Species Status Assessment Report
for the
Tennessee Heelsplitter
Version 1.0

Tennessee Heelsplitter collected from Big War Creek, Tennessee (Ostby et al. 2015, p. 14).

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Species Status Assessment Report for the Tennessee Heelsplitter (*Lasmigona holstonia*)

Prepared by the
U.S. Fish and Wildlife Service

EXECUTIVE SUMMARY

The Tennessee Heelsplitter (*Lasmigona holstonia*) is a small, thin-shelled freshwater mussel that occurs along river margins and in small headwater streams in Virginia, Tennessee, Georgia, Alabama, and historically in North Carolina. Individuals become reproductively active at approximately age three, have a lifespan of 20-30 years, and grow up to 3 inches (75 mm) in length. Adults are yellowish to greenish brown, becoming darker brown with age.

Primary factors influencing the viability of the Tennessee Heelsplitter are common to most freshwater mussels and include: siltation and sedimentation, pollution and toxic spills, drought and floods, aquatic nuisance species, and impoundments. While the timing and magnitude of these threats may differ across the range, they likely affect populations similarly at the rangewide level.

The Tennessee Heelsplitter is predominantly found in headwater streams which are inconsistently surveyed for mussels. The range of the species is well established, but it can be located in habitats along stream margins and in depositional areas, which are not often targeted during surveys. As a result, occurrences are sporadic and limited in parts of the range. Also, the species tends to occur in headwater streams that have a strong spring influence; hence, many of the streams historically occupied by this species have “spring” in the stream name. Furthermore, data to inform population metrics such as abundance and survival are not consistently available across the distribution of the species. Therefore, to describe current resiliency for the Tennessee Heelsplitter, we developed a model determining the amount of suitable habitat within the species’ range. This rangewide habitat suitability model was divided by USGS HUC-10 level, called Analysis Units (AUs), for resiliency and redundancy assessment. To evaluate representation, we used the three major river drainages, or Representation Units (RUs), of occurrence: the Cumberland, New, and Tennessee.

Our current condition analysis reveals that the strongholds for the Tennessee Heelsplitter are in the New River and Tennessee River RUs, with most of the highly resilient AUs having some level of connectivity. Across the range, there are varying levels of suitable habitat to help the species maintain viability, and our model indicates that the Tennessee Heelsplitter has the capability to withstand both stochastic and catastrophic events. Available information indicates the species’ adaptive capacity, and representation, will ensure capability to respond to environmental changes over time.

Future conditions were assessed by predicting how land use/land cover (LULC) changes, as well as climate change, impact the three Rs in the future; this is because primary factors influencing the future viability of the Tennessee Heelsplitter may be affected by such changes. We analyzed changes in resiliency at the AU level at 20 and 40 year timesteps to discern patterns in projected species habitat suitability. We found that while habitat suitability is predicted to change over the next 40 years, 78-91% of the Tennessee Heelsplitter range is

predicted to maintain resiliency (i.e., varying levels of suitable habitat) to sustain the species. This analysis does not account for the discovery of additional populations with future survey efforts which will improve our knowledge of the species.

Future predictions indicate that the distribution of resilient AUs with suitable habitat will remain throughout the Tennessee Heelsplitter range. This future redundancy will ensure that the Tennessee Heelsplitter can withstand catastrophic events. Additionally, the adaptive capacity of the Tennessee Heelsplitter highlights the many aspects of life history and ecology of the species that will enable persistence in place and ability to face future climate challenges. We do not expect future representation, or adaptive capacity, of the Tennessee Heelsplitter to change by 2060. As such, future predicted resiliency, redundancy, and representation for the Tennessee Heelsplitter will be maintained through 2060.

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ACRONYMS AND ABBREVIATIONS

ADEM	Alabama Department of Environmental Management
ANS	Aquatic Nuisance Species
AU	Analysis Unit
CBD	Center for Biological Diversity
CWA	Clean Water Act
EPA	Environmental Protection Agency
ESA	Endangered Species Act
FR	Federal Register
GDNR	Georgia Department of Natural Resources
GHG	Greenhouse gas
HUC	Hydrologic Unit Code
ICLUS	Integrated Climate and Land-Use Scenarios
IPCC	Intergovernmental Panel on Climate Change
LULC	Land use/Land cover
NOAA	National Oceanic and Atmospheric Administration
NPDES	National Pollution Discharge Elimination System
NPS	Nonpoint-Source
PPCPs	Pharmaceuticals and Personal Care Products
RRI	Reservoir Release Improvement Program
RU	Representation Unit
SDS	Sodium Dodecyl Sulfate
Service	U.S. Fish and Wildlife Service
SRP	Species Range Project
SSA	Species Status Assessment
SSP	Shared Socioeconomic Pathway
TVA	Tennessee Valley Authority
USACE	U.S. Army Corps of Engineers

CHAPTER 1. INTRODUCTION

1.1. Petition History

We, the U.S. Fish and Wildlife Service (Service), were petitioned by the Center for Biological Diversity (CBD), Alabama Rivers Alliance, Clinch Coalition, Dogwood Alliance, Gulf Restoration Network, Tennessee Forests Council, West Virginia Highlands Conservancy, Tierra Curry, and Noah Greenwald to list the Tennessee Heelsplitter (*Lasmigona holstonia*) as an endangered or threatened species under the Endangered Species Act (ESA). This request was part of a 2010 petition to list 404 aquatic, riparian, and wetland species in the southeastern United States (CBD 2010, pp. 635–639). On September 27, 2011, we found the petition presented substantial scientific or commercial information indicating that listing the Tennessee Heelsplitter may be warranted (76 FR 59836–59862); substantial findings were made for the other species in this same *Federal Register* notice, though analyses and findings for those other species are addressed separately.

1.2. Purpose of Species Status Assessment (SSA) for the Tennessee Heelsplitter

This SSA report for the Tennessee Heelsplitter was completed to evaluate current and future viability. The SSA framework (Service 2016a, Entire; Smith et al. 2018, Entire) is intended to support an in-depth review of the species' biology and threats, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain long-term viability (Figure 1). The intent is for the SSA report to be easily updated as new information becomes available, and to support all functions of the Endangered Species Program, including candidate assessment, listing, consultations, and recovery. The SSA report will be a living document upon which other documents, such as listing rules, recovery plans, and 5-year reviews, would be based if the species warrants listing under the ESA.

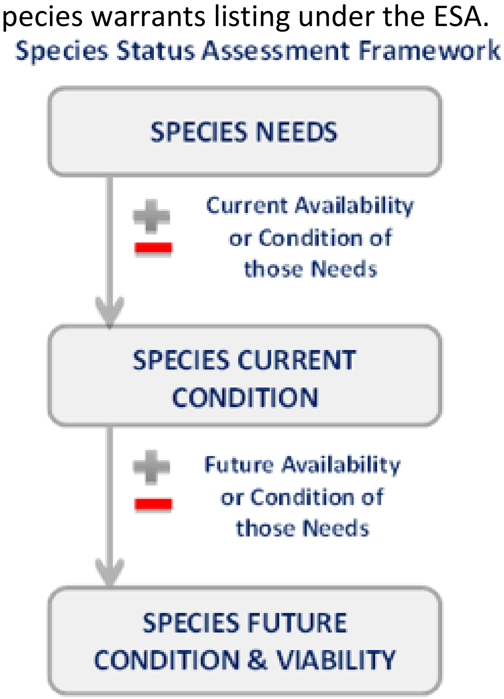

Figure 1. Species Status Assessment framework.

The intent of this report is to provide biological support for the decision on whether to propose to list the Tennessee Heelsplitter as threatened or endangered and does not result in a decision by the Service on whether this species should be proposed for listing as a threatened or endangered species under the ESA. Instead, this SSA report provides a review of the available information strictly related to the biological status of the Tennessee Heelsplitter. The listing decision will be made by the Service after reviewing this document and all relevant laws, regulations, and policies, and the results of a proposed decision will be announced in the *Federal Register,* with appropriate opportunities for public input.

We have determined what the species needs to support viable populations, its current condition in terms of those needs, and its forecasted future condition. In conducting this analysis, we took into consideration the likely changes that are happening in the environment – past, current, and future – to help us understand what factors drive the viability of the species. For this assessment, we generally define viability as the ability of the Tennessee Heelsplitter to sustain populations in natural river systems over time. Using the SSA framework, we consider what the species needs to maintain viability by characterizing the status of the species in terms of its resiliency, redundancy, and representation (Smith et al. 2018, Entire).

- **Resiliency** is the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions (e.g., temperature or rainfall), periodic disturbances within the normal range of variation (e.g., floods or storms), and demographic stochasticity (i.e., normal variation in demographic rates such as mortality and fecundity). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions. Resiliency is positively related to population size as well as growth rate and may be influenced by connectivity among populations. Populations generally need abundant individuals within habitat patches of adequate area and quality to maintain survival along with reproduction despite stochastic events.

- **Redundancy** is the ability of a species to withstand catastrophic events. Catastrophes are stochastic events that are expected to lead to population collapse regardless of population heath and for which adaptation is unlikely. Redundancy, which is about spreading the risk, can be measured through duplication and broad distribution of resilient populations connected across the range of the species. The more resilient populations a species has distributed over a larger area, the better the chance that species can withstand catastrophic events.

- **Representation** describes the ability of a species to adapt to both near-term and long-term changes in its physical (e.g., climate conditions, habitat conditions, habitat structure, etc.) and biological (e.g., pathogens, competitors, predators, etc.) environments. An ability to adapt to new environments (i.e., adaptive capacity) is essential for viability, as species need to continually adapt to their continuously changing environments. Species adapt to novel changes in their environment by either moving to new, more suitable environments, or by altering their phenotypes (i.e., physical, and behavioral traits) to match the new environmental conditions through plasticity or genetic change. The latter occurs via the evolutionary processes of natural selection, gene flow, mutations, and genetic drift.

To evaluate the current and future biological status of the Tennessee Heelsplitter, we assessed a range of conditions allowing us to consider the species' resiliency, redundancy, and representation (together, the 3Rs). This SSA provides a thorough assessment of biology and natural history, in addition to an assessment of demographic risks, stressors, and limiting factors, in the context of species viability and extinction risks. This document compiles the best available scientific and commercial information, in addition to descriptions of past, present, and likely future risk factors to the Tennessee Heelsplitter.

CHAPTER 2. SPECIES BACKGROUND

2.1. Morphological Description

Adult Tennessee Heelsplitter mussels are yellowish to greenish brown, becoming darker brown with age (Parmalee and Bogan 1998, p. 142) (see Figure 2). Their thin, slightly compressed shell is elliptical to rhomboidal in shape, and up to 3 inches (75 mm) in length (Williams et al. 2008, p. 404). The interior of the shell displays a typically white to bluish-white nacre (the lustrous interior layer of the shell), which may have a salmon tint in the shallow umbo cavity (Clarke 1985, p. 7; Williams et al. 2008, p. 404). The foot is typically white (Clarke 1985, p. 6); but specimens from the Duck River, TN sometimes have an orange or peach-colored foot (see Figure 3 for anatomical diagram).

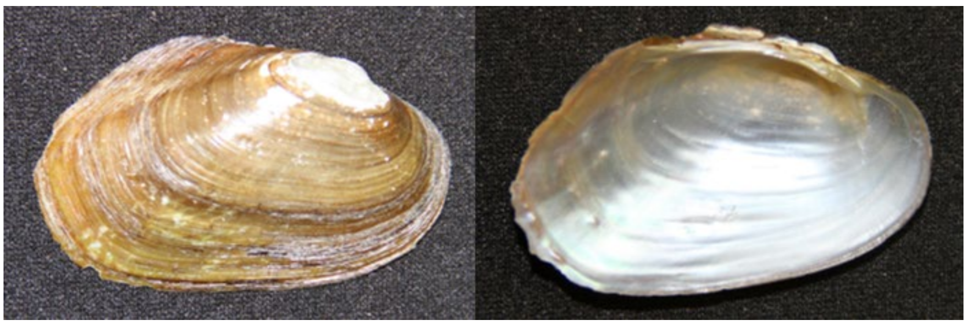

Figure 2. Tennessee Heelsplitter specimen (GDNR).

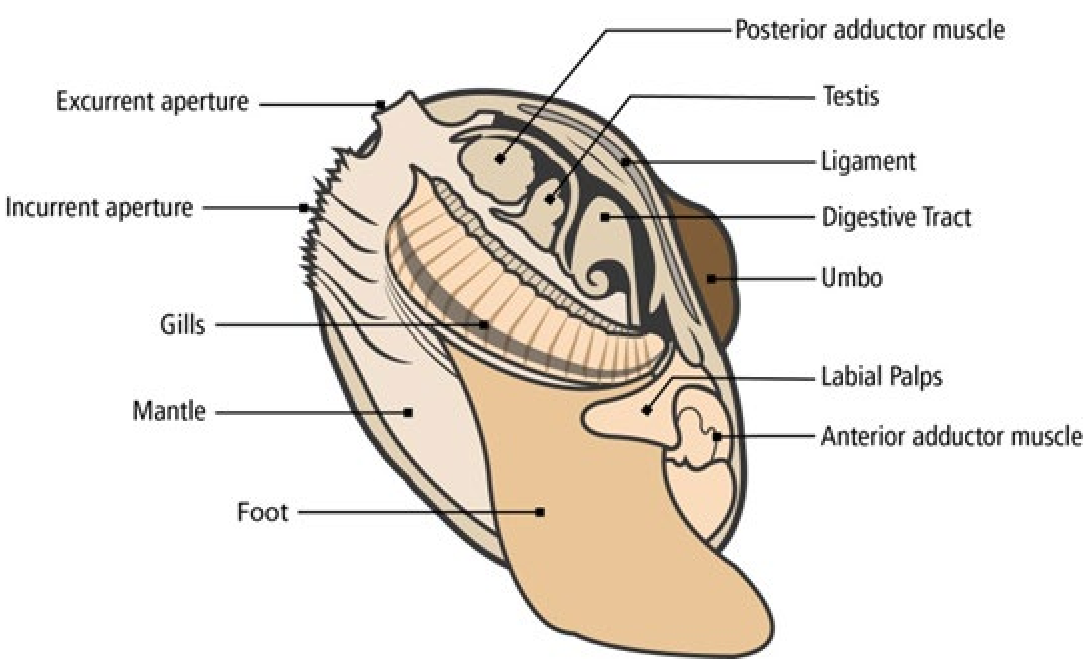

Figure 3. Diagram of mussel anatomy (Matthew Patterson, Service).

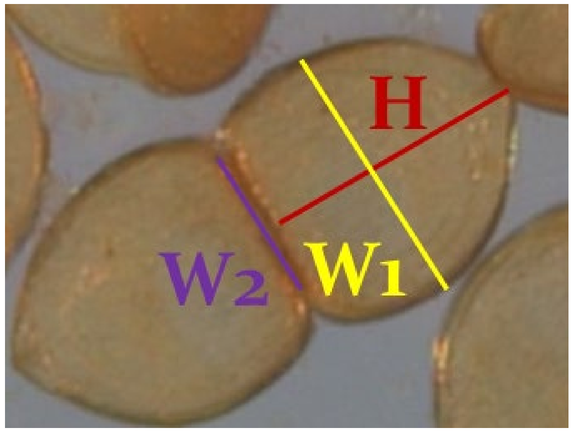

Figure 4. Tennessee Heelsplitter glochidia with shell height and width measurements marked. Photo by Alissa Ganser.

Ortmann (1924, p. 43) notes glochidia as subtriangular (see Figure 4) with large hooks. Their average height is approximately 295 µm, and average length 307 µm (Clarke 1985, p. 9).

2.2. Taxonomy

The Tennessee Heelsplitter (*Lasmigona holstonia*) is a species of freshwater mussel (Phylum Mollusca, Class Bivalvia). Recent studies indicate the genus *Lasmigona* is polyphyletic, which means it is derived from more than one common ancestor, and some species currently in the genus may be reassigned in the future based on reproductive traits (King et al. 1999, p. S65; Breton et al. 2011, p. 1653). This SSA report follows the most recently published and accepted taxonomic treatment of the Tennessee Heelsplitter (Williams et al. 2017, entire; https://molluskconservation.org/Library/Committees/Names/Appendix_1_Bivalves_Revised_Names_List_20210825.pdf) (see Figure 5).

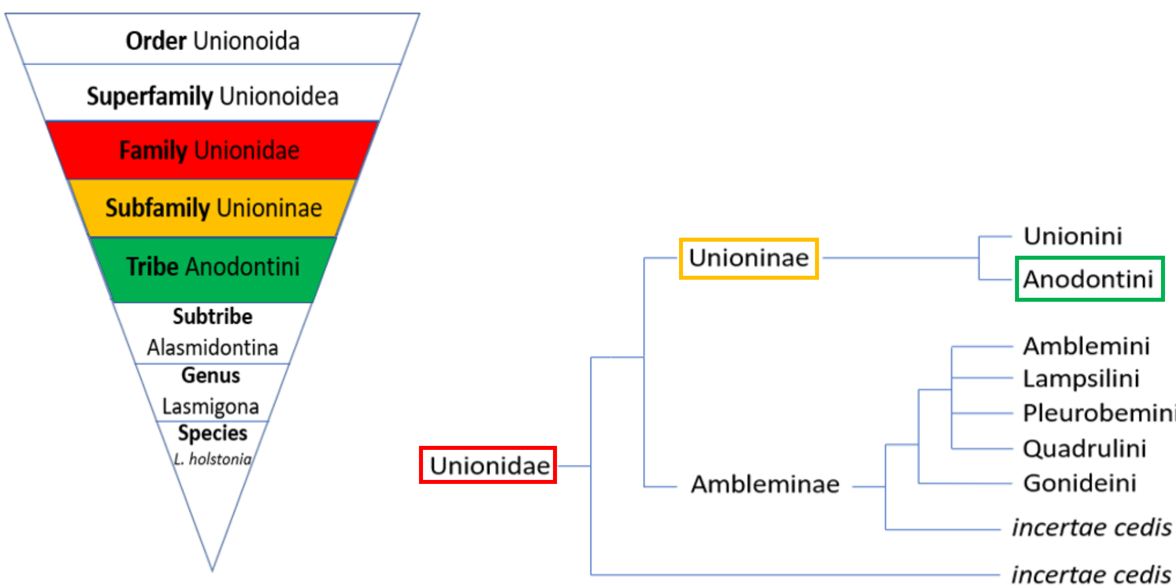

Figure 5. Taxonomic hierarchy of the Tennessee Heelsplitter (left). Genetic tree featuring Family Unionidae (right). Based on Barnhart et al. (2008, p. 371).

There is some taxonomic uncertainty regarding the Tennessee Heelsplitter populations in the Cumberland River system, as well as in populations of the upper Duck and Elk River drainages within the Tennessee River system (Campbell and Harris 2006, p. 7). These possibly represent a closely related undescribed species with morphological and slight life history differences. Specimens collected from these populations of Tennessee Heelsplitter are often referred to as the Barrens Heelsplitter or Toesplitter in some reports and publications (*Lasmigona* sp. or *Lasmigona* sp. cf. *holstonia*) (Layzer et al. 1993, p. 67; Neves et al. 1997, p. 50; Ahlstedt et al. 2017, p. 50). This potential taxonomic differentiation is not formally described, nor does it have genetic data to support recognition. The Barrens Heelsplitter is also not currently accepted as a species by the scientific community; as such, this SSA report includes this variant as a form of the Tennessee Heelsplitter (Williams et al. 2017, p. 41).

Another species, *Lasmigona diversa*, was described from the Tennessee River system by Timothy Conrad in 1856. The Barrens Heelsplitter may represent this taxon, but *Lasmigona diversa* is currently not recognized as a valid species or synonym of the Tennessee Heelsplitter. The Etowah Heelsplitter (*Lasmigona etowaensis*), which was formerly considered a subspecies of the Tennessee Heelsplitter (*Lasmigona holstonia etowahensis*), was recently separated from the Tennessee Heelsplitter based on distribution and genetic analyses; it was elevated to species status (Williams et al. 2017, p. 50). The Etowah Heelsplitter is not included in this SSA because it is now recognized as a different species, and occurs only in the Mobile Basin, where it replaces the Tennessee Heelsplitter (Williams et al. 2008, p. 405).

2.3. Genetics

Data on genetic diversity for the Tennessee Heelsplitter has not been developed. A genetic study using specimens from all RUs was initiated and funded in 2015. However, due to various factors the study has not been completed and no genetic information is currently available (Ganser et al. 2022, pp. 11-16).

2.4. Life History

Most freshwater mussel species broadcast free larvae called glochidia (Barnhart et al. 2008, p. 374). Reproduction begins with males releasing sperm into the water column, which females then siphon to fertilize their eggs (McMahon and Bogan 2001, p. 342) (Figure 6). Females brood the fertilized eggs in their gills until they become mature glochidia (Kat 1984, p. 190). Mature glochidia may be released when the female is disturbed by an appropriate host fish, attaching to the fins or gill filaments until they transform into juvenile mussels (Barnhart et al. 2008, p. 371). The Tennessee Heelsplitter has been the subject of several fish host trials and has a high transformation rate on numerous fish species (Appendix 1). Tennessee Heelsplitter individuals have limited dispersal capability and broadcast glochidia into the water column in hopes they will encounter a suitable fish host (Steg and Neves 1997, p. 34). While broadcasting is considered a more ancestral reproductive strategy among mussels, high transformation rates on multiple fish species likely improves dispersal success.

The Tennessee Heelsplitter becomes reproductively active at approximately age three (Barton 2011, p. 24). The species is likely bradytictic (Bogan 2017, p. 60), meaning the timing of spawning and brooding is long-term (Watters et al. 2001, pp. 544-545), with females gravid for several months between August and the following May (Neves 1991, p. 268; EPA 2008, p. 45; Womble and Rosenberger 2021, p. 21). Gravid specimens have been reported beginning in August; however, some populations, such as those in the Cumberland drainage, may begin spawning in the fall (Clarke 1985, p. 9; Pinder et al. 2002, p. 201). Long-term brooding species have advantages over short-term brooders in that their spawning period is much longer and females may have multiple broods. The lifespan of the Tennessee Heelsplitter is at least 24 years, and while the species might live longer, older females may have lower fecundity compared to younger individuals (Barton 2011, pp. 14-16). The Tennessee Heelsplitter is not considered to be sexually dimorphic, but because it is a long-term brooding species, gravid females may be found year-round or in most seasons. It is possible to discern gravid females, but not non-gravid females, from males. Sex ratios are therefore considered unknown, but it is assumed that sexes are equal in abundance in a population.

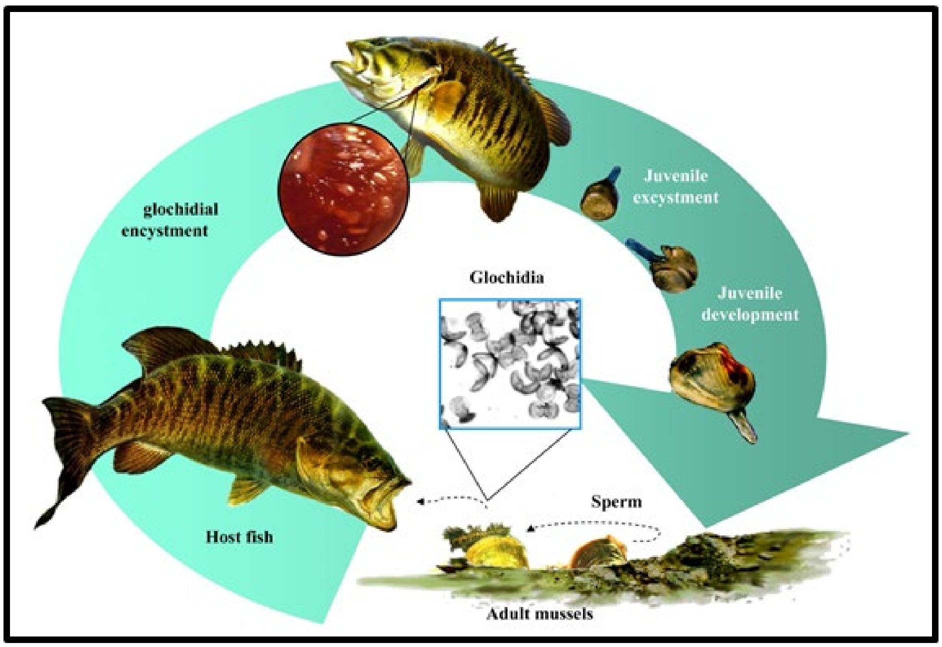

Figure 6. General life cycle of mussels (Shane Hanlon, Service).

2.5. Range and Distribution

The current range of the Tennessee Heelsplitter is based on the compilation of available data from state heritage databases, departments of natural resources, museum records, and survey reports. An occurrence was considered current if the observation was reported from the year 1990 to present, and historical if reported prior to 1990. The Tennessee Heelsplitter range is well established, though inconsistent survey methods and frequency across this range has resulted in a lack of age class structure data and population trends.

We identified representation units (RUs) for the species which contribute to their adaptive potential and are important components of assessing overall species viability (Shaffer and Stein 2000, entire; Service 2016b, p. 23). The Tennessee Heelsplitter has three RUs: the

Tennessee, Cumberland, and New, all of which are major river drainages within the greater Ohio River basin. HUC-10 analysis units (AUs) were identified to inform current condition of populations within each RU. This method provided a consistent scale of available data and is used to communicate current and future condition of the species for assessment purposes.

2.5.1. Historical Range and Distribution

The historical range of the Tennessee Heelsplitter encompassed portions of three major river drainages (i.e., Tennessee River, Cumberland River, and New River), with their distribution predominantly including the western slope of the Appalachian Mountains, the valley-ridge section of the Cumberlandian region, portions of the Cumberland Plateau, and Eastern highland rim (Figure 7) (Clarke 1985, pp. 9-11). There are four records of the species from the Blue Ridge in North Carolina, but despite surveys in rivers and streams of documented occurrence, the species has not been collected in the state since 2002 (Bogan 2017, p. 60).

