Species Status Assessment Report
Shenandoah Salamander
(*Plethodon shenandoah)*
Version 1.1

Photo credit: USGS

ACKNOWLEDGEMENTS
This document was prepared by the U.S. Fish and Wildlife Service [USFWS] (Emily Argo) and the U.S. Geological Survey (Evan Grant, Adrianne Brand). We would also like to recognize and thank Jennifer Szymanski (U.S. Fish and Wildlife Service) who provided substantive comments and edits and served as a resource throughout the process, Brian Halstead, Evan Childress, Jennifer Jones, Paul Super, Susan Walls, and two anonymous USGS reviewers.

Suggested reference:

U.S. Fish and Wildlife Service. 2025. Species status assessment report for the Shenandoah salamander (*Plethodon shenandoah*), Version 1.1. August 2025. Northeast Region. 34 pp.

EXECUTIVE SUMMARY
We conducted a species status assessment (SSA) to assess the viability of the Shenandoah salamander (*Plethodon shenandoah*). We use the proportion of occupied sites across the entire range of *P. shenandoah* in the wild over a biologically meaningful timeframe as a proxy for viability. We characterized *P. shenandoah* viability over time by assessing its ability to withstand environmental, genetic, and demographic stochasticity and disturbances (resiliency), catastrophic events (redundancy), and novel changes in its biological and physical environment (representation). *P. shenandoah* viability is enhanced by maintaining the demographic and genetic health of its populations and preserving potential habitat connections between populations which facilitate movement of salamanders.

Biology and habitat requirements
P. *shenandoah* is a small woodland salamander (adult snout-vent length 40-57 millimeters (mm), total length 85-110 mm, U.S. Fish and Wildlife Service [USFWS] 1994, p. 1) endemic to the area surrounding three peaks (Hawksbill, Stony Man, The Pinnacle) in Shenandoah National Park, Virginia, USA. The lower elevation limit of the species on these peaks is controlled by the location where clouds begin to form (the cloud base height), which define areas of high relative humidity. The species is entirely terrestrial and can be found most often in the spring and fall on the forest floor under rocks, logs, and other cover during the day, or roaming the forest floor on cool, wet nights. There is no specialized prey of the species, and individuals will forage from what is available, including insects, arachnids, worms, millipedes, and centipedes.

Little is known about *P. shenandoah* breeding behavior, and no descriptions of nesting sites have been documented in published literature; therefore, breeding behavior is assumed to be similar to other *Plethodon* species. Eggs are most likely laid in moist crevices underground or near the soil surface under rocks and woody debris with breeding most likely occurring in late spring and early summer.

Methods
We assessed *P. shenandoah* viability by evaluating the historical and current condition (e.g., species occurrence rates, habitat quality) of its populations and identifying the primary influences leading to the species' current condition. Next, we identified four plausible scenarios from a population viability

analysis (PVA) incorporating the impacts of changes in temperature, moisture, and competition over a 60-year timeframe on the proportion of occupied sites.

Results
All four scenarios predicted a decline in the proportion of occupied sites with varying levels of uncertainty after 60 years.

Viability synopsis
With the predicted decline in proportion of occupied sites, the small, disjunct distribution, and the species sensitivity to climate conditions, the species has limited ability to withstand stochastic and catastrophic events and adapt to changing environmental conditions.

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CHAPTER 1 – INTRODUCTION

Background

This report summarizes the results of a species status assessment (SSA) conducted for Shenandoah salamander (*Plethodon shenandoah*; hereafter *P. shenandoah*), a terrestrial salamander whose geographic range is restricted to three mountain peaks (Hawksbill, Stony Man, and The Pinnacle) within Shenandoah National Park (Park), Virginia (USFWS 1994, entire). The species was federally listed as endangered under the U.S. Endangered Species Act (ESA) in 1988 (53 FR 37814-37818) and a recovery plan was published in 1994 (USFWS 1994, entire). Since the species' listing and development of the recovery plan, a significant amount of research has been directed toward *P. shenandoah*, which has substantially improved scientific understanding of the species and its ecology.

In the 1994 recovery plan, the following recovery actions were identified:

1. Determine the boundaries of occupied habitat and whether additional populations exist.
2. Monitor known populations on a long-term basis.
3. Determine and minimize the impact of human-related factors.
4. Investigate relevant aspects of life history (e.g., behavior, factors that affect distribution).

5. Ensure compatibility of park maintenance and management activities.
6. Promote information exchange to the public and among relevant research and management agencies.

The U.S. Geological Survey (USGS) has conducted annual monitoring of occurrence from 2007-present and developed a standardized monitoring protocol (Recovery Action 2) and data from this research (Grant et al. 2024, entire) have been used to fit an occupancy model (Werba et al. 2024a, entire) that has refined our understanding of the species range since listing (Recovery Action 1). Additionally, research has demonstrated that the species' lower elevational limit is determined by the cloud base height (Recovery Action 2, Grant et al. 2018, entire), which provides at least partial support that the species' distribution is sensitive to climate variables. Shenandoah National Park has relocated trails, maintains a prohibition on backcountry camping in *P. shenandoah* habitat, and created guidance on rock climbing in the area where the species occurs (Recovery Action 3, 5) to minimize the impact of humans on *P. shenandoah* and its habitat. Research has also identified threats to the species that were not included in the 1994 recovery plan and our understanding of the species distribution has greatly increased (Recovery Action 4). Additionally, since 1994, a structured decision making workshop and a science panel have been convened to discuss current research and recommendations for management of *P. shenandoah* (Recovery Action 6).

Analytical framework

This SSA report documents our assessment of the extinction risk of the species. In synthesizing such information, this document is intended to support future ESA documents for *P. shenandoah*, including 5-year reviews, revised recovery plans, and potential reclassification rules. We also intend for this to be a living document, and as such have employed a flexible and transparent analytical framework, so that these analyses can be revisited in the future if new data become available or new future scenarios warrant investigation. The SSA report is not a decisional document, but rather contains 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 its long-term viability.

Herein, we have used the established SSA framework of assessing species status under the concepts of resiliency, redundancy, and representation (Wolf et al. 2015, entire). Considering the definitions provided by Smith et al. (2018, entire) and USFWS (2020, entire), we summarize these "3Rs" as follows:

- **Resiliency** the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature, rainfall), periodic disturbances within the normal range of variation (e.g., fire, floods, and storms) and demographic stochasticity (normal variation in demographic rates such as mortality and fecundity) (Redford et al. 2011, p. 40). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions.

- **Redundancy** is the ability of a species to withstand catastrophes. Catastrophes are stochastic events that are expected to lead to population collapse regardless of population health and for which adaptation is unlikely (Mangel and Tier 1993, p. 1083).

- **Representation** is 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) and biological (e.g., pathogens, competitors, predators) environments. This ability to adapt to new environments--referred to as adaptive capacity--is essential for viability, as species need to continually adapt to their continuously changing environments (Nicotra et al. 2015, p. 1269). Species adapt to novel changes in their environment by either [1] moving to new, suitable environments or [2] by altering their physical or behavioral traits (phenotypes) to match the new environmental conditions through either plasticity or genetic change (Beever et al. 2016, p. 132; Nicotra et al. 2015, p. 1270). The latter (evolution) occurs via the evolutionary processes of natural selection, gene flow, mutations, and genetic drift (Crandall et al. 2000, p. 290–291; Sgro et al. 2011, p. 327; Zackay 2007, p. 1).

We have employed this "3Rs" conceptual approach within the SSA framework to assess the viability and extinction risk of *P. shenandoah* under each of four plausible scenarios of future environmental conditions. Our primary forecasting tool was a previously published, quantitative, population dynamics model that incorporated the spatial location of observations over time (Campbell Grant et al. 2023, entire). This model was developed specifically for *P. shenandoah* through collaboration with agency stakeholders, some of whom were subsequently contracted to complete this SSA. This model, plus additional information compiled from peer-reviewed literature and other unpublished data during the development of this SSA, allows for an assessment of future resiliency, redundancy, and representation based on presumed relationships between persistence and positive and negative factors affecting the species (e.g., competition, human use of habitat, climate change). These data (Grant et al. 2024, entire) also served as inputs to model simulations that forecasted how future changes to factors affecting the species might influence the 3Rs in the future. We identified changes in moisture and temperature driven by climate change, as well as changes in competition as the factors most likely to influence the viability of the species in the foreseeable future. As such, these are the factors incorporated into future scenarios for the species. Such models can be reanalyzed in the future using updated data or new understanding of stress-response relationships.

CHAPTER 2: SPECIES INFORMATION

Taxonomy and Genetics

The Shenandoah salamander was originally described as *Plethodon richmondi shenandoah* based on morphological characteristics (trunk vertebrae, dorsal stripe width, ventral pigmentation) and was considered a "mountain form" subspecies of *P. richmondi* along with *P. nettingi* and *P. hubrichti* (Highton and Worthington 1967, entire). The Shenandoah salamander was later redefined as a subspecies of *P. nettingi* (Highton 1972, p. 144) before being elevated to a full species, *P. shenandoah* (Table 1), along with *P. nettingi*, based on electrophoretic data (Highton and Larson 1979, pp. 587-588).

