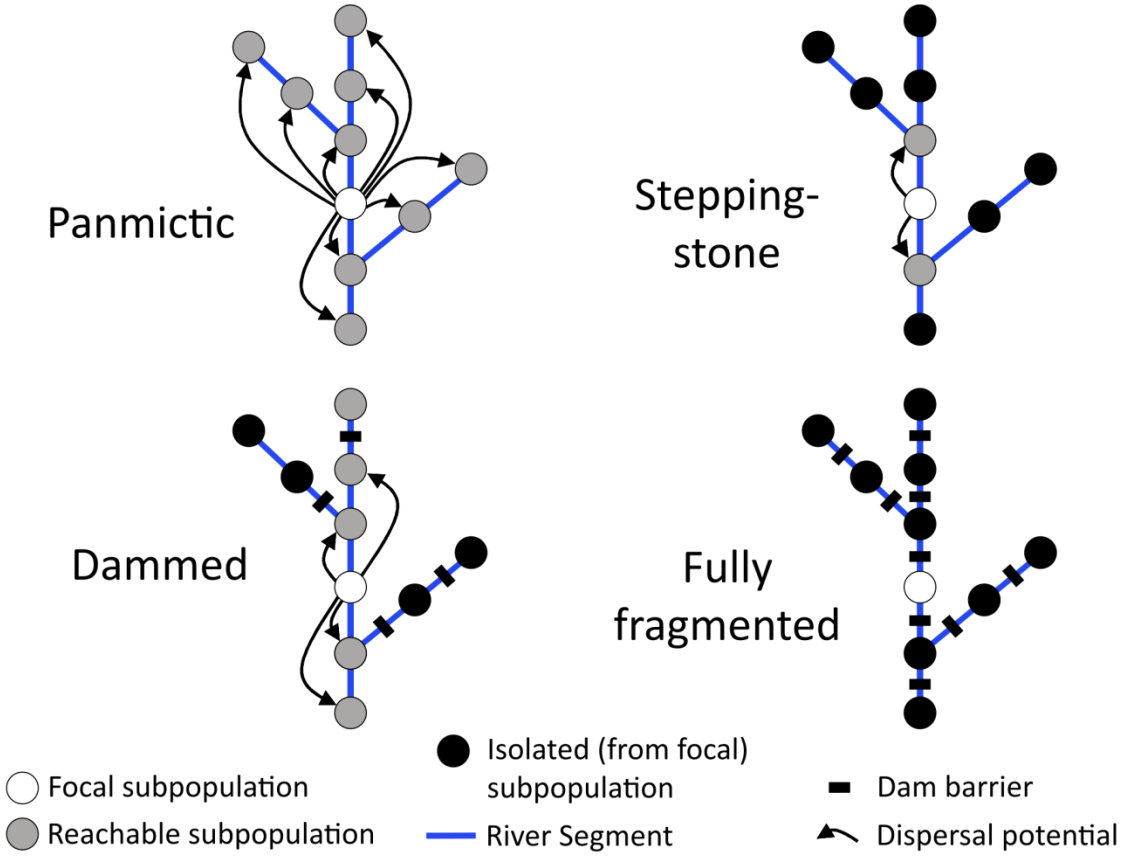


Figure 1: Conceptual diagram demonstrating potential dispersal (during a single migration event) from a single focal subpopulation in each simulation landscape. White subpopulation indicates the focal subpopulation and arrows represent the movement to reachable subpopulations (grey circles) during each time step from the focal subpopulation. Green arrows identify which subpopulations (grey circles) are available for immigration. Blue lines connecting subpopulations are river segments, while black bars perpendicular to these river segments represent dams that function as complete barriers to movement.