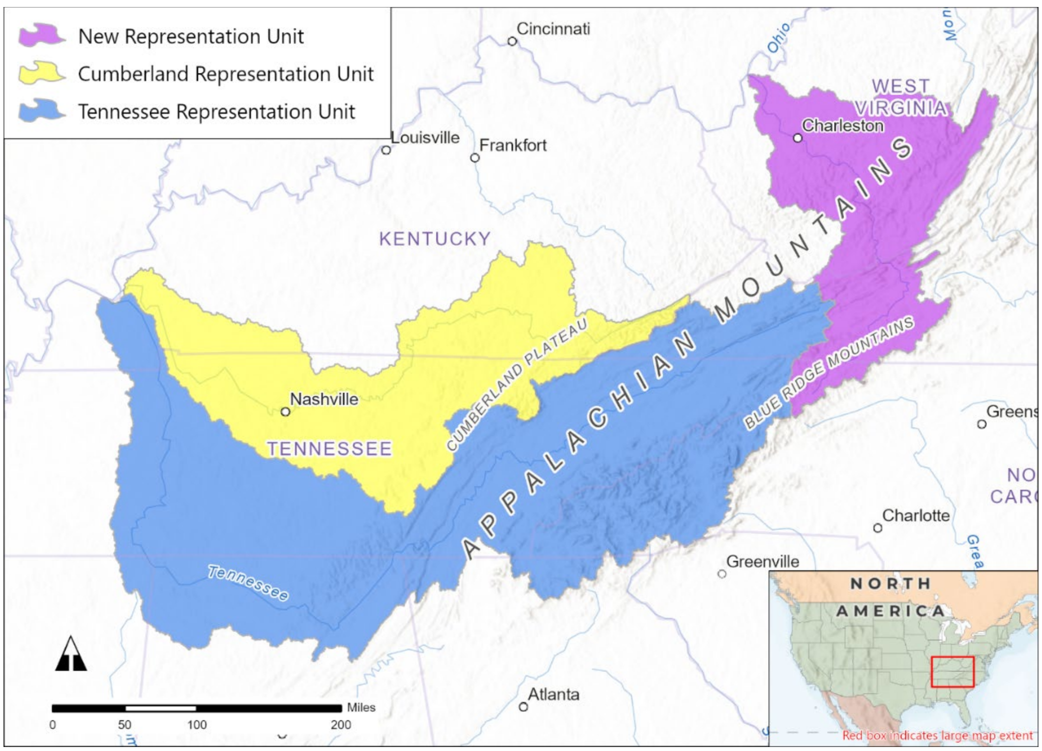

Figure 7. Map of RUs of the Tennessee Heelsplitter.

The Tennessee Heelsplitter most often occurs in small streams that, unless a mussel population was previously documented, are infrequently surveyed for mussels. As a result, there is a lack of literature and reports citing Tennessee Heelsplitter population extirpation. In some situations, mainstem populations may be considered extirpated, but the Tennessee Heelsplitter persists in tributaries (Johnson et al. 2012, p. 88). Based on historical information from museum collections, there are locations where the species was collected pre-impoundment that no longer are suitable to support the Tennessee Heelsplitter, although habitat to support the species exists at the HUC-10 (i.e., AU) level (https://water.usgs.gov/GIS/huc.html); therefore, none of the AUs are considered “extirpated” in our analysis.

2.5.2. Current Range

The current distribution of the Tennessee Heelsplitter is consistent with historical distribution, the species occurs within three RUs: Tennessee, Cumberland, and New (Figure 8). The species occurs along river margins and in small streams in Virginia, Tennessee, Georgia, and Alabama.

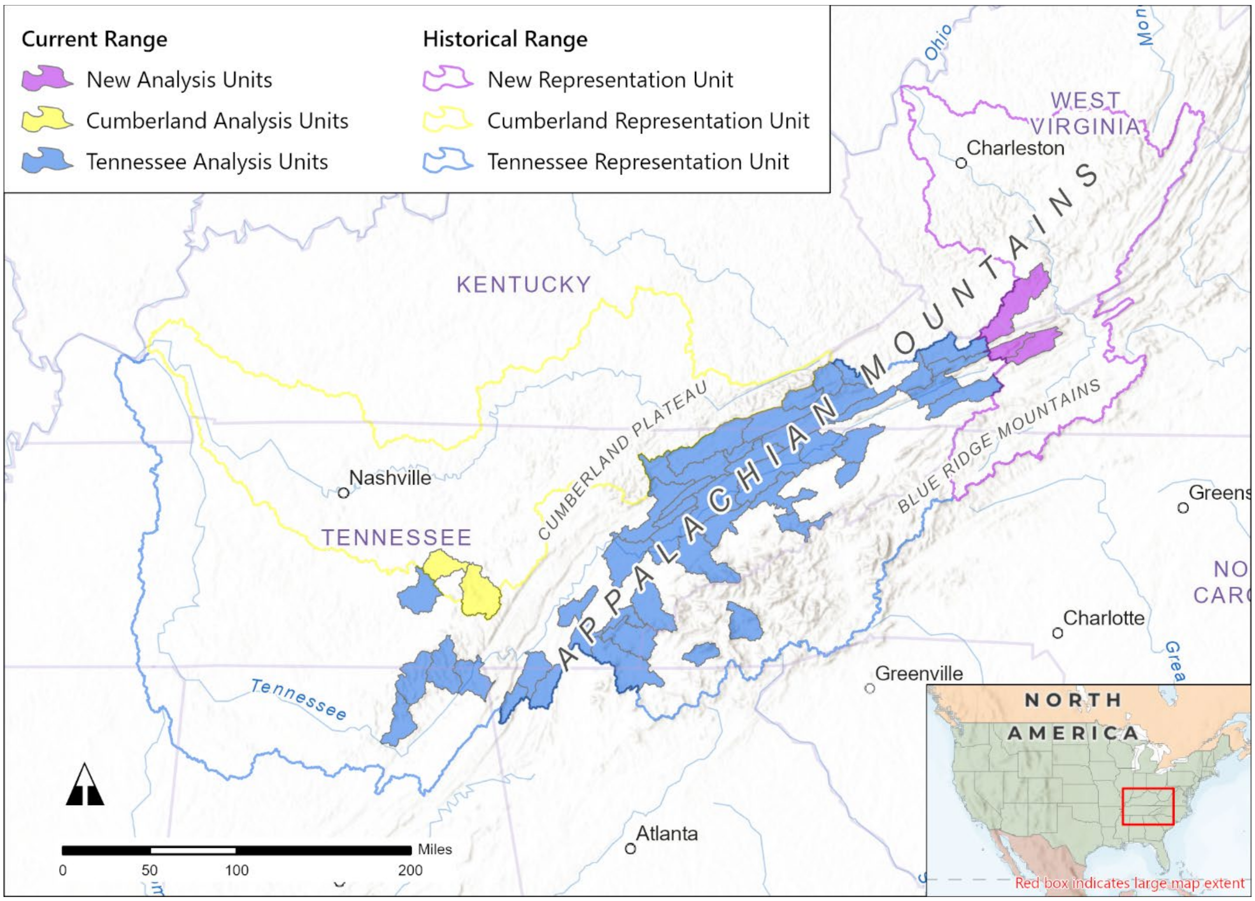

Figure 8. Map of current range of the Tennessee Heelsplitter.

CHAPTER 3. RESOURCE NEEDS

As discussed in Chapter 1, for the purpose of this assessment, we define viability as the ability of the species to sustain populations in the wild over time. Using current and future condition, we describe the species viability over time. Here we report the individual-, population-, and species-level needs of the Tennessee Heelsplitter that inform current condition of the species. Resource needs by life stage are summarized here (Table 1) and discussed in further detail below.

Table 1. Summary of resource needs and functions by life stage for the Tennessee Heelsplitter. G = Glochidia, J = Juvenile, A = Adult, B = Breeding, D = Dispersal, F = Feeding, H = Habitat, S = Sheltering.

LIFE STAGE	RESOURCE	RESOURCE FUNCTION	SOURCE(S)
G, A	Abundant host fish	S, B	Steg-Geltner (1998, pp.15-63) Barton (2011, pp.15-23)
J, A	Stable substrate	H, S, F	Haag (2012, pp.137-138)
A	Proximity to breeding individuals	B	Mosley (2012, pp.16-35)
J, A	Small or headwater streams	H	Parmalee and Bogan (1998, p.142) Williams et al. (2008, p.405) Womble and Rosenberger (2021, pp.4-12)
G, J, A	Water with neutral pH and little to no contaminants	B, F, H	Tucker and Theiling (1998, p.12) Haag (2012, p.102)
G, J, A	Spring-fed streams with low to moderate water flow	B, D, H	Parmalee and Bogan (1998, p.142) Williams et al. (2008, p.405) Womble and Rosenberger (2021, p.10)
G, J, A	Water temperature range allowing for life history functions	B, S, H	Waller and Cope (2019, p.27) Ganser et al (2021, p.8)

3.1. Individual-Level Resource Needs

This section discusses resources that influence the successful completion of each life stage for Tennessee Heelsplitter individuals (Service 2016a, p. 12). Successful completion of each life stage affects the ability of the species to withstand both catastrophic events (redundancy) and stochastic events (resiliency), as well as adapt to changing environmental conditions by way of genetic exchange or respond to environmental diversity between occupied streams (representation).

3.1.1. Abundant Host Fish

At the individual level, the Tennessee Heelsplitter requires abundant suitable host fish for glochidia while developing into juvenile mussels. Host fish studies have documented the transformation of Tennessee Heelsplitter on many species, genera, and families of host fishes (Gordon 1993, p. 7; Steg and Neves 1997, p. 34; Barton 2011, p. 22; Ganser et al. 2022, p. 62). The most successful fish species used in these studies is the Banded Sculpin (*Cottus carolinae*), a widespread and abundant component of stream fish assemblages throughout the range of the Tennessee Heelsplitter (see Appendix 1 for a list of known host fishes).

3.1.2. Substrate

Juvenile mussels need suitable substrate for burrowing and feeding (Yeager et al. 1994, p. 221). Adult mussels need substrate for stabilization to carry out life history functions, filter feeding, as well as refugia to changing environmental conditions (e.g., high flows and drought). The Tennessee Heelsplitter, while most often collected from sandy substrates in combination with mud and gravel, can also be found in silty depositional areas with low flow (Parmalee and Bogan 1998, p. 144; Williams et al. 2008, p. 405).

3.1.3. Proximity to Breeding Individuals

Access to optimal habitat and food resources to survive through to the next breeding season is of crucial importance. Adult mussels need to remain in proximity to one another for breeding, so females may siphon sperm released into the water column by males. Freshwater mussels have an efficient fertilization process, but high fertilization success achieved at low population densities happens only when populations are dominated by females (Mosley et al. 2014, p. 2,138).

Reported densities for the Tennessee Heelsplitter range from less than one to more than 15/m^2. At one location in the Cumberland RU with site area of 700m^2, density was observed as 3.4/m^2 ± 0.3 (Barton 2011, p. 33). At two different sites in the Tennessee RU with areas of 200 m^2 and 100 m^2, a density of 0.84/m^2 was observed for both (Ganser et al. 2022, pp. 39-40); when focusing on areas where most individuals were found at those two sites, which were 20 m^2 and 9 m^2, respectively, there was a much higher density of 10 mussels/m^2. At one location in the South Fork Clinch River, about 200 individuals were found in an area approximately 13 m^2 (~15/ m^2); this patch of habitat in the South Fork Clinch River occurred in a backwater area downstream of a meander which is hard to survey because of the amount of mud and silt (Watson, B. 2022, pers. comm.). These studies were at relatively small spatial scales in small, spring-fed streams; however, if there is sufficient habitat and dedicated survey effort, the Tennessee Heelsplitter can be locally abundant when found (Parmalee and Bogan 1998, p. 144). It is possible that sex ratios and spatial arrangement of subpopulations may be more important than local population densities (Mosley et al. 2014, p. 2,137), but these reported population densities are the only examples for the Tennessee Heelsplitter.

3.1.4. Headwater Streams

The Tennessee Heelsplitter is most often collected from small, shallow headwater streams with adequate flows (Figure 9). Throughout its range, the Tennessee Heelsplitter is in sand and mud substrates, sometimes with gravel. It can be located below riffles along headwater stream margins and occur in streams where it is the only freshwater mussel species present (Williams et al. 2008, p. 405). When encountered in larger streams and rivers, the species is found in small side channels or sloughs and along river margins, which are similar to small stream microhabitats (Ortmann 1918, p. 557; Neves 1991, p. 268). As a result of preferred habitats along river and stream margins, as well as in small headwater streams, the species is likely under-represented in mussel surveys (Williams et al. 2008, p. 405). The Tennessee Heelsplitter is a mussel that requires concerted effort to locate, even in rivers and streams frequently or routinely surveyed, because shallow depositional areas are not often targeted.

Figure 9. Habitat for Tennessee Heelsplitter. Top left: Sycamore Creek, TN (credit B. Ostby); Top right: South Fork Clinch River, VA (credit A. Henderson); Bottom left: Pepper Hollow Branch, TN (credit K. Womble); Bottom right: Cloud Branch, TN (credit A. Ganser).

3.1.5. Appropriate Water Quality

Freshwater mussels as a group are particularly sensitive to changes in water quality parameters, including (but not limited to): dissolved oxygen (generally below 2-3 parts per million (ppm)), salinity (generally above 2-4 ppm), ammonia (generally above 0.5 ppm total ammonia-nitrogen), excessive total suspended solids, and other pollutants such as heavy metals (Augspurger et al. 2003, p. 2,574; Chen et al. 2001, p. 214). Generally, mussels prefer high dissolved oxygen, and low salinity and ammonia. Habitats with appropriate levels of these parameters are considered suitable, while those habitats with levels outside of the appropriate ranges are considered not suitable. Field observations indicate the Tennessee Heelsplitter can be consistently located directly downstream of point and non-point sources such as wastewater discharges and pasture runoff (Pinder et al. 2002, p. 201; Ostby et al. 2015, p. 40; Lane and Neves 2014, p. 4). Therefore, groundwater connectivity and perennial flow could be more important to population persistence than specific water quality parameters or stream impairment (Catena Group 2008, p. 160-161). Spring-fed streams with continuous flow may help dilute excessive nutrients, sediments, and contaminants.

3.1.6. Appropriate Water Flow

Tennessee Heelsplitter habitat includes rivers, streams, and springs with adequate flow to deliver oxygen, enable passive reproduction, and deliver food to filter-feeding mussels. A recent habitat suitability model identified rivers and streams with mean annual flow up to 1800 cubic feet per second (cfs) as suitable (Womble and Rosenberger 2021, p. 10). Stream velocity is not static over time, and variations may be attributed to seasonal changes (with higher flows in winter or spring, and lower flows in summer or fall), extreme weather events (e.g., drought or floods), or anthropogenic influence (e.g., flow regulation via impoundments). While mussels can survive seasonally low flows and (random) short-term, periodic drying events, intermittent stream habitats generally cannot support mussel populations. Because a lotic (i.e., flowing water) environment has been shown to be critical for other freshwater mussels in the Tennessee, Cumberland, and New RUs, barriers like dams that cause permanent impoundments and disrupt natural flow patterns negatively influence Tennessee Heelsplitter resiliency. Further, flowing water reduces contaminants and fine sediments from interstitial spaces, preventing mussel suffocation.

3.1.7. Appropriate Water Temperature Range

Freshwater mussels are sensitive to water temperature changes, particularly elevated temperatures (generally above 86 °Fahrenheit (°F) (30 °Celsius (°C)), which are associated with die-offs (Waller and Cope 2019, p. 27). Habitats with appropriate temperatures are considered suitable, while those habitats with levels outside of the appropriate range are considered less than suitable, if not unsuitable. As an inhabitant of spring fed streams, the Tennessee Heelsplitter is potentially buffered from extreme water temperature changes, because these streams typically have stable temperatures and flow regimes (Barquin and Death 2011, p. 135).

Seasonal change in temperature is often noted as an important environmental cue for mussel spawning (Coker et al. 1921, pp. 142-143; Matteson 1948, p. 702; Yokley 1972, p. 351-362). Temperatures at which Tennessee Heelsplitter glochidia are released in the wild are not known, but gravid specimens have been reported beginning in August (Clarke 1985, p. 9; Pinder et al. 2002, p. 201). Also, the species has been observed closer to the substrate surface in August when compared to surveys from April through June (Ganser et al. 2022, p. 33). This vertical movement, beginning in late summer for reproduction when there are typically low flows and warm temperatures, highlights the importance of natural variations in temperature and flow regimes. Spawning for Tennessee Heelsplitter begins in periods of seasonally low flows and warm temperatures and could be associated with concentration of host fishes in shallow habitats along with temperature cues.

In a recent study, temperature data gathered in streams occupied by the Tennessee Heelsplitter did not differ from documented optimal temperatures for freshwater mussels (19-23 °C) (Ganser et al. 2022, pp. 7-8). In host fish studies of the Tennessee Heelsplitter, infested fishes were held in recirculating systems at 66-71 °F (19-21.5 °C), which is a typical temperature range for conducting host fish trials; transformation of glochidia occurred, though Tennessee Heelsplitter glochidia will transform at a much wider temperature range (Steg and Neves 1997, p. 34; Barton and Layzer 2011, p. 11; Ganser et al. 2022, p. 77; Watson, B. 2022, pers. comm.).

3.2 Population- and Species-Level Resource Needs

Resiliency of Tennessee Heelsplitter populations (which we defined as occupied stream reaches within AUs), as well as representation and redundancy of the species, are influenced by access to necessary resources. In this section, resource needs required to maintain Tennessee Heelsplitter viability are explained.

3.2.1. Abundance and Distribution

For Tennessee Heelsplitter populations to be considered healthy and resilient, they need to show evidence of recruitment as well as being numerous and representing multiple age classes. In a stream reach, mussel abundance is a product of the number of mussel beds and density of mussels within those beds (aggregations of freshwater mussels). This abundance facilitates reproduction, because mussels do not actively seek mates; rather, males release sperm into the water column, where it drifts until a female siphons it (Moles and Layzer 2008, p. 212).

Abundant populations need to be spatially arranged in a manner that enables interaction between males and females, though populations may potentially maintain resilience when experiencing lower relative population density if those populations are skewed towards females (Mosley et al. 2014, p. 2137). Ultimately, successful population viability requires enough female mussels to be in proximity of a sufficient number of male mussels. While it is possible for mussels to spread over a larger area and still exhibit high fertilization success, consideration of sex ratios and spatial arrangement of subpopulations may be more important than local population densities.

3.2.2. Suitable and Abundant Host Fish

At the population and species level, host relationships with common fish species can benefit mussels by potentially increasing mussel recruitment and range due to larger numbers of glochidia transformations, and by transporting glochidia upstream and downstream (Barton 2011, p. 23; Gordon and Layzer 1993, pp. 148-149). Wide-ranging suitable host fish with high transformation rates for the Tennessee Heelsplitter include the Banded Sculpin (Steg and Neves 1997, p. 34; Ganser et al. 2022, p. 82) and Rock Bass (Steg and Neves 1997, p. 34), as well as Eastern Blacknose Dace and Central Stoneroller (Ganser et al. 2022, p. 82).

These widespread and common host fish species are tolerant of a wide array of stream habitat types and have abundant populations in many river systems throughout the eastern U.S. The Tennessee Heelsplitter, which has high transformation rates on a variety of common host fishes, is less susceptible to host fish extirpation than a mussel species with fragmented distribution and host fish specificity (McNichols et al. 2011, p. 69). Host fish adaptability and high transformation rates are traits which are conducive to reproductive success.

3.2.3. Habitat Connectivity

Connection between habitat patches and occupied reaches is necessary for mussel populations to persist, as they are heavily dependent on gene exchange, host fish movement, and dispersal within river corridors to maintain viable populations (Newton et al. 2008, p. 425). Barriers to movement can cause isolated or patchy distributions of mussels, which may limit both genetic exchange and recolonization (Jones et al. 2006, p. 528). Fragmentation results in barriers to host fish movement, which in turn influences mussel distributions. Habitat connectivity enabling a non-linear distribution over a large area (occurrence in tributaries, in addition to the mainstem) helps buffer against stochastic events that may impact populations, with tributary connection to river or stream mainstems allowing movement of fishes and facilitating dispersal and colonization of appropriate habitat patches by mussels.

CHAPTER 4. INFLUENCES ON VIABILITY

Freshwater mussels are susceptible to human-induced impacts because they have a long life span, delayed sexual maturity, low fecundity, limited dispersal, and poor juvenile survival (McMahon and Bogan 2001, p. 368). Many mussel life-history traits, particularly long life spans and low fecundity, make it difficult to recover once decimated by a pollution event or other human- or naturally caused habitat disturbance (McMahon and Bogan 2001, p. 368). When mussels are confronted with adverse conditions, their active dispersal to a new patch of suitable habitat is limited by their relatively limited movement. While passive movement occurs over long distances when any mussels are dislodged by flows and carried downstream, active horizontal movement varies between species (Schwalb and Pusch 2007, pp. 269-270; Allen and Vaughn 2009, pp. 96-97; Gough et al. 2012, p. 2360; Galbraith et al. 2015, pp. 47-48).

Several influences affect the Tennessee Heelsplitter and may work synergistically to enhance or threaten the species' viability. We focus on the influences included in the diagram below that have been identified as having the greatest impact to current habitat suitability according to the literature and species experts (Figure 10). All influences listed in the diagram, apart from conservation actions, have adverse effects on habitat factors.

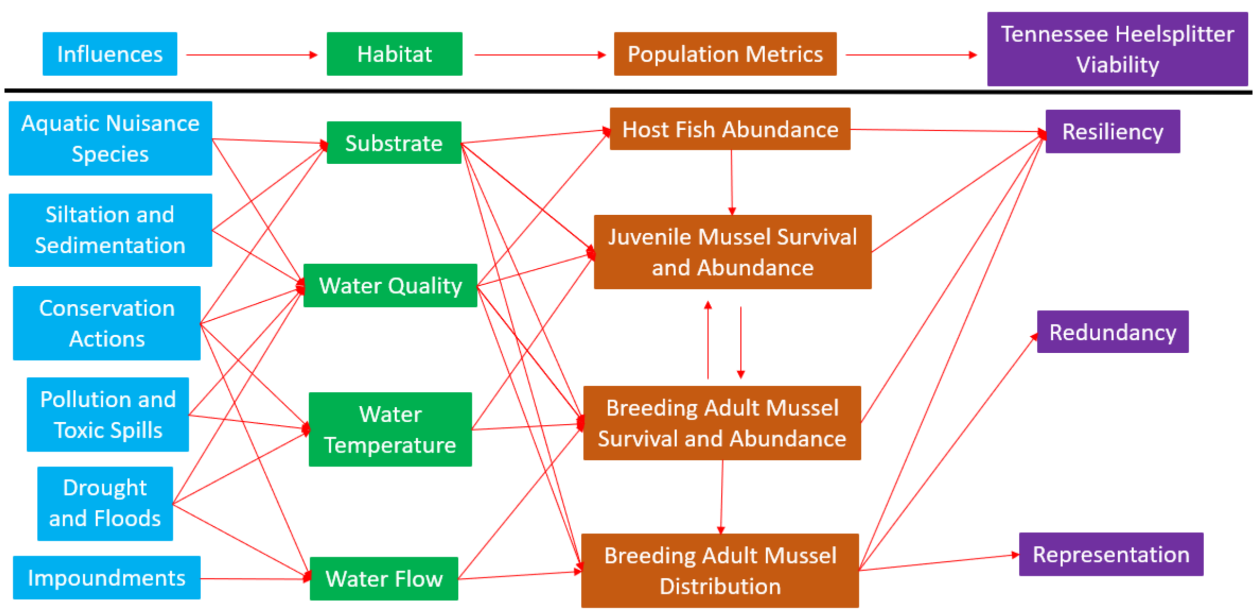

Figure 10. Influence diagram for the Tennessee Heelsplitter.

4.1. Aquatic Nuisance Species

Abundance and extent of the Asian Clam (*Corbicula fluminea*) throughout the range of the Tennessee Heelsplitter is considered a threat; though the complete impact of these invasive bivalves on native unionids is not completely understood, competitive interactions and effects of their massive die-offs have been documented. Methods of Asian Clam introduction include, among others, bait buckets and boat ballasts (GISD 2022, unpaginated) as well as passive movement via water currents (Isom 1986, p. 3). With humans demonstrated to be the primary agent of dispersal, no large-scale geographic features function as dispersal barriers (Isom 1986,

p. 3). The first collection of the Asian Clam in the U.S. occurred in 1938 along the banks of the Columbia River near Knappton, Washington (Burch 1944, p. 18). This invasive species, now a ubiquitous presence in rivers and streams of eastern North America, is present throughout the range of the Tennessee Heelsplitter.

The Asian Clam, which can be found at the sediment surface or slightly buried, has several competitive advantages over the Tennessee Heelsplitter; for instance, its ability to uproot burrowed native freshwater mussels (Fuller and Richardson 1977, p. 52). Additionally, this invasive species alters benthic substrates (Hakenkamp et al. 2001, pp. 495-497), may filter mussel sperm or glochidia, and competes with native species for limited resources. It also causes ammonia spikes in surrounding water when they die off en masse (Scheller 1997, p. 2), causing a reduction in available dissolved oxygen, which can result in stress or mortality for the Tennessee Heelsplitter (Cherry et al. 2005, p. 377). The ability of the Asian Clam to reproduce rapidly without needing a host, coupled with low tolerance of cold temperatures (2-30°C), can produce swings in population sizes from year to year and result in boom-and-bust population cycles. Populations commonly grow to thousands of individuals per square meter (Benson and Williams 2021, entire), which would undoubtedly cause both food resource and space competition with the Tennessee Heelsplitter. The Asian Clam, like the Tennessee Heelsplitter, is a filter feeder, and can threaten food availability for adult Tennessee Heelsplitter through their association with phytoplankton decline in rivers (Marescaux et al. 2016, pp. 2-10). Asian Clam may rapidly clear the sediment boundary layer of food (Leff et al. 1990, p. 409), thereby threatening food availability for juvenile mussels that typically feed while buried in sediment.