Highton (1995, p. 590; 2012, p. 288) hypothesized that most of the species of eastern *Plethodon* arose as a result of isolation on cool, moist mountain tops during the Pliocene Epoch (about 5.3–1.8 million years ago [mya]) when warm, dry conditions transformed lowland forests into arid grasslands. These speciation events resulted in four eastern species groups, each with many closely related extant species. *P. shenandoah* is one of 10 known species that form a group all closely related to *P. cinereus*, which is believed to be the most morphologically primitive group of the eastern *Plethodon*. More recent results of mitochondrial data for *P. shenandoah* and *P. cinereus* estimate the split between these species approximately 7.5-9.5 mya (Mulder 2019, p. 5098). Species such as *P. cinereus* appear to have expanded their range dramatically since the Pleistocene Epoch, indicated by its northern spread into territory that was under the last maximum extent of the continental ice sheet 21,000 years ago (Highton 1995, p. 591). Other species appear to have persisted only in their restricted mountain habitats and have limited contemporary ranges, most with distributions surrounded by *P. cinereus*, as is the case with *P. shenandoah* (Highton 1995, p. 590). See Table 1 for current taxonomy.

Table 1. Taxonomy of *P. shenandoah* (Highton and Larson, 1979).

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Caudata
Family:	Plethodontidae
Genus:	Plethodon
Species:	shenandoah

Species Description

P. *shenandoah* is a small woodland salamander (adult snout-vent length 40-57 millimeters, total length 85-110 millimeters, USFWS 1994, p. 1) that is endemic to the area that surrounds three peaks (Hawksbill, Stony Man, The Pinnacle) in Shenandoah National Park, Virginia, USA. The species is entirely terrestrial and can be found most often in the spring and fall on the forest floor under rocks, logs, and other cover during the day, or roaming the forest floor on cool, wet nights. The species occurs in two forms: one with a dorsal stripe (usually varying from red to yellow, with variations in stripe colors across the species range) and one with a brassy-flecked dorsum. Both forms have a mostly dark venter, with absence of or very little white or yellow mottling (Highton and Worthington 1967, p. 619). The species is distinguished from other similar species (including the sympatric *P. cinereus*) by the narrower stripe (if the stripe is present) and the comparatively reduced white ventral flecking (Highton and Worthington 1967, p. 619). However, the original species description for *P. shenandoah* notes possible introgression between *P. shenandoah* and the sympatric *P. cinereus* at one location on Hawksbill based on morphological characteristics, and the presence of individuals with intermediate characteristics (stripe width, ventral coloration) of both species occasionally presents identification challenges (Sevin 2014, p. 21, Chambert et al. 2018, p. 1475).

Little is known about breeding behavior in *P. shenandoah*, and no descriptions of nesting sites have been documented in published literature; therefore, breeding behavior is assumed to be similar to other *Plethodon* species with breeding occurring in late spring and early summer (USFWS 1994, p. 6). *Plethodon* salamanders have been observed sexually mature at three years of age, and females lay a clutch of 4-18 eggs with a mean of 13 eggs per female in moss, logs, or moist crevices every other summer (Jaeger 1980, p. 619; 1981, p. 192). Like other woodland salamander species, females generally guard the eggs during incubation, and their young develop completely within the eggs before hatching in September (Lannoo 2005, p. 840). Lifespan of the species is likely similar to that for other small *Plethodon* (7-16 yr; Staub 2016, p. 119), but some individuals may live up to 20-30 years.

Physical Setting

Prior to its establishment as a National Park in 1935, the area that is now Shenandoah National Park was primarily in smaller, private land holdings and used for timber production, grazing, hunting, and agriculture (National Park Service [NPS] 2019, entire). In addition to land cover change, the loss of American chestnut (*Castanea dentata*) by the 1930s induced a rapid shift in composition of remaining upland hardwood forest. Since Park establishment, the composition of the forests has changed further from primarily chestnut oak (*Quercus montana*) and northern red oak (*Quercus rubra*) in 1940 to oak and oak-hickory forests by 2009. Yellow poplar and cover of hardwood species such as maples (*Acer saccharum, Acer rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*) have increased. Cover of pitch pine (*Pinus rigida*) and bear oak (*Quercus ilicifolia*) have decreased as natural succession has taken place (Young et al. 2009, entire). The forests are continuing to change due to factors such as invasive species like the spongy moth (*Lymantria dispar*) and hemlock woolly adelgid (*Adelges tsugae*), severe weather events (e.g., droughts, hurricanes, ice storms), or other human-caused disturbances (e.g., public use, wildfire, artificial light). Climate change is expected to drive rapid changes in forest composition and condition. Although the Park is currently approximately 95 percent forested (Young et al. 2009, entire), loss of eastern hemlock (*Tsuga canadensis*) has been particularly notable in some portions of *P. shenandoah* range, and a wildfire on The Pinnacle in 2000 burned approximately 17,000 acres in and adjacent to the known range of *P. shenandoah* (NPS 2020, entire).

Skyland Resort is located on Stony Man Mountain directly adjacent to *P. shenandoah* habitat and began as a popular vacation destination for travelers from urban areas in the late 1800s (NPS 1999, p. 2). The construction of the first section of Skyline Drive further facilitated daytrips into the area, and Skyland Resort was a popular overnight destination within the newly established National Park. Construction of the Appalachian Trail began simultaneously with the evolution of the idea of Shenandoah National Park and Skyline Drive. A trail on a network of private lands that would eventually become the Appalachian Trail had been created by 1931 and was supported and frequently used by Skyland guests as the trail was easily accessible from the resort (NPS 1999, p. 20). As Skyline Drive was built, much of the original Appalachian Trail was relocated and rebuilt at a lower elevation (NPS 2007, p. 4).

The creation of Shenandoah National Park was authorized by Congress in 1926, but it was not until 1936 that enough land was acquired to officially dedicate the Park. As described in the enabling legislation, Shenandoah National Park "preserves and protects nationally significant natural and cultural resources, scenic beauty, and congressionally designated wilderness within Virginia's northern Blue Ridge Mountains, and provides a broad range of opportunities for public enjoyment, recreation, inspiration, and stewardship" (NPS 2015, p. 4).

Individual needs

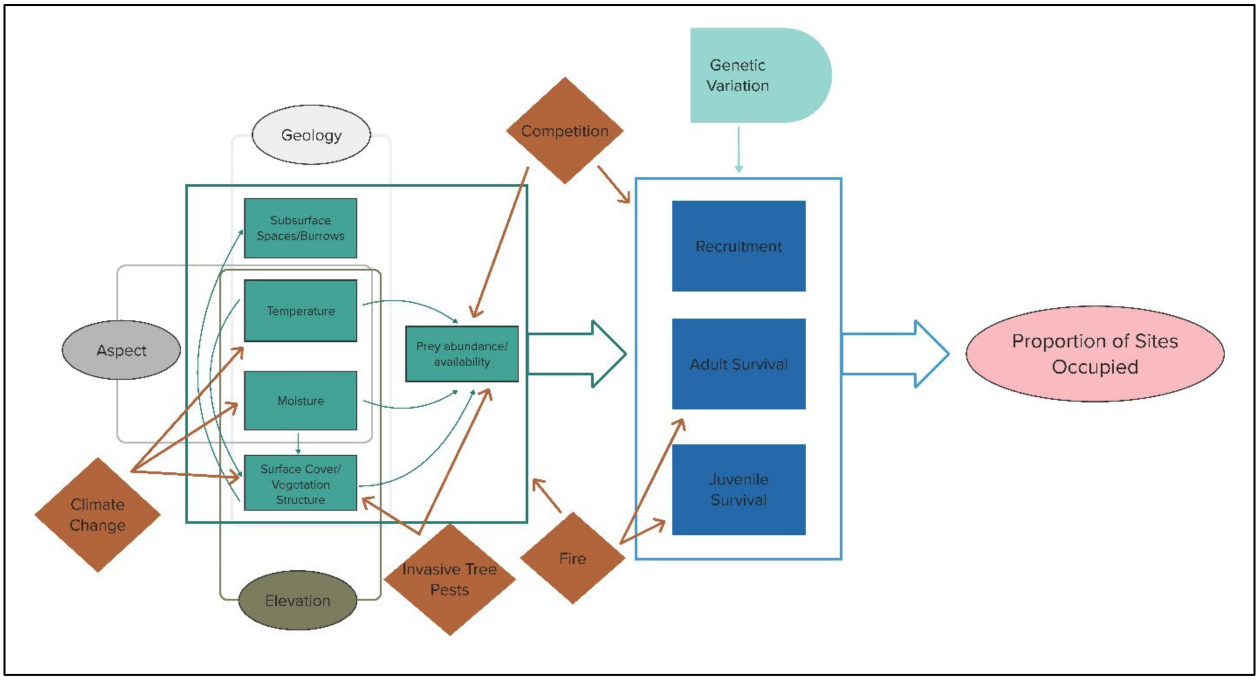

Figure 1. Influence diagram with species needs shown in teal rectangles, gray ovals and corresponding boxes identify geographic components that relate to the species needs, and threats are shown in tan diamonds.

