IMPACTS OF CLIMATE CHANGE ON MAMMALIAN SPECIES OF CONCERN WITHIN THE APPALACHIAN ECOREGION

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Degree

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DEDICATION

To the unwavering support that kept me sane through it all and endured the pandemic with me, Mr. Peepers, Jaws, Stripes, Jasper, Marten, Fisher, and my love, Wally, as well as my Parents, Grandparents, Nala-Roo, and Chris-Chris.

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ABSTRACT

Climate change and growth anthropogenic presence is a phenomenon impacting all species globally. Fortunately, with protection of key areas of suitable habitat and climate, we can alleviate the worst of biodiversity loss utilizing climate change refugia. This is apparent in the eastern United States, where the Appalachian Ecoregion naturally form a refugium compared to the surrounding landscape for many taxa and rare ecosystems. Particularly of interest are the at-risk relict boreal ecosystems found at elevation, which are otherwise restricted to the northern US and Canada, and numerous endemic taxa found only in this biodiverse region.

Recent studies have focused either on the distant future (2080s or beyond), continental scale models, and/or a wide array of taxonomic groups to produce studies of broad ecological trends. Focus has also been given primarily to birds, amphibians, and plants, with a large gap in studies of mammals at a regional scale focused on climate change. To address this gap, I assessed the effects of climate change on species distributions, dispersal, and even relocation, for Appalachian mammals, giving focus to protected areas and landcover to highlight key refugial areas for these mammals focusing first on a wide array of species of greatest conservation need, then narrowing the scope to focus on the overlap of a single large family with a single charismatic flagship species, and finally to the reintroduced subspecies of a single taxon within the region.

Results highlighted the versatility of methods used based on species ecology and the importance of post-model processing across numerous scenarios. I provided (1) recommendations to practitioners on key conservation areas for mammalian refugia as well as areas for partnership programs in the Appalachian Ecoregion, (2) proposed areas for modification of impermeable barriers in biodiverse areas to allow better connectivity of refugia

for species with varying dispersal abilities, and (3) provided recommendations to state agencies based on ecological and genetic literature and our subspecies models of suitable climate to increase reestablishment success in suitable areas for the wapiti.

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SUPPLEMENTARY MATERIAL

The following supplementary material can be utilized to replicate the results of this dissertation and are included to promote transparency and foster continued research in these areas. The following are contained within a word document under the zip file titled as "LyonDissertationSupplement.zip":

Supplementary 1.1. Mammalian Species Data

Supplementary 1.2. Evaluation Metrics and Detailed Calculations

Supplementary 1.2.1. GCM Assessment

Supplementary 1.2.2. Model Evaluation

Supplementary 1.2.3. Results for Each Species under 2-4.5 CNRM-CM6-1 Climate Scenario

Supplementary 1.2.4. Results for Each Species under 3-7.0 CanESM Climate Scenario

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INTRODUCTION

In the face of the ongoing global biodiversity crisis, species persistence is more dependent than ever on areas to shelter them from climate change and other anthropogenic impacts (Davis et al., 2018; Finn et al., 2023; O'Connor et al., 2020; Rull, 2022; Thomas et al., 2004). Specific geographic areas may naturally act as "refugia" from these adverse conditions in part due to their geologic history and structure of the topography compared to the surrounding landscape (Barratt et al., 2017; Bilton et al., 1998; Cartwright & Wolfe, 2016; García et al., 2022; Graham et al., 2010; G. Hewitt, 2000). Some of the oldest mountains on the planet are the Appalachian Mountains, having long served as climate refugia in the face of changing landscapes, such as through the Miocene grassland expansion and Pleistocene glaciations, and must do so again in the face of rapid changing climate driven by anthropogenic activities (Ashcroft, 2010; Berry & Smith, 2013; Crespi et al., 2003; DeSantis & Wallace, 2008; Tribsch & Schönswetter, 2003; Wallace & Wang, 2004).

Pleistocene glaciation events within the eastern Nearctic facilitated dispersal and period of rapid colonization that created the Appalachian biodiversity hotspot containing high richness of biodiversity in freshwater fish, amphibians, reptiles, and mammals (Cartwright & Wolfe, 2016; Graham et al., 2010; G. Hewitt, 2000; Morelli et al., 2016; R. Smith et al., 2002). Even today, relict boreal ecosystems persist at high elevation within the south-central Appalachian Mountains (hereafter Appalachian Ecoregion) (Berry & Smith, 2013; Browne & Ferree, 2007; Gross, 2010; Reese et al., 2001; Sipe & Browne, 2004). However, given the rapid rate of climate change and growing urban areas in the region, a number of these relict species and ecosystems are becoming of conservation concern, thus it is imperative to evaluate the impacts of climate change and areas of potential refugia (Carroll, 2010; Lawler et al., 2015; McKinley et al., 2019; Minor & Lookingbill, 2010).

A pitfall in planning for the conservation of protected areas and climate refugia can be the over-reliance on a single charismatic taxon to inform actions (Bifolchi & Lodé, 2005; Simberloff, 1998; F. Wang et al., 2021). Variable species-specific dispersal abilities, particularly in animals small in size or home range can compound conservation planning issues (Lugon-Moulin & Hausser, 2002; Segelbacher et al., 2010; Sutherland et al., 2000, 2000; Van Vuren, 1998). Though dispersal barriers can inhibit gene flow between populations, mitigation is possible through implementation of wildlife corridors (Frankham, 2015; Gracanin & Mikac, 2023; Pertoldi et al., 2007; Ralls et al., 2020; Shafaghat et al., 2022). The Appalachian Ecoregion in particular, has been identified as a key dispersal route for species shifting their distributions to alleviate the pressures of climate change, making it an ideal region for these corridors to promote landscape connectivity (Hamaide et al., 2022; Lawler et al., 2013; Newmark, 1993; Zhu et al., 2021). Indeed, given the successful utilization of wildlife corridors in the western US (e.g., for mule deer, mountain lions, California quail, and various rodents) and in the eastern US (for the endangered Florida Panther), demand for corridors near populous regions and National Parks in the Appalachian Ecoregion has increased tremendously (Barnick et al., 2022; Beckmann et al., 2012; Caldwell & Klip, 2020; Donaldson, 2007; Foster & Humphrey, 1995; Shepherd et al., 2023). Similarly, avoidance of road mortalities is needed in the Appalachian Ecoregion for all species.

The wapiti (*Cervus canadensis*) was once an abundant, widely distributed cervid species, with population estimates of over 10 million individuals, consisting of three subspecies ranging from the Piedmont of the east to the western edge of the Rocky Mountains, two subspecies along the Pacific Coast, and a single subspecies spanning from the Temperate Sierras of Arizona and New Mexico southward into Mexico (O'Gara & Dundas, 2002; Popp et al., 2014). By the mid-

twentieth century, the most southern and eastern subspecies had become extinct, with remaining populations of the other four subspecies extirpated from much of their range due to overhunting in all but the most remote regions (O'Gara & Dundas, 2002; Popp et al., 2014). Given the conservation success of numerous keystone species in the west (e.g. sea otters, gray wolves, and prairie dogs), various states have begun efforts to restore wapiti populations to the east (Hale & Koprowski, 2018; Martínez-Meyer et al., 2006; O'Gara & Dundas, 2002; Popp et al., 2014; Sarrazin & Barbault, 1996). Eastern restoration efforts have had mixed results, with noted lack of studies of the wapiti herds established in the east compared to their western counterparts (O'Gara & Dundas, 2002; Padilla et al., 2023; Popp et al., 2014). There is a need for intensive planning to ensure successful reestablishment and long-term persistence of populations, particularly given that different subspecies introduced to the Appalachian Ecoregion experienced different degrees of genetic drift due to overhunting and habitat loss within the past 200 years (IUCN, 1998; Martínez-Meyer et al., 2006; O'Gara & Dundas, 2002; Popp et al., 2014).

Broadly, this dissertation evaluates the impact of climate change in the near future (by the 2040s) for mammals in the Appalachian Ecoregion. Chapter 1 focuses on identifying priority climate refugial areas and opportunity areas for conservation for 59 mammalian species, of which three are federally listed species, three have federally listed subspecies, and one is a proposed candidate species for listing. The rest of the species were identified as of greatest conservation by the Appalachian Land Scape Conservation Cooperative and State Wildlife Action Plans of the 13 states overlapping the Appalachian Ecoregion. Chapter 2 focuses on comparing the outcomes of planning corridors and wildlife crossings when using a flagship species, the American Black Bear, and the most diverse order of mammals, rodents. Finally, Chapter 3 focuses on the importance of careful consideration of species' ecology and genetics

across state boundaries when planning for species' reintroductions, coupled with climate niche models and distribution predictions for the wapiti and the differences in climatic niches among subspecies.

In Chapter 1, I determined the extent of climate refugia for each mammalian species of conservation concern, as well as biodiversity hotspots and measures of losses/gains/stable refugia within the Appalachians. I also highlighted key protected areas overlapping with these biodiversity hotspots for mammals and noted areas that do not fall under protection that will be essential for forming partnerships and collaborations between conservation practitioners and private landowners to maintain climate and habitat connectivity for these species. In Chapter 2, I identified key priority areas for rodent species and major dispersal barriers in the form of primary roadways, as well as corridors needed to maintain connectivity between stable climate refugia for each species, compared to corridors for the American Black Bear. Proximity to protected areas was also factored into these analyses to highlight areas that fell under priority areas for the rodents that overlapped with those for the bear. Areas that were crossed by primary roadways were found to be in need of wildlife overpasses/underpasses. Lastly, in Chapter 3 I provided a detailed literature review of wapiti populations and reintroduction efforts in the Appalachians by state, while also evaluating the climatic niche of the four remaining subspecies in combination with ecological and genetic data. These models were then forecast to the reintroduced regions in the east from population ranges in the west, as well as into the near future, to determine whether current release sites for the two subspecies of wapiti in the Appalachians were suitable for their respective subspecies. Utilizing the results of the three chapters, I proposed specific conservation priority areas as well as conservation actions to help

mitigate the effects of climate change on mammals in such a unique and biodiverse region as the Appalachian Mountains.

REFERENCES

Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, *37*(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Barnick, K. A., Green, A. M., Pendergast, M. E., & Şekercioğlu, Ç. H. (2022). The effects of human development, environmental factors, and a major highway on mammalian community composition in the Wasatch Mountains of northern Utah, USA. *Conservation Science and Practice*, *4*(7), e12708. https://doi.org/10.1111/csp2.12708

Barratt, C. D., Bwong, B. A., Onstein, R. E., Rosauer, D. F., Menegon, M., Doggart, N., Nagel, P., Kissling, W. D., & Loader, S. P. (2017). Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa. *Diversity and Distributions*, *23*(8), 875–887. https://doi.org/10.1111/ddi.12582

Beckmann, J. P., Clevenger, A. P., Huijser, M., & Hilty, J. A. (2012). *Safe Passages: Highways, Wildlife, and Habitat Connectivity*. Island Press.

Berry, Z. C., & Smith, W. K. (2013). Ecophysiological importance of cloud immersion in a relic spruce–fir forest at elevational limits, southern Appalachian Mountains, USA. *Oecologia*, *173*(3), 637–648. https://doi.org/10.1007/s00442-013-2653-4

Bifolchi, A., & Lodé, T. (2005). Efficiency of conservation shortcuts: An investigation with otters as umbrella species. *Biological Conservation*, *126*(4), 523–527. https://doi.org/10.1016/j.biocon.2005.07.002

Bilton, D. T., Mirol, P. M., Mascheretti, S., Fredga, K., Zima, J., & Searle, J. B. (1998). Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1402), 1219–1226. https://doi.org/10.1098/rspb.1998.0423

Browne, R. A., & Ferree, P. M. (2007). Genetic Structure of Southern Appalachian "Sky Island" populations of the Southern Red-Backed Vole (Myodes gapperi). *Journal of Mammalogy*, *88*(3), 759–768. https://doi.org/10.1644/06-MAMM-A-049R1.1

Caldwell, M. R., & Klip, J. M. K. (2020). Wildlife Interactions within Highway Underpasses. *The Journal of Wildlife Management*, *84*(2), 227–236. https://doi.org/10.1002/jwmg.21801

Carroll, C. (2010). Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. *Biological Conservation*, *143*(6), 1432–1437. https://doi.org/10.1016/j.biocon.2010.03.018

Cartwright, J. M., & Wolfe, W. (2016). *Insular ecosystems of the southeastern United States—A regional synthesis to support biodiversity conservation in a changing climate*. https://www.semanticscholar.org/paper/Insular-ecosystems-of-the-southeastern-United-to-in-Cartwright-Wolfe/24f40322117d69212560c27cc05bc80c340fd77b

Crespi, E. J., Rissler, L. J., & Browne, R. A. (2003). Testing Pleistocene refugia theory: Phylogeographical analysis of Desmognathus wrighti, a high-elevation salamander in the southern Appalachians. *Molecular Ecology*, *12*(4), 969–984. https://doi.org/10.1046/j.1365-294X.2003.01797.x

Davis, M., Faurby, S., & Svenning, J.-C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences*, *115*(44), 11262–11267. https://doi.org/10.1073/pnas.1804906115

Donaldson, B. (2007). Use of Highway Underpasses by Large Mammals and Other Wildlife in Virginia: Factors Influencing Their Effectiveness. *Transportation Research Record*, *2011*(1), 157–164. https://doi.org/10.3141/2011-17

Finn, C., Grattarola, F., & Pincheira-Donoso, D. (2023). More losers than winners: Investigating Anthropocene defaunation through the diversity of population trends. *Biological Reviews*, *98*(5), 1732–1748. https://doi.org/10.1111/brv.12974

Foster, M. L., & Humphrey, S. R. (1995). Use of Highway Underpasses by Florida Panthers and Other Wildlife. *Wildlife Society Bulletin (1973-2006)*, *23*(1), 95–100.

Frankham, R. (2015). Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology*, *24*(11), 2610–2618. https://doi.org/10.1111/mec.13139

García, M. B., Miranda, H., Pizarro, M., Font, X., Roquet, C., & González-Sampériz, P. (2022). Habitats hold an evolutionary signal of past climatic refugia. *Biodiversity and Conservation*, *31*(5), 1665–1688. https://doi.org/10.1007/s10531-022-02419-4

Gracanin, A., & Mikac, K. M. (2023). Evaluating modelled wildlife corridors for the movement of multiple arboreal species in a fragmented landscape. *Landscape Ecology*, *38*(5), 1321–1337. https://doi.org/10.1007/s10980-023-01628-8

Graham, S. P., Steen, D. A., Nelson, K. T., Durso, A. M., & Maerz, J. C. (2010). An Overlooked Hotspot? Rapid Biodiversity Assessment Reveals a Region of Exceptional Herpetofaunal Richness in the Southeastern United States. *Southeastern Naturalist*, *9*(1), 19–34. https://doi.org/10.1656/058.009.0102

Gross, D. A. (2010). Pennsylvania boreal conifer forests and their bird communities: Past, present, and potential. *In: Rentch, James S.; Schuler, Thomas M., Eds. 2010. Proceedings*

from the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains. 2009 May 14-15; Slatyfork, WV. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 48-73., *p-64*, 48–73.

Hale, S. L., & Koprowski, J. L. (2018). Ecosystem-level effects of keystone species reintroduction: A literature review. *Restoration Ecology*, *26*(3), 439–445. https://doi.org/10.1111/rec.12684

Hamaide, V., Hamaide, B., & Williams, J. C. (2022). Nature reserve optimization with buffer zones and wildlife corridors for rare species. *Sustainability Analytics and Modeling*, *2*, 100003. https://doi.org/10.1016/j.samod.2022.100003

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, *405*(6789), 907–913. https://doi.org/10.1038/35016000

IUCN. (1998). *Guidelines for Re-introductions* (p. 10). IUCN. https://www.iucn.org/resources/publication/iucn-guidelines-re-introductions

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., Heller, N. E., Pressey, R. L., Sanderson, E. W., & Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change: Conserving Nature's Stage in a Time of Rapid Change. *Conservation Biology*, *29*(3), 618–629. https://doi.org/10.1111/cobi.12505

Lawler, J. J., Ruesch, A. S., Olden, J. D., & McRae, B. H. (2013). Projected climate-driven faunal movement routes. *Ecology Letters*, *16*(8), 1014–1022. https://doi.org/10.1111/ele.12132

Lugon-Moulin, N., & Hausser, J. (2002). Phylogeographical structure, postglacial recolonization and barriers to gene flow in the distinctive Valais chromosome race of the common shrew (Sorex araneus). *Molecular Ecology*, *11*(4), 785–794. https://doi.org/10.1046/j.1365-294X.2002.01469.x

Martínez-Meyer, E., Peterson, A. T., Servín, J. I., & Kiff, L. F. (2006). Ecological niche modelling and prioritizing areas for species reintroductions. *Oryx*, *40*(4), 411–418. https://doi.org/10.1017/S0030605306001360

McKinley, P. S., Belote, R. T., & Aplet, G. H. (2019). An assessment of ecological values and conservation gaps in protection beyond the corridor of the Appalachian Trail. *Conservation Science and Practice*, *1*(6), e30. https://doi.org/10.1111/csp2.30

Minor, E. S., & Lookingbill, T. R. (2010). A Multiscale Network Analysis of Protected-Area Connectivity for Mammals in the United States. *Conservation Biology*, *24*(6), 1549–1558. https://doi.org/10.1111/j.1523-1739.2010.01558.x

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

Newmark, W. D. (1993). The Role and Design of Wildlife Corridors with Examples from Tanzania. *Ambio*, *22*(8), 500–504.

O'Connor, B., Bojinski, S., Röösli, C., & Schaepman, M. E. (2020). Monitoring global changes in biodiversity and climate essential as ecological crisis intensifies. *Ecological Informatics*, *55*, 101033. https://doi.org/10.1016/j.ecoinf.2019.101033

O'Gara, B. W., & Dundas, R. G. (2002). Distribution: Past and present. *North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, DC, USA*, 67–119.

Padilla, B. J., Banfield, J. E., Corondi, A., & Larkin, J. L. (2023). Seasonal variation in size and composition of elk (Cervus canadensis) home range in central Appalachia. *Canadian Journal of Zoology*, *101*(6), 448–461. https://doi.org/10.1139/cjz-2022-0099

Pertoldi, C., Bijlsma, R., & Loeschcke, V. (2007). Conservation genetics in a globally changing environment: Present problems, paradoxes and future challenges. *Biodiversity and Conservation*, *16*(14), 4147–4163. https://doi.org/10.1007/s10531-007-9212-4

Popp, J. N., Toman, T., Mallory, F. F., & Hamr, J. (2014). A Century of Elk Restoration in Eastern North America. *Restoration Ecology*, *22*(6), 723–730. https://doi.org/10.1111/rec.12150

Ralls, K., Sunnucks, P., Lacy, R. C., & Frankham, R. (2020). Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biological Conservation*, *251*, 108784. https://doi.org/10.1016/j.biocon.2020.108784

Reese, C. L., Waters, J. M., Pagels, J. F., & Brown, B. L. (2001). Genetic Structuring Of Relict Populations Of Gapper's Red-Backed Vole (*Clethrionomys Gapperi*). *Journal of Mammalogy*, *82*(2), 289–301. https://doi.org/10.1644/1545-1542(2001)082<0289:GSORPO>2.0.CO;2

Rull, V. (2022). Biodiversity crisis or sixth mass extinction? *EMBO Reports*, *23*(1), e54193. https://doi.org/10.15252/embr.202154193

Sarrazin, F., & Barbault, R. (1996). Reintroduction: Challenges and lessons for basic ecology. *Trends in Ecology & Evolution*, *11*(11), 474–478. https://doi.org/10.1016/0169-5347(96)20092-8

Segelbacher, G., Cushman, S. A., Epperson, B. K., Fortin, M.-J., Francois, O., Hardy, O. J., Holderegger, R., Taberlet, P., Waits, L. P., & Manel, S. (2010). Applications of landscape genetics in conservation biology: Concepts and challenges. *Conservation Genetics*, *11*(2), 375–385. https://doi.org/10.1007/s10592-009-0044-5

Shafaghat, A., Keyvanfar, A., & Wui Ket, C. (2022). A decision support tool for evaluating the wildlife corridor design and conservation performance using analytic network process (ANP). *Journal for Nature Conservation*, *70*, 126280. https://doi.org/10.1016/j.jnc.2022.126280

Shepherd, B. J., Houck, J., & Lyon, C. (2023). On the road again: A study valuing wildlife crossings for wetland mitigation on State Road 40 in Volusia County, Florida. *Ecosphere*, *14*(6), e4566. https://doi.org/10.1002/ecs2.4566

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Conservation Biology and Biodiversity Strategies*, *83*(3), 247–257. https://doi.org/10.1016/S0006-3207(97)00081-5

Sipe, T. W., & Browne, R. A. (2004). Phylogeography Of Masked (Sorex Cinereus) And Smoky Shrews (Sorex Fumeus) In The Southern Appalachians. *Journal of Mammalogy*, *85*(5), 875–885. https://doi.org/10.1644/214

Smith, R., Freeman, P., Higgins, J., Wheaton, K., FitzHugh, T., Ernstrom, K., & Das, A. (2002). Priority areas for freshwater conservation action: A biodiversity assessment of the southeastern United States. *The Nature Conservancy*, *3*.

Sutherland, G., Harestad, A., Price, K., & Lertzman, K. (2000). Scaling of Natal Dispersal Distances in Terrestrial Birds and Mammals. *Conservation Ecology*, *4*(1). https://doi.org/10.5751/ES-00184-040116

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), Article 6970. https://doi.org/10.1038/nature02121

Tribsch, A., & Schönswetter, P. (2003). Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. *TAXON*, *52*(3), 477–497. https://doi.org/10.2307/3647447

Van Vuren, D. (1998). Mammalian Dispersal and Reserve Design. In T. M. Caro (Ed.), *Behavioral Ecology and Conservation Biology* (pp. 369–393). Oxford University Press, USA.

Wang, F., Winkler, J., Viña, A., McShea, W. J., Li, S., Connor, T., Zhao, Z., Wang, D., Yang, H., Tang, Y., Zhang, J., & Liu, J. (2021). The hidden risk of using umbrella species as conservation surrogates: A spatio-temporal approach. *Biological Conservation*, *253*, 108913. https://doi.org/10.1016/j.biocon.2020.108913

Zhu, G., Papeş, M., Giam, X., Cho, S.-H., & Armsworth, P. R. (2021). Are protected areas well-sited to support species in the future in a major climate refuge and corridor in the United States? *Biological Conservation*, *255*, 108982. https://doi.org/10.1016/j.biocon.2021.108982

CHAPTER I:

CLIMATE CHANGE REFUGIA FOR APPALACHIAN MAMMALS OF CONSERVATION CONCERN

ABSTRACT

The Appalachian ecoregion of the United States encompasses the greatest diversity of mammalian species in the eastern Nearctic, thus the potential impact of climate change may affect numerous mammalian species, including currently imperiled ones. Our study had two objectives: (1) to aide decision-makers and conservation practitioners by identifying mammalian species that are most susceptible to climate change and mapping mammalian richness hotspots and climate refugia within the Appalachian ecoregion; and (2) to provide a case study for montane regions globally that are facing similar conservation challenges. Using ecological niche modeling we forecasted potential range shifts under six climate scenarios for 59 mammalian species of greatest conservation need in this ecoregion. We identified two types of climate refugia for these species: (i) maintained refugia, representing areas of climatic suitability presently and into the near future (2040s) and (ii) potential refugia, representing areas that could become climatically suitable in the near future. Key refugia identified in the Appalachian ecoregion fall into three large regions: along the Tennessee-North Carolina border, the Kentucky-Virginia border, and much of south and central West Virginia. These regions are a major component of the Appalachian biodiversity that is threatened by climate change in a landscape matrix of urban and agricultural land uses. Ultimately, 45% of predicted climatic refugia for mammals of greatest conservation need fall outside of the current network of protected areas, indicating that partnerships with private landowners will be essential to mitigate climate change effects on these mammals. Practitioners should foster collaborations in areas identified for conservation opportunities if species of greatest conservation need are to persist into the future.

INTRODUCTION

Globally, refugia and species endemism are strongly linked in numerous studies focusing on the Alps of Europe, forested refugia of Africa, Australia, and Asia (Barratt et al., 2017; Bilton et al., 1998; García et al., 2022; Harrison & Noss, 2017; Keppel et al., 2015; Parisod, 2021; Tribsch & Schönswetter, 2003; Wu et al., 2017). In the northern hemisphere, "refugium" traditionally describes an area that a warm-adapted species may have used as refuge during Pleistocene glaciation events (Crespi et al., 2003), leading to high levels of species endemism (Morelli et al., 2016). A prime example of this is the southeastern United States, long recognized as a hotspot of richness and endemism for freshwater fishes, amphibians, reptiles, and mammals (Cartwright & Wolfe, 2016; Graham et al., 2010; Hewitt, 2000; Jenkins et al., 2015; Smith et al., 2002). Much of the diversity in this region is due to the north-south orientation of the Appalachian Mountains (Appalachians hereafter) that acted as a corridor for cold-adapted taxa to spread southward during the Pleistocene (Hewitt, 2000), while valleys served as refugia for warm-adapted taxa that became isolated due to widespread unfavorable climatic conditions (Crespi et al., 2003; Hewitt, 2000; Tribsch & Schönswetter, 2003). Presently, the Appalachians may once again play a large role in preserving diversity, this time in the face of warming temperatures due to anthropogenic climate change. The definition of a "refugium" has expanded in the last couple of decades to consider areas that maintain suitable climate and habitat for the survival of a particular species (Ashcroft, 2010; Morelli et al., 2016; Tribsch & Schönswetter, 2003). Historically, the high topographic and climatic heterogeneity of the Appalachians has allowed refugia to persist within a broader scale context of climate warming. This is evident in the number of relict boreal and northern taxa present at elevation within the Appalachians since the last glacial maximum (Berry & Smith, 2013; Browne & Ferree, 2007; Gross, 2010; Reese et al., 2001; Sipe & Browne, 2004).

Refugia may emerge in the context of anthropogenic climate change, if species' current ranges are proximal to areas of stable suitable conditions in the future (Ackerly et al., 2020; Ashcroft, 2010; Doxa et al., 2022). However, lack of refugia and unsuitable future climate conditions threaten species' survival, often compounded by minimal overlap of protected areas with biodiversity hotspots and poor connectivity of the landscape (Carroll, 2010; Lawler et al., 2013, 2015; McKinley et al., 2019; Minor & Lookingbill, 2010; Zhu et al., 2021). The spatial mismatch between protected areas and biodiversity hotspots is often a result of protected areas historically being established where conflict with human use of resources (e.g. fertile lands and natural resources) is low rather than where biodiversity is high (Jenkins et al., 2015; Joppa & Pfaff, 2009; Scott et al., 2001). Additionally, the "umbrella approach", that is protecting charismatic or flagship species under the assumption that a larger number of co-occurring species will also achieve protection, is commonly used to select conservation areas (Bifolchi & Lodé, 2005; Simberloff, 1998; Wang et al., 2021). However, umbrella species are often of high trophic level or have distinct habitat requirements that do not align with most of the species within the region (Bifolchi & Lodé, 2005; Simberloff, 1998; Wang et al., 2021). In the Appalachians, this effect of umbrella species could easily result from conservation actions targeting flagship species such as *Ursus americanus* (the American black bear) and *Cervus canadensis* (the wapiti). In this study, we propose a more comprehensive approach for the conservation of mammals in the Appalachians through determination of the greatest overlap of climatically suitable ranges under current and forecasted climatic conditions for the greatest number of species, leading to the conservation of a greater variety of habitats and ecosystems.

Of the 78 mammalian species that occur in the Appalachians, 59 are considered of conservation concern. Our main goal was to identify which of these species are most susceptible

to range contraction due to forecasted climate change as this information could be useful to practitioners and decision-makers tasked with protecting biodiversity. This is of particular importance given overlapping biodiversity surveys, climate resiliency of the Appalachians, and ongoing efforts by organizations such as The Nature Conservancy to acquire parcels and collaborate with stakeholders in these key regions capable of sustaining refugia (Anderson et al., 2023; Dreiss et al., 2024; Lawler et al., 2015; Trombulak, 2015). We estimated species' distribution shifts in response to these climatic changes through the widely used approach of ecological niche modeling (Anderson, 2013; Brun et al., 2020; Carroll, 2010; Peterson et al., 2002, 2018; Thuiller et al., 2006; Warren et al., 2014; Wiens et al., 2009). Additionally, we focused on species endemic to Appalachians and species that colonized the Appalachians during the Pleistocene that otherwise have a predominantly northern/boreal distribution (Jantz et al., 2016; hereafter northern relict species). In this study, we aimed to aid practitioners and decision-makers by identifying: (i) richness hotspots for mammals of conservation concern under current and future climate conditions; (ii) species projected to lose climatically suitable areas in the future, and whether these were Appalachian endemic or northern relict species; and (iii) stable and potential climate refugia outside of currently protected areas that could be targeted for partnerships, conservation planning, and outreach. More broadly, our study could serve as a comparison to other montane climate refugia globally and as a model system of estimating multi-species refugia for management and policy, placing the biodiverse region that is the south-central Appalachians into the broader conservation and refugial context globally.

METHODS

Study area and species data

To delineate the study area, we used ecoregions defined by the Environmental Protection Agency (EPA) (Commission for Environmental Cooperation, 1997), specifically the Ozark, Ouachita-Appalachian Forest Level II ecoregion (Appalachian Ecoregion hereafter). We focused on mammalian species and subspecies of conservation concern within the Appalachian Ecoregion and included subspecies contiguous with Appalachian populations within the broader Eastern Temperate Forest and southern Northern Forest ecoregions.

We compiled a list of 59 mammals (Appendix I: Table 1.1) from the following entities that identified species and subspecies in need of conservation management: (i) the United States Fish and Wildlife Service (USFWS) Endangered Species Act (ESA); (ii) the United States Geological Survey (USGS) State Wildlife Action Plans (SWAPs); (iii) and the Appalachian Landscape Conservation Cooperative (LCC). The list contained species that are found broadly in eastern temperate forests, as well as species endemic to the Appalachian Ecoregion and northern relict species, that have ranges extending from Canada or the northern United States into the higher elevations of the Appalachians. Seven species from our list occur on the fringes of the Appalachian Ecoregion: *Lasiurus seminolus, Myotis austroriparius, Nycticeius humeralis, Tadarida brasiliensis, Oryzomys palustris, Peromyscus polionotus*, and *Sylvilagus aquaticus*. We included these species to explore potential range expansions into the Appalachian Ecoregion under future climate scenarios. Lastly, our list excluded *Cervus canadensis* due to recent reintroductions of stock from various western populations into our study area (Popp et al., 2014).

We downloaded occurrence data for 59 species from the Global Biodiversity Information Facility (GBIF https://www.gbif.org/), USGS Biodiversity Information Serving Our Nation (BISON), and VertNet (http://vertnet.org/) databases. The BISON online database was replaced

by the US node to GBIF in December 2021 (https://www.gbif.us). We cleaned the data to exclude records that were duplicate, that represented fossils or were outside the known species' ranges, and that had missing dates or latitude/longitude coordinates (see Appendix I: Supplementary 1.1). To ensure that the species' occurrences aligned temporally with climate data, we only used in our models those with collecting dates within 1970-2000.

Climate data

We trained our models with 19 bioclimatic variables at 2.5 arc minute resolution (~5 km) from WorldClim 2 (https://www.worldclim.org/data/index.html) representing current (baseline) minima, maxima, means, and seasonal variation of temperature and precipitation for 1970-2000 (Fick & Hijmans, 2017). We projected our models on future climatic conditions from CMIP6 (Coupled Model Intercomparison Projects 6) for 2021-2040 from two Shared Socioeconomic Pathways (SSPs), 2-4.5 and 3-7.0. These SSPs represented "middle of the road" and "regional rivalry" greenhouse gasses emission scenarios, respectively, and were between emission scenarios of economies that are fully sustainable (lowest emissions) and those that are driven by fossil fuels (highest emissions). Using the Zonal Statistics Tool in ESRI ArcGIS 10.8.1 we calculated the mean annual temperature and mean annual precipitation for the Appalachian Ecoregion within an SSP scenario to summarize the differences in projections across the nine Global Circulation Model (GCM) outputs available from WorldClim 2 (Appendix I: Supplementary 1.2). We then selected three GCMs to represent a low temperature/low precipitation scenario (CNRM-CM6-1), medium temperature/medium precipitation scenario (CNR-ESM2-1), and high temperature/high precipitation scenario (CanESM) for each SSP.

Ecological niche modeling parameters and evaluation

We generated ecological niche models with Maximum Entropy (Maxent), a machine-learning algorithm that estimates environmental suitability and corresponding potential distributions from species' presence records, background data, and environmental data (Elith et al., 2011). For background sampling, we clipped climate data from WorldClim within a taxon-specific spatial extent that encompassed the subspecies within eastern North America that were contiguous with the subspecies occurring within the Appalachian Ecoregion. To delineate ranges and create the background sampling area for each taxon, we used the respective Mammalian Species articles (Appendix I: Supplementary 1.2) coupled with species accounts from Mammals of North America (Hall, 1981); see Appendix I: Supplementary 1.3 for species ranges and presence points.

To train the models with presence data that best captured the heterogeneity of climatic conditions across the study area, we used SDMToolbox (Brown et al., 2017) for ESRI ArcGIS 10.8.1 to run a Principal Component Analysis (PCA) of the 19 bioclimatic variables. The climate heterogeneity is calculated following two steps: (1) PCA analysis of climatic variables and (2) sum of first three PCs, weighted by their respective eigenvalue percentage. The final output is a heterogeneity raster (Brown et al., 2017). For each species, we extracted the values of the heterogeneity raster for all occurrences and selected for model training the occurrences that captured the most climatic heterogeneity (25% of occurrences in first quartile, 50% in second quartile, 75% in third quartile, and 100% of occurrences in fourth quartile); we used the remaining occurrences to test the models (see Appendix I:: Supplementary Code 1.1).

We trained the Maxent models with 10,000 random background samples from each species' range and used the following Maxent parameters: logistic output of models, no extrapolation or clamping of models, default regularization parameter, and 5000 iterations for

model convergence (see Appendix I: Supplementary Code 1.2). For each species we ran an initial model with all 19 bioclimatic variables, and then we ran final models with the subset of variables that contributed more than 1% to increasing the performance of individual species' models (see full list of variables and their contributions to initial models in Appendix I: Supplementary 1.4). The final model runs were projected onto six datasets of forecasted climate conditions (three GCMs x two SSPs). We then applied the minimum training presence (MTP) threshold to convert the model outputs (continuous suitability maps) to binary (suitable-unsuitable maps) for the baseline and all six future climate scenarios (Appendix I: Supplementary 1.5). The MTP is used to evaluate the lowest predicted suitable value for the training occurrence points, and thresholds the model to show areas at or above this value for the model's output. We chose this threshold because inclusion of all training data was important to the model performance given our deliberate selection of training presences to emphasize climatic heterogeneity.

We evaluated model performance with two metrics. The Area under the Curve (AUC) of the Receiver Operating Characteristic (ROC) is frequently used in the literature but has limitations and can be misleading (Bohl et al., 2019; Muscarella et al., 2014; Peterson et al., 2008; Veloz, 2009), thus we also calculated test omission error for each model. We removed from the analysis species whose models had 30% or greater test omission error (Appendix I: Supplementary 1.2).

Refining climate suitability estimates with land cover data

Given that our models only estimated climatic suitability, and land cover changes have occurred between 1970-2000 and the present, we refined Maxent potential distributions with current land cover information. We used a 2019 land cover classification based on plant

functional types from Moderate Resolution Imaging Spectroradiometer (MODIS MCD12Q1 version 6) (Friedl et al., 2019) to remove climatically suitable pixels that overlapped with land cover classes defined as barren, croplands, or urban/developing. Though it is possible for some species to occur within these land cover types, these are not optimal for long-term, stable populations due to the high degree of disturbance, particularly given the preference for deciduous forest of these priority species in the Appalachians.

Identifying climatic refugia as stability and expansion of climatic suitability

We calculated for each species the range expansion, range contraction, and stable ranges between current and future estimates of climatic suitability with SDMToolbox (Brown et al., 2017) in ESRI/span>ArcGIS 10.8.1. To assess the role of protected areas in preserving climatically suitable areas, we used the Protected Areas Database of the United States (PAD-US) maintained by the United States Geological Survey (USGS) (U.S. Geological Survey, 2022), and included all categories of protected areas (ranging from federal, state, and private conservation easements) in our analysis to distinguish between any level of protection and no protection. The protected areas did not overlap with land cover types that were unsuitable for our study species. For each species, we determined the area (km2) of range contraction, stable range, and range expansion that overlapped with protected areas using Tabulate Area tool in ESRI ArcGIS 10.8.1. We then averaged expansion, stability, and contraction by order of mammals as area measurement (km2) and as an average percentage (relative to baseline potential distributions). We performed this analysis for the combination of lower emission scenario (SSP 2-4.5) and lower temperature/lower precipitation GCM (CNRM-CM6-1), as well as the combination of higher emission scenario (SSP 3-7.0) and higher temperature/higher precipitation GCM (CanESM) to span the range of possible outcomes.

We defined two types of refugia: (i) maintained climatic refugia represented by areas estimated as climatically suitable currently and in the future (stable climatic suitability), and (ii) potential climatic refugia represented by novel areas projected to become climatically suitable in the future (expansion of climatic suitability). We then identified mammalian hotspots of maintained and potential climatic refugia as the areas of stable and novel climatic suitability, respectively, for at least 75% of the species included in our study. For this purpose, we summed the individual species maps of climatic stability and separately climatic expansion within each SSP and GCM. Lastly, we generated consensus maps by overlaying the maps of hotspots of maintained refugia and separately potential refugia from each climate change scenario. The consensus maps highlight target areas for conservation practitioners and land managers as these areas represent the least variability among the potential distributions forecasted under different climate change scenarios.

RESULTS

Species data and model performance

Half of all presence records were missing latitude/longitude coordinates, collection year, or were fossil specimens in the GBIF and VertNet databases thus were removed from our datasets (754,511 and 321,029 records remained, respectively); by comparison, 30% of BISON records lacked collection year, latitude/longitude coordinates, or were fossils (428,444 remained) (Supplementary 1). We further cleaned the data to match the temporal range of climate baseline (records from 1970-2000) within the combined dataset of GBIF, BISON, and VertNet; only about 20% of all points met this temporal criterion. After we removed duplicates among databases and selected the records within the study area of Eastern North America, only 1.3% of

the initial dataset remained (32,527 records total). The models performed well when evaluated with test AUC, averaging 0.896 (0.796:0.985); removal of 11 taxa with an omission error greater than 30% lead to an average omission error rate decreasing from 13.5% to 7.79% (0%:29.21%) (Appendix I: Supplementary 1.2). The models of the following species had testing omission error above 30% and were removed from all subsequent analysis (Appendix I: Supplementary 1.2): *Corynorhinus townsendii, Lasiurus cinereus, Microtus chrotorrhinus, Reithrodontomys humulis, Sorex hoyi, Sorex palustris, Spilogale putorius, Sylvilagus obscurus, Synaptomys cooperi, Tadarida brasiliensis,* and *Zapus hudsonius*.