Reproduction and larval release in Asian Clam occur biannually in spring and late summer, with both yellow and brown morphs being simultaneous hermaphrodites that brood their larvae in the inner demibranchs (Qiu et al. 2001, p. 323). Hermaphroditism enables fast colonization, and the species is believed to practice self-fertilization, enabling rapid colony regeneration when populations are low (Cherry et al. 2005, p. 378). Furthermore, Asian Clam can reproduce by self-fertilization at different ploidy levels, and is capable of androgenesis, a type of male quasi-sexual male reproduction (Hsu et al. 2020, p. 642).

Under simulated heat wave conditions, Asian Clam have been found competitively superior to native freshwaters mussels in areas where they co-occur (Ferreira-Rodriguez et al. 2018, p. 941). Depletion of energetic reserves of native mussels to cope with increasing temperatures could compromise the tolerance to additional stressors such as competition with invasive species, including the Asian Clam, or food reduction (Ferreirra-Rodriguez and Pardo 2017, p. 171). Reduction in reproduction, abundance, and distribution of the Tennessee Heelsplitter is possible due to reduced carrying capacity of areas with Asian Clam because of competition for resources is likely to continue.

4.2. Siltation and Sedimentation

While the Tennessee Heelsplitter appears to be generally more tolerant of siltation and sedimentation compared to other mussel species, their effects are widely documented as detrimental to mussel populations. For example, siltation has been cited as a limiting factor to mussel survival, specifically in the Tennessee RU (Dennis 1984, p. 150; Ciparis et al. 2019, pp. 103-104). A major source of siltation and sedimentation is development, which accelerates the loss of wetlands and forest (Hasse and Lathrop 2003, p. 159). Legacy sediment resulting from past landscape development continues to persist in rivers and affect mussel habitat (86 FR 47916); for example, upper reaches of the Powell River in Virginia have been heavily silted by runoff from unreclaimed strip-mined lands in the headwaters (Ciparis et al. 2019, p. 98; Merovich et al. 2021, p. 269). While legacy sediment remains, current human activities further affect sedimentation in river systems (Wohl 2015, p. 31; 86 FR 47916). In addition to development, there are several sources of sediment in the range of the Tennessee Heelsplitter, primarily from human activities: agriculture, construction (e.g., roads), impoundments, and resource extraction.

Goldsmith et al. discusses impacts of sedimentation (when silt and sediment particles accumulate on the river or stream bottom) to include reduced reproduction (2020, pp. 9-13), feeding (pp. 13-15), respiration (pp. 15-16) and survival (pp. 17-19). The Tennessee Heelsplitter relies on fishes as part of its life cycle; therefore, turbidity and high levels of suspended solids during critical reproductive periods may affect glochidial attachment and ultimately decrease recruitment in any given population (McLeod et al. 2017, p. 348). Sedimentation affects mussel reproduction as elevated levels of suspended sediment may cause host fish to avoid such areas, thereby decreasing the likelihood of physical interaction between host fish and gravid female mussels (Goldsmith et al. 2020, p. 12).

Elevated levels of suspended sediment affect freshwater mussel ability to filter sperm from the water column and their ability to filter food. Suspended silt can inhibit their filtering and consumption rates (McMahon and Bogan 2001, p. 382), and may dilute freshwater mussels' food source (Dennis 1984, p. 212). Stream beds can become inundated with fine sediment, which may lead to smothering of mussels (Goldsmith et al. 2020, p. 18). Additionally, silt on the landscape hinders surface water infiltration into groundwater (Rajendran et al. 2020, p. 1). Groundwater presence and spring-fed streams are important to the Tennessee Heelsplitter. Increased sedimentation can reduce or stop groundwater recharge, causing a decline in groundwater levels (Abdalla and Rawahi 2013, p. 1,956). In the future, siltation and sedimentation associated with human disturbance activity is expected to increase in rivers and streams.

4.3. Pollution and Toxic Spills

Historically, contamination from pollution events and spills has occurred in several parts of the range of the Tennessee Heelsplitter. For example, several reaches within the Tennessee RU are degraded by pollution from agriculture, development, logging, and surface coal mining (ADEM 2003, pp. 56-69; Zipper et al. 2016, p. 613). Agricultural sources of chemical contaminants, including nutrients and pesticides, have the potential to adversely affect mussel species. Nutrients (such as nitrogen and phosphorus) can impact streams when their concentrations reach levels that cannot be assimilated, known as over-enrichment. Over-enriched conditions are exacerbated by low-flow conditions. Additionally, environmental impacts on waterways are concentrated in developed areas (EPA 2022a, unpaginated), with small increases in developed land percentage having a disproportionately large influence on pollutant generation (Ai et al. 2015, p. 404).

Notable toxic chemical spills that released large quantities of highly concentrated chemicals took place on the Clinch River at Carbo, Virginia, from a power plant alkaline fly ash pond spill in 1967, and a sulfuric acid spill in 1970, resulting in mortality to mussels and host fish (Crossman et al. 1973, p. 6). In 1998, a tanker truck overturned on U.S. Route 460 in Tazewell County, VA, and released approximately 1,350 gallons of a rubber accelerant into a tributary about 530 feet from its confluence with the Clinch River (Service 2004, p. ii). An estimated eighteen thousand freshwater mussels were killed by this single spill (Service 2004, pp. ii, 8). In a 2007 survey, the Tennessee Heelsplitter was not recorded in this area, but it had been observed there in 1981 (Eckert and Pinder 2009, p. 17). The North Fork Holston River also has a history of being chronically affected by mercury releases (Neves 1991, p. 268; EPA 1995, p. 7). More recently, in January 2021, 5,000 pounds of ethylene glycol were released into the South Fork Holston River; this was followed by 300,000 gallons of wastewater and hydraulic oil released in early 2022, and additional ethylene glycol and hydraulic oil released due to steam line failures at the Eastman Chemical Plant on July 22, 2022 (WJHL 2022, entire).

Chronic exposure to lower concentrations of contaminants, which is more likely to be found in aquatic environments, can adversely affect mussels (Cope et al. 2021, p. 30). Such concentrations may not be immediately lethal, but over time, can result in mortality, reduced filtration efficiency, reduced growth, decreased reproduction, and behavioral changes to all mussel life stages. Juveniles may be especially vulnerable to contaminants in sediment, as they both burrow and feed in substrate (Newton et al. 2003, p. 2554). The duration of any toxicant avoidance response by an adult mussel is likely to be affected by several variables, such as species, age, shell thickness and gape, properties of the toxicant, and water temperature (Van Hassel and Farris 2007, p. 6). In the female mollusk, the marsupial region of the gill is thought to be physiologically isolated from respiratory functions; this isolation may provide some level of protection from contaminant interference with a female's ability to achieve fertilization or brood glochidia (Cope et al. 2008, p. 454). However, a major exception to this hypothesis is with chemicals that act directly on the neuroendocrine pathways controlling reproduction.

Research has demonstrated that mussels readily bioaccumulate PPCPs (pharmaceuticals and personal care products). Exposure to toxicant chemicals that act directly on the neuroendocrine pathways controlling reproduction can cause premature release of viable or nonviable glochidia, alter mussel behavior and influence successful attachment of glochidia on fish hosts, and may have population-level implications (De Solla et al. 2016, p. 495). Nutritional and ionic exchange is possible between a brooding female and her glochidia, providing a route for chemicals (accumulated or waterborne) to disrupt biochemical and physiological pathways (such as maternal calcium transport for construction of the glochidial shell) (78 FR 59269).

Other toxicants that may negatively affect biological processes of mussels include heavy metals, which occur in industrial and wastewater effluents. Mussels are affected by heavy metals such as cadmium, chromium, copper, mercury, and zinc; these metals can negatively affect growth, filtration efficiency, enzyme activity, valve closure, and behavior (Keller and Zam 1991, p. 543; Naimo 1995, pp. 351–355; Jacobson et al. 1997, p. 2,390; Valenti et al. 2005, p. 1,244). EPA water quality standards for mercury should be protective of juvenile mussels and glochidia, except in cases of illegal dumping, permit violations, or spills, though impacts to mussels from mercury toxicity may be occurring in some streams (78 FR 59269).

4.4. Drought and Floods

Extended droughts occurred in the Southeast during 1998 to 2002, and again in 2006 to 2008 (Figure 11). Substantial declines in mussel diversity and abundance as a direct result of drought have been documented in some southeastern streams (Golladay et al. 2004, pp. 494–503; Haag and Warren 2008, p. 1,165).

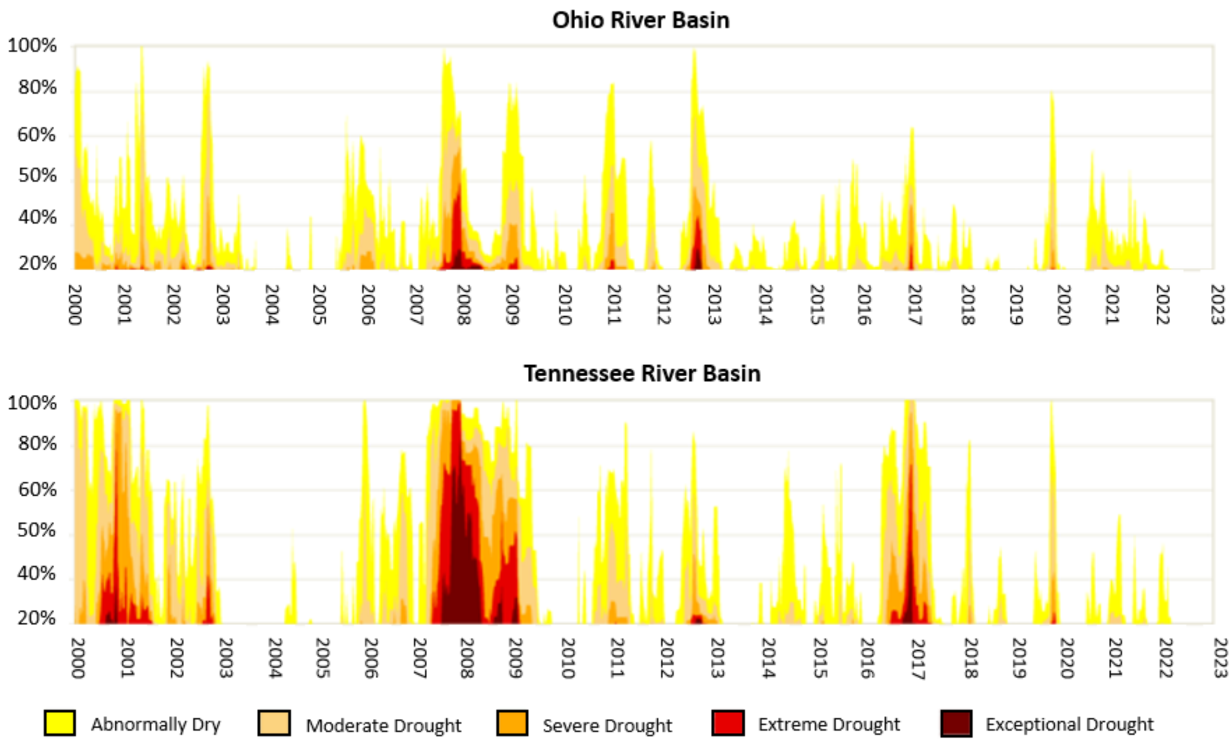

Figure 11. Percent area in drought monitor categories for the Ohio and Tennessee River Basins. The Cumberland River and New River RUs are both components of the Ohio River Basin (UNL 2021, unpaginated).

Climate change is predicted to lead to increased frequency of severe storms and droughts (McLaughlin et al. 2002, p. 6,074; Cook et al. 2004, p. 1,015; Golladay et al. 2004, p. 504). Climate change can affect mussels, their habitats, and fish hosts due to changes in timing and levels of precipitation. During high flows, flood scour can dislodge mussels, potentially causing them to be injured, buried, swept into unsuitable habitats, or stranded to perish when flood waters recede (Vannote and Minshall 1982, p. 4,105; Tucker 1996, p. 435; Hastie et al. 2001, pp. 107–115; Peterson et al. 2011, unpaginated). Increased human demand and competition for surface and ground water resources for irrigation and consumption during drought can cause drastic reductions in stream flows and alterations to hydrology (Golladay et al. 2004, p. 504; Golladay et al. 2007, unpaginated).

Juvenile mussels, which typically remain buried in sediment (Amyot and Downing 1991, p. 283), may cope better with rapidly changing water levels than adult mussels that come to the surface for filter feeding and reproduction (Hernandez 2016, p. 2). Different species have different strategies for drought and water fluctuations, including tracking of receding water, tracking of receding water then burrowing, and burrowing alone (Hernandez 2016, p. 2). There is also uncertainty around how long individuals may stay burrowed without adverse effects to their health.

Other members of the Anodontini tribe, of which the Tennessee Heelsplitter is a member, are considered "periodic," meaning they are predicted to have intermediate desiccation tolerance, and limited colonization potential during and after drying events (Chambers and Woolnough 2016, p. 13; Mitchell 2020, p. 20-26). However, a recent study indicates in some streams it is possible the Tennessee Heelsplitter can burrow considerable depths for a small thin-shelled mussel (Ganser et al. 2022, pp. 58-59). This may be in response to receding water levels, drought conditions, or to find cool substrate sub-surface temperatures or flow (Figure 11). Twenty-seven individuals at one site in Cloud Branch (Ocoee AU) were observed buried greater than 15 centimeters (cm) during a mark recapture study conducted from 2019-2020 (Table 2). Burrowing behavior for differing mussel species is not well documented under varying seasonal flows and temperatures, but for the Tennessee Heelsplitter this capability may help explain persistence of some populations in streams where no other mussel species occur.

Die-offs of the mussel community in the Clinch River, beginning at the Tennessee-Virginia state line and extending at least 27 river miles (43 km) downstream, have occurred since 2016 and as recent as Fall 2021. The Tennessee Heelsplitter has not been represented in shell material associated with the die-off, likely because of less abundance in the mainstem and a preference for smaller tributary streams. These die-offs are thought to be triggered by seasonal drought, a combination of low flows and increased river temperatures in late summer and fall. The die-offs have been preliminarily linked to undescribed species of densoviruses that may be contributing to development of an unknown mussel disease (Richard et al. 2020, p. 4).

Table 2. Depth of Tennessee Heelsplitter individuals observed during a mark recapture study (Ganser et al. 2022, pp. 58-59).

Depth (cm)	South Fork Clinch River, VA (n)	Cloud Branch, TN (n)
< 5	17	13
5 – 10	5	2
10 – 15	0	0
> 15	0	27

4.5. Impoundments

Extinction and extirpation of North American freshwater mussels can be traced to impoundment and inundation of riffle habitats in all major river basins of the central and eastern U.S. (Haag 2009, p. 107). Impoundments continue to be a range-wide threat to the Tennessee Heelsplitter (Figure 12).

The survival of mussels and their overall reproductive success are influenced:

- Upstream of dams – the change from flowing to impounded waters, increased depths, increased buildup of sediments, decreased dissolved oxygen, and the drastic alteration in resident fish populations.

- Downstream of dams – large fluctuations in flow regimes often in combination with periods of minimum flow releases and scouring flows, seasonal dissolved oxygen depletion, reduced or increased water temperatures, and changes in fish assemblages.

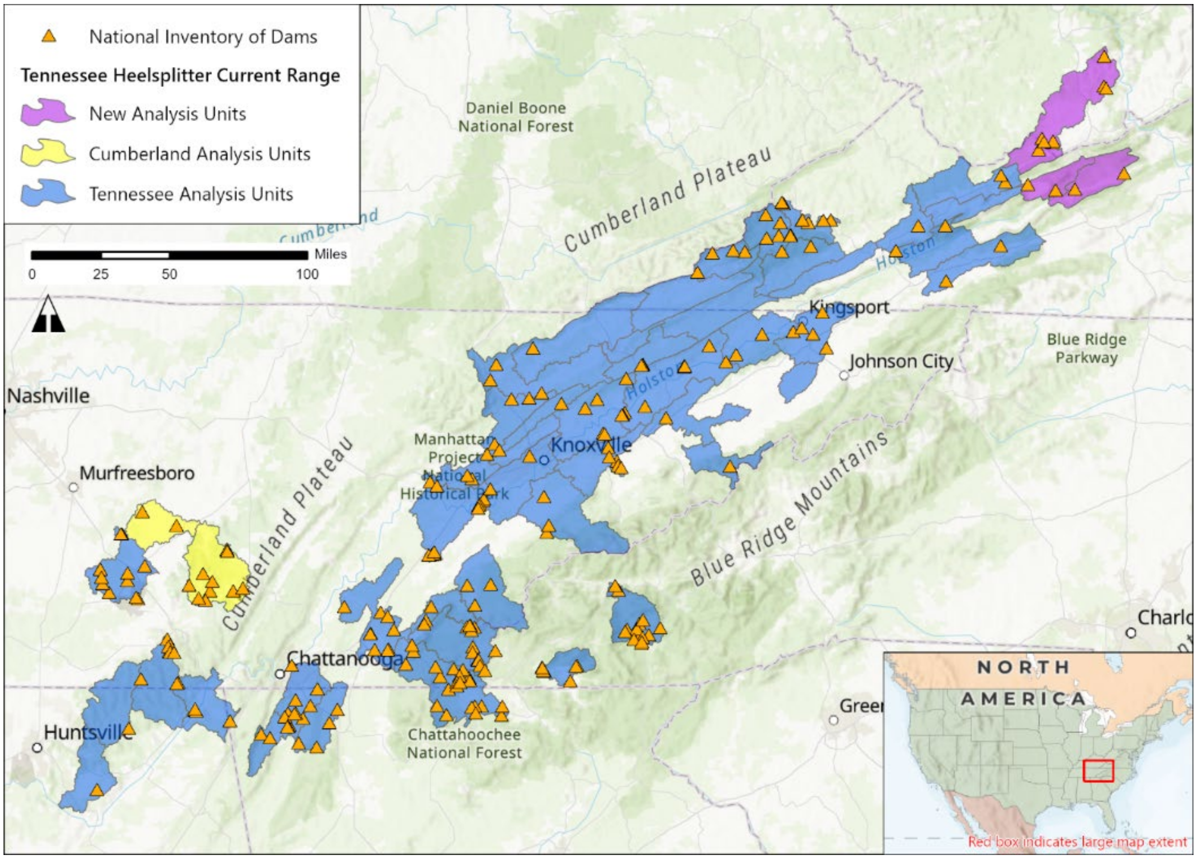

Figure 12. Large dam locations (orange triangles) within the Tennessee Heelsplitter current range. These large dams represent structures related to hydropower, flood control, or water supply.

These barriers, whether man-made or from beavers (*Castor canadensis*) or large woody debris, fragment habitats within river and stream networks and along river and stream courses. Dams also have a profound impact on in-stream habitat, as they can change lotic systems (flowing water) to lentic systems (stationary or relatively still water). Moreover, fragmentation by dams or culverts generally involves loss of access to quality habitat for one or more life stages of freshwater species.

Within the Tennessee Heelsplitter range, impoundments fall into two categories: large (e.g., hydropower, flood control, water supply) and small (e.g., farm ponds). Large dams isolate populations and result in restricted host fish movement and gene flow, whereas small dams for farm ponds, or even culverts that represent passage barriers eliminate habitat or fragment seeps and springs from downstream connectivity. There are some small dams, called leaky check dams, that have been installed to slow flows and improve habitat for trout, and these types of dams can also benefit the Tennessee Heelsplitter (Watson, B. 2022, pers. comm.).

Physical barriers limit fish host presence and Tennessee Heelsplitter ability to disperse to suitable habitat. Population isolation by distance or physical barriers prohibits the natural interchange of genetic material between occupied stream reaches, and reduced population size lessens the reservoir of genetic diversity within populations, which can lead to inbreeding depression (Allendorf and Luikart 2007, pp. 117– 146). Isolated populations are more susceptible to environmental pressures, including habitat degradation and stochastic events, and thus are the most susceptible to extinction (Primack 2004, pp. 84-118).

4.6. Summary of Factors Affecting Tennessee Heelsplitter Viability

To help communicate how some of the primary influences (Figure 10) affect Tennessee Heelsplitter throughout the range, we developed a threat calculation matrix to characterize the risk for a given stressor (see CSAS 2014, entire). We considered the primary effect of the influence to the species, the spatial threat extent, the threat frequency, and the estimated overall level of impact (Tables 3, 4).

Table 3. Definitions of metrics used in the threat matrix (modified from CSAS 2014). Threat Frequency refers to the temporal extent of a given threat over the next 10 years or 3 generations, whichever is shorter. Threat Extent refers to the proportion of the population(s) affected by a given threat. Level of Impact refers to the magnitude of the impact caused by a given threat, and the level to which it affects the viability of the population(s).

Term	Definition
Recurrent Threat Frequency	The threat occurs periodically, or repeatedly.
Continuous Threat Frequency	The threat occurs without interruption.
Widespread Spatial Threat Extent	> 50% of the population(s) is affected by the threat currently and would be by any given event.
Localized Spatial Threat Extent	< 50% of the population(s) is affected by the threat currently and would be by any given event.
High Level of Impact	Threat likely reduces resilience, and populations cannot withstand effects.
Moderate Level of Impact	Threat likely reduces resilience, but populations can withstand effects.
Low Level of Impact	Threat is unlikely to reduce resilience.

Table 4. Threat calculation matrix, characterizing level of impact, or risk, for known stressors affecting Tennessee Heelsplitter.

Threat or Influence	Primary Effect	Extent	Frequency	Level of Impact
Aquatic Nuisance Species	Competition	Widespread	Continuous	Moderate
Siltation and Sedimentation	Habitat Degradation	Widespread	Continuous	Moderate
Pollution and Toxic Spills	Contamination	Localized	Recurrent	Moderate
Drought and Floods	Stranding/Displacement	Localized	Recurrent	Low
Impoundments	Habitat Loss	Localized	Continuous	High

These are broad categorizations intended to summarize current negative influences on the Tennessee Heelsplitter at the individual and population levels. These influences are evaluated in isolation in the matrix but may be acting synergistically on some populations, which would be expected to increase the level of impact. However, all influences are not considered to be acting on all Tennessee Heelsplitter populations concurrently. While the magnitude of these threats may differ across Tennessee Heelsplitter populations, they likely affect populations similarly at the range wide level. Examples include timing of toxic spills, which are extremely difficult to predict; or rate of spread and densities of aquatic nuisance species in an AU and RU, which can vary substantially and are driven by multiple biotic and abiotic factors, including repeated human introduction.

Aquatic nuisance species such as Asian Clam affect the Tennessee Heelsplitter through competition for resources. Asian Clam are found throughout the range, persist in native mussel habitat once established, and have the capability to reproduce much faster than Tennessee Heelsplitter. They have a widespread spatial extent and have the potential to affect most Tennessee Heelsplitter populations. Temporally, Asian Clam continuously affect the Tennessee Heelsplitter due to their capability to rapidly colonize new areas and reproduce at faster rates than native freshwater mussels. While the presence of Asian Clam likely reduces overall resilience, they co-occur with Tennessee Heelsplitter in many locations. Therefore, we rated the level of impact as moderate.

As described earlier, siltation and sedimentation degrade Tennessee Heelsplitter habitat. This species appears to be more tolerant of fine substrates than other species of freshwater mussels and can be found in depositional areas (Cordiero 2004, entire; Williams et al. 2008, p. 405). However, excessive sediment buildup can suffocate mussels, affect reproduction, or even affect groundwater availability (see Section 4.2). The spatial extent of this threat is widespread, affecting nearly all populations of Tennessee Heelsplitter, and the temporal frequency is considered continuous, or without interruption, thus this threat has a moderate level of impact, reducing species resilience, but populations are withstanding effects.

Pollution and toxic spills result in contamination of Tennessee Heelsplitter habitat. These events are considered spatially localized, thus affect less than 50% of the populations in any given event. They also are considered temporally recurrent or occurring periodically. However, in the North and South Fork Holston River mainstems, toxic spills occur every year or frequently over long timeframes. The Tennessee Heelsplitter persists in tributaries within these AUs and may have never been common in chronically affected river reaches. Acute events have a moderate level of impact, meaning they reduce resilience, but their effects can be difficult to measure and only through consistent surveys and dedicated research efforts are we able to track trends in mussel decline or recovery. This information is not generally available for Tennessee Heelsplitter populations (see 2.5, above). Persistence of populations within the HUC are considered an indication of resiliency. If chronic events occur, toxic spills and pollution are expected to result in the decline and loss of Tennessee Heelsplitter populations.

Droughts can result in stranding and floods may result in either stranding or displacement of the Tennessee Heelsplitter. Droughts and floods have the potential to affect both Tennessee Heelsplitter habitat and population size. The spatial extent is localized, as any given drought or flood may not affect all populations due to underlying geology and differ in timing, severity, or duration. The Tennessee Heelsplitter is frequently associated with spring-fed streams, which have a continuous source of groundwater and relatively stable flow regimes, so the species may be less affected by drought and floods due to preferred habitat. This threat is temporally considered recurrent, or happening periodically, and is least likely to reduce resilience, but highly dependent on the severity of the event and the location.

Impoundments, or dams, result in habitat loss, fragmentation, restricted host fish movement, and alteration of flow conditions. Dams are widespread throughout the range of the species (Figure 12), but their effects on populations are linearly related to habitat alteration downstream and habitat loss due to lentic conditions upstream of the impoundment. These effects vary substantially depending on the location or size of the impoundment and a single dam may affect multiple rivers and streams. Impoundments affect habitat sometimes for large distances and on multiple tributaries, and isolate Tennessee Heelsplitter populations from one other. Unregulated and free-flowing rivers and streams in the New, Cumberland, and Tennessee RUs are uncommon.