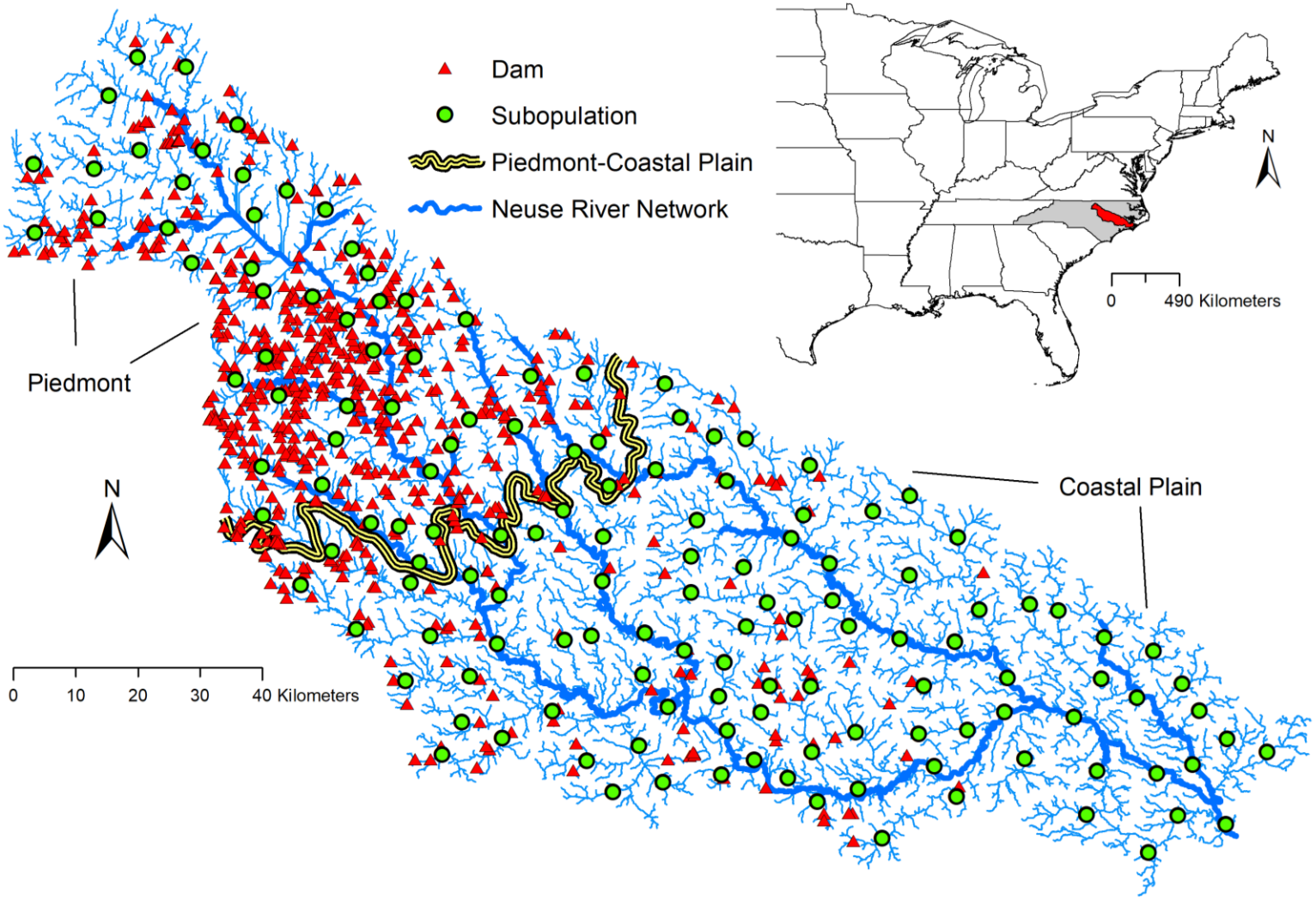


Figure 2: Map of simulation subpopulations (circles) and dams (triangles) in the Neuse River network.