The proportion of sites occupied within the range of locations considered suitable for *P. shenandoah* depends on specific individual, population, and species-level needs. We describe these needs below and provide a diagram for reference (Figure 1).

Substrate Spaces/Burrows

As *P. shenandoah* use gaps between rocks, soil, and underground crevices for refuge during multiple life stages, the availability of these subsurface habitats is important for growth and survival. The availability of cool, moist retreats with access to the surface following rain events is important for foraging in the spring and fall for juveniles as well as adults. These retreats can be created by rocky substrates, plant roots, burrowing animals, and freeze/thaw dynamics near the soil surface (Caceres-Charneco and Ransom 2010, entire; Drake et al. 2012, entire).

Availability of nesting sites is critical for reproduction, and like most small *Plethodon*, eggs are likely laid in moist crevices underground or near the surface under rocks and woody debris (Jaeger 1971a, p. 637). Given their ectothermic physiology and cutaneous respiration, the stability of temperature and moisture of nesting sites likely influences hatching success, survival of hatchlings, and the condition of the attending females after brooding. However, ideal temperature and moisture conditions for nesting sites is unknown.

Temperature

Plethodontid salamanders prefer cooler temperatures than other salamander species. *P. shenandoah* is surface-active across a range of temperatures, but peak activity is in the autumn and spring seasons (Sevin 2014, p. 108). Studies on the conspecific *P. cinereus* show a decrease in surface activity above and below soil temperatures around 7-10°C (Munoz et al. 2016, p. 8745); there are no available data to indicate *P. shenandoah* surface activity has a substantially different pattern. Both species are found on the surface under microhabitats with a range of temperatures (Amburgey et al. 2020, p. 129; leaf litter [17.3 ± 0.638°C]; log [15.6 ±0.168°C]; rock [14.6 ± 0.118°C]). Generally, *P. shenandoah* are less often detected under all types of cover objects at the surface as temperatures increase (Amburgey et al. 2020, p. 132).

In an experimental setting, Dallalio et al. (2017, p. 192) found that individuals have better outcomes for survival and growth in cooler (24-25°C) than warmer (27-28°C) temperatures. Assimilation efficiency of ingested food items is known to decrease as temperatures increase from 10-20°C in *P. shenandoah* (Bobka et al. 1981, p. 419); like other ectotherms, metabolic rate is directly correlated with temperature. Availability of cooler underground retreats and surface cover objects allows salamanders to behaviorally modify exposure to environmental conditions such as warmer temperatures (Heatwole 1962, p. 470; Jaeger 1980, p. 267) and thus regulate metabolic demands.

Moisture

Following hatching, young can be found near moist pockets of soil and leaf litter in late summer and fall (Jaeger 1970, p. 640). There is no known differentiation between habitat preferences of juveniles and adults, and both can be found together on the surface at low densities (0.1 individual/square meter [m^2]; Griffis and Jaeger 1998, p. 2497). *P. shenandoah* prefers moist microhabitats but can tolerate relatively drier conditions than the conspecific *P. cinereus* (Jaeger 1971, p. 120). Plethodon salamanders are lungless and need to keep their skin moist to breathe (cutaneous respiration), the amount of dehydration an individual species can tolerate varies (Spotila 1972).

Occupancy (a measure of the probability that *P. shenandoah* is present at a site) is positively correlated with topographic metrics associated with increased moisture (Werba et al. 2024a, p. 6). The lower elevation limit of the species on two of the mountain peaks is controlled by the location where clouds begin to form (the cloud base height; Grant et al. 2018, entire), which we interpret as defining areas of high relative humidity and higher frequency of dew/fog formation. There is likely a similar relationship with humidity and occurrence on the third mountain (The Pinnacle), but data are not available to confirm.

Surface Cover/Vegetation Structure

Surface activity of *P. shenandoah* peaks in the spring and fall seasons, but the species can also be found (albeit less frequently) under surface cover throughout the summer (Sevin 2014, p. 28). They prefer sites with areas of high moss cover (Grant et al. 2018, p. 7555), presumably because moss is associated with high environmental moisture. During the day they are found under cover objects of various types (Jaeger 1971b, p. 206; Amburgey et al. 2020, p. 129) and emerge at night to forage. Vegetation structure is important to facilitate vertical climbing behavior and foraging at night to access plant-dwelling prey (Jaeger 1971b, p. 206; Jaeger 1978, entire).

Prey Abundance/Availability

Like other Plethodontid salamanders, *P. shenandoah* is gape-limited and does not have specialized prey. Individuals will forage from what is available, including: insects, arachnids, worms, millipedes, and centipedes (Jaeger 1972, p. 543–545). Cannibalism and ingestion of other salamanders has been noted anecdotally in both captive and wild populations of *Plethodon* salamanders (Thurow 1976, p. 286; Gade et al. 2017, entire), but diet studies do not include conspecifics as a major prey item. Diet studies on *P. cinereus* in Shenandoah National Park found prey ingestion rates fluctuate with changes in rainfall and moisture content of the forest floor (Jaeger 1980, p. 338), likely due to restrictions on salamander movement to forage and not lack of prey available in the habitats (Jaeger 1972, p. 545).

Population/Species Needs

The species' viability ultimately depends on its ability to withstand environmental, demographic, and genetic stochasticity (resiliency), catastrophic events (redundancy), and novel biotic and abiotic changes in its environment (representation). For species viability, measured by proxy as the proportion of sites occupied, individuals need suitable habitat that includes substrate spaces/burrows for growth, survival, and reproduction, suitable temperature and moisture levels that create a cool and moist environment to prevent desiccation, diverse surface cover and vegetation structure for shelter and foraging, and adequate prey abundance and availability to support individual survival and resiliency. These aspects of suitable habitat are needed within each of the three populations to maintain an adequate population size by facilitating adult and juvenile survival (representation, resiliency) and recruitment (resiliency). Maintaining multiple populations increases species viability to survive natural variability or catastrophic events (redundancy).

CHAPTER 3: HISTORICAL AND CURRENT CONDITIONS

In this chapter, we describe the historical and current demographic and habitat conditions of the three known *P. shenandoah* populations. The historical period (defined here as <2007) provides the baseline condition from which we evaluate changes in *P. shenandoah* viability (measured as the proportion of sites occupied) over time, while the current (2007–2022) period is the starting point for estimating the future viability of *P. shenandoah* using population projection models.

Historical range

Maps of *P*. *shenandoah* range in listing documentation used a combination of known occurrences and presumed occurrence, mapped using topographic maps and field visits of north-facing talus slope habitats above 800 m (USFWS 1994, p. 2). The entire potential range of the species was thought to consist of up to 6 square kilometers (km^2) of high-elevation forested habitat, distributed across three mountain peaks in the Park (Highton and Worthington 1967, p. 620–621; Jaeger 1970, p. 633; 1971a, p. 632; 1971b, p. 191–192; Carpenter et al. 2001, p. 111). It is also likely that *P. shenandoah* occupied the area that is now Skyland Resort and portions of Skyline Drive.

Current range

The current estimated range of *P. shenandoah* is approximately 8.6 km^2 (6.02–17.3 km^2) spread across the three occupied mountains (Figure 2); calculated as the area with a mean expected count of at least one individual using data from visits to 500 sites from 2007 to 2022 (Werba et al. 2024a, entire) (Figure 2). There is no evidence to support that there has been an increase in the species range, this larger range may be a result of different methodology and increased survey effort. This updated analysis estimates that *P. cinereus* is present over much of the range of *P. shenandoah*. This is in contrast to earlier work, where *P. shenandoah* was believed to only occupy habitats which were inhospitable to *P. cinereus* (Jaeger 1970, entire; 1971b, entire); however, these previous studies were based on limited surveys and did not include quantitative estimates or report the associated uncertainty. Nonetheless, the historical data do not allow inference to conclude that *P. cinereus* has invaded all the sites where it is now estimated to occur. We define three separate populations that correspond to the three mountains within the species range. The three populations are separated by a considerable distance (approximately 5 km) and natural barriers; the population on each mountain is considered functionally isolated from the other mountains (Mulder et al. 2019, p. 8)