In major rivers and many streams where there are a series of impoundments, mussel habitat is restricted to short linear reaches below the dam. The frequency of this threat is continuous because their presence continues to affect habitat long after construction. Of all threats to native freshwater mussels, the effects of dams are perhaps best documented, and it is indisputable they have a high level of impact. Where they are constructed, the population is not considered to be able to withstand the effect, although there may be a recovery gradient further downstream. Tennessee Heelsplitter population persistence despite the presence of dams throughout the range of the species is potentially a result of the species preference for the headwaters of river systems, where impoundments are generally less common. However, spring fed streams are often ditched or locations for farm pond construction, and the population is not able to withstand the permanent effects. It is worth noting that leaky check dams are the exception when considering impacts of dams, as they slow the flow and actually provide suitable habitat for Tennessee Heelsplitter.

4.7 Conservation Actions

4.7.1. State Status Designations

The Tennessee Heelsplitter is currently found in the New, Cumberland, and Tennessee RUs within the states of Alabama, Virginia, Georgia, and Tennessee. It has not been collected since 2002 in North Carolina and the state considers the status currently unknown. Of the states where the Tennessee Heelsplitter occurs, it is state protected by statute as endangered only in Virginia. Virginia, in addition to other states of occurrence, have blanket protective regulatory measures for all native freshwater mussels prohibiting take or possession without a scientific collector’s permit. These regulations are associated with wildlife management agency mandates and authorities vested in their respective state governments.

A variety of additional designations or status descriptions are assigned to the Tennessee Heelsplitter within other states, making it unlawful for anyone to take, possess, transport, export, process, sell, offer for sale or ship, and for any contract carrier to knowingly transport or receive for shipment. However, these designations are typically accompanied by wildlife management agency mandates and are not state statutory protections (Table 5). Nationally and globally, NatureServe ranks the species as N3/G3 – vulnerable (Cordiero 2004, entire).

Table 5. State and NatureServe conservation status of the Tennessee Heelsplitter throughout its range (NatureServe 2022, unpaginated). P1 = highest conservation concern; NR = not ranked; E = endangered; Tier 2 = Very High Conservation Need; SH = Possibly Extirpated; S1 = Critically Imperiled; S2 = Imperiled.

State Status	AL	GA	TN	NC	VA
State Rank (Wildlife Action Plans) 2015	P1	S1	NR	P1	Tier 2 (E)
NatureServe (as of 2009)	S1	S1	S2	SH	S1

The states of Alabama and Tennessee have mussel sanctuaries, or designated reaches of rivers where it is unlawful to take, catch, or kill freshwater mussels, and the degradation of aquatic habitat is prohibited. These sanctuaries provide some indirect protection to mussels in the Clinch, Powell, and Duck River mainstems, but not tributaries where the Tennessee Heelsplitter commonly occurs. Commercial harvest is not considered a threat to the species. The Tennessee Heelsplitter is most often located in tributaries and small streams on private lands. The actual protection afforded to mussels through these sanctuaries is limited without considerable enforcement effort and trained regulatory personnel.

4.7.2. Clean Water Act (CWA)

Section 401 of the Federal Clean Water Act (CWA) requires Federal license or permit applicants to provide certification that any discharges from the facility will not degrade water quality or violate water-quality standards, including those established by states. Section 404 of the CWA establishes a program to regulate the discharge of dredged and fill material into waters of the United States. Permits to fill wetlands and fill, culvert, bridge, or re-align streams or water features are issued by the U.S. Army Corp of Engineers (USACE) under Nationwide Permits, Regional General Permits, or Individual Permits.

- Nationwide Permits are for “minor” impacts to streams and wetlands, and do not require an intense review process. These impacts usually include stream impacts under 150 ft (45.7 m), and wetland fill projects up to 0.50 ac (0.2 ha). Mitigation is usually provided for the same type of wetland or stream affected and is usually at a 2:1 ratio to offset losses and make the “no net loss” closer to reality.
- Regional General Permits are for various specific types of impacts that are common to a particular region; these permits will vary based on location in a certain region/state.
- Individual Permits are for the larger, higher impact projects. These require a complex permit process with multi-agency input and involvement. Impacts in these types of permits are reviewed individually and the compensatory mitigation chosen may vary depending on the project and types of impacts.

Current State regulations regarding pollutants are designed to be protective of aquatic organisms; however, unionids may be more susceptible to some pollutants than the test organisms commonly used in bioassays, and water quality criteria may not incorporate data available for freshwater mussels (March et al. 2007, pp. 2,066–2,067). A multitude of bioassays conducted on 16 mussel species (summarized by Augspurger et al. 2007, pp. 2,025–2,028) show that freshwater mollusks are more sensitive than previously known to some chemical pollutants, including chlorine, ammonia, copper, fungicides, and herbicide surfactants.

Another study found that nickel and chloride were toxic to a federally threatened mussel species at levels below the current criteria (Gibson 2015, p. 80). The study also found mussels are sensitive to sodium dodecyl sulfate (SDS), a surfactant commonly used in household detergents, for which water quality criteria do not currently exist (Gibson 2015, p. 90). In 2013 the EPA revised its recommended criteria for ammonia after having considered newer toxicity data on sensitive freshwater mollusks (78 FR 52192). National pollutant discharge elimination system (NPDES) permits are valid for 5 years; thus, even after the new criteria are adopted, it could take several years before facilities must comply with the new limits, or decades for new infrastructure to be installed at facilities which assures compliance.

4.7.3. Aquatic Nuisance Species Task Force (ANS)

The Aquatic Nuisance Species (ANS) Task Force, co-chaired by the Service and the National Oceanic and Atmospheric Administration (NOAA), encourages state and interstate planning entities to develop management plans describing detection and monitoring efforts of aquatic nuisance and nonnative species, prevention efforts to stop their introduction and spread, and control efforts to reduce their impacts. Management plan approval by the ANS Task Force is required to obtain funding under Section 1204 of the ANS Prevention and Control Act. Regardless of financial incentives, plans are a valuable and effective tool for identifying ANS problems and concerns under many jurisdictions and other interested entities. Each state within the current range of the Tennessee Heelsplitter has a plan. These plans have raised awareness at the state level of the severity of ecological damage that nonnative and nuisance species are capable of, but many are in early stages of implementation.

4.7.4. Reservoir Release Improvements

The Reservoir Release Improvement (RRI) Program was initiated by TVA in 1988 at many large impoundments within the range of the Tennessee Heelsplitter. The RRI focuses on improvements in dissolved oxygen concentrations below dams, including initiating minimum flows (Higgins and Brock 1999, p. 4). The RRI program has resulted in improved oxygen, decreased bank erosion, and stabilized habitat in several river systems in the Tennessee RU (Scott et al. 1996, p. 5). Despite these improvements, habitat conditions and thermal regimes below hydropower dams continue to be limiting for most mussel species (Layzer and Scott 2006, p. 475).

Records of the Tennessee Heelsplitter from the lower reaches of many rivers are from museum collections, at the mouths of small streams, and usually pre-impoundment, but remaining reaches below dams represent one of the only opportunities for mussel restoration to lower mainstem rivers post-impoundment. If flows, habitat, and temperature conditions can remain stable and approximate a natural flow regime, there is potential for mussel population re-establishment.

Despite ecological improvements in reservoir operations because of the RRI, lack of suitable flows, temperature, and mussel habitat suitability continues to limit recolonization and reintroduction potential in major river systems occupied by Tennessee Heelsplitter in the lower French Broad, Holston, and Hiwassee rivers within the Tennessee RU (Parmalee and Hughes

1994, p. 27; Layzer and Scott 2006, p. 475; Parmalee and Faust 2006, p. 73). Additional studies and research exploring opportunities to manipulate reservoir releases at dams, to improve not only habitat conditions downstream of the dam, but also reservoir pool levels and inflow of tributaries upstream of the dam into the reservoir, are needed to evaluate the effectiveness of the RRI on a species such as the Tennessee Heelsplitter.

CHAPTER 5. CURRENT CONDITION OF THE TENNESSEE HEELSPLITTER

To assess current condition, Tennessee Heelsplitter occurrence information was organized so that multiple spatial scales could be used to inform resiliency, redundancy, and representation analyses (Figure 13). We used occurrences that included georeferenced locality information, consistent with Womble and Rosenberger (2021, entire). In the absence of genetic information, we arranged occurrences into populations by occupied river or stream. This approach is consistent with other SSAs for freshwater mussels lacking genetic data and was only used for data organization purposes (Service 2018, 2019, 2021).

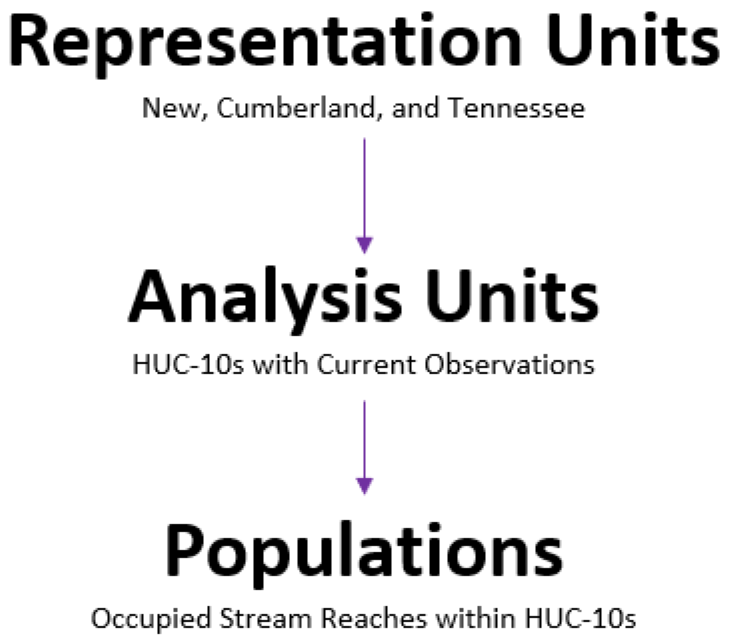

Figure 13. Hierarchy of the Tennessee Heelsplitter occurrence information used for current condition analyses.

Most freshwater mussels are found in aggregations (mussel beds) often separated by river or stream reaches of unsuitable or unoccupied habitat (Vaughn 2012, p. 983). Additionally, dams or barriers to dispersal are common throughout the species range (see Figure 12). The Tennessee and Cumberland River mussel faunas are similar and often referred to as the Cumberlandian Region, but high levels of aquatic endemism in the Cumberland River basin and mussel species originating from within can support its consideration separate from the Tennessee River basin (Gordon and Layzer 1989, p. 3; Haag 2010, p. 19; Haag and Cicerello 2016, p. 38). The New River mussel fauna represents a similar but distinct mussel province as part of the Ohio Region (Haag 2010, p. 19). We assume that populations in large and medium-sized streams exhibit relatively larger amounts of within-population genetic variation and less differentiation over large spatial scales than populations in small streams (Berg et al. 2007, p. 1,437).

For resiliency and redundancy, AUs were defined and displayed at the HUC-10 level. The HUC-10 has been used to inform current and future condition for mussels sympatric with the

Tennessee Heelsplitter (Fitzgerald et al. 2021, p. 2). The AUs are the fundamental basis for our current condition analysis and discussion. For representation, we identified three RUs for the Tennessee Heelsplitter corresponding with river drainages of occurrence: Cumberland, New, and Tennessee. Each RU contributes to the adaptive potential for species and are important components of assessing overall species' viability (Shaffer and Stein 2000, entire; Service 2016b, p.23).

Occurrence throughout multiple RUs buffers response of a species to environmental changes over time. The RU level informs adaptive capacity and representation. An overview of methods used to determine current condition, based on percent predicted suitable habitat within AUs and most recent occurrence on record, is provided. This is followed by a section for each of the three RUs discussing the current condition of their respective AUs. Variable responses for the model that informed current condition can be found in Appendix 3, and a list of current condition scores for each AU can be found in Appendix 4. This chapter ends with a summary of overall current condition for the Tennessee Heelsplitter, informed by the current condition of AUs in each RU, and the impact of the current condition on redundancy, representation, and resiliency of the species.

5.1. Methods for Determining Current Condition of the Tennessee Heelsplitter

The Service's Species Range Project (SRP) has developed a nationwide species distribution modelling platform specific to aquatic species using a variety of stream network and both catchment- and watershed-level abiotic landscape metrics (https://storymaps.arcgis.com/stories/b27fb1a49e4a4113b0343c67de49e504). Species occurrence data points, from the Service and other data sources, are used in conjunction with appropriate biotic and abiotic covariates to build an inductive model to delineate species ranges.

The SRP developed a model determining the amount of suitable aquatic habitat within the Tennessee Heelsplitter range. Using this model, we selected all HUC-10s, or AUs, that had known Tennessee Heelsplitter occurrence. Occurrences were incorporated if a live individual or fresh dead specimen was collected since 2000, or collections of the species were made since 1990 with no available negative mussel survey data to dispute that the species still occurs within the water body.

The Tennessee Heelsplitter most frequently occurs in under-surveyed small streams and inconsistently surveyed habitats. Incorporating available occurrences since 1990 supplied sufficient data with which to inform the habitat model and current condition. This timeframe criterion for occurrence data resulted in 200 locations for model creation, but many occurrences were from the same locations. To prevent pseudo-replication, only one occurrence point per stream segment was used, resulting in 99 spatially separated unique occurrences across the range of the species used for model building.

The model determined the percent river miles per catchment that were deemed suitable habitat for the Tennessee Heelsplitter based on 12 predictor variables that are biologically relevant for the species and serve as proxies for the threats identified in Chapter 4. These factors were determined to be explanatory variables for Tennessee Heelsplitter occurrence:

- Watershed Developed Land Percent
- Watershed Nitrogen Fertilizer Use
- Watershed Soil Erodibility
- Watershed Runoff
- Average Water Temperature
- Stream Order
- Catchment Average Annual Precipitation
- Catchment Pasture Land Percent
- Catchment Forested Landcover
- Flow Rate
- Velocity
- Slope

We used Cohen's kappa criterion (Κ) as the metric to assess model accuracy by considering both sensitivity and specificity. Sensitivity, also known as the true positive rate, measures the proportion of occurrence data in the test sample that were correctly identified as positives. Conversely, specificity is a measure of the true negative rate or the proportion of catchments in the test sample that were correctly identified as negatives. Fifty individual models were created, and a threshold applied to each that maximized Cohen's kappa for that individual model. A stream catchment had suitable habitat conditions if the suitability value was at or above the value that maximized Cohen's kappa for that model.

These threshold model representations were then summed together to develop a model concordance map. The model concordance map identifies how often an individual catchment exceeded the threshold suitability value based on Cohen's kappa. Our final map of suitable habitat only retained those catchments where the Cohen's kappa threshold was exceeded in at least 18 individual models. The 18 individual model threshold was the minimum Cohen's kappa concordance value in catchments with a known occurrence of the Tennessee Heelsplitter.

We consider our representation of suitable habitat to be conservative. As the threshold value increases, the amount of area identified as suitable habitat decreases. Selection of an 18-model threshold requires that 36% of the individual threshold models predict suitable habitat in order to be included in our final representation of suitable habitat. Lastly, we summarized the overall percentage of river miles identified as potential habitat within each AU, categorized those percentages using a natural breaks classification scheme, and scored each category (Table 6).

Table 6. Ranges for each level of habitat suitability for the Tennessee Heelsplitter.

Suitability Level	Percent Suitable Habitat
0	0
1	0.01 – 3.64
2	3.65 – 14.53
3	14.54 – 49.73

For evaluating current condition in areas deemed as potentially suitable habitat for the species, five confidence levels were created and summarized by AU (Table 7). General mussel habitat quality and sometimes quantity were estimated in most surveys since 1990, and recent targeted survey work has habitat notes or estimated Tennessee Heelsplitter available habitat at a given locality. By incorporating this qualitative information, more weight was given to areas with the most recent occurrence records. This allocation incorporates available habitat notes and assumes that recent observation AUs have the highest levels of current suitable habitat.

Table 7. Confidence levels for areas deemed as suitable habitat for the Tennessee Heelsplitter.

Confidence Level	Time Since Last Observation
0	No occurrence
1	Historical occurrence (pre-1990)
2	1990-1999
3	2000-2009
4	2010-Present

Current condition for each AU is determined by a combination of percent of river miles predicted as potentially suitable habitat (Table 6) and time since last confirmed observation (Table 7); the "point values" of each suitability and observation level result in a combined score that ranks the overall current condition of each AU (Table 8 and Figure 14). While all AUs have suitable habitat (and thus, resiliency and redundancy), this amount varies across the range of the species. Therefore, current condition for each AU is ranked as moderate, high, or most resiliency.

Table 8. Combined suitability and observation levels and associated resiliency levels.

Combined Score	Current Condition
0 – 1	Moderate Resiliency
2 – 4	High Resiliency
5 – 7	Most Resiliency

5.2 Cumberland Representation Unit

Within the Cumberland RU, there are 4 total AUs (Figure 14). Although the greater Cumberland RU extends into the state of Kentucky, the species occurs only in Tennessee.

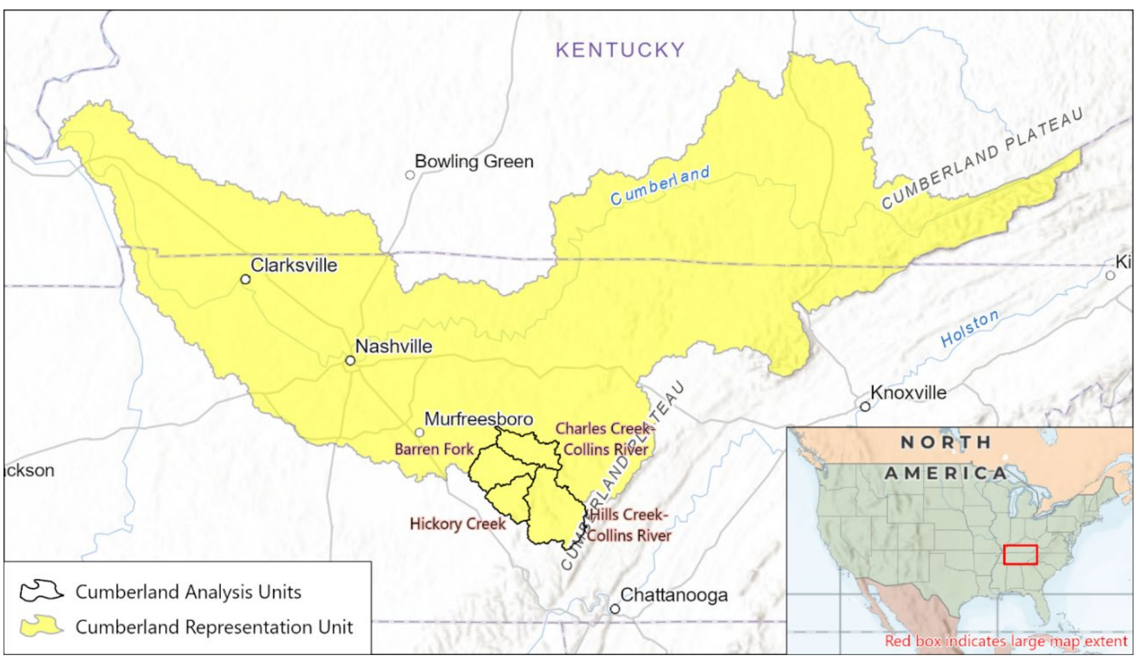

Figure 14. Cumberland RU containing four AUs.

Barren Fork and Hills Creek – Collins River are the AUs with the most resiliency, indicating substantial quality habitat suitability and confidence in species occurrence (Figure 15). Hickory Creek has high resiliency and Charles Creek – Collins River has moderate resiliency (Table 9). With only four AUs in the Cumberland RU, the species has more limited redundancy when compared to the New and Tennessee RUs. However, there is no indication of loss of AUs compared to historical conditions, indicating the species has always had less overall redundancy within this RU.

Table 9. Number of AUs within each current condition category for the Cumberland RU.

Representation Unit	**Moderate**	**High**	**Most**	***TOTAL***
Cumberland River	1	1	2	4

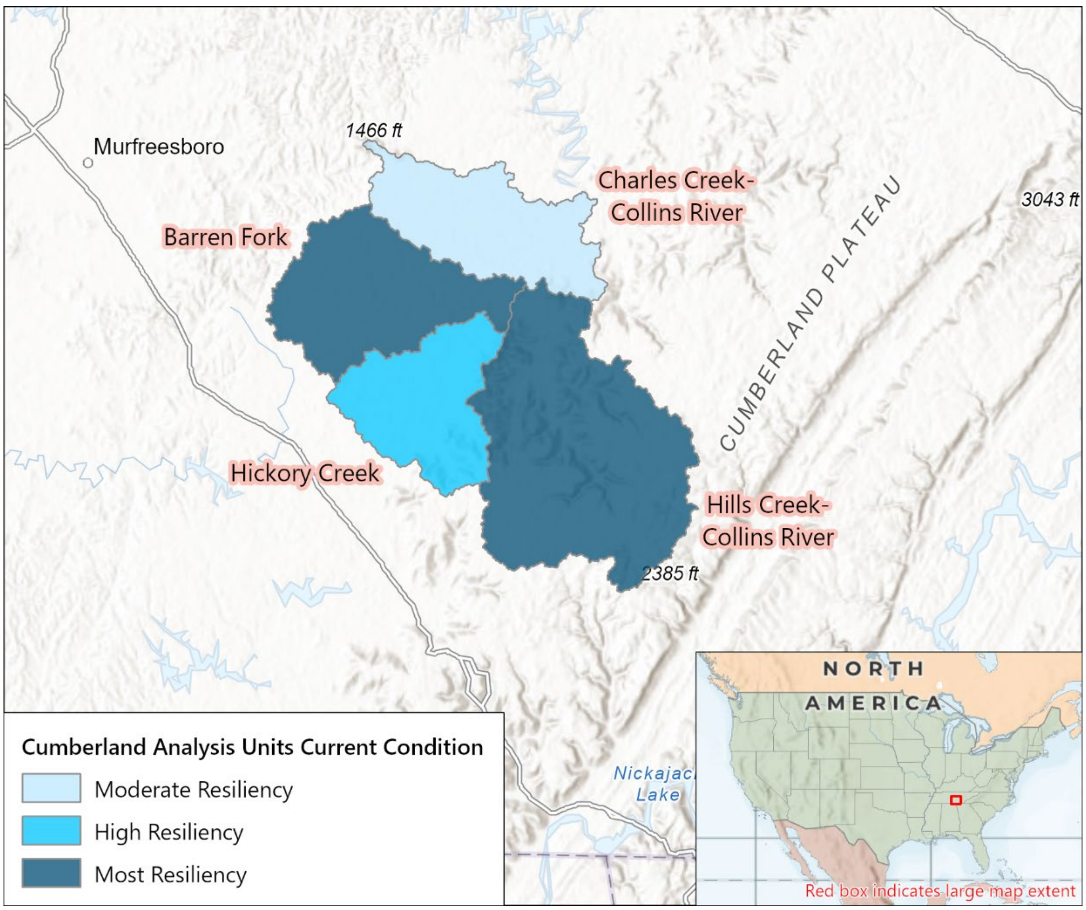

Figure 15. Current Condition Cumberland AUs.

5.3. New Representation Unit

Within the New RU, there are 10 AUs (Figure 16). Although the New RU extends into the states of North Carolina and West Virginia, the species occurs only in Virginia.

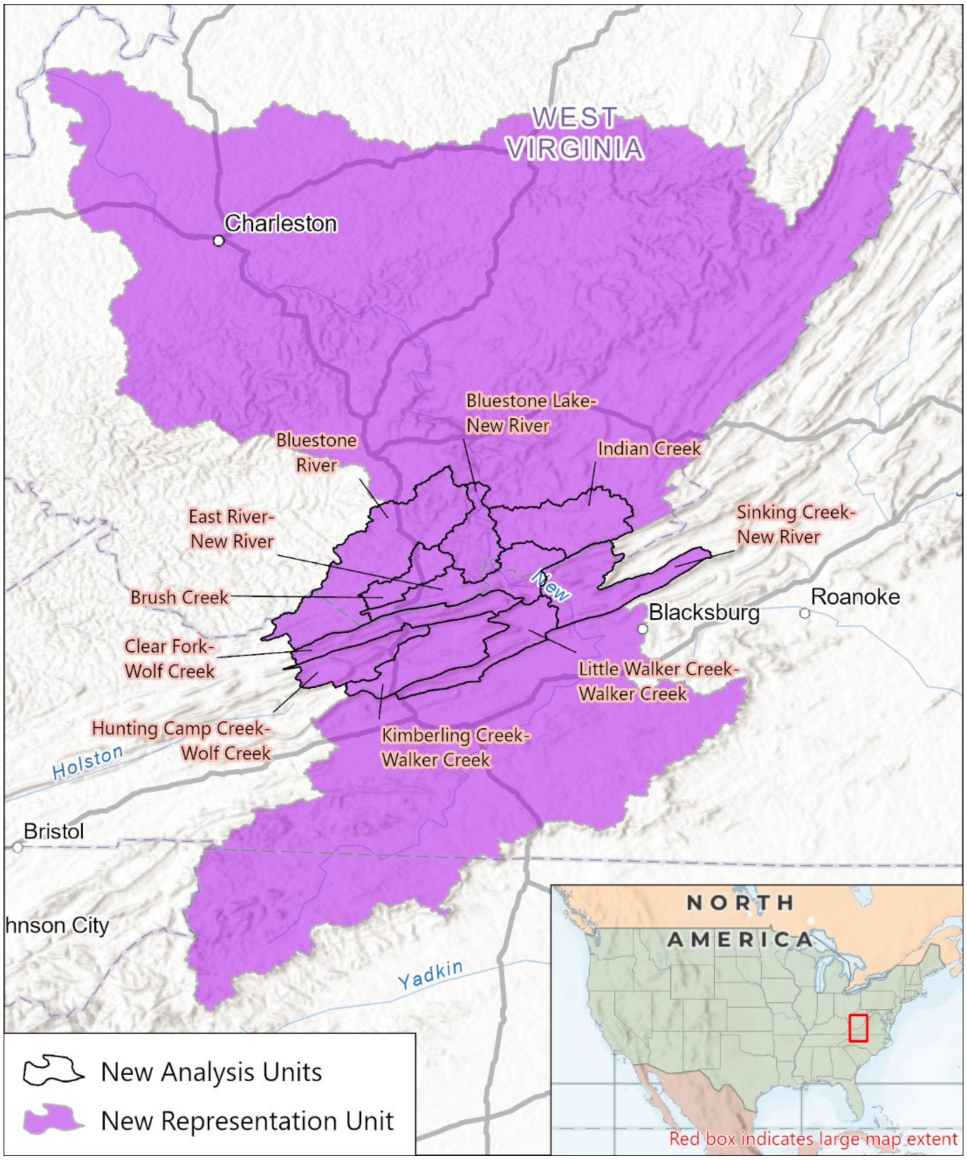

Figure 16. New RU containing ten AUs.

