AN ABSTRACT OF THE DISSERTATION OF

Marie Irene Tosa for the degree of Doctor of Philosophy in Wildlife Science presented on December 6, 2023.

Title: Leveraging Next Generation Natural History to Examine Biota and Evaluate the Role of Old Growth in Temperate Rainforests of the Pacific Northwest.

Abstract approved:_____

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Forests support the majority (ca. 70%) of terrestrial biodiversity on Earth, but the demand for economic outputs from these areas has resulted in global biodiversity decline during the Anthropocene. In particular, removal of large old trees and conversion of old growth forests into single-species, single-age plantations have degraded forests and have drawn much attention in the last 50 years. Despite decades of research, especially in the Pacific Northwest, we still do not understand how many species, taxonomic communities, and ecosystems respond to these disturbances. In this dissertation, my objective was to examine the role of disturbance and the importance of remaining old growth forests in the Pacific Northwest at multiple scales ranging from the response of a single species to a whole ecosystem. Between 2017 and 2019, I collected traditional and next generation natural history data using carnivore scats, camera traps, radiotelemetry, bulk invertebrate traps, soil cores, and observations in the H. J. Andrews Experimental Forest and the surrounding Willamette National Forest, which are located on the western slope of the Oregon Cascade Range.

In chapter 2 and 3, I investigated the diet and spatial ecology of western spotted skunks in a landscape that consisted of a mosaic of previously logged stands and old growth forest and showed that western spotted skunks are generalist carnivores that consume vertebrates, invertebrates, and plants and utilize forests of varying ages. In chapter 2, I demonstrated that western spotted skunks provide important connections between arboreal, terrestrial, and aquatic systems and that they could switch their primary food source from mammals in the wet season to insects, mainly wasps, during the dry season. Their diet could be influenced by the landscape of disturbance because scats collected in areas with a greater proportion of forest that was previously logged within 1 km (a skunk's home range size) were less likely to contain insects. In chapter 3, I combined detections by camera traps and locations of radio-collared individuals to conduct a multi-spatial-scale analysis on the habitat requirements of western spotted skunks. At both the home range and landscape scales, western spotted skunks selected wetter areas and local valleys that could provide resources such as food items described in chapter 2. At the home-range scale, I found that western spotted skunks selected areas with lower predation risk and areas surrounded by more previously logged forest, but at the landscape scale, occupancy models revealed that predicted occupancy was higher in areas with more mature forest within 5 km. Despite being widely distributed across the study area and highly detectable with baited camera traps, seasonal western spotted skunk occupancy was sensitive to disturbance, cold temperatures, and accumulated snow, which was evident when seasonal occupancy declined significantly following a severe heavy snow event in February 2019.

In chapter 4, I explored methods of quantifying the abundance of a single taxonomic group, the small mammal community, in old growth stands. By pairing capture-recapture data where individual identities are known with unmarked camera trap data where identities of individuals are unknown, I compared the performance of a suite of unmarked methods including average encounter rates, N-mixture models, time-to-event, space-to-event, and unmarked spatial-capture recapture models for estimating densities of deer mice, Townsend's chipmunks, and Humboldt flying squirrels at 8 independent sites. I was able to produce accurate density estimates using

unmarked models for Townsend's chipmunks, a species for which the sampling scheme fit its natural history and occurred at medium densities at the sites studied. Despite its simplicity, average encounter rates consistently yielded positively correlated relative density estimates in relation to marked model density estimates for all three species tested. These results provide a way forward to directly estimate densities of small mammals across large spatial extents with less effort than traditional invasive capture-recapture methods, which can be used to understand relationships between vegetation structure, small mammals, and higher trophic levels.

Finally in chapter 5, I quantified biodiversity of multiple taxa harbored in temperate rainforest stands and evaluated how biodiversity changed with elevation and time since disturbance. I found that sites in previously logged forests generally had higher species diversity across all taxa except for overstory trees, but sites in old growth forests had distinct communities. Even though many species were resilient to disturbance, many species benefited from longer times since disturbance in terms of abundance. Patterns observed in one taxon were not immediately apparent in other taxa and each taxon responded differently to site-level and landscape-level environmental variables, suggesting that studying one species let alone one taxon is not sufficient to make landscape-level conservation or management decisions.

Together, findings from this dissertation advance our understanding of old growth forests in the temperate rainforests of the Pacific Northwest. By studying a single species in detail, I showed how nuanced the relationships between a species and its environment can be. Scaling up to the perspective of an entire ecosystem, I demonstrated how information about a single species can be combined with others to understand community dynamics and the drivers of species loss and accumulation. Furthermore, these studies provide examples of methods and information necessary to make science-based informed decisions for biodiversity conservation.

Leveraging Next Generation Natural History to Examine Biota and Evaluate the Role of Old Growth in Temperate Rainforests of the Pacific Northwest

by
Marie Irene Tosa

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented December 6, 2023
Commencement June 2024

Doctor of Philosophy dissertation of Marie Irene Tosa presented on December 6, 2023.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Marie Irene Tosa, Author

ACKNOWLEDGEMENTS

First and foremost, I thank my advisors Dr. Damon Lesmeister and Dr. Taal Levi for their support, guidance, and encouragement. This work would not have been possible without their infinite enthusiasm for science. I thank my committee members, Clint Epps, Matt Betts, and Rebecca Terry, and all the coauthors on my manuscripts, especially Jenn Allen, Matt Weldy, Hankyu Kim, Doug Yu, and Dana Morin, who provided valuable input throughout the dissertation. Thanks to the support from both the Lesmeister and Levi lab members that have helped pave a path of success and folks at the USDA Forest Service PNW Research Station and the Department of Fisheries, Wildlife, and Conservation Sciences. Special thanks to Jenn Allen, who organized and processed endless samples and provided guidance in the lab.

Funding for this research was provided by Oregon State University, the USDA Forest Service (16-JV-11261952-047), the National Science Foundation and the Long Term Ecological Research Program (LTER7 DEB 1440409), the Key Research Program of Frontier Sciences, CAS (QYZDY-SSW-SMC024), the Strategic Priority Research Program of Chinese Academy of Sciences, Grant No. XDA20050202, the State Key Laboratory of Genetic Resources and Evolution (GREKF19-01, GREKF20-01, GREKF21-01) at the Kunming Institute of Zoology, the University of Chinese Academy of Sciences, the Provost's Distinguished Graduate Fellowship, the HJ Andrews Experimental Forest Graduate Student GRA Support Award, Teaching Assistantships and scholarships through the Department of Fisheries, Wildlife, and Conservation Sciences, the Achievement Rewards for College Scientists (ARCS) Oregon Chapter, NatureMetrics, and the Northwest Ecological Research Institute.

I was incredibly lucky to spend such a large chunk of time among the old growth trees at the H. J. Andrews Experimental Forest and the Willamette National Forest and am forever grateful to all members that maintain this forest. Mark Schulze, Greg Cohn, Rod Fouts, Kathleen Turnley, Brenda Hamlow, thank you for putting up with our stench over the years and for being my sanity and safety net in the

mountains. Thanks to Michael Nelson, Lina DiGregorio, Brooke Penaluna, Dave Bell, Suzanne Remillard, and Stephanie Schmidt who made work at the HJA possible and ensured that my data will be useful to future scientists. Support was also provided by the folks at the McKenzie River Ranger Station.

This project would not have been possible without the tireless effort of numerous field and lab technicians. Thank you, Brian Doyle, Julian Grudens, Hannah Haeussler, Allison Hay, Ruby Hayes, Lynn Hodnett, Lindsey Howard, DeAnn Jakobsma, Mark Linnell, Tom Manning, Dustin Marsh, Asch McDonnel, Ben Murley, Rebecca Peterson, Keke Ray, Richard Rich, Leilani Rivera, Scott Sparrow, Kristen Van Neste, and Maggie Yates for field support. Thank you, Heath Smith, Jennifer Hartman, Mairi Poisson, Collette Yee, Chester, Scooby, and Jack from Rogue Detection Teams for their assistance in locating carnivore scats. Thank you, Catie Boucher, Dominee Cagle, Olyvia Childress, Anna Froelich, Nikolias Griffith, Jared Hedges, Amy Hilger, Rayanne Mock, Alex Saucedo, Heather Thomas, Sam Speir, and other lab technicians and volunteers. Thanks to Research Experiences for Undergraduate students, Alix Prybyla, Alex Coombs, Sriram Narasimhan for allowing me to pursue research interests outside of my dissertation. Special shout out to Catie Boucher, Alex Coombs, Jared Hedges, and Sriram Narasimhan for being rockstar mentees and reminding me of the joys of science and mentoring.

I especially thank Eric Forsman and Jim Swingle for inspiring me and teaching me to explore the third dimension of the PNW forests; Hankyu Kim and Allie Swartz for their collaboration and friendship at the HJA; Cara Appel and Leila Duchac for embarking on many adventures, and The Goon Squad, Julia Smith and Shelby Adams for their infinite encouragement. I thank the Sparrows for their love and support through the years and for providing an endless supply of blue crabs, and the Tosas for instilling in me a love and appreciation of science, and Kenji and Molly for always making me smile. Finally, I could not have done this without Scott Sparrow and Blueberry. Thank you for being my editor, chef, and trainer. Your patience, delicious meals, adventures, and walks when I needed them most made this all possible.

CONTRIBUTION OF AUTHORS

Marie I. Tosa conceived and designed the studies, collected the data, performed statistical analyses, wrote, edited, and revised all chapters in this dissertation. Damon B. Lesmeister and Taal Levi helped conceive and design the studies, consulted on statistical analyses, and edited and revised all chapters included in this dissertation.

Chapter 2:
Jennifer Allen processed samples in the laboratory and generated data used in this chapter.

Chapter 4:
Clinton W. Epps and Matthew J. Weldy helped conceive and design the study, contributed data, consulted on statistical analyses, and edited and revised this chapter. Mattew J. Weldy also conducted statistical analyses for this chapter.

Chapter 5:
Douglas W. Yu and Matthew G. Betts helped conceive and design the study, consulted on statistical analyses, and edited and revised this chapter. Douglas W. Yu also provided equipment and processed samples. Mingjie Luo processed samples used in this chapter.

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CHAPTER 1 – GENERAL INTRODUCTION

The majority of terrestrial biodiversity on Earth is supported by forested systems (International Union for Conservation of Nature 2017), but the demand for economic outputs from these areas has resulted in widespread deforestation and forest degradation (Betts et al. 2017*b*). Forest loss and degradation have contributed significantly to what some call "the sixth extinction crisis" (Ceballos et al. 2015), where population trends across multiple taxa including invertebrates (Hallmann et al. 2017), amphibians (Stuart et al. 2004), birds (Rosenberg et al. 2019), and mammalian carnivores (Ripple et al. 2015), show alarming rates of decline during the Anthropocene (Dirzo et al. 2014). Despite growing concerns about the extinction crisis, we are limited in our ability to stymy the rapid decline of species because we generally have a poor understanding of the natural history of single species, species interactions, and emerging threats such as climate change (Román-Palacios and Wiens 2020), changes in wildfire regimes (Reilly et al. 2017), and species invasions (Mollot et al. 2017).

To combat biodiversity loss, the conservation of large old trees and old growth forests has drawn much attention in the last 50 years because following disturbance, time can be a critical mechanism for species accumulation and biodiversity maintenance (Peterken and Game 1984). Thus, it has been assumed that these individual old trees and old growth forests harbor unique biota that are lost when old trees and old growth forests are removed from the landscape. This relationship between species richness and old growth forests has been tested empirically, but with mixed results. In global analyses of forest loss, risks of species extinction based on IUCN Red List data were predicted to be disproportionately greater for species in relatively intact landscapes (Betts et al. 2017*b*). In the tropics, bird, dung beetle, and leaf-litter ant species richness increased with age and recovery towards old growth forest (Edwards et al. 2014, Owen et al. 2020), but others have observed declines in species richness (Müller et al. 2023). In Canada, even though there was little change in overall forest cover, there were substantial population declines in avian species related to the decline of old growth forests (Betts et al. 2022)

Additionally, old growth forests may possess the ability to buffer biota from the negative effects of climate change (Chen et al. 2011, Betts et al. 2017*a*). Moreover, the benefits of old growth forests may not be limited to the living components of these forests because even the removal of large dead old trees, both standing and fallen, from the landscape can have negative effects on biodiversity (Sandström et al. 2019). Together, these studies indicate that old growth forests may be important for biodiversity maintenance and persistence.

In the Pacific Northwest, conservation of old growth forests was formalized with the adoption of the 1994 Northwest Forest Plan, a revolutionary plan that halted logging of old growth stands on approximately 10 million hectares of federally administered forest lands. This plan was the culmination of the rapid decline of old growth forests in the Pacific Northwest, increased conservation concerns for the Northern Spotted Owl, and growing environmental activism and civil unrest during a period referred to as the "Timber Wars" of the 1980s and early 1990s. Decades of research on a single species, the Northern Spotted Owl (which started at the H. J. Andrews Experimental Forest) and the decision to list the species under the US Endangered Species Act in 1990 were critical catalysts for this historic and unprecedented plan of great geographic scale that prioritized ecological diversity. Prior to the Northwest Forest Plan, timber harvest in Oregon alone typically exceeded 8 billion board feet annually, where almost half occurred on federally owned land (Simmons et al. 2016). Following the Northwest Forest Plan, timber harvest in Oregon still exceeds 4 billion board feet annually, produces ~$7 billion in revenue, and supports over 43,000 jobs, but the majority of this occurs on private lands (Simmons et al. 2016). Within the greater footprint of the forests managed by the Northwest Forest Plan, there was approximately an 80-90% decrease in the amount of timber harvesting after the plan was adopted (Spies et al. 2019).

During the Timber Wars, significant progress was made on identifying the diversity of biota in old growth stands during the USDA Forest Service's Old Growth Wildlife Habitat Research Program (Ruggiero et al. 1991), but we still only have detailed information of relationships between forest age and species abundance for a few flagship species such as *Lobaria oregana* (Sillett et al. 2000), a lichen species,

Northern Spotted Owls (Forsman et al. 1984), and Marbled Murrelets (Raphael et al. 2002), old-growth obligate birds. Even for these species, we do not have a good understanding of the scale and configuration of protection of old growth necessary to recover populations. Although harvest of old growth trees has almost entirely ceased on federal land, intensive logging has continued on private land, wildfires have eroded existing patches of old growth forests, and other external threats such as unfavorable ocean conditions, climate change, and invasion by novel species continue to threaten old-growth associated species in such a way that they continue to decline (Lesmeister et al. 2018, Raphael et al. 2018, Reeves et al. 2018, Phalan et al. 2019). In this context, it is necessary to revisit questions concerning the value of old growth forests in maintaining biodiversity in temperate rainforests of the Pacific Northwest. In particular, it is necessary to understand the role of old growth forests for and responses to disturbance by 1) individual animals, 2) individual species, 3) communities within taxa, and 4) ecosystems as a whole.

Until recently, it was difficult to survey biodiversity at broad landscape scales. Traditional methods (e.g., morphological identification, call identification) of surveying biodiversity were expensive, labor intensive, and required taxonomic expertise, but advances in technology (e.g., camera traps, radiotelemetry, DNA metabarcoding, shotgun sequencing) now allow us to survey taxonomic groups in extreme detail across broad spatial and temporal extents (Tosa et al. 2021). These "next generation natural history" (Tosa et al. 2021) datasets can now leverage modern aircraft- and satellite-based remote sensing, which allow us to quantify empirical relationships of biodiversity to environmental factors, predict biodiversity across landscapes (Gillespie et al. 2008, Bush et al. 2017), and use these predictions for conservation and management.

For this dissertation, my objective was to examine the biota in temperate rainforests in the Pacific Northwest at multiple scales and to evaluate the role of old growth forests and disturbance. Specifically, I centered my research around the H. J. Andrews Experimental Forest, which is a Long Term Ecological Research site and investigated the natural history of an understudied small forest carnivore, the western spotted skunk. First, I opportunistically and systematically collected western spotted

skunk scat while hiking trails and using detection dog teams. By combining western spotted skunk diet composition with the logging legacy of a site, I evaluated how diets shifted between seasons and differed in areas with more mature forests. Second, I radio-collared individuals and surveyed the landscape using baited camera traps to understand the spatial ecology of individual western spotted skunks and the western spotted skunk population. Third, I evaluated statistical models for estimating the density of small mammal community with baited camera traps and unmarked individuals at 8 different old growth forest sites. By evaluating these statistical models, I established a method of estimating densities of small mammals that can be replicated across large landscapes and can be used to evaluate changes in densities related to changes in the amount of old growth forest. Finally, I conducted a multi-taxa biodiversity survey to quantify the relationship between biodiversity and time since forest harvest at the ecosystem scale. At this level, I was able to ask whether old growth forests were more species rich and identified gradients that drive differences in community composition. This research not only provides new baseline natural history knowledge for an understudied forest carnivore species, but also provides additional evidence that old growth forests in the Pacific Northwest harbor unique biota. Moreover, this dissertation shows that next generation natural history methods can be applied and replicated to monitor biota efficiently and rapidly, which can increase our understanding of the effects of the Northwest Forest Plan, a plan that was intended to last for 100 years. Finally, these data can be used to answer questions on the mechanisms driving biodiversity and generate new hypotheses about species interactions.