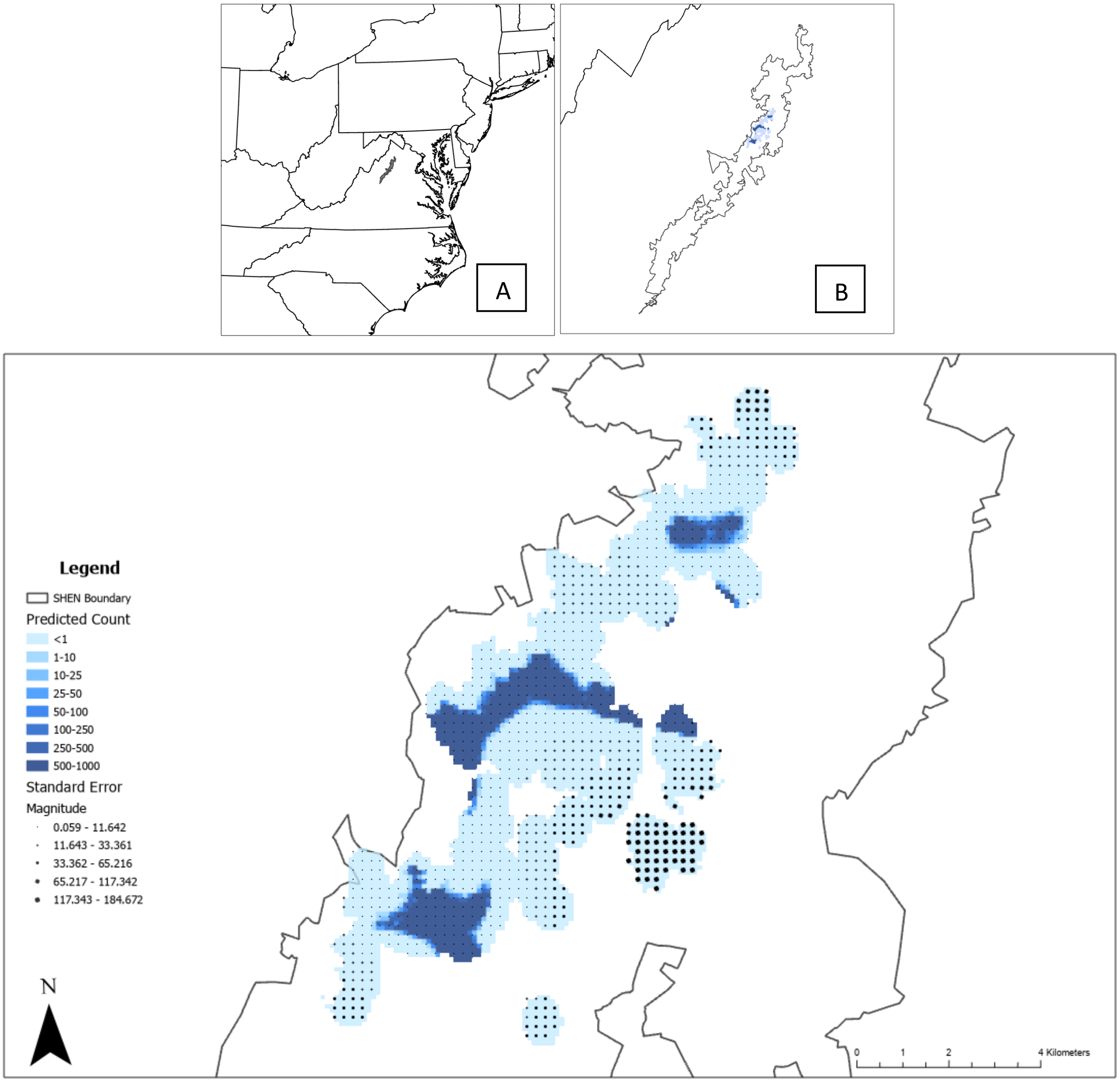

Figure 2. Map of current estimated range of *Plethodon shenandoah* in terms of predicted surface counts of salamanders (grid cell size = 0.01 km^2)(under average conditions) and corresponding standard error estimates of counts (Werba et al. 2024a, entire). Insets show the location of the species range in the region (A) and Shenandoah National Park (B). SHEN boundary line indicates border of Shenandoah National Park (SHEN). Maximum predicted counts (dark blue) cluster around populations on The Pinnacle (northernmost), Stony Man (central), and Hawksbill (southernmost) mountains. Thorofare Mountain is where the eastern-most dark blue area is found, and while analysis of the data predicts the species may be present, they have yet to be found on this peak. Therefore, Thorofare Mountain is not included in discussions.

Connectivity

Population genetics analyses offer additional insight into the climate-related constraints on the dispersal of *P. shenandoah* at larger scales among the mountains. Genetic evidence supports the Pinnacle and Stony Man populations as one genetic group, while the Hawksbill population has not mixed with the other populations. The higher prevalence of northfacing slopes between Pinnacle and Stony Man was most strongly related to this population genetic pattern (Mulder et al. 2019, entire), which corresponds to inferences about the cloud base height setting the lower elevation limit for the salamander's distribution (Grant et al. 2018, entire). These lines of evidence indicate that long-distance dispersal likely occurs along north-facing slopes where cool, moist conditions and/or the presence of clouds or fog facilitate movement of salamanders between occupied habitats.

Distribution and Habitat Conditions

The Hawksbill population has high habitat quality with relatively continuous habitat occupied by the species. The area occupied by this population has several maintained trails, including the Appalachian Trail, which results in associated backcountry camping and off-trail use impacts in localized areas. Spongy moth outbreaks have recently been documented within the occupied areas and caused widespread defoliation; occurrence of favorable host tree species within the population indicates there is a high risk of future outbreaks. Threat of fire is lowest in this population, but potentially catastrophic if it were to occur.

The Stony Man population has the largest total occupied area, but it is comprised of several smaller patches, some of which are separated by Skyline Drive and the infrastructure of Skyland Resort. Maintained trails are present within occupied habitats, and some occupied areas are adjacent to Skyland Resort and other large canopy openings, reducing suitability for surface occupancy by *P. shenandoah*. Dispersal across these barriers is presumed to be unlikely in the event of localized extirpation of an individual habitat patch, though transient opportunities for dispersal are possible when environmental conditions are suitable. Habitat conditions of the patches vary, with some heavily impacted by eastern hemlock decline in recent years. Threat of fire is moderate relative to the other units due to standing and fallen dead eastern hemlock trees in some habitats, proximity to Skyland human use areas, and nearby Skyland electrical infrastructure. A wildfire occurred near occupied habitat in 2023. Spongy moth outbreaks have also occurred in this population, with high risk of future occurrence due to favorable host tree species. Impacts of off-trail use are evident in localized areas that are frequented by climbers, overnight illegal camping, and Skyland visitors.

The Pinnacle population, in comparison to Hawksbill and Stony Man, is the smallest in area, has the lowest habitat quality, and generally has the least number of individuals observed in field surveys although individuals of all age classes are observed in good survey conditions. Multiple wildfires have impacted the area near *P. shenandoah* habitat, with the most recent in 2000 (NPS 2020, entire). Given the generally drier habitats in this population, risk of fire is higher. There are maintained trails on the periphery of occupied habitat, and off-trail use is minor and mostly around overlooks near the peak on the Appalachian Trail.

Factors influencing Current and Future Conditions

Habitat quality

Defoliation/invasive insects

Invasive forest pest species have been present in *P. shenandoah* habitats since species listing (and presumably earlier) as spongy moth defoliation was considered a threat to the species in the Recovery

Plan (USFWS 1994, p. 8). Currently, two pest species in particular have potential to affect populations of *P. shenandoah* through similar negative impacts on canopy cover which can reduce surface soil moisture. Spongy moth was found in the Park in 1984, and outbreaks since 1986 have resulted in periodic near total defoliation of overstory primary host trees (such as oaks, Kasbohm et al. 1994, p. 462). For the area where *P. shenandoah* occurs, spongy moth outbreaks have been noted as recently as 2023/2024 (NPS 2024, entire), as well as in 2007-2009 (Manderino et al. 2014, p. 3), the late 1980s (Kasbohm et al. 1994, p. 463; Highton 1999, p. 68), and potentially multiple times in epidemic years from 1986-1995 when overstory primary host trees were defoliated along the entire length of the Park (Manderino et al. 2014, p. 3). Analysis of aerial imagery shows defoliation due to spongy moth may have occurred up to seven times from 1984-2014 (Asaro and Chamberlin 2015, p. 183). Outbreaks are exacerbated by dry conditions in the spring, which reduce the effectiveness of viruses and pathogens (Reilly et al. 2014, p.639) that target the caterpillar stages of the spongy moth, thus reducing herbivory. Defoliated trees in good condition are able to produce a second set of smaller leaves in the same year, but multiple years of defoliation can kill overstory trees. Shenandoah National Park treats heavily infested areas of the park with an aerial bacterial application of BtK (*Bacillus thuringiensis Kurstaki*), including areas occupied by *P. shenandoah* (NPS 2024, entire); it is unknown if aerial spraying significantly affects *P. shenandoah* or their potential prey, but potential effects are expected to be minimal (USFWS 2022, entire).