Forecasted changes in potential distributions of Appalachian mammals in relation to current protected areas

We present in the main text the results of SSP 2-4.5 and GCM CNRM-CM6-1 combination (lower intensity climate change) and provide supplemental figures and tables showing comparison to the combination of SSP 3-7.0 and GCM CanESM (higher intensity climate change). For each species, we provide as supplementary materials the potential distribution estimates under each GCM and SPP combination (Appendix I: Supplementary 1.2 & 1.5) and future distributional changes relative to the baseline potential distributions (Appendix I: Supplementary 1.6), as well as consensus models across all species (Appendix I: Supplementary 1.7); consensus for climatic stability (maintained climatic refugia), separately under scenarios of lower and higher intensity climate change, are available in Appendix I: Supplementary 1.8. Additionally, in Appendix I: Supplementary 1.8, overlapping areas of predicted suitable climate (both expansion and stable) through 2040 are highlighted by major taxonomic grouping.

At the level of order, we calculated the average overlap between protected areas and stability, loss, and gain of climatic suitability. We repeated the same calculations for unprotected areas as well (Appendix I: Figure 1.1 shows the scenario of low intensity climate change). For all

mammal orders, our models estimated that climatic stability (maintained refugia) in protected areas was high (average above 93%) under both scenarios of low intensity and high intensity climate change, with the exception of Lagomorpha for which maintained refugia in protected areas dropped to an average of 79% under high intensity climate change (Table 3). The expansion of climatic suitability for Lagomorpha in protected areas was the largest compared to the other orders: on average 45% under low intensity climate change and 34% under high intensity climate change, in contrast with Carnivora, Chiroptera, and Eulipotyphla that showed small expansion (up to 3%) under low intensity and slightly higher under high intensity climate change (up to 7%); the models for Rodentia predicted same climatic expansion into protected areas between the two scenarios (4%). The estimated range contractions in protected areas for Carnivora, Lagomorpha, and Rodentia were on average more severe under the scenario of high intensity climate change (up to 21%), compared to Eulipotyphla experiencing greater contraction in the low intensity scenario (4%), and Chiroptera experiencing similar levels of contraction in protected areas in either scenario (5%).

Outside protected areas, all orders were estimated to have high stability (on average over 92%), with the exception of the Lagomorpha (on average 86%) under high intensity climate change. Expansion of climatic suitability outside protected areas was on average greater for Carnivora, Chiroptera, and Eulipotyphla under the high intensity scenario (up to 12%), whereas for Lagomorpha expansion was slightly greater under the low intensity scenario (1%), and Rodentia was predicted to expand similarly under both scenarios (5%). Contraction outside protected areas was greatest in every order under the high intensity scenario, with Lagomorpha predicted to experience the most suitability loss (on average 14%).

To evaluate the climate change risk to individual species, we focused on changes to the baseline potential distribution and defined high risk as a combination of 15% or higher contraction of baseline distribution and 85% or lower stability of the baseline distribution. Under the scenario of low intensity climate change, the species predicted at highest risk within protected areas was Erethizon dorsatum (Rodentia), with only half of its range forecasted to remain stable within protected areas and half of its range contracting; additionally, our models did not project an expansion of suitable climate in protected areas for this species. Other at risk species include two chiropterans (*Lasionycteris noctivagans* and *Perimyotis subflavus*), two rodents (*Glaucomys sabrinus*, a northern relict species, and *Neotoma magister*, an Appalachian endemic species), and the carnivoran *Mustela frenata* (Appendix I: Supplementary 1.3). Outside of protected areas, under the scenario of low intensity climate change, *M. frenata* was also predicted to be at risk while *E. dorsatum* remained at high risk. Compared to species identified as at risk in protected areas, outside of protected areas only one chiropteran, *L. noctivagans*, one rodent, *Microtus pennsylvanicus*, and one eulipotyphlan, *Sorex longirostris* were predicted to be at risk.

The projected distributions under higher intensity climate change (SSP 3-7.0 and GCM CanESM) identified *S. longirostris* as losing 81% of its suitable climatic range and maintaining 19% of climatically stable range in the protected areas. Other at risk species in protected areas under this scenario were, in decreasing levels of risk, *Mustela erminea* (northern relict species), *G. volans, Myotis sodalis, Condylura cristata, U. americanus, Mustela nivalis* (northern relict species), *Microtus ochrogaster, Lepus americanus* (northern relict species), *Tamiasciurus hudsonicus* (northern relict species), *Eptesicus fuscus*, *and Peromyscus gossypinus*. In unprotected areas *E. dorsatum* remained most at risk and several additional species were

predicted at risk: *M. pennsylvanicus, L. noctivagans, C. cristata, Myotis septentrionalis, Pekania pennanti* (northern relict species), *P. polionotus, L americanus* (northern relict species), *P. subflavus, Sorex fumeus* (northern relict species), *N. magister* (endemic Appalachian species), *M. austroriparius, G. sabrinus* (northern relict species), and *Lasiurus borealis*.

Hotspots of maintained and potential climate refugia for mammalian species

Within the Appalachian Ecoregion the dominant land cover by plant functional type is Deciduous Broadleaf Trees (94.2%; 324,832 km2) and most of our occurrence records coincided with this land cover type (~92% of occurrences). The unsuitable land cover types that overlapped with maintained and potential refugia represented only 3.8% (13,246 km2) of the ecoregion. Additionally, though a climatically suitable area should have some level of protection in place to act as a refugium in practice, most of the climatic suitability was forecasted on privately owned lands. Currently, privately owned lands represent about 6% of protected areas in the Appalachian Ecoregion, indicating that partnerships with private landowners can provide another avenue for conservation.

Our consensus mapping of stable climate refugia indicated that most of the Appalachian Ecoregion is climatically stable for at least half of the species studied (Supplementary I: Figure 1.2A), with the caveat that the hotspots of maintained refugia (climatic stability) represented different combinations of species in different areas. When considering stable climatic suitability, hotspots of maintained refugia for 36-40 species emerged along the eastern edge of the Appalachian Ecoregion. We also examined the Appalachian Ecoregion for hotspots of potential refugia (novel climatic suitability; Appendix I: Figure 1.2B) and for contraction of climate suitability (Appendix I: Figure 1.2C). Our analyses indicated limited hotspots of potential refugia, for up to 9 species, concentrated in the southernmost portion of the Appalachian

Ecoregion. Contraction of climatic suitability was projected to be minimal and sparse, with no clear climatic sink for species, and with a maximum overlap of only 7 species of greatest conservation need that we included in our study.

When analyzing the overlap between protected areas and the consensus map of maintained refugia (Appendix I: Figure 1.3) two National Parks are of importance, the Great Smoky Mountains National Park (Tennessee-North Carolina) and New River Gorge National Park (West Virginia), and six National Forests: Chattahoochee National Forest (Georgia), Nantahala and Pisgah National Forest (North Carolina), Cherokee National Forest (Tennessee), Daniel Boone National Forest (Kentucky), Jefferson and George Washington National Forest (Virginia), and Monongahela National Forest (West Virginia). Some of the stable climatic refugia are not connected but potential climatic refugia outside protected areas could partially mitigate this issue. Many of these potential refugia fall within one of three contiguous regions within the Appalachian Ecoregion: (1) on the Tennessee-North Carolina border and into southern Virginia; (2) from Frozen Head State Park in Tennessee northward along the Kentucky-Virginia border into West Virginia; and (3) the central interior of West Virginia northward.

DISCUSSION

Our study forecasted that the climatic conditions within the Appalachian Ecoregion would remain suitable in 2021-2040 for the majority of mammals of conservation concern. This possible future scenario would allow practitioners and land managers vital time needed for conservation planning long-term, as many taxa, including mammals, are expected to experience high range loss in the region by 2100 due to warming temperatures (Michalak et al., 2018; Zhu et al., 2021, 2022). Studies have shown that the Appalachians exhibit low change in climate

velocity compared to much of eastern North America, indicating that connectivity of the landscape will be critical for species migrating to refugial areas (Carroll et al., 2018; Lawler et al., 2013; Zhu et al., 2021, 2022). Given the findings of previous studies and our study, conservation partnerships with landowners will be key to connectivity and preservation of preferred habitat that would allow persistence or migration of species to refugia in response to climate change (Block & Levine, 2021; Clancy et al., 2020; Enquist et al., 2017; Jenkins et al., 2015; Lutter et al., 2018; Morelli et al., 2020, 2021; Roberts & Parker, 1998). Some caveats worth noting for this study include: refugial areas are projected to be centered around the Appalachians within eastern North America given the partial-pooling of presence points to focus on gene flow into that region, meaning more periphery areas may have different genetics contributing to those populations/subspecies than those in the Appalachians; the models here estimate the abiotic climatic niche (of the BAM diagram of a species' niche; e.g. Peterson & Soberón, 2012; Qiao et al., 2015; Soberón, 2010) and assume unlimited dispersal within suitable climatic areas with suitable landcover, thus excluding biotic factors and presence of fine scale habitat under 30m and beyond dominant land cover.

We included in our analyses 48 mammalian species; potential distributions for additional 11 species for which the models had low performance are presented in Appendix I: Supplementaries 1.4, 1.5, 1.6, & 1.7. Following mammalian diversity trends (Amori & Gippoliti, 2000; Hall, 1981; Pagel et al., 1991; Venditti et al., 2011) most of the species in our study were from two orders: (i) Rodentia, with 19 species across four families of which Cricetidae comprised the majority of rodents studied, and (ii) Chiroptera, with 13 species, all from the family Vespertillionidae (Appendix I: Table 1.1). Eighteen other species were from two additional orders: nine species of Carnivora from three families and nine species of Eulipotyphla

from two families. Lastly, Lagomorpha was represented by two species (both in family Leporidae), which our models estimated that would be most susceptible to high intensity climate change. This is consistent with global findings within this order, particularly for species unable to shift latitudinally or in elevation (Leach et al., 2015; Rehnus et al., 2018). Our study forecasted that mammalian richness would remain high, as the potential distribution of 24 or more species overlapped in the Appalachian Ecoregion under the projections for 2021-2040; additionally, we identified regional hotspots of 36 or more taxa in much of the Blue Ridge and Central Appalachian regions (EPA Ecoregion Level III; Commission for Environmental Cooperation, 2021). This aligns with predictions of other terrestrial vertebrates, trees, and climate corridors in the Appalachians (Jenkins et al., 2015; Michalak et al., 2018; Stralberg et al., 2020; Zhu et al., 2021, 2022) and highlights the conservation importance of the region as one of the richest temperate forests globally in terms of endemic species and relict lineages (Olson et al., 2012).

Our individual species models suggest that loss due to climate change could affect several endemic Appalachian and northern relict species, particularly the porcupine (*E. dorsatum*), Allegheny woodrat (*N. magister*), northern flying squirrel (*G. sabrinus*), and long-tailed weasel (*M. frenata*). Our models projected expansion of suitable climatic conditions for more than 40 taxa across scenarios, but these model estimates are limited to climatic conditions; additional factors, such as lag in vegetation turnover (Corlett & Westcott, 2013; Ding et al., 2020; Stralberg et al., 2015; Svenning & Sandel, 2013; D. Wu et al., 2015) and dispersal abilities determined by the small body and home range sizes of all but a few species (even bats to some degree) will limit dispersal to novel environments (Bowman et al., 2002; Schloss et al., 2012; Whitmee & Orme, 2013). At the systematic level of mammalian order, and even at the species

level in most cases, the overall trend of our model estimates was towards stability in the near future, particularly in protected areas. Eulipotyphlans (the shrews and moles) had, on average, the greatest predicted area of suitable stable climate, with Rodentia (squirrels, porcupines, mice, and voles), Chiroptera (bats), and Carnivora (weasels, skunks, felines, bears, and canines) occupying similar breadths of stability. The models for Lagomorpha (rabbits) were more restricted in both geographic range and suitable climate, occupying at most 10% of the range of the other orders. Lagomorphs should be a target for local outreach given compounded effect of hunting pressure and species misidentification even by experts, i.e. the swamp rabbit (*Sylvilagus aquaticus*) and the Appalachian cottontail (*S. obscurus*) are difficult to distinguish from the highly abundant eastern cottontail (*S. floridanus*).

Species projected to experience the greatest contraction of climatic suitability within protected areas may be prioritized for conservation. Within the Appalachian Ecoregion only 58,779 km2 of land (17%) falls under some degree of protection and parcel size and degree of connectivity are highly variable (U.S. Geological Survey, 2022). This means that many climatic refugia identified by our models exist as patches within the fragmented Appalachian landscape. As suggested in previous studies, we can best aide conservation efforts by identifying refugia for species and potential connectivity corridors among refugia (Barrows et al., 220; Block & Levine, 2021; Clancy et al., 2020; Enquist et al., 2017; Jenkins et al., 2015; Lutter et al., 2018; Michalak et al., 2018; Morelli et al., 2020, 2021; Roberts & Parker, 1998). In the Appalachian Ecoregion, partnerships with private landowners and community outreach in the Blue Ridge and Central Appalachians will be critical to improve connectivity of hotspots of climate refugia and survival of species studied. Building relationships with landowners, encouraging voluntary surveys and monitoring of private lands, and sharing information about species' management

recommendations have been found to benefit conservation efforts in the Appalachians for target bird species (Lutter et al., 2018). Given the overlap of refugia in this region for several taxonomic groups (Carroll et al., 2018; Lawler et al., 2013; Zhu et al., 2021, 2022), similar surveys and management support for corridors and refugia on private lands would likely improve conservation of key habitats and many taxa, including mammals of greatest conservation need.

Finally, from a modeling methodological standpoint, we observed that for some of the species we studied as much as half of species' presence records lack collection date or latitude and longitude coordinates. This is even more apparent in species that are understudied or rarely observed such as the microtine rodents, soricids, and talpids of the Appalachian Ecoregion. The reliability of ecological niche models and their future climate projections depends in part on availability of species' records matching temporally the baseline climate data, as well as on the spatial extent of the records to account for regional variation in environmental conditions. Our method of selecting model training data to maximize climatic heterogeneity mitigated spatial clustering of records, however support is critical for institutions to continue digitization efforts of natural history collections that will enable future research. The species' records available highlighted knowledge gaps in distributions of these species during the middle and end of the 20th century, by showing the need to concentrate data digitization efforts on historical specimens collected prior to 2000.

In summary, for most mammals of greatest conservation need analyzed in this study, the Appalachian Ecoregion appears to be climatically stable in the next couple of decades, particularly when compared to the surrounding landscape. However, beyond the next couple of decades, other studies forecast contractions and range shifts in 2050-2100 for many vertebrate species (Zhu et al., 2021, 2022). Our results suggest that there is a narrow window of time in

which conservation planning is needed for key refugial areas and connectivity corridors in the Blue Ridge and Central Appalachian landscapes. A major concern is the extent of climate stability occurring outside of protected areas. Thus, outreach efforts by decision-makers could be focused on communicating to private landowners and local communities the importance of climate refugia for biodiversity persistence. Information to disseminate could include facts about rare species and actions that can help with species' conservation, and the role of corridors to increase connectivity of refugia while climate conditions remain suitable in the region. Maintaining these biodiversity hotspots is going to be critical for species persistence in the coming decades, and this will be possible only by building partnerships between decision-makers and local communities and landowners.

REFERENCES

Ackerly, D. D., Kling, M. M., Clark, M. L., Papper, P., Oldfather, M. F., Flint, A. L., & Flint, L. E. (2020). Topoclimates, refugia, and biotic responses to climate change. *Frontiers in Ecology and the Environment*, *18*(5), 288–297. https://doi.org/10.1002/fee.2204

Amori, G., & Gippoliti, S. (2000). What do mammalogists want to save? Ten years of mammalian conservation biology. *Biodiversity & Conservation*, *9*(6), 785–793. https://doi.org/10.1023/A:1008971823774

Anderson, R. P. (2013). A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, *1297*(1), 8–28. https://doi.org/10.1111/nyas.12264

Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, *37*(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Barratt, C. D., Bwong, B. A., Onstein, R. E., Rosauer, D. F., Menegon, M., Doggart, N., Nagel, P., Kissling, W. D., & Loader, S. P. (2017). Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa. *Diversity and Distributions*, *23*(8), 875–887. https://doi.org/10.1111/ddi.12582

Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., Rodgers, J., & Mahalovich, M. F. (2020). Validating climate-change refugia: Empirical bottom-up approaches to support management actions. *Frontiers in Ecology and the Environment*, *18*(5), 298–306. https://doi.org/10.1002/fee.2205

Berry, Z. C., & Smith, W. K. (2013). Ecophysiological importance of cloud immersion in a relic spruce–fir forest at elevational limits, southern Appalachian Mountains, USA. *Oecologia*, *173*(3), 637–648. https://doi.org/10.1007/s00442-013-2653-4

Bifolchi, A., & Lodé, T. (2005). Efficiency of conservation shortcuts: An investigation with otters as umbrella species. *Biological Conservation*, *126*(4), 523–527. https://doi.org/10.1016/j.biocon.2005.07.002

Bilton, D. T., Mirol, P. M., Mascheretti, S., Fredga, K., Zima, J., & Searle, J. B. (1998). Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1402), 1219–1226. https://doi.org/10.1098/rspb.1998.0423

Block, S., & Levine, J. M. (2021). How dispersal evolution and local adaptation affect the range dynamics of species lagging behind climate change. *The American Naturalist*, *197*(6), E173–E187. https://doi.org/10.1086/714130

Bohl, C. L., Kass, J. M., & Anderson, R. P. (2019). A new null model approach to quantify performance and significance for ecological niche models of species distributions. *Journal of Biogeography*, *46*(6), 1101–1111. https://doi.org/10.1111/jbi.13573

Bowman, J., Jaeger, J. A. G., & Fahrig, L. (2002). Dispersal distance of mammals is proportional to home range size. *Ecology*, *83*(7), 2049–2055. https://doi.org/10.1890/0012-9658(2002)083[2049:DDOMIP]2.0.CO;2

Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, *5*, e4095. https://doi.org/10.7717/peerj.4095

Browne, R. A., & Ferree, P. M. (2007). Genetic Structure of Southern Appalachian "Sky Island" populations of the Southern Red-Backed Vole (*Myodes gapperi*). *Journal of Mammalogy*, *88*(3), 759–768. https://doi.org/10.1644/06-MAMM-A-049R1.1

Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R. O., Wang, Z., & Zimmermann, N. E. (2020). Model complexity affects species distribution projections under climate change. *Journal of Biogeography*, *47*(1), 130–142. https://doi.org/10.1111/jbi.13734

Carroll, C. (2010). Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. *Biological Conservation*, *143*(6), 1432–1437. https://doi.org/10.1016/j.biocon.2010.03.018

Carroll, C., Parks, S. A., Dobrowski, S. Z., & Roberts, D. R. (2018). Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Global Change Biology*, *24*(11), 5318–5331. https://doi.org/10.1111/gcb.14373

Cartwright, J. M., & Wolfe, W. (2016). Insular ecosystems of the southeastern United States—A regional synthesis to support biodiversity conservation in a changing climate. https://www.semanticscholar.org/paper/Insular-ecosystems-of-the-southeastern-United-to-in-Cartwright-Wolfe/24f40322117d69212560c27cc05bc80c340fd77b

Clancy, N. G., Draper, J. P., Wolf, J. M., Abdulwahab, U. A., Pendleton, M. C., Brothers, S., Brahney, J., Weathered, J., Hammill, E., & Atwood, T. B. (2020). Protecting endangered species in the USA requires both public and private land conservation. *Scientific Reports*, *10*(1), 11925. https://doi.org/10.1038/s41598-020-68780-y

Commission for Environmental Cooperation. (1997). *Ecological Regions of North America: Toward a common perspective* (Revised 2006) [Map]. http://www.cec.org/publications/ecological-regions-of-north-america/

Commission for Environmental Cooperation. (2021). *Terrestrial Ecoregions: Level III* [Map]. http://www.cec.org/north-american-environmental-atlas/terrestrial-ecoregions-level-iii/

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, *28*(8), 482–488. https://doi.org/10.1016/j.tree.2013.04.003

Crespi, E. J., Rissler, L. J., & Browne, R. A. (2003). Testing Pleistocene refugia theory: Phylogeographical analysis of *Desmognathus wrighti*, a high-elevation salamander in the southern Appalachians. *Molecular Ecology*, *12*(4), 969–984. https://doi.org/10.1046/j.1365-294X.2003.01797.x

Ding, Y., Li, Z., & Peng, S. (2020). Global analysis of time-lag and -accumulation effects of climate on vegetation growth. *International Journal of Applied Earth Observation and Geoinformation*, *92*, 102179. https://doi.org/10.1016/j.jag.2020.102179

Doxa, A., Kamarianakis, Y., & Mazaris, A. D. (2022). Spatial heterogeneity and temporal stability characterize future climatic refugia in Mediterranean Europe. *Global Change Biology*, *n/a*(n/a). https://doi.org/10.1111/gcb.16072

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Enquist, C. A., Jackson, S. T., Garfin, G. M., Davis, F. W., Gerber, L. R., Littell, J. A., Tank, J. L., Terando, A. J., Wall, T. U., Halpern, B., Hiers, J. K., Morelli, T. L., McNie, E.,

Stephenson, N. L., Williamson, M. A., Woodhouse, C. A., Yung, L., Brunson, M. W., Hall, K. R., … Shaw, M. R. (2017). Foundations of translational ecology. *Frontiers in Ecology and the Environment*, *15*(10), 541–550. https://doi.org/10.1002/fee.1733

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Friedl, M., Gray, Josh, & Sulla-Menashe, Damien. (2019). *MCD12Q2 MODIS/Terra+Aqua Land Cover Dynamics Yearly L3 Global 500m SIN Grid V006* [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MCD12Q2.006

García, M. B., Miranda, H., Pizarro, M., Font, X., Roquet, C., & González-Sampériz, P. (2022). Habitats hold an evolutionary signal of past climatic refugia. *Biodiversity and Conservation*, *31*(5), 1665–1688. https://doi.org/10.1007/s10531-022-02419-4

Graham, S. P., Steen, D. A., Nelson, K. T., Durso, A. M., & Maerz, J. C. (2010). An Overlooked Hotspot? Rapid Biodiversity Assessment Reveals a Region of Exceptional Herpetofaunal Richness in the Southeastern United States. *Southeastern Naturalist*, *9*(1), 19–34. https://doi.org/10.1656/058.009.0102

Gross, D. A. (2010). Pennsylvania boreal conifer forests and their bird communities: Past, present, and potential. *In: Rentch, James S.; Schuler, Thomas M., Eds. 2010. Proceedings from the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains. 2009 May 14-15; Slatyfork, WV. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 48-73.*, *p-64*, 48–73.

Hall, E. R. (1981). *The mammals of North America* (2nd ed). Wiley.

Harrison, S., & Noss, R. (2017). Endemism hotspots are linked to stable climatic refugia. *Annals of Botany*, *119*(2), 207–214. https://doi.org/10.1093/aob/mcw248

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, *405*(6789), 907–913. https://doi.org/10.1038/35016000

Jantz, P., Monahan, W. B., Hansen, A. J., Rogers, B. M., Zolkos, S., Cormier, T., & Goetz, S. J. (2016). Potential Impacts of Climate Change on Vegetation for National Parks in the Eastern United States. In A. J. Hansen, W. B. Monahan, S. T. Olliff, & D. M. Theobald (Eds.), *Climate Change in Wildlands: Pioneering Approaches to Science and Management* (pp. 151–173). Island Press/Center for Resource Economics. https://doi.org/10.5822/978-1-61091-713-1_8

Jenkins, C. N., Van Houtan, K. S., Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences*, *112*(16), 5081. https://doi.org/10.1073/pnas.1418034112

Joppa, L. N., & Pfaff, A. (2009). High and Far: Biases in the Location of Protected Areas. *PLoS ONE*, *4*(12), e8273. https://doi.org/10.1371/journal.pone.0008273

Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., & Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*, *13*(2), 106–112. https://doi.org/10.1890/140055

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., Heller, N. E., Pressey, R. L., Sanderson, E. W., & Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change:

Conserving Nature's Stage in a Time of Rapid Change. *Conservation Biology*, *29*(3), 618–629. https://doi.org/10.1111/cobi.12505

Lawler, J. J., Ruesch, A. S., Olden, J. D., & McRae, B. H. (2013). Projected climate-driven faunal movement routes. *Ecology Letters*, *16*(8), 1014–1022. https://doi.org/10.1111/ele.12132

Leach, K., Montgomery, W. I., & Reid, N. (2015). Biogeography, macroecology and species' traits mediate competitive interactions in the order Lagomorpha. *Mammal Review*, *45*(2), 88–102. https://doi.org/10.1111/mam.12035

Lutter, S. H., Dayer, A. A., Heggenstaller, E., & Larkin, J. L. (2018). Effects of biological monitoring and results outreach on private landowner conservation management. *PLOS ONE*, *13*(4), e0194740. https://doi.org/10.1371/journal.pone.0194740

McKinley, P. S., Belote, R. T., & Aplet, G. H. (2019). An assessment of ecological values and conservation gaps in protection beyond the corridor of the Appalachian Trail. *Conservation Science and Practice*, *1*(6), e30. https://doi.org/10.1111/csp2.30

Michalak, J. L., Lawler, J. J., Roberts, D. R., & Carroll, C. (2018). Distribution and protection of climatic refugia in North America. *Conservation Biology*, *32*(6), 1414–1425. https://doi.org/10.1111/cobi.13130

Minor, E. S., & Lookingbill, T. R. (2010). A multiscale network analysis of protected-area connectivity for mammals in the United States. *Conservation Biology*, *24*(6), 1549–1558. https://doi.org/10.1111/j.1523-1739.2010.01558.x

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020).

Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*(5), 228–234. https://doi.org/10.1002/fee.2189

Morelli, T. L., Brown-Lima, C. J., Allen, J. M., Beaury, E. M., Fusco, E. J., Barker-Plotkin, A., Laginhas, B. B., Quirion, B. R., Griffin, B., McLaughlin, B., Munro, L., Olmstead, N., Richburg, J., & Bradley, B. A. (2021). Translational invasion ecology: Bridging research and practice to address one of the greatest threats to biodiversity. *Biological Invasions*, *23*(11), 3323–3335. https://doi.org/10.1007/s10530-021-02584-7

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210X.12261

Olson, D., DellaSala, D. A., Noss, R. F., Strittholt, J. R., Kass, J., Koopman, M. E., & Allnutt, T. F. (2012). Climate Change Refugia for Biodiversity in the Klamath-Siskiyou Ecoregion. *Natural Areas Journal*, *32*(1), 65–74. https://doi.org/10.3375/043.032.0108

Pagel, M. D., May, R. M., & Collie, A. R. (1991). Ecological Aspects of the Geographical Distribution and Diversity of Mammalian Species. *The American Naturalist*. https://doi.org/10.1086/285194

Parisod, C. (2021). Plant speciation in the face of recurrent climate changes in the Alps. *Alpine Botany*. https://doi.org/10.1007/s00035-021-00259-6

Peterson, A. T., Cobos, M. E., & Jiménez-García, D. (2018). Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences*, *1429*(1), 66–77. https://doi.org/10.1111/nyas.13873

Peterson, A. T., Ortega-Huerta, M. A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R. H., & Stockwell, D. R. B. (2002). Future projections for Mexican faunas under global climate change scenarios. *Nature*, *416*(6881), Article 6881. https://doi.org/10.1038/416626a

Peterson, A. T., Papeş, M., & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, *213*(1), 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Popp, J. N., Toman, T., Mallory, F. F., & Hamr, J. (2014). A century of elk restoration in Eastern North America. *Restoration Ecology, 22*, 723–730. https://doi.org/10.1111/rec.12150

Reese, C. L., Waters, J. M., Pagels, J. F., & Brown, B. L. (2001). Genetic structuring of relict populations of Gapper's Red-Backed Vole (*Clethrionomys gapperi*). *Journal of Mammalogy*, *82*(2), 289–301. https://doi.org/10.1644/1545-1542(2001)082<0289:GSORPO>2.0.CO;2

Rehnus, M., Bollmann, K., Schmatz, D. R., Hackländer, K., & Braunisch, V. (2018). Alpine glacial relict species losing out to climate change: The case of the fragmented mountain hare population (Lepus timidus) in the Alps. *Global Change Biology*, *24*(7), 3236–3253. https://doi.org/10.1111/gcb.14087

Roberts, S. D., & Parker, G. R. (1998). Ecosystem Management: Opportunities for Private Landowners in the Central Hardwood Region. *Northern Journal of Applied Forestry*, *15*(1), 43–48. https://doi.org/10.1093/njaf/15.1.43

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, *109*(22), 8606–8611. https://doi.org/10.1073/pnas.1116791109

Scott, J. M., Davis, F. W., McGhie, R. G., Wright, R. G., Groves, C., & Estes, J. (2001). Nature Reserves: Do They Capture the Full Range of America's Biological Diversity? *Ecological Applications*, *11*(4), 999–1007. https://doi.org/10.1890/1051-0761(2001)011[0999:NRDTCT]2.0.CO;2

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Conservation Biology and Biodiversity Strategies*, *83*(3), 247–257. https://doi.org/10.1016/S0006-3207(97)00081-5

Sipe, T. W., & Browne, R. A. (2004). Phylogeography of the Masked (*Sorex cinereus*) and Smoky Shrews (*Sorex fumeus*) in the Southern Appalachians. *Journal of Mammalogy*, *85*(5), 875–885. https://doi.org/10.1644/214

Smith, R., Freeman, P., Higgins, J., Wheaton, K., FitzHugh, T., Ernstrom, K., & Das, A. (2002). Priority areas for freshwater conservation action: A biodiversity assessment of the southeastern United States. *The Nature Conservancy*, *3*.

Stralberg, D., Bayne, E. M., Cumming, S. G., Sólymos, P., Song, S. J., & Schmiegelow, F. K. A. (2015). Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: A modified refugia approach. *Diversity and Distributions*, *21*(9), 1112–1128. https://doi.org/10.1111/ddi.12356

Stralberg, D., Carroll, C., & Nielsen, S. E. (2020). Toward a climate-informed North American protected areas network: Incorporating climate-change refugia and corridors in conservation planning. *Conservation Letters*, *13*(4), e12712. https://doi.org/10.1111/conl.12712

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266–1286. https://doi.org/10.3732/ajb.1200469

Thuiller, W., Lavorel, S., Sykes, M. T., & Araújo, M. B. (2006). Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, *12*(1), 49–60. https://doi.org/10.1111/j.1366-9516.2006.00216.x

Tribsch, A., & Schönswetter, P. (2003). Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. *TAXON*, *52*(3), 477–497. https://doi.org/10.2307/3647447

U.S. Geological Survey. (2022). *Protected Areas Database of the United States (PAD-US) 3.0 (ver. 2.0, March 2023)* [Data set]. U.S. Geological Survey. https://doi.org/10.5066/P9Q9LQ4B

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography*, *36*(12), 2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Venditti, C., Meade, A., & Pagel, M. (2011). Multiple routes to mammalian diversity. *Nature*, *479*(7373), Article 7373. https://doi.org/10.1038/nature10516

Wang, F., Winkler, J., Viña, A., McShea, W. J., Li, S., Connor, T., Zhao, Z., Wang, D., Yang, H., Tang, Y., Zhang, J., & Liu, J. (2021). The hidden risk of using umbrella species as

conservation surrogates: A spatio-temporal approach. *Biological Conservation*, *253*, 108913. https://doi.org/10.1016/j.biocon.2020.108913

Warren, D. L., Wright, A. N., Seifert, S. N., & Shaffer, H. B. (2014). Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions*, *20*(3), 334–343. https://doi.org/10.1111/ddi.12160

Whitmee, S., & Orme, C. D. L. (2013). Predicting dispersal distance in mammals: A trait-based approach. *Journal of Animal Ecology*, *82*(1), 211–221. https://doi.org/10.1111/j.1365-2656.2012.02030.x

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19729–19736. https://doi.org/10.1073/pnas.0901639106

Wu, D., Zhao, X., Liang, S., Zhou, T., Huang, K., Tang, B., & Zhao, W. (2015). Time-lag effects of global vegetation responses to climate change. *Global Change Biology*, *21*(9), 3520–3531. https://doi.org/10.1111/gcb.12945

Wu, Y., DuBay, S. G., Colwell, R. K., Ran, J., & Lei, F. (2017). Mobile hotspots and refugia of avian diversity in the mountains of south-west China under past and contemporary global climate change. *Journal of Biogeography*, *44*(3), 615–626. https://doi.org/10.1111/jbi.12862

Zhu, G., Papeş, M., Armsworth, P. R., & Giam, X. (2022). Climate change vulnerability of terrestrial vertebrates in a major refuge and dispersal corridor in North

America. *Diversity and Distributions*, *28*(6), 1227–1241. https://doi.org/10.1111/ddi.13528

Zhu, G., Papeş, M., Giam, X., Cho, S.-H., & Armsworth, P. R. (2021). Are protected areas well-sited to support species in the future in a major climate refuge and corridor in the United States? *Biological Conservation*, *255*, 108982. https://doi.org/10.1016/j.biocon.2021.108982

APPENDIX I:

TABLES

Table 1.1. Mammalian Species of Greatest Conservation Need in the Appalachian Ecoregion.

Mammalian Species of Greatest Conservation Need (59) evaluated due to species/subspecies listing Federally, on a State Wildlife Action Plan, and/or by the Appalachian Land Conservation Cooperative. Mammalian species marked with an asterisk (*) are those referred to as "northern relict or Appalachian endemic mammals" throughout the manuscript (19).

Order	Family	Scientific name	Common name	Training/ Testing sample size	DOI of GBIF dataset
Rodentia	Cricetidae	Microtus chrotorrhinus*	Rock Vole	47/79	https://doi.org/10.15468/dl.t246x6
		Microtus ochrogaster	Prairie Vole	135/224	https://doi.org/10.15468/dl.p96duv
		Microtus pennsylvanicus	Meadow Vole	612/975	https://doi.org/10.15468/dl.f4dsmt
		Microtus pinetorum	Woodland Vole	239/384	https://doi.org/10.15468/dl.uqk32b
		Myodes gapperi*	Southern Red-backed Vole	367/587	https://doi.org/10.15468/dl.q6tx73
		Neotoma floridana	Eastern Woodrat	99/161	https://doi.org/10.15468/dl.bxcxe7
		Neotoma magister*	Allegheny Woodrat	542/64	https://doi.org/10.15468/dl.wkw9fu
		Ochrotomys nuttalli	Golden Mouse	93/147	https://doi.org/10.15468/dl.jueku4
		Oryzomys palustris	Marsh Rice Rat	114/179	https://doi.org/10.15468/dl.7c58vc
		Peromyscus gossypinus	Cotton Mouse	420/667	https://doi.org/10.15468/dl.n23x74
		Peromyscus leucopus	White-footed Mouse	1199/1903	https://doi.org/10.15468/dl.3vc4xw
		Peromyscus maniculatus	Deer Mouse	470/751	https://doi.org/10.15468/dl.6ksurg
		Peromyscus polionotus	Oldfield mouse	44/72	https://doi.org/10.15468/dl.ngxdfk
		Reithrodontomys humulis	Eastern Harvest Mouse	55/92	https://doi.org/10.15468/dl.3xq5f7
		Synaptomys cooperi*	Southern Bog Lemming	96/236	https://doi.org/10.15468/dl.mkmt97
	Dipodidae	Napaeozapus insignis*	Woodland Jumping Mouse	169/266	https://doi.org/10.15468/dl.t6zd4s
	Erethizontidae	Erethizon dorsatum*	North American Porcupine	66/107	https://doi.org/10.15468/dl.657jwx
	Sciuridae	Glaucomys sabrinus*	Northern Flying Squirrel	61/104	https://doi.org/10.15468/dl.y74cy7
		Glaucomys volans	Southern Flying Squirrel	213/345	https://doi.org/10.15468/dl.n8vnsw
		Sciurus niger	Fox Squirrel	274/445	https://doi.org/10.15468/dl.w322kg
		Tamias striatus	Eastern Chipmunk	536/920	https://doi.org/10.15468/dl.q7hk3z
		Tamiasciurus hudsonicus*	American Red Squirrel	2055/3257	https://doi.org/10.15468/dl.sfd8bq
	Zapodidae	Zapus hudsonius	Meadow Jumping Mouse	203/391	https://doi.org/10.15468/

Table 1.1. Continued

Lagomorpha	Leporidae	Lepus americanus*	Snowshoe Hare	38/57	https://doi.org/10.15468/dl.m6xact
		Sylvilagus aquaticus	Swamp Rabbit	87/137	https://doi.org/10.15468/dl.mxugyk
		Sylvilagus obscurus*	Appalachian Cottontail	20/38	https://doi.org/10.15468/dl.2q3pcx
Carnivora	Felidae	Lynx rufus	Bobcat	298/471	https://doi.org/10.15468/dl.j4ry42
	Mephitidae	Spilogale putorius	Eastern Spotted Skunk	20/34	https://doi.org/10.15468/dl.sbwpt2
	Mustelidae	Mustela erminea*	Stoat	65/106	https://doi.org/10.15468/dl.dsr2vz
		Mustela frenata	Long-tailed Weasel	122/198	https://doi.org/10.15468/dl.apwdxd
		Mustela nivalis*	Least Weasel	56/102	https://doi.org/10.15468/dl.c78wwp
		Neovison vison	American Mink	147/236	https://doi.org/10.15468/dl.zwgxqw
		Pekania pennanti*	Fisher	341/534	https://doi.org/10.15468/dl.8b9swm
	Ursidae	Ursus americanus	American Black Bear	62/101	https://doi.org/10.15468/dl.6mzsvc
Chiroptera	Molossidae	Tadarida brasiliensis	Mexican Free-tailed Bat	158/512	https://doi.org/10.15468/dl.tny6ty
	Vespertilionidae	Corynorhinus rafinesquii	Rafinesque's Big-eared Bat	120/191	https://doi.org/10.15468/dl.yumh4p
		Corynorhinus townsendii	Townsend's Big-eared Bat	10/18	https://doi.org/10.15468/dl.rm2rjr
		Eptesicus fuscus	Big Brown Bat	363/579	https://doi.org/10.15468/dl.hbedyb
		Lasionycteris noctivagans	Silver-haired Bat	49/98	https://doi.org/10.15468/dl.cxgg8u
		Lasiurus borealis	Eastern Red Bat	275/440	https://doi.org/10.15468/dl.mybp8m
		Lasiurus cinereus	Hoary Bat	68/111	https://doi.org/10.15468/dl.2343te
		Lasiurus seminolus	Seminole Bat	59/96	https://doi.org/10.15468/dl.m3mu6f
		Myotis austroriparius	Southeastern Bat	79/135	https://doi.org/10.15468/dl.8cgktj
		Myotis grisescens	Gray Bat	91/150	https://doi.org/10.15468/dl.taszr8
		Myotis leibii	Eastern Small-footed Bat	56/90	https://doi.org/10.15468/dl.hbnkra
		Myotis lucifugus	Little Brown Bat	186/301	https://doi.org/10.15468/dl.a7w8mw
		Myotis septentrionalis	Northern Long-eared Bat	61/100	https://doi.org/10.15468/dl.7jng5j
		Myotis sodalis	Indiana Bat	91/146	https://doi.org/10.15468/dl.hdbsjx
		Nycticeius humeralis	Evening Bat	147/242	https://doi.org/10.15468/dl.d5bcca
		Perimyotis subflavus	Tricolored Bat	149/239	https://doi.org/10.15468/dl.hzfcxm
Eulipotyphla	Soricidae	Cryptotis parva	North American Least Shrew	211/340	https://doi.org/10.15468/dl.22rtz4
		Sorex cinereus*	Masked Shrew	552/875	https://doi.org/10.15468/dl.zy8p3n
		Sorex dispar*	Long-tailed Shrew	22/37	https://doi.org/10.15468/dl.7tmee4
		Sorex fumeus*	Smoky Shrew	262/426	https://doi.org/10.15468/dl.r4ym4t
		Sorex hoyi*	American Pygmy Shrew	75/118	https://doi.org/10.15468/dl.e586ve
		Sorex longirostris	Southeastern Shrew	131/214	https://doi.org/10.15468/dl.25yrnf
		Sorex palustris*	American Water Shrew	47/74	https://doi.org/10.15468

Table 1.1. Continued

Talpidae	Condylura cristata	Star-nosed Mole	180/291	https://doi.org/10.15468/dl.c3sxcj
	Parascalops breweri*	Hairy-tailed Mole	83/140	https://doi.org/10.15468/dl.6uzrx4

Table 1.2. Mammalian Occurrences Summary. Mammal occurrences obtained through GBIF and VertNet. Averages by species within the five orders shown followed by the range of points in parenthesis.

