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FEATURE ARTICLE

Genetic predictors of population resilience: A case study of native Brook Trout in headwater streams

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Abstract

Objective: Populations of eastern Brook Trout *Salvelinus fontinalis* face threats from several sources, such as habitat fragmentation, climate change, and competition with introduced salmonids. As a native species, understanding how these populations will respond to disturbances is paramount to their management and effective conservation. A population's ability to respond to disturbance, its resilience, is influenced by several factors. One such group of factors is population genetics.

Methods: We calculated population resilience metrics based on transient dynamics using population projection matrix models. Long-term demographic data from 23 headwater stream Brook Trout populations were used to parameterize models. Genetic data were collected, and genetic indices were calculated. Partial redundancy analysis was then used to evaluate relationships between resilience metrics and genetic indices.

Result: Inbreeding coefficient, rarefied allelic richness, pairwise genetic differentiation (F_{ST}), and effective population size were all found to be important variables in predicting resilience.

Conclusion: Our results suggest that genetic isolation may increase the demographic resilience in Brook Trout through faster generation times and higher juvenile survival, but this likely comes at the cost of increased extinction risk and truncated size structures. Genetic indices can provide insight into gene flow between populations, thus the relationship between population connectivity and resilience. Given the importance of connectivity to population resilience, restoring and maintaining movement corridors could affect resilience in headwater Brook Trout populations.

KEYWORDS

ecology, genetics, life history, population dynamics, riparian and stream

INTRODUCTION

Demographic resilience is a topic of great interest to ecologists and conservation biologists. In an era of rapidly changing environmental conditions, disturbances and perturbations are occurring more frequently and with greater severity (Intergovernmental Panel on Climate Change 2021). In lotic systems, this generally comes in the form of altered flow regimes (Novotny and Stefan 2007), more extreme temperatures (Daraio and Bales 2014), altered land use (Maloney and Weller 2011), and degraded water quality (Peters and Meybeck 2000). The ability of a population to withstand disturbances by resisting changes in abundance induced by disturbance and recovering from them defines its resilience (Holling 1973; Hodgson et al. 2015). Resilience can largely be broken into three components: resistance, compensation, and recovery time. Demographic resistance describes a population's ability to avoid a decrease in density following a disturbance, while compensation describes the ability of a population to respond to a disturbance by increasing in density (Capdevila et al. 2020).

The life history strategies within a population have been linked to its demographic resilience, with species that exhibit high turnover and population growth rates generally having higher resilience than species that live longer and turn over more slowly (Winemiller 2005). The different aspects of resilience—resistance, compensation, and recovery time—are also related to life history strategies, with different life histories taking advantage of different aspects defining population resilience (Capdevila et al. 2021).

Despite interest in resilience by ecologists, it has proven potentially difficult to define. Many studies and conservation strategies evoke the idea of resilience without consideration of any quantifiable measure therein. Attempts have been made to develop quantifiable measures of resilience. Ives (1995) developed a method for estimating resilience of stochastic environments based on relationships between the population growth rates of species within a community. Indicators based on critical slowing down, the tendency of a system to recover more slowly from a disturbance as it approaches a tipping point, have been linked to the probability of community collapse and the timing of species extinction (Dakos and Bascompte 2014). Scheffer et al. (2015) also recommended the use of critical slowing down based metrics as an indication of ecological resilience but also endorsed using long time series data or satellite imagery to characterize alternative ecological states. Other researchers suggested that no one metric can capture the resilience of a population, but the aspects of a population that drive its resilience can be measured and defined (Hodgson et al. 2015). Based on this idea, Capdevila et al. (2020) laid out a framework for estimating demographic resilience based on a suite of metrics associated with a population's transient dynamics.

Transient dynamics describe a population's departure from its stable state following a disturbance and processes driving its return to the stable state (Stott et al. 2011). The metrics calculated to describe the transient dynamics of a population fall into four groups: three based on the aspects of resilience, compensation, resistance, and recovery time and one that acts as a combination of resilience and compensation, transient envelope (Capdevila et al. 2020). Three metrics are used for each compensation and resistance and are associated with how a population reacts to a disturbance in the first time step, the maximum displacement of a population during the transient period, and the long-term displacement of a population after the transient period. For compensation, these metrics are reactivity, maximum amplification, and amplification inertia, respectively. For resistance, they are first-step attenuation, maximum attenuation, and attenuation inertia, respectively. Transient envelope metrics represent a population's overall response to disturbance and are a combination of compensation and resistance metrics. Two metrics are used to describe a population's transient envelope: reactivity envelope and inertia envelope. These can be thought of as a population's immediate and long-term response to a disturbance, respectively. Finally, two metrics are calculated for recovery time: convergence time and damping ratio. These metrics are similar and differ mostly regarding unit. Convergence time is time stamped and can provide managers with estimates of how long it will take a population to recover, while damping ratio is unitless and thus useful for comparing resilience among populations or species with different generation times. While the aforementioned techniques are used to define ecological resilience at the community or ecosystem level, the framework proposed by Capdevila et al. (2020) can provide insight to demographic resilience at the population level.

> **Impact statement**
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> Understanding the ability of a population to respond to disturbance, its resilience, is incredibly important in ecology and fisheries management. Many factors go into resilience, and this study explores how genetics can affect resilience in eastern Brook Trout populations and why genetics alone might not tell the whole story of a population's resilience.

Genetic indices have also been used to evaluate the resilience of a population. Using genetic parameters, insights into connectivity and isolation dynamics among subpopulations (Lowe and Allendorf 2010), population persistence (Lande and Shannon 1996), and evolutionary potential (Frankham et al. 1999) can be gained. Interconnectivity between spatially structured metapopulations has been linked to population resilience due to several processes. Hypotheses such as the rescue effect and propagule rain describe how immigration from surrounding populations can reduce the risk of localized extinctions (Gotelli 1991). A lack of genetic diversity in a population can impact its fitness through inbreeding depression and reduction of adaptive ability (Markert et al. 2010). Minimum viable population size has been assessed using effective population size based on genetic indices, with a general rule of thumb being an effective population size of 50 to avoid inbreeding depression and 500 to ensure maintenance of evolutionary potential (Jamieson and Allendorf 2012). Given the links observed between genetic indices and population resilience, a connection between these indices and demographic resilience metrics based on transient dynamics may also exist.

Populations of stream-dwelling eastern Brook Trout *Salvelinus fontinalis* often experience disturbances, largely from sources such as increasing water temperature, land-use changes, competition with introduced salmonids, sedimentation, and other stressors (Hudy et al. 2005). It has been estimated that Brook Trout populations have been extirpated from 28% of previously occupied subwatersheds, with 35% of subwatersheds having less than 50% of Brook Trout habitat intact (Hudy et al. 2008). Previous genetic analyses of lotic Brook Trout populations have found variability in levels of gene flow between spatially structured populations. In a Virginia watershed, pronounced fragmentation was observed between populations, with smaller patches having lower genetic diversity and higher risk of extinction (Whiteley et al. 2013). Kelson et al. (2015) observed connectivity between below-barrier populations, but populations above natural barriers showed little evidence of gene flow with below-barrier populations. Other environmental factors, such as temperature, stream gradient, and the presence of tributaries, have also been associated with the magnitude of gene flow (Kanno et al. 2011b). A simulation study found that gene flow could occur at the watershed scale but would be limited by watershed development (Nathan et al. 2019). For isolated populations, evidence of genetic rescue has been observed when individuals from a high-diversity population were introduced into a low-diversity, above-barrier population (Robinson et al. 2017). Barrier removal has also been found to be effective in reconnecting populations with migrants present in previously isolated populations in the first year following barrier removal (Wood et al. 2018). Given the previously stated relationships between connectivity and resilience, there likely exists a spectrum of resilience among Brook Trout populations that can be detected using genetic data. Therefore, our objectives were to investigate the potential relationships between indices of population genetics and demographic resilience. Using long-term ecological monitoring data, we aimed to estimate population resilience metrics. These metrics were then related to genetic measures associated with those populations.

METHODS

Study area

Brook Trout genetic samples and demographic data were collected from 23 headwater streams in eastern West Virginia (Figure 1). These streams stratified across six 10-digit hydrologic unit code (HUC10) watersheds, each containing between one and eight streams (Table 1). Fifteen of the study streams were located on the Monongahela National Forest, while the remaining eight were located on adjacent private commercial forest lands largely used as private hunting leases and for timber harvest. This region of West Virginia is dominated by maple–beech–birch and oak–hickory forests, but some spruce–fir forests are also present (Morin et al. 2016). The study streams ranged in elevation from 613 to 1129 m, in drainage area from 1.7 to 18.7 km^2, and in stream order from 1 to 3.