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CHAPTER 2 – MULTI-LOCUS DNA METABARCODING REVEALS SEASONALITY OF FORAGING ECOLOGY OF WESTERN SPOTTED SKUNKS IN THE PACIFIC NORTHWEST

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Ecosphere
Published: January 20, 2023
DOI: 10.1002/ecs2.4386

Abstract

There are increasing concerns about the declining population trends of small mammalian carnivores around the world. Their conservation and management is often challenging due to limited knowledge about their ecology and natural history. To address one of these deficiencies for western spotted skunks (*Spilogale gracilis*), we investigated their diet in the Oregon Cascades of the Pacific Northwest during 2017 – 2019. We collected 130 spotted skunk scats opportunistically and with detection dog teams and identified prey items using DNA metabarcoding and mechanical sorting. Western spotted skunk diet consisted of invertebrates such as wasps, millipedes, and gastropods, vertebrates such as small mammals, amphibians, and birds, and plants such as *Gaultheria*, *Rubus*, and *Vaccinium*. Diet also consisted of items such as black-tailed deer that were likely scavenged. Comparison in diet by season revealed that spotted skunks consumed more insects during the dry season (June – August), particularly wasps (75% of scats in the dry season), and marginally more mammals during the wet season (September – May). We observed similar diet in areas with no record of human disturbance and areas with a history of logging at most spatial scales, but scats collected in areas with older forest within a skunk's home range (1 km buffer) were more likely to contain insects. Western spotted skunks provide food web linkages between aquatic, terrestrial, and arboreal systems and serve functional roles of seed dispersal and scavenging. Due to their diverse diet and prey-switching, western spotted skunks may dampen the effects of irruptions of prey, such as wasps during dry springs and summers. By studying the natural history of western spotted skunks in the Pacific Northwest forests while they are still abundant, we provide key information necessary to achieve the conservation goal of keeping this common species common.

Introduction

Globally, many small mammalian carnivores (< 16 kg) face decreasing population trends due to multiple threats including land use change, disease, and overhunting (Belant et al. 2009, Marneweck et al. 2021). Even small carnivore species that were previously widely distributed and considered "least concern" by the

IUCN, such as weasels (*Mustela* spp. and *Neogale* spp.), have shown signs of significant population decline (Gompper 2017, Jachowski et al. 2021). These declines are problematic because small carnivores can play important roles in ecosystem function, predator-prey dynamics, and disease transmission dynamics (Roemer et al. 2009). Despite their potentially important roles, many small carnivores remain neglected in ecological research, data deficient, or understudied (Proulx 2010, Marneweck et al. 2021). Limited knowledge about small carnivore ecology and natural history continues to hinder management and conservation of declining populations.

In the Pacific Northwest, the western spotted skunk (*Spilogale gracilis*) is putatively a common forest carnivore, but little is known about their ecology due to their nocturnal nature (Verts et al. 2001) (Doty and Dowler 2006, Neiswenter and Dowler 2007, Neiswenter et al. 2010). Most spotted skunk literature is derived from the island spotted skunk subspecies (*S. g. amphialus*) (Crooks 1994*a*, *b*), the congeneric eastern spotted skunk (*S. putorius*) (Kinlaw 1995, Lesmeister et al. 2009, 2010) and plains spotted skunk subspecies (*S. p. interrupta*) (Crabb 1948), or other skunk species such as the pygmy skunk (*S. pygmaea*) (Cantú-Salazar et al. 2005). These spotted skunks, however, inhabit markedly different ecosystems such as on islands, prairie, or desert where there is limited forest vegetation. The Pacific Northwest, in comparison, is a temperate rainforest system that is dominated by large coniferous trees, and the functional role of western spotted skunks in this system is largely unknown. Due to their dietary plasticity, spotted skunks could vary from omnivorous generalist (e.g., eastern and plains spotted skunk) (Selko 1937, Crabb 1941, Baker and Baker 1975, Cheeseman et al. 2021), insectivorous specialist (e.g., pygmy skunk) (Cantú-Salazar et al. 2005), or key carnivorous predator of small vertebrates (e.g., island spotted skunk) (Crooks and Van Vuren 1995) in Pacific Northwest forests.

Eastern and plains spotted skunk populations are in severe decline and, as a result, the eastern spotted skunk is now listed as Vulnerable by the IUCN (Gompper and Jachowski 2016), and the plains spotted skunk subspecies had been petitioned for listing under the US Endangered Species Act (US Fish and Wildlife Service 2012).

The mechanism for these declines are poorly understood, but multiple mechanisms have been proposed, including land-use change, disease outbreaks, or changes in predator communities (Gompper and Hackett 2005, Gompper 2017, Sasse 2021). Although western spotted skunks are still relatively common and considered a species of Least Concern by the IUCN (Cuarón et al. 2016), western spotted skunks may be prone to future, rapid declines similar to those of eastern and plains spotted skunks. Studying western spotted skunks provides an opportunity to understand the functional roles of the species and amass basic ecological knowledge that may inform conservation and land management decisions.

Land use change is a potent disturbance in the Pacific Northwest given that it is an internationally important center of timber production (Simmons et al. 2016). Forest management can influence the structure and composition of forests with unknown consequences on the ecology of western spotted skunks. One way that land use change could cause declines in spotted skunk population densities is by causing declines in prey populations. For example, potential small mammal prey such as Trowbridge's shrews (*Sorex trowbridgii*), shrew moles (*Neurotrichus gibbsii*), red tree voles (*Arborimus longicaudus*), and flying squirrels (*Glaucomys oregonensis*), are less abundant in young forest stands than in mature and old-growth forest stands (Carey 1989, 1995, Gilbert and Allwine 1991). Disturbances such as commercial thinning can reduce density of some small mammal prey such as flying squirrels (Manning et al. 2012). In contrast, forest management can increase the abundance of flowers and fruits of understory plants through increased light penetration onto the forest floor (Wender et al. 2004). Thus, it remains important to investigate how western spotted skunk diets are impacted by forest management.

Characterizing the diet of small carnivores, however, has been difficult. New techniques such as detection dogs and DNA metabarcoding have improved our ability to find scat and identify prey items, respectively. Previously, diets of spotted skunks were difficult to study because scats were often deposited in rest sites (Selko 1937, Lesmeister et al. 2008*a*), not on trails, and because spotted skunks exhibit an omnivorous diet consisting of insects, small vertebrates, and fruit (Howell 1906, Crabb 1941, Baker and Baker 1975, Crooks and Van Vuren 1995). These scats were

typically collected opportunistically, mechanically sorted, and morphologically identified (Ewins et al. 1994, Sándor and Ionescu 2009), but these processes had biases related to digestion that may render prey items unrecognizable (Symondson 2002, Galan et al. 2012) and misidentification of rare species (Massey et al. 2021). This can be particularly problematic for small omnivorous predators that consume a wide breadth of prey items including plants, animals, and invertebrates because identifiers must have taxonomic expertise. Moreover, misidentification of carnivores from scat morphology has been problematic and has potentially led to biased results (Morin et al. 2016). Newer genetic approaches such as DNA metabarcoding (Eriksson et al. 2019, Monterroso et al. 2019, Roffler et al. 2021) can increase confidence in correctly identifying the carnivore (Morin et al. 2016), increase the number of prey items that can be correctly identified (Massey et al. 2021), and increase efficiency of identifying diet for a high volume of samples (Kartzinel et al. 2015), especially for omnivorous species (De Barba et al. 2014).

Here we use DNA metabarcoding and mechanical sorting to provide the first comprehensive analysis of western spotted skunk diet in the Pacific Northwest, and quantified seasonal variability in diet as a function of land use change. This improved understanding of western spotted skunk foraging ecology can elucidate their functional role as small vertebrate predators, insectivores, and frugivores.

Methods

Study Area

This study was centered around the H. J. Andrews Experimental Forest (HJA), which is located on the western slope of the Cascade Mountain Range near Blue River, Oregon (Figure 2.1). The is surrounded by the McKenzie River Ranger District of the Willamette National Forest. Elevations range from 410 m to 1,630 m. The maritime climate consists of warm, dry summers and mild, wet winters. Mean monthly temperatures range from 1°C in January to 18°C in July. Precipitation falls primarily as rain, is concentrated from November through March, and averages 230 cm at lower elevations and 355 cm at higher elevations (Greenland 1993, Swanson and Jones 2002). During 2018 – 2019, western Oregon experienced an extreme

drought (USDM 2022). In Lane County, drought severity was greatest during August 2018 – February 2019, but abnormally dry conditions began as early as January 2018 and moderate drought conditions began as early as June 2018 (Figure S2.1).

Lower elevation forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Upper elevation forests are dominated by noble fir (*Abies procera*), Pacific silver fir (*Abies amabilis*), Douglas-fir, and western hemlock. The understory is variable and ranged from open to dense shrubs. Common shrubs included Oregon grape (*Mahonia aquifolium*), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), vine maple (*Acer circinatum*), Pacific rhododendron (*Rhododendron macrophyllum*), huckleberry (*Vaccinium* spp.), and blackberry and salmonberry (*Rubus* spp.).

Before timber cutting in 1950, 65% of the HJA was covered in old-growth forest. Approximately 30% of the HJA was clear cut or shelterwood cut to create plantation forests varying in tree composition, stocking level, and age. In 1980, the HJA became a charter member of the Long Term Ecological Research network and no logging has occurred since 1985. The Willamette National Forest immediately surrounding the HJA has a similar logging history, but logging continues to occur. Currently, the HJA consists of a higher percentage of old-growth forest than the surrounding Willamette National Forest (approximately 58% in the HJA vs. 37% in the study area) (Davis et al. In Press). Wildfires are the primary disturbance type, followed by windthrow, landslides, root rot infections, and lateral stream channel erosion. Mean fire return interval of partial or complete stand-replacing fires for this area is 166 years and ranges from 20 years to 400 years (Teensma 1987, Morrison and Swanson 1990).

Field methods

Our western spotted diet study was part of a larger study on their spatial ecology in the temperate rainforest ecosystem of western Oregon that was conducted between April 2017 – September 2019. During this study, we set and maintained 112 baited trail cameras and captured and tracked western spotted skunks ($n_F = 12$, $n_M = 19$) using Tomahawk traps (Model 102 and 103, Tomahawk Live Trap Co.,

Hazelhurst, WI) and VHF radio-collars (M1545, 16 g; Advanced Telemetry Systems, Isanti, MN). Cameras placed in the HJA were paired with previously established long-term songbird monitoring (Frey et al. 2016*a*) and small mammal monitoring sites (Weldy et al. 2019). Cameras placed outside of the HJA were stratified based on elevation and old-growth structural index (Spies and Franklin 1988) and chosen randomly within logistical constraints. Both cameras and live traps were baited with a frozen house mouse (*Mus musculus*), a can of sardines (*Culpidae*), and/or various carnivore scent lures. We located skunks using radio-telemetry triangulation and homing techniques daily, weather permitting. Homing techniques were mainly used to locate rest site locations during the day whereas triangulation was used to locate skunks during the night when skunks were most active. All animal capture and handling were conducted in accordance with the guidelines set by the American Society of Mammalogists and were approved by the USDA Forest Service Institutional Animal Care and Use Committee (IACUC #2016-015) and the Oregon Department of Fish and Wildlife (Permit #107-17, 059-18, 081-19).

We collected western spotted skunk scat in multiple ways: 1) during western spotted skunk capture, 2) opportunistically while tracking western spotted skunks with radio-collars and checking trail cameras, and 3) using detection dog teams (summer and fall of 2018). Detection dog teams either surveyed 3 x 3 km grids within the study area for a minimum of 6 hours near camera trap locations where we detected western spotted skunk or focused their surveys around known spotted skunk rest sites. Focused surveys were necessary to increase scat sample sizes and increase spotted skunk scat detection rates. Moreover, western spotted skunk scats were difficult to locate opportunistically because typically, they were deposited after we tracked skunks to their rest sites, were in hard to search locations such as in hollow logs or a short distance from the rest site. We froze all scat samples until we processed them in the laboratory, and processed scats were dried for long-term storage.

Laboratory methods

In the lab, we identified the diet of western spotted skunks using DNA metabarcoding (Eriksson et al. 2019, Massey et al. 2021) and mechanical sorting. For

DNA metabarcoding, we extracted DNA in a laboratory dedicated to processing degraded DNA using the DNeasy Blood and Tissue kit (Qiagen, Germantown, Maryland) or the QIAamp Fast DNA Stool Mini Kit (Qiagen, Germantown, Maryland). We included an extraction blank with every batch of extractions as a negative control, where we used the same protocol but without a fecal sample (hereafter called extraction blanks). We kept extraction blanks throughout the DNA metabarcoding process.

Following DNA extraction, we amplified 3 regions of the mitochondria and chloroplast DNA. First, we amplified a ~100 base-pair DNA segment of the ribosomal mitochondrial 12S gene using universal vertebrate primers (12S-V5-F': YAGAACAGGCTCCTCTAG and 12S-V5-R: TTAGATACCCCACTATGC) (Riaz et al. 2011, Kocher et al. 2017) and the chloroplast-encoded intron region of the trnL gene using universal plant primers (g-F: GGGCAATCCTGAGCCAA and h-R: CCATYGAGTCTCTGCACCTATC) (Taberlet et al. 2007) in a multiplex polymerase chain reaction (PCR). In a separate singleplex PCR reaction, we amplified the mitochondrial-encoded cytochrome oxidase subunit I (COI) gene using ANML universal arthropod primers (LCO1490-F: GGTCAACAAATCATAAAGATATTGG and CO1-CFMRa-R: GGWACTAATCAATTTCCAAATCC) (Jusino et al. 2019). We performed 3 PCR replicates per sample using the QIAGEN Multiplex PCR kit (Qiagen, Germantown, Maryland) (**Supplemental Text S2.1**). To aid in identifying contamination, we performed PCR on a negative control on each plate (hereafter called PCR blanks) in addition to the extraction blanks. Each reaction was amplified with identical 8 base pair tags on the 5' end of the forward and reverse primer that were unique to each sample to identify individual sample after pooling and to prevent misidentification of prey samples due to tag jumping (Schnell et al. 2015). We normalized and pooled the PCR products and used NEBNext Ultra II Library Prep Kit (New England BioLabs, Ipswich, Massachusetts) to adapt the library pools into Illumina sequencing libraries (Illumina Inc., San Diego, California). We purified libraries using the Solid Phase Reversible Immobilization beads and sent libraries to the Center for Genome Research and Biocomputing at Oregon State University for 150 base pair paired-end sequencing on the Illumina HiSeq 3000.

We paired raw sequence reads using PEAR (Zhang et al. 2014) and demultiplexed samples based on the 8-base pair-index sequences using a custom shell script (Supplemental Text S2.2). We counted unique reads from each sample replicate and assigned taxonomy using BLAST against the 12S, COI, and trnL sequences in a local database and GenBank (www.ncbi.nlm.nih.gov/blast). Scat amplification was considered successful if DNA sequencing produced over 100 total reads per replicate, and we limited the effects of contamination by retaining only species that consisted of more than 1% of the total reads. Furthermore, we used extraction and PCR negative controls to set additional filtering thresholds for species read counts. Species were only retained in the final species list if it was present in at least 2 of the 3 replicates and if their species distribution maps included our study area or were included on the species lists of the study area (https://andrewsforest.oregonstate.edu/about/species). We identified plants to genus since congeners are difficult to differentiate using these primers.

To mechanically sort scats, we placed dried scat contents in a petri dish and separated items using forceps. We identified remains macroscopically to the lowest taxonomic order possible (typically class or order). If we had used all fecal matter for DNA metabarcoding, we relied on notes on identifiable parts from when the scat was collected or processed samples for DNA extraction. Once mechanically sorted, we compared our findings to the DNA metabarcoding results for each scat. If the identified taxon was not included in the DNA metabarcoding results, we augmented the results with the missing taxon. We used mechanical sorting to augment results from DNA metabarcoding because of known biases introduced by mismatches in the universal invertebrate ANML primers we used, which is attributed to a lack of conserved regions across all invertebrates (Deagle et al. 2014).