Dataset type	Carnivora	Chiroptera	Eulipotyphla	Lagomorpha	Rodentia
Initial number of records	14,157 (7,386:77,855)	7,156 (2,897:67,456)	7,956 (1,237:140,203)	4,424 (360:10,067)	22,250 (3,584:601,162)
Extant records with lat/long and year	8,921 (4,170:55,810)	4,462 (1,454:42,900)	5,403 (510:11,513)	2,551 (251:15,052)	13,448 (1,267:319,940)
Records between 1970-2000	6,122 (606:16,850)	3,960 (606:12,724)	5,894 (141:37,402)	903 (139:1,666)	13,732 (564:103,512)
Unique records within the study area	363 (54:884)	346 (28:942)	453 (59:1,427)	77 (58:95)	878 (106:5,312)
Training records	139 (20:341)	126 (10:363)	174 (22:552)	29 (20:38)	335 (42:2,055)
Testing records	224 (34:534)	221 (18:579)	279 (37:875)	48 (38:57)	544 (64:3,257)

Table 1.3. Protected and Unprotected Refugial Areas. Key findings of comparison of protected (PA) to unprotected areas (UA) within the Appalachian Ecoregion from 1970-2040 by average per mammalian order for the low temperature/low precipitation scenario in a less intense emission scenario (low; SSP 2-4.5 GCM CNRM-CM6-1) evaluated in this study, and a higher emission high temperature/high precipitation scenario (high; SSP 3-7.0 GCM CanESM) evaluated in this study. Additional data are available in Supplementary 2 of individual species in both scenarios.

Order	Climate change scenario	% and area expansion in PA	% and area expansion in UA	% and area of stability in PA	% and area of stability in UA	% and area of contraction in PA	% and area of contraction in UA
Carnivora	Low	3% 1,220 km^2	3% 5,849 km^2	96% 38,124 km^2	95% 216,682 km^2	4% 1,417 km^2	5% 11,317 km^2
	High	2,252 km2 6%	8,301 km2 4%	37,260 km2 93%	204,713 km2 92%	2,792 km2 7%	18,595 km2 8%
Chiroptera	Low	1,125 km2 3%	10,359 km2 6%	40,050 km2 95%	160,113 km2 95%	1,996 km2 5%	8,864 km2 5%
	High	2,922 km2 7%	20,349 km2 12%	40,412 km2 95%	154,444 km2 92%	2,079 km2 5%	14,042 km2 8%
Eulipotyphla	Low	1,184 km2 2%	13,342 km2 6%	47,073 km2 96%	215,703 km2 95%	1,984 km2 4%	10,497 km2 5%
	High	2,270 km2 5%	13,311 km2 7%	48,875 km2 99%	189,996 km2 94%	568 km2 1%	12,233 km2 6%
Lagomorpha	Low	2,236 km2 45%	3,384 km2 1%	4,815 km2 97%	269,891 km2 99%	174 km2 3%	2,302 km2 1%
	High	1,181 km2 23%	496 km2 <1%	4,020 km2 79%	234,553 km2 86%	1 071 km2 21%	37,304 km2 14%
Rodentia	Low	1,841 km2 4%	11,096 km2 6%	41,542 km2 96%	176,241 km2 96%	1,560 km2 4%	7,710 km2 4%
	High	1,704 km2 4%	11,577 km2 6%	40,620 km2 93%	173,589 km2 95%	2,866 km2 7%	9,987 km2 5%

FIGURES

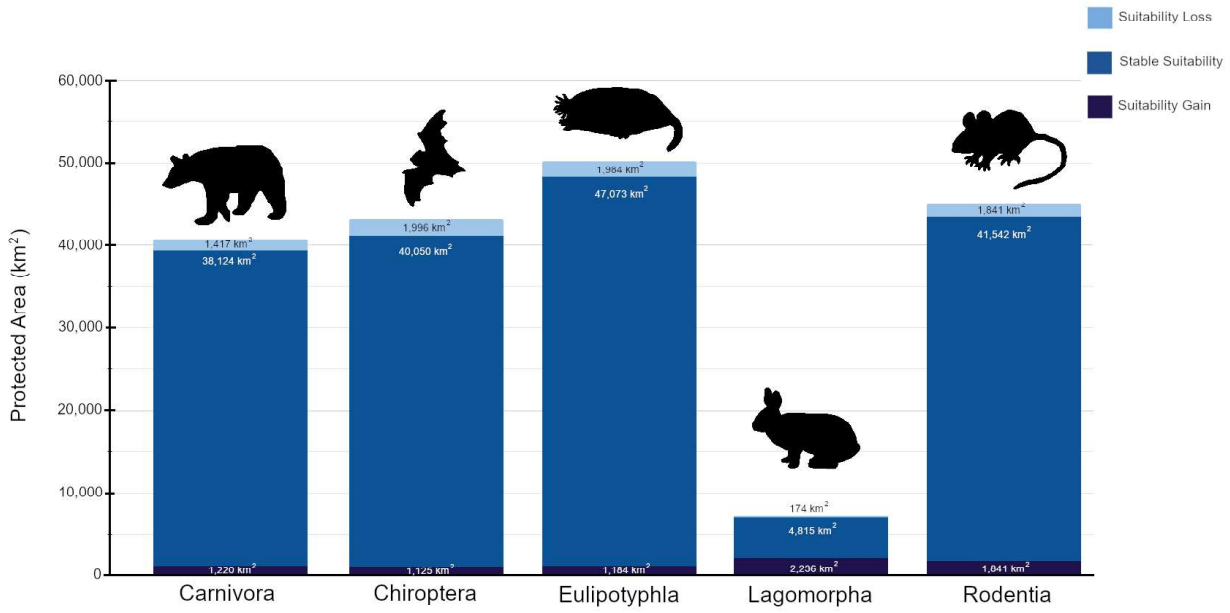


Figure 1.1. Climate Change by Family. Estimated climatic loss, stability, and gain between the baseline (1970-2000) and future (2021-2040) climatic conditions for 48 mammalian species of greatest conservation concern from the Appalachian ecoregion in the eastern United States. The analysis was restricted to protected areas and estimates were averaged by mammalian order. The suitability projections were estimated for a low intensity greenhouse gas emissions scenario (SSP 2-4.5), combined with CNRM-CM6, a Global Circulation Model that forecasted the least changes in temperature and precipitation of eight models examined in this study.

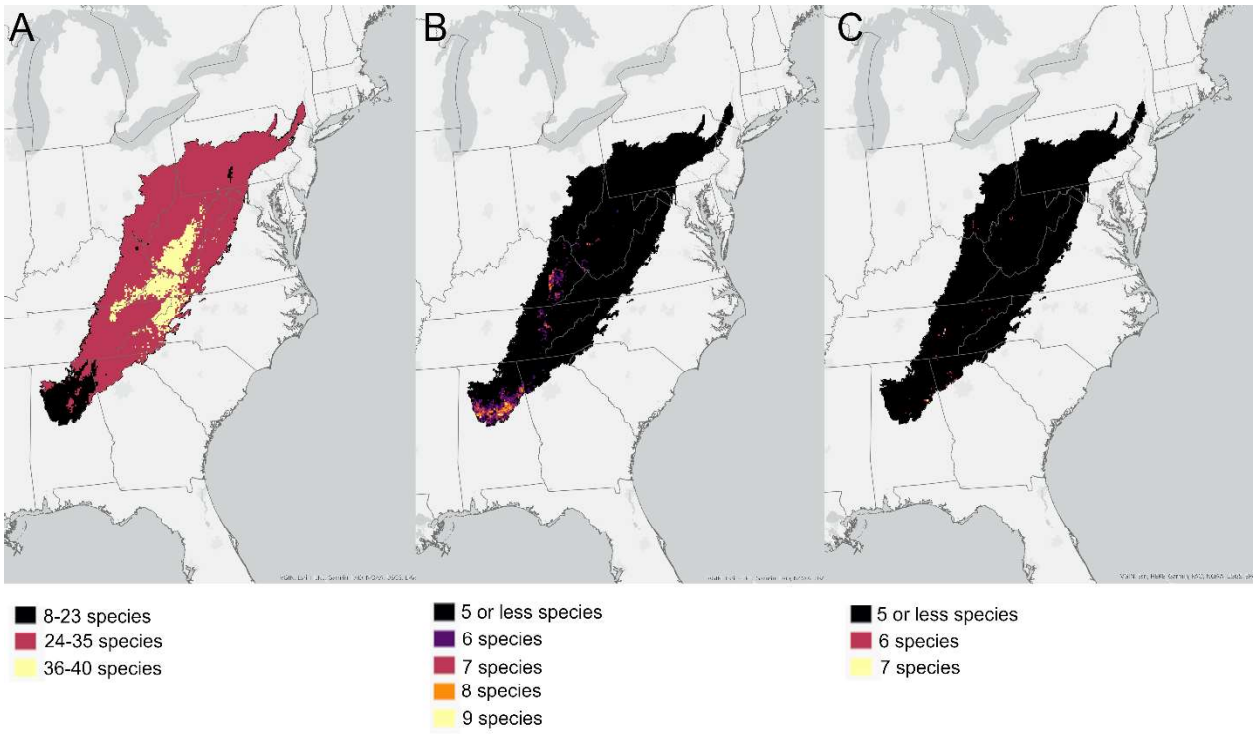


Figure 1.2. Consensus of Climate Change. Consensus of potential distribution estimates for Appalachian mammalian species under a scenario of lower intensity climate change. A. Consensus of climatic stability with yellow representing 75% or greater species overlap (a biodiversity hotspot; maximum 40 species), red representing 50% species overlap or greater, and black representing fewer than half of the species (minimum of 8 species). B. Consensus for expansion of climatic suitability, with at most 19% of examined species overlapping (9 species maximum), indicating a lack of an expansion hotspot. C. Consensus for contraction of climatic suitability, with a maximum of 14% (7 species) overlapping in an area of contraction, indicating low risk of species experiencing climatic contraction.

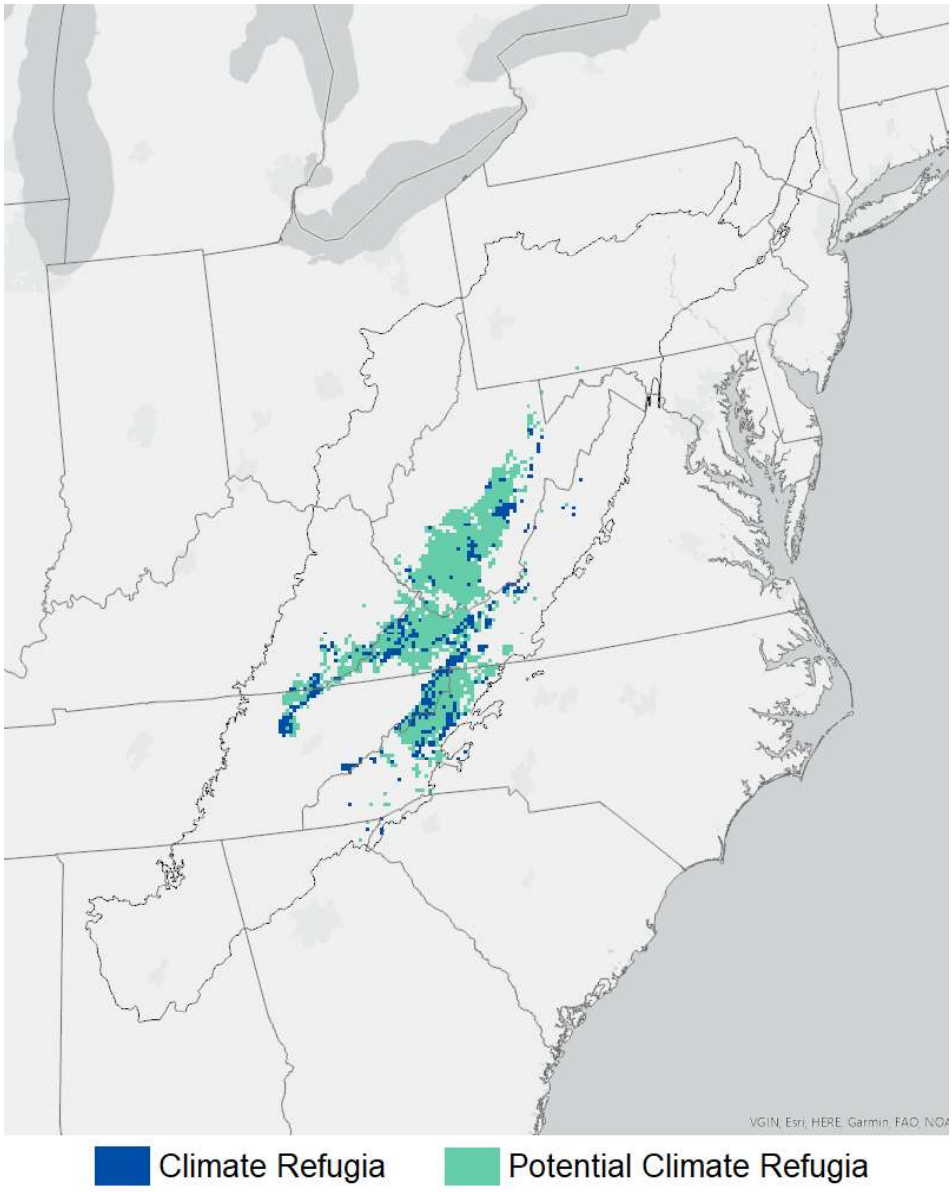


Figure 1.3. Climate Refugia of the Appalachian Ecoregion. Consensus of climatically stable areas for mammalian species across Shared Socioeconomic Pathways and Global Circulation Models within the Appalachian Ecoregion. Areas in blue represent refugia, which are protected areas with stable climate and suitable land cover for 75% of species of greatest conservation need. Light green shows unprotected areas with suitable land cover for 75% of species of greatest conservation need, representing potential refugia and target areas for private land partnerships and outreach.

CHAPTER II:

A RIGHT OF PASSAGE: REFUGIAL CORRIDORS AND WILDLIFE CROSSINGS IN THE APPALACHIANS

ABSTRACT

Given the rapid rate of changing climate, identification and preservation of stable regions of climate refugia has become a global priority for researchers and practitioners alike. However, concerns have been raised about loss of connectivity between key refugial areas globally, as relict ecosystems are at risk of being lost or experiencing severe inbreeding depression at best. One such region, the Appalachian Mountains of the eastern United States, is predicted to maintain stable climate refugia through at least 2040, growing populations in the region are encroaching on these refugia. To address these concerns, we used ecological niche modeling and least cost pathways to identify key climate refugia and corridors for maintaining connectivity. We focused on rodents, the largest group of mammals in the Appalachians, given their close ties to ecosystem composition and health, as well as their diversity of life histories. Past research has utilized charismatic flagship species for conservation and gaining public interest, therefore we chose to compare the designation of refugia and corridors based solely on the one remaining large mammal iconic of the Blue Ridge and Appalachia, the American black bear. Results highlighted that though the bear's refugia and corridors encompassed the majority of the rodents in the region, for specific planning of wildlife crossings and protection of key corridors a multi-species approach including non-generalist taxa should be utilized. This approach to corridor planning for connecting refugia can be used in other geographic regions globally. With this approach, taxa that are often overlooked but critical to certain rare ecosystems will be included in planning that needs to occur prior to beginning road construction projects. To illustrate this possibility and to aide in conservation decision making in the south-central Appalachians, we identified three key areas of interrupted corridors for the overwhelming majority of rodents on I-26 and I-40 in the Blue Ridge (Tennessee and North Carolina), and I-75 in the Central Appalachians (Tennessee) and recommend surveys for incorporation of new wildlife

overpasses/underpasses and/or modification of existing structures. In doing this, we aim to provide key information for planning to help mitigate vehicular collisions with large taxa, facilitate movement of small species unable to cross surfaces with large swaths of concrete median, and promote connectivity of stable climate refugia in a key biodiversity region of the United States.

INTRODUCTION

Anthropogenic climate change is an active threat predicted to cause high extinction rates due to temperatures rising to levels that haven't been present since the Eocene Epoch 40 mya (Houghton et al., 2001; Thomas et al., 2004). In response, a number of species have shifted their ranges in latitude, elevation, water depth or towards buffered microhabitats (Moritz et al., 2008; Parmesan & Yohe, 2003; Pelini et al., 2011; Perry et al., 2005; Spence & Tingley, 2020). A meta-analysis by Parmesan and Yohe (2003) focuses on global trends, noting that across taxa the average shift of a species range was 6.1 km towards higher latitudes and 6.1m higher in elevation per decade. However, a major pitfall to shifting to track suitable climate is habitat fragmentation, which can both lessen the overall availability of suitable habitat and increase distance between suitable patches (Gibson et al., 2013; Synes et al., 2020; Travis, 2003). Indeed, it has been predicted that in the Appalachians, many species that are already dispersal limited, such as moles, shrews, and rodents, may be further impacted by extensive areas of anthropogenic land use (Parmesan & Yohe, 2003).

Rodents play key roles in every ecological system in which they are found, with a number considered keystone species or ecosystem engineers (Jones et al., 1994, 1997), having disproportionate impacts on the landscape around them and the species that inhabit them. For example the American beaver (*Castor canadensis*) facilitating emergent wetland habitat, prairie dogs (*Cynomys spp*.) increasing diversity of the flora in arid landscapes, or ground squirrels supporting entire carnivoran food webs in Idaho (Davidson et al., 2008; Miller et al., 1994; Power et al., 1996; Whicker & Detling, 1988; Wright et al., 2002). Rodents can also significantly alter ecosystems through seed dispersal (often through caching) and consumption of plants (increasing diversity), spread of fungi and mycorrhizae (the latter particularly by fungal specialists such as *Tamiasciurus* and *Clethrionomys*), aeration of the soil both below ground and

along the surface, and facilitate nutrient cycling and mineral turnover through decomposition of old vegetation and waste excretion (Dickman, 1999; Godó et al., 2022; Lacher et al., 2016; Stephens & Rowe, 2020; Yensen & Hafner, 1998). Though, large mammals are often predicted to be more at risk due to slower reproductive rates and greater resource requirements, consideration should also be given to those with low dispersal traits (Isaac, 2009; Morrison et al., 2018). In choosing rodents, despite their fast reproduction, we accounted for elusive, small, dispersal limited taxa tied to rare ecosystems (e.g. Appalachian balds, Appalachian spruce-fir forests) that would be dispersal limited, with the assumption that many of these taxa serve as a "best case" persistence scenario for taxa that reproduce/adapt more slowly in those systems. Loss of rodent diversity can have profound impacts on a region, particularly given the cascading trophic effects that could cause the direct extinction of other species (Hafner et al., 1998; Lacher et al., 2016; Yensen et al., 1992; Yensen & Hafner, 1998). Of concern are rodent species of greatest conservation need threatened by climate change, especially those in relict systems such as the Appalachian boreal forests.

In a time of rapid climate change, connectivity of refugia (=suitable persisting habitats) and dispersal to these refugia is another challenge faced by rodents, if not all taxa. Unfortunately, natal dispersal distance (hereafter referred to as "dispersal distance") is often poorly known in small mammals, though typically dispersal distance of North American mammals typically correlates to both body size and home range size (Bowman et al., 2002; Sutherland et al., 2000; Van Vuren, 1998; Whitmee & Orme, 2013). Whitme and Orme (2013) noted strong trends in dispersal ability and phylogeny as well. A number of small rodents (<100g), e.g. arvicolines, occupy only a few hundred square-meter home ranges within their entire life (Le Galliard et al., 2012). The mean dispersal distance based on the literature review of Le Galliard et al (2012)

suggests that though capable of dispersing into the multi-kilometer range each year (the bulk of studies showed dispersal of small rodents as less than 1km per year), the mean yearly dispersal distance of small rodents such as the arvicolines to be closer to 10 meters. However, it should be noted that a number of small rodents will also produce more than one liter per year, enabling a number of dispersal events (Le Galliard et al., 2012). A key problem facing rodents, like many other taxa, is growing anthropogenic disruption of the landscape (e.g. roadways, urban sprawl, removal of native land cover), which is thought to be a compounding factor to geographic isolation of populations, particularly for small mammals (Brunke et al., 2019; Chambers & Garant, 2010; Ćosić et al., 2013; Lugon-Moulin & Hausser, 2002; Segelbacher et al., 2010). Barriers to dispersal are a major concern because populations can become isolated and experience inbreeding depression if not genetically rescued (Ćosić et al., 2013; Frankham, 2015; Pertoldi et al., 2007; Ralls et al., 2020; Tallmon et al., 2004). Prior to reaching this level of genetic isolation, an alternative is to try to bridge these populations utilizing wildlife corridors (Gracanin et al., 2023; Shafaghat et al., 2022; Thapa et al., 2018).

Wildlife corridors can be defined as habitat allowing dispersal between otherwise isolated ecological areas (Hamaide et al., 2022; Liu et al., 2018; Loro et al., 2015; Newmark, 1993). In addition to providing means of dispersal to suitable habitat in an increasing anthropogenic landscape, wildlife corridors are also key to connecting persisting suitable habitats (=refugia) in the face of global climate change (Carroll, 2010; Lawler et al., 2013, 2015; McKinley et al., 2019; Minor & Lookingbill, 2010; Zhu et al., 2021). Indeed, Lawler et al. (2013) identified the Appalachian Mountains (hereafter Appalachians) as a key dispersal route in the western hemisphere for a number of vertebrate taxa in the face of climate change at coarse resolution (i.e. 50 km grids). Zhu et al. (2021) conducting a study at finer resolution (i.e. 1 km), and found this

region to have a high percentage of protected areas overlapping with high diversity of species richness across vertebrate taxa, even into the future (2070), ideal for the placement of wildlife corridors (Hamaide et al., 2022; Liu et al., 2018; Loro et al., 2015; Newmark, 1993). It has also been stressed that when planning for wildlife corridors, the goal should be to physically connect designated protected patches together through means such as wildlife overpasses, underpasses, and bridges; as opposed to placing an overpass that leads to unprotected land that could easily end up developed urban landscape (e.g. a subdivision) (Beier & Loe, 1992).

Corridors for wildlife and climate corridors have been studied at the continental scale (e.g., McGuire et al., 2016; Nuñez et al., 2013; Rose & Burton, 2009) and at regional and localized scales (e.g., Alexander & Waters, 2000; Erb et al., 2012; Wilson & Belote, 2022). Our study focuses on the Appalachians as known climate refugia at the regional level and includes a diverse and representative group for mammals, both well-studied and cryptic taxa, for comparison to other taxonomic groups in the region. The potential climate refugia for mammals were estimated for near future climatic conditions (2040s). We take a regional connectivity approach in identifying specific sites for climate connectivity corridors by modeling where refugial patches within the region could be found as well as overlap with a charismatic flagship species, making this a novel method for providing specific corridor advice in the region. Much of this type of work has been conducted globally (e.g., Denneboom et al., 2021; Glista et al., 2009; Mata et al., 2008; Olsson et al., 2008; Pell & Jones, 2015), as well as in the western United States (e.g., Barnick et al., 2022; Caldwell & Klip, 2020; Gloyne & Clevenger, 2001; Huijser et al., 2016; Mccollister & Van Manen, 2010) and has shown that corridors have been used by a wide diversity of taxa of varying sizes to cross otherwise impenetrable sections of major roadways. In the eastern United States, wildlife corridors are becoming more common (Austin &

Garland, 2001; Donaldson, 2007; Jones et al., 2008; Parker et al., 2011), with successful implementation in Florida connecting habitat for large charismatic species such as the federally listed Florida Panther (*Puma concolor coryi*) (Beckmann et al., 2012; Foster & Humphrey, 1995; Shepherd et al., 2023). As a result of public outcry, there is interest in the Appalachians to implement more corridors, particularly in the Blue Ridge (https://smokiessafepassage.org/); this study may assist corridor planning by providing another metric for identifying optimal areas for placement, which has been met with enthusiasm by stakeholders (e.g. National Parks Conservation Association and The Nature Conservancy) in the region.

Given the key role of the Appalachians as climate refugia for relict boreal species and endemics (see Chapter 1; Berry & Smith, 2013; Browne & Ferree, 2007; Cartwright & Wolfe, 2016; Graham et al., 2010; Gross, 2010; G. Hewitt, 2000), connectivity on the landscape and establishing wildlife corridors is of the utmost importance (Anderson et al., 2015; Anderson et al., 2023). For this study, we investigate whether protecting climate refugia for charismatic flagship species secondarily aids in the conservation of more rare and elusive species that have important ecological roles. To do this we analyzed the degree of overlap between stable climate refugia for a flagship species (the American black bear, see below) and rodent species within the Appalachian Ecoregion. We also investigated whether major road systems in the Appalachians could impede movement of species with limited dispersal abilities attempting to track geographic shifts of their climate suitability. To do this, we identified key refugial parcels for each rodent species, and determined whether roads intersected potential corridors between these refugial areas.

METHODS

Study area and species data

The potential for stable climate refugia (Chapter 1), combined with existing large protected areas in a landscape matrix of agriculture and urban areas makes the Appalachians an ideal candidate region for wildlife corridors. Our study area was represented by Level II Ozark, Ouachita-Appalachian Forest as defined by the Environmental Protection Agency (EPA) that comprises the Appalachians as the "Appalachian Ecoregion" (Commission for Environmental Cooperation, 1997).

Similar to global trends, the order Rodentia is the most specious mammalian group (28 species) within the Appalachian Ecoregion (78 species total); five families and seven subfamilies of rodents are represented in the region. These species range in ecology from habitat generalists such as the deer mice (*Peromyscus maniculatus)* to habitat specialists such as the Allegheny woodrat (*Neotoma magister*) and have adapted to diverse lifestyles, from semi-fossorial ground squirrels to the semi-aquatic beaver and muskrat to arboreal gliding flying squirrels. Of these Appalachian rodent species, 16 are found on at least one State Wildlife Action Plan (SWAP) list of species of greatest conservation need. The ranges of three federally listed subspecies, *Glaucomy sabrinus coloratus, Microtus chrotorrhinus carolinensis,* and *N. floridana haematoria*, overlap with the Appalachian Ecoregion (Appendix II: Table 2.1).

We selected a charismatic species, the American black bear (*Ursus americanus*) for comparison of climate refugia and corridor needs with our focal group of rodent species. The American black bear is a generalist species from the order Carnivora and is listed on SWAPs for three states in the Appalachian Ecoregion. Additionally, the American black bear has gained considerable media attention with videos emerging of bears with cubs struggling to cross

Interstate-40 along the edge of the Great Smoky Mountains National Park, thus strengthening the case for corridors to connect the remaining habitat patches for this species.

We included in our study all rodent subspecies overlapping the Appalachian Ecoregion and the larger EPA Level I Eastern Temperate Forest and Northern Forest Ecoregion, to account for possible links with populations and regions outside of our study area. We downloaded occurrence data for these 29 species (28 rodents and the bear; Appendix II: Table 2.1) from GBIF and VertNet, and cleaned, geographically clipped, and temporally aligned the data following the procedures used in Chapter 1.

Climate Data

To determine stability of climate into the future, we followed standard methodology: we utilized the 19 bioclimatic variables from WorldClim 2 representing current (baseline) temperature and precipitation variables for 1970-2000 (https://www.worldclim.org/data/index.html) and future climate projections at the finest available resolution from the newest of the Climate Model Intercomparison Project (CMIP) 6 (2.5 arc minute resolution; ~5 km) (Fick & Hijmans, 2017). We used standard future climatic variables, representing two middle-of-the road emission scenarios (SSP 2-4.5 and 3-7.0) for greenhouse gases and three Global Circulation Models representing a range of warmer/wetter and cooler/drier scenarios (CNRM-CM6-1, CNR-ESM2-1, and CanESM) to predict climate refugia into 2040 (Fick & Hijmans, 2017).

Ecological niche modeling parameters and evaluation

To generate ecological niche models and estimate current and future potential distributions, we used Maximum Entropy (Maxent) machine-learning algorithm given its versatility and widely accepted use (Elith et al., 2011; see Chapter 1). In Chapter 1, we ran

models for 23 rodent species of greatest conservation need (SGCN) and for the American black bear. In this chapter we used the same modeling parameters as in Chapter 1 for five additional rodent species occurring in the Appalachian Ecoregion (*Castor canadensis, Marmota monax, Ondatra zibethicus, Sciurus carolinensis,* and *Sigmodon hispidus*). Lastly, to improve model performance, we applied a more standard model training approach for four rodent SGCNs with restricted ranges and few occurrence points (*M. chrotorrhinus, Reithrodontomys humulis, Synaptomys cooperi,* and *Zapus hudsonius*) by utilizing all occurrence data to train and test the model through crossvalidation, rather than selecting data to train and test the model based on climatic heterogeneity. These species have narrow ranges and limited occurrence data; thus we ran five crossvalidation iterations with all occurrence data and obtained models with higher performance (as measured by AUC and omission error). The resulting models were then overlaid to produce a consensus climate model showing stability from the baseline into the future across climate scenarios (SSP and GCM). These consensus models were considered "stable climate refugia" throughout the manuscript. The consensus models represent a conservative estimate of stable climate refugia. This is less problematic for those species with a high degree of connectivity between source refugia but is worth keeping under consideration for taxa with a more uncertain climatic future with less consensus (see Chapter 1 for extent of predictions by scenario relative to consensus models).

Land cover, protected areas, and primary roadways

We refined climate suitability estimates for stable refugia by excluding areas on the landscape that would be difficult for the vast majority, if not all species, to disperse through or inhabit for a prolonged period of time based on land cover type and species' habitat requirements (Brunke et al., 2019; Dewitz, 2021; Emmons, 2000; Kuefler et al., 2010; Wells et al., 2006).

Following the methods of Chapter 1, we removed developed areas, barren spaces, cropland, hayfields, and pasture from the National Land Cover Database (Dewitz, 2021) because we assumed that these areas are unsuitable for long term stability of the species studied. The class "open water" was retained only for semi-aquatic rodent species, for which we buffered open water and wetlands by 0.5 km. The buffer was necessary, albeit erring on the side of overestimation, to encompass shorelines and account for fluctuations in the water table, as well as to allow for dispersal between patches of wetland and open water areas (Cotner & Schooley, 2011; Cox & Nelson, 2009; Eubanks et al., 2011; Nadeau et al., 1995; Wang et al., 2019). We used the United States Geological Survey's (USGS) Protected Area Database of the United States (PAD-US; U.S. Geological Survey, 2022) to identify where protected areas overlap with these rodents, following Chapter 1, where we assume stable climate, suitable landcover, and protected land constitute highest likelihood of persistence for a species. Additionally in this chapter, we documented these protected climate refugia that were in close proximity (1 kilometer or less) to a key dispersal barrier for species, primary roadways (Brunke et al., 2019; Chambers & Garant, 2010; Ćosić et al., 2013; Lugon-Moulin & Hausser, 2002; Segelbacher et al., 2010). Primary roadways (=Interstates and Major US Highways) were derived from the United States Census Bureau 2021 TIGER/Line Primary Roads shapefile for the Appalachian Ecoregion (U.S. Census Bureau, Geography Division, 2021). We then buffered by 1 km each greater urban area derived from the U.S. Census Bureau's TIGER/Line Urban Areas shapefile (U.S. Census Bureau, Geography Division, 2020) to determine areas of overlap with hotspots and priority areas for 2022 for major cities in the region with populations over 50,000 (U.S. Census Bureau, Population Division, 2023).

Identifying climate connectivity

Given the variability in body size and dispersal ability of rodents, we assessed separately for each species the feasibility of connectivity of stable climate refugia by species within the Appalachian Ecoregion by using Least Cost Pathway (LCP) analysis given its widespread use (e.g., Balbi et al., 2019; Cushman et al., 2009; Li et al., 2010; Poor et al., 2012; Pullinger & Johnson, 2010; C. Wang & Liu, 2020). We calculated the size of climate refugia patches and the distance between patches to create connectivity corridors, or the shortest and easiest traversal paths. Individual refugial patches were sorted by size (sq km) and binned, with the top 75% of size distribution values kept and identified as "core refugial patches" (a necessity for LCP; e.g. see Belote et al., 2016 or Alexander et al., 2016). The centroid for each patch was used in corridor calculations in ArcGIS Pro v3.2, under the assumption that the centroid was less susceptible to leading/trailing edge effects beyond the 2040 time frame (Garden et al., 2015; Hagerty et al., 2011; Heintzman & McIntyre, 2021; Koen et al., 2014; Parra-Olea et al., 2012; Skov & Svenning, 2004). Leading edge effects of phylogeography are long-distance or rare dispersal events that lead to colonization of novel areas, whereas trailing edge effects are remnant populations in areas quickly deteriorating in climate and habitat suitability (Bennett et al., 1991; Davis & Shaw, 2001; Hampe & Petit, 2005; Hewitt, 2000; Hewitt, 2004) The largest core refugial patch was considered as the primary refugial "source" relative to the network of all core refugial patches.

To estimate landscape resistance to the movement for each species, we considered two characteristics: climatic suitability and land cover type (from the NLCD dataset). We classified climatically unsuitable cells as difficult to traverse (high resistance, value of 9), and climatically suitable cells as easily traversable (no resistance, value of 1). For land cover we created a gradient of resistance values from 1 (least resistant; e.g., forest cover) to 9 (most resistant; e.g.

high intensity development; see Appendix II: Supplementary 2.1; Chapter 1 accompanying *Mammalian Species* accounts). We created two separate land cover dispersal rasters: one for aquatic/semi-aquatic obligates (*C. canadensis, O. zibethicus,* and *Oryzomys palustris*) and the other for terrestrial species. We added the climatic and land cover resistance rasters in ESRI ArcGIS Pro v.3.2 to produce an overall "travel cost raster" with values ranging from 2 representing areas of easiest traversal (suitable climate and least resistant land cover) to 18 showing areas nearly impossible to move through (unsuitable climate and most resistant land cover).

A combination of the travel cost raster and the source refugial patches was used to calculate the output distance raster (=the least cost distance between each cell based on the lowest accumulative cost from the source) and path direction raster (=the direction to the neighboring cell when retracing the shortest path to the source based on lowest accumulative cost) utilized in calculating the distance accumulation of a species through the Distance Accumulation tool in ESRI's ArcGIS Pro v.3.2. This was then utilized to calculate the least cost corridor between the main refugial source and other sources of refugia that were smaller in size. The final outputs were both lines and a raster showing overlapping optimal connectivity corridors between key climate refugial patches by each 5 km raster cell. We made the assumption that this output distance raster shows the "best case scenario" for connectivity and potential dispersal between stable climate refugia in the future, with the acknowledgement that there are a multitude of travel corridors and dispersal routes between different edges of suitable habitat that could be utilized. We buffered the core refugial areas by 10km, 30km, and 50km for all rodents, given that most rodents are small and tend to move under 1 km per year; the two larger extents (30km and 50km) account for larger rodents (porcupines and beavers) and the rare

possibility of a long distance dispersal event through the 2021-2040 period (Bowman et al., 2002; Le Galliard et al., 2012; Littlefield et al., 2019; Sutherland et al., 2000; Van Vuren, 1998; Whitmee & Orme, 2013). Each core possesses a ring that indicates distance from the surrounding core climate refugia areas, with the assumption that refugial areas separated by >50km may represent sink subpopulations, whereas areas within 10 km or less could likely be targeted for mammalian stepping stones to maintain population connectivity (Bowman et al., 2002; Le Galliard et al., 2012; Littlefield et al., 2019; Sutherland et al., 2000; Van Vuren, 1998; Whitmee & Orme, 2013). Distances 30-50km or greater should be considered low probability of maintaining connectivity among populations, thus higher likelihood of these populations becoming isolated. For comparison, the 10, 30, and 50 km buffers were placed around *U. americanus* core refugial areas, however it should be noted that a bear can easily travel over 100 km and should be assumed as close to "unlimited dispersal". Lastly, our predictions led us to set the following criteria for this particularly study to determine species "at risk" to fragmentation and potential climatic isolation: 1) core climate areas, excluding land cover, should consist of an area of at least 100,000 square kilometers; and 2) distances between fragmented core areas should be minimal relative to the size of the species in question given the small home ranges and poor dispersal ability of most of these animals (i.e. arvicoline rodents should have core refugial parcels within 10 kilometers of one another to maintain some climate connectivity). The first criterion of 100,000 square kilometers is slightly less than a third of the area of the Appalachian Ecoregion (Beier & Loe, 1992), and this value also was a natural delineation in the amount suitable climate among taxa falling well above this area; for some species the value was smaller, around 50,000 square kilometers, and a few taxa were below 10,000 square kilometers, particular species that are known to be restricted climatically and in habitat use. The second criterion is tied

directly to the size and dispersal ability that varies by species, with distance between core refugia preferably adjacent, but noting that this distance may be traversable if it falls within the formula proposed by Bowman et al. (2002).