Hemlock woolly adelgid is a forest pest that causes loss of needles and eventual death of eastern hemlock trees which are present in some areas of the *P. shenandoah* range. The National Park Service treats approximately 2,500 trees annually in the park for hemlock woolly adelgid with a combination of injections of an insecticide and an anthropogenic, or human-influenced, introduction of a predatory beetle that targets the forest pest (NPS 2022, entire). Of the 29,000 trees treated to date, approximately 770 of those occur in the Skyland, Hawksbill, and Stony Man areas (NPS 2022, pg. 8). The effects of these treatments on P. *shenandoah* are unknown and have not been evaluated. High-elevation eastern hemlocks in Shenandoah National Park have fared much better than those at lower elevations, as measured by better crown condition and lower mortality since 1990, likely due to cold weather limitations on hemlock woolly adelgid growth (Abella 2014, p. 28). The eastern hemlock overstory experienced near-complete loss in at least one patch occupied by *P. shenandoah* since 2009, but the salamander was still detected in the patch as of 2023 (Grant et al. 2024, entire). Eastern hemlock is known to create a dark, cool, and moist microclimate below the canopy in summer and moderate temperatures extremes in the winter (Abella 2014, p. 19), so it can be expected that loss of eastern hemlock overstory will influence temperature and moisture availability at the soil surface and thus salamander surface activity. Whether loss of eastern hemlock overstory has or will lead to negative effects on populations of *P. shenandoah* is unknown.

Fire

Wildfires have not affected most areas that are known to be occupied by Shenandoah salamanders since 1925 (NPS 2020, entire). However, the entire forest habitat across the Pinnacle population was affected by a large wildfire in 2000. Impacts of wildfire for the species are unknown, but decreased canopy cover and loss of leaf litter due to even low intensity fires can be expected to impact surface activity for multiple years, as has been described for other Plethodontid salamanders (Wilk and

Peterman 2024, p.203). Field survey data in the Pinnacle population support this contention, with generally low observed abundance since the initiation of field surveys in 2007 (Grant et al. 2024, entire). Smaller fires have occurred near the *P. shenandoah* range on Stony Man as recently as 2023, but current data suggest none have impacted occupied habitats in this population.

Competition

Terrestrial salamanders spend a disproportionately higher amount of time in underground retreats than on the surface (Bailey et al., 2004, p. 89), most likely to avoid desiccation threats (e.g., wind and solar radiation) at the surface. *Plethodon* competitive interactions observed on the surface may involve territorial behavior that extends from surface to sub-surface habitats.

It has long been hypothesized that competition with *P. cinereus* is a principal factor in the decline and extinction risk of *P. shenandoah* (Jaeger 1970, entire; 1971b, entire; 1974, p. 35; Griffis and Jaeger 1998, entire). While there is some evidence that *P. cinereus* exhibits more aggressive behavior than *P. shenandoah* (Wrobel et al. 1980, p. 1038), other historical evidence suggests that *P. shenandoah* is not always an inferior competitor (Griffis and Jaeger 1998, p. 2500). Colonization experiments resulted in *P. shenandoah* colonizing surface cover objects (rocks, woody debris) following the removal of *P. cinereus* (Griffis and Jaeger 1998, p. 2500), which could be interpreted as a higher colonization ability for *P. shenandoah* for unoccupied sites. However, a second experiment found that, contrary to the expectation if the species were competing for space, there was no difference in aggressive behaviors among the two species when competing for a cover object (Griffis and Jaeger 1998, p. 2499).

Estimating range boundaries between species is particularly difficult due to imperfect detection (i.e., the failure to observe a species when it is present at a site), which was not accounted for in work prior to the 2000s. Amburgey et al. (2019, p. 4) used multiple visits to locations near the lateral range boundaries of *P. shenandoah* on Hawksbill and Stony Man mountains to examine factors that influence the estimation of range edges between the species. They found that co-occurrence zones are underestimated when imperfect detection is not accounted for; the observed breadth of contact zones typically varied from 60-170m, which was wider than previously inferred (Jaeger 1972, p. 543). Disjunct contact zones were frequently observed that varied in location and area over time, and habitat covariates were not sufficient to explain range boundaries. More recently, Amburgey et al. (2020, p. 130) found limited evidence for character displacement (differences in traits between the species) in body size, microhabitat use, stripe color, age class, or tail damage, which had been suggested in past studies as potential outcomes of competition for food, territory, or space use. Disjunct distributions of two species (resulting in ‘apparent’ competition) may arise from differential sensitivity to environmental conditions. Experimental desiccation trials (Jaeger 1971b, p. 200) found that *P. shenandoah* was more resilient to desiccation than *P. cinereus*. Combined with observations of higher *P. cinereus* densities in the more shaded deep soil habitats outside talus slopes, Jaeger (1971a, p. 636) inferred that *P. shenandoah* persists in the high-elevation habitat because it is outcompeted for preferred habitats (i.e., in the shaded deep soil), but persists in isolated microhabitats where it can tolerate warmer and drier conditions compared to *P. cinereus*. Lack of strong differentiation at the range edge additionally weakens support for a hypothesis of competition relative to previous research.

Altogether, the evidence suggests that a combination of abiotic factors (temperature/humidity) and biotic interactions (competition) may affect species distributions and future extinction risk for *P. shenandoah*, which is a similar finding for other taxa (e.g., Dunson and Travis 1991, entire). Dallalio (2013, entire) investigated how the ecological relationship between *P. shenandoah* and *P. cinereus* may be altered under future climate change, and found evidence that, under current climate conditions, *P. cinereus* outperforms *P. shenandoah*. However, under future climate conditions the reverse was observed – *P. shenandoah* outperformed *P. cinereus*. Therefore, direct competition with *P. cinereus* may not increase the extinction risk for *P. shenandoah* under future climate conditions in some habitats. *P. shenandoah* appears to be more sensitive to increases in surface temperature, while both species appear similarly sensitive to declines in environmental moisture, as expected for *Plethodon* salamanders (Spotila 1972, p. 122).

Finally, a study using detection data from 2007–2016 found reduced colonization by *P. shenandoah* when *P. cinereus* is present (Werba et al. 2024b, p. 2). They also found that moisture-related variables had a larger effect on colonization and persistence than temperature. This work combined with other recent research (Dallalio et al. 2017, entire; Grant et al. 2018, entire; Amburgey et al. 2019, entire) indicate competition alone is insufficient to explain *P. shenandoah* occupancy dynamics at the range scale, and it is expected that human-induced climate change is at least partially responsible for the extinction risk to the species. As neither competition nor climate factors alone can fully explain current species occurrence dynamics, models predicting *P. shenandoah* occupancy dynamics benefit from including the influence of both abiotic (temperature/humidity) and biotic (competition) factors.

Barriers

Barriers to salamander movement include trails and roads. Historic impacts of trail construction were likely confined to the immediate disturbance area and although this construction may have caused temporary movement of individual salamanders due to soil and rock relocation, trails likely had minimal effect on the species and the influences of trails have presumably not changed given that the entire range is within the Shenandoah National Park.

Roads are currently expected to be a minor factor for most populations of *P. shenandoah*. There are fire roads for emergency access on each mountain where the species occurs, but only the fire road on Stony Man has known populations of *P. shenandoah* in adjacent forested habitats. It is unknown if this limited-use, gravel fire road is acting as a barrier to movement of salamanders. The larger, paved, and high-use Skyline Drive and several overlook pull-off areas are adjacent to *P. shenandoah* habitat in some locations (Werba et al. 2024a, entire). The paved surface, size, and breaks in canopy associated with Skyline Drive likely serve as barriers to salamander movement and may impact nearby temperature and moisture conditions in forested habitats. Occupied habitats in proximity to larger roads or other Park infrastructure are largely in the Stony Man population, with two overlooks, Skyline Drive, and Skyland Resort adjacent to occupied forested habitats. Considering the species' current proximity to the developed areas, it is likely that historically the mountaintop area that is now Skyland Resort was occupied by the species. Similarly, the construction of Skyline Drive likely historically impacted habitats on Stony Man and possibly Hawksbill, as large sections of habitat were modified to support Skyline Drive and overlooks were created to facilitate open viewsheds. While the footprint of these developed areas has largely not changed in the past few decades, presumably large impacts to the immediate modified areas may have resulted from initial construction. Occurrence of *P. shenandoah* in these places prior to its description in 1967 is not known.