We confirmed scats as defecated by western spotted skunks using the metabarcoding data following criteria: 1) western spotted skunk was the only carnivore (order: Carnivora) identified in the scat, or 2) western spotted skunk was one of the carnivores identified in the scat and the other carnivores consisted of less than 10% of the read count. We confirmed the predator in this way because predators

are frequently misidentified through scat morphology (Lonsinger et al. 2015, Morin et al. 2016).

Data analysis

We conducted analyses and produced figures using the Program R (R Core Team 2019). We quantified the importance of each taxonomic group by first calculating the frequency of occurrence of broader taxonomic group of prey (i.e., vertebrate, invertebrate, or plant). We calculated frequency of occurrence as a proportion of the number of scats in which each taxonomic group was present divided by the total number of scats. Due to the broad breadth of diet, we then calculated conditional frequency of occurrence of each species as the number of scats that contained the prey species divided by the total number of scats containing the broader taxonomic group. We also calculated the importance of each prey item by calculating the relative read abundance (RRA) for items identified through DNA metabarcoding by:

$$RRA_i = \frac{1}{S}\sum_{k=1}^{S}\frac{n_{i,k}}{\sum_{i=1}^{T} n_{i,k}}$$

where $n_{i,k}$ is the number of sequences of prey species *i* in sample *k*, *S* is the number of scat samples, and *T* is the number of species. We produced figures relating taxonomy of prey items using the *metacoder* package (Foster et al. 2017), and we produced rarefaction curves for each taxonomic group (species for vertebrates, genus for invertebrates and plants) using the *iNEXT* package (Hsieh et al. 2016) to estimate completeness and expected taxonomic richness of diet based on sample size.

To investigate the effect of season and disturbance history on western spotted skunk diet, we summarized the presence or absence (i.e., 1 for present, 0 for absent) of each taxonomic class (e.g., Mammalia, Insecta, Gastropoda) per sample and fit a binomial generalized linear model for multivariate data using the manyglm function in the *mvabund* package (Wang et al. 2012). We defined season as wet (1 for scat collected between October – Mary) or dry (0 for scat collected between June – September) and characterized past disturbance to the area at multiple scales: where the scat was collected (1 for previously logged, 0 for no record of logging) and within a 0.1 km, 0.5 km, 1 km and 5 km buffer of where the scat was collected (0-100% area

within buffer that had been previously logged). We included season and past disturbance in additive models.

Results

During October 2017 – August 2019, we collected and genetically confirmed 130 western spotted skunk scats (n_{summer} = 47, n_{fall} = 62, $n_{opportunistic}$ = 21). 58 scats (n_{dry} = 32, n_{wet} = 26) were collected from previously logged areas and 72 (n_{dry} = 25, n_{wet} = 47) scats were collected from areas with no record of timber harvest.

We identified 27 vertebrate species, 43 plant genera, 15 arthropod species, and 3 mollusk species as prey using DNA metabarcoding (Figure 2.2). The most frequent prey item (n = 15) was Atlantic herring (*Clupea harengus*), which we used to bait skunks to trail cameras and traps. Atlantic herring was the only prey item in 2 scats, so we removed these samples from the following analyses. After removing Atlantic herring, invertebrates were the most common prey items identified through metabarcoding and mechanical sorting (Figure 2.3, Figure 2.4, Figure 2.5). Invertebrates, especially insects, occurred in 85.2% of all scats (n = 109) (Figure 2.3). Vertebrates were the next most common prey item (58.6%, n = 75), and we detected mammals in 46.9% (n = 60), birds in 14.1% (n = 18), and amphibians in 13.3% (n = 17) of all scats (Figure 2.4). Finally, we detected plants in 28.9% of all scats (n = 37) (Figure 2.5).

Wasps (*Vespula* spp.) and millipedes (Diplopoda) were the top invertebrate prey items comprising 67.0% (n = 73) and 40.4% (n = 44) of scats containing invertebrates, respectively (Figure 2.3). The most frequent vertebrate naturally occurring prey items were shrew mole (*Neurotrichus gibbsii*), Pacific tree frog (*Pseudacris regilla*), Townsend's chipmunk (*Neotamias townsendii*), Swainson's thrush (*Catharus ustulatus*), clouded salamander (*Aneides ferreus*), and Humboldt's flying squirrel (*Glaucomys oregonensis*) (Figure 2.4). The most frequent plant items were Douglas fir (*Pseudotsuga*), maple (*Acer*), Hemlock (*Tsuga*), Gaultheria (*Gaultheria*), Alder (*Alnus*), and Rhododendron (*Rhododendron*) (Figure 2.5).

Of the 130 scats, 51 scats (39.2%) only amplified western spotted skunk DNA and 67 scats (51.5%) did not contain any vertebrate DNA other than Atlantic herring

or western spotted skunk. Manual inspection of all scat samples revealed that the majority consisted of invertebrate body parts such as wasps (Vespidae) (n = 71), millipedes (Diplopoda) (n = 43), and snail shells (Gastropoda) (n = 6) that failed to amplify with ANML primers. Invertebrate remains mainly consisted of exoskeletons and head parts, indicating that skunks primarily consumed individuals in the adult life stage. We also found feathers (n = 3), snake skin (n = 4), and plant material such as Douglas fir needles and bark (likely consumed incidentally along with other food items), indicating that primers and DNA quality in some scats did not allow for detection of all diet items.

Diet composition of western spotted skunks differed based on season ($LRT_{season} = 32.0$, $p = 0.001$), but not based on the collection site's logging history ($LRT_{logged} = 10.7$, $p = 0.35$). During the dry season, diet was composed primarily of insects ($LRT_{season, insect} = 25.4$, $p = 0.001$) (Figure 2.6) and wasps were detected in 75% (n=43) of scats. Although plant material consumed was similar across season and the collection site's logging history ($LRT_{season, plant} = 0.36$, $p = 0.996$; $LRT_{logged, plant} = 0.007$, $p = 0.98$), there were more plants from genera that produce fruit during the dry season including *Rubus* (n = 6), *Vaccinium* (n = 1), and *Gaultheria* (n = 10). During the wet season, western spotted skunks consumed *Gaultheria* (n = 3) and *Vaccinium* (n = 3), but no *Rubus*. Similarly, although mammals and amphibians consumed were similar across season and collection site's logging history ($LRT_{season, mammal} = 5.8$, $p = 0.12$; $LRT_{season, amphibian} = 0.05$, $p = 0.999$), wet season scats consisted of more small mammals (*Neotamias townsendii*, *Neurotrichus gibbsii, Myodes* spp., *Sorex* spp.) and amphibians such as salamanders (*Rhyacotriton*, *Plethodon*, *Ambystoma*, and *Aneides*) (Figure 2.6).

When examining the effect of the amount of disturbance in the area surrounding each scat at multiple scales, composition of scats only differed with the percentage of logged area within a 1 km buffer ($LRT_{p\_logged\ 1\ km} = 20.3$, $p = 0.03$). Insect presence in the scat decreased with increasing percentage of area that was previously logged and was the only taxonomic class that showed a slight response to the percentage of area logged ($LRT_{p\_logged\ 1\ km, insect} = 6.43$, $p = 0.105$) (Figure 2.7).

Discussion

This study provides the first data on the diet of western spotted skunks in the Pacific Northwest and represents the first use of DNA metabarcoding for high resolution spotted skunk diet analysis. In the coniferous forests of the Oregon Cascades, the western spotted skunk diet was highly diverse and included mammals, birds, amphibians, reptiles, insects, gastropods, and plants. The combined methods of DNA metabarcoding and mechanical sorting revealed that invertebrates were the primary diet items and mammals were the secondary diet item for western spotted skunks, which is consistent among other food habit studies conducted on skunks (Selko 1937, Crabb 1941, Baker and Baker 1975, Cantú-Salazar et al. 2005). The importance of these diet items shifted by season, where skunks consumed more insects during the dry season.

We detected substantially higher frequency of Vespidae than in diets reported on the island spotted skunk (Crooks and Van Vuren 1995), the pygmy skunk (Cantú-Salazar et al. 2005), and the plains spotted skunk (Howell 1906, Selko 1937, Crabb 1941). In these studies, grasshoppers and crickets (Orthoptera) and beetles (Coleoptera) were consumed more frequently (Howell 1906, Crabb 1941, Baker and Baker 1975, Cantú-Salazar et al. 2005). The scats collected for this study were collected during a year when the Oregon Cascades were unusually dry during the spring and summer **(**Figure S2.1). These conditions have been shown to be correlated with irruptions in wasp populations (Akre and Reed 1981, Dejean et al. 2011), and wasps were observed to be more abundant on the landscape (W. Gerth, personal communication). Thus, higher consumption of wasps during these irruptions suggests that western spotted skunks can switch from one prey item to another and capitalize on abundant resources as generalist predators.

As expected, the vertebrate prey base of the western spotted skunk in Oregon was more diverse than that of the island spotted skunk that only consumed one mammal species (*Peromyscus maniculatus*) (Crooks and Van Vuren 1995) considering mammal diversity is greater in the Oregon Cascades. Unlike many of the other studies on skunks (except Howell 1906; Sprayberry and Edelman 2016), the western spotted skunk in the Oregon Cascades consumed a variety of amphibian

species, which are tightly associated with aquatic systems. DNA metabarcoding also revealed that western spotted skunks consumed 11 avian species that would have been difficult to identify with mechanical sorting. During mechanical sorting, we were only able to identify avian species in 3 scats through the presence of feathers, suggesting that skunks may be consuming eggs rather than adult birds. Still, these avian and flying squirrel prey species connect western spotted skunks to the arboreal system. Together, western spotted skunks consumed a great diversity of prey including arthropods, small and large mammals, amphibians, and birds, which is more diverse than all other mammalian carnivores in this region. Given their generalist diet, relatively high abundance, and terrestrial habits, the western spotted skunk may provide substantial linkages between terrestrial, aquatic, and arboreal systems in the Pacific Northwest by facilitating energy and nutrient transfer.

In addition to linking these disparate systems, western spotted skunks may perform important roles in ecosystem as seed dispersers, scavengers, and disease reservoirs. We identified plants in western spotted skunk scats with fruiting bodies including berries (e.g., *Vaccinium*, *Rubus*, *Gaultheria*) and mast (e.g., *Acer*, *Quercus*, *Corylus*). Western spotted skunks may provide key movements that allow for long-distance dispersal of seeds and may influence plant communities similar to martens and foxes (Jordano et al. 2007, González-Varo et al. 2013). We also identified black-tailed deer in 3 scats that we collected opportunistically. We observed radio-collared western spotted skunks scavenging on kills made by mountain lions (*Puma concolor*) on trail camera videos on multiple occasions and tracked western spotted skunks to rest sites adjacent to mountain lion kill sites. This behavior has been observed in other systems (e.g., California scrub oak forest), where the western spotted skunk has the ability to displace gray fox (*Urocyon cinereoargenteus*) from carcasses and mountain lions from their kill sites (Allen et al. 2013, 2016). Furthermore, this signifies the importance of these kill sites and carrion as food resources that are worth the risks associated with being near or directly encountering larger predators (Briffa and Sneddon 2007, Allen et al. 2016, J. Ruprecht et al. 2021). Finally, we identified possible direct and indirect pathways for transmission of nematode parasites such as *Skrjabingylus* spp. which require spotted skunks as definitive hosts to complete their

life cycle (Kirkland Jr. and Kirkland 1983, Lesmeister et al. 2008*b*, Higdon and Gompper 2020, LaRose et al. 2021). Western spotted skunks have been shown to exhibit high prevalence and high severity of *Skrjabingylus* spp. infection (Higdon and Gompper 2020). Direct transmission of this nematode may occur through consumption of gastropods, which are the obligate intermediate host (Lankester and Anderson 1971, Kirkland Jr. and Kirkland 1983), and indirect transmission may occur through consumption of gastropod-consuming vertebrates that serve as paratenic hosts such as chipmunks *(Neotamias townsendii),* shrew moles (*Neurotrichus* gibsii), shrews (*Sorex trowbridgii*), voles *(Myodes spp.),* and amphibians (Gamble and Riewe 1982). Given that *Skrjabingylus* spp. can cause significant osteologic damage to the cranium, it is possible that this parasite could have significant impacts on individual fitness and population dynamics (Lankester and Anderson 1971, Hughes et al. 2018).

Seasonal changes in diet for western spotted skunks were similar to other skunk species, where skunks switched from consuming more insects during the dry season to more vertebrate prey during the wet season (Crabb 1941, Crooks and Van Vuren 1995). Island spotted skunks increased their consumption of crickets during the dry season and mice during the wet season (Crooks and Van Vuren 1995). Prairie spotted skunks primarily consumed rabbits and mice during the winter and spring and insects during the summer and fall (Crabb 1941). These seasonal changes in diet likely reflect changes in availability and abundance of invertebrate resources and plasticity in spotted skunk diet (Cantú-Salazar et al. 2005). In addition to the changes in availability of invertebrate resources, western spotted skunks may switch their diet to one that includes more vertebrates because they need more caloric and protein-rich input to thermoregulate and survive the harsher, colder weather (Moors 1977). Moreover, western spotted skunks breed during the fall during the wet season (Mead 1968) and, if like eastern spotted skunks (Lesmeister et al. 2009), males have larger home ranges when questing for mates, this could increase their energetic requirements, and therefore require an increase in caloric input.

Although they are challenging to collect because they are difficult to find, western spotted skunk scats could serve as a rapid and efficient biodiversity sampler (Shao et al. 2021). As widely distributed and relatively abundant predators with

broad, generalist and opportunistic diet, western spotted skunks could provide valuable information on species co-occurrence and interspecies relationships, ecosystem dynamics, and biodiversity through non-invasive collection of their scats (Boyer et al. 2015, Shao et al. 2021). Western spotted skunk diet analysis may detect cryptic species such as shrew moles, coast moles (*Scapanus orarius*), Pacific tree frogs, and other amphibians that may be difficult to detect using traditional methods.

This was the first study to examine western spotted skunk diet across scat collected from areas with different logging histories. Similarities in diet across logging history across most scales, however, is not surprising. As a generalist species and as an efficient sampler of biodiversity, spotted skunk diet may indicate that many prey species such as chipmunks may be distributed equally across these forest types and these areas may have similar biotic communities. Although some prey species are associated with old-growth forest such as flying squirrels, these species still occur in logged forest at lower densities (Carey 1989). A relatively large portion of our study area (41.5%) is still composed of old-growth forest (Davis et al. In Press), which may help support old-growth associated species within logged areas. Results may differ in landscapes with few remaining old-growth stands, a different configuration of old-growth stands, or in landscapes with more intensive logging operations. Alternatively, spotted skunks are highly mobile (Lesmeister et al. 2009) and can easily move between logged and unlogged areas in this area. This landscape can be characterized as a mosaic of previously logged and unlogged areas without clear boundaries, and scats do not necessarily represent the prey consumed within the stand in which they were defecated. This is supported by the difference in scat composition at the 1 km buffer size (Figure 2.7), which corresponds to the size of a spotted skunk home range (Lesmeister et al. 2009), and fewer insects in the diet if more area in the buffer had been logged. Since many insects such as wasps and beetles depend on the presence of dead wood (e.g., nesting substrate and nutrition; Siitonen and Jonsson 2012), change in diet composition likely reflects differences in insect abundance within these areas.

Although we detected a wide variety of diet items in western spotted skunk scats using DNA metabarcoding, we did not amplify and detect any DNA besides western spotted skunk in 51 scats (39.2%) and only amplified predator and bait DNA

in 67 scats (51.5%). Upon manual inspection, discrepancies between DNA metabarcoding and mechanical sorting indicated that the ANML invertebrate primers that we used poorly amplified Vespidae even though we detected Vespula in some of our samples. The potential for mismatch in the universal invertebrate primers and the biases introduced by the ANML primers we used is well-known because of a lack of conserved regions across all invertebrates (Deagle et al. 2014). Still, we used these primers because of the extensive COI reference library and prior research suggesting that they outperformed other primers for invertebrate biodiversity surveys (Elbrecht et al. 2019, Jusino et al. 2019). This highlights the need for taxa-specific primers, better universal invertebrate primers, a panel of invertebrate primers, or shotgun sequencing that does not rely on PCR to amplify target sequences so that key prey items are not missed in the future (Alberdi et al. 2018).

We detected a wide variety of plants in the western spotted skunk diet through DNA metabarcoding, but many of the genera identified may not have been consumed by western spotted skunks as a food source. When mechanically sorting scats, we discovered many intact Douglas fir needles and bark imbedded in the scat that were likely consumed incidentally, environmentally contaminated following defecation, or contaminated during scat collection (Tercel et al. 2021). Although we tried to reduce the amount of contamination by extracting DNA from fecal material from the interior of the scat, care should be taken when interpreting some DNA metabarcoding results using plant primers.