RESULTS

Taxonomic trends and refugial overlap filtering for land cover

Of the 28 rodents that occur within the Appalachian Ecoregion, 61% (17 species) are members of the family Cricetidae: 7 species are of the subfamily Arvicolinae (voles, lemmings, and muskrats), 8 species are Neotominae (North American rats and mice), and 2 species are Sigmodontinae (New World rats and mice). The next largest family within the Appalachian Ecoregion are the Sciuridae with 7 species (25%): 5 species are members of the subfamily Sciurinae (tree squirrels) and the other 2 species are Xerinae (ground squirrels). The remaining families occurring within the Appalachian Ecoregion are Castoridae (1 species), Erethizontidae (1 species), and Zapodidae (2 species). Of the federally listed taxa, 2 are cricetids (1 arvicoline and 1 neotomine), whereas the other is a sciurine.

Stable climate refugia overlapping suitable land cover for the family Ursidae occupies 65% of the Appalachian Ecoregion (Appendix II: Figure 2.1; Supplementary 2.2). By individual family average, *U. americanus* occupies 48% of climate refugial areas of Castoridae, 93% of Erethizontidae, 82% of Cricetidae (subfamilies: 80% of Arvicolinae, 88% of Neotominae, and 61% of Sigmodontinae), 88% of Sciuridae (subfamilies: 88% of Sciurinae and 90% of Xerinae), and 92% of Zapodidae. Inversely, the proportion of *U. americanus* climate refugial area occupied by the families are <1% by Castoridae, 41% by Erethizontidae, 48% by Cricetidae

(subfamilies: 51% by Arvicolinae, 54% by Neotominae, and 13% by Sigmodontinae), 79% by Sciuridae (subfamilies: 77% by Sciurinae and 84% by Xerinae), and 50% by Zapodidae.

At the species level (Appendix II: Supplementary 2.3 and 2.4), *U. americanus* has low overlap (<50%) with the following climate refugial area of the following taxa: the sigmodontine *O. palustris*, the cricetid *O. zibethicus*, and the castorid *C. canadensis*. *Ursus americanus* had moderate overlap (50-75%) with the climate change refugia of the arvicoline *M. chrotorrhinus* and the neotomine *P. polionotus*; whereas all other taxa fell within the high overlap category (>75%). Inversely, the species with extremely low overlap (<10%) of the climate refugial area of *U. americanus* were: the sigmodontine *O. palustris*, the castorid *C. canadensis*, the arvicolines *M. chrotorrhinus* and *O. zibethicus*, and the neotomine *P. polionotus*. Species with low overlap (10-49%) included: the neotomines *R. humulis* and *P. gossypinus*, the sigmodontine *S. hispidus*, the arvicoline *M. ochrogaster*, the zapodid *Z. hudsonius*, and the erethizontid *E. dorsatum.* Moderate overlap (50-75%) of the climate refugial area of *U. americanus* occurred in the neotomines *Ochrotomys nuttalli, N. magister,* and *N. floridanus*, the arvicoline *C. gapperi*, the zapodid *N. insignis*, the sciurines *G. sabrinus*, *G. volans*, *S. niger*, and *Tamiasciurus hudsonicus*, and the xerine *Ma. monax*. Species with high overlap (>75%) were the arvicolines *S. cooperi, M. pennsylvanicus,* and *M. pinetorum,* the xerine *Tamias striatus*, the sciurine *S. carolinensis*, and the neotomines *P. maniculatus* and *P. leucopus*.

We created an overlay of stable climate refugia for all rodent species in the Appalachians, which ranged in overlap from 2-23 species (Appendix II: Supplementary 2.5). Areas with the most species overlapping within the Appalachians can be found in the following EPA Level III ecoregions: the Blue Ridge along the Tennessee-North Carolina border, the Southwestern Appalachians along the Tennessee-Kentucky border, throughout the Central Appalachians, and

the Ridge and Valley of southwestern Virginia. In terms of refugial "hotspots" for rodents in the Appalachians, we used the same definition as in Chapter 1, and kept 75% of total possible rodent overlap (17 species or more; 127,820 km²) to be considered for conservation, with areas of 90% overlap (21 species or more; 75% of total rodent species in the Appalachians; 7,249 km²) to be targeted as "priority areas" for refugia (Appendix II: Supplementary 6). Of the 127,820 km² of rodent climate refugia hotspots (including suitable land cover) in the Appalachian Ecoregion: 34% can be found in the Central Appalachians; 31% in the Ridge and Valley; 17% can be found in the Blue Ridge; 12% in the Western Allegheny Plateau; and 5% in the Southwestern Appalachians.

Priority areas (21 or more species overlap) occupy 7,249 km², or 2%, of the Appalachian Ecoregion, distributed as follows: 45% occurs in the Central Appalachians; 40% in the Blue Ridge; 11% in the Ridge and Valley; 4% in the Southwestern Appalachians; and no areas with 21 rodent refugia or more overlapping in the Western Allegheny Plateau. Most of these 21+ species priority areas can be found in the Central Appalachians and the Blue Ridge, which are comparable in size and together comprise 85% of all priority areas. The Ridge and Valley (11%) is followed by the Southwestern Appalachians distantly, with the Western Allegheny Plateau containing no priority refugial areas under this criteria. At most, 6% of the total land area of the Blue Ridge falls under the priority area criteria, followed by 5% of the Central Appalachians. The Southwestern Appalachians and Ridge in Valley, comparably, both have <1% of their total land area as priority areas. Finally, to compare overlap, we overlaid these rodent refugial hotspots and priority areas with the stable climate refugia of *U. americanus* to determine which areas the charismatic species could be most useful as a "flagship species" for conserving the more cryptic rodents (Appendix II: Figure 2.2). *Ursus americanus* overlapped with 89% of

refugial hotspots and 97% of priority areas; whereas the refugial hotspots occupied 50% of the climate refugial area of *U. americanus* and priority areas occupied 3% of *U. americanus*' climate refugial area.

Roadways and urban areas as barriers to dispersal on the landscape

Of the 15,666 km² of the 1 km buffered interstate and primary roads crossing the Appalachian Ecoregion, 42% overlap with the climate refugia of *U. americanus,* 22% overlap with rodent refugial hotspots, and less than 1% overlap with priority areas. There are 12 major cities with populations above 50,000 within the Appalachian Ecoregion: Birmingham, AL; Asheville, NC; Knoxville, Chattanooga, Johnson City, and Kingsport, TN ; Allentown, Reading, Scranton, Harrisburg, and Pittsburgh PA; and Roanoke, VA (U.S. Census Bureau, Population Division, 2023). Of these U.S. Census defined metropolitan areas, *U. americanus* climate refugia overlap with all of them to some degree. Rodent refugial hotspots overlapped with Asheville, Johnson City, Kingsport, Roanoke, Pittsburgh, Reading, Allentown, and Scranton; and rodent priority areas only overlapped with a portion of the eastern Asheville metropolitan area.

Given that protected areas often serve as refuge from habitat loss and certain disturbance events, we evaluated the degree of overlap of protected climate refugia with primary roadways within the Appalachian Ecoregion. It is worth noting that 1,015 km² of primary roadways intersect with protected areas of the Appalachian Ecoregion (Appendix II: Supplementary 2.7). Of this area, 60% (604 km²) overlapped with *U. americanus* climate refugia, 47% (476 km²) overlapped with rodent refugial hotspots, and less than 1% (4 km²) overlapped with rodent refugial priority areas. A particular focus was given to practicality and feasibility of planning for mitigating the negative effects of roads in the priority areas of overlap (90% or greater; 21 or more species). These priority areas occurs in three regions: the first and largest priority area is

bisected by Interstate-26 (I-26) at the Tennessee-North Carolina border at the intersection of Cherokee National Forest in Unicoi County, TN and Pisgah National Forest in Madison County, NC; the second smaller priority area is adjacent to Interstate-75 (I-75) overlapping the Royal Blue Unit of the North Cumberland Wildlife Management Area in Campbell County, TN; and the smallest priority area is in close proximity to I-40 in Buncombe County Park in Buncombe County, North Carolina. In comparison, *U. americanus* has stable climate refugia within protected areas overlapping interstates in an area of 604 km². Overlap of these areas with rodent hotspots was 80% (380 km²), and with rodent priority areas 100% of the time (4 km²) (Appendix II: Figure 2.3; Supplementary 2.8).

Connectivity of core climate refugia

We mapped climate connectivity between the largest "core" areas of contiguous stable climate refugia for all species (Supplementary 9). Our models predict that most rodent species were to maintain a high degree of contiguous stable climate through the 2021-2040 period. Eight species (29% of the rodents in the Appalachian Ecoregion) were predicted to be susceptible to climatic isolation in the 2021-2040 period: the castorid, *C. canadensis*; the arvicolines, *M. chrotorrhinus* and *M. ochrogaster*; the sigmodontines, *O. palustris* and *S. hispidus*; the neotomines, *P. polionotus* and *R. humulis*; and the zapodid, *Z. hudsonius* (Appendix II: Table 2.2).

Finally, we overlaid these "best case scenario" paths between refugia for each individual species, allowing us to predict trends in areas with potential for high species traffic and travel corridors. Individual least cost pathways for all taxa led to 386 potential corridors ranging in length from 5km to 1357km. We buffered by 1 km the least cost pathway of each individual species between climate refugia (typical maximum dispersal range for an individual for most of

rodents examined) and calculated the number of overlapping pathways within that 1 km buffer, with areas with 25% or more overlap (11 overlapping corridors or more) being considered as key corridor routes (Appendix II: Figure 2.4). This resulted in three major corridors running considerable contiguous distances southeast to northwest. The longest contiguous predicted corridors stretched roughly 900km from the Georgia-North Carolina border through the Blue Ridge north through the Ridge and Valley into central Pennsylvania. Consequently, this stretch also maintains the longest contiguous corridors, with several supporting over 25 intersecting pathways: most notably the 37km segment in Carter County/Johnson County (TN), 64km segment in Grayson County/Smyth County/Wythe County (VA), 67km segment in Bedford County/Blair County (PA), and 63km segment Juniata County/Mifflin County/Snyder County (PA). Additionally, the greatest number of overlapping segments also occurs in this longest Blue Ridge/Ridge and Valley Corridor, with areas in Cherokee County (NC), Carter County (TN), and Blair County (PA) having over 40 intersecting pathways. A shorter corridor in the Blue Ridge/Ridge and Valley/Central Appalachians is also present, running from northwest North Carolina roughly 260km northward to intersect with the longer Blue Ridge/Ridge and Valley Corridor and continuing northward through parts of the Central Appalachians of West Virginia and Maryland before culminating in the Ridge and Valley of southern Pennsylvania (~600km total length). A final long contiguous corridor begins in the Central Appalachians of eastern Kentucky and runs northeast 675km through the Western Allegheny Plateau of West Virginia and Pennsylvania before turning eastward through the Central Appalachians to end in the Ridge and Valley of central Pennsylvania. There were also less contiguous connectivity corridors of various lengths running from southwest to northeast: a 65 km segment from northeast Alabama into southcentral Tennessee in the Southwestern Appalachians; a 170km segment running from

the Ridge and Valley south of Knoxville (TN) to the Tennessee-Kentucky border; a 75km segment running from northcentral Tennessee in the Central Appalachians to southeastern Kentucky; a 320km segment in the Central Appalachians running from eastern Kentucky along the Virginia border into central West Virginia; and a 107km segment running from the Ridge and Valley of western Virginia northward into the Central Appalachians of southern West Virginia.

DISCUSSION

Can conservation planning for a flagship taxon account for cryptic taxa?

We found a high degree of mismatch among stable climate refugia of rodents and the flagship ursid. Our results indicate that we should plan conservation efforts around a number of overlapping taxa, rather than solely relying on a single flagship species as an "umbrella" for the region. Given the prevalence of souvenirs, signs, and advertisements in the Appalachians, one could argue that the beloved and charismatic American black bear (*U. americanus*) appears more often than not, though the other large charismatic taxon would be the newly reintroduced wapiti (*Cervus canadensis*). Either taxon could be utilized as a flagship in this instance for the region, however given the generalist nature of the wapiti, the results would likely be similar, with most of the region climatically suitable and habitat and biotic factors driving most of the distribution. It is worth noting that this study could focus on any size or group of taxa, however we specifically chose the ill-reputed but ecologically significant rodents (Bogoni et al., 2020; Corlett, 2007; Godó et al., 2022; Hafner et al., 1998; Lacher et al., 2016; Stoner et al., 2007; Yensen & Hafner, 1998) given the stark contrast to the public opinion compared to the bears. Another reason for the selection of the American black bear as our flagship species is that, ecologically, these two groups (the bears and rodents) have been documented as working in tandem to disperse seeds, rodent predation of seeds occurring less often than initially expected,

and seeds dispersed through bear scat alone germinating the less often than seeds dispersed by rodents such as deer mice (*Peromyscus*) (Enders & Vander Wall, 2012; Koike et al., 2012). This clear ecological link, as well as the rodents' roles as ecological drivers in any system they inhabit allowed their usage as a proxy for their respective habitats, particularly those with restrictive ranges (Godó et al., 2022; C. G. Jones et al., 1994; Lacher et al., 2016; Miller et al., 1994).

Reliance on this flagship species alone to designate wildlife overpasses and underpasses could lead to missed opportunities in critical areas. Given that *U. americanus* is a generalist with strong dispersal abilities, placement of corridors in high traffic interstate areas within its range and refugia would overall save money and lives, however we recommend focusing on areas within its range that are occupied by a high number of refugia for rodents in the region, some of which are federally listed. It is worth noting that many of these rodents are generalist taxa, with models being most strongly driven by restricted taxa (in terms of habitat or climatic niche). It is also important to note that these refugia were based mostly on climate with overlay of the land cover, however many of these rodents occupy small habitat structures on the landscape (e.g. *Neotoma*) that inhabit a smaller portion of the predicted refugial range (BAM model of a species' niche; e.g. (Peterson & Soberón, 2012; Soberón, 2010).

In summary, our study showed that the "flagship taxon" of the Appalachians, the American black bear, did encompass many key regions of rodents, however, could not be relied upon to refine critical areas. This appears to be a conundrum widely faced and criticized of the flagship concept, with many of the species chosen globally that are large, well-known, with forward facing eyes, and overtly charismatic (McGowan et al., 2020). Instead, it is proposed by McGowan et al. (2020) that we separately highlight these key biodiversity areas while

maintaining the flagship species for funding and conservation fund raising as we propose here in our study with the American black bear accounting for less charismatic rodents.

What is the geographic distribution of key refugial areas for rodents?

Averaged by family or subfamily as appropriate, Castoridae, by far, has the smallest portion of climate refugia with suitable habitat in the Appalachian Ecoregion. This is mostly due to the sole species of this family on the continent, the North American beaver, (*C. canadensis*) being reliant on riparian, lacustrine, and wetland environments (Wang et al., 2019). It is worth noting that future endeavors should consider semi-aquatic species (even beyond rodents) separately for wildlife underpasses in riparian and wetland areas given the unique habitat occupied by these taxa, particularly those adjacent to primary roadways. Sigmodontinae follows second, with only two species: the marsh rice rat (*O. palustris*), which is restricted to similar habitats as the beaver, and the hispid cotton rat (*S. hispidus*), which is found only in the more south/central reaches of the Appalachian Ecoregion. Erethizontidae, with its single Appalachian member, the North American porcupine (*E. dorsatum*), is restricted by its boreal distribution to the northern Appalachian Ecoregion. Arvicolinae and Neotominae averaged to more middle of the road with shared climate refugia overlap with the ursid, with some wide-spread generalist taxa within each respective subfamily, such as the woodland vole (*M. pinetorum*) and the North American deer mouse (*P. maniculatus*); others were highly restricted in terms of range, suitable climate, and habitat such as the rock vole (*M. chrotorrhinus*) or inhabiting only a small southern portion of the Appalachian Ecoregion such as the oldfield mouse (*P. polionotus*). Zapodidae also falls in the middle of the road, with only two species, the woodland jumping mouse (*N. insignis*) being more widespread climatically and the meadow jumping mouse (*Z. hudsonius*) more climatically restricted. Finally, Sciurinae and Xerinae are comparable and exhibit a high degree

of climate refugia overlap with *U. americanus*, likely due to their generalist habitat preferences and ecological roles and occupy large areas of novel suitable climate refugia not occupied by the ursid (select species shown in Appendix II: Supplementary 2.10).

At the species level, as mentioned above, the rodents *C. canadensis*, *O. palustris* and the arvicoline, *O. zibethicus* (muskrat), are limited by their need for aquatic/semi-aquatic habitats, making their suitable climate refugia quite restricted. The habitat preference of the arvicoline *M. chrotorrhinus* for talus slopes (Orrock & Pagels, 2003), combined with climatic isolation of the Appalachian population, has restricted this species' distribution to the southern Appalachians, with the subspecies *M. c. carolinensis* in the Blue Ridge of federal concern. The taxon with the smallest overlap in range with *U. americanus* is *P. polionotus*, which only occurs in the southernmost portion of the Appalachians. It is worth noting that the species with the highest degree of overlap are the generalist and widespread sciurids *T. striatus* (Eastern chipmunk) and *S. carolinensis* (Eastern gray squirrel), neotomines *P. leucopus* (white-footed mouse) and *P. maniculatus*, and the arvicoline *M. pinetorum*.

Cumulatively, the Central Appalachians was projected to have the highest concentration of rodent hotspots (overlap of 17-20 rodent species), measured as total area and percentage of the region, whereas the lowest concentration of rodent hotspots was found in the Southwest Appalachians (percentage) and Western Allegheny Plateau (area). The projection of priority areas (overlap of 21-23 species) was highest by land area in the Central Appalachians and most concentrated (percentage of region) in the Blue Ridge. The Western Allegheny Plateau, despite being the second largest region in the Appalachian Ecoregion, had no priority areas, whereas both the smallest region, the Southwestern Appalachians, and the largest, the Ridge and Valley, had comparably small portions of land occupied by priority areas. These trends for both priority

areas and hotspots are worth noting given the disproportionate number of species occupying a small area in both the Central Appalachians and the Blue Ridge, highlighting key ecosystems that many of these species have been integral to since the Miocene (Abramson et al., 2021; Fabre et al., 2012; Lacher et al., 2016; Steppan & Schenk, 2017).

In terms of overall composition of land mass of the Appalachian Ecoregion, 33% is the Ridge and Valley, 24% is the Western Allegheny Plateau, 18% is the Central Appalachians, 14% is the Blue Ridge, and 11% is the Southwestern Appalachians. This is important to note given the disproportionate distribution of rodents compared to this land mass. The rodent climate refugia hotspots containing 17+ species can be found occupying 37% of the total Appalachian Ecoregion, with the most occurring in the Central Appalachians and closely followed by the Ridge and Valley (both containing nearly two-thirds of all hotspots), more distantly followed by the Blue Ridge and Western Allegheny Plateau, and behind that with 5% of the hotspots is the Southwestern Appalachians. Relative to total land area within each region, 70% of the Central Appalachians and nearly 50% of the Blue Ridge is occupied by hotspots, with around one-third of the Ridge and Valley containing these hotspots, followed by the Southwestern Appalachians and Western Allegheny Plateau.

Are roadways a barrier for species trying to track favorable climate?

The Appalachian Ecoregion contains an extensive network of primary roadways that function both as major north-south routes between metropolises in New England and those such as Atlanta, and as major east-west routes connecting the eastern seaboard to the rest of the nation. This patchwork crosses through some key climate refugia for rodents, often adjacent to or intersecting protected areas, such as National Forest. It has been noted that even in optimal

habitat conditions, many small rodents have limited dispersal given small home range and size, let alone cross large multi-lane roadways (Bakker & Van Vuren, 2004; Chen & Koprowski, 2016; Hennessy et al., 2018; Kozakiewicz, 1993; McGregor et al., 2008; Merrick & Koprowski, 2017; Oxley et al., 1974). Though some existing culverts can function as wildlife corridors, the assumption should be that, if not designed with specific parameters, they are less than ideal given their primary use as water channels, which deter use unless a dry bridge is present and the size of the culvert does not appear threatening (e.g. the "tunneling" effect is not too great nor is the distance under the roadway in a dark and enclosed area too great) (Clevenger et al., 2001; D'Amico et al., 2015; Henke et al., 2001; Jones et al., 2008; McDonald & St. Clair, 2004; Meaney et al., 2007). The extensive use of solid concrete medians in the region in combination with mitigation efforts for rock slides often lead to trapped and subsequently killed larger animals, such as bears (Bélanger-Smith, 2014; Clevenger et al., 2006; Clevenger & Kociolek, 2013; Glista et al., 2009; Kociolek & Clevenger, 2007) (Supplementary 10). This combination makes for a dire situation for species trying to track suitable habitat and climate refugia in the region.

Beier & Loe (1992) stresses the importance of highlighting not just stable areas of habitat (and in our case climate as well) to be connected with a wildlife corridor, but incorporating designated protected patches that the corridors are physically connecting together through means such as wildlife overpasses, underpasses, and bridges; as opposed to placing an overpass that leads to unprotected land that could easily end up developed urban landscape (e.g. a subdivision). In our results, we highlighted 4 square kilometers of priority refugial corridors that should be evaluated for placement of wildlife overpasses and wildlife underpasses connecting protected areas. In the Central Appalachian ecoregion, the priority corridor on I-75 in Campbell

County, TN, had 31,165 vehicles on average passing through it daily in 2022 as a major north-south transportation corridor in the Eastern U.S. (Location IDs 07000049; Tennessee Department of Transportation, 2023), in addition to being adjacent to the two extensive Wildlife Management Areass in the region, as well as Cove Lake State Park. Of note, a potential corridor site connecting the Royal Blue Unit of the North Cumberland Wildlife Management Area near mile marker (mm) 136 on I-75 has an impenetrable concrete median running its length, starting at the Cove Creek crossing (which itself is a wildlife corridor) near mm 134.5 and ending near mm 138.5. Another potential corridor site in close proximity (~2 km) of the priority area, which itself is unfortunately close to privately owned commercial property, is connecting the swath of forested median running from mm 139.2 to 140.4 to connect the Royal Blue Unit and the Sundquist Unit of the WMAs, though this may be trickier given there is a stretch of private property running the northbound length with campgrounds. A better alternative, though more distant from the priority area, would be to connect the two WMAs with wildlife corridors where they are adjacent to the interstate right-of-way further north between mm 141.6 and mm 146.4, particularly given the solid concrete median that runs between mm 145 and mm 146.4.

In the Blue Ridge ecoregion, the priority corridor on the border of TN-NC on I-26 in Unicoi County, TN/Madison County, NC has 11,089 vehicles, on average that passed through it daily in 2022 (86000066; Tennessee Department of Transportation, 2023). This area in particular serves as one of the few uninterrupted corridors (with the exception of I-26) of National Forest (NF), with Cherokee NF on the Tennessee side and Pisgah NF in North Carolina. This area, known as Sam's Gap, is less steep than the roadcuts to the north and south, and is ideal for wildlife corridors, particularly given the number of large mammals hit here and on the neighboring stretch of I-26 in both Unicoi and Madison Counties (Supplementary 10). Part of the

problem lies in the steep geology and roadcuts, which can force a large animal onto the interstate, and the other is the overuse of solid concrete medians as a central divider on this stretch of I-26 in particular. On the Tennessee side, from mm 40.6 to just past mm 54.4 there is only a small gap in the concrete median for official vehicles to change direction, which then continues unbroken to just before mm 5 on the North Carolina side where there is another small official vehicle gap, and the nearly continuous stretch of solid concrete median finally ends just past mm 8. This is nearly 22 miles of solid concrete barrier, whereas the sides are often open (barring the fence along the interstate right-of-way), which Jones et al. (2008) and personal observation suggest is often damaged to the point that animals can pass through making it easy for large animals to try to cross and become trapped. This was of particular concern given the presence of bear preserves in the region, with the Unicoi County Bear Reserve overlapping the western edge of I-26 through Sam's Gap (Tennessee Wildlife Resource Agency, 2023), and expansion of the reintroduced elk population in the Smokies, with a bull elk having been struck near exit 2 on I-26 in 2019 (personal observation; Appendix II: Supplementary 2.10). Indeed, at the county level, Jones et al. (2008) found American black bear movement to be ranked among the highest in Madison County along this stretch of the border spanning I-26. Given the struggle of larger animals, it is likely to be difficult, if not impossible, for the small rodents to cross in these areas.

In the Blue Ridge, in Buncombe County, NC, on the I-40 priority refugial corridor, 39,225 vehicles passed through daily in 2022 (Location ID 0110000217; North Carolina Department of Transportation, 2023). Fortunately, the priority areas mostly are north of this stretch, with only a small portion highlighted to the west of the Black Mountain Reservoir. Unfortunately, there are few protected areas to bridge in this priority area along the interstate.

However, about 2 miles east on I-40 in McDowell County, NC, there are hotspots within protected areas that could use overpasses to maintain connectivity of Pisgah National Forest that is bisected by I-40, from just past mm 67 to mm 71. It should be noted that for all of these proposed corridor sites, existing bridges spanning forested ravines and creeks can function as overpasses, whereas small drainage culverts not designed explicitly for wildlife should not be considered underpasses without specific evaluation of size and placement (Clevenger et al., 2001; D'Amico et al., 2015; Henke et al., 2001; Jones et al., 2008; McDonald & St. Clair, 2004; Meaney et al., 2007). On the ground surveys within these proposed areas are important given the presence of roadcuts being less than ideal for some mammals, though perhaps others relying on talus may find them more favorable, and overall steepness of the surrounding landscape in combination with surrounding landcover may make for an obvious choice of placement.

As for connectivity corridors between climate refugia, fortunately most rodents (and the bear) were predicted in this study to maintain stable and connected core climate refugia (areas over 100,000 km²). Of the species not meeting this threshold, and though predicted to be susceptible to climatic isolation, a number of species had ranges of suitable climate that were in close enough proximity to warrant migration events. In particular, *M. ochrogaster* had an area of over 67,000 km² and another over 51,000 km² within 5 km of one another. The species of most concern is the most climatically restricted of all species analyzed, *M. chotorrhinus*, which has 1,079 km² adjacent to a 338 km² refugial patch, however the next closest stable climate refugium is 43 km away. Aquatic/semi-aquatic species are always of concern given their reliance on specific habitat, with climate refugia likely tied to the underlying hydrology of the region; *C. canadensis* show large degrees of separation between climate refugia (over 440 km) and *O. palustris* reliance on marsh and wetland with a distance of 70 km separating refugial patches.

The last taxon of note is *P. polionotus*, which occurs only in the most southern Appalachians, with a high degree of separation (over 100 km). Taxa with separation greater than 50 km of climate refugia are likely to experience climate isolation or worse, extirpation, if they cannot track their preferred climate refugia; however, we should note that some taxa only occupy the Appalachians as fringe populations and should also consider populations outside of this ecoregion for connectivity corridors in future studies (i.e. *P. polionotus*).

Lastly, the least cost pathways between stable climate refugia, though considered a best-case scenario and not one the individual animal may always logically take, were useful in showing overall trends in corridors between key refugial areas. Similar to previous studies (Carroll, 2010; Lawler et al., 2013, 2015; McKinley et al., 2019; Minor & Lookingbill, 2010; Zhu et al., 2021), our study shows key corridors within the Appalachians with a regional, near future, and more taxonomically specific focus; allowing for comparison to studies at the continental level, those predicting into the more distant future (2080s), and determining whether inclusion of all vertebrates overlaps with specific groups of concern. A key central corridor runs from the Southwest Appalachians of central Tennessee northward through the Kentucky-Virginia border in the Central Appalachians through central West Virginia. The other major corridor in the Appalachian Ecoregion runs from central eastern Kentucky in the Western Allegheny Plateau northward through western West Virginia and the Central Appalachians northward into central Pennsylvania in the Ridge and Valley. In the east along the Blue Ridge from the North Carolina-Georgia border, northward until it intersects the Ridge and Valley in southeast Virginia and travels northward to central Pennsylvania. Each of these key corridors intersects a number of primary roadways in the region, highlighting the need for wildlife overpasses and underpasses in high diversity areas with unique ecosystems.

Roadways are indeed a major barrier and source of mortality for wildlife (Cruz et al., 2019; Denneboom et al., 2021; Rhodes et al., 2014), with the focus of this study being primary roadways and their intersection to climate change refugia and division of travel corridors. However it is worth noting that secondary roadways can also be a source of mortality, though speed and traffic volume are contributing factors to road mortality (Cruz et al., 2019; Denneboom et al., 2021; Rhodes et al., 2014). A key assumption was that given the high speed and volume of traffic on the interstates and primary roadways in the Appalachians compared to secondary roadways, the former would be the primary threats to wildlife and most likely to receive funding for mitigation measures. Upon implementation within a region, additional studies should be conducted to determine the feasibility of mitigating additional smaller roadways where there is a documented need in the region.

CONCLUSION

It is worthy of mention that many of the areas discussed here also overlap with the results of Chapter 1, suggesting that these corridors have a high likelihood of benefitting most of mammals in the region depending on location, and even extend beyond to benefitting other fauna and flora sharing these ecosystems in the Appalachians. Given the dependency of the ecosystems in the Appalachians on rodents for nutrient cycling, seed dispersal, and even as a food source, the impacts of bridging these climate refugia separated by anthropogenic structures would prevent loss of taxa crucial to the ecosystems. Additionally, lives and property damage through vehicular collisions could be saved in the case of large mammals, such as the charismatic American black bear. Though it is important to consider the range of these flagship species in planning of wildlife corridors, a multispecies approach with less generalist taxa is a worthwhile endeavor in targeting specific areas of stability for overlap, particularly in proximity to protected areas.

Planning based solely on a single species, like the American black bear, could omit important wildlife corridor areas for smaller and more elusive wildlife in the region. Major wildlife corridors tracking suitable climate refugia were described in this study within the Appalachian Ecoregion, with most taxa exhibiting high connectivity of climate refugia. One of the major threats to tracking these refugia and suitable climate are primary roadways, particularly those with long expanses of concrete medians. It is important that we utilize existing features for key wildlife corridors, such as roadway bridges over ravines, valleys, and creeks, while avoiding placement in locations with sheer rock faces or that funnel wildlife into areas of high anthropogenic activity. Ground truthing of these highlighted areas in the near future will be key in all rodent refugia, not just priority areas, if we are to create a connectivity network in such a diverse landscape of endemics surrounded by such a populous region.

REFERENCES

Abramson, N. I., Bodrov, S. Yu., Bondareva, O. V., Genelt-Yanovskiy, E. A., & Petrova, T. V. (2021). A mitochondrial genome phylogeny of voles and lemmings (Rodentia: Arvicolinae): Evolutionary and taxonomic implications. *PLoS ONE*, *16*(11), e0248198. https://doi.org/10.1371/journal.pone.0248198

Alexander, J. L., Olimb, S. K., Bly, K. L. S., & Restani, M. (2016). Use of least-cost path analysis to identify potential movement corridors of swift foxes in Montana. *Journal of Mammalogy*, *97*(3), 891–898. https://doi.org/10.1093/jmammal/gyw032

Alexander, S. M., & Waters, N. M. (2000). The effects of highway transportation corridors on wildlife: A case study of Banff National Park. *Transportation Research Part C: Emerging Technologies*, *8*(1), 307–320. https://doi.org/10.1016/S0968-090X(00)00014-0

Anderson, J. T., Perera, N., Chowdhury, B., & Mitchell-Olds, T. (2015). Microgeographic Patterns of Genetic Divergence and Adaptation across Environmental Gradients in *Boechera stricta* (Brassicaceae). *The American Naturalist*, *186*(S1), S60–S73. https://doi.org/10.1086/682404

Anderson, M. G., Clark, M., Olivero, A. P., Barnett, A. R., Hall, K. R., Cornett, M. W., Ahlering, M., Schindel, M., Unnasch, B., Schloss, C., & Cameron, D. R. (2023). A resilient and connected network of sites to sustain biodiversity under a changing climate. *Proceedings of the National Academy of Sciences*, *120*(7), e2204434119. https://doi.org/10.1073/pnas.2204434119

Austin, J. M., & Garland, L. (2001). Evaluation of a wildlife underpass on Vermont State Highway 289 in Essex, Vermont. https://escholarship.org/uc/item/9bt4d3gb

Bakker, V. J., & Van Vuren, D. H. (2004). Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology*, *18*(3), 689–697.

Balbi, M., Petit, E. J., Croci, S., Nabucet, J., Georges, R., Madec, L., & Ernoult, A. (2019). Ecological relevance of least cost path analysis: An easy implementation method for landscape urban planning. *Journal of Environmental Management*, *244*, 61–68. https://doi.org/10.1016/j.jenvman.2019.04.124

Barnick, K. A., Green, A. M., Pendergast, M. E., & Şekercioğlu, Ç. H. (2022). The effects of human development, environmental factors, and a major highway on mammalian community composition in the Wasatch Mountains of northern Utah, USA. *Conservation Science and Practice*, *4*(7), e12708. https://doi.org/10.1111/csp2.12708

Beier, P., & Loe, S. (1992). In my experience: a checklist for evaluating impacts to wildlife movement corridors. *Wildlife Society Bulletin (1973-2006)*, *20*(4), 434–440.

Bélanger-Smith, K. (2014). Evaluating the effects of wildlife exclusion fencing on road mortality for medium-sized and small mammals along Quebec's Route 175 [Masters, Concordia University]. https://spectrum.library.concordia.ca/id/eprint/979605/

Belote, R. T., Dietz, M. S., McRae, B. H., Theobald, D. M., McClure, M. L., Irwin, G. H., McKinley, P. S., Gage, J. A., & Aplet, G. H. (2016). Identifying corridors among large protected areas in the United States. *PLOS ONE*, *11*(4), e0154223. https://doi.org/10.1371/journal.pone.0154223

Bennett, K., Tzedakis, P., & Willis, K. (1991). Quaternary refugia of north European trees. *Journal of Biogeography*, 103–115.

Berry, Z. C., & Smith, W. K. (2013). Ecophysiological importance of cloud immersion in a relic spruce–fir forest at elevational limits, southern Appalachian Mountains, USA. *Oecologia*, *173*(3), 637–648. https://doi.org/10.1007/s00442-013-2653-4

Bogoni, J. A., Peres, C. A., & Ferraz, K. M. P. M. B. (2020). Extent, intensity and drivers of mammal defaunation: A continental-scale analysis across the Neotropics. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-72010-w

Bowman, J., Jaeger, J. A. G., & Fahrig, L. (2002). Dispersal Distance of Mammals Is Proportional to Home Range Size. *Ecology*, *83*(7), 2049–2055. https://doi.org/10.1890/0012-9658(2002)083[2049:DDOMIP]2.0.CO;2

Browne, R. A., & Ferree, P. M. (2007). Genetic Structure of Southern Appalachian "Sky Island" populations of the Southern Red-Backed Vole (Myodes gapperi). *Journal of Mammalogy*, *88*(3), 759–768. https://doi.org/10.1644/06-MAMM-A-049R1.1

Brunke, J., Radespiel, U., Russo, I.-R., Bruford, M. W., & Goossens, B. (2019). Messing about on the river: The role of geographic barriers in shaping the genetic structure of Bornean small mammals in a fragmented landscape. *Conservation Genetics*, *20*(4), 691–704. https://doi.org/10.1007/s10592-019-01159-3

Caldwell, M. R., & Klip, J. M. K. (2020). Wildlife Interactions within Highway Underpasses. *The Journal of Wildlife Management*, *84*(2), 227–236. https://doi.org/10.1002/jwmg.21801

Carroll, C. (2010). Role of climatic niche models in focal-species-based conservation planning: Assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. *Biological Conservation*, *143*(6), 1432–1437. https://doi.org/10.1016/j.biocon.2010.03.018

Cartwright, J. M., & Wolfe, W. (2016). *Insular ecosystems of the southeastern United States—A regional synthesis to support biodiversity conservation in a changing climate*. https://www.semanticscholar.org/paper/Insular-ecosystems-of-the-southeastern-United-to-in-Cartwright-Wolfe/24f40322117d69212560c27cc05bc80c340fd77b

Chambers, J. L., & Garant, D. (2010). Determinants of Population Genetic Structure in Eastern Chipmunks (Tamias striatus): The Role of Landscape Barriers and Sex-Biased Dispersal. *Journal of Heredity*, *101*(4), 413–422. https://doi.org/10.1093/jhered/esq029

Chen, H. L., & Koprowski, J. L. (2016). Barrier effects of roads on an endangered forest obligate: Influences of traffic, road edges, and gaps. *Biological Conservation*, *199*, 33–40. https://doi.org/10.1016/j.biocon.2016.03.017

Clavenger, A. P., Kociolek, A. V., & Western Transportation Institute. (2006). Highway Median Impacts on Wildlife Movement and Mortality: State of the Practice Survey and Gap Analysis. https://rosap.ntl.bts.gov/view/dot/27680

Clevenger, A. P., Chruszcz, B., & Gunson, K. (2001). Drainage Culverts as Habitat Linkages and Factors Affecting Passage by Mammals. *Journal of Applied Ecology*, *38*(6), 1340–1349.

Clevenger, A. P., & Kociolek, A. V. (2013). Potential Impacts of Highway Median Barriers on Wildlife: State of the Practice and Gap Analysis. *Environmental Management*, *52*(5), 1299–1312. https://doi.org/10.1007/s00267-013-0155-0

Commission for Environmental Cooperation. (1997). *Ecological Regions of North America: Toward a common perspective* (Revised 2006) [Map]. http://www.cec.org/publications/ecological-regions-of-north-america/

Corlett, R. T. (2007). The Impact of Hunting on the Mammalian Fauna of Tropical Asian Forests. *Biotropica*, *39*(3), 292–303. https://doi.org/10.1111/j.1744-7429.2007.00271.x

Ćosić, N., Říčanová, Š., Bryja, J., Penezić, A., & Ćirović, D. (2013). Do rivers and human-induced habitat fragmentation affect genetic diversity and population structure of the European ground squirrel at the edge of its Pannonian range? *Conservation Genetics*, *14*(2), 345–354. https://doi.org/10.1007/s10592-013-0466-y

Cotner, L. A., & Schooley, R. L. (2011). Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. *The Journal of Wildlife Management*, *75*(7), 1637–1645. https://doi.org/10.1002/jwmg.197

Cox, D. R., & Nelson, T. A. (2009). Beaver habitat models for use in Illinois streams. *T Illinois Acad Sci*, *102*, 55–64.