Environmental covariates associated with these sites were calculated in ArcGIS using remotely sensed data. Covariates included mean slope (%), mean elevation, flow accumulation difference, and drainage area. Slope was calculated as the percent rise. Mean elevation was calculated as the mean evaluation across all stream points. Flow accumulation difference was calculated using the flow accumulation tool in ArcMap. Drainage area was measured as the area drained by each study stream. Distance to confluence was also calculated in ArcGIS and was defined as the distance from the middle sampling section to the confluence with the nearest third-order or higher stream.

Data collection

Brook Trout electrofishing surveys were conducted annually during the Brook Trout spawning period (October to December) from 2003 to 2020 under annual scientific collection permits issued by the West Virginia Division of Natural Resources to the authors. Surveys were conducted with triple-pass depletion using backpack electrofishing methods on three 100-m sections (upstream, middle, and downstream) of each stream. Other species commonly occurring in the study systems included riffle daces *Rhinichthys* spp. and Mottled Sculpin *Cottus bairdii*. Sympatric populations of nonnative trouts, Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta*, were present in 8 of the 23 streams. The care and handling of all fish captured for this ongoing sampling is in accordance with protocol 15-0506 approved by the West Virginia University Institutional Animal Care and Use Committee. Brook Trout sampled during the electrofishing surveys were measured to the nearest millimeter, weighed to the nearest gram, and visually checked for sex identification. All fish sampled were held streamside in aerated stream water during subsequent electrofishing passes and returned to the stream after the final pass. During fish surveys in 2018, adipose fin clips were collected from up to 10 adult (>100 mm) Brook Trout in each stream section, for a target sample size of 30 fin clips per stream. Adipose fin clips were stored in 95% ethanol until DNA extraction.

Genetic protocols

The Wizard SV-96 DNA purification system (Promega, Madison, Wisconsin) was used for genomic DNA extraction,

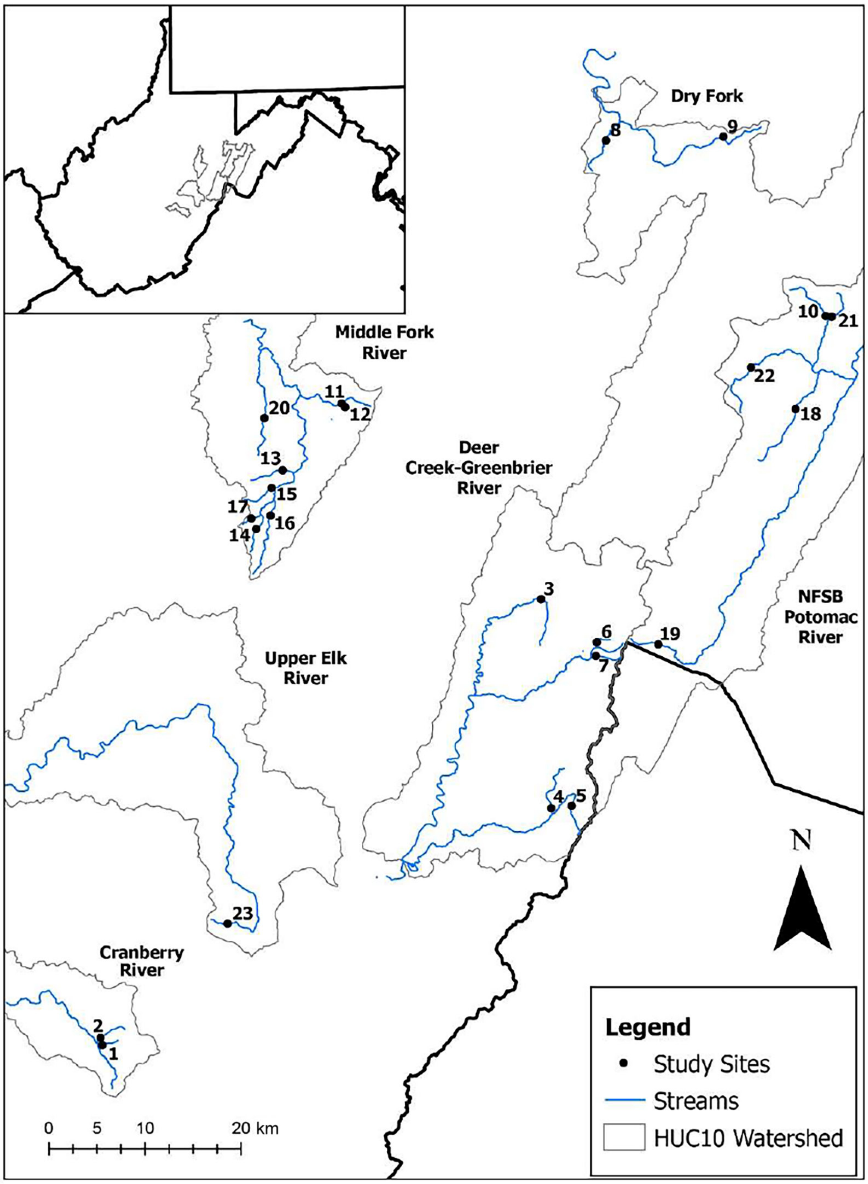

FIGURE 1 Map of the study streams, with HUC10 watersheds outlined. The name of the stream associated with the stream numbers can be found in Table 1.

following manufacturer protocols. Extracted genomic DNA was quantified using spectrophotometry (NanaDrop, Wilmington, Delaware) and diluted to a 10 ng/μL standard concentration. There were 13 microsatellite loci defined by King et al. (2012) that were amplified using a PTC-200 thermocycler (MJ Research, St. Bruno, Quebec) or a C1000 thermocycler (Bio-Rad, Hercules, California). Also, 10-μL reactions were used, each consisting of 1 X Qiagen Multiplex PCR Master kit, 0.2 μM of fluorescently labeled forward primer, 0.2 μM of reverse primer, and 20 ng of DNA.

Two different amplification protocols were used, each for a set of loci. Loci set 1 consisted of *SfoB52*, *SfoC79*, *SfoD100*. *SfoC24*, *SfoC28*, *SfoC115*, and *SfoC113*, while loci set 2 consisted of *SfoC86*, *SfoD91*, *SfoC38*, *SfoD100*, *SfoC88*, and *SfoC129*. Loci set 1 was amplified with an initial heating to 94°C. Thirty-five subsequent cycles of 94°C (30 s), 56°C (30 s), and 72°C (45 s) were then performed with a final extension of 72°C for 10 min (King et al. 2012). The amplification protocol used for loci set 2 began with an initial heating to 94°C. Fifteen subsequent cycles of 94°C (45 s), 60°C (45 s), with a decrease of 0.5°C per cycle, and 72°C (30 s) were then performed. Fifteen additional cycles were then performed of 94°C (45 s), 52°C (45 s), and 72°C (30 s) (King et al. 2012). Samples were then sent to the West Virginia University Genomics Core Facility (CTSI Grant U54 GM104942) for fragment analysis using a LIZ600 size standard. Allele peaks were identified and manually confirmed using GeneMarker Genotyping Software by SoftGenetics.

TABLE 1 Summary of study streams by genetically defined populations and HUC10 watershed. Stream numbers represent numbers in Figure 1.

Genetic population designation	Stream number	Study stream	HUC10	HUC10 name
Cranberry	1	Little Branch	0505000502	Cranberry River
	2	Sand (Red)	0505000502	Cranberry River
Clubhouse	3	Clubhouse	0505000301	Deer Creek–Greenbrier River
Lower Greenbrier	4	Block	0505000301	Deer Creek–Greenbrier River
	5	Elleber	0505000301	Deer Creek–Greenbrier River
Upper Greenbrier	6	Poca	0505000301	Deer Creek–Greenbrier River
	7	Lick	0505000301	Deer Creek–Greenbrier River
Elklick	8	Elklick	0502000404	Dry Fork
NF Red	9	North Fork Red	0502000404	Dry Fork
Long (MF)	10	Long (Middle Fork)	0502000102	Middle Fork River
Panthers	11	North Fork Panther	0502000102	Middle Fork River
	12	Panther	0502000102	Middle Fork River
Schoolcraft	13	Schoolcraft	0502000102	Middle Fork River
Upper Middle Fork	14	Birch	0502000102	Middle Fork River
	15	Light	0502000102	Middle Fork River
	16	Rocky	0502000102	Middle Fork River
	17	Sugar	0502000102	Middle Fork River
Brushy	18	Brushy	0207000101	North Fork South Branch Potomac River
Little Low Place	19	Little Low Place	0207000101	North Fork South Branch Potomac River
Long/Roaring	20	Long (Potomac)	0207000101	North Fork South Branch Potomac River
	21	Roaring	0207000101	North Fork South Branch Potomac River
Whites	22	Whites	0207000101	North Fork South Branch Potomac River
Crooked	23	Crooked	0505000701	Upper Elk River

Genetic data analysis

Possible null alleles were evaluated using the R package PopGenReport using the function null.all (Adamack and Gruber 2014). Deviations from Hardy–Weinberg equilibrium were tested using the hw.test function in the R package pegas (Paradis 2010) using a Monte Carlo procedure with 100,000 replicates. Significance was determined after a Bonferroni correction.