The Bluestone River, Clear Fork – Wolf Creek, and Kimberling Creek – Walker Creek AUs have the most resiliency, indicating high quality habitat and confidence in species occurrence (Table 10, Figure 17). Seven AUs have high resiliency: Bluestone Lake-New River, Indian Creek, Brush Creek, East River-New River, Little Walker Creek-Walker Creek, Clear Fork-Wolf Creek, and Sinking Creek-New River (Figure 18). There are no AUs with moderate resiliency, indicating that despite less AUs occupied in the New RU when compared to the Tennessee RU, the Tennessee Heelsplitter has very high habitat quality and resiliency and redundancy in this RU.

Table 10. AU totals within each current condition category for the New RU.

Representation Unit	Moderate	High	Most	*TOTAL*
New River	-	7	3	10

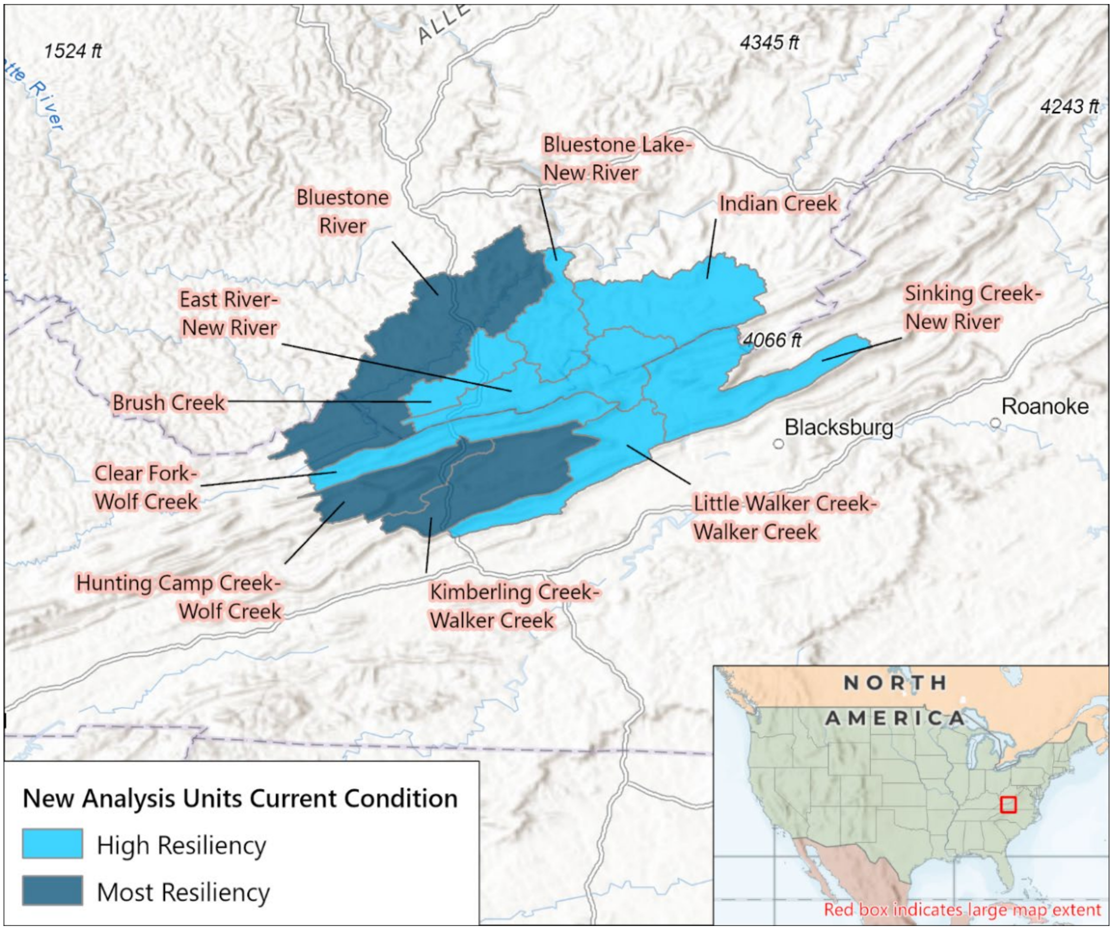

Figure 17. Current Condition of New AUs.

5.4. Tennessee Representation Unit

The Tennessee RU has 132 AUs in Virginia, North Carolina, Georgia, Alabama, and Tennessee (Figure 18). The upper Tennessee drainage in Virginia and Tennessee have what is considered the "core" of the Tennessee Heelsplitter range, past and present.

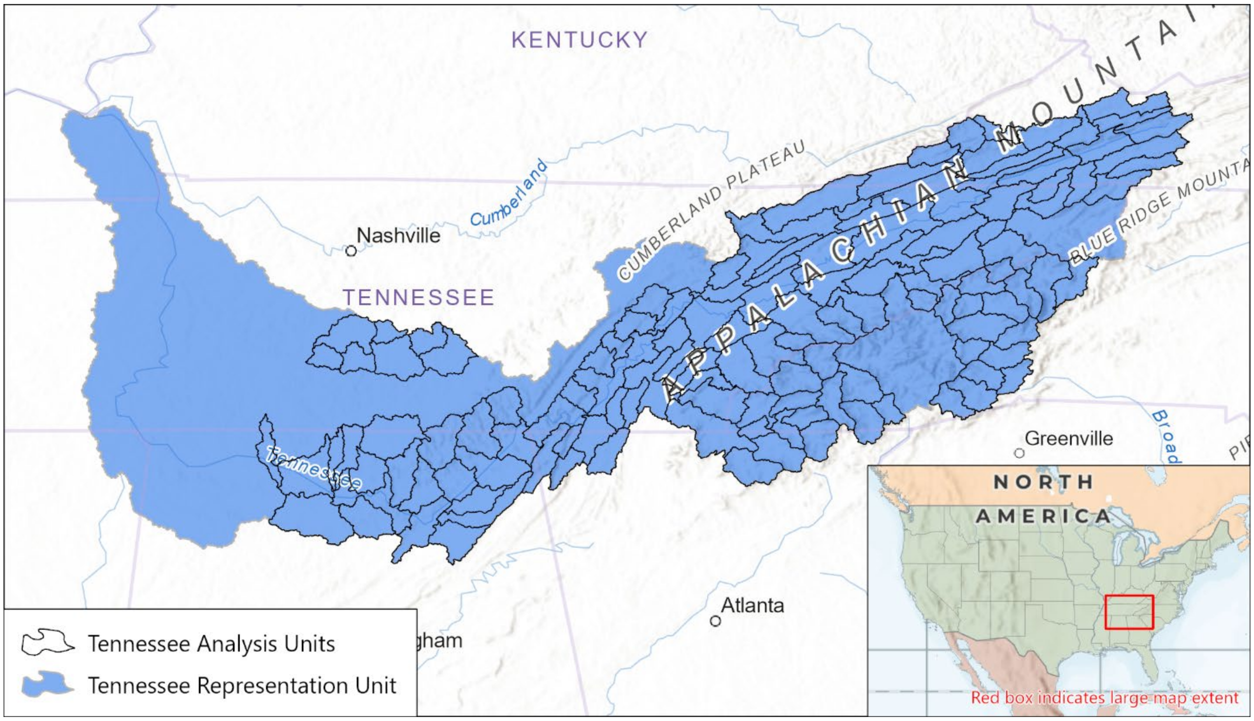

Figure 18. Tennessee River RU containing 132 AUs.

The Tennessee RU has the largest resiliency and redundancy of the three RUs for the Tennessee Heelsplitter (Figure 19). Current records since 1990 and museum collections indicate the species has historically had most occurrences within this RU. It is also where the type locality for the Tennessee Heelsplitter is located, Holston River, for which the species (i.e., *holstonia*) is named. Due to the large number of AUs, only representative examples of each resiliency category are presented here, for a full list see Appendix 3, Table 15. Approximately 43% (n=57) of AUs have moderate current condition, 40% (n=53) high condition, 17% (n=22) most resilient condition.

Table 11. Number of AUs within each current condition level for the Tennessee RU.

Representation Unit	Moderate	High	Most	*TOTAL*
Tennessee River	57	53	22	132

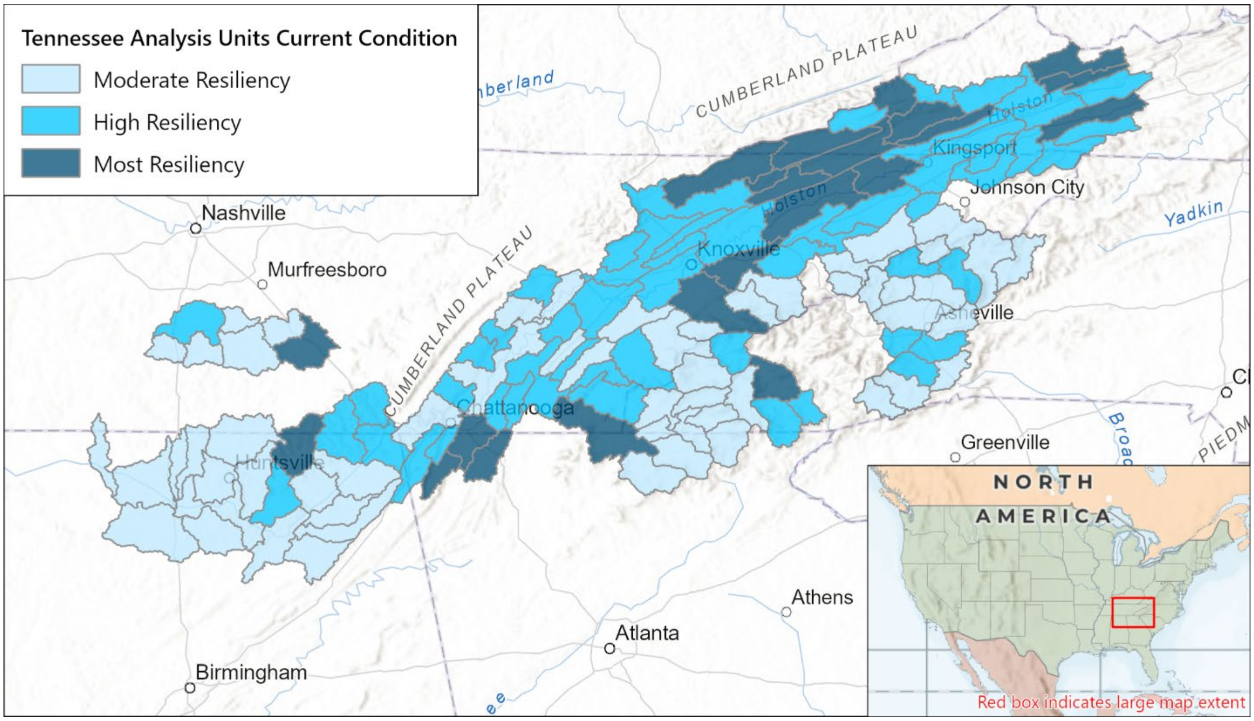

Figure 19. Current Condition of Tennessee AUs.

5.5. Current Condition

The current condition of the Tennessee Heelsplitter informs whether the species can maintain viability in the face of both stochastic events (resiliency) and catastrophic events (redundancy), as well as adapt to changing environmental conditions (representation). Although the Tennessee Heelsplitter is considered to be an under-surveyed species, the range is well established and many populations have been surveyed with occurrences at least once since 1990.

These occurrences were commonly associated with consistent or strategic mussel monitoring in river systems with high mussel diversity such as the Clinch, Powell, North Fork Holston, Paint Rock, and Duck AUs within the Tennessee RU. Targeted Tennessee Heelsplitter surveys in the Collins AU of the Cumberland RU and Wolf AU of the New RU provided recent confirmation of historical occurrences as well as some new locations (Womble and Rosenberger 2021, entire; Ganser et al. 2022, entire). We incorporated the confidence level into our analyses along with the habitat suitability level from our Tennessee Heelsplitter model to reflect these areas with moderate, high, and most habitat suitability. The summary of current condition based on each of the three Rs is provided below.

5.5.1. Resiliency

For the Tennessee Heelsplitter, demographic information and population growth rate is either scarce or unavailable. We infer resilience of each AU based on the percentage of suitable habitat for the species, in combination with recentness of observations. Small spring-fed streams are infrequently and inconsistently surveyed for freshwater mussels. As a result, with a couple of exceptions noted in section 3.1.3, not much is known about population sizes for the species, because it has rarely been targeted or the focus of surveys. However, the most consistently surveyed portion of the Tennessee Heelsplitter range in northeastern Tennessee and southwestern Virginia is a stronghold (Figure 20). Recent research and surveys in areas of potentially suitable habitat within this stronghold in the Tennessee RU has led to confirmation of large populations (Ostby et al. 2015, entire; Ganser et al. 2022, entire).

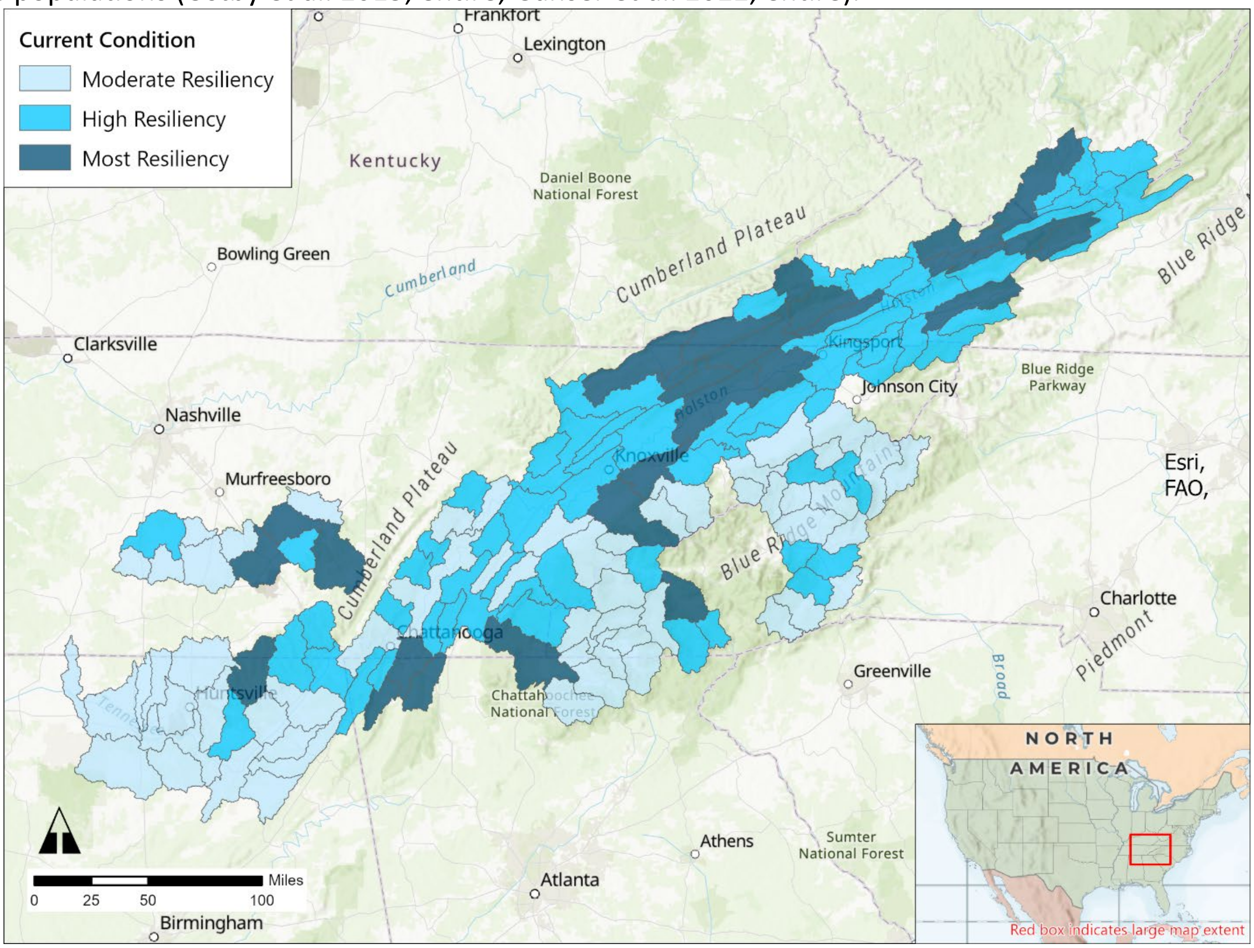

Figure 20. Current condition of AUs for the Tennessee Heelsplitter throughout the range of the species.

In Virginia, its range includes upper Walker and Wolf Creeks in the New River RU, and the Clinch, Powell, and Holston River systems, which are part of the Tennessee River RU (Jones et al. 2001, p. 21; Pinder et al. 2002, p. 190; Hanlon et al. 2009, p. 2). In Tennessee, the species occurs primarily in eastern tributary systems to the Tennessee River such as the French Broad, Holston, Little Tennessee, and Hiwassee AUs. It also occurs in upper Caney Fork and Collins in the Cumberland RU, and the upper Duck and Elk River AUs. In Alabama, it is known from tributaries of the Tennessee River in Jackson County, predominantly in the Paint Rock River drainage AUs (Williams et al. 2008, p. 405). In Georgia, the Tennessee Heelsplitter has been found recently in West Chickamauga, Little Chickamauga, and Crawfish creeks, which are part of the Tennessee River RU (Wisniewski 2014, p. 5).

Across the range, there are varying levels of suitable habitat to help the species maintain viability. Our model indicates the Tennessee Heelsplitter in all RUs has the capability to withstand stochastic events. AUs with a current condition level of high or most resilient indicate large percentages of suitable habitat, or high estimated resiliency. In the Cumberland RU, this includes three AUs (75%, n = 4), 75 AUs in the Tennessee River RU (57%, n = 132), and all the AUs in the New River RU (100%, n = 10). There are moderately resilient AUs in the Cumberland River RU (25%, n = 1), and Tennessee River RU (43%, n = 57), but not in the New River RU, which currently has proportionally the highest concentration of suitable habitat.

5.5.2. Redundancy

Redundancy is the number and distribution of resilient populations. As discussed above, Tennessee Heelsplitter resiliency is measured as moderate, high, or most, which is based on amount of suitable habitat, and these vary across the range of the Tennessee Heelsplitter. The number and distribution of high and most resilient current condition AUs in southwest Virginia and northeastern Tennessee indicates a stronghold for the species in the Upper Clinch, North Fork Holston, Powell, and Holston AUs.

In the Tennessee River RU, 57% (75 out of 132) of the AUs are high or most resilient, and these are distributed throughout the basin. In the Cumberland River RU, 75% (3 out of 4) of the AUs are high or most resilient, and in the New River RU, 100% (10 out of 10) of the AUs are high or most resilient. Within RUs, the total number of Cumberland (4) and New (10) AUs is considerably less than Tennessee (132), but large proportions of high and most resilient AUs in the Cumberland and New indicates redundant AUs with strong overall resiliency and habitat suitability.

Surveys since 1990 have improved our knowledge of Tennessee Heelsplitter distribution but range contractions or expansions are not fully understood, especially without genetic information. Multiple river and stream capture events over geologic timeframes may have played a role in shaping the distribution of the species. In review of museum data and historical information, it appears the Tennessee Heelsplitter was never widespread in the Cumberland and New RUs and these have always contained smaller portions of the species range. Across the range of the species, 60% (88 of 146) AUs contain high and most resilient categories. An additional 40% (58 of 146) of AUs have moderate resiliency, indicating consistent suitable habitat distributed throughout the range.

It is difficult to foresee a catastrophic event that would affect all RUs and result in species or even RU-level extirpation. Unpredictable weather and climate extremes in the future such as severe droughts and prolonged floods, in isolation or consecutively, could affect multiple populations within an RU. It has taken decades, or even a century, to fully grasp the devastating effects of impoundments on freshwater mussels; and similarly, the introduction of non-native species has had catastrophic effects on native mussel populations. However, these effects are a result of concurrent and successive events over long timeframes and are a direct result of human alterations of the landscape and ecosystem.

A catastrophic event such as a pollutant spill can affect multiple populations of freshwater mussels due to their linear orientation. This is a greater concern in the Cumberland and New RUs, which have less redundancy. The Tennessee Heelsplitter may have greater capability to withstand such events due to its occurrence in headwater streams and occupying multiple tributaries within a watershed. Our model indicates the Tennessee Heelsplitter has redundant AUs, habitat suitability, and high and most resiliency categories distributed within and across the Tennessee, Cumberland, and New RUs, and the species can withstand catastrophic events.

5.5.3. Representation

Maintaining representation in the form of genetic or ecological diversity is important to a species' capability to adapt to future environmental changes. There are no studies that address intraspecific divergence in genetic diversity across the range of the Tennessee Heelsplitter. The adaptive capacity to climate change is described below using the approach from Thurman et al. (2020, Entire). Thurman et al. (2020, Entire) identified 36 attributes as contributing to a species' ability to move through a landscape (shift in space) or accommodate changing climate in place, with twelve of those attributes referred to as "core attributes" to focus on for conservation decision-making if data are limited (Thurman et al. 2020, p. 522).

To inform the adaptive capacity of the Tennessee Heelsplitter, we evaluated all 36 attributes, using definitions from Thurman et al. (2020), and assigned a score to each attribute for which information applicable to the species was available (see Appendix 5 for more description of all attributes). Categories with information available were assigned a score of low, medium, or high. Figure 21 below shows the results for each adaptive capacity attribute.

Tennessee Heelsplitter extent of occurrence and area of occupancy indicates relatively high adaptive capacity, because multiple resilient populations, or AUs, over a large range will enable species persistence in the face of climate change. Large area of occupancy is also correlated with population size. Further, most of the Tennessee Heelsplitter life history strategies and movement traits are common to freshwater mussels. These include minimal parental investment, moderate to high fecundity, multiple reproductive cycles in lifetime, dispersal via host fish. Although dispersal is largely reliant on host fish, many fish species that occur in a wide range of stream habitat types are hosts for the Tennessee Heelsplitter (Appendix A). A reproductive mode of broadcast spawning is combined with a wide variety of potential host fishes to increase chances of reproductive success. Additional advantages include multiple reproductive cycles in its lifetime (parity), and age of sexual maturity being reached at approximately age 3, relatively early in the Tennessee Heelsplitter lifetime.

Broadcast spawning also enables the species to reproduce and colonize suitable areas, despite limited individual movement. Limited movement results in a higher proportion of "stayers" at sites (i.e., site fidelity), and may make populations more susceptible to changing environmental conditions. However, for the Tennessee Heelsplitter, these susceptibilities are potentially mitigated by observed burrowing capabilities (despite being a thin-shelled mussel), as well as the means for active dispersal through a variety of fish hosts during its glochidial phase. While there is not a likely way for adult Tennessee Heelsplitter individuals to disperse to high quality habitats without fish hosts or human intervention, the species increases its representation through flexibility in the habitats it occupies. The Tennessee Heelsplitter can be found in very fine substrates such as silt and mud, and since it uses many host fishes, can inhabit a variety of slow-flowing habitats and stream sizes. As a result, it displays more adaptability to a wide range of substrates compared to a riffle/run specialist, which has host fish specificity and requires swift flows over gravel and cobble and is not well adapted to fine substrates or depositional areas.

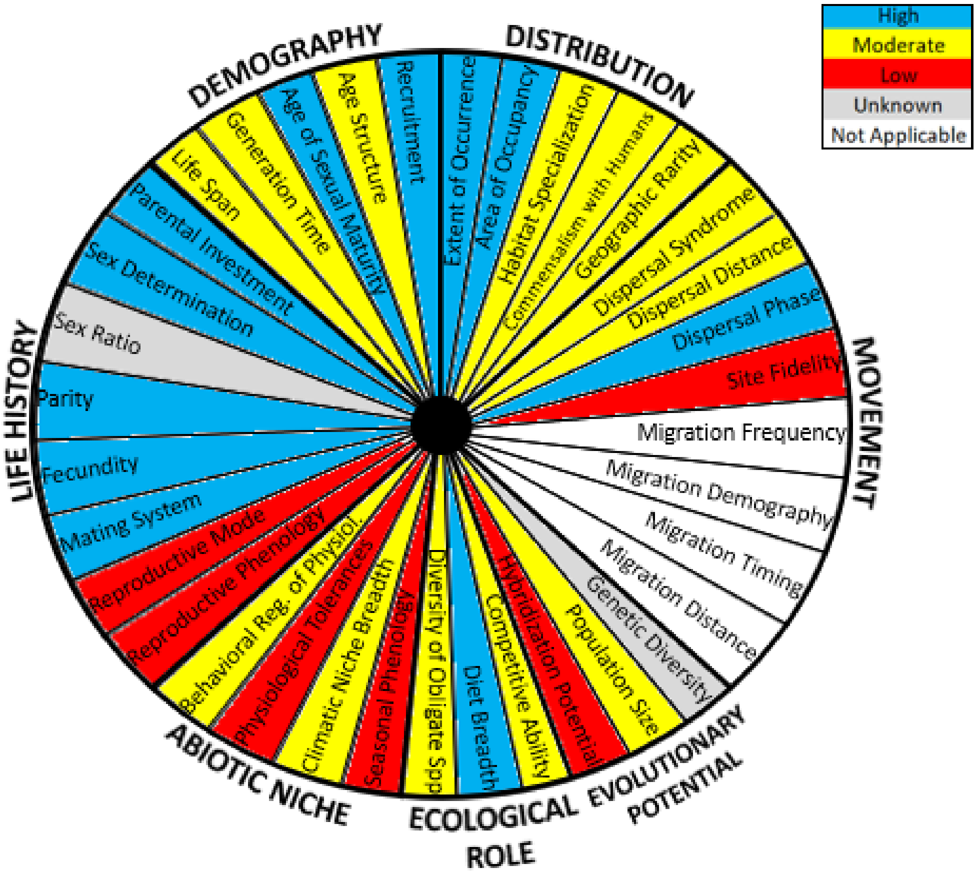

Figure 21. Adaptive capacity attribute results for the Tennessee Heelsplitter.