Cruz, T. M. R., Lima, J., Luis, A., & Azeiteiro, U. M. (2019). *Impact of secondary roads on wildlife of coastal center region Portugal and differences between before and post fire.* https://doi.org/10.21203/rs.2.15714/v1

Cushman, S. A., McKelvey, K. S., & Schwartz, M. K. (2009). Use of Empirically Derived Source-Destination Models to Map Regional Conservation Corridors. *Conservation Biology*, *23*(2), 368–376. https://doi.org/10.1111/j.1523-1739.2008.01111.x

D'Amico, M., Clevenger, A. P., Román, J., & Revilla, E. (2015). General versus specific surveys: Estimating the suitability of different road-crossing structures for small mammals. https://doi.org/10.1002/jwmg.900

Davidson, A. D., Lightfoot, D. C., & McIntyre, J. L. (2008). Engineering rodents create key habitat for lizards. *Journal of Arid Environments*, *72*(12), 2142–2149. https://doi.org/10.1016/j.jaridenv.2008.07.006

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*(5517), 673–679.

Denneboom, D., Bar-Massada, A., & Shwartz, A. (2021). Factors affecting usage of crossing structures by wildlife – A systematic review and meta-analysis. *Science of The Total Environment*, *777*, 146061. https://doi.org/10.1016/j.scitotenv.2021.146061

Dewitz, J. (2021). *National Land Cover Database (NLCD) 2019 Products* [dataset]. U.S. Geological Survey. https://doi.org/10.5066/P9KZCM54

Dickman, C. (1999). *Rodent-ecosystem relationships: A review* (pp. 113–133).

Donaldson, B. (2007). Use of Highway Underpasses by Large Mammals and Other Wildlife in Virginia: Factors Influencing Their Effectiveness. *Transportation Research Record*, *2011*(1), 157–164. https://doi.org/10.3141/2011-17

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Emmons, L. (2000). *Tupai: A Field Study of Bornean Treeshrews*. University of California Press.

Enders, M. S., & Vander Wall, S. B. (2012). Black bears *Ursus americanus* are effective seed dispersers, with a little help from their friends. *Oikos*, *121*(4), 589–596. https://doi.org/10.1111/j.1600-0706.2011.19710.x

Erb, P. L., McShea, W. J., & Guralnick, R. P. (2012). Anthropogenic Influences on Macro-Level Mammal Occupancy in the Appalachian Trail Corridor. *PLOS ONE*, *7*(8), e42574. https://doi.org/10.1371/journal.pone.0042574

Eubanks, B. W., Hellgren, E. C., Nawrot, J. R., & Bluett, R. D. (2011). Habitat associations of the marsh rice rat (*Oryzomys palustris*) in freshwater wetlands of southern Illinois. *Journal of Mammalogy*, *92*(3), 552–560. https://doi.org/10.1644/10-MAMM-A-289.1

Fabre, P.-H., Hautier, L., Dimitrov, D., & P Douzery, E. J. (2012). A glimpse on the pattern of rodent diversification: A phylogenetic approach. *BMC Evolutionary Biology*, *12*(1), 88. https://doi.org/10.1186/1471-2148-12-88

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Frankham, R. (2015). Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology*, *24*(11), 2610–2618. https://doi.org/10.1111/mec.13139

Garden, J. G., O'Donnell, T., & Catterall, C. P. (2015). Changing habitat areas and static reserves: Challenges to species protection under climate change. *Landscape Ecology*, *30*(10), 1959–1973. https://doi.org/10.1007/s10980-015-0223-3

Gibson, L., Lynam, A. J., Bradshaw, C. J., He, F., Bickford, D. P., Woodruff, D. S., Bumrungsri, S., & Laurance, W. F. (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, *341*(6153), 1508–1510.

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning*, *91*(1), 1–7. https://doi.org/10.1016/j.landurbplan.2008.11.001

Gloyne, C. C., & Clevenger, A. P. (2001). Cougar Puma concolor use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. *Wildlife Biology*, *7*(2), 117–124. https://doi.org/10.2981/wlb.2001.009

Godó, L., Valkó, O., Borza, S., & Deák, B. (2022). A global review on the role of small rodents and lagomorphs (clade Glires) in seed dispersal and plant establishment. *Global Ecology and Conservation*, *33*, e01982. https://doi.org/10.1016/j.gecco.2021.e01982

Gracanin, A., Knipler, M. L., & Mikac, K. M. (2023). Informing Wildlife Corridor Creation through Population Genetics of an Arboreal Marsupial in a Fragmented Landscape. *Genes*, *14*(2), Article 2. https://doi.org/10.3390/genes14020349

Graham, S. P., Steen, D. A., Nelson, K. T., Durso, A. M., & Maerz, J. C. (2010). An Overlooked Hotspot? Rapid Biodiversity Assessment Reveals a Region of Exceptional Herpetofaunal Richness in the Southeastern United States. *Southeastern Naturalist*, *9*(1), 19–34. https://doi.org/10.1656/058.009.0102

Gross, D. A. (2010). Pennsylvania boreal conifer forests and their bird communities: Past, present, and potential. *In: Rentch, James S.; Schuler, Thomas M., Eds. 2010. Proceedings from the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains. 2009 May 14-15; Slatyfork, WV. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 48-73.*, *p-64*, 48–73.

Hafner, D. J., Yensen, E., & Kirkland, G. L., Jr. (1998). Summary Descriptions of Rodents of Conservation Concern. In D. J. Hafner, E. Yensen, & G. L. Kirkland Jr. (Eds.), *North American Rodents: Status Survey and Conservation Action Plan* (pp. 23–31). IUCN.

Hagerty, B. E., Nussear, K. E., Esque, T. C., & Tracy, C. R. (2011). Making molehills out of mountains: Landscape genetics of the Mojave desert tortoise. *Landscape Ecology*, *26*(2), 267–280. https://doi.org/10.1007/s10980-010-9550-6

Hamaide, V., Hamaide, B., & Williams, J. C. (2022). Nature reserve optimization with buffer zones and wildlife corridors for rare species. *Sustainability Analytics and Modeling*, *2*, 100003. https://doi.org/10.1016/j.samod.2022.100003

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*(5), 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Heintzman, L. J., & McIntyre, N. E. (2021). Assessment of playa wetland network connectivity for amphibians of the south-central Great Plains (USA) using graph-theoretical, least-cost path, and landscape resistance modelling. *Landscape Ecology*, *36*(4), 1117–1135. https://doi.org/10.1007/s10980-021-01199-6

Henke, R. J., Cawood-Hellmund, P., & Sprunk, T. (2001). *Habitat connectivity study of the I-25 and US 85 corridors, Colorado*. https://escholarship.org/uc/item/6t60j9w5

Hennessy, C., Tsai, C.-C., Anderson, S. J., Zollner, P. A., & Rhodes, O. E. (2018). What's stopping you? Variability of interstate highways as barriers for four species of terrestrial rodents. *Ecosphere*, *9*(7). https://doi.org/10.1002/ecs2.2333

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, *405*(6789), 907–913. https://doi.org/10.1038/35016000

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*. https://doi.org/10.1098/rstb.2003.1388

Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., & Johnson, C. A. (2001). Climate change 2001: The scientific basis (Vol. 881, Issue 9). Cambridge university press Cambridge.

Huijser, M. P., Fairbank, E. R., Camel-Means, W., Graham, J., Watson, V., Basting, P., & Becker, D. (2016). Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife–vehicle collisions and providing safe crossing opportunities for large mammals. *Biological Conservation*, *197*, 61–68. https://doi.org/10.1016/j.biocon.2016.02.002

Isaac, J. L. (2009). Effects of climate change on life history: Implications for extinction risk in mammals. *Endangered Species Research*, *7*(2), 115–123. https://doi.org/10.3354/esr00093

John L. Orrock & John F. Pagels. (2003). Tree communities, microhabitat characteristics, and small mammals associated with the endangered rock vole, M*icrotus chrotorrhinus*, in Virginia. *Southeastern Naturalist*, *2*(4), 547–558. https://doi.org/10.1656/1528-7092(2003)002[0547:TCMCAS]2.0.CO;2

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, *69*(3), 373–386. https://doi.org/10.2307/3545850

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jones, E. R., Lancia, R., Doerr, P., & North Carolina State University. (2008). The effectiveness of wildlife crossing structures for black bears in Madison County, North Carolina. (FHWA/NC/2006-62). https://rosap.ntl.bts.gov/view/dot/21345

Kociolek, A., & Clevenger, A. P. (2007). Highway median Impacts on Wildlife Movement and Mortality. https://escholarship.org/uc/item/97v1c6ww

Koen, E. L., Bowman, J., Sadowski, C., & Walpole, A. A. (2014). Landscape connectivity for wildlife: Development and validation of multispecies linkage maps. *Methods in Ecology and Evolution*, *5*(7), 626–633. https://doi.org/10.1111/2041-210X.12197

Koike, S., Morimoto, H., Kozakai, C., Arimoto, I., Yamazaki, K., Iwaoka, M., Soga, M., & Koganezawa, M. (2012). Seed removal and survival in Asiatic black bear *Ursus thibetanus* faeces: Effect of rodents as secondary seed dispersers. *Wildlife Biology*, *18*(1), 24–34. https://doi.org/10.2981/10-049

Kozakiewicz, M. (1993). Habitat isolation and ecological barriers—The effect on small mammal populations and communities. *Acta Theriologica*, *38*(1), 1–30. https://doi.org/10.4098/AT.arch.93-1

Kuefler, D., Hudgens, B., Haddad, N. M., Morris, W. F., & Thurgate, N. (2010). The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology*, *91*(4), 944–950. https://doi.org/10.1890/09-0614.1

Lacher, T., Murphy, W., Rogan, J., Smith, A., & Upham, N. (2016). *Evolution, phylogeny, ecology and conservation of the Clade Glires: Lagomorpha and Rodentia* (pp. 15–26).

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., Heller, N. E., Pressey, R. L., Sanderson, E. W., & Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change: Conserving Nature's Stage in a Time of Rapid Change. *Conservation Biology*, *29*(3), 618–629. https://doi.org/10.1111/cobi.12505

Lawler, J. J., Ruesch, A. S., Olden, J. D., & McRae, B. H. (2013). Projected climate-driven faunal movement routes. *Ecology Letters*, *16*(8), 1014–1022. https://doi.org/10.1111/ele.12132

Le Galliard, J.-F., Rémy, A., Ims, R. A., & Lambin, X. (2012). Patterns and processes of dispersal behaviour in arvicoline rodents. *Molecular Ecology*, *21*(3), 505–523. https://doi.org/10.1111/j.1365-294X.2011.05410.x

Li, H., Li, D., Li, T., Qiao, Q., Yang, J., & Zhang, H. (2010). Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake—Case study of Wolong Nature Reserve in China. *Ecological Modelling*, *221*(6), 944–952. https://doi.org/10.1016/j.ecolmodel.2009.12.006

Littlefield, C. E., Krosby, M., Michalak, J. L., & Lawler, J. J. (2019). Connectivity for species on the move: Supporting climate-driven range shifts. *Frontiers in Ecology and the Environment*, *17*(5), 270–278. https://doi.org/10.1002/fee.2043

Liu, C., Newell, G., White, M., & Bennett, A. F. (2018). Identifying wildlife corridors for the restoration of regional habitat connectivity: A multispecies approach and comparison of resistance surfaces. *PLOS ONE*, *13*(11), e0206071. https://doi.org/10.1371/journal.pone.0206071

Loro, M., Ortega, E., Arce, R. M., & Geneletti, D. (2015). Ecological connectivity analysis to reduce the barrier effect of roads. An innovative graph-theory approach to define wildlife corridors with multiple paths and without bottlenecks. *Landscape and Urban Planning*, *139*, 149–162. https://doi.org/10.1016/j.landurbplan.2015.03.006

Lugon-Moulin, N., & Hausser, J. (2002). Phylogeographical structure, postglacial recolonization and barriers to gene flow in the distinctive Valais chromosome race of the common shrew (Sorex araneus). *Molecular Ecology*, *11*(4), 785–794. https://doi.org/10.1046/j.1365-294X.2002.01469.x

Mata, C., Hervás, I., Herranz, J., Suárez, F., & Malo, J. E. (2008). Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. *Journal of Environmental Management*, *88*(3), 407–415. https://doi.org/10.1016/j.jenvman.2007.03.014

Mccollister, M. F., & Van Manen, F. T. (2010). Effectiveness of Wildlife Underpasses and Fencing to Reduce Wildlife-Vehicle Collisions. *The Journal of Wildlife Management*, *74*(8), 1722–1731. https://doi.org/10.2193/2009-535

McDonald, W., & St. Clair, C. C. (2004). Elements That Promote Highway Crossing Structure Use by Small Mammals in Banff National Park. *Journal of Applied Ecology*, *41*(1), 82–93.

McGowan, J., Beaumont, L. J., Smith, R. J., Chauvenet, A. L. M., Harcourt, R., Atkinson, S. C., Mittermeier, J. C., Esperon-Rodriguez, M., Baumgartner, J. B., Beattie, A., Dudaniec, R. Y., Grenyer, R., Nipperess, D. A., Stow, A., & Possingham, H. P. (2020). Conservation prioritization can resolve the flagship species conundrum. *Nature Communications*, *11*(1), 994. https://doi.org/10.1038/s41467-020-14554-z

McGregor, R. L., Bender, D. J., & Fahrig, L. (2008). Do Small Mammals Avoid Roads Because of the Traffic? *Journal of Applied Ecology*, *45*(1), 117–123.

McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences*, *113*(26), 7195–7200. https://doi.org/10.1073/pnas.1602817113

McKinley, P. S., Belote, R. T., & Aplet, G. H. (2019). An assessment of ecological values and conservation gaps in protection beyond the corridor of the Appalachian Trail. *Conservation Science and Practice*, *1*(6), e30. https://doi.org/10.1111/csp2.30

Meaney, C. A., Bakeman, M. E., Reed-Eckert, M., & Wostl, E. (2007). *Effectiveness of Ledges in Culverts for Small Mammal Passage* (CDOT-2007-9). Article CDOT-2007-9. https://trid.trb.org/view/860336

Merrick, M. J., & Koprowski, J. L. (2017). Circuit theory to estimate natal dispersal routes and functional landscape connectivity for an endangered small mammal. *Landscape Ecology*, *32*(6), 1163–1179. https://doi.org/10.1007/s10980-017-0521-z

Miller, B., Ceballos, G., & Reading, R. (1994). The Prairie Dog and Biotic Diversity. *Conservation Biology*, *8*(3), 677–681. https://doi.org/10.1046/j.1523-1739.1994.08030677.x

Minor, E. S., & Lookingbill, T. R. (2010). A Multiscale Network Analysis of Protected-Area Connectivity for Mammals in the United States. *Conservation Biology*, *24*(6), 1549–1558. https://doi.org/10.1111/j.1523-1739.2010.01558.x

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, *322*(5899), 261–264.

Morrison, L., Estrada, A., & Early, R. (2018). Species traits suggest European mammals facing the greatest climate change are also least able to colonize new locations. *Diversity and Distributions*, *24*(9), 1321–1332. https://doi.org/10.1111/ddi.12769

Nadeau, S., Décarie, R., Lambert, D., & St-Georges, M. (1995). Nonlinear Modeling of Muskrat Use of Habitat. *The Journal of Wildlife Management*, *59*(1), 110–117. https://doi.org/10.2307/3809123

Newmark, W. D. (1993). The Role and Design of Wildlife Corridors with Examples from Tanzania. *Ambio*, *22*(8), 500–504.

North Carolina Department of Transportation, T. P. D. (2023). *2022 AADT Station Shapefile* [dataset]. https://connect.ncdot.gov/resources/State-Mapping/Pages/Traffic-Survey-GIS-Data.aspx

Nuñez, T. A., Lawler, J. J., Mcrae, B. H., Pierce, D. J., Krosby, M. B., Kavanagh, D. M., Singleton, P. H., & Tewksbury, J. J. (2013). Connectivity Planning to Address Climate Change. *Conservation Biology*, *27*(2), 407–416. https://doi.org/10.1111/cobi.12014

Olsson, M. P. O., Widén, P., & Larkin, J. L. (2008). Effectiveness of a highway overpass to promote landscape connectivity and movement of moose and roe deer in Sweden. *Landscape and Urban Planning*, *85*(2), 133–139. https://doi.org/10.1016/j.landurbplan.2007.10.006

Oxley, D. J., Fenton, M. B., & Carmody, G. R. (1974). The Effects of Roads on Populations of Small Mammals. *Journal of Applied Ecology*, *11*(1), 51–59. https://doi.org/10.2307/2402004

Parker, I. D., Lopez, R. R., Silvy, N. J., Davis, D. S., & Owen, C. B. (2011). Long-term effectiveness of US 1 crossing project in reducing florida key deer mortality. *Wildlife Society Bulletin*, *35*(3), 296–302. https://doi.org/10.1002/wsb.45

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42.

Parra-Olea, G., Windfield, J. C., Velo-Antón, G., & Zamudio, K. R. (2012). Isolation in habitat refugia promotes rapid diversification in a montane tropical salamander. *Journal of Biogeography*, *39*(2), 353–370. https://doi.org/10.1111/j.1365-2699.2011.02593.x

Pelini, S. L., Boudreau, M., McCoy, N., Ellison, A. M., Gotelli, N. J., Sanders, N. J., & Dunn, R. R. (2011). Effects of short-term warming on low and high latitude forest ant communities. *Ecosphere*, *2*(5), 1–12.

Pell, S., & Jones, D. (2015). Are wildlife overpasses of conservation value for birds? A study in Australian sub-tropical forest, with wider implications. *Biological Conservation*, *184*, 300–309. https://doi.org/10.1016/j.biocon.2015.02.005

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915.

Pertoldi, C., Bijlsma, R., & Loeschcke, V. (2007). Conservation genetics in a globally changing environment: Present problems, paradoxes and future challenges. *Biodiversity and Conservation*, *16*(14), 4147–4163. https://doi.org/10.1007/s10531-007-9212-4

Peterson, A. T., & Soberón, J. (2012). Integrating fundamental concepts of ecology, biogeography, and sampling into effective ecological niche modeling and species distribution modeling. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology*, *146*(4), 789–796. https://doi.org/10.1080/11263504.2012.740083

Poor, E. E., Loucks, C., Jakes, A., & Urban, D. L. (2012). Comparing Habitat Suitability and Connectivity Modeling Methods for Conserving Pronghorn Migrations. *PLOS ONE*, *7*(11), e49390. https://doi.org/10.1371/journal.pone.0049390

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the Quest for Keystones: Identifying keystone species is difficult—but essential to understanding how

loss of species will affect ecosystems. *BioScience*, *46*(8), 609–620. https://doi.org/10.2307/1312990

Pullinger, M. G., & Johnson, C. J. (2010). Maintaining or restoring connectivity of modified landscapes: Evaluating the least-cost path model with multiple sources of ecological information. *Landscape Ecology*, *25*(10), 1547–1560. https://doi.org/10.1007/s10980-010-9526-6

Ralls, K., Sunnucks, P., Lacy, R. C., & Frankham, R. (2020). Genetic rescue: A critique of the evidence supports maximizing genetic diversity rather than minimizing the introduction of putatively harmful genetic variation. *Biological Conservation*, *251*, 108784. https://doi.org/10.1016/j.biocon.2020.108784

Rhodes, J. R., Lunney, D., Callaghan, J., & McAlpine, C. A. (2014). A Few Large Roads or Many Small Ones? How to Accommodate Growth in Vehicle Numbers to Minimise Impacts on Wildlife. *PLOS ONE*, *9*(3), e91093. https://doi.org/10.1371/journal.pone.0091093

Rose, N.-A., & Burton, P. J. (2009). Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management*, *258*, S64–S74. https://doi.org/10.1016/j.foreco.2009.07.053

Segelbacher, G., Cushman, S. A., Epperson, B. K., Fortin, M.-J., Francois, O., Hardy, O. J., Holderegger, R., Taberlet, P., Waits, L. P., & Manel, S. (2010). Applications of landscape genetics in conservation biology: Concepts and challenges. *Conservation Genetics*, *11*(2), 375–385. https://doi.org/10.1007/s10592-009-0044-5

Shafaghat, A., Keyvanfar, A., & Wui Ket, C. (2022). A decision support tool for evaluating the wildlife corridor design and conservation performance using analytic network process

(ANP). *Journal for Nature Conservation*, *70*, 126280. https://doi.org/10.1016/j.jnc.2022.126280

Skov, F., & Svenning, J.-C. (2004). Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography*, *27*(3), 366–380. https://doi.org/10.1111/j.0906-7590.2004.03823.x

Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, *33*(1), 159–167. https://doi.org/10.1111/j.1600-0587.2009.06074.x

Spence, A. R., & Tingley, M. W. (2020). The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography*, *43*(11), 1571–1590. https://doi.org/10.1111/ecog.05170

Stephens, R. B., & Rowe, R. J. (2020). The underappreciated role of rodent generalists in fungal spore dispersal networks. *Ecology*, *101*(4), e02972. https://doi.org/10.1002/ecy.2972

Steppan, S. J., & Schenk, J. J. (2017). Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. *PloS One*, *12*(8), e0183070. https://doi.org/10.1371/journal.pone.0183070

Stoner, K. E., Riba-Hernández, P., Vulinec, K., & Lambert, J. E. (2007). The Role of Mammals in Creating and Modifying Seedshadows in Tropical Forests and Some Possible Consequences of Their Elimination. *Biotropica*, *39*(3), 316–327.

Sutherland, G., Harestad, A., Price, K., & Lertzman, K. (2000). Scaling of Natal Dispersal Distances in Terrestrial Birds and Mammals. *Conservation Ecology*, *4*(1). https://doi.org/10.5751/ES-00184-040116

Synes, N. W., Ponchon, A., Palmer, S. C. F., Osborne, P. E., Bocedi, G., Travis, J. M. J., & Watts, K. (2020). Prioritising conservation actions for biodiversity: Lessening the impact from habitat fragmentation and climate change. *Biological Conservation*, *252*, 108819. https://doi.org/10.1016/j.biocon.2020.108819

Tallmon, D. A., Luikart, G., & Waples, R. S. (2004). The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, *19*(9), 489–496. https://doi.org/10.1016/j.tree.2004.07.003

Tennessee Department of Transportation. (2023). *Average Annual Daily Traffic Map* [dataset]. https://tdot.public.ms2soft.com/tcds/tsearch.asp?loc=Tdot&mod=TCDS

Tennessee Wildlife Resource Agency. (2023). *Black Bear Reserves* [dataset]. https://www.tn.gov/content/tn/twra/hunting/big-game/bear.html#zones

Thapa, K., Manandhar, S., Bista, M., Shakya, J., Sah, G., Dhakal, M., Sharma, N., Llewellyn, B., Wultsch, C., Waits, L. P., Kelly, M. J., Hero, J.-M., Hughes, J., & Karmacharya, D. (2018). Assessment of genetic diversity, population structure, and gene flow of tigers (Panthera tigris tigris) across Nepal's Terai Arc Landscape. *PLOS ONE*, *13*(3), e0193495. https://doi.org/10.1371/journal.pone.0193495

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), Article 6970. https://doi.org/10.1038/nature02121

Travis, J. (2003). Climate change and habitat destruction: A deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1514), 467–473.

U.S. Census Bureau, Geography Division. (2020). *TIGER/Line 2010 Urban Areas* [dataset]. https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2010-urban-areas

U.S. Census Bureau, Geography Division. (2021). *TIGER/Line Shapefiles: Roads* [Machine-readable data files]. https://www.census.gov/cgi-bin/geo/shapefiles/index.php?year=2021&layergroup=Roads

U.S. Census Bureau, Population Division. (2023). *Annual Estimates of the Resident Population for Incorporated Places of 50,000 or More, Ranked by July 1, 2022 Population: April 1, 2020 to July 1, 2022 (SUB-IP-EST2022-ANNRNK)* [dataset]. https://www2.census.gov/programs-surveys/popest/tables/2020-2022/cities/totals/SUB-IP-EST2022-ANNRNK.xlsx

U.S. Geological Survey. (2022). *Protected Areas Database of the United States (PAD-US) 3.0 (ver. 2.0, March 2023)* [dataset]. U.S. Geological Survey. https://doi.org/10.5066/P9Q9LQ4B

Van Vuren, D. (1998). Mammalian Dispersal and Reserve Design. In T. M. Caro (Ed.), *Behavioral Ecology and Conservation Biology* (pp. 369–393). Oxford University Press, USA.

Wang, C., & Liu, H. (2020). Developing large-scale international ecological networks based on least-cost path analysis – a case study of Altai mountains. *Open Geosciences*, *12*(1), 840–850. https://doi.org/10.1515/geo-2020-0173

Wang, G., McClintic, L. F., & Taylor, J. D. (2019). Habitat selection by American beaver at multiple spatial scales. *Animal Biotelemetry*, *7*(1), 10. https://doi.org/10.1186/s40317-019-0172-8

Wells, K., Pfeiffer, M., Lakim, M. B., & Kalko, E. K. V. (2006). Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo. *Journal of Animal Ecology*, *75*(5), 1212–1223. https://doi.org/10.1111/j.1365-2656.2006.01144.x

Whicker, A. D., & Detling, J. K. (1988). Ecological Consequences of Prairie Dog Disturbances. *BioScience*, *38*(11), 778–785. https://doi.org/10.2307/1310787

Whitmee, S., & Orme, C. D. L. (2013). Predicting dispersal distance in mammals: A trait-based approach. *Journal of Animal Ecology*, *82*(1), 211–221. https://doi.org/10.1111/j.1365-2656.2012.02030.x

Wilson, M. B., & Belote, R. T. (2022). The Value of Trail Corridors for Bold Conservation Planning. *Land*, *11*(3), Article 3. https://doi.org/10.3390/land11030348

Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, *132*(1), 96–101. https://doi.org/10.1007/s00442-002-0929-1

Yensen, E., & Hafner, D. J. (1998). North American Rodents. In D. J. Hafner, E. Yensen, & G. L. Kirkland Jr. (Eds.), *North American Rodents: Status Survey and Conservation Action Plan* (pp. 1–4). IUCN.

Yensen, E., Quinney, D. L., Johnson, K., Timmerman, K., & Steenhof, K. (1992). Fire, Vegetation Changes, and Population Fluctuations of Townsend's Ground Squirrels. *The American Midland Naturalist*, *128*(2), 299–312. https://doi.org/10.2307/2426464

Zhu, G., Papeş, M., Giam, X., Cho, S.-H., & Armsworth, P. R. (2021). Are protected areas well-sited to support species in the future in a major climate refuge and corridor in the United States? *Biological Conservation*, *255*, 108982. https://doi.org/10.1016/j.biocon.2021.108982

APPENDIX II:

TABLES

Table 2.1. Taxa Included and Sample Sizes. List of taxa included in this study, as well as state wildlife action plan (SWAP)/federal listing status, sample size, DOI of datasets, and references utilized for delimiting the samples by subspecies for the data used. Taxa considered boreal relicts or Appalachian endemics are indicated with a *. The ursid of the order Carnivora is shown in gray as the charismatic outgroup.

Family	Subfamily	Scientific name	Common name	2015 SWAP Listed	Training/Testing sample size	DOI of GBIF dataset	Range utilized to delimit subspecies for models
Castoridae	none	*Castor canadensis*	North American Beaver	none	117/29	https://doi.org/10.15468/dl.cdzusb	Stephen H. Jenkins, Peter E. Busher, Castor canadensis, Mammalian Species, Issue 120, 8 June 1979, Pages 1–8, https://doi.org/10.2307/3503787
Cricetidae	Arvicolinae	*Clethrionomys gapperi**	Southern Red-backed Vole	C. g. carolinensis SC; C. g. maurus KY	367/587	https://doi.org/10.15468/dl.q6tx73	Joseph F. Merritt, Clethrionomys gapperi, Mammalian Species, Issue 146, 8 May 1981, Pages 1–9, https://doi.org/10.2307/3503900
Cricetidae	Arvicolinae	*Microtus chrotorrhinus**	Rock Vole	M. c. carolinensis federal species of concern; MD, NC, TN, VA, WV	46/11	https://doi.org/10.15468/dl.t246x6	Gordon L. Kirkland, Jr. , Frederick J. Jannett, Jr., Microtus chrotorrhinus, Mammalian Species, Issue 180, 18 June 1982, Pages 1–5, https://doi.org/10.2307/3503842
Cricetidae	Arvicolinae	*Microtus ochrogaster*	Prairie Vole	WV	135/224	https://doi.org/10.15468/dl.p96duv	Dick T. Stalling, Microtus ochrogaster, Mammalian Species, Issue 355, 26 April 1990, Pages 1–9, https://doi.org/10.2307/3504103
Cricetidae	Arvicolinae	*Microtus pennsylvanicus*	Meadow Vole	SC	612/975	https://doi.org/10.15468/dl.f4dsmt	Lawrence M. Reich, Microtus pennsylvanicus, Mammalian Species, Issue 159, 3 December 1981, Pages 1–8, https://doi.org/10.2307/3503976

Table 2.1 Continued

Cricetidae	Arvicolinae	*Microtus pinetorum*	Woodland Vole	none	239/384	https://doi.org/10.15468/dl.uqk32b	Michael J. Smolen, Microtus pinetorum, Mammalian Species, Issue 147, 8 May 1981, Pages 1–7, https://doi.org/10.1093/mspecies/147.1
Cricetidae	Arvicolinae	*Ondatra zibethicus*	Muskrat	none	76/157	https://doi.org/10.15468/dl.3nmcjg	Gale R. Willner, George A. Feldhamer, Elizabeth E. Zueker, Joseph A. Chapman, Ondatra zibethicus, Mammalian Species, Issue 141, 20 November 1980, Pages 1–8, https://doi.org/10.2307/3504016
Cricetidae	Arvicolinae	*Synaptomys cooperi**	Southern Bog Lemming	GA, MD, TN, WV	75/19	https://doi.org/10.15468/dl.mkmt97	Robert K Rose , Alicia V Linzey, Synaptomys cooperi (Rodentia: Cricetidae), Mammalian Species, Volume 53, Issue 1007, 2 August 2021, Pages 95–111, https://doi.org/10.1093/mspecies/seab009
Cricetidae	Neotominae	*Neotoma floridana*	Eastern Woodrat	N. f. haematoria federal species of concern; TN, NC; N. f. ilonoensis TN; SC	99/161	https://doi.org/10.15468/dl.bxcxe7	Robert W. Wiley, Neotoma floridana, Mammalian Species, Issue 139, 20 November 1980, Pages 1–7, https://doi.org/10.2307/3503989
Cricetidae	Neotominae	*Neotoma magister**	Allegheny Woodrat	AL, KY, MD, NC, TN, VA, WV	542/640	https://doi.org/10.15468/dl.wkw9fu	Steven B. Castleberry and others, Neotoma magister, Mammalian Species, Issue 789, 24 May 2006, Pages 1–5, https://doi.org/10.1644/789.1
Cricetidae	Neotominae	*Ochrotomys nuttalli*	Golden Mouse	TN, WV	93/147	https://doi.org/10.15468/dl.jueku4	Donald W. Linzey , Robert L. Packard, Ochrotomys nuttalli, Mammalian Species, Issue 75, 15 June 1977, Pages 1–6, https://doi.org/10.2307/3503860
Cricetidae	Neotominae	*Peromyscus gossypinus*	Cotton Mouse	KY, VA; protected heritage species KY	420/667	https://doi.org/10.15468/dl.n23x74	James L. Wolfe , Alicia V. Linzey, Peromyscus gossypinus, Mammalian Species, Issue 70, 15 June 1977, Pages 1–5, https://doi.org/10.2307/3503898
Cricetidae	Neotominae	*Peromyscus leucopus*	White-footed Mouse	subspecies outside of study area	1199/1903	https://doi.org/10.15468/dl.3vc4xw	James Alden Lackey and others, Peromyscus leucopus, Mammalian Species, Issue 247, 13

Table 2.1 Continued

Cricetidae	Neotominae	*Peromyscus maniculatus*	Deer Mouse	none	470/751	https://doi.org/10.15468/dl.6ksurg	Unavailable- utilized Hall's Mammals of North America only
Cricetidae	Neotominae	*Peromyscus polionotus*	Oldfield mouse	subspecies outside of study area	44/72	https://doi.org/10.15468/dl.ngxdfk	Unavailable- utilized Hall's Mammals of North America only
Cricetidae	Neotominae	*Reithrodontomys humulis*	Eastern Harvest Mouse	MD, WV	64/16	https://doi.org/10.15468/dl.3xq5f7	Dick T. Stalling, Reithrodontomys humulis, Mammalian Species, Issue 565, 24 October 1997, Pages 1–6, https://doi.org/10.2307/3504466
Cricetidae	Sigmodontinae	*Oryzomys palustris*	Marsh Rice Rat	subspecies outside of study area of federal concern	114/179	https://doi.org/10.15468/dl.7c58vc	James L. Wolfe, Oryzomys palustris, Mammalian Species, Issue 176, 18 June 1982, Pages 1–6, https://doi.org/10.2307/3503921
Cricetidae	Sigmodontinae	*Sigmodon hispidus*	Hispid Cotton Rat	none	237/751	https://doi.org/10.15468/dl.7k2hmy	Guy N. Cameron, Stephen R. Spencer, Sigmodon hispidus, Mammalian Species, Issue 158, 3 December 1981, Pages 1–9, https://doi.org/10.2307/3504057
Erethizontidae	Erethizontinae	*Erethizon dorsatum**	North American Porcupine	MD, WV	66/107	https://doi.org/10.15468/dl.657jwx	Charles A. Woods, Erethizon dorsatum, Mammalian Species, Issue 29, 13 June 1973, Pages 1–6, https://doi.org/10.2307/3504036
Sciuridae	Sciurinae	*Glaucomys sabrinus**	Northern Flying Squirrel	G. s. coloratus/ G. s. fuscus federally endangered; MD, NC, TN, VA, WV	61/104	https://doi.org/10.15468/dl.y74cy7	Nancy Wells-Gosling , Lawrence R. Heaney, Glaucomys sabrinus, Mammalian Species, Issue 229, 14 November 1984, Pages 1–8, https://doi.org/10.2307/3503926
Sciuridae	Sciurinae	*Glaucomys volans*	Southern Flying Squirrel	none	213/345	https://doi.org/10.15468/dl.n8vnsw	Patricia G. Dolan , Dilford C. Carter, Glaucomys volans, Mammalian Species, Issue 78, 15 June 1977, Pages 1–6, https://doi.org/10.2307/3504026
Sciuridae	Sciurinae	*Sciurus carolinensis*	Eastern Gray Squirrel	none	283/809	https://doi.org/10.15468/dl.yhrvq8	John L. Koprowski, Sciurus carolinensis, Mammalian Species, Issue 480, 2 December 1994, Pages 1–9, https://doi.org/10.2307/3504224

Table 2.1 Continued

Sciuridae	Sciurinae	*Sciurus niger*	Fox Squirrel	S. n. niger SC, VA	274/445	https://doi.org/10.15468/dl.w322kg	John L. Koprowski, Sciurus niger, Mammalian Species, Issue 479, 2 December 1994, Pages 1–9, https://doi.org/10.2307/3504263
Sciuridae	Sciurinae	*Tamiasciurus hudsonicus**	American Red Squirrel	GA, TN	2055/3257	https://doi.org/10.15468/dl.sfd8bq	Michael A. Steele, Tamiasciurus hudsonicus, Mammalian Species, Issue 586, 1 June 1998, Pages 1–9, https://doi.org/10.2307/3504443
Sciuridae	Xerinae	*Marmota monax*	Groundhog	none	87/182	https://doi.org/10.15468/dl.2fpj5w	Gary G. Kwiecinski, Marmota monax, Mammalian Species, Issue 591, 4 December 1998, Pages 1–8, https://doi.org/10.2307/3504364
Sciuridae	Xerinae	*Tamias striatus*	Eastern Chipmunk	none	274/445	https://doi.org/10.15468/dl.q7hk3z	Dana P. Snyder, Tamias striatus, Mammalian Species, Issue 168, 25 May 1982, Pages 1–8, https://doi.org/10.2307/3503819
Zapodidae	Zapodinae	*Napaeozapus insignis**	Woodland Jumping Mouse	TN, SC	169/266	https://doi.org/10.15468/dl.t6zd4s	John O. Whitaker, Jr. , Robert E. Wrigley, Napaeozapus insignis, Mammalian Species, Issue 14, 16 June 1972, Pages 1–6, https://doi.org/10.2307/3503916
Zapodidae	Zapodinae	*Zapus hudsonius*	Meadow Jumping Mouse	AL, TN, WV	134/33	https://doi.org/10.15468/dl.ekgdnd	John O. Whitaker, Jr., Zapus hudsonius, Mammalian Species, Issue 11, 16 June 1972, Pages 1–7, https://doi.org/10.2307/3504066
Ursidae	Ursinae	Ursus americanus	American Black Bear	AL, KY, SC	62/101	https://doi.org/10.15468/dl.6mzsyc	Serge Larivière, Ursus americanus, Mammalian Species, Issue 647, 23 January 2001, Pages 1–11, https://doi.org/10.2307/0.647.1

Table 2.2. Size of Core Climate Refugia by Species. Core climate refugia sizes by species, with largest cores for those that are highly fragmented and shortest distance between cores. Grayed out portions indicate that climatic isolation is not predicted for that species.