Population assignment was performed by assessing pairwise genetic differentiation (F_{ST}) between each stream sampled. Pairwise comparisons were only performed for streams within the same HUC10 watershed. Pairwise F_{ST} values were calculated using the program FSTAT version 2.9.3 (Goudet 2003). The most likely number of populations in a watershed was then assessed using the STRUCTURE software (Pritchard et al. 2000). The number of populations tested (K) for each watershed ranged from one to two more than the number of streams in that watershed to account for the potential of more populations than sampling sites. The burn-in period and the number of Monte Carlo iterations were both set to 100,000. Ten replicate runs were performed for each value of K. The STRUCTURE results were then imported into STRUCTURE HARVESTER (Earl and vonHoldt 2012) to determine the mostly likely K value visually using the $\log_e$ likelihood of the number of populations and ΔK (Evanno et al. 2005). When the most likely number of populations was greater than 1, these procedures were repeated on subsets of the data as determined by the original test until K was equal to 1 (Vähä et al. 2007).

Genetic diversity metrics within genetically defined populations were then calculated. Expected (H_e) and observed (H_o) heterozygosity were calculated in the R package adegenet (Jombart 2008). Effective population size (N_e) was estimated using the program NeEstimator version 2.1 (Do et al. 2014), with only alleles with frequencies greater than 0.02 considered in the analysis. Rarefied allelic richness (A_r) was calculated using the function allel.rich in the R package PopGenReport assuming a sample size of eight based on the lowest sample size per stream (Adamack and Gruber 2014). Mean relatedness (Queller and Goodnight 1989) was calculated using the Microsoft Excel add-in GenAlEx (Peakall and Smouse 2012) using 999 permutations and bootstraps. Inbreeding coefficient (F_{IS}) and population-specific F_{ST} were calculated using the basic.stats and betas functions in the R package hierfstat, respectively (Goudet and Jombart 2021).

Population projection matrix models

Brook Trout age-class was assigned using finite mixture models using the R package mixdist (Macdonald and Du 2018). Fish were assumed to only live to age 3 since previous research on the study streams found that Brook Trout ranged from age 0 to age 4, with fish rarely surviving to age 4 (Stolarski and Hartman 2008). A finite mixture model was constructed for each stream–year combination. A population projection matrix model was then constructed for each population as determined by the genetic structure analysis using the R package popdemo (Stott et al. 2021). Survival was estimated by following cohorts through time and was calculated as the density (Brook Trout per 100 m) of a cohort in a population for a given year divided by the density of the same cohort in the previous year. Using this method, 16 survival estimates were calculated for each of the three age-class transitions (age 0–age 1, age 1–age 2, and age 2–age 3). In rare cases (12 out of 720) where calculated survival was greater than 1, the estimate was removed. A mean survival estimate for each age transition in each population was then calculated using these estimates. Fecundity estimates were obtained using the length–fecundity relationship in Wydoski and Cooper (1966) corrected for metric measurements. The equation used was $\log(F) = 3.23 \times \log(L_T) - 5.07$, in which F is fecundity and L_T is the total length of the female Brook Trout in millimeters. Mean fecundity for age-2 and age-3 Brook Trout was calculated for each population. Egg survival to age 0 was calculated for each cohort in each population using the total number of eggs produced per 100 m based on the summed fecundity estimates of age-2 and age-3 female Brook Trout sampled in a population divided by the density of age-0 Brook Trout sampled in the following year. Mean egg survival was then calculated for each population across years. These fecundity and egg survival estimations are simplified for the sake of the model, while other factors such as spawning habitat availability also play a role in reproductive output (Blanchfield and Ridgway 2005). A template of the parameters of the population projection matrix models can be found in the Appendix.

Population resilience metrics were then calculated based on the population projection matrix models following the framework laid out in Capdevila et al. (2020). The equations used to calculate these metrics can be found in Table 2. Calculated metrics included reactivity, maximal population amplification, inertia amplification, first-step population attenuation, maximal population attenuation, long-term population attenuation, reactivity envelope, inertia envelope, damping ratio, and convergence time. Maximal population amplification always occurred in the first year after the disturbance in our models, so this metric was always equal to reactivity and as such was not used in further analyses.

Statistical analysis

Partial redundancy analysis was used to evaluate relationships between resilience metrics and genetic and environmental variables using data from all 23 streams. Analyses were performed in the R package vegan (Oksanen et al. 2020). Drainage was used as a conditioning factor to partition out the variation attributed to drainage. Forward selection ($\alpha = 0.1$) was used to select important variables from a set of candidate variables, including genetic covariates conditioned on environmental covariates to partition out the variation associated with the environmental covariates. Genetic covariates included H_e, H_o, A_r, N_e, relatedness, F_{ST}, and F_{IS}. Environmental covariates included elevation, drainage area, slope, distance to confluence, and flow accumulation difference. Variance inflation factor was used to evaluate collinearity of selected variables. Both covariance and correlation matrices of the response variables were used for redundancy analyses, and the performance of the models was compared using adjusted R^2 values. The covariance matrix was created by Hellinger transforming the response variable matrix, while the correlation matrix was untransformed. Significance was evaluated using a global permutation test using 1000 permutations and an alpha value of 0.05.

RESULTS

Across the 23 streams, a total of 506 individuals were successfully genotyped. Sample sizes per stream ranged from 8 to 32. In the 18-stream subset used for isolation by distance analysis, a total of 391 individuals were genotyped, with sample sizes ranging from 8 to 31 per stream. A total of 15 populations were designated based

TABLE 2 Calculation of resilience metrics as recommended by Capdevila et al. (2020). Each metric was calculated using population projection matrix models for each of the 25 headwater streams sampled. Subscripts associated with ρ represent the time frame of a study. The number 1 indicates the first step, max and min are maximum and minimum amplication and attenuation, and ∞ is inertia. Equations terms are as follows: A = the population matrix model; $\hat{A}$ = the standardized matrix population model, calculated as A/λ_{max}; minCS = the minimum column sum of the matrix; v = the dominant left eigenvector, the reproductive value vector of A; w = the dominant right eigenvector, the stable demographic structure of A; λ_1 = the dominant eigenvalue; λ_2 = the largest subdominant eigenvalue; λ_{max} = the dominant eigenvalue of A; and ρ = the transient bounds or damping ratio when distinguished with an overbar (amplification) or underbar (attenuation).

Resilience attribute	Metric	Calculation	Interpretation
Compensation	Reactivity	$\bar{\rho}_1 = \lVert\hat{A}\rVert_1$	The largest population density a population can achieve at the first time step following a disturbance
	Max amplification	$\bar{\rho}_{\max} = \max_{t>0}\left(\lVert\hat{A}^t\rVert_1\right)$	The largest population density a population can achieve at any time step following a disturbance
	Amplification inertia	$\bar{\rho}_\infty = \frac{v_{\max}\lVert w\rVert_1}{v^T w}$	The largest long-term population density a population can achieve
Resistance	First-step attenuation	$\underline{\rho}_1 = \mathrm{minCS}\left(\hat{A}\right)$	The lowest possible population density a population can achieve in the first time step following a disturbance
	Max attenuation	$\underline{\rho}_{\min} = \min_{t>0}\left(\mathrm{minCS}\left(\hat{A}^t\right)\right)$	The lowest population density a population can achieve at any time step following a disturbance
	Attenuation inertia	$\underline{\rho}_\infty = \frac{v_{\min}\lVert w\rVert_1}{v^T w}$	The lowest long-term population density a population can achieve
Transient envelope	Reactivity envelope	$\lVert\hat{A}\rVert_1 / \mathrm{minCS}\left(\hat{A}\right)$	Lower values indicate a population that resists changes in density following disturbance
	Inertia envelope	$\frac{v_{\max}\lVert w\rVert_1}{v^T w} / \frac{v_{\min}\lVert w\rVert_1}{v^T w}$	Higher values indicate greater displacement from its initial stable state in the long term
Recovery time	Damping ratio	$\rho = \lambda_1 / \lVert\lambda_2\rVert$	Dimensionless measure of time to convergence to a stable state. Smaller values represent slower convergence
	Convergence time	$t_x = \log(\rho)/\log(x)$	Time-stamped measure of the time required for a population to converge to a stable state. Smaller values represent quicker convergence