Noticeably missing from our analysis are the fungal components of the western spotted skunk diet. Fungi are likely to contribute important nutrients (e.g., vitamins) to the western spotted skunk diet (Maser et al. 2008) and fungal dispersal by mammals is essential to plants, fungal diversity, and ecosystem function (Nuske et al. 2017). Eastern spotted skunks have been documented bringing fungal sporocarps to den sites (Sprayberry and Edelman 2016), and we have also recorded western spotted skunks carrying fungal sporocarps on trail cameras during this study. The importance of fungal diet items remains unknown for western spotted skunks and an important area of future research. In addition, we did not characterize differences in diets between individuals and sexes. Although there may be preferences for certain

prey items by individual or sex, we were unable to estimate how many individuals from whom we collected scat for this study.

Western spotted skunks occupy a key position in the Pacific Northwest food web. Through their broad diet and omnivory, they serve as a hub species that creates high connectivity across arboreal, terrestrial, and aquatic systems. Their generalism and habitat plasticity suggest that western spotted skunks may possess greater ability to withstand environmental change (Reed and Tosh 2019, Ducatez et al. 2020). Due to their ability to prey switch to group-living invertebrates, they may even be a beneficiary of climate change if hotter summers increase the availability of wasps, which were by far the most consumed taxa during our study. Although these traits suggests that spotted skunks are resilient, the congeneric eastern spotted skunk has experienced a precipitous decline, and a lack of natural history information stymies recovery efforts. By studying the natural history of western spotted skunks while still abundant, we hope to provide key information necessary to achieve the conservation goal of keeping this common species common.

Acknowledgments

We thank field technicians A. Coombs, B. Murley, K. Van Neste, and R. Rich and Rogue Detection Dogs (formerly with Conservation Canines) – H. Smith, J. Hartman, M. Poisson, C. Yee, Chester, Jack, and Scooby – for field support. We thank Levi Lab technicians for laboratory support. We also thank J. Hedges, S. Speir, and H. Thomas for mechanically sorting scats. Facilities were provided by the H. J. Andrews Experimental Forest and the Long Term Ecological Research program, administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest. Funding for this project was provided by Oregon State University, the USDA Forest Service, the National Science Foundation (LTER7 DEB-1440409), the Northwest Ecological Research Institute, and the ARCS Oregon Chapter. This publication represents the views of the authors and any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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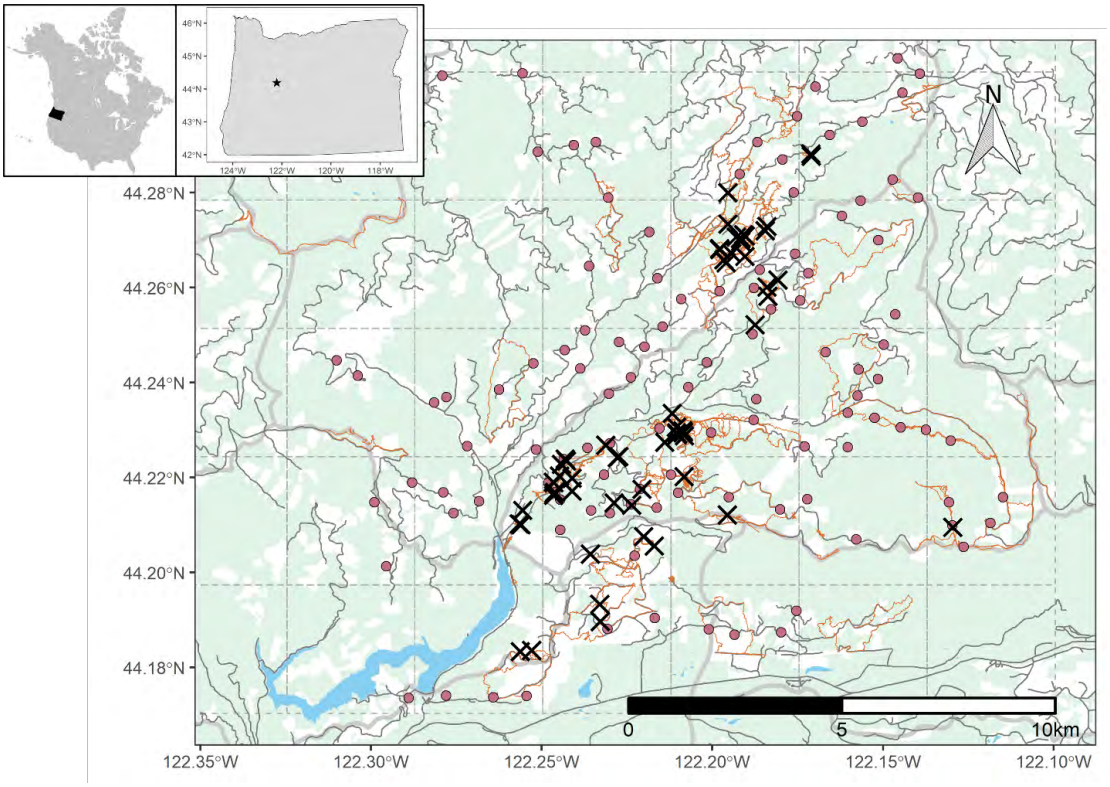

Figure 2.1. Study area within the Willamette National Forest in the Cascade Range of Oregon, USA, and locations of western spotted skunk (*Spilogale gracilis*) scats (black crosses).
Detection dog tracks during the summer and fall of 2018 shown in orange, 3 x 3 km survey grids shown in grey dashed lines, and locations of camera traps shown in maroon circles. Previously logged areas shown in white. Roads shown in dark grey lines, and outlines of watersheds shown in thick light grey lines.

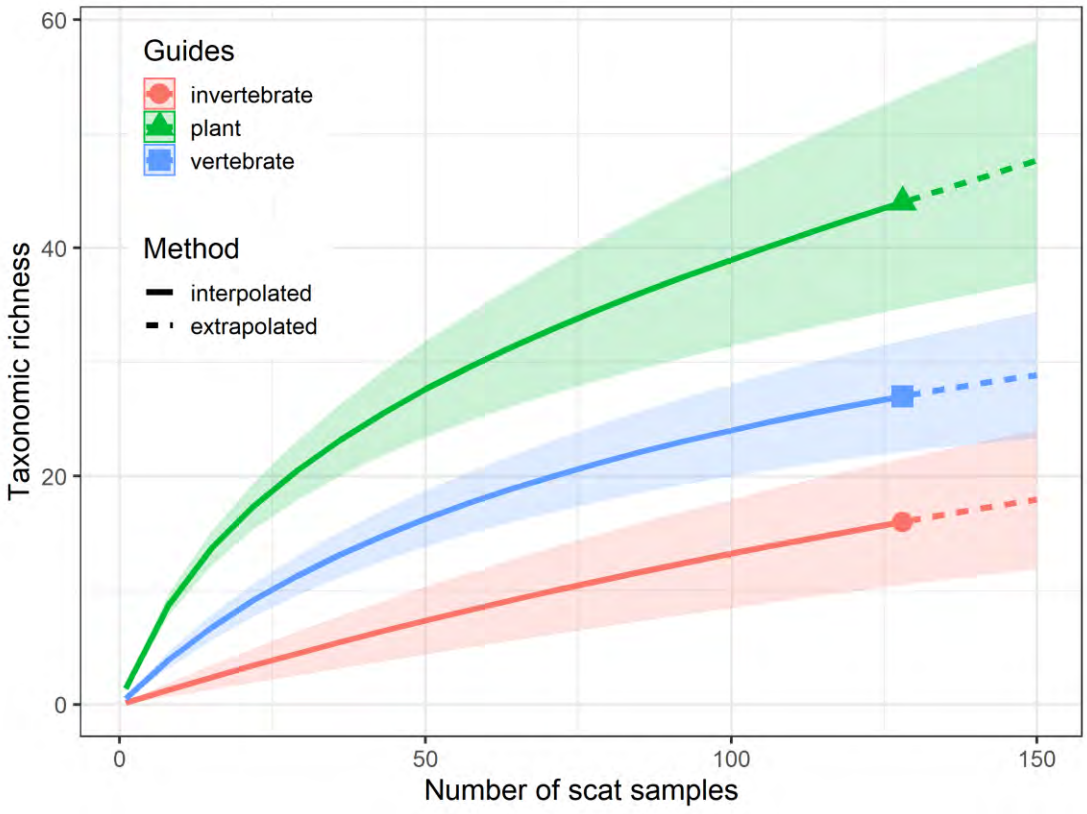

Figure 2.2. Estimation of prey taxonomic richness for western spotted skunks (*Spilogale gracilis*) in the Willamette National Forest.
Vertebrate taxonomic richness (blue line) represents species richness. Invertebrate (red line) and plant (green line) richness represents genus richness.

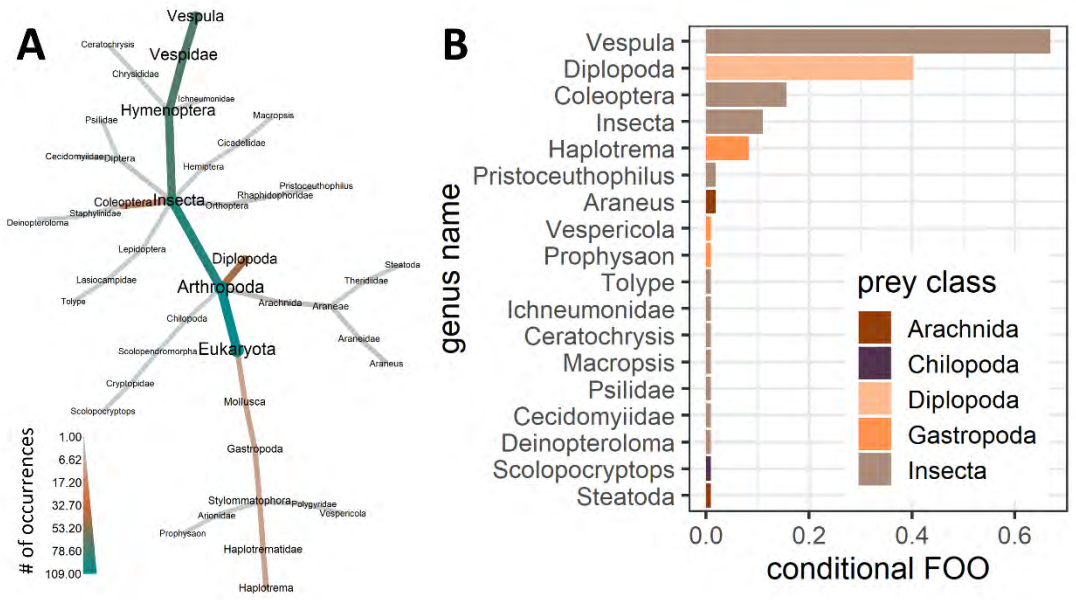

Figure 2.3. Invertebrate contents of western spotted skunk (*Spilogale gracilis*) scats (n = 130) collected from 2017 to 2019 in the Willamette National Forest were identified through DNA metabarcoding and mechanical sorting.
(A) Taxonomic relationships of vertebrate diet items where color and size of nodes represent number of occurrences. (B) Frequency of occurrence (FOO) conditional on the presence of invertebrates in scat (n = 109).

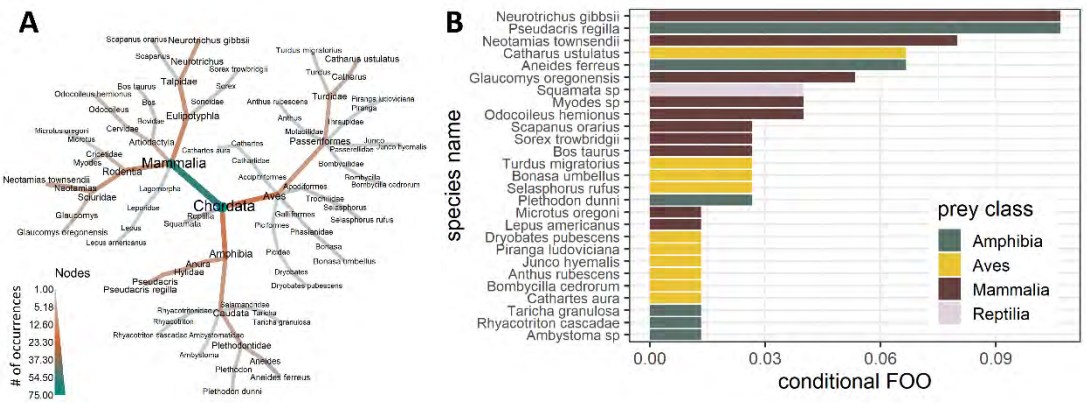

Figure 2.4. Vertebrate contents of western spotted skunk (*Spilogale gracilis*) scats (n = 130) collected from 2017 to 2019 in the Willamette National Forest were identified through DNA metabarcoding and mechanical sorting.
(A) Taxonomic relationships of vertebrate diet items where color and size of nodes represent number of occurrences. (B) Frequency of occurrence (FOO) conditional on the presence of vertebrates in scat (n = 75).

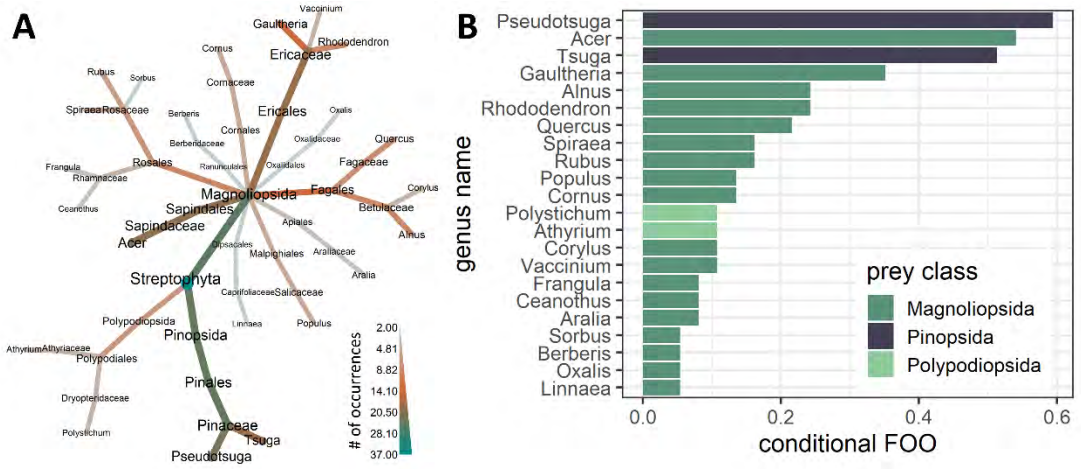

Figure 2.5. Plant contents of western spotted skunk (*Spilogale gracilis*) scats (n = 130) collected from 2017 to 2019 in the Willamette National Forest were identified through DNA metabarcoding and mechanical sorting.
(A) Taxonomic relationships of vertebrate diet items where color and size of nodes represent number of occurrences. (B) Frequency of occurrence (FOO) conditional on the presence of plants in scat (n = 37). Note only plants detected in more than one scat were shown.

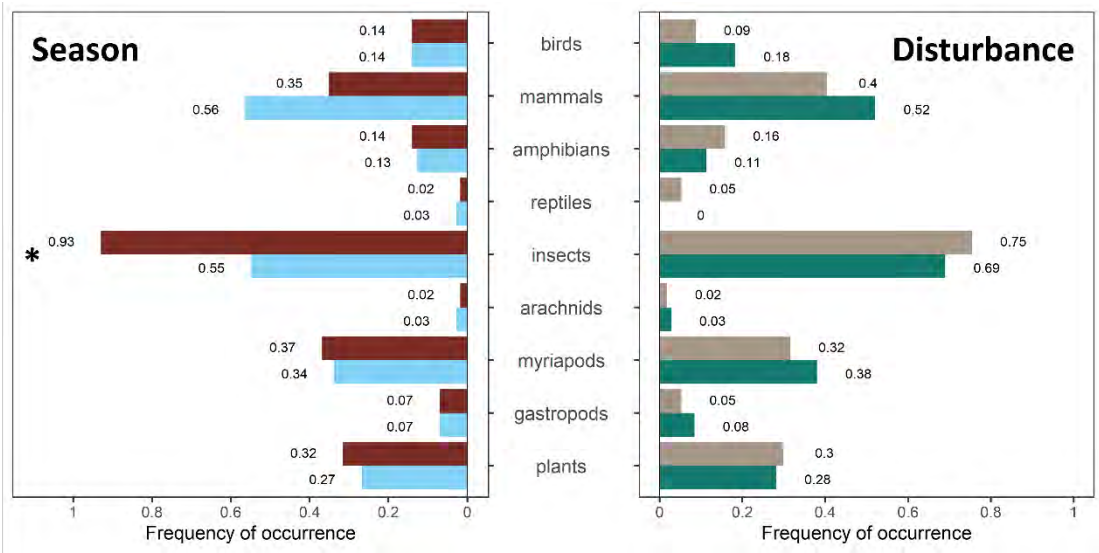

Figure 2.6. Frequency of occurrence of taxonomic groups in western spotted skunk (*Spilogale gracilis*) scats (n = 128) collected from 2017-2019 in the Willamette National Forest.