Species	Largest Core Climate Refugia (sq km)	Largest Fragmented Cores (sq km)	Shortest Distances between Cores (km)
Castor canadensis	46,442	46,422; 15,820; 8,545	753; 447
Clethrionomys gapperi	176,330		
Erethizon dorsatum	131,006		
Glaucomys sabrinus	209,254		
Glaucomys volans	250,576		
Marmota monax	252,211		
Microtus chrotorrhinus	1,079	1,079; 338; 276	Adjacent; 43
Microtus ochrogaster	67,094	67,094; 51,175; 1,225	5; 61
Microtus pennsylvanicus	287,195		
Mictrotus pinetorum	342,246		
Napaeozapus insignis	187,404		
Neotoma floridana	200,836		
Neotoma magister	158,514		
Ochrotomys nuttalli	154,124		
Ondatra zibethicus	267,190		
Oryzomys palustris	37,405	37,405; 9,529; 1,489	70; 591
Peromyscus gossypinus	124,483		
Peromyscus leucopus	342,314		
Peromyscus maniculatus	336,367		
Peromyscus polionotus	2,660	2,660; 2,527; 2,017	307; 138
Reithrodontomys humulis	71,384	71,384; 10, 228; 1,241	13; 163
Sciurus carolinensis	341,991		
Sciurus niger	254,037		
Sigmodon hispidus	62,787	62,787; 14,463; 2,987	32; 24
Synaptomys cooperi	256,501		
Tamiasciurus hudsonicus	235,759		

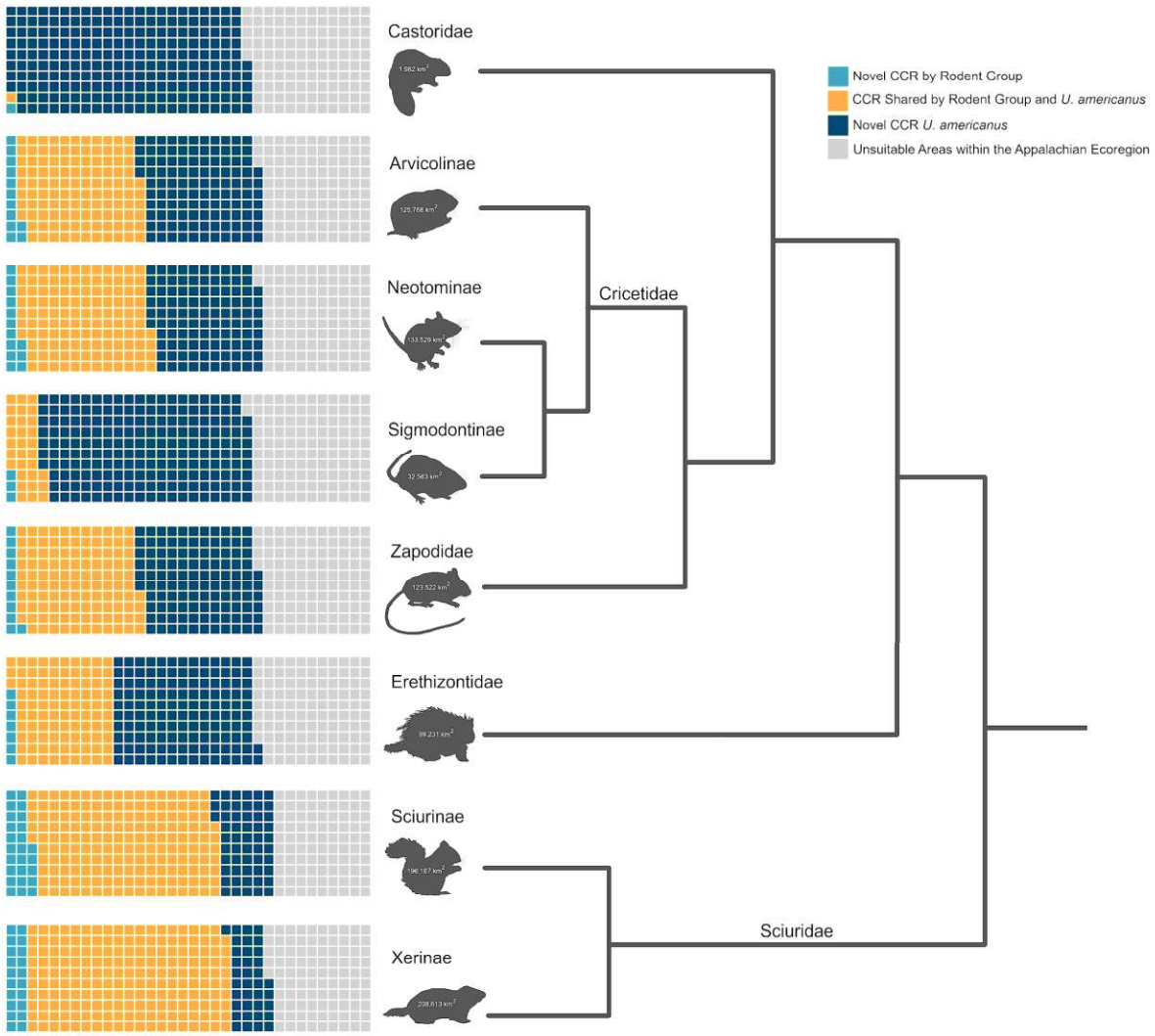
Table 2.2 Continued

Tamias striatus	319,649		
Zapus hudsonius	86,629	86,629; 17,155; 16,846; 9,760	109; 17; 17
Ursus americanus	297,717		

FIGURES

Figure 2.1. Refugia Summaries by Family/Subfamily. Breakdown of the climate refugia (CCR) overlap by family, or if applicable subfamily. The silhouette shows the average amount of CCR with appropriate land cover (in square kilometers) for each family/subfamily listed, whereas the light teal blue bar shows the average percentage of climate refugia novel to that rodent group, the light orange shows the overlap between that rodent group's CCR and the CCR of *Ursus americanus*, the dark blue shows the novel CCR to *U. americanus*, and the gray represents the parts of the Appalachian Ecoregion that have unsuitable climate or land cover. Each cube represents 1,000 square kilometers. To the right of the waffle charts is a phylogeny based on (Steppan & Schenk, 2017), showing respective relationships between the groups shown above.

Climate Change Refugia (CCR) Overlap by Rodent Family/Subfamily



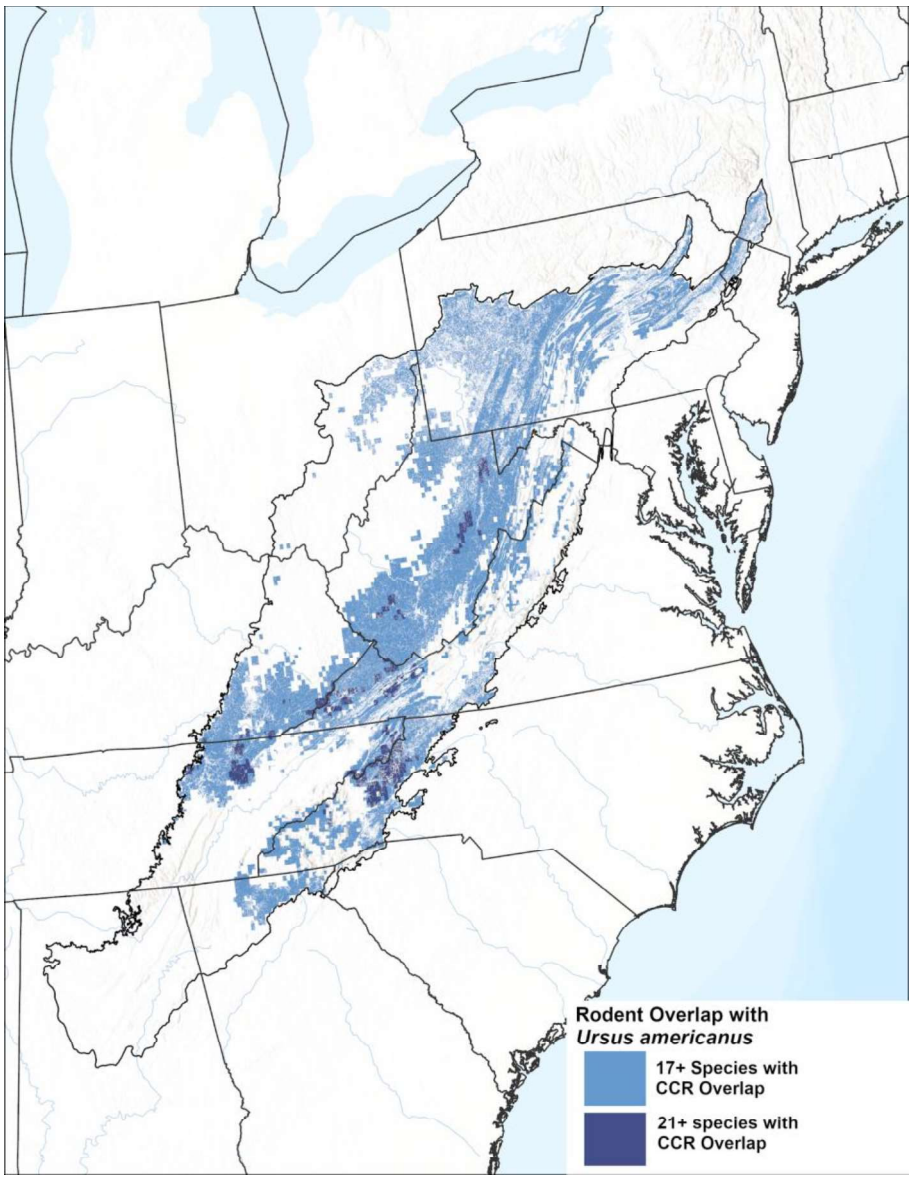


Figure 2.2. Key Rodent Refugia Overlap with Bear Refugia. Areas of highest rodent climate refugia density that overlap with the stable climate refugia of the American black bear (*Ursus americanus*) within the Appalachian Ecoregion. Areas shown in lighter blue represent a consensus of rodent stable climate refugia that have been categorized as rodent hotspots (17+ species; 113,132 km²), whereas darker blue represents a consensus of rodent priority climate refugia areas (21+ species; 7,049 km²).

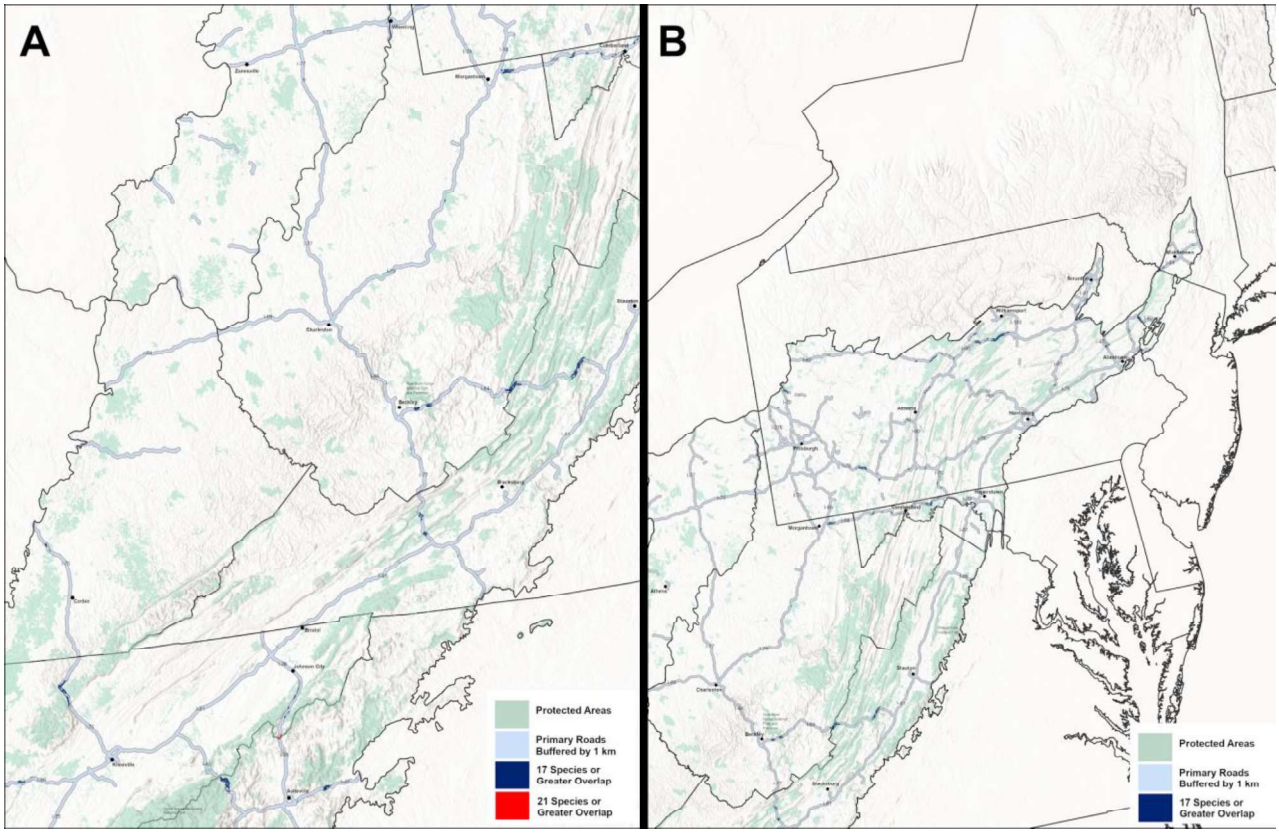


Figure 2.3. Overlap of Refugia with Primary Roadways and Protected Areas. A. Central portion of the Appalachian Ecoregion with key primary roadway barriers (gray) to dispersal in priority (red) and hotspot (blue) refugial areas for rodents and the American black bear; *B* Shows the same for the northern extent of the Appalachian Ecoregion. Major cities and National Parks are included as points of reference.

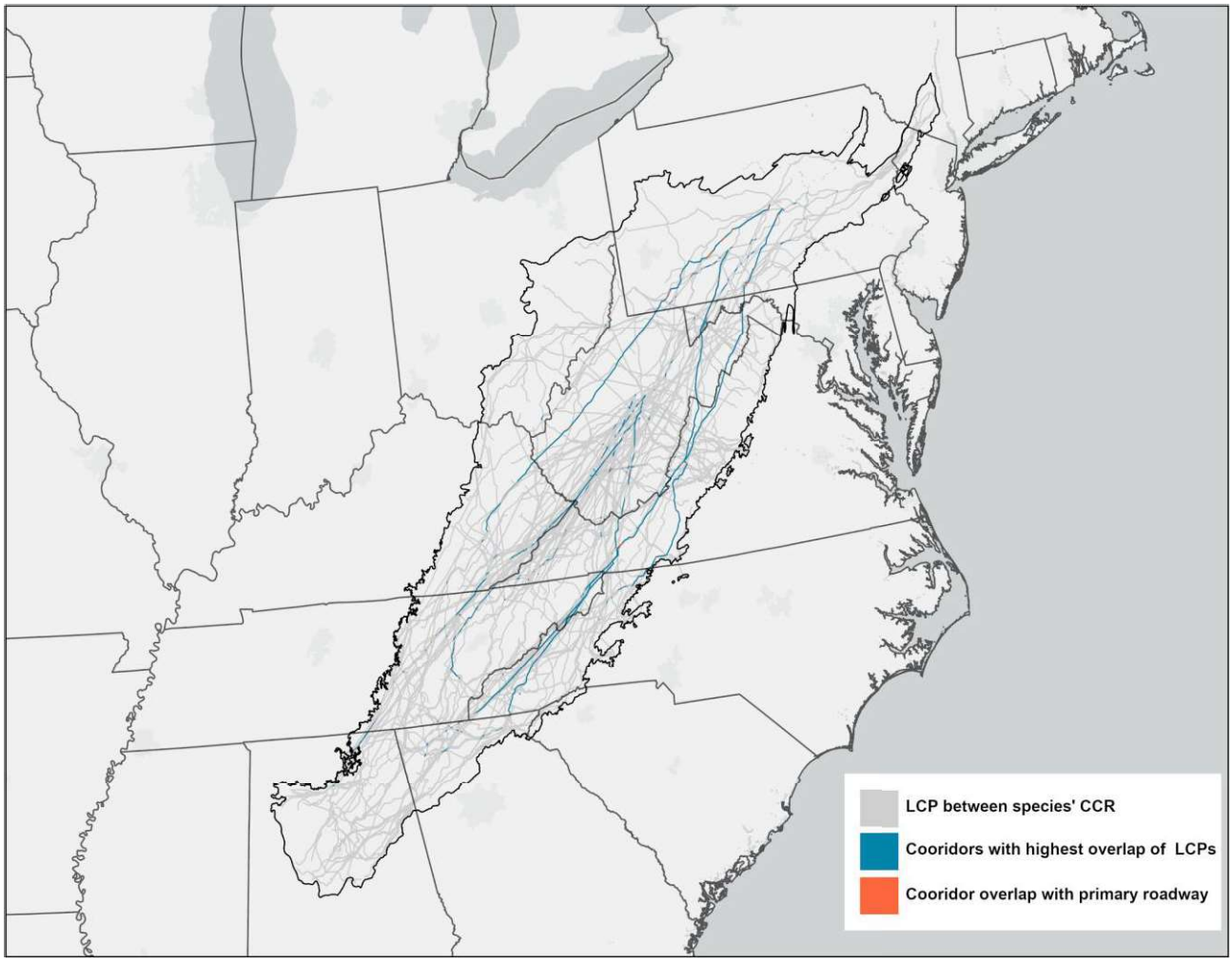


Figure 2.4. Least Cost Pathway Refugial Corridors. Climate connectivity corridors between stable climate change refugia (CCR) for rodents in the Appalachian Ecoregion. The least cost pathways (LCP), or "best case scenarios" are the shortest paths between these CCRs by species and are shown in darker gray; travel corridors that statistically have the most LCPs within a 1km radius are shown in blue; areas where these travel corridors overlap with primary roadways within the Appalachians, which are known barriers to species dispersal, are shown in red.

CHAPTER III:
REINTRODUCTION EFFORTS IN APPALACHIA AND CLIMATE SUITABILITY OF THE FOUR SUBSPECIES OF WAPITI IN NORTH AMERICA

ABSTRACT

Historically, human colonization events have had severe negatives impact on biodiversity globally. In North America, prominent examples of such negative impacts are the eradication of over 60 million American bison by the 1870s, and extirpation of the once numerous (about 10 million individuals) wapiti (*Cervus canadensis*) from most of its historical range following European colonization, including the extinction of two subspecies (*C. c. merriami* and *C. c. canadensis*). Given successful reintroductions of wapiti in the western U.S., we investigated the efforts to restore this species' range in the Appalachian Mountains, where *C. c. canadensis*, a now extinct subspecies, once lived. We utilized ecological niche modeling, coupled with an extensive literature review of wapiti genetics and ecology, to create climate suitability models through the 2040s for each of the four subspecies of wapiti both at the continental scale and focused solely on the Appalachians. Results showed that the Tule and Roosevelt wapiti have separate climatic niches from all other subspecies, whereas the Rocky Mountain wapiti showed high degrees of overlap with the Manitoba subspecies in the west. In the Appalachians, the Rocky Mountain wapiti showed the highest degree of climatic suitability through the 2040s, whereas the Manitoba wapiti had no suitable climate predicted present. Previous studies found that the populations of Manitoba wapiti, the source for reintroductions in Tennessee and North Carolina, underwent a severe bottleneck in 1906, reducing the alleles and heterozygosity to that of a founder population that was specific to Alberta, Canada. Lack of genetic diversity within release sites in Tennessee and North Carolina, small population size with low growth, and lack of suitable climate are severely limiting the restoration potential in the southern Appalachians. Through a summary of literature in the region, as well as novel climate and refugial maps for the wapiti we aim to promote greater restoration success, much like has been experienced in

Kentucky. Finally, we wish this study will serve as a research template for necessary modeling and carefully informed selection of variables for a species long considered a “generalist” ecologically, but which may be experiencing reintroduction setbacks due to a cascade of effects and potential susceptibility to stressors including maladaptation to regional climate.

INTRODUCTION

Humans have created an ongoing biodiversity crisis that has resulted in the decline in nearly half of all vertebrate populations globally (Davis et al., 2018; Finn et al., 2023; Myers, 1996; O'Connor et al., 2020; Rull, 2022). One tool to combatting these losses is species reintroductions to their historical ranges (Evans et al., 2022; Seddon et al., 2007). The International Union for the Conservation of Nature (IUCN)'s Species Survival Commission (SSC) published a series of guidelines and deemed "re-introduction" as attempting to establish a species in part of its historical range where previously extirpated or extinct (IUCN, 1998). A critical step in the reintroduction process is to determine the cause of extirpation/extinction to ensure that the reintroduced population does not meet a similar demise (IUCN, 1998). Wolf et al (1998) cite three factors as critical for reintroduction success: (a) quality of site habitat; (b) location site relative to historic range; and (c) released number of individuals at a site. Though occurring globally, extensive literature, detailed planning, and conservation success has been documented among charismatic fauna and/or keystone species, such as the black-footed ferret (*Mustela nigripes*), California condor (*Gymnogyps californianus*), gray wolf (*Canis lupus*), sea otter (*Enhydra lutris*), and prairie dogs (*Cynomys* spp.) in North America (Hale & Koprowski, 2018; Martínez-Meyer et al., 2006; Sarrazin & Barbault, 1996). More recently and as a case study for reintroduction efforts, is the wapiti, an eastern keystone species and a game species.

The wapiti (*Cervus canadensis*; or American Elk) as it is globally referred to avoid confusion with the elk (= Moose; *Alces alces*), is a name derived from the indigenous Shawnee people's word meaning "white rump" (National Park Service, 2023). It is the second largest member of the deer family Cervidae (following *A. alces*), with *C. canadensis* initially, and even in recent literature, lumped with the Eurasian species, *C. elaphus* (red deer). However, based on the litany genetic data (Doan et al., 2022; Hu et al., 2019; Lorenzini & Garofalo, 2015; Ludt et

al., 2004; Meiri et al., 2018; Pitra et al., 2004; Polziehn & Strobeck, 1998), geographical distance, and morphological and behavioral differences (e.g. difference in the larynx producing different calls, with the wapiti bugling versus the red deer which has a lower pitched "roar") (Frey & Riede, 2013), we followed recommendations of treating *C. canadensis* as its own separate species rather than a subspecies. The genus *Cervus* appears to have first originated around the Miocene-Pliocene transition and spread of C4 grasslands in Asia (Di Stefano & Petronio, 2002), with subsequent divergence about 6 mya into an "Eastern clade" consisting of *C. nippon* and *C. canadensis* of eastern Asia and North America, and a "Western clade" of *C. elaphus* from Europe, North Africa, and east-central Asia (Lorenzini & Garofalo, 2015). The *C. canadensis* lineage then split from *C. nippon* roughly 2 mya during the Pleistocene, further deriving the wapiti lineage from *C. elaphus* as the former spread across the Bering Land Bridge during variation in glacial cycles to colonize North America (Lorenzini & Garofalo, 2015). Prior to European colonization, six subspecies of wapiti (=American Elk; *Cervus canadensis*) spanned the North American continent with population estimates near 10 million individuals (O'Gara & Dundas, 2002; Popp et al., 2014). Habitat loss and overhunting through the mid-twentieth century reduced wapiti populations to only half a million individuals, mostly in the west, and caused the extirpation of the eastern wapiti (*C. c. canadensis*) and Merriam's wapiti (*C. C. merriami*) (O'Gara & Dundas, 2002; Popp et al., 2014). Today, estimates of wapiti populations are slightly over 1 million individuals (Popp et al., 2014), with reintroduction efforts having mixed results (O'Gara & Dundas, 2002).

Popp et al (2014) note that elk restoration in eastern North America has been understudied, with populations such as the Pennsylvania herd being studied over half a century post-release (Banfield & Rosenberry, 2020; Kentucky Department of Fish and Wildlife

Resources, 2015; Larkin et al., 2003). Indeed, reintroduced wapiti in the east have been noted (Padilla et al., 2023) as lacking in the research prevalent of their western counterparts (e.g., Amor et al., 2019; Bender et al., 2012; Christianson & Creel, 2007; McCorquodale, 2003; Rickbeil et al., 2019; Rowland et al., 2000). Padilla et al. (2023) note the differences in habitat type, weather, predation, and private-public land interface of the eastern North American populations compared to those out west (Brough et al., 2017; Radeloff et al., 2005; Webb et al., 2011), with additional challenges to reintroduction efforts arising from concerns of transmission of diseases (Padilla et al., 2023; Kurth, 2022).

The IUCN (IUCN, 1998) strongly encourages due diligence in researching areas for reintroductions and maintaining studies to ensure success, making study of the wapiti ideal. Martinez-Meyer et al (Martínez-Meyer et al., 2006) explicitly state the need for consideration of climate change and long term effects on a particular release site and surrounding area, particularly during the planning stage of reintroduction. Given the lack of climate studies featuring wapiti released into the Appalachians and eastern North America, we investigated whether geographically and/or genetically separated subspecies of wapiti have distinct climatic niches. To do this, we conducted a detailed review of wapiti genetics, as well as extirpation and recovery of populations across the continent, and subsequently created ecological niche models using baseline climatic conditions, when many population recovery efforts began (1970-2000), and projected the models to near future conditions (2021-2040). We also evaluated whether the wapiti released in the Appalachian Mountains were predicted to have climatic suitability in this region, hence be climatically adapted to this region now and into the future. We modeled all subspecies and projected them to the Appalachians, and evaluated the performance of all

subspecies for comparison, though with a predominant focus on the Rocky Mountain, Manitoban, and potential hybrid of the subspecies.

Literature Review: Overview of reintroductions within the Appalachians by state

Kentucky: *Cervus canadensis nelsoni*

Kentucky Department of Fish and Wildlife Resources carried out a habitat study as well as public survey prior to releasing the first herd in the state of Kentucky, finding that eastern Kentucky was biologically appropriate in terms of land base, human population, and lack of large scale agriculture (Kentucky Department of Fish and Wildlife Resources, 2015; Larkin, 2001). With overwhelming public support (Maehr et al., 1999), 1,541 wapiti were translocated to Kentucky from Arizona, Kansas, North Dakota, New Mexico, Oregon and Utah, from 1997-2002 (Kentucky Department of Fish and Wildlife Resources, 2015; Larkin, 2001; Larkin et al., 2003; Maehr et al., 1999; Seward, 2003). The initial 8 counties where wapiti in Kentucky were released were: Pike, Martin, Floyd, Knott, Letcher, Perry, Leslie, and Bell (Kentucky Department of Fish and Wildlife Resources, 2015); with the original restoration zone including the surrounding Johnson, Magoffin, Breathitt, Clay, and Knox counties, followed by the addition of Whitley and McCreary counties in 2004 to connect to Tennessee's restoration zone (Kentucky Department of Fish and Wildlife Resources, 2015). Within the Kentucky restoration zone of over 4 million acres, 87% of the land is privately owned, making management of habitat quality for the herd a challenge (Kentucky Department of Fish and Wildlife Resources, 2015). As of 2018, refined abundance estimates place the Kentucky wapiti population at around 7,000 individuals (Crank et al., 2019).

Tennessee: *Cervus canadensis manitobensis*

Tennessee Wildlife Resource Agency evaluated the potential for wapiti restoration in 1996 utilizing the following guidelines: a) 200,000 acre or greater area; (b) significant portion public land; (c) land cover significantly open or able to be converted to open; (d) potential for public hunting; and (e) avoid crop disturbance (Tennessee Wildlife Resource Agency, 2018; Wathen et al., 1997). After some initial debate as to release location, in 2000, TWRA proposed a restoration zone of 670,000 acres in Scott, Campbell, Claiborne, Anderson, and Morgan counties, contiguous with Kentucky's wapiti restoration zone (Tennessee Wildlife Resource Agency, 2000, 2018). This restoration area encompassed the North Cumberland Wildlife Management Area (WMA; = Royal Blue WMA) and was proposed to have 400 wapiti released starting in 2000 (Tennessee Wildlife Resource Agency, 2000, 2018). Source populations were imported from Elk Island National Park (Alberta, Canada) given the distance from chronic wasting disease (CWD) outbreaks and rigorous pathogen testing protocols, with releases occurring from 2000-2002 (Lupardus et al., 2011; Tennessee Wildlife Resource Agency, 2018); however, in 2003 and 2008 wapiti were obtained from Land Between the Lakes (Kentucky) given lack of availability from Elk Island National Park (Lupardus et al., 2011; Tennessee Wildlife Resource Agency, 2018). Given the prevalence of CWD and concern with disease introductions, no wapiti have been released in Tennessee since 2008 nor is there a recommendation for the release of more through 2027, resulting in a release total of 201 individuals (Tennessee Wildlife Resource Agency, 2018). Population estimates for the Tennessee wapiti herd as of 2016 was roughly 349 individuals, though uncertainty was high (Tennessee Wildlife Resource Agency, 2018).

Virginia: *Cervus canadensis nelsoni*

After failed restoration efforts in the early twentieth century due to poor habitat quality, site selection, and improper harvest management, in 1997 Virginia Department of Game and Inland Fisheries proposed a new plan to release wapiti (over 1,540 individuals) into the eastern portion of the state over the course of five years (Virginia Department of Game and Inland Fisheries, 2019). Planning commenced with identifying locations of suitable habitat for restoration site and building public support, though with pathogen spread a major concern, these efforts would stall out (Virginia Department of Game and Inland Fisheries, 2019). In 2000, given the spread and establishment of populations from Kentucky into Virginia despite legal harvest of either sex, the lack of detection of pathogens, and renewed public interest, discussions continued until 2009 when new evaluations of southwest Virginia for potential restoration sites began (Virginia Department of Game and Inland Fisheries, 2019). As such, hunting of dispersing wapiti was banned in 2011 in Buchanan, Wise, and Dickenson counties (=the Virginia Elk Restoration Area); 75 wapiti were released between 2012 and 2014 onto reclaimed mining lands in Buchanan County (Virginia Department of Game and Inland Fisheries, 2019). Release of wapiti into this region was a polarizing decision with Buchanan County being targeted for passive restoration in an attempt to further surrounding counties' acceptance of these animals (Virginia Department of Game and Inland Fisheries, 2019). The source for the wapiti translocation from 2012 to 2014 was the Kentucky herd, with harvest proposed to be banned in the surrounding restoration area counties in 2013 and again in 2015, but was met with strong opposition, preventing enactment in either instance (Virginia Department of Game and Inland Fisheries, 2019). More recent surveys and education efforts have reported positive responses to the presence of wapiti in the area, which would benefit the Virginia herd given the prediction that the currently occupied area is

likely close to carrying capacity and incapable of sustained growth of the wapiti population at the current rate (Virginia Department of Game and Inland Fisheries, 2019).

West Virginia: *Cervus canadensis nelsoni*

West Virginia Division of Natural Resources began looking at feasible options for wapiti restoration in 1972, and again in 2005 with the assessment of potential habitat and restoration areas on the landscape, particularly given the success of the Kentucky wapiti herd and subsequent natural immigration of individuals into West Virginia (West Virginia Division of Natural Resources, 2021). Initial wapiti management plans were drafted between 2011 and 2015, with an official management area and damage fund for agricultural loss being passed by state legislature (West Virginia Division of Natural Resources, 2021). The Tomblin Wildlife Management Area was designated after acquisition of 44,000 acres of habitat for an initial wapiti release site; in 2016, 24 wapiti were captured from the Kentucky Land Between the Lakes Recreation Area and released in West Virginia (West Virginia Division of Natural Resources, 2021). An additional 46 individuals were transferred from the Arizona herd and released in 2018 (West Virginia Division of Natural Resources, 2021). Given the West Virginia herd is still in early stages of release, the estimated total number of animals was 85, prior to calves being born in 2021 (West Virginia Division of Natural Resources, 2021). The restoration zone in West Virginia overlaps Wayne, Lincoln, Boone, Logan, Mingo, Wyoming, and McDowell counties, forming a contiguous patch with the Virginia and Kentucky adjacent wapiti herds (West Virginia Division of Natural Resources, 2021).

North Carolina: *Cervus canadensis manitobensis*

In 2001, 25 wapiti were released experimentally into the Great Smoky Mountains National Park, from the Land Between the Lakes in Kentucky, followed by an additional 27 individuals in 2002, to Cataloochee, NC (North Carolina Wildlife Resources Commission, 2013). In 2008, the population was deemed stable enough to be considered a successful reintroduction, with North Carolina Wildlife Resource Commission estimating between 150-200 wapiti occupying Haywood, Jackson, and Swain counties (North Carolina Wildlife Resources Commission, 2013). Overarching restoration goals for North Carolina include a harvestable population outside of the National Park, with management involving collaboration and cooperation between the Eastern Band of Cherokee Indians, NPS, public, and private landowners (North Carolina Wildlife Resources Commission, 2013).

Pennsylvania: *Cervus canadensis nelsoni*

Attempts to reintroduce wapiti to Pennsylvania in the early 20th century were poorly documented, with initial 50 individuals reintroduced from Yellowstone National Park in 1913 and additional 22 animals donated from a private reserve in Monroe County, and subsequent reintroductions in 1915 from Yellowstone National Park (95), and Wind Cave National Park in 1924 and 1926 (10 bulls total) (Banfield & Rosenberry, 2020). Most likely due to persecution in response to crop damage, this initial population became depleted, and reintroductions were considered failed mostly, with populations unknown for nearly 40 years and estimates between 14-100 individuals remaining (Banfield & Rosenberry, 2020). A management area was first defined in 1982, in a matrix of public land; public support indicated the presence of wapiti desirable in an area of 205 square miles in north-central Pennsylvania north of I-80 (Banfield &

Rosenberry, 2020). Natural dispersal to the southeast led to expansion of this management area by 2006 to include an area of 835 square miles in a landscape matrix with over 70% public land (Banfield & Rosenberry, 2020), Currently the wapiti management area in Pennsylvania occupies the north-central part of the state including Cameron, McKean, Elk, Clinton, Clearfield, Tioga, Potter, Lycoming, and Jefferson counties (3,757 square mile area); much of this is public land, with only 26% privately-owned (Banfield & Rosenberry, 2020). Estimates show that roughly half of this area is occupied, giving the wapiti room for population growth and expansion in the future. Population estimates for 2017 suggested the minimum number of individuals to be upward of 900 (Banfield & Rosenberry, 2020). Concerns from the Pennsylvania Game Commission have arisen due to the genetic bottleneck that occurred in the early-mid 20th century, with studies showing poor genetic diversity relative to Yellowstone stock, and though the population appears healthy, reproductive rates are "suspiciously low" (Banfield & Rosenberry, 2020).

METHODS

Species data and study area

All wapiti records were downloaded from the Global Biodiversity Information Facility (GBIF; see Appendix III: Supplementary 3.1). Fossil records were removed, as well as those missing latitude and longitude data, a year, and those with uncertainty greater than 10km. To match the temporal range of climate data with that of occurrence records, while ensuring that sample size needs for modeling were met, only records from 1960 to 2015 were used in this study. Points were then rarified to avoid biasing the model using the same grain as the climate data (2.5 arc minute resolution ~5km). For the creation of the models, points from the eastern US were excluded as those were introduced populations, however these were later used to

evaluate projections to the eastern half of the continent. Initial models were run utilizing the following groupings: *Cervus canadensis* (species level), *C. c. manitobensis, C. c. nannodes, C. c. nelsoni,* and *C. c. roosevelti*. There is also a debate regarding the validity of *C. c. manitobensis* and *C. c. nelsoni* as individual subspecies or if this is a result of extirpation. Therefore, we modeled *C. c. manitobensis* x *C. c. nelsoni* together and projected it as well for comparison. This is of particular importance given that both of these subspecies have been reintroduced to the Appalachians (*C. c. manitobensis* in Tennessee and North Carolina), and there is potential for hybridization. The models were run with the background sampling extent of wapiti in the west created using available points and overlaying the Environmental Protection Agency (EPA) Level III Ecoregions (Commission for Environmental Cooperation, 1997) in that region (Appendix III: Supplementary 3.2).

Climate data

All models were run initially with all 19 bioclimatic variables from WorldClim 2 (ttps://www.worldclim.org/data/index.html; (Fick & Hijmans, 2017) at 2.5 arc minute resolution for a baseline climate of 1970-2000. Following the methods of Chapters 1 and 2, the baseline ecological niche models were projected onto future climatic conditions from two Shared Socioeconomic Pathways, SSP 2.45 and SSP 3.70, across a range of low, medium, and high temperature and precipitation change Global Circulation Models from CMIP6 (Coupled Model Intercomparison Projects 6), GCM CNR-ESM2-1, GCM CNRM-CM6-1, and GCM CanESM, for the near future (2021-2040) (Fick & Hijmans, 2017). Consensus forecasts were created to determine a minimum-maximum predicted climatically suitable area from each model for near future, as well as individual models for comparison.

Ecological niche model parameters and evaluation metrics

Models were trained to the extent of species, subspecies, or hybrid ranges utilizing all variables initially, and then rerun a second time with a subset of variables contributing to the model (greater than 1%) and projected to estimate the potential climatic suitability continent-wide (Appendix III: Supplementary 3.3). We ran maximum entropy (Maxent) models with standard methodology including no clamping or extrapolation, 5,000 iterations crossvalidated among ten replicates, logistic output, and the average raster of all replicates was thresholded to minimum training presence, the suitability probability value at which all training data are classified as present or suitable. Models were evaluated internally via AUC, and externally through Sensitivity (=calculated with additional data that was not used in the models). Additionally, we ran a third set of models to determine the ability of one taxon to predict the distribution (known occurrences) of another taxon by using all known records to test the reciprocal prediction (training+testing+external testing). The degree of climatic niche overlap between subspecies was evaluated using training/testing points as well as those points omitted from the model due to close proximity for that subspecies range. These reciprocal models were projected across the historic range of the wapiti for each species, subspecies, and the hybrid, and evaluated for degree of overlap with other subspecies through known occurrence points post-2020. For projections we also utilized Multivariate Environmental Similarity Surfaces (MESS) to measure the degree of similarity between the environments of the training data with respect to the variables utilized in model creation and the projected new environments (i.e. the Appalachian Ecoregion) (Elith et al., 2010). In MESS analysis, negative values represent dissimilarity in that the values present in the new environment fall outside of the range of training environments; scores will vary by the number of variables and degree of difference in environments (Elith et al., 2010). We also utilized Limiting Factor analysis (LF) to highlight the areas driving dissimilarity

in predictions; for this analysis, each variable in the new environment was changed to the mean value of that particular variable for the training region while measuring model response (Elith et al., 2010). The Limiting Factor is determined when that particular variable change results in a higher predicted probability of a species occurring in the new environment relative to all other variables (Elith et al., 2010). Through examination of the LFs of each subspecies, we determined why a particular area may be predicted unsuitable. This information may inform future studies predicting thermal tolerance or even provide linkages to particular habitat management strategies for vegetation types preferred by the wapiti.

Post-model processing: Appalachian Ecoregion

For our focal area of wapiti reintroduction in the Appalachian ecoregion, we eliminated unsuitable land cover for long term persistence for the wapiti using the National Land Cover Dataset (NLCD CONUS) for 2019 at 30-meter resolution (Dewitz, 2021). The areas removed included developed areas, barren spaces, and croplands, given the generalist nature of this species. In evaluating the climate suitability of the reintroduced wapiti subspecies to the Appalachian ecoregion, we also specifically evaluated counties of initial wapiti release as well as the neighboring counties to predict climate suitability in the event of population expansion.

RESULTS

Baseline climate

Species level: Wapiti

Grouping *Cervus canadensis* at the species level (534 occurrences) and running the model based on current ecoregion distribution based on species-level occurrences across the continent led to the following most contributing variables: precipitation of the coldest quarter (23.9%), isothermality (20.7%), mean temperature of the warmest quarter (14.3%), mean

temperature of the wettest quarter (8.6%), precipitation of the warmest quarter (6.1%), mean diurnal range (5.5%); maximum temperature of the warmest month, precipitation of the driest month and quarter, temperature seasonality, temperature annual range, precipitation seasonality, mean temperature of the coldest quarter, and annual mean temperature had low contributions to model accuracy gain (<5% each). Variables excluded were minimum temperature of the coldest month, mean temperature of the driest quarter, annual precipitation, precipitation of the wettest month and quarter. A commonality between this and all subspecies/hybrid models was the exclusion of the precipitation of the wettest quarter variable. Model projections to the baseline climate (1970-2000) predicted the largest suitable climate range for the wapiti, encompassing 99.7% of all wapiti points, including occurrences not used in the model for a total of 2280/2288 throughout the historic range, including all points in the east (72/72) (Appendix III: Supplementary 3.4). Predictions projected through the historic range are shown in Figure 3.1A, with the mean AUC value 0.854 (Appendix III: Supplementary 3.4). MESS analysis and Limiting Factor analysis (Appendix III: Supplementary 3.5; range of MESS -380 to 55) showed some differences in climatic niche present along the North Carolina-Georgia-South Carolina border (scores ranging from -30 to 0) within the Appalachian ecoregion. Throughout the Appalachian Ecoregion, aside from the dissimilar areas, MESS scores were predominantly 0 to 10, with isothermality as the limiting factor isothermality in that area.