on genetics, each containing between one and four streams (Table 1). No null alleles or significant deviations from Hardy–Weinberg equilibrium were detected. Mean (SD) calculated values for genetic diversity metrics were H_o = 0.58 (0.08), H_e = 0.62 (0.08), A_r = 5.28 (0.87), N_e = 95.71 (125.98), relatedness = −0.04 (0.02), F_{IS} = 0.08 (0.07), and population-specific F_{ST} = 0.21 (0.10) (Table 3). Mean pairwise F_{ST} values were similar by drainage. Watersheds with more than one pairwise comparison, the Greenbrier River, Middle Fork, and North Fork South Branch Potomac River watersheds, had mean (SD) F_{ST} values of 0.087 (0.042), 0.091 (0.044), and 0.092 (0.039), respectively. The Cranberry River and Dry Fork watersheds only contained two study streams and thus only had one pairwise comparison. The streams in the Cranberry watershed had an F_{ST} of 0.16, and the Dry Fork streams had an F_{ST} of 0.14. A summary of remotely sensed environmental covariates can be found in Table A.1.

Genetic differentiation was observed across all streams, generally associated with watershed designation. When all streams were run together, 11 was the most likely number of populations, where mean ln[$P(K|D)$ = −2072.2]. Based on this global analysis, the Cranberry, Dry Fork, North Fork South Branch Potomac, and Upper Elk contained one population while the Greenbrier contained three and the Middle Fork contained four (Figure 2). When subsets of the data based on these populations were analyzed, genetic differentiation was observed in four of the six watersheds sampled. Single populations were found in each the Upper Elk (Figure 3A) and Cranberry River (Figure 3B)

TABLE 3 Summary of genetic indices calculated for headwater Brook Trout populations in central Appalachia.

Population	H_o	H_e	A_r	N_e	Relatedness	F_{IS}	F_{ST}
Cranberry	0.63	0.67	6.46	54.90	−0.03	0.07	0.16
Clubhouse	0.54	0.54	5.77	39.00	−0.04	0.01	0.32
Lower Greenbrier	0.44	0.50	4.89	46.30	−0.05	0.14	0.37
Upper Greenbrier	0.56	0.68	6.01	46.30	−0.03	0.18	0.14
Elklick	0.70	0.67	5.04	35.70	−0.04	−0.03	0.14
NF Red	0.63	0.67	5.91	38.50	−0.05	0.10	0.14
Long (MF)	0.69	0.70	5.79	30.00	−0.07	0.05	0.09
Panthers	0.51	0.55	4.91	37.40	−0.03	0.06	0.30
Schoolcraft	0.47	0.49	3.34	43.00	−0.04	0.07	0.37
Upper Middle Fork	0.56	0.62	5.63	161.20	−0.02	0.11	0.22
Brushy	0.63	0.64	4.97	483.00	−0.03	0.03	0.19
Little Low Place	0.70	0.74	6.53	168.90	−0.04	0.07	0.06
Long/Roaring	0.51	0.64	4.80	12.60	−0.08	0.23	0.17
Whites	0.59	0.64	5.20	196.30	−0.03	0.09	0.19
Crooked	0.48	0.48	3.99	25.50	−0.05	0.03	0.38

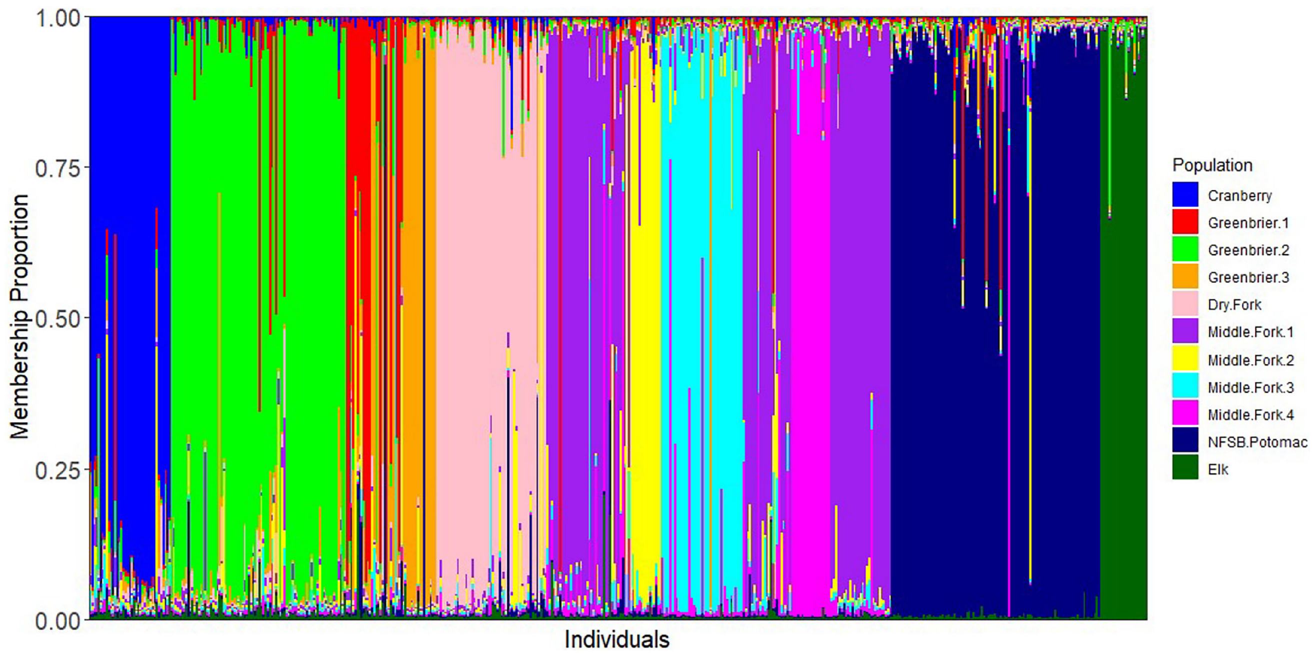

FIGURE 2 A STRUCTURE plot based on all sample streams. The most likely number of populations based on the global analysis based on $\log_e$ likelihood and change in ΔK (Evanno et al. 2005) was 11. The populations were largely differentiated based on watershed, but the Greenbrier and Middle Fork watersheds each contained more than one population. Subsets of the global data set were analyzed further for more fine-scale differentiation.

watersheds. The Upper Elk watershed only contained one study stream and the Cranberry only contained two, which were close in proximity (distance between middle sampling section = 1531 m). All other watersheds contained more than one population. Two populations were observed in the Dry Fork watershed, each population corresponding to a study stream (Figure 3C). The Greenbrier watershed had three separate populations, Upper Greenbrier containing Poca and Lick runs, Lower Greenbrier containing Block and Elleber runs, and a population containing only Clubhouse Run (Figure 3D). Four populations were observed in the Middle Fork watershed. The populations defined in the Middle Fork watershed included Upper Middle Fork (Birch Run, Light Run, Rocky Run, and Sugar Drain), Panthers (Panther and North Fork Panther runs), a Long (Middle Fork) Run population, and a Schoolcraft Run population (Figure 3E). Four populations were also detected in