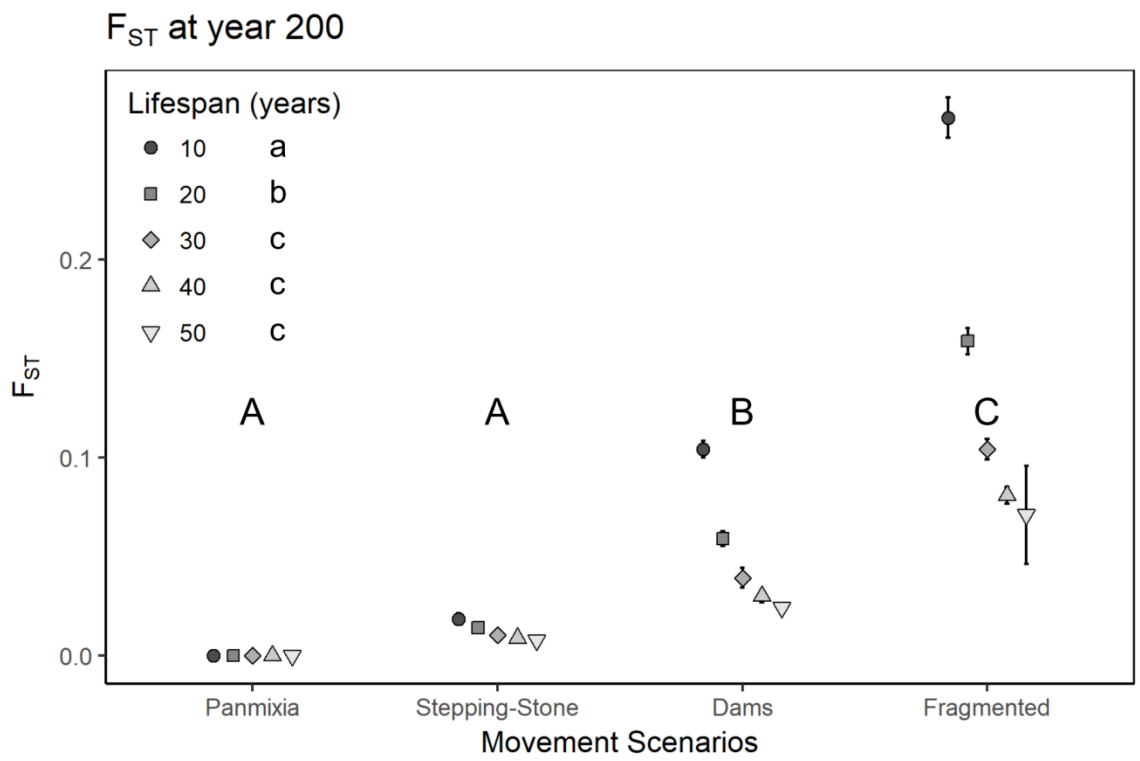
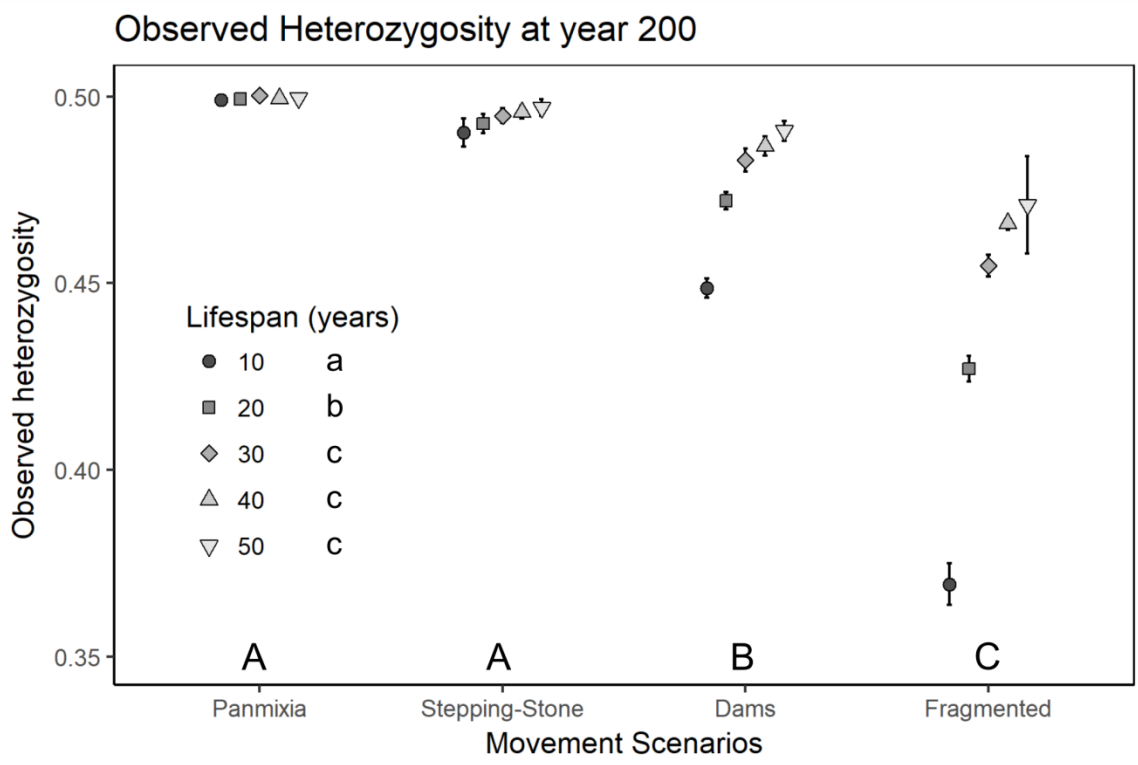