Changing Climate Conditions

Temperature

The climate of Shenandoah National Park has remained relatively stable over the last 50 years, but future climate change is expected to increase temperatures in high elevation habitats where *P. shenandoah* occurs (Lee et al. 2014, p. 7). Increased temperatures are expected to increase food requirements for salamanders due to increased metabolism and lower assimilation efficiency (Bobka and Jaeger 1981, p.419; Novarro et al. 2018, p. 8) if peak activity periods do not shift with climate change. Reduced energy budgets could reduce reproductive output through smaller clutch sizes or fewer opportunities to reproduce (Riddel and Sears 2020, p. 316). Thus, climate warming could result in local extinction of habitat patches that are currently on the edge of environmental suitability for *P. shenandoah* in terms of temperature if resident salamanders cannot maintain positive energy balance through increased foraging or access to subsurface refugia. Increased temperatures could also further fragment populations by increasing the distances between occupied patches (due to reduction in size of current occupied areas) or further reduce the likelihood of recolonization of locally extinct patches.

Behavioral plasticity in the timing or extent of surface activity could potentially ameliorate some negative effects of temperature in a warmer future for *P. shenandoah*. We currently lack data on plasticity in respiration rate or surface activity for *P. shenandoah*, but temporary exposure to realistic future summer temperatures induced mass loss in captive *P. shenandoah* even when cooler subsurface retreats and unrestricted food were available (Dallalio et al. 2017, p. 194). Given the small geographic range of *P. shenandoah* and its physiologic adaptation to cooler high-elevation temperatures, the species may not have large potential for behavioral or phenotypic plasticity in response to increased temperature given the already narrow range of conditions in which it occurs.

Moisture

The future status of *P. shenandoah* is expected to be influenced by the timing and duration of precipitation as well as the frequency and duration of high relative humidity (presence of dew or fog) at the soil surface. As predictions for the range of *P. shenandoah* are highly uncertain in terms of timing and duration of moisture (Fan et al. 2014, p. 160), it is unclear how available time for foraging and other surface activity during spring and fall may change for *P. shenandoah.* It is likewise uncertain how quickly a reduction in surface activity may affect survival and growth of *P. shenandoah* individuals or populations. The timing, duration, and amount of surface activity is related to water balance, which for individual salamanders is related to many factors such as body size (lower as size increases), topographic position (lower in ravines compared to ridgelines), canopy cover (lower as canopy cover increases), proximity to streams (lower closer to streams), and days since rainfall (lower after rain events) (Peterman and Semlitsch 2014, p. 362). Given the challenges of downscaling climate predictions for temperature to salamander-relevant scales (Lee et al. 2014, p. 5), predicting the fine-scale variation in future relative humidity and water balance for habitats where *P. shenandoah* occurs would be exceptionally challenging.

Early research hypothesized that *P. shenandoah's* ability to survive in the talus may be facilitated by the presence of dew or fog (Jaeger 1971b, p. 205), but current evidence indicates coexistence is likely mediated by the frequency of clouds (Grant et al. 2018, p. 7559). The lower elevation limit for distribution of *P. shenandoah* occurs between 850 m (on Stony Man) and 900 m (on Hawksbill) (Grant et al. 2018, p. 7557–7558). Notably, the cloud base height elevation (i.e., the elevation at which clouds form) is also located at 850-900m. This provides evidence for a relationship between the species' range limit and climate-related variables, including moss cover which is sensitive to environmental moisture, indicating that the lower elevational distribution of *P. shenandoah* may be sensitive to the frequency of high humidity and/or clouds. With increasing temperatures due to climate change, the elevation limit (and the cloud base height) is expected to increase by 2.4-4.1 m per decade (Grant et al. 2018, p. 7559) given there is no change in precipitation as the climate warms. Although highly uncertain for the region, predictions generally forecast a decrease in summer precipitation (Fan et al. 2014, p. 159), which would further restrict cloud or fog cover and the areas suitable for *P. shenandoah* at lower elevations.

Similar to responses to changes in temperature, it is expected that salamanders may be able to behaviorally avoid some changes in environmental moisture by utilizing subsurface retreats. The degree of plasticity in surface activity is unknown for *P. shenandoah*, but the species has been documented to tolerate experimental dehydration better than *P. cinereus* (Jaeger 1971b, p. 204) and larger individuals are expected to be able to be more active on the surface in drier conditions due to lower water loss rates (Spight 1968, p. 203; Peterman and Semlitsch 2014, p. 365). Nevertheless, *P. shenandoah* may have relatively low capacity to adapt to different moisture conditions in the future due to the already narrow range of conditions where they are found.

Other influences considered

Hybridization

Earlier research hypothesized that hybridization between *P. shenandoah* and *P. cinereus* was common as evidenced by a number of individuals with intermediate morphological traits (Highton and Worthington 1967, p. 624–625) and supported with analysis of protein variation (Highton 1999, p. 46), however frequency of hybridization was not widespread across all populations. Considering the low documented incidence of hybridization and no evidence of species- or population-level effects, hybridization is not likely a major threat to *P. shenandoah*, although our understanding remains limited by a lack of data.

Predation

There are no predators known to specifically prey on *P. shenandoah*, but predators are likely to include snakes, birds, and various mammals that forage on the forest floor (Jaeger 1971b, p.637). Some research has indicated that forest edges can attract certain predators such as snakes and this can increase predation on forest salamanders (Bradshaw 2010, p. 55). However, the habitat of *P. shenandoah* naturally includes many areas that have forest edges or more open canopy (e.g. rock outcrops) and there is no available information to indicate that predation on *P. shenandoah* is increased by those conditions.

Soil pH/Acid Rain

Acid deposition and other sources of air pollution are well-documented at the Park (Cosby et al. 2006, entire), but direct effects of these factors on *P. shenandoah* have not been investigated. Although some amphibians are vulnerable to the effects of acid deposition (Pierce 1993, entire), study results for the closely related *P. cinereus* offer conflicting evidence. There is some indication that *P. cinereus* is limited by acidic soils with pH values less than 3.7 (Wyman and Hawksley-Lescault 1987, p. 1819), but more recent information suggests it tolerates a wide range of soil pH conditions without adverse effects (Bondi et al. 2016, entire). It is possible that acidification of *P. shenandoah* habitat could indirectly affect individual foraging success through reduction of invertebrate prey. Increased soil sulfate levels from acid deposition have been shown to correlate with decreases in the abundance of insects upon which *P. shenandoah* could feed (Bromenshenk 1980, entire; Leetham et al. 1980, entire; McNary et al. 1980, entire). Because salamanders forage preferentially during rainy or foggy weather, they may be particularly susceptible to the effects of acid deposition on their ability to maintain water balance (Frisbie and Wyman 1995, p. 331) and thus their foraging efficiency could be affected. Results of the Shenandoah Watershed Study (a monitoring project initiated in 1979) indicate that effects of acid deposition are beginning to wane in the well-buffered soil types that underlie *P. shenandoah* habitat (Jastram et al. 2013, p. 66). In particular, sulfate is beginning to flush from shallow soils (Scanlon et al. 2021, p. 1); thus, any potential effects of acidification on *P. shenandoah* are expected to currently be small and not a major threat.

Talus Weathering

The status of *P. shenandoah* was previously thought to be threatened due to weathering of the exposed rock (talus) habitat to which the species was restricted by competition with *P. cinereus* (Jaeger 1970, entire; 1971b, p. 192; Griffis and Jaeger 1998, entire). However, recent research has indicated that *P. shenandoah* range edges are much wider and more complex than previously thought (Grant et al. 2018, entire; Amburgey et al. 2020, entire). Further, *P. shenandoah* co-occurs with *P. cinereus* throughout most of its current estimated range as predicted by elevation and environmental moisture variables (Werba et al. 2024a, p. 7). Thus, talus weathering is not currently considered a primary threat to *P. shenandoah* status given research supporting primarily climate-related controls on distribution.

Infectious disease

Amphibians worldwide are vulnerable to highly infectious pathogens that can cause rapid mortality or die offs in certain conditions. The pathogens *Batrachochytrium dendrobatidis* (*Bd*) and ranavirus are present in amphibian populations in the eastern U.S. (Rothermel et al. 2008, p. 11; Olson et al. 2013, p. 3) but have not been documented in *P. shenandoah* populations or other *Plethodon* species near *P. shenandoah's* range (Muletz et al. 2014, p. 4; Muletz-Wolz et al. 2017, p. 1). A large study of museum specimens that included 51 *P. shenandoah* and 315 *P. cinereus* collected from Hawksbill from 1957–1979 were all negative when tested for presence of *Bd* (Muletz et al. 2014, p. 4). A separate study of bacterial communities on terrestrial salamanders found high prevalence of anti-*Bd* bacteria on salamanders in Shenandoah National Park but did not detect *Bd* in any individuals sampled (Muletz-Wolz et al. 2017, p. 3). It is unknown if the presence of these bacteria are sufficient to confer resistance to Bd infection or if these bacteria are a result of past exposure to *Bd* within the populations.