Contents determined by DNA metabarcoding and mechanical sorting. Left panel shows frequency of occurrence by season (dry in red, wet in blue), right panel shows frequency of occurrence by amount of disturbance in the location we collected the scat (previously logged in tan, no record of logging in green). * represents significant differences in frequency of occurrence by taxonomic group.

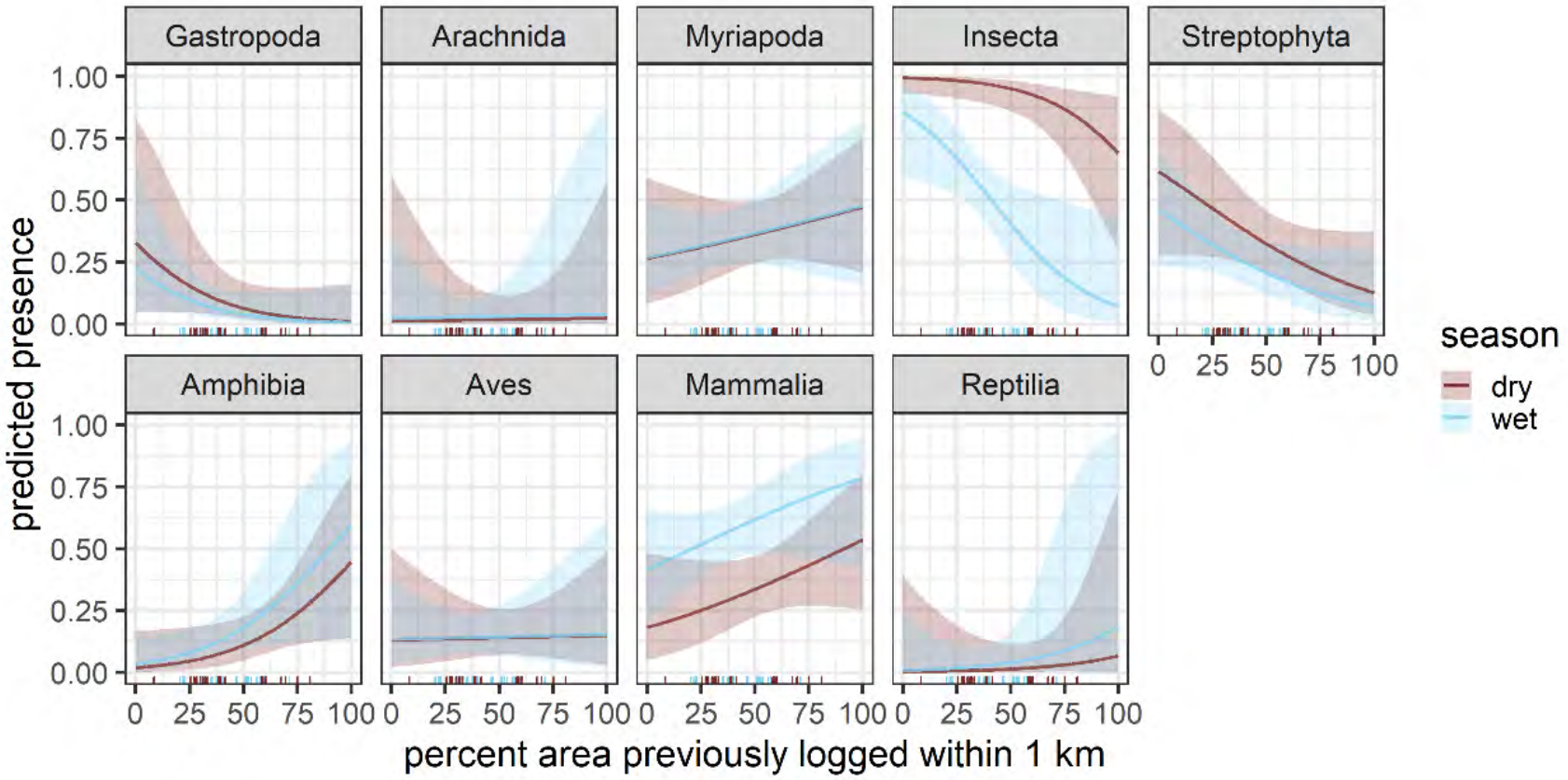

Figure 2.7. Predicted response curves representing probability of presence of each taxonomic class in western spotted skunk scat to percent area that was previously logged within a 1 km buffer of the location where scat was collected.
Response curve for dry season (June – September) in red and wet season (October – Mary) in blue. Ribbons represent 95% confidence interval.

CHAPTER 3 – WESTERN SPOTTED SKUNK SPATIAL ECOLOGY IN THE TEMPERATE RAINFORESTS OF THE PACIFIC NORTHWEST

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Abstract

A major threat to small mammalian carnivore populations is human-induced land use change, but conservation and management are inhibited by limited knowledge about their ecology and natural history. To fill a key knowledge gap for the western spotted skunk (*Spilogale gracilis*), we investigated their spatial ecology at the landscape and home range scale in the temperate rainforests of the Oregon Cascades during 2017-2019. For the landscape scale analysis, we used detections of western spotted skunks at 112 baited camera traps and fitted a dynamic occupancy model to investigate spatial distribution and drivers of inter-seasonal and inter-annual changes in occupancy. Concurrently, we radio-collared 25 spotted skunks (9 female, 16 male) and collected 1,583 relocations. Using continuous-time movement models, we estimated large home range sizes for both male and female spotted skunks, relative to their body mass. Using these home ranges, we fitted a resource selection function using environmental covariates that we assigned to various hypotheses such as resources, predator avoidance, thermal tolerance, and disturbance. Overall, western spotted skunks were widely distributed across our study area (seasonal occupancy up to 63.7 ± 5.3%) and highly detectable (weekly detection probability = 41.2%). At both landscape and home range spatial scales, spotted skunks selected wetter areas and local valleys, which we attributed to areas with more resources. At the home range scale, spotted skunks selected locations with lower predation risk and areas surrounded by more previously logged forests. In this montane environment, inter-seasonal contractions in the spatial distributions of spotted skunks were strongly driven by their response to cold temperature and accumulated snow. This was especially evident when seasonal occupancy declined significantly following a severe heavy snow event in February 2019. Given that there is little information available on the natural history of the western spotted skunk, these results provide essential information about their ecology to focus future monitoring efforts and may help identify potential threats (e.g., forest management, severe snow events, or wildfires) to this species.

Introduction

Small carnivores (< 21.5 kg) are among the most sensitive mammals to changes in environmental conditions (Marneweck et al. 2022, Jachowski et al. 2023). Recent evidence suggests that small carnivore populations are declining globally (Belant et al. 2009, Marneweck et al. 2021), threatening their ecological function as predators, insectivores, frugivores, and seed dispersers (Do Linh San et al. 2022, Marneweck et al. 2022). One of the major threats to small carnivores is human-induced land use change such as the conversion of forest into large-scale agricultural plantations, which can cause habitat fragmentation and degradation (Marneweck et al. 2021) and rapid localized extinction even for common species (Gompper and Hackett 2005, Lindenmayer et al. 2011). Some mechanisms for localized extinction of small carnivores in these degraded landscapes could include an increase in the abundance of other larger predators or a decrease in the amount of cover, which would hinder their ability to avoid predation. Therefore, understanding the habitat requirements of species and restoring their habitat can strongly influence the success of conservation efforts (Wilcove et al. 1998), but determining habitat requirements of a species can be challenging once habitat has been converted or once the species is rare or extirpated from a region. This has led to a growing recognition of the need to study common species while they are still common (Lindenmayer et al. 2011).

In western North America, the decline of small forest carnivores such as fishers (*Pekania pennanti*) (Aubry and Lewis 2003, Zielinski et al. 2004, Aubry et al. 2013) and martens (*Martes caurina humboldtensis*) (Slauson et al. 2007, Moriarty et al. 2011, Tweedy et al. 2019) is associated with even-aged forest management practices that convert complex multi-level forests into simple single-canopy plantations (Hayes et al. 1997) that reduce the availability of large-diameter trees, snags, logs, dense cover, and plant diversity. Another small forest carnivore, the western spotted skunk (*Spilogale gracilis*), is still relatively common within a large geographical range that spans from southwestern Canada to Mexico and as far east as Wyoming and Colorado (McDonough et al. 2022). Its congener, the eastern spotted skunk (*Spilogale putorius*), which was also common throughout its range in the Midwest and Southeast United States, declined by > 90% within a decade (1940-

1950) and > 99% within 4 decades (1940-1980) (Gompper and Hackett 2005). Although the causes of decline are poorly understood, population declines have been linked to habitat loss (Gompper and Hackett 2005). The eastern spotted skunk is now listed as Vulnerable by the IUCN (Gompper and Jachowski 2016) and the plains spotted skunk (*Spilogale interrupta*) is being considered for listing under the Endangered Species Act (US Fish and Wildlife Service 2012). Eastern spotted skunk recovery efforts have been hindered by limited information due to low capture rates (< 2.8%; Hackett et al. 2007) and have relied on a handful of studies conducted after the population had already declined (Lesmeister et al. 2008*a*, 2009, 2013).

The limited available research on western spotted skunks is restricted to non-forested ecosystems including the island spotted skunk subspecies (*S. g. phiala*) (Crooks 1994*b*, *a*, Crooks and Van Vuren 1995), deserts of Texas (Doty and Dowler 2006, Neiswenter et al. 2006, Neiswenter and Dowler 2007), and the chaparral biome of the Sierra Nevada mountains of California (Carroll 2000). In these ecosystems, spotted skunks selected for dense cactus patches (Doty and Dowler 2006), large mesquite (*Prosopis glandulosa*) trees (Neiswenter and Dowler 2007), canopy cover, logs, snags, shrubs (Carroll 2000), and ravines (Crooks and Van Vuren 1995). Western spotted skunk ecology in forests in mountainous environments remains understudied, particularly in areas with large spatial and interannual variation in snow, but some evidence suggests the species may be associated with old-growth forests in the temperate rainforests of the Pacific Northwest (Carey and Kershner 1996).

To better understand the natural history of the western spotted skunk in forested ecosystems, we studied the species' spatial ecology in the Oregon Cascade Mountains using camera traps and radio-collars. The objectives of our study were to quantify the habitat selection of the western spotted skunk at the landscape scale and at the individual home range scale, and to investigate the seasonal changes in space use. We designed our analyses to reflect hypotheses related to anthropogenic disturbance and the need for resources, thermoregulation, and cover from predators (Table 3.1). We predicted that western spotted skunk spatial ecology would be negatively impacted by anthropogenic disturbance (Carey and Kershner 1996),

positively related to areas that provide food resources and water (Tosa et al. 2023), positively related to areas with coarse woody debris (Buskirk et al. 1989, Lesmeister et al. 2008*a*) and lower snow fall, and driven by a need for cover from predators (Lesmeister et al. 2009, 2013, Tweedy et al. 2019, Delheimer et al. 2023) as suggested in other spotted skunk and small carnivore studies.

Study Area

This study was conducted in the McKenzie River District of the Willamette National Forest and the H. J. Andrews Experimental Forest (HJA), which are located on the western slope of the Cascade Mountain Range near Blue River, Oregon (Figure 3.1). Elevations range from 410 m to 1,630 m. The maritime climate is typical of the Pacific Northwest region and consists of warm, dry summers and mild, wet winters. Mean monthly temperatures range from 1°C in January to 18°C in July. Precipitation falls primarily as rain, is concentrated from November through March, and averages 230 cm at lower elevations and 355 cm at higher elevations.

Lower elevation forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) but also include deciduous trees such as bigleaf maple (*Acer macrophyllum*). Upper elevation forests are dominated by noble fir (*Abies procera*), Pacific silver fir (*Abies amabilis*), Douglas-fir, and western hemlock. The understory is variable and ranged from open to dense shrubs. Common shrubs included Oregon grape (*Berberis* spp.), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), vine maple (*Acer circinatum*), Pacific rhododendron (*Rhododendron macrophyllum*), huckleberry (*Vaccinium* spp.), and blackberry and salmonberry (*Rubus* spp.).

Before timber cutting in 1950, 65% of the HJA was covered in old-growth forest. Approximately 30% of the HJA was clear cut or shelterwood cut to create plantation forests varying in tree composition, stocking level, and age. In 1980, the HJA became a charter member of the Long Term Ecological Research network and no logging has occurred since 1985. The Willamette National Forest immediately surrounding the HJA has a similar logging history, but logging continued through the duration of our study. The HJA consisted of a higher percentage of old-growth forest

than the surrounding Willamette National Forest (approximately 58% in the HJA vs. 37% in the study area; Davis et al. 2022). In addition to logging, wildfires are a primary disturbance, followed by windthrow, landslides, root rot infections, lateral stream channel erosion, and tree fall caused by heavy snow events. On 24 February 2019, near the end of the study, the Oregon Cascades experienced a large heavy snow event that resulted in a massive tree fall event (DiGregorio 2019, The White House 2019, Stoelb 2020). There were no fires during the study, but mean fire return interval of partial or complete stand-replacing fires for this area is 166 years and ranges from 20 years to 400 years (Teensma 1987; Morrison and Swanson 1990).

Methods

We studied the resource selection of western spotted skunks at two scales because we were interested in the spatiotemporal dynamics of the population as a whole and the responses of individual animals to their environment (Johnson 1980, Mayor et al. 2009). To investigate the inter-seasonal and interannual variability in the spatial distribution of western spotted skunks across the study area (2^{nd} order habitat selection; Johnson 1980), we implemented multi-season occupancy models using detections of spotted skunks at baited camera traps. Specifically, we were interested in the changes in occupancy between seasons and years because our study was conducted in mountainous terrain where precipitation in the winter can fall as rain at low elevations and heavy snow at high elevations and the weather was quite variable during the study (e.g., wet cold spring in 2017, warm dry spring in 2018, drought conditions during summer 2018, severe snow event during winter 2019). Next, we used fine-scale locations of spotted skunks from radiotelemetry and GPS data to estimate western spotted skunk home range sizes and overlap and to model western spotted skunk resource selection within home ranges (3^{rd} order habitat selection). We conducted all analyses using Program R (R Core Team 2019) and produced figures using the *ggplot2* package (Wickham 2016).

Field methods

Camera traps

We set and maintained 112 baited camera traps (HC500, Reconyx, Holmen, WI or TrophyCam, Bushnell, Overland Park, KS) between April 2017 – August 2019. We stratified placement of camera traps based on disturbance (i.e., old growth stand characteristics) and elevation gradients. Camera traps were part of a larger biodiversity study (Frey et al. 2016*a*, *b*, Weldy et al. 2019, Kim et al. 2022). The camera traps located in the surrounding Willamette National Forest were deployed in May and June 2018 (n= 58). To increase detection probabilities of carnivores, we baited each camera trap with a can of fish flavored cat food or sardines, a fresh dead mouse (*Mus musculus*), and a commercially available carnivore lure (e.g., Gusto, Caven's Lure, Pennock, MN). We manually tagged species presence in camera trap photographs in DigiKam (V6.1.0, www.digikam.org), extracted metadata using the *exifr* package (Dunnington and Harvey 2021), converted western spotted skunk detections into weekly encounter histories.

Capture

We captured spotted skunks from August – May during 2017 – 2019 using Tomahawk live traps (Model 102 [12.7 cm x 12.7 cm x 40.6 cm] and 103 [15.2 cm x 15.2 cm x 48.3 cm], Tomahawk Live Trap Co., Hazelhurst, WI). We placed traplines of 10-30 live traps at 100 – 250 m intervals along accessible trails and roads near detections of western spotted skunks on camera traps. To reduce trap injuries, we modified Tomahawk traps with corrugated plastic to eliminate gaps between the trap door and floor. We also included polyester insulation in traps during the winter to help trapped animals with thermoregulation. We covered traps with burlap and bark or leaf litter. We baited each trap with one or a combination of the following: sardines, a frozen dead house mouse, or commercially available carnivore lures. We checked traps daily between 0600 and 1000.