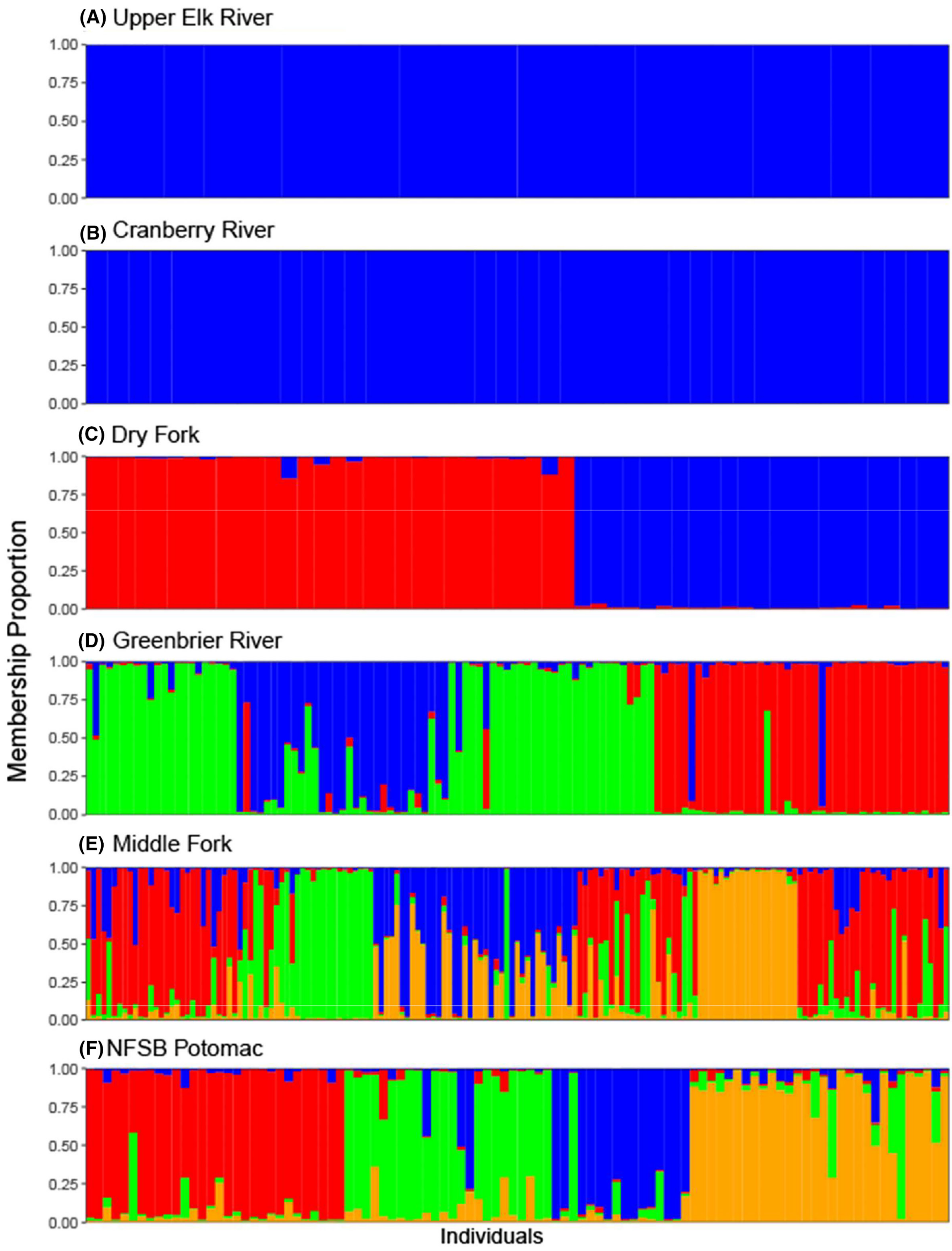

FIGURE 3 Multiple STRUCTURE plots used to designate headwater Brook Trout populations within each watershed evaluated in the long-term Brook Trout monitoring project. Each plot represents the most likely number of populations in the watershed based on $\log_e$ likelihood and change in ΔK (Evanno et al. 2005). The watersheds represented in this study include (A) Upper Elk River, (B) Cranberry River, (C) Dry Fork, (D) Greenbrier River, (E) Middle Fork, and (F) North Fork South Branch (NFSB) Potomac River.

the North Fork South Branch Potomac watershed and included Brushy Run, Little Low Place (Vance Run), Long/Roaring (Long [Seneca] and Roaring runs), and Whites Run (Figure 3F).

Resilience metrics were calculated for each of the 15 genetically identified populations (Table 4). For all models, maximum amplification occurred in the first time step, so reactivity and maximum amplification were always equal. Mean (SD) for each of the resilience metrics was reactivity or maximum amplification = 14.08 (5.52), amplification inertia = 6.67 (2.31), first-step attenuation = 0.31 (0.05), maximum attenuation = 0.13 (0.04), attenuation inertia = 0.48 (0.03), reactivity envelope = 48.14 (24.23), inertia envelope = 129.63 (82.15), damping ratio = 1.11 (0.04), and convergence time = 59.17 (27.97).

Forward selection procedure indicated that population-specific F_{ST}, F_{IS}, A_r, and N_e were important variables in predicting resilience metrics. No collinearity was observed between these variables since all variance inflation factors were <10. The redundancy analysis (RDA) using the correlation matrix (untransformed response variables; adjusted $R^2 = 0.832$) performed better than the model using the covariance matrix (Hellinger-transformed response variables; adjusted $R^2 = 0.469$). Variance partitioning procedures on the correlation RDA indicated that drainage described 69.7% of the variation in the resilience metrics by population, while genetic variables described 13.5%, and 0% of the variance was described by both drainage and genetic variables combined. The overall adjusted R^2 for the partial RDA was 0.832 (Figure 4). The global permutations test indicated that the strength of the linear relationships between resilience and genetic variables was significant ($p = 0.042$). Axis-specific eigenvalues, proportion of variance explained, and cumulative proportion of variance explained can be found in Table 5, and the results from the forward selection procedure are found in Table 6.

The results of the partial RDA indicated that F_{IS} was correlated with higher levels of maximum attenuation and negatively associated with reactivity envelope. Population-specific F_{ST} was correlated with higher levels of first-step attenuation, a metric of resistance, and negatively correlated with reactivity envelope metrics, especially reactivity envelope. Rarefied allelic richness was found to have a negative relationship with maximum attenuation and a positive relationship with reactivity envelope. Effective population size was correlated positively with long-term attenuation and negatively with convergence time.

DISCUSSION

Genetic factors appear to be related to population resilience metrics in our study systems. Inbreeding coefficient (F_{IS}), population-specific F_{ST}, rarefied allelic richness, and effective population size were all correlated with resilience in our populations. Inbreeding coefficient and population-specific F_{ST} were found to be positively associated with resistance metrics, specifically maximum and first-step attenuation, respectively. Maximum attenuation describes the lowest population density that can be reached following a disturbance and can be seen as a measure of overall resistance to disturbance, and first-step attenuation describes the lowest density a population can achieve in the first time step following a disturbance (Capdevila et al. 2020). Conversely, negative relationships between F_{IS} and F_{ST} with reactivity envelope were observed. Reactivity envelope describes how a population responds in the short term to a disturbance by changes in abundance, with lower values representing higher resistance to change (Capdevila et al. 2020). The negative relationship we observed between F_{IS} and F_{ST} and the reactivity envelope metric would support that higher F_{IS} and F_{ST} result in greater resistance to change. High levels of inbreeding and isolation could be a consequence of population fragmentation (Beer et al. 2019). Brook Trout populations have been observed to respond to isolation with high juvenile survival and faster generation times (Letcher et al. 2007) potentially accounting for the positive relationship we observed between F_{IS} and F_{ST} and resistance metrics. While a positive relationship between isolation or inbreeding and resistance may seem counterintuitive, previous studies have found that populations with longer generation times are less resistant to disturbance (Neilson et al. 2020; Capdevila et al. 2021). Additionally, high survival rates have also been linked to high demographic resistance (Buckley and Puy 2022).

Rarefied allelic richness was positively associated with reactivity envelope and negatively associated with maximum attenuation. In dendritic networks such as stream systems, A_r has been linked to connectivity between populations, with high A_r being associated with more connected populations (Paz-Vinas and Blanchet 2015). This result further illustrates relationships we previously discussed between isolation and high resilience, specifically resistance. These relationships may be driven by the inverse of the relationships between F_{IS} and demographic resistance. High levels of connectivity among Brook Trout populations may result in lower juvenile survival and longer generation times (Letcher et al. 2007), which may result in lower resistance (Neilson et al. 2020; Capdevila et al. 2021; Buckley and Puy 2022). Rescue effects associated with connectivity could mitigate some of the negative effects associated with low demographic resistance though through lower extinction probability (Gotelli 1991).

Effective population size was found to have a positive relationship with long-term attenuation and a negative relationship with first-step attenuation. Large effective

TABLE 4 Results from the population projection matrix models evaluating nine population resilience metrics from headwater stream Brook Trout populations in central Appalachia. Maximum amplification is not displayed here because in all runs, maximum amplification occurred in the first time step, resulting in reactivity and maximum amplification being equal.