The pathogen *Batrachochytrium salamandrivorans* (*Bsal*) is closely related to *Bd* but is not known to be present in wild amphibian populations in North America (Waddle et al. 2020, p.2). The pathogen has been implicated in mortality events in Europe and has been identified as a severe threat to populations of some North American amphibian species if it is introduced (Yap et al. 2015, p. 481; Richgels et al. 2016, p. 6). Lab studies have indicated that some *Plethodon* species can become infected with *Bsal* but do not exhibit mortality and are generally tolerant of Bsal (DiRenzo et al. 2021, p. 2804; Gray et al. 2023, p. 2). Given there are no known pathogens to which *P. shenandoah* or other closely related species are highly susceptible and pathogens have yet not been documented on *P. shenandoah* or in nearby habitats, we did not consider infectious disease a major factor influencing the current status of *P. shenandoah* populations.

NPS Maintenance

Maintenance activities occur near known *P. shenandoah* habitat due to its close proximity to Skyline Drive, scenic overlooks, hiking trails, and Park infrastructure to support visitor services. To address concerns for possible impacts, NPS has outlined several restrictions to minimize harm from Park maintenance activities. According to park policy, there will be no use of herbicides along corridors within predicted *P. shenandoah* habitat and instead mechanical vegetation management techniques will be used. Additionally, during these maintenance activities no cover objects are to be moved and work is to be conducted during the day to minimize the risk of direct harm to surface-active salamanders. Considering these precautions, and others outlined in an associated Biological Opinion (USFWS 2022, entire), we did not include NPS maintenance further as a considerable source of impact on the current condition or recovery of the species.

Current Condition

Resiliency: While threats vary slightly in each population, all three populations have a low-moderate resiliency.

Redundancy/Representation: The species in only known from three peaks in Shenandoah National Park and is not expected to occur elsewhere. Given the proximity of these populations to one another, it is possible for all three to be exposed to catastrophic events, resulting in low or limited redundancy and representation.

CHAPTER 4: ANALYSIS METHODS

For the purposes of this assessment, we defined three separate populations that correspond to the three mountains within the species range. Each population is considered an analytical unit, defined as groups of 100*100 m grid cells, also referred to as 'sites' (Grant et al. 2021, p. 11). Sites were selected from across all known suitable habitat for the species, defined as forested habitat above 700 m elevation across the three mountains that comprise the species range. These analytical units were assessed collectively for changes in occupancy over time (both historical to current, and projected into the future) to inform current and future viability of each population.

The historical period (defined here as <2007) provides the baseline condition from which we evaluate changes in *P. shenandoah* viability (measured as the proportion of sites occupied) over time, while the current (2007–2022) period is the starting point for estimating the future viability of *P. shenandoah* using population projection models. We identified changes in moisture and temperature driven by climate change, and competition with *P. cinereus* as factors most likely to affect viability for *P. shenandoah* in the foreseeable future. We developed plausible future scenarios (described below) based on projections of how these three factors may change over time. Campbell Grant et al. (2023, entire) used field data from 2007–2016 to estimate annual occupancy dynamic rates (i.e., site extinction and colonization probabilities) of *P. shenandoah* and *P. cinereus*, then used the parameter estimates under different future temperature and moisture scenarios and models representing hypotheses of the relative importance of biotic (competition with *P. cinereus*) interactions to estimate a range of future occurrence rates, while accommodating climate and ecological (i.e., whether competition and climate are important factors driving salamander extinction risk) uncertainty. To assess extinction risk over time, we relied on Campbell Grant et al. (2023, entire) who used multiple hypotheses of occurrence and future climate projections to project the extinction risk for *P. shenandoah* over 60 years. This time horizon corresponds to approximately 10 generations of the species based on estimated longevity of 6-17 years (Staub 2016, p. 119).

Future Scenarios

Climate scenarios were extended from downscaled climate projections for Shenandoah National Park (Lee et al. 2014, entire), which predict an increase of 3.3–7°C in the July mean maximum temperature over 60 years in *P. shenandoah* habitat. While there is high certainty of warming of *P. shenandoah* habitat, there is less certainty about how precipitation and thus moisture availability may change. To address this, Campbell Grant et al. (2023, entire) used two predicted future moisture scenarios for forecasting occupancy: a drier scenario (linear decrease in moisture by two standard deviations) and a wetter scenario (linear increase in moisture by two standard deviations). Evidence regarding the current dynamics/effect of competition is mixed, as described in the competition section, and linked to climate impacts on the two species individually. Whether the influence will be exacerbated in the future is unknown so we treated this effect as constant. We include the multiple hypotheses related to competition in the future scenarios because, in addition to the uncertainty about its current role in viability for *P. shenandoah*, there is uncertainty as to how competition may change in the future. As such, outcomes for *P. shenandoah* were estimated under four possible hypotheses including the combinations of two different moisture levels (drier vs. wetter) under two hypotheses of competition (i.e., including or excluding the conditional effect of *P. cinereus* on local extinction and colonization).

Predictions of future occupancy detailed below assume all analytical units are one continuous population and do not account for potential differences in site colonization or extinction between occupied patches of habitat across the different analytical units. This is due to insufficient data available to conduct a robust analysis for individual populations. Viability is assessed across the entire range and may be higher than true viability because the species occurs in smaller, fragmented areas across the range. Additionally, the steep initial decline in occurrence in all scenarios is an artifact of the model and it is better to consider the overall trajectory and not attempt to interpret specific annual estimates.

Scenario 1: Warmer, drier future with abiotic and biotic influence

Warmer and drier conditions are expected to result in the largest declines in *P. shenandoah* occupancy when both abiotic (temperature and moisture) and biotic (negative influence of *P. cinereus*) factors are used to forecast future occupancy (Figure 3, panel 1). Less than 5 percent of sites are expected to be occupied after 60 years as compared to just over 50 percent current site occupancy. Uncertainty of these estimates decreases over time, but even upper bounds of predicted occupancy do not exceed approximately 10 percent of sites and lower bounds are at 0.

Scenario 2: Warmer, wetter future with abiotic and biotic influence

The predicted status of *P. shenandoah* in wetter future conditions is similar to Scenario 1. Estimates of occupancy after 60 years are approximately 5 percent of sites, with lower bounds of estimated error near zero and upper bounds near 15 percent. Uncertainty around the occupancy estimates is slightly larger than Scenario 1, but also decreases over time, particularly after 30 years.

Scenario 3: Warmer, drier future, abiotic influence only

When only abiotic (temperature and moisture) variables are included in predictions, occupancy of *P. shenandoah* in a warmer, drier future is much more uncertain in the next 30-40 years. Occupancy at 60 years is still expected to be low (<10 percent of sites occupied), but bounds of the estimated error indicate it could be as high as 35 percent or as low as zero. This larger estimated error is a result of uncertainty in how moisture may affect site extirpation and colonization rates.

Scenario 4: Warmer, wetter future, abiotic influence only

The best predicted outcome for *P. shenandoah* is a wetter future with no negative influence of *P. cinereus*; however, this scenario still is expected to result in a decrease in occupancy to <15 percent of sites after 60 years. The uncertainty around occupancy estimates is large but decreases after approximately 30 years. Lower error bounds of the occupancy estimate do not reach zero but are low by year 60 (<5 percent of sites). Upper error bounds indicate occupancy could be as high as approximately 35 percent of sites, but estimated error remains large at year 60 due to uncertainty in the response of site colonization and extirpation due to moisture changes.

Warmer/drier future impacts

Warmer and drier conditions (Scenario 1 and Scenario 3) may reduce time for foraging and prey capture on the surface during spring and fall seasons if surface moisture conditions become unsuitable for salamanders. At the same time, higher temperatures may also increase energy requirements via higher metabolic costs to foraging and surface activity if salamander activity windows (which peak in spring/fall) remain stable as the climate changes (Gade et al. 2020, p. 9). Generally, prey availability is lower in drier conditions (Jaeger 1980, p. 339), so salamanders may not be able to compensate for higher metabolism with increased bouts of foraging.

At the range scale, model results indicate that warmer and drier conditions will reduce the likelihood of colonization of sites where *P. shenandoah* is absent and will decrease persistence probability at occupied sites (Campbell Grant et al. 2023, p.1692–1693). This could lead to disappearance of small, occupied patches with little chance of recolonization due to lack of conditions to facilitate long-distance dispersal. Further, warmer and drier future conditions may decrease the frequency of dew and fog, which has been correlated with *P. shenandoah* occurrence and could further restrict the range of all populations at lower elevations (Grant et al. 2018, p. 7559). Warmer and drier conditions could also increase risk of potential catastrophic wildfire that could impact large portions of a population. Outbreaks of pests such as the spongy moth may also increase the risk of widespread defoliation, as fungal pathogen growth that kills caterpillars are inhibited in dry conditions (Reilly et al. 2014, p. 639). Defoliation from forest pests is often patchy, but outbreaks would further decrease surface moisture through increased solar incidence and may exacerbate dry conditions in localized areas (USFWS 1994).