The Tennessee Heelsplitter displays some traits that indicate potentially higher adaptive capacity than other mussel species. Additionally, the species exhibits strong association with spring-fed streams, and the largest concentration of AUs is found in the Ridge and Valley physiographic province, where these habitats are abundant. Spring-fed streams where they are most often found show muted or delayed hydrograph peaks (Jefferson et al. 2007, p. 392), which respond to higher flow events but provide more consistent flow than runoff-dominated streams (Jefferson et al. 2007, p. 399). Spring-fed waters will likely act as cool and cold-water refuges in the face of climate change, with water volume and temperatures in these systems more resilient to changing environmental conditions (EPA 2022b, unpaginated).

Small spring-fed streams are infrequently and inconsistently surveyed for freshwater mussels. As a result, with a couple of exceptions noted in section 3.1.3, not much is known about population sizes for the species, because it has rarely been targeted or the focus of surveys. However, the most consistently surveyed portion of the Tennessee Heelsplitter range in northeastern Tennessee and southwestern Virginia is a stronghold. Recent research and surveys in areas of potentially suitable habitat within this stronghold in the Tennessee RU has led to confirmation of large populations (Ostby et al. 2015, entire; Ganser et al. 2022, entire).

Additionally, in the New and Cumberland RUs, where the species has less redundancy than the Tennessee RU, previously unknown populations have recently been discovered (Womble and Rosenberger 2021, entire; Lane, T. 2022, pers. comm.). While these populations do not expand the range, this indicates with targeted survey effort the Tennessee Heelsplitter may have further documented additional populations and higher adaptive capacity than is currently known. The Tennessee Heelsplitter is not extirpated from any RUs, and recent targeted survey efforts have either documented new populations or confirmed many populations throughout the range.

5.5.4. Current Viability Summary

The strongholds for the Tennessee Heelsplitter are in the New River and northeast Tennessee River RUs, and most AUs with "high" or "most" resiliency have some level of connectivity (see Figure 14). Redundancy, or the number and distribution of AUs with suitable habitat, is high, as suitable habitat exists throughout the range of the Tennessee Heelsplitter. Representation is maintained across all three RUs of historical and current occurrence, the Cumberland, New, and Tennessee. Targeted surveys need to be conducted in AUs with historical-only observations to determine whether populations (if still present) in those AUs have a higher level of resiliency than current information indicates (since current condition in this SSA is informed by observations since 1990). Additionally, available information indicates the species' adaptive capacity will ensure survival despite predicted climate impacts (see section 5.5.3 and Appendix 4), particularly because of the strong association with spring-fed streams that will likely act as cold-water and drought refugia in the face of climate change.

CHAPTER 6. FUTURE VIABILITY

We focused our future conditions analysis on how land use/land cover (LULC) changes, as well as climate change, impact the three Rs in the future. Outlined in Chapter 4, primary factors influencing the viability of the Tennessee Heelsplitter include siltation and sedimentation; pollution and toxic spills; drought and floods; aquatic nuisance species, particularly the Asian clam; and impoundments. These influences may be affected by LULC, or climate changes, which in turn indicate future habitat suitability for the Tennessee Heelsplitter.

Siltation, sedimentation, pollution, and toxic spills may be affected by LULC changes in agriculture (ADEM 2003, pp. 56-69), mining (Merovich et al. 2021, pp. 246-247), or developed land (Hasse and Lathrop 2003, p. 159; Ai et al. 2015, p. 404), as major sources of these influences include those land-use types. Impoundments and aquatic passage barriers such as hanging culverts have dramatically affected the landscape and eliminated habitat and altered hydrology. However, impoundments in some urban settings help buffer amounts of impervious surfaces and provide infrastructure for sediment capture, stormwater storage, and reuse (Wenger et al. 2009, p. 1091). Run-of-river dams and barriers in some situations mitigate the effects of flooding, scour, and head-cutting of streams, and stable reaches below dams may harbor diverse aquatic species assemblages (Gangloff 2013, p. 477).

It is not expected that the eastern U.S. will undertake construction of large impoundments on large rivers in the future, in part, because most are already impounded in many locations. However, the potential for small impoundment construction for water supply and agricultural uses is expected to increase. Road density and construction as well as other transportation infrastructure associated with developed land-use are also expected to increase into the future. Both agricultural and developed land uses are expected to contribute to small impoundment construction, and concentration, in the future. ANS, drought, and floods may be informed by these LULC changes under different climate change scenarios. This is because climate change is predicted to lead to an increased frequency of severe storms and floods (McLaughlin et al. 2002, p. 6,074; Cook et al. 2004, p. 1,015; Golladay et al. 2004, p. 504), and the Asian clam possessing several competitive advantages over native freshwater mussels in the face of climate change (see section 4.1).

All AUs currently have suitable habitat, but factors influencing species viability may reduce current levels of suitable habitat (i.e., resiliency) in the future; as such, future condition includes a ranking of “reduced” resiliency in addition to “moderate”, “high”, or “most” resiliency. We considered two 20-year intervals, and an estimated future time frame of 40 years (out to 2060). This timeframe was chosen based on data availability and our understanding of the heelsplitter’s life history.

Based on life history and age data, we estimate the species to live 20-30 years maximum, and capable of reproduction at age 3 (Barton and Layzer 2011, entire). Older mussels do not reproduce at the same rate and fecundity varies greatly across species (Haag 2013, p. 760). Based on professional judgement, Tennessee Heelsplitter peak reproductive output is potentially achieved between ages 5-15. While generation time and age of peak reproductive output are not documented, using the best available information and professional judgement, we estimate a 20-year (out to 2040) timeframe to capture at least 2 generation cycles of maximum reproductive output and a 40-year (out to 2060) timeframe captures 4, thus allowing us to predict how the species may respond to changing future conditions.

6.1. Data

6.1.1. Future Climate Conditions

To predict future changes in climate, scientists rely on climate model simulations that are driven by assumptions about future human population growth, changes in energy generation and land use, socio-economic development, and technology change. The Intergovernmental Panel on Climate Change (IPCC) was created to provide policymakers with regular scientific assessments on climate change, its implications, and potential future risks, as well as to put forward adaptation and mitigation options (IPCC 2022, unpaginated). Groups like IPCC use multiple scenarios that depict trajectories of future greenhouse gas (GHG) emissions (i.e., emission scenarios) because it is difficult to accurately predict how human societies will change over multiple decades.

These scenarios are based on assumptions about plausible future changes for four factors that are the dominant drivers of GHG emissions: population growth, economic growth or per capita gross domestic product (GDP), energy intensity of GDP, and the carbon intensity of energy production (Blanco et al. 2014, p. 357). Collectively, these four factors form the core of socioeconomic scenarios used in IPCC assessment reports (AR). A combination of scenarios can produce a reasonable range of plausible outcomes (Kunkel et al. 2020, p. 5). The use of different emission scenarios in climate models leads to different projections that reflect a range of possible climate futures.

The sixth Assessment Report (AR6), published in 2021, presents the most recent climate findings based on a set of scenarios that use Shared Socioeconomic Pathways (SSPs). The SSPs are scenarios of projected socioeconomic global changes out to the year 2100. The SSPs look at five different ways the world might evolve in the absence of climate policy. The SSP scenarios are (Hausfather 2018, p. 2):

- SSP1: Sustainability - Taking the Green Road (low challenges to mitigation and adaptation)
- SSP2: Middle of the Road (medium challenges to mitigation and adaptation)
- SSP3: Regional Rivalry - A Rocky Road (high challenges to mitigation and adaptation)
- SSP4: Inequality - A Road Divided (low challenges to mitigation, high challenges to adaptation)
- SSP5: Fossil-Fueled Development - Taking the Highway (high challenges to mitigation, low challenges to adaptation)

We considered the climate futures under SSP2 and SSP5 at timesteps 2040 and 2060, with SSP5 (“Higher Emissions”) projecting a possible future where global emissions of heat-trapping gases continue to increase through the 21st century, whereas SSP2 (“Lower Emissions”) projects a possible future where global emissions of heat-trapping gasses peak around 2040 and then decline (U.S. Climate Resilience Toolkit 2019, entire).

6.1.2. Future Land Use Change

The EPA's Integrated Climate and Land-Use Scenarios (ICLUS) explore future changes in human population, housing density, and impervious surface (soon to be available for ICLUS version 2) for the U.S. (EPA 2022c, unpaginated). These projections are broadly consistent with peer-reviewed storylines of population growth and economic development that are now widely used by the climate change impacts community.

The different population and land use change scenarios stem from global population and development assumptions underlying two different future trajectories from the SSPs (explained above) effort: SSP2, which represents a 'business as usual' trajectory, similar to the U.S. Census population projection, and SSP5, which represents a trajectory with higher fertility and higher net migration into the United States (National Climate Assessment, undated).

Two ICLUS projections are provided, based on the 2010 U.S. Census and using fertility, mortality and immigration rates from the Wittgenstein Centre (http://witt.null2.net/shiny/wic/) to project decadal population, consistent with the demographic assumptions of the SSP2 and SSP5 socioeconomic scenarios, respectively. These ICLUS population projections are used as inputs to a land use model, which spatially allocates five residential land uses (exurban-low, exurban-high, suburban, urban-low, urban-high) as well as commercial and industrial uses. For our analysis, we considered projections at the 2040 and 2060 timesteps.

6.2. Methods for Determining Future Conditions for the Tennessee Heelsplitter

To focus our future condition land-use assessment, we first simplified the ICLUS land-use categories to 7 major land-use types (Table 12).

Table 12. Major land-use type classification of ICLUS data.

Major land-use type	Original ICLUS Classification
Water	Natural Water
Water	Reservoirs, Canals
Wetlands	Wetlands
Recreation, Conservation	Recreation, Conservation
Timber	Timber
Agriculture	Grazing
Agriculture	Pasture
Agriculture	Cropland
Mining	Mining, Barren Land
Developed	Parks, Golf Courses
Developed	Exurban, Low
Developed	Exurban, High
Developed	Suburban
Developed	Urban Low
Developed	Urban High
Developed	Commercial
Developed	Industrial
Developed	Institutional
Developed	Transportation

With our major land-use type classification we then summarized current condition, 2040, and 2060 for SSP2 and SSP5 future condition scenarios by 10-digit HUC AU. Originally, we summarized the developed, timber, and agriculture major land-use type groupings, but after assessing the future condition values, it was apparent that the developed land change forecasted into the future predominantly came from timber and agriculture groupings and we decided to assess developed land, assuming an inverse relationship with timber and agriculture groupings.

We calculated future condition (SSP2 and SSP5 scenarios) percent of developed land for each AU and identified the percentage of developed land gained or lost within each AU, as compared to current condition, represented by a 2020 timestep. The percentage of developed land gained or lost within each AU was calculated for the two SSP scenarios, with the future condition (2040 and 2060 timesteps) percent developed total being subtracted from the current condition (2020 timestep) percent developed total. The calculated percent changes were assigned a level (score) of 1, 2, or 3 (Table 13):

Table 13. Levels for percent developed change in future condition.

Level	Percent Developed Change
0	< 5%
1	5-10%
2	10-20%
3	> 20%

To calculate the future condition, we subtracted the assigned levels for developed land change from the current condition level (see Section 6.1), using the following equation:

Future Condition Level = Current Condition Level – Developed Land Change Level

Thus, the future condition level (score) could be a value between -3 and 7 (Table 14). The mapped future habitat conditions for both scenarios under both timesteps can be seen in Figure 23. AUs with changes in resiliency from current conditions under SSP2 and SSP5, which indicate projected resiliency reductions in the future are shown in Figure 23. These are also listed in Appendix 3, Table 19.

Table 14. Future condition score and future condition level.

Future Condition Score	Future Condition Level
-3 - -1	Reduced Resiliency
0 – 1	Moderate Resiliency
2 – 4	High Resiliency
5 – 7	Most Resiliency

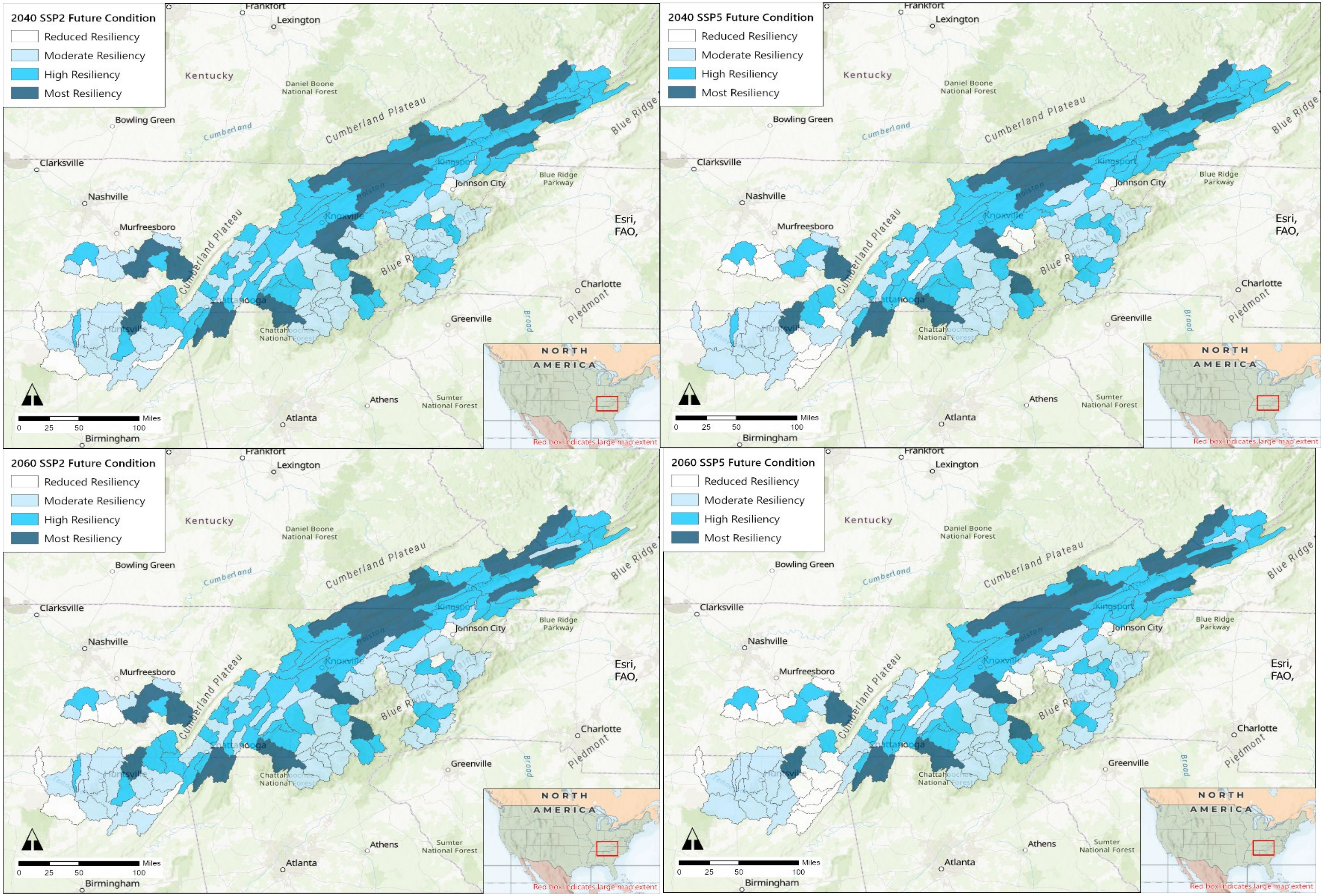

Figure 22. Future condition of Tennessee Heelsplitter AUs. SSP2 (left) and SSP5 (right) from 2040 (top) and 2060 (bottom).

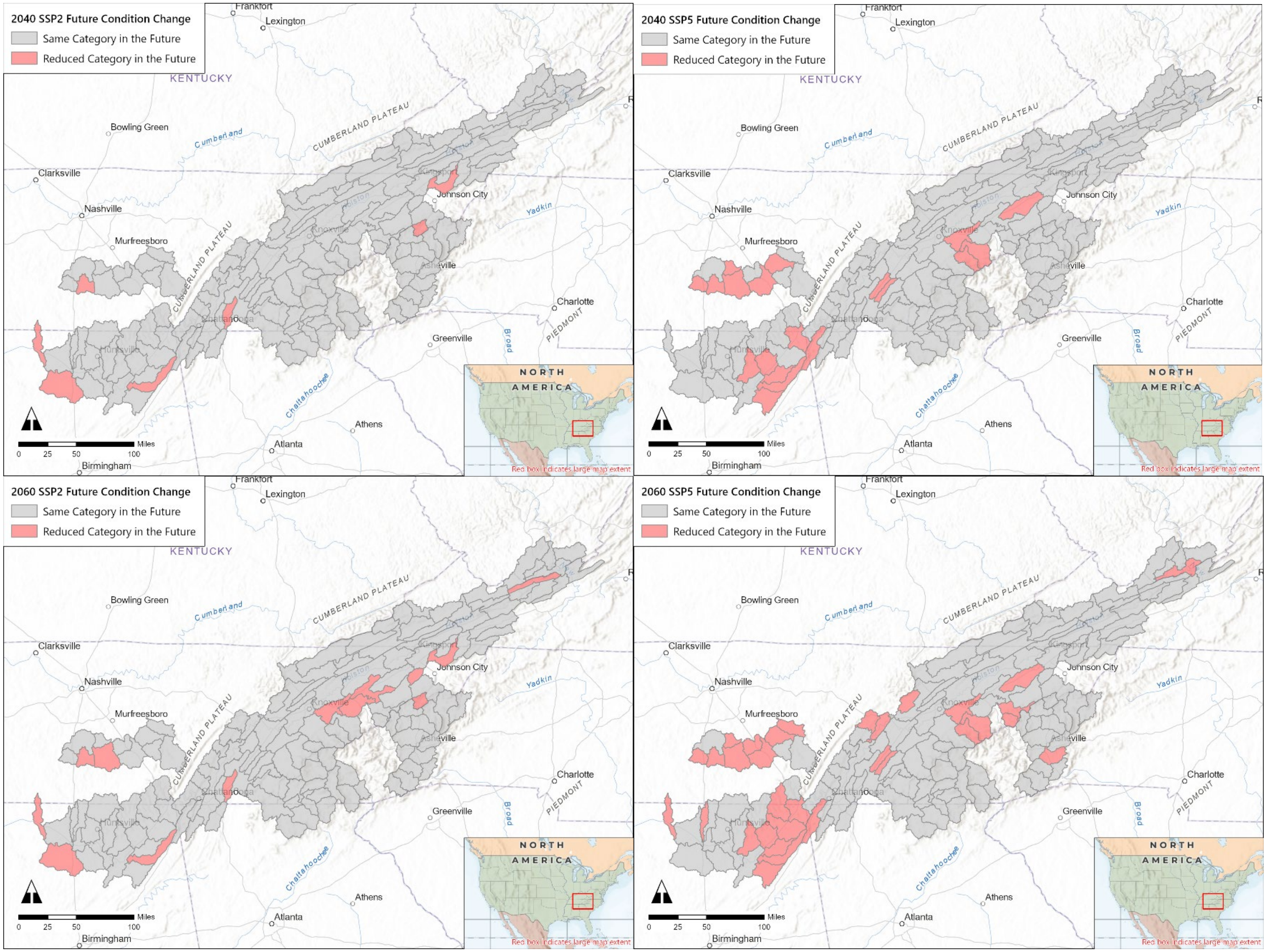

Figure 23. Future habitat suitability change by AU, at timesteps 2040 and 2060, under two future scenarios SSP2 and SSP5.

6.3. Future Habitat Suitability Conditions

Changes in future habitat suitability for the Tennessee Heelsplitter under both SSP2 and SSP5 scenarios at 2040 and 2060 timesteps are displayed in Figure 24. These maps capture differences in future habitat suitability summarized from model outputs displayed in Figure 23. More detailed information is included in Appendix 5.

6.3.1. Resiliency

Overall, habitat suitability is predicted to change within the Tennessee Heelsplitter range over the next 40 years (to 2060). Under SSP2, compared to current condition, habitat suitability decreases in 7 AUs by 2040, and in 13 AUs by 2060. Under this moderate future scenario, in 40 years (2060), it is predicted that 91% of AUs (n=133) will maintain varying levels of suitable habitat for the Tennessee Heelsplitter, with 5% of AUs (n=7) predicted to have less suitable habitat than under current conditions, and 4% of AUs (n=6) no longer having suitable habitat.

Under SSP5, compared to current condition, habitat suitability decreases in 19 AUs by 2040, and 32 AUs by 2060. Under this more extreme future scenario, in 40 years (2060), it is predicted that 77% of AUs (n=113) will maintain varying levels of suitable habitat for the Tennessee Heelsplitter, with 9% of AUs (n=13) with less suitable habitat than under current conditions, and 14% of AUs (n=20) no longer with suitable habitat for the species. Decreases in suitable habitat could mean reduced resiliency for the Tennessee Heelsplitter; however, our analysis shows that by 2060, 77-91% of the Tennessee Heelsplitter's range is predicted to maintain varying levels of suitable habitat to sustain the species. ICLUS projections into the future indicate slight reductions in comparison to current resiliency for the Tennessee Heelsplitter.

We analyzed changes in resiliency at the AU level at 20 and 40 year timeframes to discern patterns in projected species habitat suitability. These patterns of reduced resiliency generally are expected in or around existing urban centers or large cities that correlate with continued human population growth and expansion into non-urban areas currently dominated by agriculture and forest. Our future conditions analysis does not account for the potential rediscovery of populations, or discovery of new populations within the range through future survey efforts, which will improve our knowledge and understanding of the species.

6.3.2. Redundancy

The predicted changes in future suitable habitat are generally clustered around the more developed areas near and east of Huntsville, AL, as well as Lynchburg/Tullahoma, TN and Knoxville, TN. These are areas of developing urban centers. In 40 years, the number of AUs with suitable habitat for the Tennessee Heelsplitter remains high (ranging from 113 to 133 AUs) and the distribution of higher levels of AUs with suitable habitat remains throughout the range. This future redundancy will help the species withstand potential future catastrophic events.

6.3.3. Representation

There are predicted changes in future suitable habitat in all three RUs, although the Tennessee River RU, by virtue of encompassing the majority of AUs, is predicted to have more overall AUs with decreased habitat suitability than the Cumberland or New River RUs. The adaptive capacity of the Tennessee Heelsplitter (as described in section 6.5.3) indicates that there are many aspects of life history and ecology of the species that will enable the species to persist in place and face future climate challenges. We do not expect the future representation, or adaptive capacity, of the Tennessee Heelsplitter to change by 2060.

6.3.4. Additional Considerations

While future impacts are accounted for when looking at changes in developed land-use coverage under multiple climate change scenarios (see Chapter 6 introduction on p. 42), we acknowledge that our future conditions analysis did not account for all potential influences on Tennessee Heelsplitter viability, and only indirectly accounted for some of the influences discussed in Chapter 4. This was primarily a result of limited availability of data for future projections on these influences.

For instance, there are other ANS, in addition to the Asian Clam that may affect the Tennessee Heelsplitter. Hydrilla (*Hydrilla verticillata*) is a widespread aquatic plant in the Ohio and Tennessee River systems that alters stream habitat, decreases flows, and contributes to sediment buildup in streams (Balciunas et al. 2002, p. 92). However, there is not enough information to make reasonable assumptions about how Hydrilla might impact the Tennessee Heelsplitter in the future.

Additionally, there are many possible sources of siltation, sedimentation, pollution, and toxic spills. While our future condition analysis did not account for an exhaustive list of potential sources driving these influences, it indirectly accounted for the most likely sources associated with development, using data from which reasonable assumptions could be drawn. In other words, despite limited information available on future influences, justifiable interpretations could be made about future condition of the Tennessee Heelsplitter because of documented relationships these influences have related to LULC, with these LULC changes determining future condition being informed by the empirically based ICLUS model.

6.3.5. Future Viability Summary

Our analysis of future condition for the Tennessee Heelsplitter, when compared to current condition, predicts slight changes to levels of suitable habitat and overall resiliency throughout the range of the species. Redundancy is sustained through varying levels of suitable habitat across RUs being maintained over the next 40 years (2060) in 77-91% of all AUs. This analysis considers expected changes to suitability of habitat in areas of developing urban centers and changes in major land-use classifications. Our projections do not include the potential discovery of additional populations, but all AUs and RUs are within the historical documented range, so any new populations are expected to be within this geographical area. Potential conservation actions, such as barrier removals, may lead to population expansion or improvements in resiliency, but are opportunistic and difficult to consistently predict into the future. Our future condition analyses using ICLUS data predicts the Tennessee Heelsplitter will maintain substantial resiliency through 2060.