Population	Reactivity	First-step attenuation	Amplification inertia	Attenuation inertia	Max attenuation	Reactivity envelope	Inertia envelope	Damping ratio	Convergence time
Cranberry	24.92	0.27	11.34	0.46	0.09	92.44	291.22	1.05	114.50
Clubhouse	15.09	0.26	6.88	0.46	0.09	58.50	159.39	1.13	43.50
Lower Greenbrier	13.86	0.35	6.72	0.48	0.14	40.05	97.19	1.13	43.50
Upper Greenbrier	11.73	0.28	6.09	0.52	0.14	41.46	85.50	1.08	65.50
Elklick	9.23	0.29	4.41	0.48	0.13	31.62	70.30	1.15	34.50
NF Red	7.07	0.45	4.12	0.53	0.23	17.11	34.01	1.10	53.50
Long (MF)	16.22	0.29	7.29	0.45	0.09	56.57	178.80	1.08	65.50
Panthers	11.38	0.35	5.37	0.47	0.12	32.29	91.63	1.08	63.50
Schoolcraft	12.85	0.34	6.34	0.49	0.13	38.05	98.48	1.05	114.50
Upper Middle Fork	10.90	0.27	5.44	0.50	0.13	39.84	86.80	1.12	44.50
Brushy	8.41	0.31	4.30	0.51	0.15	27.35	54.98	1.14	37.50
Little Low Place	20.46	0.23	9.65	0.47	0.10	87.80	203.91	1.14	40.50
Long/Roaring	8.18	0.40	3.90	0.48	0.16	20.67	52.23	1.15	33.50
Whites	17.41	0.34	7.80	0.45	0.12	50.93	143.35	1.15	36.50
Crooked	23.48	0.27	10.42	0.44	0.08	87.42	296.65	1.06	96.50

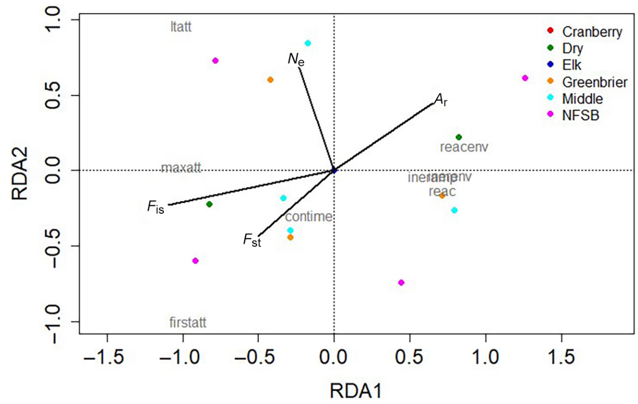

FIGURE 4 Distance triplot displaying weighted species sums of a partial redundancy analysis (RDA) of resilience metrics and genetic variables associated with headwater Brook Trout populations in central Appalachia. Circles represent genetically assigned Brook Trout populations, with colors representing different HUC10 watersheds (NFSB = North Fork South Branch). Gray text represents resilience metrics, and black arrows and black text represent vectors associated with genetic diversity indices.

TABLE 5 Summary of statistical results of the redundancy analysis (RDA) performed relating resilience metrics to genetic and environmental indices associated with headwater Brook Trout populations. Eigenvalues represent the importance of the individual axes. Proportion variation explained is the percentage of the total variance explained by each individual axis, and cumulative proportion represents the cumulative proportion of the variance explained by that axis and more important axes.

Importance of components	RDA1	RDA2	RDA3
Eigenvalue	1.364	0.306	0.142
Proportion variance explained	0.752	0.169	0.078
Cumulative proportion	0.752	0.921	0.999

TABLE 6 Statistical results of the RDA performed relating resilience metrics to genetic and environmental indices associated with headwater Brook Trout populations, showing the results from the forward selection procedure.

Variable	df	F	p
F_{ST}	1	3.11	0.04
F_{IS}	1	2.14	0.08
A_r	1	1.09	0.09
N_e	1	1.01	0.09
H_o	1	0.77	0.45
H_e	1	0.66	0.61

population sizes can indicate that populations are more stable over time in terms of abundance and have a more balanced breeding sex ratio (Caballero 1994). These results would suggest that populations with high N_e are resistant to long-term fluctuations while being susceptible to short-term fluctuations. Stream-dwelling Brook Trout populations have been observed to have highly fluctuating abundances (Kanno et al. 2016; Andrew et al. 2022) and have a nearly 1:1 breeding sex ratio (Kanno et al. 2011a). In our study streams, Brook Trout populations have been observed to experience >60% reductions in abundance due to environmental factors such as drought disturbance (Hakala and Hartman 2004). Some populations within our study systems have been observed to respond to disturbances differently than what is observed in the majority of the streams due primarily to demographic and habitat factors (Andrew 2018). Since Brook Trout populations, including our study populations, fluctuate naturally, the N_e of our populations may be largely driven by long-term stability and gene flow rather than short-term stability. This relationship is reflected in the positive correlation observed between N_e and long-term attenuation. Effective population size has been linked to population viability both in the short term (mitigating inbreeding depression) and in the long term (maintaining evolutionary potential) (Frankham et al. 2014). Long-term attenuation describes a population's ability to resist long-term decreases in population density following a disturbance (Capdevila et al. 2020). Intuitively then, this resilience attribute would be predicted to be positively correlated with N_e, illustrating how population stability may impact demographic resilience.

Our data show trends that would be consistent with what would be predicted by Letcher et al. (2007). There was a negative trend between population-specific F_{ST} and mean length and a positive relationship between population-specific F_{ST} and age-0 survival probability, but neither of these relationships was statistically significant. As stated above, Letcher et al. (2007) found that isolated populations have smaller average body sizes and higher juvenile survival, both of which can result in higher population resilience as derived from demographic rates. Additional effort into looking at these relationships is likely warranted though since our sample sizes were low, only 15 populations, and the relationships were not strong.

While this study focused on genetic factors, it is also clear that other factors also play a role in determining population resilience. Drainage level covariates explained a large amount of the variation observed in population resilience. Factors such as presence of nonnative salmonids (Budy et al. 2020), harvest characteristics (Clarke et al. 2022), and habitat condition (Murphy et al. 2020) have also been linked to population resilience. These factors are also likely contributing to resilience in the study populations as well, and this variation would be contained within the partitioned variation of the redundancy analysis.

Understanding the factors that result in high resilience in Brook Trout populations appears to require the consideration of many variables. Genetic measures were good predictors of resilience in this study. While several factors were found to contribute to resilience, a general pattern of connectivity associated with resilience was observed. Metrics indicative of connectivity between populations (F_{IS}, A_r, and F_{ST}) were generally good predictors of population resilience metrics. Effective population size, N_e, was also an important variable and is another possible indicator of connectivity or isolation gradients. Connectivity between populations has been linked to higher resilience and persistence capabilities in stream-dwelling fishes (Campbell et al. 2019). Our data seem to contradict these hypotheses. While our results suggest that resilience is higher in more isolated systems based on their demographics, isolated populations are more prone to localized extinctions (Van Schmidt and Beissinger 2020). Given these concerns, it is possible that the resilience we have observed in isolated streams is a negative consequence of isolation as populations demographically adjust to survive less desirable conditions. As such, other factors beyond simply population demographic resilience should be accounted for when managing Brook Trout populations. In another West Virginia watershed, barrier removal projects have proven successful in rapidly connecting previously disconnected populations, opening up the possibility of rescue effects from potential extinction events (Wood et al. 2018). When barriers to movement do not exist, Brook Trout populations within headwater streams in central Appalachia likely display high levels of connectivity. Studies of other stream-dwelling salmonids suggest that high connectivity results in higher population resilience (Neville et al. 2009; Campbell et al. 2019), while our results suggest that population dynamics resulting from isolation result in higher demographic resilience, likely at the expense of other desirable population traits. Given the evidence we present in the light of other literature, fully understanding a population's connectivity and isolation dynamics and population demographics can help to provide a more complete picture of the resilience of that population. As such, genetic data or demographic data alone may not tell the entire story of a population's resilience, and it may be necessary to consider both when evaluating population resilience.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data associated with this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The care and handling of all fish captured for this ongoing sampling is in accordance with protocol 15-0506 approved by the West Virginia University Institutional Animal Care and Use Committee.