Once captured, we physically restrained and chemically immobilized skunks using an intramuscular injection of 15 mg/kg ketamine HCl (Zoetis Services LLC, Parsippany, NJ) and 40 mcg/kg dexmedetomidine HCl (Zoetis Services LLC, Parsippany, NJ). Following chemical immobilization, we determined sex, recorded

mass and morphometric measurements, and examined tooth wear. We fit each skunk with two metal ear tags (Monel size 1; National Band and Tag Co., Newport, KY) and a VHF radio-collar < 5% of their body mass (M1545, 16 g; Advanced Telemetry Systems, Isanti, MN). We also fit 4 large male skunks (> 550 g) with GPS collars (LiteTrack20, 20 g; SirTrack, New Zealand) during the breeding season (September – October). All capture and handling protocols were approved by the United States Department of Agriculture Forest Service Animal Care and Use Committee (USFS 2016-015) under Oregon Department of Fish and Wildlife Scientific Take Permits (ODFW 107-17, ODFW 059-18, and ODFW 081-19) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Relocations

For our 3rd order of resource selection analysis, we collected spatial data on western spotted skunks from August 2017 – August 2019 in three ways: 1) we recorded location information for any skunk that we captured in a trap, 2) we triangulated collar VHF signals from the roads nightly when skunks were more active, and 3) we used homing techniques on collar VHF signal daily to identify diurnal rest site locations. We derived skunk locations from triangulations of ≥ 3 signal bearings with ≥ 20 degrees difference within 20 min. from a hand-held 3-element Yagi antenna in the program Locate III (Nams 2006). To gain finer-scale movement data, we programmed the 4 GPS collars to collect locations at 30-minute fix intervals during the night (21:00 – 09:00) when skunks were more active and at 4-hour fix intervals during the day (09:00-21:00) when skunks are less active (Moriarty and Epps 2015). We used 2 types of GPS location acquisition technology (SWIFT fix and standard fix) and programmed 2 collars for each. SWIFT fixes were recently developed to improve GPS fix success rates and reduce battery energy consumption compared to standard fix devices, especially in forested ecosystems (Forrest et al. 2022). We conservatively only analyzed GPS locations where the horizontal dilution of precision was < 20 (n = 14) (D'Eon et al. 2002).

Model covariates

We assessed western spotted skunk habitat at local and landscape levels with environmental covariates derived from satellite imagery, light detection and ranging

(LiDAR) maps (collected from 2008 to 2016), and other maps acquired from the USDA Forest Service and Oregon Explorer (https://oregonexplorer.info/) (Table 3.1). We assigned each covariate to a category based on our hypotheses related to resources, predation, thermal tolerance, and disturbance. In addition to linear functional forms of each variable, we explored the quadratic form for elevation and the logarithmic form of distance to features of stream, waterbody, road, and areas logged within the last 100 years. We averaged landscape level variables using buffer sizes of 100 m, 500 m, 1 km, and 5 km to represent minimum and mean step length traveled in 1 hour when skunks were active (estimated from GPS locations), approximate core area size (also maximum step length traveled in 1 hour), and home range size of a western spotted skunk (this study), respectively (McGarigal et al. 2016). To determine the appropriate scale and functional forms of variables, we fitted single covariate models and compared models using Akaike's Information Criterion corrected for small sample size (AIC_C) (Burnham and Anderson 2011). For each covariate, the scale or functional form of the model with the lowest AIC_C score was identified as the most-supported scale or functional form, respectively. To prevent multi-collinearity and confounding factors, we computed Pearson's correlation coefficients between each pair of covariates and retained the covariate with the greater average deviance explained when 2 or more covariates were highly correlated (i.e., $|r| \geq 0.6$) (Wan et al. 2017). All covariates were centered and scaled prior to fitting models to facilitate effect size comparisons and model convergence.

Statistical analyses

Occupancy models

To evaluate the inter-seasonal and interannual variability in 2nd order selection by western spotted skunks across the landscape, we conducted dynamic occupancy analyses. Dynamic occupancy analyses allowed us to formally address our anecdotal observations of declines in spotted skunk detections at higher elevations during the winter when there was consistent snow cover. We separated encounter histories into 17- and 18-week biologically meaningful seasons for summer (June – September), fall (October – January), and spring (February – May). Summer corresponded to the

dry season in the Oregon Cascades, fall represented the wet season and the mating season of western spotted skunks, and spring represented a period in the Oregon Cascades when there was consistent snow cover at high elevations and food resources were likely most scarce. This resulted in 7 seasons (summer 2017 through summer 2019) and allowed us to investigate seasonal shifts in space use by western spotted skunks. Since it was possible for western spotted skunks to visit multiple cameras, occupancy model results should be interpreted as space use instead of occupancy of sites.

We calculated naïve occupancy for each season by dividing the number of sites where western spotted skunks were detected on baited camera traps by the total number of sites monitored during that season. We estimated each of the four parameters, detection (p), initial occupancy (ψ), colonization (γ), and extinction (ε) as a function of environmental covariates (Table 3.1) using the *unmarked* package (Fiske and Chandler 2011). Since the unmarked dynamic occupancy models require balanced encounter histories for each season, we augmented encounter histories with NA values so that each season consisted of 18 weeks. We started with the null model ($p \sim 1$, $\psi \sim 1$, $\gamma \sim 1$, $\varepsilon \sim 1$) and fit a detection only model with temporal variables: season, skunk year, and number of weeks since bait. Then, for occupancy, colonization, and extinction parameters, we fitted univariate models using environmental or temporal covariates for each hypothesis category and separately evaluated which covariates to include in each additive hypothesis model (i.e., resource model, predation model, thermal model, disturbance model, temporal model) and ranked univariate models based on AIC_C scores (Burnham and Anderson 2011). Only covariates from univariate models that were more supported than the null model and those that were not highly correlated with one another (|Pearson's r| < 0.6) were included in each hypothesis model. We fitted a parameter model for occupancy, colonization, and extinction by combining all four hypothesis models. To prevent overparameterization and to be conservative in our biological interpretations of covariates, we removed variables with 95% confidence intervals overlapping 0. We combined all parameter models into the final global model (Figure 3.2).

For our final model, we conducted a goodness-of-fit test using a parametric bootstrap with 1000 replicates and the chi-square statistic (Fiske and Chandler 2011, Kéry and Chandler 2012, Kellner et al. 2023). Finally, we estimated standard errors of predicted occupancy in each season using a non-parametric bootstrap with 1000 replicates using the *nonparboot* function and predicted occupancy across the landscape. To explore whether occupancy probability was declining over time, we fit a post-hoc linear regression to the predicted seasonal occupancy (predicted occupancy ~ season).

Home Range Estimation

We calculated home range metrics using a continuous-time movement model in the *ctmm* package (Fleming and Calabrese 2022). For each telemetry location, we incorporated variance and covariance of 95% error ellipses. We removed outlier locations when indicated by the *outlie* function. For GPS locations, we assumed that 1 horizontal dilution of precision (HDOP) value was equivalent to 10 m error and set degrees of freedom to 2. Then, we estimated core range (50% isopleth) and home range (95% isopleth) for each spotted skunk with ≥ 5 locations using autocorrelated kernel density estimation with the *akde* function (Fleming and Calabrese 2017). We used this method because it incorporates error in locations, performs well with low sample sizes, and allows us to combine multiple sources of location information with different fix intervals (e.g., rest sites, capture locations, VHF triangulation, and GPS locations). We calculated the degree of overlap in home ranges using the Bhattacharyya method (Bhattacharyya 1943) in the *overlap* function to assess territoriality within and between sexes of western spotted skunks (Winner et al. 2018). In addition, because there were apparent differences in home range and core area sizes, we explored clustering within the home range sizes using the *kmeans* function (k = 1-5). To verify significant differences between home range sizes of groups, we ran an ANOVA and Tukey's honestly significant difference (HSD) test. Post-hoc, we also explored whether the large differences in home range size we observed in males but not females could be explained by body mass, total body length, or environmental variables (i.e., mean elevation, proportion of logging, or proportion of old growth within the home range) using linear regressions.

To explore whether skunks shifted their home ranges by season, we calculated seasonal home ranges using the same methods as above. We split locations based on the same seasons used in the occupancy modeling: summer (June – September), fall (October – January), and spring (February – May). We calculated seasonal home ranges if an animal had ≥ 5 locations multiple seasons. Using the Bhattacharyya method in the *overlap* function, we calculated fidelity of home ranges across seasons (e.g., summer vs. fall).

Within Home Range Resource Selection

To investigate resource selection at the home range scale, we explored the same environmental variables from our occupancy models. Again, we tested different scales for landscape variables and linear, quadratic, and log functional forms for environmental variables with these data to determine which was the most supported. Since seasonal home range fidelity was high, we selected 25 available points for each used location within each home animal's overall home range to estimate resource selection. We fitted a binomial generalize linear mixed effects regression to used and available points within the home range and included individual as a random intercept in the *blme* package (Chung et al. 2013). To determine which variables to include in the global model, we fitted univariate models to used and available points. We ranked univariate models against the null model using AICc and included any variables with a univariate model that ranked higher than the null and were not correlated with one another (|Pearson's r| < 0.6) in an additive global model. Similar to the dynamic occupancy analysis, we fit additive hypothesis models for resources, predation, thermal, and disturbance and combined all hypothesis models into the final global model. We took this approach for the resource selection analysis because our analysis was largely exploratory and a global model would better reflect relationships of western spotted skunks with variables of interest for forest management such as amount of logging. We excluded skunks with < 25 used locations from this analysis because of model convergence issues.

From observations in the field, we suspected that some western spotted skunks had opposite relationships with some environmental variables, specifically elevation, percentage of area logged, and percentage of area mature. To test this, we added a

random slope by individual term for one environmental covariate at a time to the final global model and ranked these models using AICc. We only added a random slope by individual term for one environmental covariate at a time to prevent overparameterization and facilitate model convergence.

Results

Over the course of 7970 trap nights, we captured 31 western spotted skunks (12 female, 19 male) 177 times (2.2% capture success) and tracked 25 of those individuals (9 female, 16 male) for various durations between October 2017 – August 2019 (Figure S3.1). Males weighed 1.5 times more ($mass_{male}$ = 595.3 ± 22.3 g, $mass_{female}$ = 392.4 ± 11.2 g; $F_{1,29}$ = 47.2, $p < 0.001$) and total body lengths were 4.5 cm longer ($length_{male}$ = 42.2 ± 0.5 cm, $length_{female}$ = 37.7 ± 0.5 cm; $F_{1,29}$ = 36.7, $p < 0.001$) than females. We recorded 170 skunk capture events, 293 rest site uses, 1011 telemetry locations, and 109 GPS locations. We excluded 34 reuses of a single site by a female (SG-008) during the summer that we suspect was used for denning and raising kits. During the spring of 2019, many of our VHF collars failed because the VHF antenna broke off the collars within 1 month of deployment. We recovered location data from 2 GPS collars (1 swift fix and 1 standard fix): the swift fix collar recorded 121 points and 107 points met our error threshold criteria (11.0% fix success rate; Figure S3.2), whereas the standard fix collar only recorded 2 successful locations, both of which met the error threshold criteria (0.8% fix success rate).

The western spotted skunks in this study had relatively large home ranges relative to their body mass compared to other mammalian carnivores (Figure 3.3). One skunk (SG-001) had 2 distinct home ranges, suggesting the spotted skunk dispersed on 10 May 2018 (Figure S3.3). Therefore, we treated the 2 home ranges as separate for the remainder of the analysis. K-means clustering revealed 2 groups of home ranges ($F_{2,22}$ = 15.2, $p < 0.001$): a smaller home range consisting of females (mean = 10.93 km^2, 95% CI = 6.63 – 16.86) and males (mean = 16.38 km^2, 95% CI = 12.83 – 20.49) and a distinctly larger home range consisting of males (mean = 35.83 km^2, 95% CI = 31.52 – 40.40) (Table 3.2). Home range size and clustering was independent of the number of locations used to calculate the home range ($\beta_{total\ locs}$ = -

0.05, $p < 0.56$; Figure S3.4), length or body mass of the skunk ($\beta_{length} = 2.21$, $p = 0.23$, $\beta_{mass} = 0.05$, $p = 0.09$), and other environmental variables including mean elevation within the home range, percent of forest logged, or percent old growth (Figure S3.5). Females had similar home range size across seasons, and male home range sizes differed by season, but there was no consistent trend among individuals (Figure 3.4A). Some males had larger home ranges during the spring whereas other males had larger home ranges during the fall (Figure 3.4A). Home range overlap between neighboring skunks was high regardless of sex (Table 3.3; Figure S3.6), and individual home range fidelity was high across seasons (fall-spring overlap: 87.6 ± 2.6%, fall-summer overlap: 80.2 ± 4.5%, spring-summer overlap: 82.0 ± 5.8%; Figure 3.4B).

Occupancy models

We detected western spotted skunks at 80 of 112 camera sites (naïve occupancy = 71.4%). The final multi-season occupancy model revealed that detection probability declined with more weeks since bait ($\beta_{bait} = -0.09 \pm 0.01$) (Figure 3.5; Table S3.3). Detection probability was highest in the fall and in 2019 and lowest in the summer and in 2017 ($\beta_{p.SPRING} = -0.56 \pm 0.10$, $\beta_{p.SUMMER} = -1.03 \pm 0.10$, $\beta_{p.2018} = 0.25 \pm 0.08$, $\beta_{p.2019} = 0.36 \pm 0.23$). Initial occupancy was also higher when there was more mature forest in the landscape ($\beta_{P.MATURE.5KM} = 0.99 \pm 0.67$), in local valley bottoms ($\beta_{TOPO\_POS.1KM} = -0.71 \pm 0.45$), and areas with dense vegetation ($\beta_{B4} = -1.23 \pm 1.19$). Colonization probability was higher in areas with more moisture ($\beta_{B6} = -0.69 \pm 0.26$), areas with rougher topography ($\beta_{ROUGH} = 0.25 \pm 0.20$), and areas with lower basal area of Pacific silver fir ($\beta_{ABAM} = -0.53 \pm 0.32$). Extinction probability was higher at low and high elevations ($\beta_{ELEVATION} = -5.14 \pm 1.53$, $\beta_{ELEVATION2} = 5.76 \pm 1.67$), at ridge tops ($\beta_{TOPO\_POS.0.5KM} = 0.45 \pm 0.19$), and in areas with more Pacific silver fir ($\beta_{ABAM} = 0.65 \pm 0.46$). Extinction probability was also higher immediately following a disturbance ($\beta_{YRS\_SINCE\_DIST} = 0.88 \pm 0.76$, $\beta_{LOG(YRS\_SINCE\_DIST)} = -1.47 \pm 0.92$) and in areas with less mature forest in the landscape ($\beta_{P.MATURE.5KM} = -0.41 \pm 0.20$). Probability of colonization was highest between summer and fall ($\beta_{\gamma.SUMMER} = 1.70 \pm 0.51$), and probability of extinction was highest between spring and summer ($\beta_{\varepsilon.SPRING}$

= 1.10 ± 0.43) and between 2018 and 2019 ($\beta_{\varepsilon.2018}$ = 1.04 ± 0.35). After accounting for detection, colonization, and extinction, predicted seasonal occupancy was highest during the fall of 2017 (63.7 ± 5.3%) and lowest during the summer of 2019 (19.9 ± 4.2%) following the severe heavy snow event (Figure 3.6). Overall, seasonal occupancy had a declining trend over the duration of the study (β_{season} = -0.05 ± 0.02, p = 0.038), but this trend was primarily driven by the low predicted occupancy rate during summer 2019.

Home Range Resource Selection

We censored 5 skunks from the resource selection analysis due to small sample size (n < 25). Used locations within the western spotted skunk home range were best predicted by predation variables, followed by resource, thermal, and disturbance variables. The best performing model was one that included a term for random slope by individual on elevation (Table S3.6). When we fitted the global model with random slopes for each skunk, we found that each skunk had distinct responses to elevation where some individuals selected for low elevations whereas other selected for intermediate elevations (Figure S3.11). Coefficients for covariates were similar between the global model that only included random intercepts by individuals (Table S3.6) and the global model that included random intercepts and random slopes for elevation by individuals (Table S3.7). Overall, spotted skunks selected for variables related to predation avoidance including shorter understory canopy (β_{CANOPY_HT} = -0.13 ± 0.03) and flatter terrain (β_{ROUGH} = -0.22 ± 0.03) (Figure 3.7; Table S3.7). Spotted skunks selected for resources such as local valley bottoms ($\beta_{TOPO\_POS.1KM}$ = -0.29 ± 0.04), areas near streams ($\beta_{DIST.STREAM}$ = -0.10 ± 0.05, $\beta_{LOG(DIST.STREAM)}$ = 0.02 ± 0.05), and wetter areas (β_{B4} = -0.10 ± 0.04). Spotted skunks also selected for variables related to thermal tolerance including northerly aspects (β_{NORTH} = 0.30 ± 0.04), intermediate elevations ($\beta_{ELEVATION}$ = 0.02 ± 0.15, $\beta_{ELEVATION2}$ = -0.39 ± 0.13), and more disturbed areas such as locations closer to roads ($\beta_{DIST.ROAD}$ = -0.14 ± 0.06, $\beta_{LOG(DIST.ROAD)}$ = -0.15 ± 0.03) and locations with more previously logged areas in the landscape ($\beta_{P.LOGGED.1KM}$ = 0.17 ± 0.04).