With resiliency being maintained range-wide, it is also predicted that the concentration of resilient AUs in the southwestern Virginia and northeastern Tennessee strongholds will remain intact. Connectivity of these resilient AUs within the upper Tennessee RU bolster the likelihood of persistence into the future. In the future, stochastic events associated with threats to the species will likely affect population resilience in portions of the range, and these are more likely to occur or be observed in developed areas. However, our future condition projections indicate Tennessee Heelsplitter resiliency is sufficient to withstand disturbance stochasticity, due to prevalent suitable habitat and life history traits that reduce risk currently and into the future.

The New and Tennessee RUs currently have the largest number of most resilient AUs. All RUs maintain at least 91% resilient AUs under future condition SSP2 and 77% resilient AUs under SSP5 future condition projections. Resilient and redundant AUs maintained in future condition projections across RUs are predicted to help buffer changes in environmental conditions in 2040 and 2060.

The Tennessee Heelsplitter has several adaptive life history traits, such as capability to transform on a wide variety of common host fish species, occurring in varying stream sizes, and tolerance of silty and sandy substrates and depositional areas with low flows. Spring-fed streams where the Tennessee Heelsplitter are most frequently located are ubiquitous throughout the species range and have year-round groundwater contributions with continuous flow and comparatively stable temperature regimes. These characteristics are expected to help the Tennessee Heelsplitter persist in most AUs throughout the range into the future and withstand projected climate effects.

Additionally, the Tennessee Heelsplitter can be locally abundant when found; when taken with its occurrence in headwater streams, the result could potentially be large populations in multiple tributary streams within AUs. The dendritic population and AU orientation may enable the species to withstand stochastic and potentially catastrophic events such as contaminant spills, which are likely to increase in developed land use areas.

Our representation analysis indicates that there are many aspects of Tennessee Heelsplitter life history and ecology that will enable the species to persist in place in the future. We do not expect the future representation, or adaptive capacity, of the Tennessee Heelsplitter to change by 2060. As such, future predicted resiliency, redundancy, and representation for the Tennessee Heelsplitter will be maintained in 2040 and through 2060.

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Appendix 1. Host Fish for the Tennessee Heelsplitter

Table 15. Host fishes documented for the Tennessee Heelsplitter. Only includes species for which transformation and excystment occurred. The RU from which the species was collected is indicated in parentheses.

Common Name	Scientific Name	Source (Representation Unit)
Central Stoneroller	*Campostoma anomalum*	Gordon 1993 (Tennessee); Ganser et al. 2022 (New)
Bluntnose Minnow	*Pimephales notatus*	Gordon 1993 (Tennessee); Barton and Layzer 2011 (Cumberland)
Flame Chub	*Hemitremia flammea*	Barton and Layzer 2011 (Cumberland)
Creek Chub	*Semotilus atromaculatus*	Gordon 1993 (Tennessee); Barton and Layzer 2011 (Cumberland)
Striped Shiner	*Luxilus chrysocephalus*	Gordon 1993 (Tennessee); Barton and Layzer 2011 (Cumberland)
Southern Redbelly Dace	*Chrosomus erythrogaster*	Barton and Layzer 2011 (Cumberland)
Eastern Blacknose Dace	*Rhinichthys atratulus*	Ganser et al. 2022 (Tennessee, New)
Rock Bass	*Ambloplites rupestris*	Gordon 1993; Steg and Neves 1997; Ganser et al. 2022 (Tennessee)
Green Sunfish	*Lepomis cyanellus*	Barton and Layzer 2011 (Cumberland)
Western Mosquitofish	*Gambusia affinis*	Barton and Layzer 2011 (Cumberland)
Banded Sculpin	*Cottus carolinae*	Gordon 1993; Steg and Neves 1997 (Tennessee); Barton and Layzer 2011 (Cumberland); Ganser et al. 2022 (New)
Cherry Darter	*Etheostoma etnieri*	Barton and Layzer 2011 (Cumberland)
Corrugated Darter	*Etheostoma basilare*	Barton and Layzer 2011 (Cumberland)
Redline Darter	*Etheostoma rufulineatum*	Gordon 1993 (Tennessee)
Rainbow Darter	*Etheostoma caeruleum*	Gordon 1993 (Tennessee)
Snubnose Darter	*Etheostoma simoterum*	Gordon 1993 (Tennessee)
Fantail Darter	*Etheostoma flabellare*	Ganser et al. 2022 (Tennessee, New)

Appendix 2. Variable Responses and Descriptions for Tennessee Heelsplitter Current Condition Model

Table 16. Model responses for variables used to inform habitat suitability of the Tennessee Heelsplitter.

Variable	BRT	GAM	GLM	MAX	RF	Average
Slope	0.05	0.50	0.37	0.29	0.06	0.254
Watershed Nitrogen Fertilizer Use	0.01	0.26	0.38	0.33	0.02	0.2
Watershed Soil Erodibility	0.01	0.33	0.34	0.24	0.03	0.19
Catchment Average Annual Precipitation	0.01	0.34	0.35	0.23	0.02	0.19
Flow Rate	0.18	0.08	0.15	0.29	0.07	0.154
Catchment Pasture Land Percent	0.00	0.28	0.32	0.15	0.01	0.152
Stream Order	0.02	0.11	0.57	0.02	0.02	0.148
Velocity	0.00	0.27	0.33	0.07	0.01	0.136
Watershed Runoff	0.12	0.24	0.12	0.12	0.07	0.134
Catchment Forested Landcover Percent	0.00	0.20	0.22	0.19	0.00	0.122
Average Water Temperature	0.01	0.22	0.03	0.23	0.02	0.102
Watershed Developed Land Percent	0.00	0.17	0.14	0.16	0.00	0.094

Table 17. Descriptions of variables used in the final Tennessee Heelsplitter habitat suitability model.

Variable	Description
Watershed Developed Land Percent	Percent of watershed developed, open space, low-intensity, medium-intensity, and high-intensity
Watershed Nitrogen Fertilizer Use	Mean rate of synthetic nitrogen fertilizer application to agricultural land in kg N/ha/yr, within watershed.
Watershed Soil Erodibility	Mean soil erodibility (Kf) factor (unitless) of soils within watershed. The Kf factor is used in the Universal Soil Loss Equation (USLE) and represents a relative index of susceptibility of bare, cultivated soil to particle detachment and transport by rainfall.
Watershed Runoff	Mean runoff (mm) within watershed.
Catchment Average Annual Precipitation	PRISM climate data - 30-year normal mean precipitation (mm): Annual period: 1981-2010 within the catchment.
Catchment Pasture Land Percent	Sum percent of catchment area classified as hay land use (NLCD 2016 class 81) and grassland/herbaceous land cover (NLCD 2016 class 71).
Catchment Forested Landcover	Sum percent of catchment area classified as deciduous land cover (NLCD 2016 class 41), evergreen forest land cover (NLCD 2016 class 42), and mixed deciduous/evergreen forest land cover (NLCD 2016 class 43).
Average Water Temperature	Predicted mean annual stream temperature (Jan-Dec) for year 2014.
Stream Order	Modified Strahler stream order.
Flow Rate	Mean Annual Flow from gage adjustment (cfs). Best EROM estimate of actual mean flow.
Velocity	Mean Annual Velocity from gage adjustment (fps). Best EROM estimate of actual mean velocity.
Slope	Slope of flowline (meters/meters) based on smoothed elevations; a value of -9998 means that no slope value is available.

Appendix 3. Current & Future Condition Analysis Unit Rankings

Table 18. Current Condition Level for Each AU.

Representation Unit	Analysis Unit Name	Current Condition
Cumberland	Charles Creek-Collins River	*Moderate Resiliency*
	Hickory Creek	*High Resiliency*
	Barren Fork	*Most Resiliency*
	Hills Creek-Collins River	*Most Resiliency*
New	Bluestone Lake-New River	*High Resiliency*
	Indian Creek	*High Resiliency*
	Brush Creek	*High Resiliency*
	East River-New River	*High Resiliency*
	Little Walker Creek-Walker Creek	*High Resiliency*
	Clear Fork-Wolf Creek	*High Resiliency*
	Sinking Creek-New River	*High Resiliency*
	Bluestone River	*Most Resiliency*
	Kimberling Creek-Walker Creek	*Most Resiliency*
	Hunting Camp Creek-Wolf Creek	*Most Resiliency*
Tennessee	Big Rock Creek	*Moderate Resiliency*
	Flint Creek	*Moderate Resiliency*
	Fountain Creek	*Moderate Resiliency*
	Guntersville Lake-Short Creek	*Moderate Resiliency*
	Guntersville Lake-South Sauty Creek	*Moderate Resiliency*
	Guntersville Lake-Town Creek	*Moderate Resiliency*
	Limestone Creek	*Moderate Resiliency*
	Little Pigeon River	*Moderate Resiliency*
	Lower Tellico Lake	*Moderate Resiliency*
	Mud Creek	*Moderate Resiliency*
	Nantahala River	*Moderate Resiliency*
	North Fork Creek	*Moderate Resiliency*
	Nottely River	*Moderate Resiliency*
	Piney Creek	*Moderate Resiliency*
	Piney River	*Moderate Resiliency*
	Second Creek-Wheeler Lake	*Moderate Resiliency*
	South Indian Creek	*Moderate Resiliency*
	Swan Creek-Wheeler Lake	*Moderate Resiliency*
	Upper Guntersville Lake	*Moderate Resiliency*
	Watts Bar Lake-Tennessee River	*Moderate Resiliency*
	West Prong Little Pigeon River	*Moderate Resiliency*
	Wheeler Lake-Cotaco Creek	*Moderate Resiliency*
	Abrams Creek	*Moderate Resiliency*
	Brasstown Creek-Hiwassee River	*Moderate Resiliency*
	Cheoah River	*Moderate Resiliency*
	Chestuee Creek	*Moderate Resiliency*
	Clear Creek-French Broad River	*Moderate Resiliency*
	Cove Creek-Nolichucky River	*Moderate Resiliency*
	Dallas Lake-Tennessee River	*Moderate Resiliency*

Representation Unit	Analysis Unit Name	Current Condition
Tennessee	Davidson River-French Broad River	*Moderate Resiliency*
	Fall Creek-Duck River E	*Moderate Resiliency*
	Garrison Fork	*Moderate Resiliency*
	Gulf Fork Big Creek	*Moderate Resiliency*
	Headwaters French Broad River	*Moderate Resiliency*
	Headwaters North Toe River	*Moderate Resiliency*
	Hiwassee Lake-Hiwassee River	*Moderate Resiliency*
	Hiwassee River-Chatuge Lake	*Moderate Resiliency*
	Huntsville Spring Branch-Indian Creek	*Moderate Resiliency*
	Ivy Creek	*Moderate Resiliency*
	Lower Flint River	*Moderate Resiliency*
	Lower Guntersville Lake	*Moderate Resiliency*
	Mud Creek-Tennessee River	*Moderate Resiliency*
	Nickajack Lake-Tennessee River	*Moderate Resiliency*
	North Indian Creek-Nolichucky River	*Moderate Resiliency*
	North Mouse Creek	*Moderate Resiliency*
	Nottely River-Nottely Lake	*Moderate Resiliency*
	Sandymush Creek-French Broad River	*Moderate Resiliency*
	South Toe River-North Toe River	*Moderate Resiliency*
	Spring Creek-French Broad River	*Moderate Resiliency*
	Swannanoa River	*Moderate Resiliency*
	Tennessee River-Wheeler Lake	*Moderate Resiliency*
	Toccoa River-Blue Ridge Lake	*Moderate Resiliency*
	Tusquitee Creek-Hiwassee River	*Moderate Resiliency*
	Upper Flint River	*Moderate Resiliency*
	Upper Tellico Lake	*Moderate Resiliency*
	Valley River	*Moderate Resiliency*
	Walnut Creek-French Broad River	*Moderate Resiliency*
	Battle Creek	*High Resiliency*
	Big Laurel Creek	*High Resiliency*
	Boone Lake-South Fork Holston River	*High Resiliency*
	Cane Creek-French Broad River	*High Resiliency*
	Cane River	*High Resiliency*
	Chattanooga Creek	*High Resiliency*
	Cullasaja River	*High Resiliency*
	Douglas Lake-French Broad River	*High Resiliency*
	Flat Creek-Duck River W	*High Resiliency*
	Fontana Lake	*High Resiliency*
	Headwaters Little Tennessee River	*High Resiliency*
	Hominy Creek	*High Resiliency*
	Laurel Creek-South Fork Holston River	*High Resiliency*

Representation Unit	Analysis Unit Name	Current Condition
Tennessee	Lick Creek	*High Resiliency*
	Lookout Creek	*High Resiliency*
	Mills River-French Broad River	*High Resiliency*
	North Chickamauga Creek	*High Resiliency*
	Oostanaula Creek	*High Resiliency*
	Poplar Creek	*High Resiliency*
	Richland Creek	*High Resiliency*
	Sale Creek	*High Resiliency*
	Sinking Creek-Tennessee River	*High Resiliency*
	South Holston Lake-South Fork Holston River	*High Resiliency*
	Spring Creek-Hiwassee River	*High Resiliency*
	Tellico River	*High Resiliency*
	Whites Creek	*High Resiliency*
	Widows Creek-Tennessee River	*High Resiliency*
	Abrams Creek-North Fork Holston River	*High Resiliency*
	Beaver Creek TN	*High Resiliency*
	Beaver Creek VA	*High Resiliency*
	Big Coon Creek-Crow Creek	*High Resiliency*
	Big Limestone Creek	*High Resiliency*
	Big Moccasin Creek-North Fork Holston River	*High Resiliency*
	Candies Creek	*High Resiliency*
	Clinch River	*High Resiliency*
	Conasauga Creek	*High Resiliency*
	Dumps Creek-Clinch River	*High Resiliency*
	Laurel Creek-North Fork Holston River	*High Resiliency*
	Little Chucky Creek-Nolichucky River	*High Resiliency*
	Lower Paint Rock River	*High Resiliency*
	Norris Lake-Clinch River	*High Resiliency*
	North Fork Powell River-Powell River	*High Resiliency*
	Rowland Creek-South Fork Holston River	*High Resiliency*
	Sewee Creek	*High Resiliency*
	Wolftever Creek	*High Resiliency*
	Big Cedar Creek-Clinch River	*High Resiliency*
	Bullrun Creek	*High Resiliency*
	Chickamauga Lake-Hiwassee River	*High Resiliency*
	Fort Patrick Henry Lake-South Fork Holston River	*High Resiliency*
	Guest River	*High Resiliency*
	Holston River	*High Resiliency*
	Pond Creek-Tennessee River	*High Resiliency*
	Tumbling Creek-North Fork Holston River	*High Resiliency*

Representation Unit	Analysis Unit Name	Current Condition
Tennessee	Alarka Creek-Little Tennessee River	*Most Resiliency*
	Cherokee Lake-Holston River	*Most Resiliency*
	French Broad River	*Most Resiliency*
	Little River TN	*Most Resiliency*
	South Fork Powell River-Powell River	*Most Resiliency*
	Normandy Lake-Duck River	*Most Resiliency*
	Ocoee River	*Most Resiliency*
	Powell River	*Most Resiliency*
	Stony Creek-Clinch River	*Most Resiliency*
	Upper Paint Rock River	*Most Resiliency*
	Ball Creek	*Most Resiliency*
	Big Creek-Holston River	*Most Resiliency*
	Copper Creek	*Most Resiliency*
	Indian Creek-Clinch River	*Most Resiliency*
	Little Chickamauga Creek-East Chickamauga Creek	*Most Resiliency*
	Little River VA	*Most Resiliency*
	Middle Fork Holston River	*Most Resiliency*
	North Fork Clinch River-Clinch River	*Most Resiliency*
	South Chickamauga Creek	*Most Resiliency*
	Swords Creek-Clinch River	*Most Resiliency*
	Wallen Creek-Powell River	*Most Resiliency*
	West Chickamauga Creek	*Most Resiliency*

Table 19. AUs with reduced resiliency in the future under SSP2 (2040, 2060) and SSP5 (2040, 2060).

Climate Scenario	SSP 2	SSP 5	SSP 2	SSP 5
Timeframe	**2040**	**2040**	**2060**	**2060**
Representation Unit	**Analysis Unit**			
Tennessee	Guntersville Lake-Town Creek	Widows Creek-Tennessee River	Guntersville Lake-Town Creek	Widows Creek-Tennessee River
	Big Rock Creek	Guntersville Lake-South Sauty Creek	Big Rock Creek	Guntersville Lake-South Sauty Creek
	Second Creek-Wheeler Lake	Upper Guntersville Lake	Second Creek-Wheeler Lake	Upper Guntersville Lake
	Flint Creek	Guntersville Lake-Town Creek	Flint Creek	Guntersville Lake-Town Creek
	Boone Lake-South Fork Holston River	Guntersville Lake-Short Creek	Boone Lake-South Fork Holston River	Guntersville Lake-Short Creek
	Candies Creek	Lower Paint Rock River	Candies Creek	Lower Paint Rock River
	South Indian Creek	West Prong Little Pigeon River	South Indian Creek	West Prong Little Pigeon River
		Little Pigeon River	French Broad River	Little Pigeon River
		French Broad River	Fall Creek-Duck River E	French Broad River
		Lick Creek	Douglas Lake-French Broad River	Lick Creek
		Oostanaula Creek	Big Limestone Creek	Oostanaula Creek
		North Mouse Creek	Little Chucky Creek-Nolichucky River	North Mouse Creek
		Normandy Lake-Duck River		Normandy Lake-Duck River
		Fall Creek-Duck River E		Fall Creek-Duck River E
		Big Rock Creek		Big Rock Creek
		Fountain Creek		Fountain Creek
		Lookout Creek		Lookout Creek
		North Fork Creek		North Fork Creek
				Mud Creek-Tennessee River
				Piney Creek
				Second Creek-Wheeler Lake
				Gulf Fork Big Creek
				Whites Creek
				Watts Bar Lake-Tennessee River
				Poplar Creek
				Garrison Fork
				Big Coon Creek-Crow Creek
				Clear Creek-French Broad River
				Cane Creek-French Broad River
New			Clear Fork-Wolf Creek	East River-New River
Cumberland		Barren Fork		Barren Fork
				Charles Creek-Collins River

Appendix 4. Adaptive Capacity for the Tennessee Heelsplitter

Table 20. Results for adaptive capacity of the Tennessee Heelsplitter, including definitions and justifications.

Ecological Theme	Trait	Definition	Justification
Abiotic Niche	Moderate Behavioral Regulation of Physiology	Behavior temporarily restricts foraging or reproductive activities, but is not detrimental to survivability or fitness.	The Tennessee Heelsplitter is one of the few mussels that can be found year-round in some small streams. Most mussels generally burrow into the substrate during winter months and cold temperatures and the Tennessee Heelsplitter is no exception, but the species is thought to be adaptable and capable of modifying its physiological tolerance, and can be found at the substrate surface in the fall and winter.
Abiotic Niche	Moderate Climatic Niche Breadth	50– 90% of occurrences or range restricted to particular climatic (or hydrological) condition that may be reduced as a result of climate change.	The Tennessee Heelsplitter has been most frequently found in small spring fed streams but also can be found in larger streams such as the North Fork Holston River and Clinch River. The dynamics of these populations occurring in varying size streams is unknown, but it is assumed the species has the capability to adapt to a variety of flowing waters as long as appropriate microhabitats, such as substrate conditions, and host fishes are present.
Abiotic Niche	Low Physiological Tolerances	Range of novel conditions are known to cause lethal effects (intolerable); OR variation in historical conditions for limiting abiotic factor is highly restricted.	Droughts, floods, and changes in stream temperature could cause lethal effects (78 FR 59269), particularly for headwater streams. Proper water flow is necessary for species viability. Species that are reliant on stable conditions, such as temperature or hydrological flow regimes, for survival and reproduction can be negatively impacted by extreme events (pulse disturbances) or press disturbances beyond conditions to which they are adapted.
Abiotic Niche	Low Seasonal Phenology	Dependence on environmental cue.	Seasonal change in temperature is an important environmental cue for mussel spawning (Coker et al. 1921, pp. 142-143; Matteson 1948, p. 702; Yokley 1972, p. 351-362). For more information, see Section 3.1.7.
Demography	High Age of Sexual Maturity	Early relative to lifespan.	The Barrens Heelsplitter, a form of *Lasmigona holstonia*, sexually mature at three years old (Barton 2011, p. 14)
Demography	Moderate Age Structure	Balanced (age classes are roughly equal).	Barton (2011, p. 16) examined 103 shells from a single population of Barrens Heelsplitter. Ages ranged from 2-24 years, with 61 (56%) being between 4-9 years old.
Demography	Moderate Generation Time	1–25 years.	*Lasmigona holstonia* has a minimum reproductive age of three years (Barton 2011, p. 35), but peak reproductive output is probably 10.
Demography	Moderate Lifespan	10-25 years.	Periodic species like the Tennessee Heelsplitter exhibit a lifespan of up to 30 years (Mitchell 2020, p. 23); however, a life history study indicated a

			life span of 24 years for the Barrens heelsplitter, a form of *Lasmigona holstonia* (Barton 2011, p. 14).
Demography	High Recruitment	Large proportion of juveniles in a population surviving to maturity.	Barton (2011, p. 14) found that older individuals (i.e., >20 years) were uncommon; however, a large proportion of individuals were past first age of reproduction (p. 16).
Distribution	High Area of Occupancy	>2000km^2	The area of the Tennessee Heelsplitter's range is above 2000km^2.
Distribution	Moderate Commensalism with Humans	Moderately tolerant of human influences, utilization of semi-natural landscapes (e.g., agricultural fields, suburban parks, etc.).	Tennessee Heelsplitter individuals have been observed buried greater than 15cm (Ganser et al. 2022, pp. 58-59), which may help provide a greater desiccation tolerance for the species to survive short-term drought caused by human actions. Other members of the Anodontini tribe, of which the Tennessee Heelsplitter is a member, are considered "periodic," meaning they are predicted to have intermediate desiccation tolerance, and limited colonization potential during and after drying events (Chambers and Woolnough 2016, p. 13; Mitchell 2020, p. 20-26).
Distribution	High Extent of Occurrence	Area contained within the shortest continuous boundary that can be drawn to encompass all known, inferred, or projected sites of present occurrence, excluding cases of vagrancy.	Broad distribution (> 5,000 km^2). This broad distribution confers higher adaptive capacity because multiple populations over a large range will enable species persistence given varying climate futures.
Distribution	Moderate Geographic Rarity	Broadly distributed with sparse or isolated populations	The Tennessee Heelsplitter has some degree of connectivity of populations in waterways and moderate dispersal distances via fish hosts and high flow events.
Distribution	Moderate Habitat Specialization	Moderately dependent on a particular uncommon habitat, or an indicator of, but not an endemic to that habitat (contains 65–85% of occurrences).	Even though the Tennessee Heelsplitter is found in small to medium streams, they can occur in rivers. The species requires flowing waters for all life stages but is tolerant of a wide range of substrates that other mussels are not (such as silt and mud), and also occurs in depositional areas along river margins not frequently surveyed.
Ecological Role	Moderate Competitive Ability	Moderately affected by native or non-native species likely to be favored by climate change.	Biological interactions between exotic and native species may contribute to mussel declines in the Tennessee Heelsplitter range. The Asian clam has demonstrated cold tolerance following acclimation (Cvetanovska et al. 2021, pp. 729-738); this adaptive approach to thermal tolerance, and its observed resistance to desiccation (Guareschi and Wood 2020, p. 2818), may make it a strong competitor for the Tennessee Heelsplitter in the face of climate change.