Figure 3: Mean (±2SD) population genetic structure (FST) for each movement and lifespan scenario at year 200. Lowercase letters in legend indicate significant differences between lifespan life history strategies while capital letters across figure indicate significant differences between movement scenarios based on Tukey's HSD test.



492

493 **Figure 4: Mean (±2SD) observed heterozygosity for each movement and lifespan scenario**

494 **at year 200. Lowercase letters in legend indicate significant differences between lifespan life**

495 **history strategies while capital letters across figure indicate significant differences between**

496 **movement scenarios based on Tukey's HSD test.**

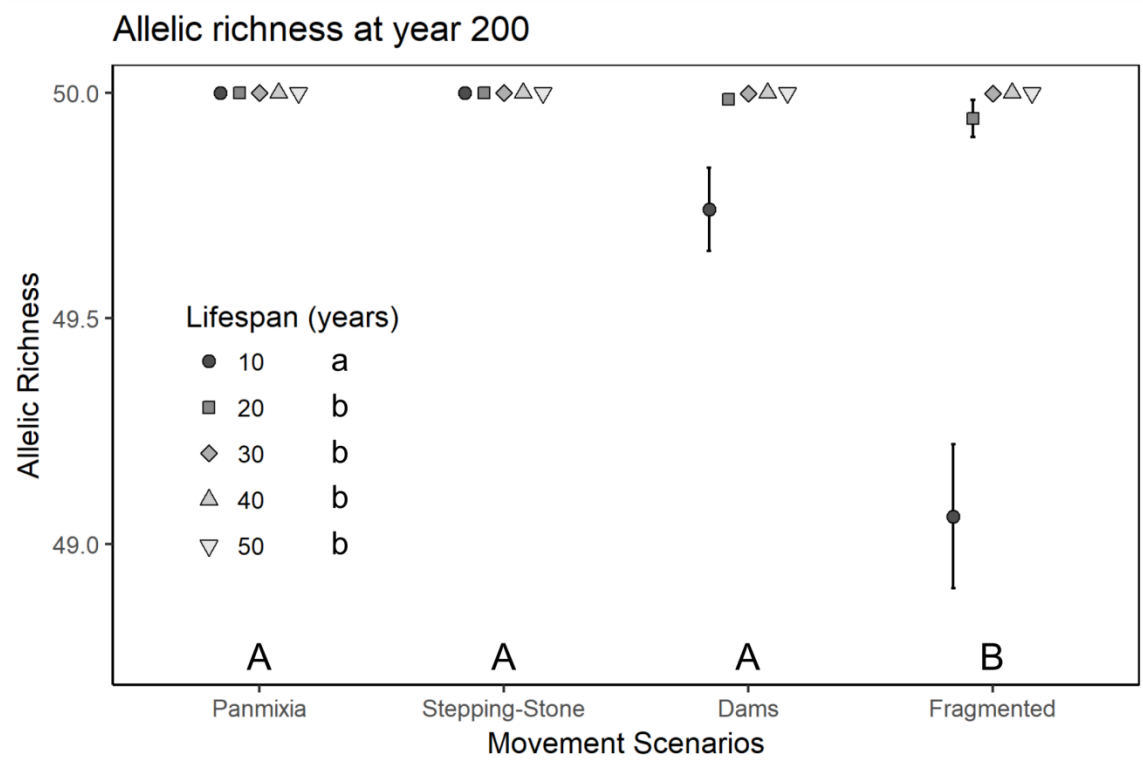


Figure 5: Mean (±2SD) allelic richness for each movement and lifespan scenario at year 200. Lowercase letters in legend indicate significant differences between lifespan life history strategies while capital letters across figure indicate significant differences between movement scenarios based on Tukey's HSD test.