Warmer/wetter future impacts

Warmer and wetter futures (Scenario 2 and Scenario 4) may allow salamanders to offset some effects of increased temperatures with increased foraging and surface activity to compensate for higher metabolic costs (Munoz et al. 2016, p. 8747). However, the timing of moisture is critical, and climate forecasts that involve timing and duration of precipitation are uncertain (Fan et al. 2014, p. 160). Surface activity increases with rainfall during the spring and fall, so more nights with suitable, moist surface conditions may increase the total activity time that is available for salamanders in these seasons (Gade et al. 2020, p. 9). Whether greater total activity time is sufficient to compensate for the increased metabolic demand is uncertain and dependent on a variety of factors, including the response in prey abundance to changing conditions.

Broadly, wetter future conditions lower the risk of catastrophic events such as wildfire and could reduce the intensity and extent of outbreaks of forest pests such as spongy moth (Reilly et al. 2014, p. 639) or hemlock woolly adelgid (Chandler et al. 2022, p.546). Wetter conditions are expected to positively affect salamander colonization and persistence (Campbell Grant et al. 2023, p. 1692–1693), so occupied patches may be more likely to be re-colonized or persist longer as compared to a drier climate future. However, current predictions indicate increased moisture will likely not be enough to compensate for lower probability of long-distance dispersal (to colonize empty sites) or lower persistence due to warmer temperatures as indicated by overall predicted declines of the species (Campbell Grant et al. 2023, entire). Wetter conditions may slow the expected negative effect of higher temperatures on the frequency of dew or fog at the lower elevational limit of *P. shenandoah*. Instead, wetter conditions could slow the rate of change in frequency of clouds and fog at lower elevations if an increase in precipitation occurs simultaneously with warming (Grant et al. 2018, p. 7559), allowing salamanders at lower elevations to potentially persist longer than expected when compared with drier climate scenarios.

Competition is expected to have a negative effect on *P. shenandoah* regardless of the abiotic model warmer/wetter or warmer/drier. In the drier scenario, the inclusion of competition did not seem to have a greater impact on the occupancy of *P. shenandoah* than the abiotic factors alone (scenarios 1 and 3, Figure 3). Alternatively, competition may have a more pronounced impact in the wetter scenario (scenario 2, Figure 3). However, in both abiotic scenarios the uncertainty around predicted occupancy estimates was considerably larger.

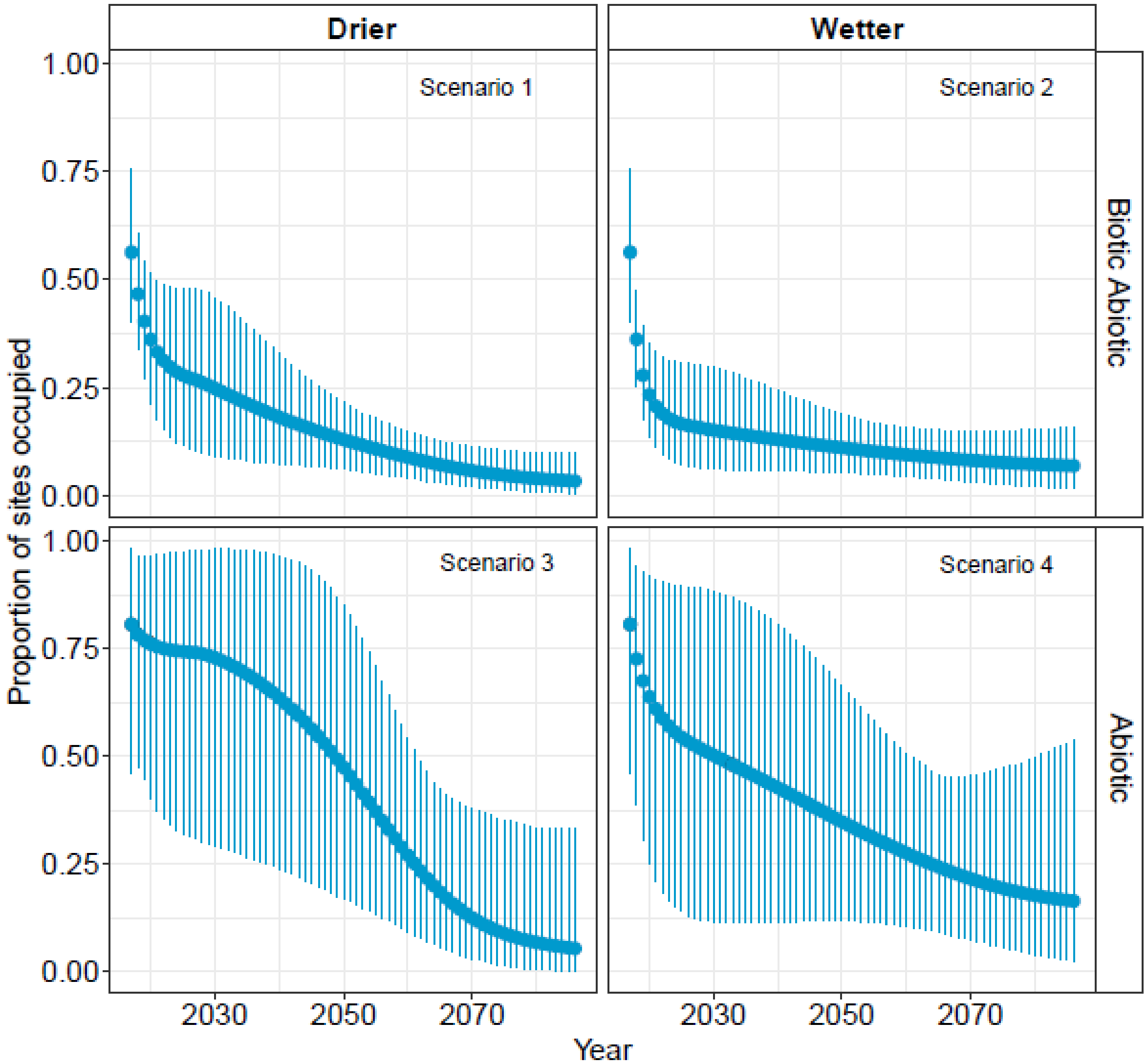

Figure 3. Bayesian population viability analysis results for the proportion of sites occupied by *Plethodon shenandoah* for each scenario over 60 years. Top row includes results under hypothesis of both abiotic and biotic controls on *P. shenandoah* occurrence, bottom row includes results assuming only abiotic influence on species occurrence. Results for +3.3°C temperature scenario are shown, as results for +7°C temperature scenario are virtually identical. Difference in starting occupancy estimates is a result of the inclusion of the presence of *P. cinereus* on occupancy of *P. shenandoah* the Biotic Abiotic model (see Campbell Grant et al. 2023 for further explanation of models). The steep initial decline in occurrence is an artifact of the model and it is better to consider the overall trajectory and not attempt to interpret specific annual estimates.

CHAPTER 5: VIABILITY AND EXTINCTION RISK

Under all future scenarios, *P. shenandoah* occurrence is expected to decline. In the near-term, most scenarios indicate a steep decline. Looking further out, *P. shenandoah* occurrence continues to decline, owing to climate change impacts on temperature and moisture. The implications of these changes on *P. shenandoah* viability (3Rs and extinction risk) are described below.

P. shenandoah requires multiple healthy, resilient populations that are distributed across its range to withstand normal environmental stochasticity, disturbances, catastrophic events, and changing environmental conditions. *P. shenandoah's* ability to withstand normal stochasticity likely varies across populations, though overall the ability of the populations to withstand catastrophic events is expected to be low, as total area for each population is relatively small.

Given the declining occurrence, the species' viability is likely to decline in both the near- and far-term. The species currently is estimated to exist within a limited geographic area (8.6 km^2, 6.02 - 17.3 km^2), which is characterized by similar habitats, elevations, and latitudes. The three populations are separated by a considerable distance (approximately 5 km) and natural barriers. This restricted geographic extent and homogeneity of conditions make the populations more vulnerable to the impact of environmental stochasticity and catastrophic events, such as fire. Moreover, natural recolonization of areas is unlikely given that the population on each mountain is functionally isolated from the other mountains (Mulder et al. 2019, p. 8). As the climate changes, species occupancy is expected to decline, further isolating populations and reducing overall abundance. The future impacts of competition with *P. cinereus* are uncertain and may depend on climate conditions, but there is potential for competition to exacerbate future climate-related impacts. In turn, populations will be more vulnerable to the impact of environmental stochasticity, disturbances, and catastrophic events.

Additionally, *P. shenandoah's* ability to adapt in place (evolutionary potential) will likely decline as population abundance is reduced. This is because as population size declines, so too does within- and among-population genetic diversity, which is the substrate upon which natural selection (thus adaptation) operates. Furthermore, given its habitat constraints and dispersal ability, *P. shenandoah* is unlikely to shift its range to track suitable environmental conditions. For these reasons, *P. shenandoah* is expected to face increasing extinction risk over the next 60 years.

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