REFERENCES

Adamack, A. T., & Gruber, B. (2014). PopGenReport: Simplifying basic population genetic analyses in R. *Methods in Ecology and Evolution*, *5*(4), 384–387. https://doi.org/10.1111/2041-210X.12158

Andrew, R. G. (2018). *Examination and characterization of brook trout before and after a broad scale disturbance event in headwater streams of West Virginia, USA* [Doctoral dissertation, West Virginia University]. https://doi.org/10.33915/etd.7153

Andrew, R. G., Schwinghamer, C. W., Hartman, K. J., & Briggs, E. E. (2022). Climate change influence on Brook Trout populations in the central Appalachians. *Ecology of Freshwater Fish*, *31*(4), 710–725. https://doi.org/10.1111/eff.12664

Beer, S. D., Bartron, M. L., Argent, D. G., & Kimmel, W. G. (2019). Genetic assessment reveals population fragmentation and inbreeding in populations of Brook Trout in the Laurel Hill of Pennsylvania. *Transactions of the American Fisheries Society*, *148*(3), 620–635. https://doi.org/10.1002/tafs.10153

Blanchfield, P. J., & Ridgway, M. S. (2005). The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine Brook Trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(12), 2694–2705. https://doi.org/10.1139/f05-176

Buckley, Y. M., & Puy, J. (2022). The macroecology of plant populations from local to global scales. *New Phytologist*, *233*(3), 1038–1050. https://doi.org/10.1111/nph.17749

Budy, P. E., Walsworth, T., Thiede, G. P., Thompson, P. D., McKell, M. D., Holden, P. B., Chase, P. D., & Saunders, W. C. (2020). Resilient and rapid recovery of native trout after removal of a non-native trout. *Conservation Science and Practice*, *3*(2), Article e325. https://doi.org/10.1111/csp2.325

Caballero, A. (1994). Developments in the prediction of effective population size. *Heredity*, *73*, 657–679. https://doi.org/10.1038/hdy.1994.174

Campbell, T., Simmons, J., Sáenz, J., Jerde, C. L., Cowan, W., Chandra, S., & Hogan, Z. (2019). Population connectivity of adfluvial and stream-resident Lahontan Cutthroat Trout: Implications for resilience, management, and restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(3), 426–437. https://doi.org/10.1139/cjfas-2017-0483

Capdevila, P., Stott, I., Beger, M., & Salguero-Gómez, R. (2020). Towards a comparative framework of demographic resilience. *Trends in Ecology & Evolution*, *35*(9), 776–786. https://doi.org/10.1016/j.tree.2020.05.001

Capdevila, P., Stott, I., Cant, J., Beger, M., Grace, M., & Salguero-Gómez, R. (2021). Life history mediates the trade-offs among different components of demographic resilience. *Ecology Letters*, *25*(6), 1566–1579. https://doi.org/10.1111/ele.14004

Clarke, S. H., McCracken, G. R., Humphries, S., Ruzzante, D. E., Grant, J. W. A., & Fraser, D. J. (2022). Demographic resilience of Brook Trout populations subjected to experimental size-selective harvesting. *Evolutionary Applications*, *15*(11), 1792–1805. https://doi.org/10.1111/eva.13478

Dakos, V., & Bascompte, J. (2014). Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(49), 17546–17551. https://doi.org/10.1073/pnas.1406326111

Daraio, J. A., & Bales, J. D. (2014). Effects of land use and climate change on stream temperature I: Daily flow and stream temperature projections. *Journal of the American Water Resources Association*, *50*(5), 1155–1176. https://doi.org/10.1111/jawr.12179

Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillet, B. J., & Ovenden, J. R. (2014). NeEstimator V2: Re-implementation of software for the estimation of contemporary effective population size (N_e) from genetic data. *Molecular Ecology*, *14*(1), 209–214. https://doi.org/10.1111/1755-0998.12157

Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE and implementing the Evanno method. *Conservation Genetics Resources*, *4*, 359–361. https://doi.org/10.1007/s12686-011-9548-7

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*, *170*, 56–63. https://doi.org/10.1016/j.biocon.2013.12.036

Frankham, R., Lees, K., Montgomery, M. E., England, P. R., Lowe, E. H., & Briscoe, D. A. (1999). Do population size bottlenecks reduce evolutionary potential? *Animal Conservation*, *2*(4), 255–260. https://doi.org/10.1111/j.1469-1795.1999.tb00071.x

Gotelli, N. J. (1991). Metapopulation models: The rescue effect, the propagule rain, and the core-satellite hypothesis. *The American Naturalist*, *138*(3), 768–776. https://doi.org/10.1086/285249

Goudet, J. (2003). *FSTAT, a program to estimate and test gene diversities and fixation indices*. Department of Ecology and Evolution, Université de Lausanne. https://www2.unil.ch/popgen/softwares/fstat.htm

Goudet, J., & Jombart, T. (2021). hierfstat: Estimation and tests of hierarchical F-statistics. R package version 0.5-10. https://CRAN.R-project.org/package=hierfstat

Hakala, J. P., & Hartman, K. J. (2004). Drought effects on stream morphology and Brook Trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia*, *515*(1–3), 203–213. https://doi.org/10.1023/B:HYDR.0000027330.12182.24

Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, "resilient"? *Trends in Ecology & Evolution*, *30*(9), 503–506. https://doi.org/10.1016/j.tree.2015.06.010

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*, 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hudy, M., Thieling, T. M., Gillespie, N., & Smith, E. P. (2005). Distribution, status and threats to Brook Trout within the eastern United States. In *Eastern Brook Trout joint venture*. Trout Unlimited.

Hudy, M., Thieling, T. M., Gillespie, N., & Smith, E. P. (2008). Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the eastern United States. *North American Journal of Fisheries Management*, *28*(4), 1069–1085. https://doi.org/10.1577/M07-017.1

Intergovernmental Panel on Climate Change. (2021). *Climate Change 2021 – The physical science basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://www.ipcc.ch/report/ar6/wg1/

Ives, A. R. (1995). Measuring resilience in stochastic systems. *Ecological Monographs*, *65*(2), 217–233. https://doi.org/10.2307/2937138

Jamieson, I. G., & Allendorf, F. W. (2012). How does the 50/500 rule apply to MVPs? *Trends in Ecology & Evolution*, *27*(10), 578–584. https://doi.org/10.1016/j.tree.2012.07.001

Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kanno, Y., Pregler, K. C., Hitt, N. P., Letcher, B. H., Hocking, D. J., & Wofford, J. E. B. (2016). Seasonal temperature and precipitation regulate Brook Trout young-of-the-year abundance and population dynamics. *Freshwater Biology*, *61*(1), 88–99. https://doi.org/10.1111/fwb.12682

Kanno, Y., Vokoun, J. C., & Letcher, B. H. (2011a). Sibship reconstruction for inferring mating systems, dispersal and effective population size in headwater Brook Trout (*Salvelinus fontinalis*) populations. *Conservation Genetics*, *12*(3), 619–628. https://doi.org/10.1007/s10592-010-0166-9

Kanno, Y., Vokoun, J. C., & Letcher, B. H. (2011b). Fine-scale population structure and riverscape genetics of Brook Trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. *Molecular Ecology*, *20*(18), 3711–3729. https://doi.org/10.1111/j.1365-294X.2011.05210.x

Kelson, S. J., Kapuscinski, A. R., Timmins, D., & Ardren, W. R. (2015). Fine-scale genetic structure of Brook Trout in a dendritic stream network. *Conservation Genetics*, *16*(1), 31–42. https://doi.org/10.1007/s10592-014-0637-5

King, T. L., Lubinski, B. A., Burnham-Curtis, M. K., Stott, W., & Morgan, R. P. (2012). Tools for the management and conservation of genetic diversity in Brook Trout (*Salvelinus fontinalis*): Tri- and tetranucleotide microsatellite markers for the assessment of genetic diversity, phylogeography, and historical demographics. *Conservation Genetics Resources*, *4*(3), 539–543. https://doi.org/10.1007/s12686-012-9603-z

Lande, R., & Shannon, S. (1996). The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, *50*(1), 434–437. https://doi.org/10.2307/2410812

Letcher, B. H., Nislow, K. H., Coombs, J. A., O'Donnell, M. J., & Dubreuil, T. L. (2007). Population response to habitat fragmentation in a stream-dwelling Brook Trout population. *PLoS ONE*, *2*(11), Article e1139. https://doi.org/10.1371/journal.pone.0001139

Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, *19*(15), 3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x

Macdonald, P., & Du, J. (2018). mixdist: Finite mixture distribution models. https://rdrr.io/cran/mixdist/

Maloney, K. O., & Weller, D. E. (2011). Anthropogenic disturbance and streams: Land use and land-use change affect stream ecosystems via multiple pathways. *Freshwater Biology*, *56*(3), 611–626. https://doi.org/10.1111/j.1365-2427.2010.02522.x

Markert, J. A., Champlin, D. M., Gutjahr-Gobell, R., Grear, J. S., Kuhn, A., Mcgreevy, T. J., Roth, A., Bagley, M. J., & Nacci, D. E. (2010). Population genetic diversity and fitness in multiple environments. *BMC Evolutionary Biology*, *10*, Article 205. https://doi.org/10.1186/1471-2148-10-205