Manitoba Wapiti: *Cervus canadensis manitobensis*

The variables contributing most to the model of the subspecies\ *C. c. manitobensis* (40 occurrences) were: precipitation of the coldest quarter (28.3 %), mean temperature of the wettest quarter (17.5%) and driest quarter (12.1%) precipitation of the wettest month (10.8%), annual precipitation (10.7%), temperature seasonality (5.3%); maximum temperature of the warmest

month, precipitation seasonality, annual mean temperature, temperature annual range, precipitation of the driest and coldest quarters, and mean temperature of the coldest quarter each contributed <5%. Variables excluded were mean diurnal range, isothermality, minimum temperature of the coldest month, mean temperature of the warmest quarter, and precipitation of the driest month and wettest quarter. Baseline projections showed overlapping suitability with all points of this subspecies, including 28 occurrences not used in the model training (100% correctly predicted; total 68/68), with the mean AUC value 0.774. Outside of the initially examined background region of the Great Plains, climate suitability was also predicted overlapping with 48.9% of the *C. c. nelsoni* points (906/1854), particularly in Arizona and New Mexico, large portions of Colorado and Montana, southern Utah, eastern Idaho, and parts of Alberta and British Columbia (Fig. 3.1B). Additionally, the population of *C. c. manitobensis* for the baseline did not show predicted climate suitability in the east south of Michigan. MESS and Limiting Factor analysis showing strong differences in the southeast, particularly in southwest North Carolina-South Carolina-Georgia borders within the Appalachian ecoregion (scores -175 to -75). Most of the Appalachians falls within the highly dissimilar category, with negative MESS scores ranging from -1 in the northwestern part of the Appalachian ecoregion in Ohio and Pennsylvania to -175 as mentioned above in the southwestern Appalachians. The most limiting variable in this area was the precipitation of the coldest quarter.

Tule Wapiti: *Cervus canadensis nannodes*

The variables contributing most to the models for *C. c. nannodes* (11 occurrences) were: precipitation seasonality (40.8%), precipitation of the warmest quarter (26.2%), mean temperature of the wettest quarter (16.3%), precipitation of the driest quarter (9.4%); the variables that contributed least were: precipitation of the wettest month, isothermality, and

precipitation of the driest month and coldest quarter (<5% each). Variables excluded from the model were annual mean temperature, mean diurnal range, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the driest quarter, mean temperatures of the warmest and coldest quarters, and precipitation of the wettest quarter. Only a few areas northward in south-central Washington were found to be climatically similar to their current range (Fig. 3.1C), and no region predicted suitable for *C. c. nannodes* was found to overlap the other subspecies. All points used in the model were predicted suitable for *C. c. nannodes*, including an additional 16 occurrences (100%; total 27/27), with the mean AUC 0.94. *Cervus canadensis nannodes* was not predicted to have suitable climate outside of California and Washington state. MESS and Limiting Factor analysis showed strong climatic differences along the Georgia-South Carolina-North Carolina border (-380 to -100) within the Appalachian Ecoregion, though the entirety is the most dissimilar of all the subspecies according to MESS analyses with the majority of the Ecoregion showing MESS values from -250 to -100 and at most -75 within the northeastern portion of the Appalachian Ecoregion. The limiting factors were precipitation of the warmest quarter and precipitation of the driest month.

Rocky Mountain Wapiti: *Cervus canadensis nelsoni*

For *C. c. nelsoni* (356 occurrences), the variables with the highest contribution were on average: precipitation of the driest month (29.3%), mean diurnal range (23.4%), precipitation of the warmest quarter (12%), isothermality (11.8%), annual precipitation (5.5%), mean temperature of the wettest quarter (5%); least contributing variables were: mean temperature of the coldest quarter, annual mean temperature, precipitation seasonality, minimum temperature of the coldest month, and mean temperature of the driest quarter (<5% each). Excluded from the

model were temperature seasonality, maximum temperature of the warmest month, temperature annual range, mean temperature of the warmest quarter, precipitation of the wettest month, and precipitation of the wettest, driest, and coldest quarters. All points utilized in the model were predicted correctly, with additional occurrence predictions leading to a total of 99.9% predicted suitable (1852/1854), with the mean AUC value 0.885. When projected onto the historic range of the wapiti (Fig. 3.1D), *C. c. nelson* models predicted suitable areas that overlapped with 98.5% of all *C. c. manitobensis* occurrences (67/68), 4.5% of *C. c. roosevelti* occurrences (12/267), and all reintroductions into the eastern US and Canada as of 2015 (72/72). This includes known sites not shown due to high spatial uncertainty (random placement in a 28km x 28km grid) intentionally generated by iNaturalist for critically endangered taxa. Of note, this also includes overlap with the reintroduced *C. c. manitobensis* in Tennessee/North Carolina. MESS and Limiting Factor Analysis shows some mild climate dissimilarity in the Appalachians in central West Virginia (-10 to 0) and higher climate dissimilarity along the Georgia-South Carolina-North Carolina borders (-75 to -20), into southwest North Carolina along the southern half of the Tennessee-North Carolina border near the Great Smoky Mountains National Park (-20 to 0). The overwhelming majority of the Appalachian Ecoregion falls within 0-10 MESS scores, making this subspecies the most similar in terms of climatic conditions and greatest area predicted with climate suitability of the four subspecies of wapiti. Limiting factors in these areas are precipitation of the warmest and driest quarters and precipitation of the driest month.

Roosevelt's Wapiti: *Cervus canadensis roosevelti*

The variables contributing to *C. c. roosevelti* models (78 occurrences) were: precipitation seasonality (28.5%), temperature seasonality (24.6%), and mean diurnal range (18.1%), temperature annual range (9.2%), precipitation of the coldest quarter (6.9%); precipitation of the

warmest and driest quarters, isothermality, annual mean temperature, and maximum temperature of the warmest month each contributed <5%. Variables excluded were minimum temperature of the coldest month, mean temperatures of the wettest, driest, warmest, and coldest quarters, annual precipitation, precipitation of the wettest and driest months, and precipitation of the wettest quarter. All occurrences were predicted correctly with points not included in the model bringing the total occurrences predicted correctly (264/267) to have suitable climate to 98.9%, with the mean AUC 0.854. When projected across the historic range of the wapiti, there were a few scattered areas of predicted climate suitability through eastern California into northern Baja and throughout the highlands of Arizona and central New Mexico, as well as northward along the coast of British Columbia and along the front range within that province. The climatic niche of *C. c. roosevelti* is distinct in that the overlap with other subspecies is nearly minimal (1 occurrence of *C. c. nannodes* and 2 occurrences of *C. c. nelsoni*). Except for a small area along the Minnesota-Wisconsin border, there is no climate similarity found in the eastern U.S. or Appalachian ecoregion, with MESS and limiting factor analysis showing moderate niche dissimilarity in the Appalachians (-20 to 10). Most of the Appalachians had MESS values from -10 to 0, with the limiting factors precipitation seasonality and annual mean temperature.

Hybrid Model: *Cervus canadensis manitobensis* x *C. c. nelsoni*

We generated an ecological niche model for the two subspecies together to evaluate the scenario of admixture (=hybrid), particularly given that both were released into the eastern US (438 occurrences). Therefore, this should be treated as more of a "best case" scenario for Tennessee and North Carolina in terms of climate predictions. On average, the following variables contributed most to the hybrid model: isothermality (26.7%), mean temperature of the warmest quarter (21.7%), precipitation of the coldest quarter (14.6%), mean diurnal range

(13.3%), precipitation of the warmest quarter (8%); the least contributing variables were: precipitation of the driest month and quarter, annual mean temperature, precipitation seasonality, temperature seasonality, mean temperature of the coldest quarter, annual precipitation, and mean temperature of the driest quarter (<5%). Variables excluded from the model were the maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, precipitation of the wettest month, and precipitation of the wettest quarter. Total occurrences predicted correctly were 1920/1922 (99.9%), with all (72/72) occurrences in the east predicted correctly as well, and the mean AUC value was 0.881. Additionally, overlap increased to 9/27 for *C. c. nannodes* (33.3%) and 24/267 for *C. c. roosevelti* (9%). Predictions for the hybrid subspecies were more extensive than those resulting from the model for *C. c. nelsoni*, but more restricted than those for that of *C. canadensis*. MESS and Limiting Factor analysis showed high climate dissimilarity along the Georgia-South Carolina-North Carolina border (-75 to 0), and a small swath along the Tennessee-North Carolina border (-30 to 0). The majority of the Appalachian Ecoregion was predicted to fall within the 0 to 10 MESS score range, with limiting factors precipitation of the warmest and driest quarters and precipitation of the driest month.

Future projections

Species level: Wapiti

For the species level prediction of *C. canadensis*, there is a high degree of projection consensus in the future, across all both SSPs and all GCMs, throughout the east and west. The most disagreement was found in the Great Plains, in northern Iowa, central-west Minnesota, northern Kansas, western South Dakota, most of North Dakota, eastern Montana, and southern Texas (model consensus numbers ranging from 0-6 shown in Fig. 3.2). It should be noted that

areas of full consensus are most likely to be climatically suitable for the wapiti in the near future (2021-2040), whereas areas predicted absent in even minimal consensus should be considered unsuitable in the near future (detailed individual models by SSP and GCM can be found in Appendix 3: Supplementary 3.6). Areas with the most loss of predicted suitable climate from baseline to the near future across all models occur in much of North Dakota, eastern Montana, eastern South Dakota, western Minnesota, northern Iowa, and southwest Texas; whereas additional loss is predicted in small portions of the montane areas of Utah, Nevada, Arizona, California, and eastern New Mexico (future projections for any consensus, moderate consensus, and full consensus are shown overlaid with baseline climate in Appendix III: Supplementary 3.7; losses detailed in the results and discussion of this chapter are the result of those areas predicted unsuitable under at least one future scenario). Potential areas of climatic expansion are predicted to occur in Iowa, southeastern South Dakota, and small montane portions of Utah, Arizona, California, and Nevada.

Manitoba Wapiti: *Cervus canadensis manitobensis*

Future projections for *C. c. manitobensis* were the second most variable in terms of suitable predicted climate, with consensus among all climate scenarios occurring predominantly within the Rocky Mountains, parts of British Columbia, much of Manitoba, western Ontario, and central Arizona and New Mexico. Large swaths of Saskatchewan, western Colorado, central New Mexico, and the Great Plains show a lack of consensus, as well as northeast Wisconsin and northern Michigan. Climate suitability in Kansas was predicted in only one climate projection, as were periphery areas around the western Oklahoma herd, and much of the central-eastern portion of North Dakota also fell within the single projection suitability category. Loss of suitable climate was predicted within the Great Plains predominantly, with Saskatchewan, eastern

Montana, southern North Dakota, west-central South Dakota and Nebraska, eastern Colorado, western Kansas, east-central New Mexico, most of Texas, and parts of central Oklahoma experiencing the greatest areas of lack of climate suitability in the near future. Areas of expansion of suitable climate in the near future were predicted further north in the Canadian Provinces, as well as eastern Montana, Wyoming, and Colorado, western North Dakota, South Dakota, Nebraska, east-central Kansas, and western Oklahoma.

Tule Wapiti: *Cervus canadensis nannodes*

Future projections of suitable climate *C. c. nannodes* were the most variable of all subspecies, with consensus among all projections occurring in Inyo, Ventura, Santa Barbara Kern, San Benito, Fresno, Sonoma, and Lake counties (CA); climate suitability was also predicted in in Grant, Yakima, Klickitat, and Benton counties in Washington, though this subspecies is confined to California. Largest areas of disagreement occurred along the coast of California from Mendocino County to San Luis Obispo County and along the Sierra Nevadas in the areas surrounding Tulare County northward to Tuolumne County, and north in Nevada County (CA) to Lassen County (CA); additional disagreement areas were predicted in Nevada in Lyon and Washoe counties. Largest areas of climate suitability loss in the near future were from Glenn County (CA) southward to the San Francisco Bay area in Contra Costa County, as well as San Mateo and Santa Clara counties southward into Santa Barbara County; additional losses were predicted along the Los Angeles-San Bernardino County border, western Inyo County, and Mariposa County (CA). Expansion was predicted further northward in Mendocino and Lake counties, Tulare, Fresno, Madera, and Tuolumne counties, and Nevada (CA), Yuba, Sierra, Butte, Plumas, and Lassen counties (CA); expansion of suitable climate was also predicted predominantly in Washoe County (NV), Klickitat County (WA), and Gilliam County (OR).

Rocky Mountain Wapiti: *Cervus canadensis nelsoni*

The future projections for *C. c. nelsoni* showed the second highest degree of consensus across climate scenarios ranging from predicted suitable climate in southern Alaska southward to the Mexican states of Chihuahua and Sonora, eastward into northern Texas, northern Georgia and northward into the Canadian provinces of Nova Scotia and Quebec. The largest areas of disagreement in suitable climate are in southern Nevada and western Utah, as well as south-central Arkansas in the east. Largest areas of suitable climate loss include most of California, Oregon, and Washington with the exclusion of the Sierra Nevadas and Cascade Range, much of western Nevada, southwest Idaho, and areas to the south and west of the Great Salt Lakes in Utah, most of Mexico with the exception of the border with New Mexico and Arizona, much of southern Texas, and central Alabama and Georgia. Notable areas of suitable climatic expansion in the near future are projected for parts of eastern Texas, west-central Arkansas, and northern Georgia.

Roosevelt's Wapiti: *Cervus canadensis roosevelti*

C. c. roosevelti was predicted with the greatest degree of consensus across all climate scenarios and subspecies, with areas of consensus in the Sierra Nevadas, and the northwest coast of California spanning northward to the southern Alaska-Canadian border. Largest areas with a lack of consensus are in the Rockies of British Columbia as well as west of the Coast Mountains. Loss of suitable climate was minimal for this subspecies, with areas outside of their range showing slight loss such as in central Arizona, and areas on the edge of their historic range such as the Cascades of northern California. Expansion of suitable climate was predicted along north Vancouver Island, parts of the eastern Coast Mountains and small portions of the Rockies in British Columbia.

Hybrid Model: *Cervus canadensis manitobensis* x *C. c. nelsoni*

The degree of consensus for the projection of the hybrid model was greater than that of the species level model, but less than that of *C. c. nelsoni*, with consensus ranging from Alaska southward into Mexico and eastward into Georgia and Nova Scotia to the north. Areas lacking consensus for suitable climate were greatest in north-east Iowa and southern Minnesota, east Texas, and all but western Arkansas. Major areas of climatic suitability loss predicted by the hybrid model in the near future were in southern Arizona into Sonora (Mexico), to the west of the Salt Lakes in Utah, southern Texas near the border with Mexico, most of Louisiana and eastern Mississippi, parts of Manitoba, and eastern Ontario along the border with Michigan. Expansion of suitable climate was predominantly predicted along the northern edge of its range in Canada, as well as eastern Texas, central and east Arkansas, central Tennessee, and northern Georgia.

Appalachian reintroductions

Species level: Wapiti

Projecting the wapiti at the species level shows climate suitability in the near future for all counties of the initial release/management in the Appalachian Ecoregion (Appendix III: Supplementary 3.8), as well as throughout much of the eastern U.S. (Appendix III: Supplementary 3.9), with the exception of those in North Carolina (Fig. 3.3). Climate suitability is predicted absent near the Georgia-South Carolina-North Carolina border in Macon, Jackson, Transylvania, and Henderson (NC) counties, northern Rabun County (GA), and the southernmost edge of Haywood County (NC). Surrounding this area of predicted unsuitable climate there is slight variance by 5-10 km in model consensus ranging from 2-5 projection agreement. Typically, north of the town of Balsam Grove, near Shining Rock Wilderness and east of

Tuckasegee (NC), projection agreement was at least 4 projections or more (Appendix III: Supplementary 3.10).

Manitoba Wapiti: *Cervus canadensis manitobensis*

Projecting *C. c. manitobensis,* which is the subspecies on record for release into both Tennessee and North Carolina, yielded no suitable future climate predicted within the Appalachians, or within the eastern U.S. outside of portions of Michigan and Wisconsin (Appendix III: Supplementary 3.7 and 3.9).

Rocky Mountain Wapiti: *Cervus canadensis nelsoni*

Release of *C. c. nelsoni* occurred in Kentucky, Virginia, West Virginia, and Pennsylvania within the Appalachian ecoregion. Projections predicted climate suitability with full consensus in all of the Pennsylvania management areas for 2021-2040, and most of West Virginia, Virginia, and Kentucky. Outside areas of full consensus in these three states, high agreement (>4) of predicted suitable climate was obtained in Kanawha, Boone, Raleigh, Lincoln, Logan, Mingo, and Wyoming counties (WV), Wise, Russell, Scott, and Lee (VA) counties, and Harlan, Letcher, Leslie, Clay, Knox, Bell, Whitley, McCreary, and Wayne counties (KY). In Tennessee consensus for this subspecies (not released) was variable, with full consensus of suitable climate mostly occurring in the counties of the Ridge and Valley ecoregion (EPA Ecoregion Level III; (Commission for Environmental Cooperation, 1997). Areas of agreement of 4-5 projections were found in Claiborne, Campbell, Union, Grainger, Scott, Morgan, Pickett, Fentress, Cumberland, Anderson, Roane, Monroe, Blount, Sevier, and Cocke counties (TN). Counties with full projection agreement for predicted unsuitable climate included Morgan, Anderson, Monroe, Blount, Sevier, and Cocke counties (TN). Along the Cumberland Plateau, projection agreement was higher (4-5 models), particularly along the I-75 corridor, compared to those counties in the

east of the state, with areas of 1-3 projection agreement only occurring north of Petros (TN) and south-west of Caryville and Norris Dam State Park (TN). In the eastern counties within the Blue Ridge, full consensus of projected suitability was observed within the Ridge and Valley northward towards Newport, and Harford near the Tennessee-North Carolina border, particularly in Cherokee National Forest. This transitions to 4-5 projection consensus in the foothills of the Great Smoky Mountains near Seymour and Pigeon Forge (TN) eastward. At higher elevation and north of Townsend and surrounding Gatlinburg (TN) consensus fell to 1-3 projection predicting suitable climate, with much of the Great Smoky Mountains National Park on the Tennessee side predicted not to have suitable climate for this subspecies. Within North Carolina, full consensus climate projections predicted suitable climate in only Madison and Buncombe counties (NC), with 4-5 consensus suitability projections in these two counties, as well as Jackson, Henderson, and Haywood counties (NC). Full projection consensus for absence of suitable climate was predicted in Graham, Cherokee, Macon, Jackson, Swain, Haywood, Transylvania, Henderson, Buncombe, and Madison counties (NC) as well as those adjacent in Georgia and South Carolina. Highest projection consensus in North Carolina was predicted from Hot Springs in Pisgah National Forest southward through Marshall and Sandy Mush Game Land to northwest Asheville (NC). There is 4-5 projection consensus along the I-40 corridor from the Tennessee-North Carolina border through Cove Creek, including parts of the Cataloochee Valley in the Great Smoky Mountains National Park, to just south of Lake Junaluska and east to Canton (NC). The area surrounding Cherokee, Bryson City, Whittier, and southeast to Cullowhee (NC) was variable with 1-3 projections predicting suitable climate, and the area 5 km east of Whittier predicted suitable by 4-5 models. Some of the edges of the 4-5 projection consensus along the I-40 corridor dropped to 1-3 projection consensus before a consensus of no suitable climate was

reached. All projections showed a lack of suitable climate from Lake Santeetlah northward to the border with Tennessee and northeast through the Great Smoky Mountains National Park with the exceptions of the western border along the Cataloochee Valley mentioned above near the I-40 corridor.

The hybrid projection shows a greater degree of full consensus among future projections in Kentucky, Virginia, and West Virginia, to full consensus in Pennsylvania. Though counties with 4-5 projection consensus are close or identical to *C. c. nelsoni* projections in these states, the hybrid model shows this congruence occurring in less than half of the area than the former models. In West Virginia, these 4-5 projection areas are centered predominantly around Boone County, with only a 5 km patch in Wise County and Lee County (VA). In Kentucky they are centered around: Cumberland Gap National Historical Park; Corrigan WMA northward towards Kentucky Ridge Forest WMA; Shillalah Creek WMA; northeast of Wailsend to Beverly in Bell county; from Rosspoint and Mary Alice westward to the county border; a small patch northeast of Holmes Mill in Harlan County; south of Mozelle to the county border in Leslie County; surrounding the Elk Forest WMA; northward towards Ashers Fork in Clay County; east of Erose and Walker in Knox County; immediately adjacent to the Tennessee-Kentucky border south of Creekmore, Strunk, and Fidelity (KY) in McCreary County; and much of the southern edge of Wayne County (KY). In Tennessee 4-5 projection consensus occupies most of Pickett, Fentress, Cumberland, Morgan, and Scott counties, with western portions of Anderson, Campbell, Roane, and Clairborne counties as well. In the eastern part of the state, projection consensus was highest in the foothills of the Blue Ridge near the transition for the Ridge and Valley through central Monroe, Blount, and Sevier counties, as well as southern Cocke County. This includes 4-5 projection consensus of suitability through Tellico Plains; Fort Loudon Lake (Monroe);

Townsend and the northern border of the Great Smoky Mountains National Park (Blount); Pigeon Forge and Gatlinburg and the northern edge of the National Park (Sevier); and Cocke County. In North Carolina, the western edge of Cherokee county has 4-5 projection consensus, as well as surrounding Whittier and Cherokee (Swain); near Webster and west of Oliver (Jackson); with the largest areas of 4-5 projection consensus occurring north of the area surrounding Lake Junaluska and Canton towards Cove Creek along the National Park's eastern edge and Cataloochee; Waterville at the border of Tennessee-North Carolina (Haywood); the eastern edge of Buncombe County; the areas surrounding Royal Pines, Swannanoa, and Barnardsville (Buncombe); the area surrounding Fletcher and Mills River (Henderson); surrounding Trust (Madison); along the border of Madison and Yancey counties; along the Tennessee-North Carolina border near Sams Gap; and north of Allegheny and Mars Hill (Madison). Areas with low consensus of 1-3 projections only occurred in North Carolina and Tennessee, with some uncertainty near Frozen Head State Park and the confluence of Morgan, Anderson, and Scott counties (TN). Low consensus was also predicted for much of the transition from the foothills to higher elevations along the edges of the Great Smoky Mountains National Park (TN). In North Carolina, the low consensus of 1-3 projections was predicted throughout the central and southern half of Cherokee County, surrounding Cullowhee and North of Cherokee (Jackson) and Bryson City (Swain) into the edge of the Great Smoky Mountains National Park surrounding and just north of the Oconaluftee Visitor's Center. Additional low consensus areas in North Carolina included the Madison-Haywood County borders to west of Luck (NC), and east of Fairview (Buncombe) and surrounding Fruitland (Henderson). Areas with full consensus of unsuitable climate for the hybrid wapiti are most of the Great Smoky Mountains National Park (both the Tennessee and North Carolina side), the eastern half of Monroe County (TN) and

Cherokee County (NC), all of Graham, Macon, and Transylvania counties (NC), Rabun County (GA), and Oconee County (SC), most of Swain, Jackson, and Henderson counties (NC), roughly half of Haywood County (NC), and small periphery portions of Buncombe County (NC).

DISCUSSION

Do the wapiti subspecies have distinct climatic niches?

A growing number of studies have noted the importance of utilizing biologically relevant populations in the creation of niche models, often due to the local adaptation and shaping the environmental tolerances and optimal niches of an animal both at and below the species level (Banta et al., 2012; Godoy et al., 2018; Hällfors et al., 2016; Maguire et al., 2018; Marcer et al., 2016; Pearman et al., 2010; Smith et al., 2019). Smith et al. (2019) note the particular differences in outputs depending on lumping or splitting of training data, and advisee against splitting models to populations and subspecies based solely on null model tests of niche overlap and model differences. Smith et al. (2019) instead encouraged the utilization of genetic, environmental, geographic limits, and knowledge of a species' ecology to determine if subdivisions are necessary to inform the model at the entire species level. Indeed, Smith et al. (2019) recommend partial-pooling in the event that there is potential for gene flow in populations or subspecies (as shown in Chapter 1), hence we chose to address these concerns in this study. Our findings showed that whole species wapiti models overpredicted suitable climate, making them less useful in conservation decision making, and highlighted the need for models tailored to the reintroduced populations based on subspecies. Climatically, only *C. c. nannodes* and *C. c. roosevelti* were shown to have distinct niches, whereas *C. c. manitobensis* and *C. c. nelsoni* showed significant if not almost complete overlap, which could indicate these populations were not separate subspecies prior to human intervention, or highlight that the maintained genetic

diversity, wider distribution, and reintroduction success of *C. c. nelsoni* allows for adaptability to a greater range of climatic conditions.

The overlap of the climatic niche of *C. c. manitobensis* with *C. c. nelsoni* likely is tied to its ecology, with *C. c. manitobensis* climate suitability found predominantly in the Great Plains, with some suitability in the Temperate Sierras, Northern Forests, Northwestern Forested Mountains, and Deserts (EPA Ecoregion Level I; (Commission for Environmental Cooperation, 1997). Historically, *C. c. manitobensis* mostly inhabited the prairies and plains, with recovery of fossils in Alberta indicative that this subspecies has been present for at least 10,000 years (early Holocene) (Burns, 1986; Naughton, 2003; Shackleton & Hills, 1977; Speller et al., 2014). Given the rapid decline due to overhunting across the continent with the arrival of European settlers, Canada began regulating and protecting remaining wapiti populations in the late 1800s with some of the earliest conservation efforts occurring for the wapiti, specifically *C. c. manitobensis* (Speller et al., 2014). The wildlife reserve Elk Island National Park was established in 1906 (then Elk Park) (Speller et al., 2014), which is notable as one of the source populations for the reintroduction efforts in Tennessee-North Carolina. There is currently an argument that there is strong genetic influence from *C. c. nelsoni* and that it is not genetically distinct from *C. c. manitobensis*, having once formed a continuous population prior to extirpation (Polziehn et al., 2000; Polziehn & Strobeck, 1998), which was then subsequently admixed due to translocation and reintroduction efforts (Speller et al., 2014). Results from Speller et al. (2014) suggest that gene flow was much higher historically and subsequently limited by human influence, with *C. c. nelsoni* possessing much higher haplotype and nucleotide diversity at present than *C. c. manitobensis*, likely due to the significant bottleneck experienced by the latter, which consist mostly of relict Elk Island National Park populations. The bottleneck caused by this extirpation

and limitation to a population in Elk Island National Park, and subsequent genetic work (Polziehn et al., 2000; Polziehn & Strobeck, 1998; Speller et al., 2014) are indicative of a population of wapiti that exhibits founder effects, is locally adapted to a small area in Alberta, Canada, and has likely lost genetic diversity that once tied it to its geographic neighbor, the now extinct eastern wapiti (*C. c. canadensis*).

Ecologically, the climate predictions and projections agree with the ecological niches and genetic separation of the smallest subspecies of wapiti, *C. c. nannodes*, which was restricted to remnant marshlands in Kern County by the early 1900s (Sacks et al., 2024) from the once wider expanses of grasslands and woodlands of the Central Valley and Coast Range (California Department of Fish and Wildlife, 2018). *Cervus canadensis nannodes* is suspected of having been reduced to as few as 3 individuals in the region by the late 1800s (McCullough, 1969; Sacks et al., 2024). Reintroduction efforts renewed in the 1970s, with Sacks et al. (2024) documenting gene flow between the three subspecies in California, with *C. c. nannodes* estimated to exceed 5,700 animals (California Department of Fish and Wildlife, 2018). However, along the Mendocino coast there is genetic admixture with the remnant populations of *C. c. roosevelti*; though it was noted that there is little to no evidence of admixture between *C. c. nannodes* and the reintroduced *C. c. nelsoni*, which occupy a smaller portion of northeastern California than originally documented (Sacks et al., 2024). It was also mentioned that the *C. c. nelsoni* were introduced from Montana source populations which are otherwise predicted to have been mostly naturally separated by the Great Basin from the other subspecies (California Department of Fish and Wildlife, 2018). Therefore, a higher degree of reproductive isolation with *C. c. nannodes* was expected (Sacks et al., 2024), lending credence to the prediction that *C. c. nannodes* and *C. c. roosevelti* have been isolated from the remaining subspecies for some time

(California Department of Fish and Wildlife, 2018; McCullough, 1969). The California Department of Fish and Wildlife (2018) specifically lists climate change as an area in need of research, mentioning the impact of regional effects and local habitat type may have on the presence of the three subspecies that occur there. California Department of Fish and Wildlife, (2018) proposed that climate impacts are unforecastable given the wide distribution and habitat variety, as well as the wapiti's generalist nature and dispersal abilities. The variability in the models may reflect this, or it may also be a result of a small sample size restricted in range, however we recommend examining the outputs produced here in relation to protected areas in California and known distributions before dismissing climate models altogether as there are some areas of consensus.

Predicted suitable climate for this subspecies was geographically extensive, with suitability shown throughout the Great Plains and much of Eastern North America, though there was a high degree of omission in the area occupied by *C. c. roosevelti* and complete omission of the habitat occupied by *C. c. nannodes*. This likely reflects the isolation from the two subspecies, lending support to the niches of the aforementioned wapiti being distinct from this subspecies. Genetically, *C. c. nelsoni* is presumed to be the most diverse of the subspecies, given that it retained a strong population both within and surrounding Yellowstone National Park when other subspecies were being extirpated, and that over 13,500 wapiti were subsequently restored from 1912-1967 across North America, with most of the stock originating from the Greater Yellowstone area (Hicks et al., 2007; O'Gara & Dundas, 2002; Toweill & Thomas, 1982). Like the Manitoba subspecies, initial source populations in the Greater Yellowstone area could be split into northern and southern herds, however unlike the Manitoba subspecies, genetic diversity and structure was comparable across herds, indicating high gene flow (Hicks et al., 2007). Hicks

et al. (Hicks et al., 2007) proposed that this was due to shared summer ranges given the migration tendencies of this subspecies. Overall diversity in the western US was found to be homogenous and populations sampled showed little differentiation, with gene flow prevalent though potentially limited between certain subpopulations (Hicks et al., 2007; Polziehn et al., 2000). This may be because the dispersal distance in wapiti can be great, with a radio collared male traveling from Montana to Missouri in a matter of days (over 1,500 km) (Demarais & Krausman, 2000; Hicks et al., 2007), which may contribute to overall gene flow, even if such a long distance dispersal event is rare.

Climate predictions for this wapiti subspecies were the most in agreement across future climate scenarios and encompassed the coastal and Cascade regions of the Pacific Northwest into northern California, likely reflecting the specialized climate and niche occupied by this subspecies. *Cervus canadensis roosevelti* has long been isolated in the Pacific Northwest as a monophyletic lineage, (much like *C. c. nannodes* in California), but was eliminated in all except a few small herds in the Cascade Mountains (OR), Olympic Peninsula (WA), and Vancouver Island (British Columbia, Canada) by the early 1900s (Polziehn et al., 2000). The near extirpation of the wapiti in the region due to over-hunting on the peninsula led to Washington outlawing wapiti hunting at that time and to the creation of Mt. Olympus National Monument by President Roosevelt as a protected area to aid in wapiti recovery (Washington Department of Fish and Wildlife, 2004). It is estimated that roughly 9,000 wapiti occupied the peninsula at that time (greater than elsewhere in the state) and maintained core isolated populations in this area where other populations were continuing to decline across its range (Washington Department of Fish and Wildlife, 2004). The timber industry and logging in the region outside of the Monument led to more of a mosaic of habitat and created more foraging areas for the wapiti, which caused

the population to rebound enough for an annual hunting season starting in 1936 (Washington Department of Fish and Wildlife, 2004).

Climate predictions for the hybrid model are more heavily influenced by the wide array of suitable climate and training data of *C. c. nelsoni*, compared to the more restricted range and likely local adaptation of *C. c. manitobensis*. This is suspected to reflect the distribution of genetics and potential climatic limits in the event that hybridization were to occur in a particular population and along contact zones near the front range, as well as potentially in the east (discussed below).

Lastly, it should be noted that a concern and an assumption of this study is that lack of climatic suitability is an added stressor to the reintroduced wapiti that increases susceptibility to pathogens, particularly in the east. We also assumed that, though generalist in nature and able to tolerate a wide array of habitats and conditions, the wapiti does have a niche that is defined by biotic interactions, in addition to abiotic (climatic) preferences and dispersal abilities (Peterson & Soberón, 2012; Soberón, 2010).

Are the wapiti released in the Appalachians climatically adapted to this region now and into the future?

Wapiti released into Pennsylvania, West Virginia, Kentucky, and Virginia are all *C. c. nelsoni*, which was predicted to have suitable climate and stable climate refugia at least through the 2040s in the introduced counties and surrounding areas, which is an ideal situation. The presence of stable climate across such a large area can be beneficial in allowing for selection of new release sites and maintained management areas without the restriction of suboptimal or unsuitable climate weighing on populations. This is particularly notable given genetic pressure and founder population risks even within *C. c. nelsoni* if the small size of introduced herds experience a severe bottleneck. For example, the Pennsylvania herd, showed remarkably low

allele diversity and heterozygosity compared to source populations and even insular populations separated from the mainland 7,000 years ago (Polziehn et al., 2000; Williams & Collazo, 2013). Contrasting this is the wide array of sources of *C. c. nelsoni* and numerous animals released into Kentucky, which Youngmann et al. (2020) call the most successful of wapiti restorations in eastern North America, with populations comparable to sources in terms of genetic diversity. Though Chronic Wasting Disease has been a major concern to states and federal agencies (e.g. (Banfield & Rosenberry, 2020; Carlson et al., 2018; Kentucky Department of Fish and Wildlife Resources, 2015; Tennessee Wildlife Resource Agency, 2018; Virginia Department of Game and Inland Fisheries, 2019), in the event of renewed reintroduction efforts to supplement genetic diversity in the region, our climate maps showed the majority of the region to be suitable for populations of *C. c. nelsoni*.

The reintroduction case in Tennessee and North Carolina is interesting in that the models of *C. c. manitobensis* predicted no suitable climate or refugia where released, though given the generalist nature of wapiti, survival is not necessarily the issue. This does raise the question of whether noted population growth is slower than expected because a less climatically suited subspecies has been released. Bryant and Maser (1982) note that *C. c. manitobensis* is the closest subspecies to the extinct eastern wapiti that would have inhabited the region, *C. c. canadensis.* However, given the results of Speller et al. (2014) it could be argued that the bottleneck and genetic drift of *C. c. manitobensis* likely eliminated a high percentage of the genetics remaining of *C. c. canadensis* (Clutton-Brock et al., 1982; Muller et al., 2018; Nussey et al., 2005). It has been documented that the wapiti from Elk Island National Park (genetic source material of the Tennessee and North Carolina populations) were reduced to 24 animals in 1906 (Muller et al., 2018; Polziehn & Strobeck, 1998). Additionally, Muller et al. (2018) found that the division of

Elk Island National Park by Highway 16 and fencing of populations at different points in time (northern population in 1906 and the southern in 1947) has led to genetic isolation between the two populations within the park given that this separation has persisted for over 15 generations (over 100 years). Muller et al. (2018) also note that post-translocation to Tennessee and North Carolina, populations continue to maintain genetic separation between those from the northern portion of Elk Island National Park and those from the south, reducing population viability given the initial small introduced population sizes. If this is indeed the case, then the animals released into Tennessee and North Carolina are less genetically diverse and likely more locally adapted to those conditions of Alberta, Canada.

Perhaps a best case scenario, would be that the wapiti released into Tennessee and North Carolina eventually hybridize with existing populations to the north, or managers release into the region individuals from the more genetically diverse and better climatically suited *C. c. nelsoni* in hopes that this becomes the dominant subspecies or there is renewed hybrid vigor compared to the populations currently in Tennessee and North Carolina. Unfortunately though, hybridization seems very unlikely given the rate of spread of populations and the lack of admixture between populations within the subspecies of *C. c. manitobensis* once translocated (Muller et al., 2018). Model predictions for both the hybrid and *C. c. nelsoni* show the North Cumberland WMA to be suitable in the majority of scenarios, as well as areas northwest of Asheville, North Carolina. Unfortunately, though Cataloochee (GSMNP) was predicted to have suitable climate for the hybrid and *C. c. nelson*, most of the Great Smoky Mountains National Park will not have suitable climate in the future. Supplementary data shows more suitable climate in Pisgah and Cherokee National Forest to the north of the National Park.

CONCLUSIONS

Prior to reintroduction efforts, we should be estimating climatic niches and future potential distributions to ensure that in the face of rapidly changing global conditions we are equipping a species with the best chance of long-term persistence. This is particularly important given the cost of these programs and potential for ecological imbalance/restoration. We should also be cognizant of the implications of releasing certain populations and their genetic characteristics into an area, especially when efforts span state boundaries within a region, and ensure coordination and careful planning to avoid population crashes or potential introduction of maladaptive genes. Since the wapiti released prefer the mosaic of forested and grassland habitats species (Figure 3.4), we recommend pairing these climate results with existing habitat studies and reports in planning, particularly in Tennessee and North Carolina (e.g. (Lupardus et al., 2011; Williams & Collazo, 2013). Given efforts to restore grasslands in the region, practitioners should also consider the effects and possible benefits of having a large herbivore in maintaining these ecosystems and whether the extinct eastern wapiti would have fulfilled a similar ecological role. If the current subspecies are valid, we should also consider the possibility of hybridization between the two subspecies, or even the implications of lack of hybridization, that of releasing a lesser adapted subspecies to the region. Based on the literature review of genetic data, ecological data, and now our climate models, a sound alternative is to release only the *C. c. nelsoni* subspecies into the Appalachians from diverse source populations. It is our hope that by outlining stable climate refugia surrounding current population distributions of the reintroduced wapiti, managers choose to address misalignment of climatic niches and potential for alternative release sites in the future to ensure that these animals are not additionally stressed and adversely affected by climate conditions that are suboptimal, particularly along the Tennessee-North Carolina border. Future research needs to include the spread of pathogens adversely affecting

reintroduced and existing wapiti populations, particularly if there is potential for synergistic effects of spread, climate change, host reservoirs, and stress increasing susceptibility of the wapiti (Kurth, 2022). Finally, we continue to build on existing literature and encourage rigorous modeling and planning both at present and into the future for reintroduction of species, particularly those that may be culturally and ecologically significant to a region.