Discussion

This study provides the first detailed movement and habitat analysis of western spotted skunks in temperate rainforests of the Pacific Northwest. By studying habitat selection at multiple spatial and temporal scales and with multiple methods, we found that responses to some environmental variables, such as complex forest structure, were scale specific, whereas responses to other environmental variables, such as topographic position index, were consistent at all scales. Given that there is little information available on the natural history of the western spotted skunk, these results provide evidence for key aspects of their ecology to focus monitoring efforts and may be beneficial to understand and identify potential threats (e.g., forest management, severe snow events, or wildfires) to this species.

We found that western spotted skunks were widely distributed across our study area (seasonal occupancy up to 63.7 ± 5.3%) and highly detectable (weekly detection probability = 41.2%), suggesting that populations are common in the Willamette National Forest. We also found that western spotted skunks exhibited sexual dimorphism in body mass, body length, and home range size. Females were consistently lighter, smaller, and had smaller home ranges. Some male western spotted skunks had relatively small home range sizes (16.38 km^2) that were similar to female western spotted skunks (10.93 km^2), but other males had home ranges that were 2.4-fold larger (35.83 km^2). The differences in male home range size were independent of the physical characteristics of the individuals, proportion of forest type, elevation, or the number of relocations we were able to collect (Figure S3.5). The home ranges of western spotted skunks in our study were considerably larger than those previously reported for other western spotted skunk populations (0.50 km^2 for males, 1.59 km^2 for females; Carroll 2000), island spotted skunks (0.29 km^2 – 0.61 km^2; Crooks and Van Vuren 1995, Jones et al. 2008). We also found that this population of western spotted skunks had larger home ranges than other similarly sized or closely related carnivores (Lindstedt et al. 1986, Doty 2003, Gehring and Swihart 2004, Jachowski 2007, King and Powell 2007) (Figure 3.3). The smaller male western spotted skunk home ranges in this study (95% CI: 12.83 – 20.49 km^2) were similar to the breeding season home ranges for male prairie spotted skunks (2.22

– 18.24 km^2), and female western spotted skunk home ranges in this study (6.63 – 16.86 km^2) were 5.9-fold larger than home ranges reported for female prairie spotted skunks (0.21 – 1.48 km^2; Lesmeister et al. 2009).

Western spotted skunk occupancy was higher in local valleys and areas with greener, wetter areas and close to streams, which typically corresponded to areas near ephemeral creeks and was consistent with previous studies (Brown 1985, Crooks and Van Vuren 1995, Carey and Kershner 1996). These areas likely provide spotted skunks with food resources such as invertebrates (e.g., wasps, millipedes, beetles) (Tosa et al. 2023). Occupancy was also higher in areas surrounded by higher proportions of mature forests, not of old growth forest, at the 5 km buffer scale, which was not aligned with our predictions given a past study that suggested that spotted skunks were associated with old growth forest (Carey and Kershner 1996).

Seasonal occupancy (i.e., landscape use) estimates were highest during the fall, which may have been driven by higher movement rates by males during the breeding season. This could have resulted in individual western spotted skunk detections on multiple camera traps. Lesmeister (2009) found that the highest movement rates of prairie spotted skunks occurred during the spring when males quested for reproductive females. Because seasonal home range fidelity of western spotted skunks was high (> 80%), increases in seasonal occupancy rates during the fall may also have been due to birth and dispersal events. Conversely, we suspect decreases in seasonal occupancy rates during the spring may be due to increased mortality in winter.

Seasonal extinction probabilities appear to reflect sensitivity to recent forest harvest (harvest within 25 years) and thermal tolerance of western spotted skunks. Extinction probability was highest in areas with a recent disturbance but dropped off sharply thereafter (Figure 3.5; Figure S3.9). Extinction probability was also higher at higher elevations, on ridges, and in areas with more Pacific silver fir. These attributes represent areas that experience greater volumes of precipitation in the form of snow, consistent snow cover, especially during the spring, and prolonged snowmelt. This was especially apparent when we mapped predicted extinction probabilities across our study area (Figure S3.8). Western spotted skunk sensitivity to snow and cold

temperatures was apparent when we observed the greatest decline in seasonal occupancy between spring and summer 2019 following the severe wet snow event that occurred in February 2019 (Figure 3.6). Not only did this event provide a downfall of heavy, wet snow, this event also caused widespread tree damage, tree falls, and landslides (Stoelb 2020). Therefore, declines in spotted skunk occupancy may have resulted from tree mortality or ground movement (e.g., landslides). It remains uncertain what population level impact these extreme events may have on western spotted skunks, but warrants further investigation given extreme weather events are projected to increase in frequency and severity with climate change (Seneviratne et al. 2022).

Other similarly sized carnivores are also sensitive to snow and cold temperatures because of their morphology, high metabolic demands, and limited energy reserves (Buskirk and Harlow 1989). For example, long-tailed weasels (*Neogale frenata*) may be limited in their northward distribution because of snow cover (Simms 1979). Other species such as ermine (*Mustela erminea*) and American marten (*Martes americana*), however, may be better suited to these conditions through behavioral adaptations. Ermines are highly adept predators that can balance their energetic demands by hunting voles in the subnivean zone (Simms 1979). American marten behaviorally cope with colder temperatures and heavy snow by selecting subnivean rest sites (Buskirk et al. 1989, Wilbert et al. 2000). Although we were generally unsuccessful in tracking western spotted skunks when there was deep snow cover, we regularly detected spotted skunks in camera trap photos walking on top of the snow, which suggests that spotted skunks were not restricted to the subnivean zone, at least when active.

While dynamic occupancy models revealed general patterns of space use by western spotted skunks, resource selection at the home range scale revealed more detailed responses to environmental variables. In both models, predicted use by western spotted skunks was higher in local valleys and in greener, wetter areas. Use of wetter areas was further supported by the greater use of northerly aspects, which typically remained moister, compared to southerly aspects. Our hypotheses about spotted skunk use of local valleys were further refined by home range scale analysis

that showed use was higher with less bigleaf maple basal area and lower canopy height. Spotted skunks may have avoided lowland riparian forests prone to flooding. Western spotted skunks are susceptible to predation by barred owls (*Strix varia*) (Tosa et al. 2022), which may be a driving factor for selecting areas with more shrubby vegetation that could reduce predation risk (Figure 3.7). Selection for vegetative cover to reduce predation risk is consistent with other studies on prairie spotted skunks and eastern spotted skunks (Lesmeister et al. 2009, Sprayberry and Edelman 2018, Eng and Jachowski 2019).

At the home range scale, western spotted skunk use was greater in locations surrounded by more logged area at the 1 km scale, also contrary to the observations by Carey and Kershner (1996). This was also counter to our findings in the landscape-level occupancy analysis where occupancy was higher in areas surrounded by more mature forest at the 5 km scale and extinction probability was higher in areas with recent disturbances. A possible reason for selection for previously logged forest could be because light is able to penetrate through the canopy and create denser shrub cover (Bunnell 1990), which in turn could provide more cover from predators. These areas, however, may attract other predators, such as bobcats, and may not support the persistence of western spotted skunks.

In addition, we found that individuals had different responses to environmental variables, especially elevation. Most skunk home ranges were at intermediate elevations, but some individuals selected low elevation sites and one individual selected high elevation sites (Figure S3.11). This suggests that western spotted skunks exhibit high plasticity and can employ a variety of strategies to survive in the forests of the Pacific Northwest. Conflicting selection of resources by individuals has also been noted by a previous study on island spotted skunks, where 1 individual preferred a vegetation type that was avoided by all other monitored animals (Crooks and Van Vuren 1995). Although spotted skunks may be highly adaptable to their environmental, they may experience varying mortality risks in these different environments (Lesmeister et al. 2010). Together, our results suggest that western spotted skunks are a common, habitat generalist species.

Although spotted skunks have been described as having more of an “area of familiarity” instead of a home range (Crabb 1948), we found that western spotted skunks generally used the same area over the course of the study, apart from one dispersing skunk. We found that western spotted skunk home ranges of both males and females overlapped considerably, suggesting that western spotted skunks are not territorial, unlike other solitary small carnivores (Powell 1979, Inman et al. 2012, Moriarty et al. 2017). There were no obvious correlations between seasonal male home range sizes and body mass or body length (Figure S3.5). Male spotted skunk home ranges appeared to be driven by the size of their summer home ranges, where males with large summer home ranges had large overall home ranges and male skunks with small summer home ranges had small overall home ranges. Male home ranges in the fall and spring were similar (Figure 3.4A). Since food resources are most abundant during the summer, male skunks with large home ranges may require larger home ranges to acquire enough food resources to meet their energetic requirements. Female western spotted skunk home ranges, on the other hand, were small overall and consistently small across all seasons.

The montane temperate rainforests of the Pacific Northwest can be a challenging landscape to conduct animal GPS and VHF tracking studies. Dense canopy cover in valley bottoms are known to hinder communication between GPS devices and satellites and may prevent fixes from occurring in those location (Moriarty and Epps 2015) (Figure S3.2). VHF signal strength was limited by weight of the battery in comparison to the small body size of the western spotted skunk and prevented us from locating animals far from roads or if the animal was inside a dense structure (Frair et al. 2010). Therefore, our sample of locations may be biased, so the apparent selection of areas close to roads by spotted skunks may be artificial. Still, many carnivores take advantage of road networks for travelling and hunting because there are fewer obstructions. Furthermore, we found that western spotted skunks consistently selected areas of low topographic position index, even with these biases, suggesting that selection for these areas may be higher than quantified in our analyses.

Although the use of bait at cameras may bias the detection rates and occupancy rates by increasing detection rates for western spotted skunks, this method was necessary to obtain adequate observations of our focal species. Other studies were not able to detect spotted skunks without bait whereas those with bait in the same area were able to detect spotted skunks (Kelly and Holub 2008, Thorne et al. 2017).

Future studies of western spotted skunks should explore co-occurrence patterns with other species and finer scales of selection, such as the characteristics and availability of rest sites, which may limit spotted skunk distribution (Lesmeister et al. 2008*a*). For example, western spotted skunks may depend on mountain beaver burrows for rest site structures where old-growth forest legacies such as large coarse woody debris or hollow live trees are scarce. Previous studies have also noted that associations between western spotted skunks and mountain beavers (Pfeiffer 1953, Lovejoy 1972). Moreover, associations may exist between western spotted skunks and their prey species (Tosa et al. 2023) or between western spotted skunks and their competitors such as the striped skunk (*Mephitis mephitis*) (Neiswenter et al. 2006, Neiswenter and Dowler 2007) or Pacific marten (*M. caurina*).

Forest stand age was not an important predictor of western spotted skunk space use or resource selection at any scale as it was for prairie spotted skunks (Lesmeister et al. 2013). This may be because forest structure and understory complexity are not strictly correlated to forest age in the Pacific Northwest. Most federally managed forest, regardless of age, typically consist of complex vegetation structure that can provide ample rest sites and protection from predators. Stands in the stem-exclusion stage, however, have simple structure and may lack the necessary resources and protection needed for stable occupancy. Thorne et al. (2017) found that for eastern spotted skunk, occupancy was high in both young-aged forest and mature stands that had complex forest structure. If we had not studied western spotted skunks in old-growth stands that have high vegetation complexity and structure, we may have concluded that western spotted skunks favor young stands. Therefore, studying western spotted skunk spatial ecology in a variety of forest types provides important conservation and forest management information.

Acknowledgments

We thank field technicians A. Coombs, B. Doyle, H. Haeussler, D. Marsh, B. Murley, R. Peterson, R. Rich, L. Rivera, and K. Van Neste for field support. We thank C. Boucher, D. Cagle, O. Childress, A. Froelich, N. Griffith, J. Hedges, R. Mock, A. Saucedo, S. Spiers, H. Thomas for photo tagging. Facilities were provided by the H. J. Andrews Experimental Forest and the Long Term Ecological Research program, which is administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest. Funding for this project was provided by Oregon State University, the USDA Forest Service (16-JV-11261952-047), the National Science Foundation (LTER7 DEB-1440409), and the ARCS Oregon Chapter. This publication represents the views of the authors and any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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Table 3.1. Descriptions of candidate environmental variables used to develop occupancy and resource selection models for the western spotted skunk (*Spilogale gracilis*) in temperate rainforests in the Oregon Cascades.

Category	Variable name	Range	Units	Description	Rationale
Disturbance	D.ROAD[1]	0-1,385	m	Euclidean distance from nearest road using rgeos::gDistance Transformations tested: linear, log	Areas closer to roads are more disturbed and exhibit more edge characteristics
Disturbance	P.LOGGED[1]	0-83	%	Percent within buffer that was logged within the last 100 years calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More previously logged areas, more disturbed
Disturbance	P.MATURE[1]	5-21	%	Percent within buffer categorized as OGSI 80 but not OGSI 200 calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More mature stands, more legacy of disturbed
Disturbance	P.OLDGROWTH[1]	7-92	%	Percent within buffer categorized as OGSI200 calculated with landscapemetrics::sample_lsm Buffer sizes tested: 0.1, 0.5, 1.0, 5.0 km	More old growth stands, less disturbed
Disturbance	YRS_SINCE_DISTURB[1]	3-103	Year	Years since location was logged Transformations: linear, log	More time since disturbance, less disturbed
Disturbance	OGSI[2]	0-88		Old growth structural index as defined by Spies and Franklin 1988	More old growth characteristics, less disturbed
Predation	COVER[2,3]	0-1	%	Vegetation cover based on the proportion of total returns between 4 m and 16 m	More cover, more visual obstruction from avian predators
Predation	CANOPY_HT[3]	2-83	m	25th percentile height for first returns (P25)	Lower canopy height, more obstruction from predators
Predation	ROUGH	0-22		Topographic roughness index (TPI) at site calculated from DEM and Raster::terrain	Rougher terrain, more opportunities to escape predators
Predation	TREE_DENSITY[2]	1-4,247	trees/ha	Density of live trees, conifers, hardwoods >= 2.5 cm DBH	Lower tree density, more area between trees for avian predators
Resource	STAND_DIVERSITY[2]	1-837		DDI = measure of the structural diversity of a forest stand, based on tree densities in different DBH classes SDI = Reineke's stand diversity index	More stand diversity, more food and rest site resources
Resource	TOPO_POS	-453-685		Topographic position index at site calculated from DEM and Raster::terrain Buffer sizes tested: 0, 0.5, 1.0 km	Lower topographic position, more food resources
Resource	D.WATER[4,5]	0-1,507	m	Euclidean distance from nearest waterbody or perennial stream using rgeos::gDistance Transformations: linear, log	Closer to water, more food resources
Resource	LANDSAT_VEG	0-5,340		Landsat8 reflectance bands: 2 (blue), 3 (green), 4 (red), 5 (near-infrared), 6 (Shortwave infrared 2), 7 (Shortwave infrared 2)	Greener areas and more moist areas, more food resources

Resource	STAND_AGE[2]	1-5,486	Years	Basal area weighted stand age based on field recorded or modeled ages of dominant/codominant trees	Older stand, more coarse woody debris for potential rest sites
Resource	SNAG[2]	1-257,697	trees/ha	STPH = Density of snags >= 25 cm DBH and >= 2 m tall SBPH, SVPH	More snags, more potential rest sites
Thermal tolerance	ELEVATION[3]	368-1,590	m	Elevation Transformations: linear, quadratic, log	Higher elevation sites, lower ambient temperature and more snow precipitation
Thermal tolerance	BASAL_AREA_SP[2]	0-2,609	m^2/ha	Basal area of *Abies amabilis* (ABAM), *Acer macrophyllum* (ACMA), *Pseudotsuga menziesii* (PSME), *Tsuga heterophylla* (TSHE)	More ABAM, lower temperatures and more persistent snow More ACMA, more riparian area
Thermal tolerance	BASAL_AREA_TYPE[2]	0-12,004	m^2/ha	Basal area of live trees, conifers, or hardwoods ≥ 2.5 cm DBH	Larger trees provide more insulation for rest sites
Thermal tolerance	ASPECT	0-6.28	Radians	Aspect at site calculated from DEM and Raster::terrain northness = COS(Aspect); eastness = SIN(Aspect)	South-facing slopes get more sun exposure

Sources:

1. USDA Forest Service
2. GNN structure: https://lemma.forestry.oregonstate.edu/
3. LiDAR
4. National Hydrography Dataset
5. Oregon Explorer, https://spatialdata.oregonexplorer.info/geoportal/
6. Landsat 8; https://earthexplorer.usgs.gov/

Table 3.2. Mean ± 95% confidence intervals of western spotted skunk (*Spilogale gracilis*) home ranges (95% utilization distributions) and core areas (50% utilization distributions) estimated using continuous time movement models in the Willamette National Forest, Oregon during August 2017 – August 2019.