Morin, R. S., Cook, G. W., Barnett, C. J., Butler, B. J., Crocker, S. J., Hatfield, M. A., Kurtz, C. M., Lister, T. W., Luppold, W. G., McWilliams, W. H., Miles, P. D., Nelson, M. D., Perry, C. H., Piva, R. J., Smith, J. E., Westfall, J. A., Widmann, R. H., & Woodall, C. W. (2016). *West Virginia forests, 2013* (Resource Bulletin NRS-105). U.S. Forest Service, Northern Research Station. https://www.fs.usda.gov/nrs/pubs/rb/rb_nrs105.pdf

Murphy, B. P., Walsworth, T. E., Belmont, P., Conner, M. M., & Budy, P. (2020). Dynamic habitat disturbance and ecological resilience (DyHDER): Modeling population responses to habitat condition. *Ecosphere*, *11*(1), Article e03023. https://doi.org/10.1002/ecs2.3023

Nathan, L. R., Welsh, A. B., & Vokoun, J. C. (2019). Watershed-level brook trout genetic structuring: Evaluation and application of riverscape genetics models. *Freshwater Biology*, *64*(3), 405–420. https://doi.org/10.1111/fwb.13230

Neilson, E. W., Lamb, C. T., Konkolics, S. M., Peers, M. J. L., Majchrzak, Y. N., Doran-Myers, D., Garland, L., Martinig, A. R., & Boutin, S. (2020). There's a storm a-coming: Ecological resilience and resistance to extreme weather events. *Ecology and Evolution*, *10*(21), 12147–12156. https://doi.org/10.1002/ece3.6842

Neville, H., Dunham, J., Rosenberger, A., Umek, J., & Nelson, B. (2009). Influences of wildfire, habitat size, and connectivity on trout in headwater streams revealed by patterns of genetic diversity. *Transactions of the American Fisheries Society*, *138*(6), 1314–1327. https://doi.org/10.1577/T08-162.1

Novotny, E. V., & Stefan, H. G. (2007). Streamflow in Minnesota: Indicator of climate change? *Journal of Hydrology*, *334*, 319–333. https://doi.org/10.1016/j.jhydrol.2006.10.011

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). vegan: Community ecology package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Paradis, E. (2010). pegas: An R package for population genetics with an integrated-modular approach. *Bioinformatics*, *26*, 419–420. https://doi.org/10.1093/bioinformatics/btp696

Paz-Vinas, I., & Blanchet, S. (2015). Dendritic connectivity shapes spatial patterns of genetic diversity: A simulation-based study. *Journal of Evolutionary Biology*, *28*(4), 986–994. https://doi.org/10.1111/jeb.12626

Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics*, *28*, 2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Peters, N. E., & Meybeck, M. (2000). Water quality degradation effects on freshwater availability: Impacts of human activities. *Water International*, *25*(2), 185–193. https://doi.org/10.1080/02508060008686817

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotypes. *Genetics*, *155*, 945–959. https://doi.org/10.1093/genetics/155.2.945

Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution*, *43*(2), 258–275. https://doi.org/10.2307/2409206

Robinson, Z. L., Coombs, J. A., Hudy, M., Nislow, K. H., Letcher, B. H., & Whiteley, A. R. (2017). Experimental test of genetic rescue in isolated populations of Brook Trout. *Molecular Ecology*, *26*(17), 4418–4433. https://doi.org/10.1111/mec.14225

Scheffer, M., Carpenter, S. R., Dakos, V., & Van Nes, E. H. (2015). Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 145–167. https://doi.org/10.1146/annurev-ecolsys-112414-054242

Stolarski, J. T., & Hartman, K. J. (2008). An evaluation of the precision of fin ray, otolith, and scale age determinations for Brook Trout. *North American Journal of Fisheries Management*, *28*(6), 1790–1795. https://doi.org/10.1577/M07-187.1

Stott, I., Hodgson, D. J., & Townsley, S. (2021). popdemo: Demographic modelling using projection matrices. R package version 1.3-1. https://CRAN.R-project.org/package=popdemo

Stott, I., Townley, S., & Hodgson, D. J. (2011). A framework for studying transient dynamics of population projection matrix models. *Ecology Letters*, *14*(9), 959–970. https://doi.org/10.1111/j.1461-0248.2011.01659.x

Vähä, J. P., Erkinaro, J., Niemelä, E., & Primmer, C. R. (2007). Life-history and habitat features influence the within-river genetic structure of Atlantic Salmon. *Molecular Ecology*, *16*(13), 2638–2654. https://doi.org/10.1111/j.1365-294X.2007.03329.x

Van Schmidt, N. D., & Beissinger, S. R. (2020). The rescue effect and inference from isolation–extinction relationships. *Ecology Letters*, *23*(4), 598–606. https://doi.org/10.1111/ele.13460

Whiteley, A. R., Coombs, J. A., Hudy, M., Robinson, Z., Colton, A. R., Nislow, K. H., & Letcher, B. H. (2013). Fragmentation and patch size shape genetic structure of Brook Trout populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(5), 678–688. https://doi.org/10.1139/cjfas-2012-0493

Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian*

Journal of Fisheries and Aquatic Sciences, *62*(4), 872–885. https://doi.org/10.1139/f05-040

Wood, D. M., Welsh, A. B., & Todd Petty, J. (2018). Genetic assignment of Brook Trout reveals rapid success of culvert restoration in headwater streams. *North American Journal of Fisheries Management*, *38*(5), 991–1003. https://doi.org/10.1002/nafm.10185

Wydoski, R. S., & Cooper, E. L. (1966). Maturation and fecundity of Brook Trout from infertile streams. *Journal of the Fisheries Research Board of Canada*, *23*(5), 623–649. https://doi.org/10.1139/f66-055

APPENDIX: Population Project Matrix Models

Population projection matrix model framework was used to evaluate population resilience of headwater Brook Trout populations:

$$\begin{bmatrix} 0 & 0 & F_2 \times S_{\text{egg}} & F_3 \times S_{\text{egg}} \\ S_{\text{age}-0} & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix},$$

where $\boldsymbol{F}$ represents age-class-based fecundity estimates calculated using the length–fecundity relationship from Wydoski and Cooper (1966): $\log(F) = 3.23 \times \log(L_T) - 5.07$, where $\boldsymbol{L_T}$ represents stream-specific mean total length at age of Brook Trout sampled across the entire time span (2003–2019) of the long-term Brook Trout monitoring study. The term $\boldsymbol{S}$ represents survival of Brook Trout as they transition between age-classes. For example, $\boldsymbol{S}_{\text{age-0}}$ represents the proportion of young of the year (age-0) Brook Trout that will survive and transition to age 1. Survival was estimated by following cohorts within a stream across time. Survival ($\boldsymbol{S}_{\text{age}}$) was calculated by dividing the density per 100 m of a cohort in a year by the density per 100 m of the same cohort in the previous year, e.g., $\left(\frac{\text{Catch}_{1[t]}}{\text{Catch}_{0[t-1]}}\right)$. Egg survival ($\boldsymbol{S}_{\text{egg}}$) was calculated by dividing estimated total population fecundity by the number of young of year caught in the following year, $\left(\frac{F_{\text{Tot}[t-1]}}{\text{Catch}_{0[t]}}\right)$. Total population fecundity was calculated by taking the sum of the estimated fecundity of all of the age-2 and age-3 fish sampled in a stream in a year. Population projection matrix models were executed using package popdemo in R (Stott et al. 2021) (Table A.1).

TABLE A.1 Remotely sensed covariates from headwater Brook Trout populations in the study streams in central Appalachia.

Population	Drainage area (km^2)	Slope (%)	Mean elevation (m)	Distance to confluence	Flow accumulation difference
Cranberry	3.27	5.45	1070.00	40.00	25.37
Clubhouse	8.09	7.80	955.00	194.00	28.30
Lower Greenbrier	6.46	13.90	1076.00	127.50	11.69
Upper Greenbrier	2.56	11.45	1013.50	38.00	5.32
Elklick	13.65	18.10	613.00	636.00	1.32
North Fork Red	13.89	13.10	942.00	3016.00	4.82
Long (Middle Fork)	7.65	7.50	695.00	3476.00	8.41
Panthers	4.56	10.80	757.50	30.00	4.57
Schoolcraft	7.94	17.00	736.00	668.00	51.26
Upper Middle Fork	5.34	7.15	827.75	604.50	10.01
Brushy	18.65	6.40	697.00	3803.00	10.19
Little Low Place	5.51	13.20	970.00	35.00	2.46
Long/Roaring	9.93	10.20	762.00	130.00	10.00
Whites	12.80	10.90	728.00	222.00	27.27
Crooked	8.36	5.40	1020.00	2378.00	8.36