Ecological Role	High Diet Breadth	Diet flexible; not strongly dependent on one or a few species	The Tennessee Heelsplitter is an obligate filter feeder. While most suspended organic matter in water is particulate organic detritus or heterotrophic bacteria and fungi (Nelson and Scott 1962, entire) the species filters everything in the water.
Ecological Role	Moderate Diversity of Obligate Species	Obligated to a restricted network (or pool) of species.	The Tennessee Heelsplitter is a host fish generalist.
Evolutionary Potential	Unknown Genetic Diversity	The genetic variability within a species	There is no currently available comprehensive study on genetic diversity for the Tennessee Heelsplitter.
Evolutionary Potential	Low Hybridization Potential	Hybridization does not occur OR hybridization occurs but offspring are not viable, or have lower fitness.	Hybridization is not known to occur for the species.
Evolutionary Potential	Moderate Population Size	< 2500 mature individuals.	The relevant scale for this category may be based on the lowest known size in lieu of averaging population sizes across the species. The Tennessee Heelsplitter has one location, Pocahontas Branch, with an estimated population size of 1,518 (90% CI: ± 133) (Barton 2011, p. 13).
Life History	High Fecundity	Many offspring or propagules (> 10).	*Lasmigona sp.* gravid females (N=34) were reported as having 9,000 – 54,000 glochidia per mussel (Barton 2011, p. 14). Haag (2013, p. 748) reports lower fecundity with a mean of 2,883 (13 individuals).
Life History	High Mating System	Promiscuity.	The Tennessee Heelsplitter is a broadcast spawner, and multiple paternity has previously been reported for freshwater mussels (Wacker et al. 2018, Entire; Christian et al. 2007, Entire).
Life History	High Parental Investment	Precocial (young are relatively mature and mobile from the moment of birth or hatching and capable of feeding themselves).	After juvenile mussels detach from their host fish, they burrow in substrate and feed themselves by sweeping the sediment with their foot (Yeager et al. 1994, pp. 217-221).
Life History	High Parity	Iteroparous.	The Tennessee Heelsplitter has multiple reproductive cycles in its lifetime., but females are not guaranteed to reproduce each year (Bauer 1987, p. 700; Saha and Layzer 2008, p. 88); this may occur with *Lasmigona sp.*, as individuals not gravid in 2009 had shell widths like gravid individuals (Barton 2011, p. 20).
Life History	Low Reproductive Mode	Broadcast spawning.	Most Unioninae species broadcast free larvae (Barnhart et al. 2008, p. 374).
Life History	Low Reproductive Phenology	Dependence on environmental cue; species is incapable of adjusting the	Temperature changes could impact the reproductive cycle, as seasonal change in temperature is an important environmental cue for spawning (Coker et al. 1921, pp.142-143; Matteson 1948, p. 702; Yokley 1972, p.

		timing or duration of reproductive events.	351-362). Small temperature increases can reduce freshwater mussel glochidia and juvenile survival.
Life History	High Sex Determination	Chromosomal.	Sex determination is chromosomal in freshwater mussels (Breton et al. 2011, p. 1645).
Life History	Unknown Sex Ratio	Can be skewed, balanced, or capable of facultative adjustments to account for skews.	There is no currently available information on sex ratios for the Tennessee Heelsplitter.
Movement	Moderate Dispersal Distance	Large percentage (at least 50%) of propagules or individuals disperse periodically or irregularly occurs.	Dispersal for mussels is accomplished by fish host and high flow rain events. This generally small, thin shelled species is likely frequently dispersed by high flows.
Movement	High Dispersal Phase	Long period or throughout life.	While it is important to note that the Tennessee Heelsplitter does not actively disperse on its own, it is capable of being dispersed throughout its lifetime. Dispersal is not tied to a particular life stage, as juvenile mussels may be dispersed by host fish, in addition to glochidia and adults being dispersed by high flow events.
Movement	Moderate Dispersal Syndrome	Dependence on vertebrate vectors with high mobility.	Species relies on host fish for dispersal.
Movement	Migration Demography	Can be complete (most individuals in population), partial (some individuals reside on breeding grounds year-round), or differential (individuals migrate different distances).	Adaptive capacity attribute is not applicable to the species.
Movement	Migration Distance	The total, geographic distance spanned during a migratory event.	Adaptive capacity attribute is not applicable to the species.
Movement	Migration Frequency	Once during lifetime, or throughout lifetime.	Adaptive capacity attribute is not applicable to the species.
Movement	Migration Timing	Can be obligate (migrate given a specific cue), or facultative (individuals “choose” to migrate or not).	Adaptive capacity attribute is not applicable to the species.
Movement	Low Site Fidelity	High site fidelity (high proportion of “stayers”).	There is very limited movement in freshwater mussels during their lifetime. Note: score for this metric is “low” in terms of adaptive capacity which is why the trait box reads “Low Site Fidelity” but as the definition suggests, the species has “high” site fidelity because it is a sessile species.

Appendix 5. Future Condition Output

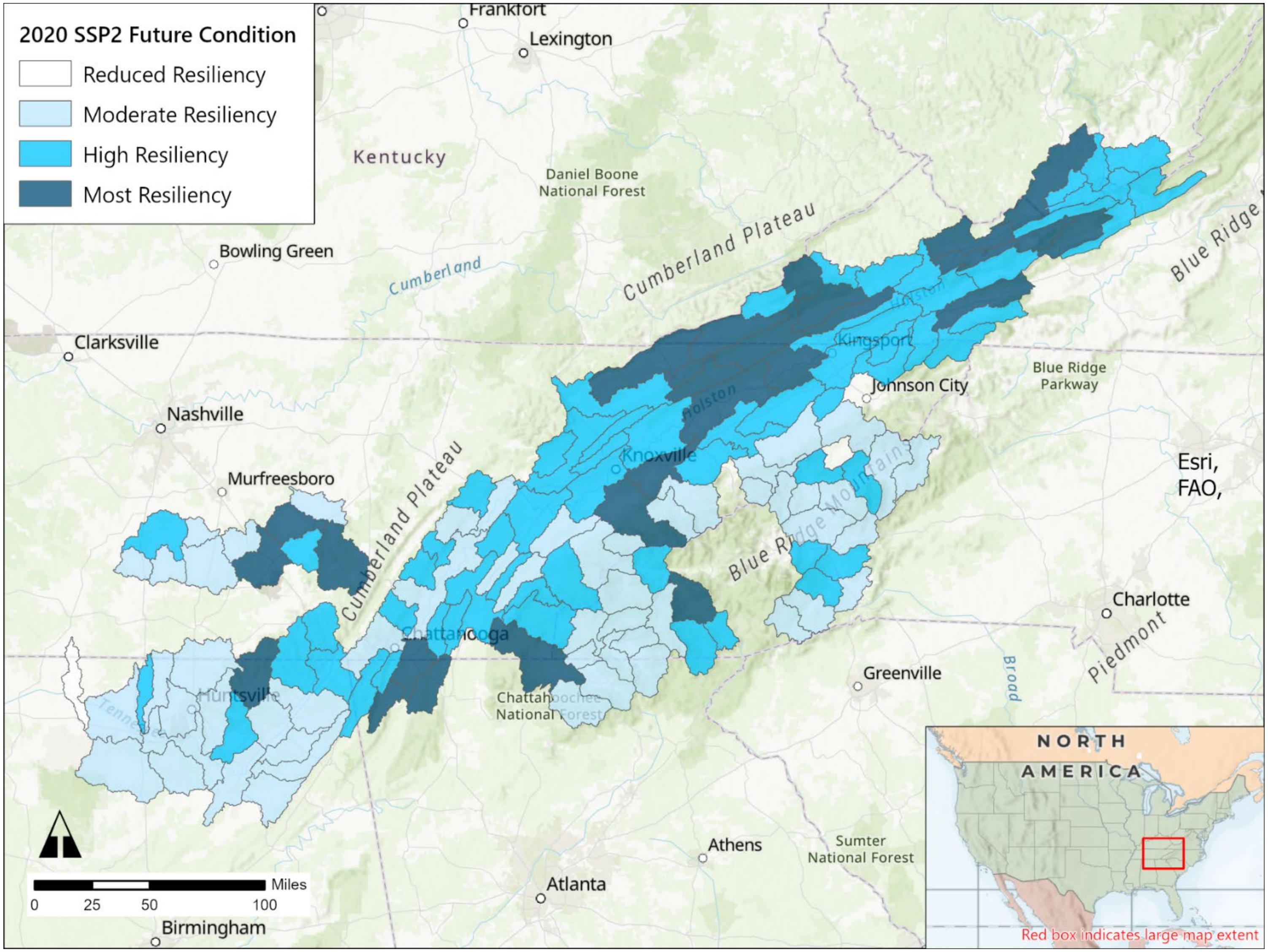

Figure 24. Future condition scores for each AU under SSP2 (Middle of the Road) in 2020. This year was used as a baseline for 2040 and 2060.

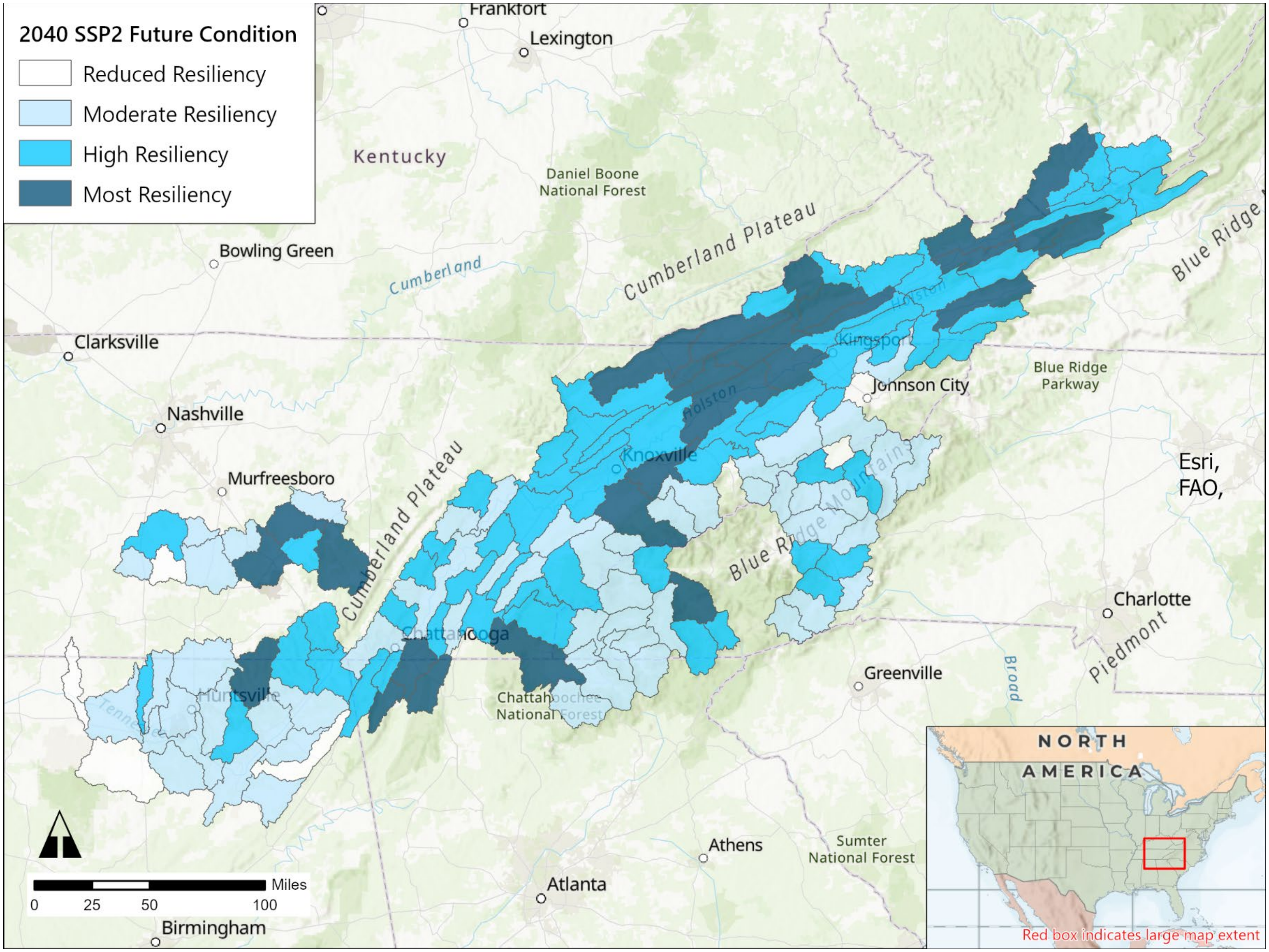

Figure 25. Future condition scores for each AU under SSP2 (Middle of the Road) in 2040.

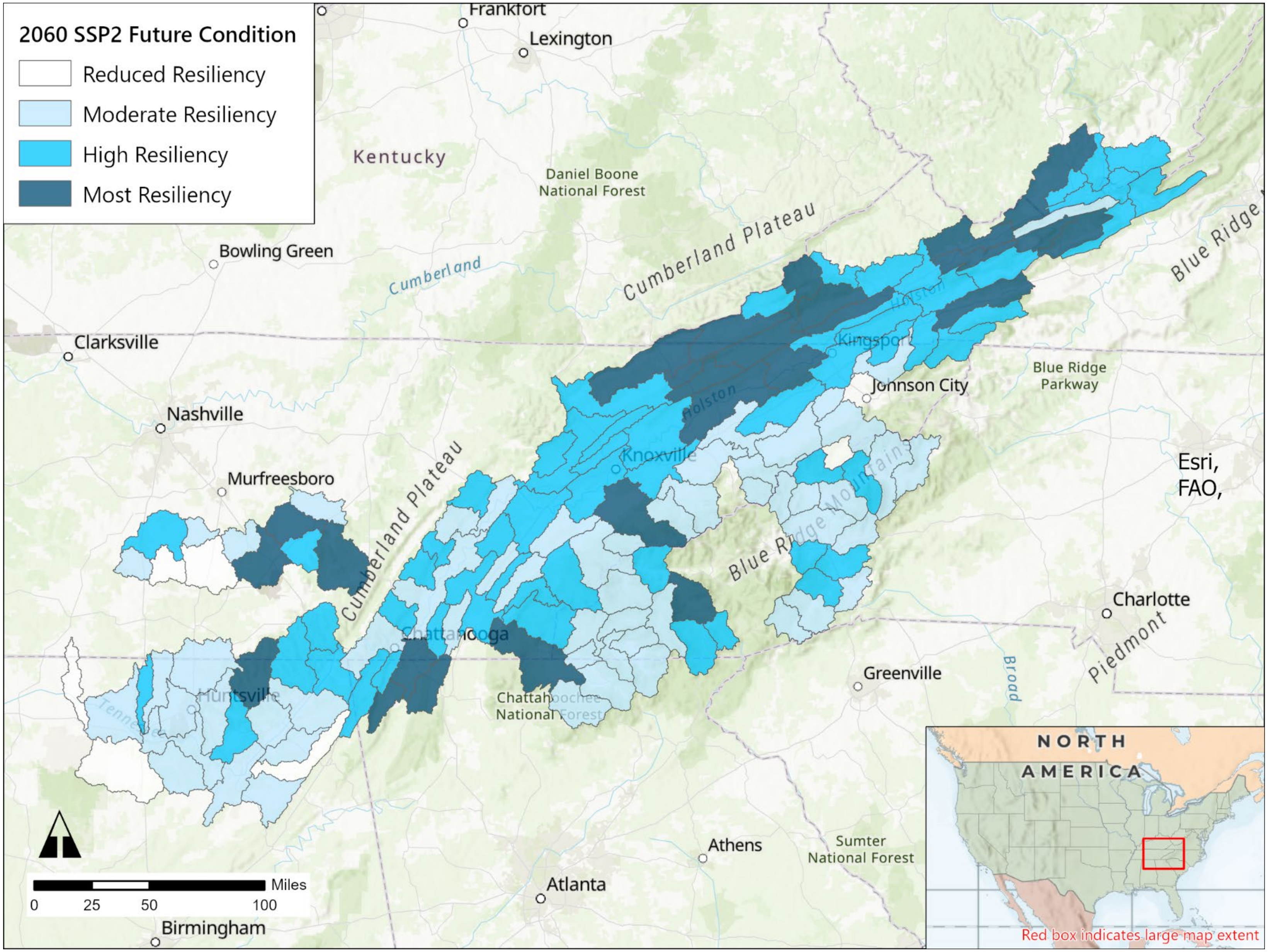

Figure 26. Future condition scores for each AU under SSP2 (Middle of the Road) in 2060.

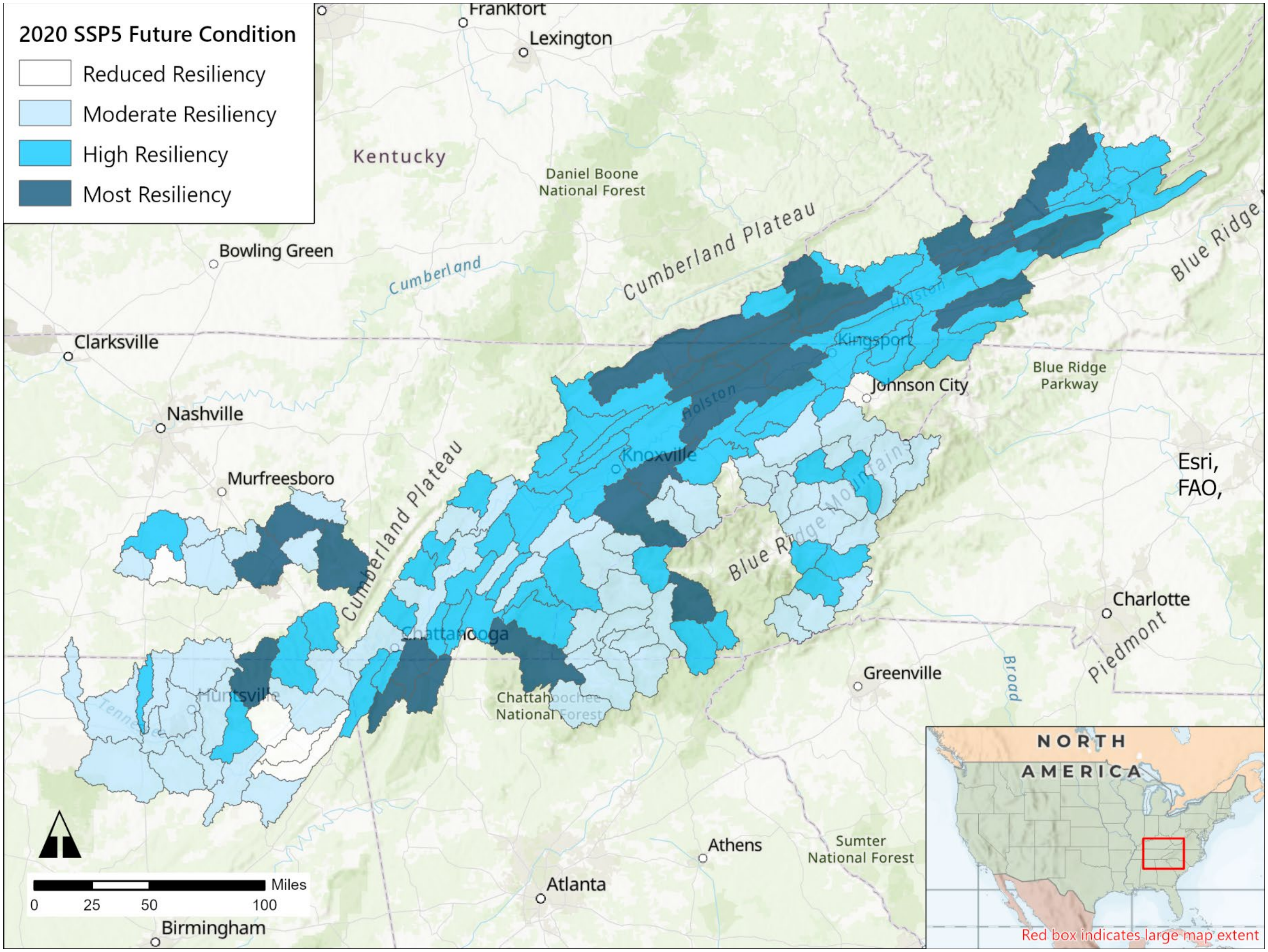

Figure 27. Future condition scores for each AU under SSP5 (Fossil-fueled Development) in 2020.

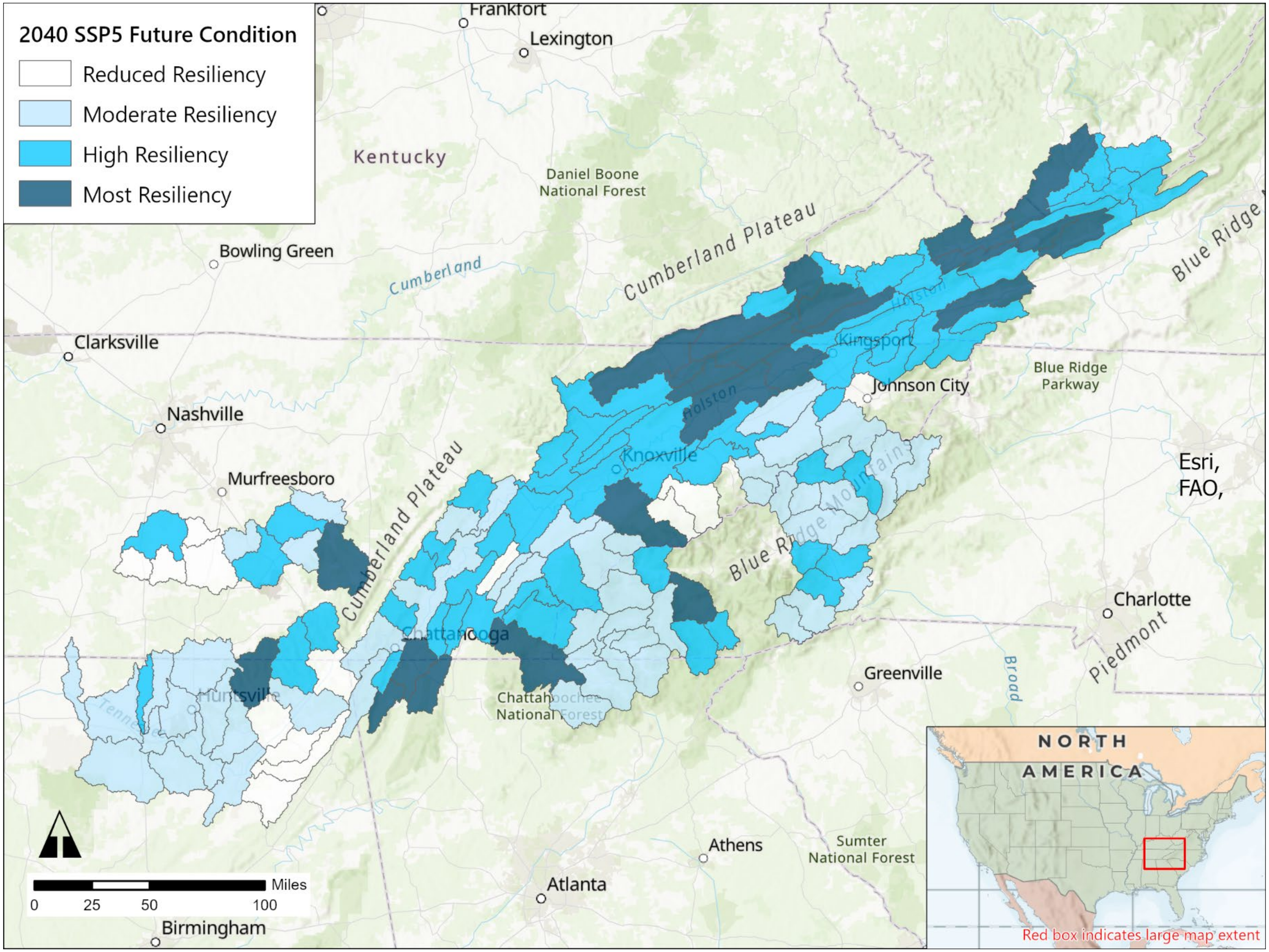

Figure 28. Future condition scores for each AU under SSP5 (Fossil-fueled Development) in 2040.

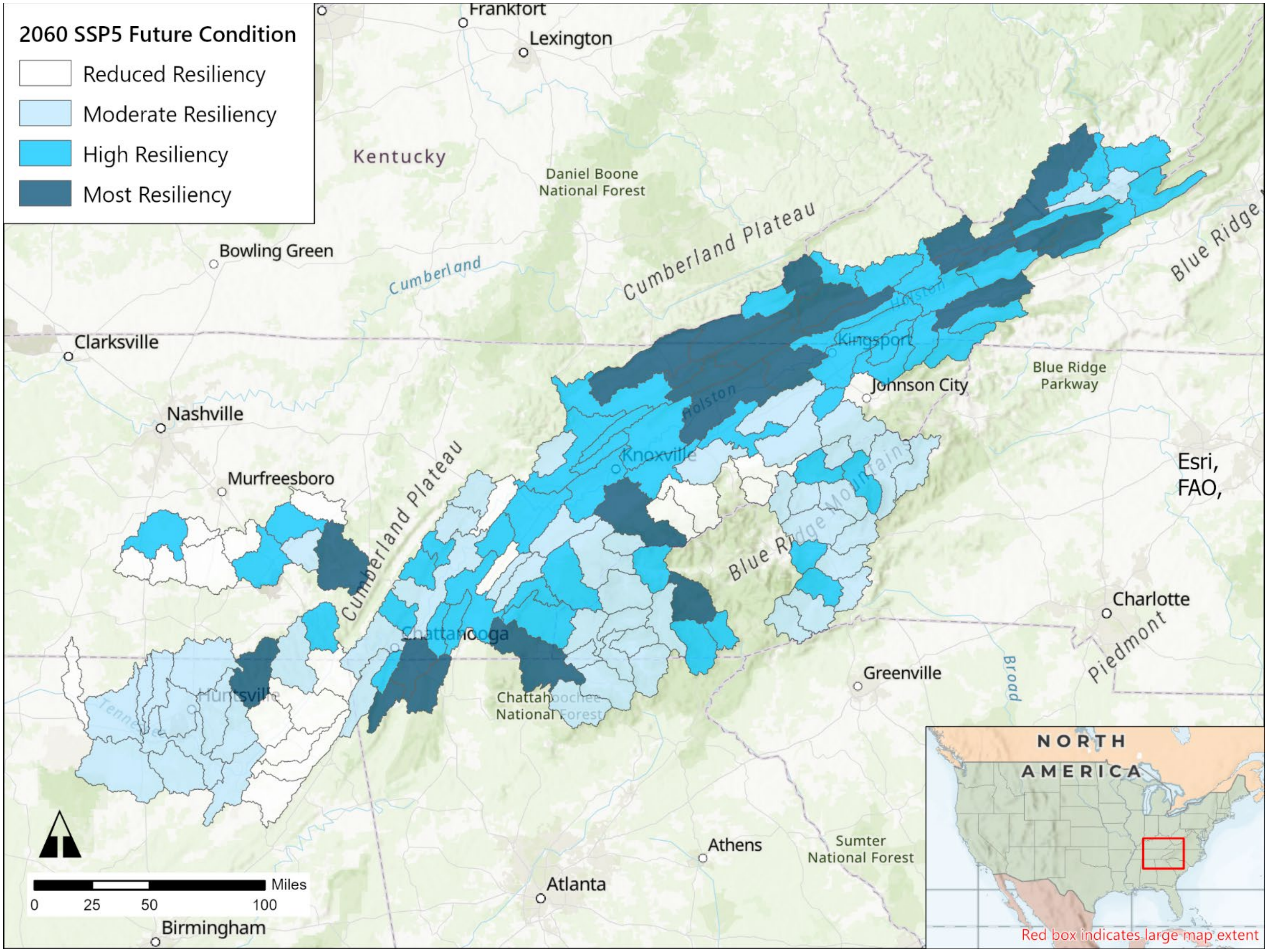

Figure 29. Future condition scores for each AU under SSP5 (Fossil-fueled Development) in 2060.