REFERENCES

Amor, J. M., Newman, R., Jensen, W. F., Rundquist, B. C., Walter, W. D., & Boulanger, J. R. (2019). Seasonal home ranges and habitat selection of three elk (*Cervus elaphus*) herds in North Dakota. *PLOS ONE*, *14*(2), e0211650. https://doi.org/10.1371/journal.pone.0211650

Banfield, J. E., & Rosenberry, C. S. (2020). Pennsylvania Elk Management Plan (2020-2025). Pennsylvani Game Commission.

Banta, J. A., Ehrenreich, I. M., Gerard, S., Chou, L., Wilczek, A., Schmitt, J., Kover, P. X., & Purugganan, M. D. (2012). Climate envelope modelling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. *Ecology Letters*, *15*(8), 769–777. https://doi.org/10.1111/j.1461-0248.2012.01796.x

Bender, L. C., Baldwin, R. A., & Piasecke, J. R. (2012). Habitats occupied by Elk (*Cervus elaphus*) in desert grassland–scrublands of northwestern New Mexico. *The Southwestern Naturalist*, *57*(4), 361–369. https://doi.org/10.1894/0038-4909-57.4.361

Brough, A. M., Justin DeRose, R., Conner, M. M., & Long, J. N. (2017). Summer-fall home-range fidelity of female elk in northwestern Colorado: Implications for aspen management. *Forest Ecology and Management*, *389*, 220–227. https://doi.org/10.1016/j.foreco.2016.11.034

Bryant, L., & Maser, C. (1982). Classification and Distribution. In *Elk of North America* (pp. 1–59). Stackpole Books.

Burns, J. A. (1986). A 9000-year old wapiti (*Cervus elaphus*) skeleton from northern Alberta, and its implications for the early Holocene environment. *Géographie Physique et Quaternaire*, *40*(1), 105–108.

California Department of Fish and Wildlife. (2018). Elk Conservation and Management Plan 2018. California Department of Fish and Wildlife.

Carlson, C. M., Hopkins, M. C., Nguyen, N. T., Richards, B. J., Walsh, D. P., & Walter, W. D. (2018). Chronic wasting disease—Status, science, and management support by the U.S. Geological Survey. In *Open-File Report* (2017–1138). U.S. Geological Survey. https://doi.org/10.3133/ofr20171138

Christianson, D. A., & Creel, S. (2007). A Review of Environmental Factors Affecting Elk Winter Diets. *The Journal of Wildlife Management*, *71*(1), 164–176. https://doi.org/10.2193/2005-575

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behavior and ecology of two sexes*. University of Chicago press.

Commission for Environmental Cooperation. (1997). *Ecological Regions of North America: Toward a common perspective* (Revised 2006) [Map]. http://www.cec.org/publications/ecological-regions-of-north-america/

Crank, D., Fusaro, J., Jenkins, G., & McDermott, J. (2019). 2019-2020 Kentucky Department of Fish and Wildlife Resources Elk Report. Kentucky Department of Fish and Wildlife Resources.

Davis, M., Faurby, S., & Svenning, J.-C. (2018). Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences*, *115*(44), 11262–11267. https://doi.org/10.1073/pnas.1804906115

Demarais, S., & Krausman, P. R. (2000). Ecology and management of large mammals in North America.

Dewitz, J. (2021). *National Land Cover Database (NLCD) 2019 Products* [dataset]. U.S. Geological Survey. https://doi.org/10.5066/P9KZCM54

Di Stefano, G., & Petronio, C. (2002). Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). *Geologica Romana*, *36*(311), e334.

Doan, K., Niedziałkowska, M., Stefaniak, K., Sykut, M., Jędrzejewska, B., Ratajczak-Skrzatek, U., Piotrowska, N., Ridush, B., Zachos, F. E., Popović, D., Baca, M., Mackiewicz, P., Kosintsev, P., Makowiecki, D., Charniauski, M., Boeskorov, G., Bondarev, A. A., Danila, G., Kusak, J., … Stanković, A. (2022). Phylogenetics and phylogeography of red deer mtDNA lineages during the last 50 000 years in Eurasia. *Zoological Journal of the Linnean Society*, *194*(2), 431–456. https://doi.org/10.1093/zoolinnean/zlab025

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Evans, M. J., Gordon, I. J., Pierson, J. C., Neaves, L. E., Wilson, B. A., Brockett, B., Ross, C. E., Smith, K. J., Rapley, S., Andrewartha, T. A., Humphries, N., & Manning, A. D. (2022). Reintroduction biology and the IUCN Red List: The dominance of species of Least Concern in the peer-reviewed literature. *Global Ecology and Conservation*, *38*, e02242. https://doi.org/10.1016/j.gecco.2022.e02242

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Finn, C., Grattarola, F., & Pincheira-Donoso, D. (2023). More losers than winners: Investigating Anthropocene defaunation through the diversity of population trends. *Biological Reviews*, *98*(5), 1732–1748. https://doi.org/10.1111/brv.12974

Frey, R., & Riede, T. (2013). The anatomy of vocal divergence in North American Elk and European red deer. *Journal of Morphology*, *274*(3), 307–319. https://doi.org/10.1002/jmor.20092

Godoy, B. S., Camargos, L. M., & Lodi, S. (2018). When phylogeny and ecology meet: Modeling the occurrence of *Trichoptera* with environmental and phylogenetic data. *Ecology and Evolution*, *8*(11), 5313–5322. https://doi.org/10.1002/ece3.4031

Hale, S. L., & Koprowski, J. L. (2018). Ecosystem-level effects of keystone species reintroduction: A literature review. *Restoration Ecology*, *26*(3), 439–445. https://doi.org/10.1111/rec.12684

Hällfors, M. H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G. C., & Hellmann, J. J. (2016). Addressing potential local adaptation in species distribution models: Implications for conservation under climate change. *Ecological Applications*, *26*(4), 1154–1169. https://doi.org/10.1890/15-0926

Hicks, J. F., Rachlow, J. L., Rhodes, O. E., Jr., Williams, C. L., & Waits, L. P. (2007). Reintroduction and genetic structure: Rocky Mountain Elk in Yellowstone and the Western States. *Journal of Mammalogy*, *88*(1), 129–138. https://doi.org/10.1644/06-MAMM-A-051R1.1

Hu, P., Shao, Y., Xu, J., Wang, T., Li, Y., Liu, H., Rong, M., Su, W., Chen, B., Cui, S., Cui, X., Yang, F., Tamate, H., & Xing, X. (2019). Genome-wide study on genetic diversity and

phylogeny of five species in the genus Cervus. *BMC Genomics*, *20*(1), 384. https://doi.org/10.1186/s12864-019-5785-z

IUCN. (1998). *Guidelines for Re-introductions* (p. 10). IUCN. https://www.iucn.org/resources/publication/iucn-guidelines-re-introductions

Kentucky Department of Fish and Wildlife Resources. (2015). *2015-2030 Kentucky Elk Management Plan*. Kentucky Department of Fish and Wildlife Resources.

Larkin, J. L. (2001). *Demographic and spatial characteristics of a reintroduced elk population*. University of Kentucky.

Larkin, J. L., Maehr, D. S., Cox, J. J., Bolin, D. C., & Wichrowski, M. W. (2003). Demographic characteristics of a reintroduced Elk population in Kentucky. *The Journal of Wildlife Management*, *67*(3), 467–476. https://doi.org/10.2307/3802704

Lorenzini, R., & Garofalo, L. (2015). Insights into the evolutionary history of Cervus (Cervidae, tribe Cervini) based on Bayesian analysis of mitochondrial marker sequences, with first indications for a new species. *Journal of Zoological Systematics and Evolutionary Research*, *53*(4), 340–349. https://doi.org/10.1111/jzs.12104

Ludt, C. J., Schroeder, W., Rottmann, O., & Kuehn, R. (2004). Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Molecular Phylogenetics and Evolution*, *31*(3), 1064–1083. https://doi.org/10.1016/j.ympev.2003.10.003

Lupardus, J. L., Muller, L. I., & Kindall, J. L. (2011). Seasonal Forage Availability and Diet for Reintroduced Elk in the Cumberland Mountains, Tennessee. *Southeastern Naturalist*, *10*(1), 53–74.

Maehr, D. S., Bldg, C., Grimes, R., Larkin, J. L., & Bldg, C. (1999). *Initiating Elk Restoration:The Kentucky Case Study*.

Maguire, K. C., Shinneman, D. J., Potter, K. M., & Hipkins, V. D. (2018). Intraspecific Niche Models for Ponderosa Pine (*Pinus ponderosa*) Suggest Potential Variability in Population-Level Response to Climate Change. *Systematic Biology*, *67*(6), 965–978. https://doi.org/10.1093/sysbio/syy017

Marcer, A., Méndez-Vigo, B., Alonso-Blanco, C., & Picó, F. X. (2016). Tackling intraspecific genetic structure in distribution models better reflects species geographical range. *Ecology and Evolution*, *6*(7), 2084–2097. https://doi.org/10.1002/ece3.2010

Martínez-Meyer, E., Peterson, A. T., Servín, J. I., & Kiff, L. F. (2006). Ecological niche modelling and prioritizing areas for species reintroductions. *Oryx*, *40*(4), 411–418. https://doi.org/10.1017/S0030605306001360

McCorquodale, S. M. (2003). Sex-Specific Movements and Habitat Use by Elk in the Cascade Range of Washington. *The Journal of Wildlife Management*, *67*(4), 729–741. https://doi.org/10.2307/3802679

McCullough, D. (1969). The tule elk, its history, behavior, and ecology. In *University of California Publications in Zoology*. University of California Press.

Meiri, M., Kosintsev, P., Conroy, K., Meiri, S., Barnes, I., & Lister, A. (2018). Subspecies dynamics in space and time: A study of the red deer complex using ancient and modern DNA and morphology. *Journal of Biogeography*, *45*(2), 367–380. https://doi.org/10.1111/jbi.13124

Muller, L. I., Murrow, J. L., Lupardus, J. L., Clark, J. D., Yarkovich, J. G., Stiver, W. H., Delozier, E. K., Slabach, B. L., Cox, John. J., & Miller, B. F. (2018). Genetic structure in Elk persists after translocation. *The Journal of Wildlife Management*, *82*(6), 1124–1134. https://doi.org/10.1002/jwmg.21482

Myers, N. (1996). The biodiversity crisis and the future of evolution. *Environmentalist*, *16*(1), 37–47. https://doi.org/10.1007/BF01325613

National Park Service. (2023). *Elk (Cervus canadensis)—Jewel Cave National Monument (U.S. National Park Service)*. https://www.nps.gov/jeca/learn/nature/elk-cervus-canadensis.htm

Naughton, D. (2003). *Annotated bibliography of Quaternary vertebrates of northern North America: With radiocarbon dates*. University of Toronto Press.

North Carolina Wildlife Resources Commission. (2013). *North Carolina Wildlife Resources Commission Elk Management Plan 2013-2015*. North Carolina Wildlife Resources Commission.

Nussey, D. H., Clutton-Brock, T. H., Albon, S. D., Pemberton, J., & Kruuk, L. E. B. (2005). Constraints on plastic responses to climate variation in red deer. *Biology Letters*, *1*(4), 457–460. https://doi.org/10.1098/rsbl.2005.0352

O'Connor, B., Bojinski, S., Röösli, C., & Schaepman, M. E. (2020). Monitoring global changes in biodiversity and climate essential as ecological crisis intensifies. *Ecological Informatics*, *55*, 101033. https://doi.org/10.1016/j.ecoinf.2019.101033

O'Gara, B. W., & Dundas, R. G. (2002). Distribution: Past and present. *North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, DC, USA*, 67–119.

Padilla, B. J., Banfield, J. E., Corondi, A., & Larkin, J. L. (2023). Seasonal variation in size and composition of elk (*Cervus canadensis*) home range in central Appalachia. *Canadian Journal of Zoology*, *101*(6), 448–461. https://doi.org/10.1139/cjz-2022-0099

Pearman, P. B., D'Amen, M., Graham, C. H., Thuiller, W., & Zimmermann, N. E. (2010). Within-taxon niche structure: Niche conservatism, divergence and predicted effects of

climate change. *Ecography*, *33*(6), 990–1003. https://doi.org/10.1111/j.1600-0587.2010.06443.x

Peterson, A. T., & Soberón, J. (2012). Integrating fundamental concepts of ecology, biogeography, and sampling into effective ecological niche modeling and species distribution modeling. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology*, *146*(4), 789–796. https://doi.org/10.1080/11263504.2012.740083

Pitra, C., Fickel, J., Meijaard, E., & Groves, C. (2004). Evolution and phylogeny of old world deer. *Molecular Phylogenetics and Evolution*, *33*(3), 880–895. https://doi.org/10.1016/j.ympev.2004.07.013

Polziehn, R. O., Hamr, J., Mallory, F. F., & Strobeck, C. (2000). Microsatellite analysis of North American wapiti (*Cervus elaphus*) populations. *Molecular Ecology*, *9*(10), 1561–1576. https://doi.org/10.1046/j.1365-294x.2000.01033.x

Polziehn, R. O., & Strobeck, C. (1998). Phylogeny of Wapiti, Red Deer, Sika Deer, and Other North American Cervids as Determined from Mitochondrial DNA. *Molecular Phylogenetics and Evolution*, *10*(2), 249–258. https://doi.org/10.1006/mpev.1998.0527

Popp, J. N., Toman, T., Mallory, F. F., & Hamr, J. (2014). A Century of Elk Restoration in Eastern North America. *Restoration Ecology*, *22*(6), 723–730. https://doi.org/10.1111/rec.12150

Radeloff, V. C., Hammer, R. B., Stewart, S. I., Fried, J. S., Holcomb, S. S., & McKeefry, J. F. (2005). The Wildland–Urban Interface in the United States. *Ecological Applications*, *15*(3), 799–805. https://doi.org/10.1890/04-1413

Rickbeil, G. J. M., Merkle, J. A., Anderson, G., Atwood, M. P., Beckmann, J. P., Cole, E. K., Courtemanch, A. B., Dewey, S., Gustine, D. D., Kauffman, M. J., McWhirter, D. E., Mong, T., Proffitt, K., White, P. J., & Middleton, A. D. (2019). Plasticity in elk migration timing is a response to changing environmental conditions. *Global Change Biology*, *25*(7), 2368–2381. https://doi.org/10.1111/gcb.14629

Rowland, M. M., Wisdom, M. J., Johnson, B. K., & Kie, J. G. (2000). Elk Distribution and Modeling in Relation to Roads. *The Journal of Wildlife Management*, *64*(3), 672–684. https://doi.org/10.2307/3802737

Rull, V. (2022). Biodiversity crisis or sixth mass extinction? *EMBO Reports*, *23*(1), e54193. https://doi.org/10.15252/embr.202154193

Sacks, B. N., Davis, T. M., & Batter, T. J. (2024). Genetic structure of California's elk: A legacy of extirpations, reintroductions, population expansions, and admixture. *The Journal of Wildlife Management*, *n/a*(n/a), e22539. https://doi.org/10.1002/jwmg.22539

Sarrazin, F., & Barbault, R. (1996). Reintroduction: Challenges and lessons for basic ecology. *Trends in Ecology & Evolution*, *11*(11), 474–478. https://doi.org/10.1016/0169-5347(96)20092-8

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the Science of Reintroduction Biology. *Conservation Biology*, *21*(2), 303–312. https://doi.org/10.1111/j.1523-1739.2006.00627.x

Seward, N. W. (2003). Elk calf survival, mortality, and neonatal habitat use in eastern Kentucky. https://www.semanticscholar.org/paper/elk-calf-survival%2c-mortality%2c-and-neonatal-habitat-seward/8bb59d238eb48598a734cd02a5c28a4a3ea3410a

Shackleton, D., & Hills, L. (1977). Post-glacial ungulates (*Cervus* and *Bison*) from Three Hills, Alberta. *Canadian Journal of Earth Sciences*, *14*(5), 963–986.

Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.-H., & Warren, D. (2019). Niche Estimation Above and Below the Species Level. *Trends in Ecology & Evolution*, *34*(3), 260–273. https://doi.org/10.1016/j.tree.2018.10.012

Soberón, J. M. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, *33*(1), 159–167. https://doi.org/10.1111/j.1600-0587.2009.06074.x

Speller, C. F., Kooyman, B., Rodrigues, A. T., Langemann, E. G., Jobin, R. M., & Yang, D. Y. (2014). Assessing prehistoric genetic structure and diversity of North American elk (*Cervus elaphus*) populations in Alberta, Canada. *Canadian Journal of Zoology*, *92*(4), 285–298. https://doi.org/10.1139/cjz-2013-0253

Tennessee Wildlife Resource Agency. (2000). Proposal: Elk restoration in the northern Cumberland Plateau, Tennessee. Tennessee Wildlife Resource Agency.

Tennessee Wildlife Resource Agency. (2018). *Tennessee Strategic Elk Management Plan 2018-2027.* Tennessee Wildlife Resource Agency.

Toweill, D. E., & Thomas, J. W. (1982). *North American elk: Ecology and management*. Smithsonian Institution Press.

Virginia Department of Game and Inland Fisheries. (2019). Virginia elk management plan, 2019-2028. Virginia Department of Game and Inland Fisheries.

Washington Department of Fish and Wildlife. (2004). Olympic Elk Herd Plan. Wildlife Program, Washington Department of Fish and Wildlife.

Wathen, G., Marcum, L., Peterson, A., Dykes, S., & Layton, B. (1997). Elk reintroduction in Tennessee: An evaluation of its potential (Technical Report 97–07). Tennessee Wildlife Resource Agency.

Webb, S. L., Dzialak, M. R., Harju, S. M., Hayden-Wing, L. D., & Winstead, J. B. (2011). Influence of land development on home range use dynamics of female elk. *Wildlife Research*, *38*(2), 163–167. https://doi.org/10.1071/WR10101

West Virginia Division of Natural Resources, W. R. S. (2021). West Virginia Elk Management Plan FY2021-FY2025. West Virginia Division of Natural Resources.

Williams, S., & Collazo, J. (2013). Elk Habitat Suitability Index Map for North Carolina. North Carolina Wildlife Resources Commission.

Wolf, M., Garland, T., & Griffith, B. (1998). Predictors of avian and mammalian translocation success: Reanalysis with phylogenetically independent contrasts. *Biological Conservation*, *86*(2), 243–255. https://doi.org/10.1016/S0006-3207(97)00179-1

Youngmann, J. L., Deyoung, R. W., Demarais, S., Strickland, B. K., & Jenkins, G. (2020). Genetic Characteristics of Restored Elk Populations in Kentucky. *The Journal of Wildlife Management*, *84*(3), 515–523. https://doi.org/10.1002/jwmg.21817

APPENDIX III:

FIGURES

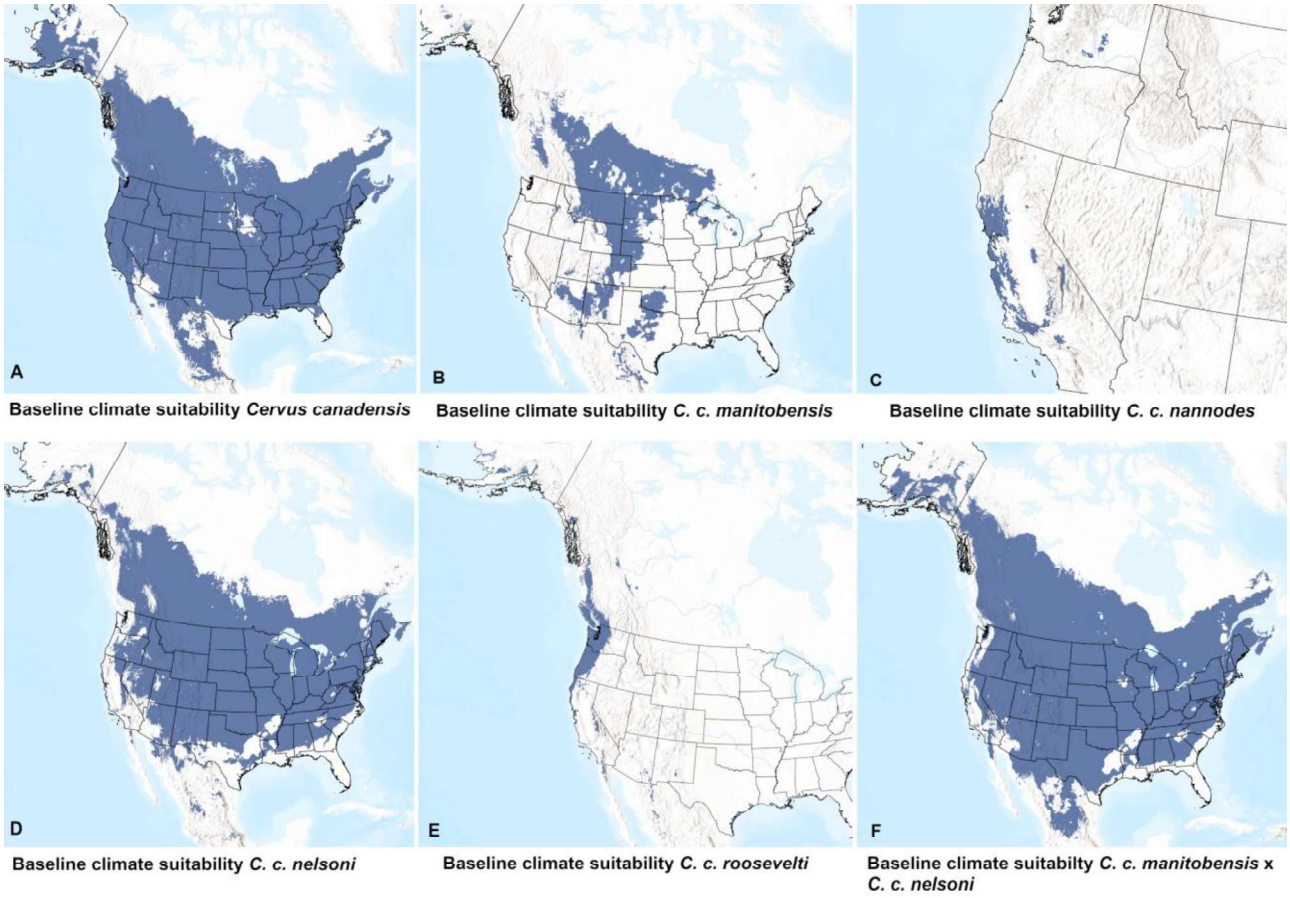


Figure 3.1. Baseline Models of the Wapiti Subspecies. Predicted baseline (1970-2000) climatic suitability at the species level for *Cervus canadensis* (**A**), individual subspecies (**B-E**), and hybrid *C. canadensis* (**F**). Suitable climate is shown in dark blue.

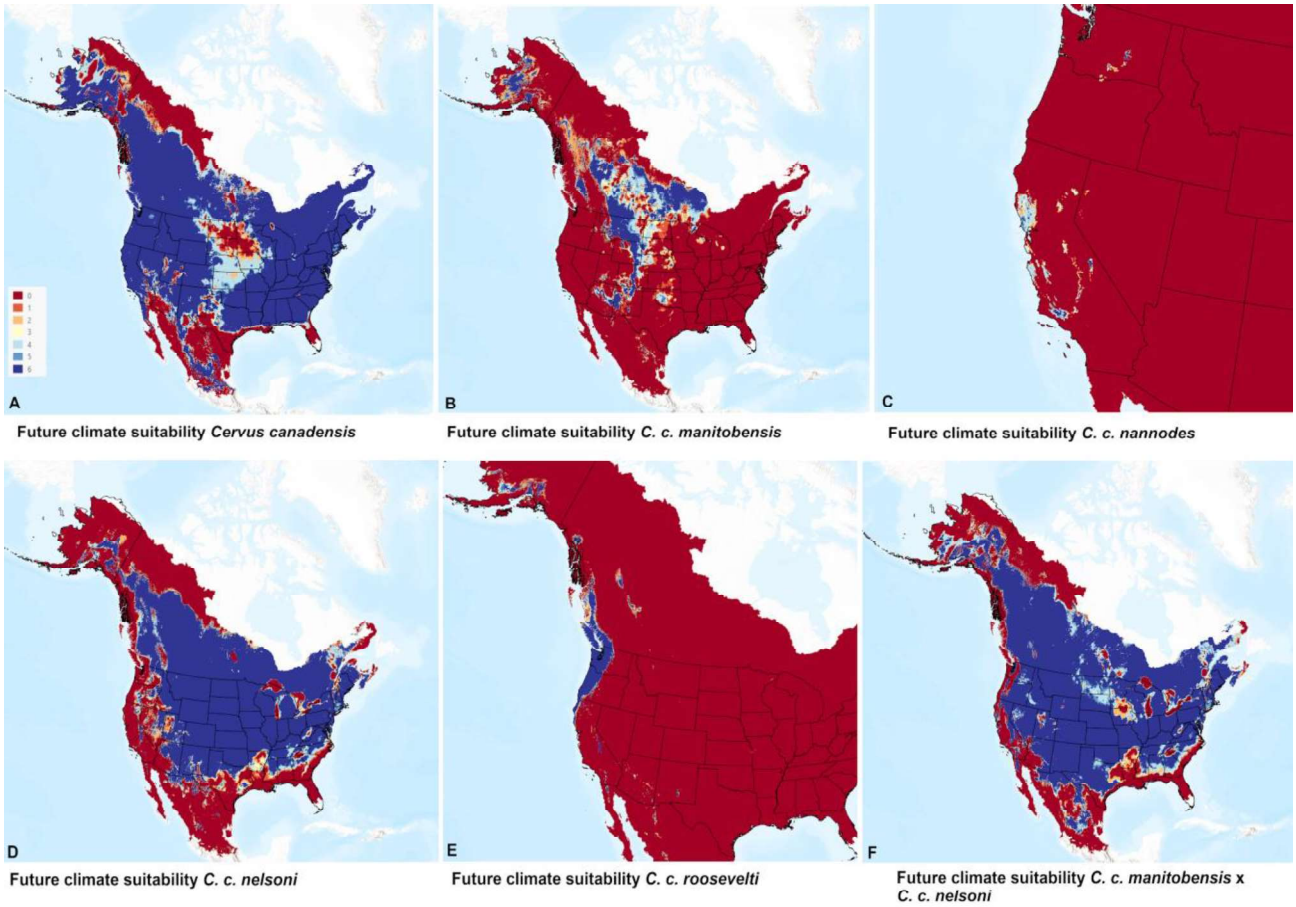


Figure 3.2. Consensus in Future Predictions of Climatic Suitability for the Wapiti Subspecies. Predicted near future (2021-2040) climatic suitability at the species level for *Cervus canadensis* (**A**), individual subspecies (**B-E**), and hybrid *C. canadensis* (**F**). Degrees of prediction consensus across SSPs and GCMs are shown ranging from no predictions (0, darkest red) to full prediction consensus (6, darkest blue).

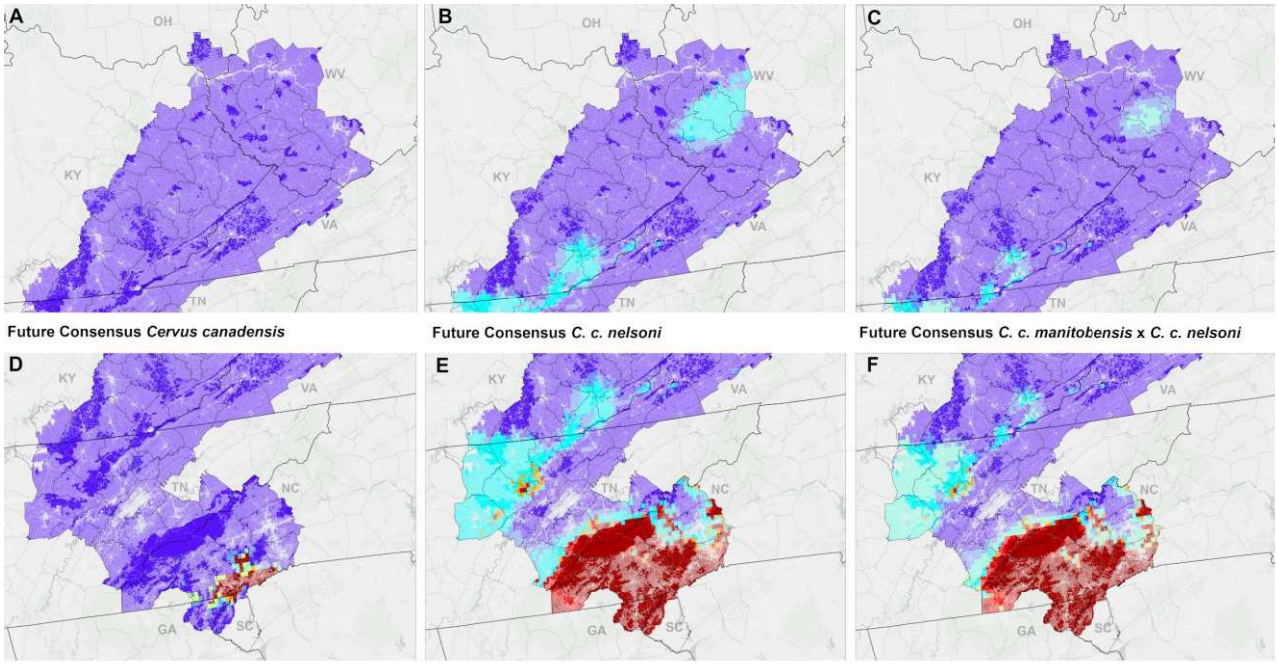


Figure 3.3. Consensus in Future Predictions of Climatic Suitability within the Appalachians. Predicted near future (2021-2040) climatic suitability overlaid with suitable land cover at the species level within the Appalachian reintroduced populations for *Cervus canadensis* (**A & D**), *C. c. nelsoni* (**B & E**), and the hybrid (**C & F**). *Cervus canadensis manitobensis* was released in both Tennessee and North Carolina, but is not shown due to the subspecies having zero predicted climatic suitability in the Appalachian ecoregion. **A-C** show the northern Appalachian ecoregion release locations for the wapiti, whereas **D-F** show the southern release locations. Degrees of prediction consensus for the near future across SSPs and GCMs are shown ranging from no predictions (0, dark red) to full prediction consensus (6, dark blue), whereas the light/dark distinction within colors represents protected areas (darker) versus unprotected (lighter). Note the full consensus of suitable climate in Pennsylvania for all models but *C. c. manitobensis* which was predicted to have no suitability across all predictions (shown in Appendix III: Supplementary 3.9).

Figure 3.4. Comparison of Two Wapiti Subspecies in Different National Parks and Habitats. A. A large herd of *C. c. nelsoni* cows and calves in Rocky Mountain National Park (RMNP) emerging from cover to forage along Trail Ridge Road at high elevation (near alpine tundra). *B.* A small herd of cows and immature bulls feeding along Trail Ridge Road near Medicine Bow Curve highlighting the diversity of occupied habitats within RMNP**.** ***C.*** One of a number of large bull wapiti in velvet foraging in the grassy fields around the Beaver Creek Picnic area (RMNP). *D.* A small herd of *C. c. manitobensis* cows and calves from the reintroduced population foraging in the Oconaluftee Visitor Center fields of the Great Smoky Mountains National Park (GSMNP). *E.* One of the dominant bull wapiti strolling through the Oconaluftee Visitor Center fields, highlighting the habitat occupied in the GSMNP. *F.* A non-dominant bull wapiti with a drop-tine foraging near the original release site in the Cataloochee Valley (GSMNP). *All photographs shown were taken by Lauren M. Lyon.*


A
B
C
D
E
F

CONCLUSIONS

Key findings of my dissertation included the importance of the Blue Ridge and Central Appalachians as hotspots of mammalian species richness, key dispersal corridors for maintaining climate connectivity, and as refugia for mammals. I stress the importance of performing climate modeling prior to decision making, analyzing numerous taxa, and incorporating species ecology and traits, whether implementing a new road construction project, designating a new protected area, or reintroducing an extirpated taxon to the region.

In my first dissertation chapter, I found that for the majority of mammals of conservation concern within the Appalachian Ecoregion, climatic conditions would remain stable through the 2040s. This affords resource managers and practitioners at least a short amount of time to implement refugia conservation strategies and develop partnerships in the key areas outlined for mammalian diversity in the region. Unfortunately, there were a few taxa at risk due to climate change in the near future, which were predominantly Appalachian endemic mammals and relict boreal taxa. Hotspots of diversity for mammalian species of greatest conservation need (stable refugia overlap for 36 or more species) were found in the Blue Ridge and Central Appalachians, aligning with predictions for other major faunal and plant groups in the Appalachians. Secondarily, I identified a number of gaps in occurrence records and areas in need of museum specimen data to be digitalized to supplement these gaps, particularly with rare and secretive species.

In my second chapter I found that the American Black Bear (*Ursus americanus*) is far too generalist in climate and habitat preferences to solely base climate connectivity corridors on its needs. Reliance on this flagship species could result in missed opportunity areas, which I identified utilizing a multispecies modeling approach focused on a secretive yet abundant and ecologically significant group of mammals, the rodents. Given the limited dispersal abilities of

most rodents, I modelled the feasibility of refugial connections and determined key dispersal corridors for species likely to experience range shifts. I also highlighted the overlap of bear refugia and rodent biodiversity hotspots and priority areas with the highest degree of refugial overlap within protected areas that were interrupted by primary roadways. Based on these results I recommend 4 km of priority areas to survey in the Blue Ridge and Central Appalachians for potential modification of existing or construction of new structures to allow wildlife crossing of roadways.

In my final chapter, I found that most of the Appalachian Ecoregion is predicted to have suitable climate for the Rocky Mountain Wapiti (*Cervus canadensis nelsoni*) both at present and into the 2040s. This is likely in part to much of the population persisting in montane and remote regions relative to the other subspecies. I also found that the Manitoban Wapiti (*C. c. manitobensis*) did not have any climate suitability predicted at present or into the future, likely due to the strong founder effect exhibited by the bottleneck in the population that left this subspecies restricted to a narrow area within Alberta, Canada. I evaluated the reciprocity of the climatic niches of the other two subspecies of wapiti (*C. c. nannodes* and *C. c. roosevelti*) and described potential changes in range as well as their distinct climatic niches, likely a result historical distributions and isolation. Due to the near extirpation, genetic work, well studied ecology, and known historical distributions of the wapiti (*C. canadensis*), I determined that this species is a prime candidate for separate subspecies modeling or partially-pooled modeling, particularly with regards to conservation planning. Lastly, I recommended that conservation practitioners in Tennessee and North Carolina strongly consider future release efforts of the Rocky Mountain subspecies, noting that the added stressor of non-optimal climate in

combination with poor genetics appears to be hindering population growth compared to the rest of the Appalachian reintroductions.

This dissertation focused on specific mammalian species distributions and susceptibility to climate change, which will be useful to state agencies overlapping the Appalachian Ecoregion that must incorporate climate data for species of greatest conservation need into their State Wildlife Action Plans (SWAPs) in 2025, 2035, and 2045. It can also be utilized to identify overlap with other taxonomic groups to designate Conservation Opportunity Areas within these SWAPs. Previous research predominantly focused on meta-analysis of various taxa without individually refined maps, either focusing continentally or at a very localized scale, and/or into the distant future (2100s) which is less pertinent for planning in the immediate future. I detailed the feasibility of connecting stable climate refugia for dispersal limited species, as well as determined the degree of refugial representation by a flagship taxon, which has traditionally been utilized in conservation decision making, and proposed options within a region that is actively planning for wildlife crossings. Results also demonstrated the importance of incorporating climate models into reintroduction efforts, particularly during such a period of rapid climate change, as well as ensuring the models are consistent and justifiable for the splitting of a species into subspecies or pooling population occurrences in potential areas of genetic overlap.

Future Directions

Future directions include refining climate refugial models to finer resolution (<1km) and incorporating additional species from digitized museum collections in biodiverse regions, namely the Blue Ridge and Central Appalachians. I plan to work with various Southeastern Climate Adaptation Science Center partners to incorporate my data into the larger US Fish and Wildlife Service Southeast Conservation Adaptation Strategy Blueprint. I want to collaborate

with National Parks Conservation Association out of Asheville, NC to assist in the planning phase and potential implementation of wildlife overpasses/underpasses on I-26 based on a combination of road mortality data, my climate models, and their research. Finally, future work needs to be conducted on the genetics of the four wapiti subspecies to interpret climatic tolerance while acknowledging the wapiti as a separate species from the European red deer (*Cervus elaphus*) to avoid potential bias. I would like to initiate conversation with current wapiti researchers and management agencies regarding plans for reintroduction of more wapiti into Tennessee and North Carolina and urge them to consider the Rocky Mountain subspecies for future reintroduction projects, if not because of my models then because of genetics of this subspecies.

VITA

Lauren is a Tennessee native, growing up near Chattanooga and spending much of her childhood exploring nature and volunteering at the Tennessee Aquarium with her parents' encouragement. Prior to joining the Biodiversity Matters Lab run by Dr. Mona Papeş in 2018, Lauren graduated *cum laude* from the University of Tennessee at Chattanooga with a B.S. in Biology, zookeeper intern experience, and two publications on fossil xenarthrans from her undergraduate research in the Gaudin Lab. Lauren later received her M.S. in Geosciences from East Tennessee State University where she immediately fell in love with GIS and red panda, spending her free time collaborating with Zoo Knoxville and researchers at the Gray Fossil Site, resulting in several publications. During her time at UTK in the Department of Ecology and Evolutionary Biology, Lauren gained experience teaching a number of courses including Human Anatomy, Comparative Vertebrate Zoology, and her favorite, Ichthyology. Though Lauren's dissertation focused on mammals, her first love will always be fish and she can often be found snorkeling or sampling in creeks in her spare time. Lauren received numerous awards during her time at UT ranging from departmental to societal to federal funding ranging upward of $27,000: the Alexander Hollaender Graduate Fellowship, the Biology Outstanding Graduate Student Publication Award, Chancellor's Funds, the American Society of Mammalogist Travel Award, the Graduate Student Senate Travel Award, the United States Geological Survey's National Climate Adaptation Science Center's (CASC) Science to Action Fellowship (2022), and the United States Fish and Wildlife Service's Directorate Fellowship (2023). Lauren has presented her research at numerous conferences and workshops as well as featured in several press releases and as part of the Refugia Research Coalition's website on climate change refugia in the southeast. She was heavily involved with the USGS's Southeastern CASC and NCASC

participating in early career workshops through invitation, as well as field intensive workshops on coastal resilience and climate change in the southeast and serving as a mentor on the Science to Action panel for two years. Lauren more recently worked with the Lower Mississippi Valley Joint Venture on priority wetland areas for waterfowl as part of her USFWS fellowship, which culminated in models and research that is being utilized in their JV planning. She has Direct Hire Authority upon graduation with the Department of Interior and plans on pursuing a career with the USFWS.