Group	Core area (km^2)	Home range (km^2)
Female	2.52 (1.55 – 3.83)	10.93 (6.63 – 16.86)
Male (small)	3.55 (2.68 – 4.60)	16.38 (12.83 – 20.49)
Male (large)	6.81 (6.00 – 7.69)	35.83 (31.52 – 40.40)

Table 3.3. Mean and 95% confidence intervals of home range overlap between western spotted skunk (*Spilogale gracilis*) estimated using continuous time movement models and the Bhattacharyya coefficient. Values range between 0 and 1, where 0 indicates no shared areas and 1 indicates identical distributions of 95% utilization distributions.

Dyad	Home range overlap
Female-Female	0.78 (0.67 – 0.86)
Male-Female	0.76 (0.61 – 0.89)
Male-Male	0.83 (0.65 – 0.94)

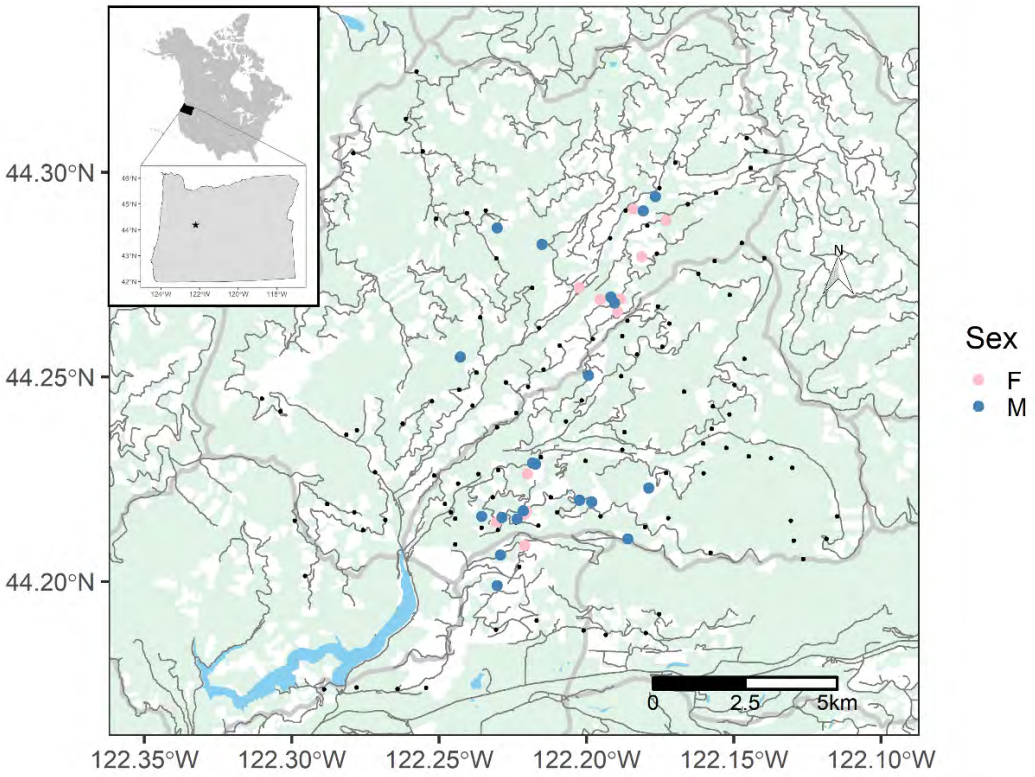

Figure 3.1. Study area and western spotted skunk (*Spilogale gracilis*) home range centroids for females (pink circles) and males (blue circles). White areas indicate previously logged stands. Trail camera locations shown as black circles. Thick grey lines represent watershed boundaries.

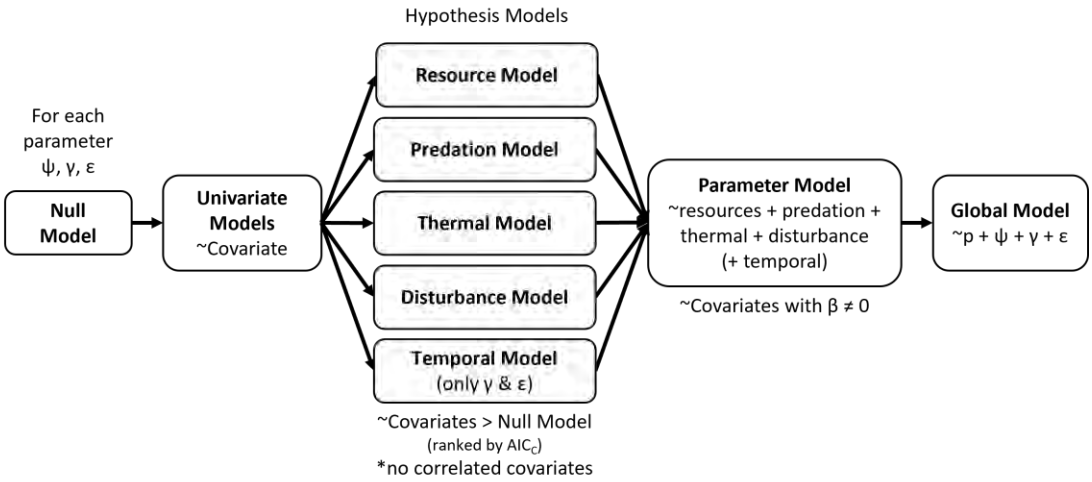

Figure 3.2. Flowchart for construction of global parameter models for each parameter initial occupancy (ψ), colonization (γ), and extinction (ε) in multi-season occupancy model.

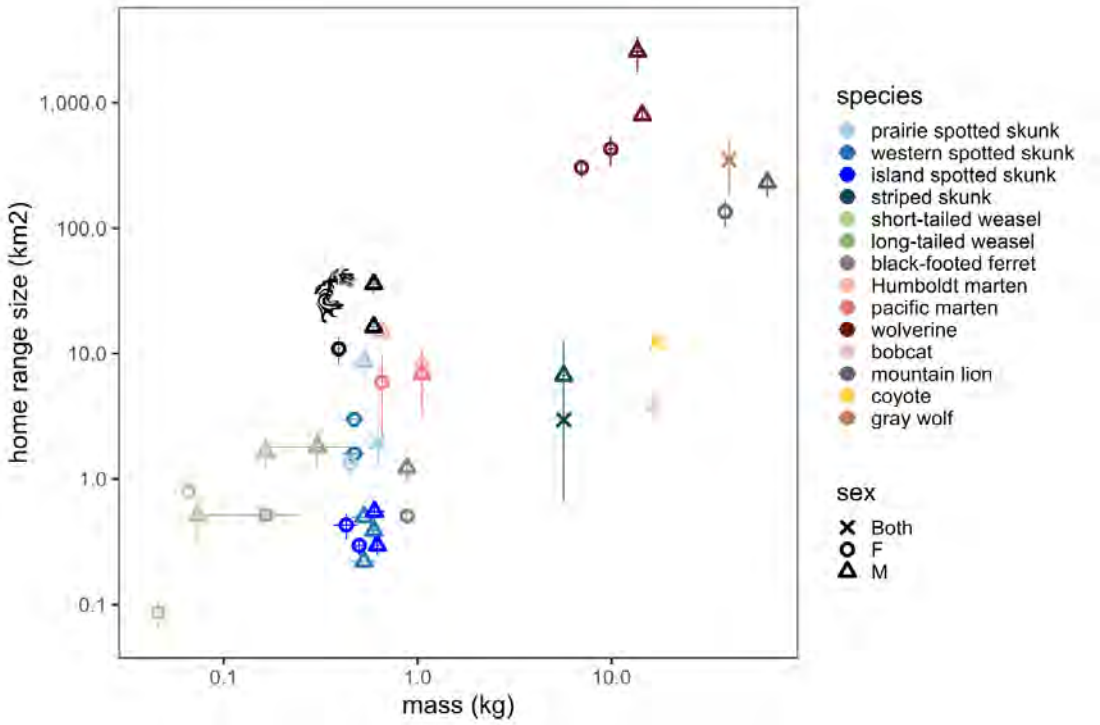

Figure 3.3. Comparison of mean home range sizes and mean body mass of mammalian carnivores in North America. Lines represent standard error or range of values presented in study. Values from Crooks and Van Vuren 1995, Lisgo 1999, Carroll 2000, Doty 2003, Gehring and Swihart 2004, Jachowski 2007, Jones et al. 2008, Lesmeister et al. 2009, Dawson et al. 2010, Inman et al. 2012, Linnell et al. 2017, 2018, Mastro et al. 2019, Orning 2019, Martin et al. 2021, Schmidt et al. 2023. Values from this study in black. Note mass and home range size axes are on log10 scale.

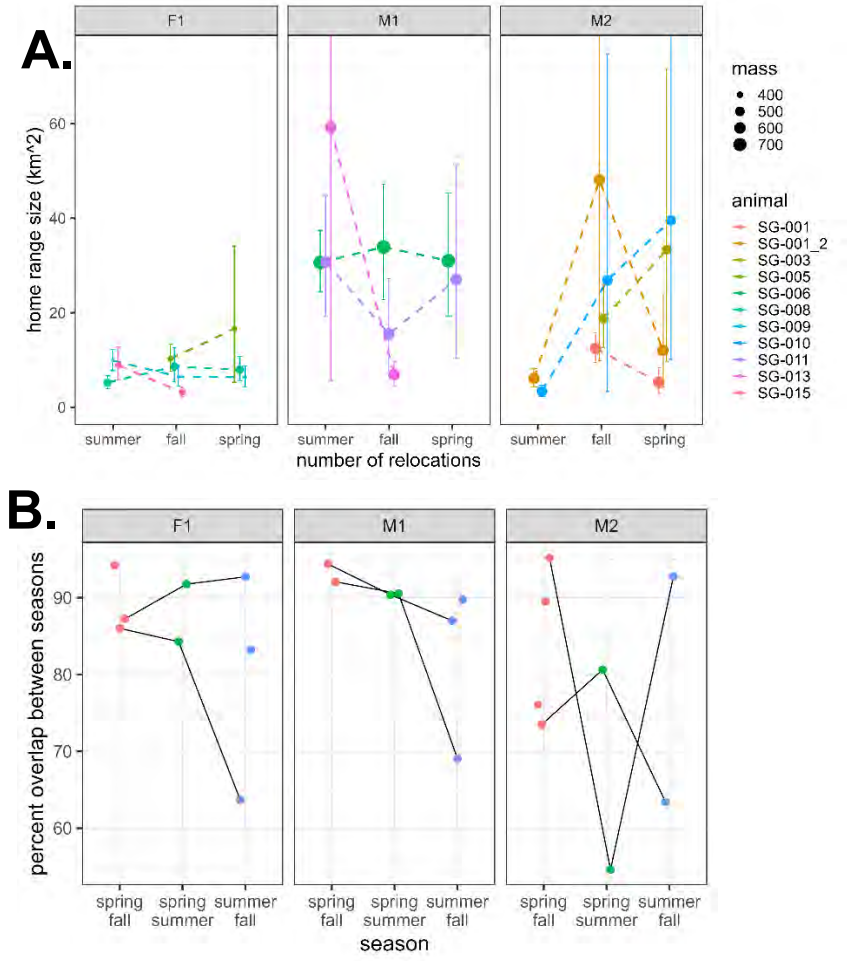

Figure 3.4. (A) Changes in seasonal home range size estimates and (B) fidelity of home ranges across seasons (spring: February – May, summer: June – September, fall: October – January) of western spotted skunks. Point size in panel A represents body mass size of skunk. Points connected with lines represent the same animal. Panels represent female western spotted skunks (F1), male western spotted skunks with large home ranges (M1), and male spotted skunks with small home ranges (M2).

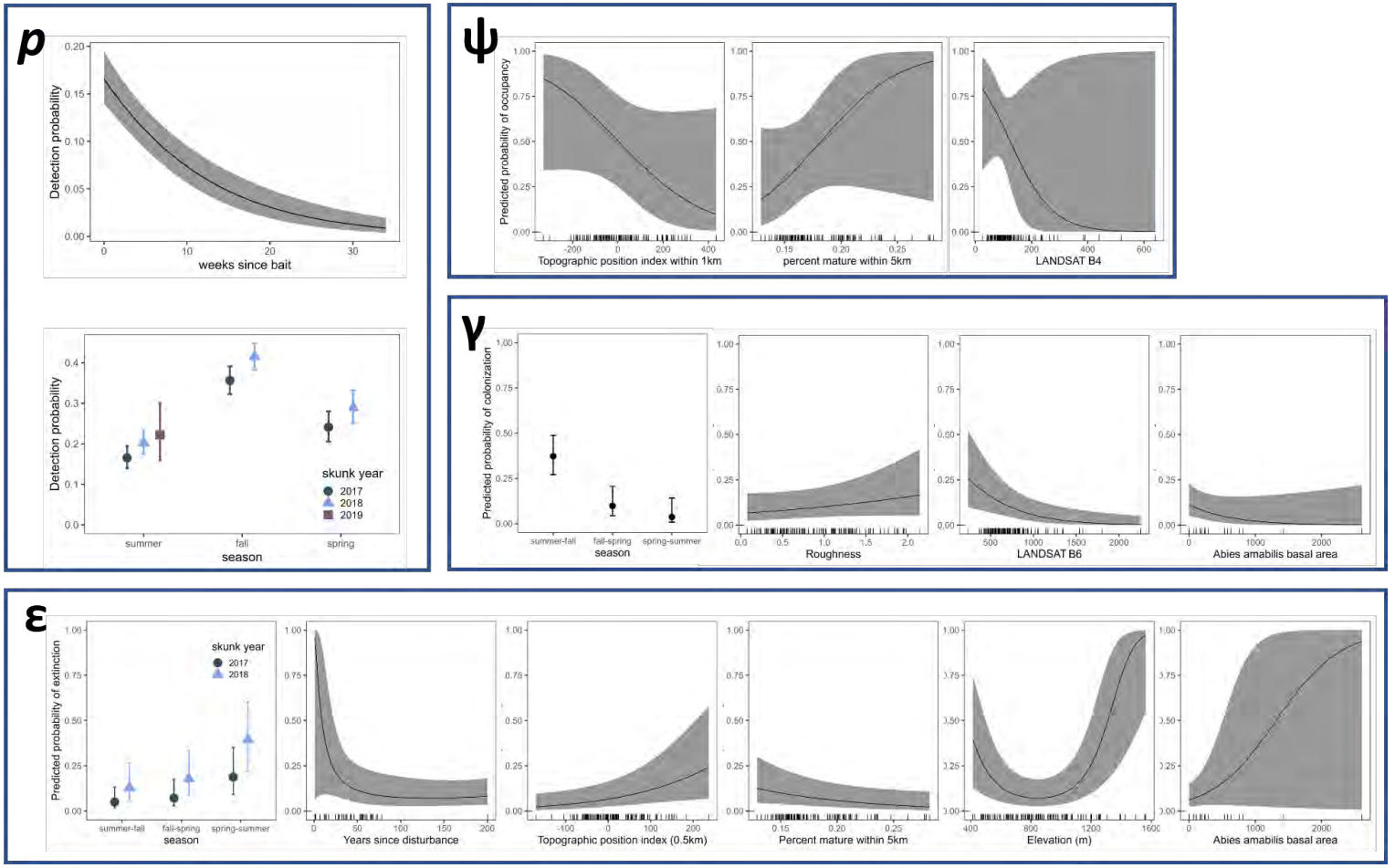

Figure 3.5. Marginal plots for detection (*p*), initial occupancy (ψ), colonization (γ), and extinction (ε) from multi-season occupancy models of western spotted skunks in the Oregon Cascades from 2017-2019.

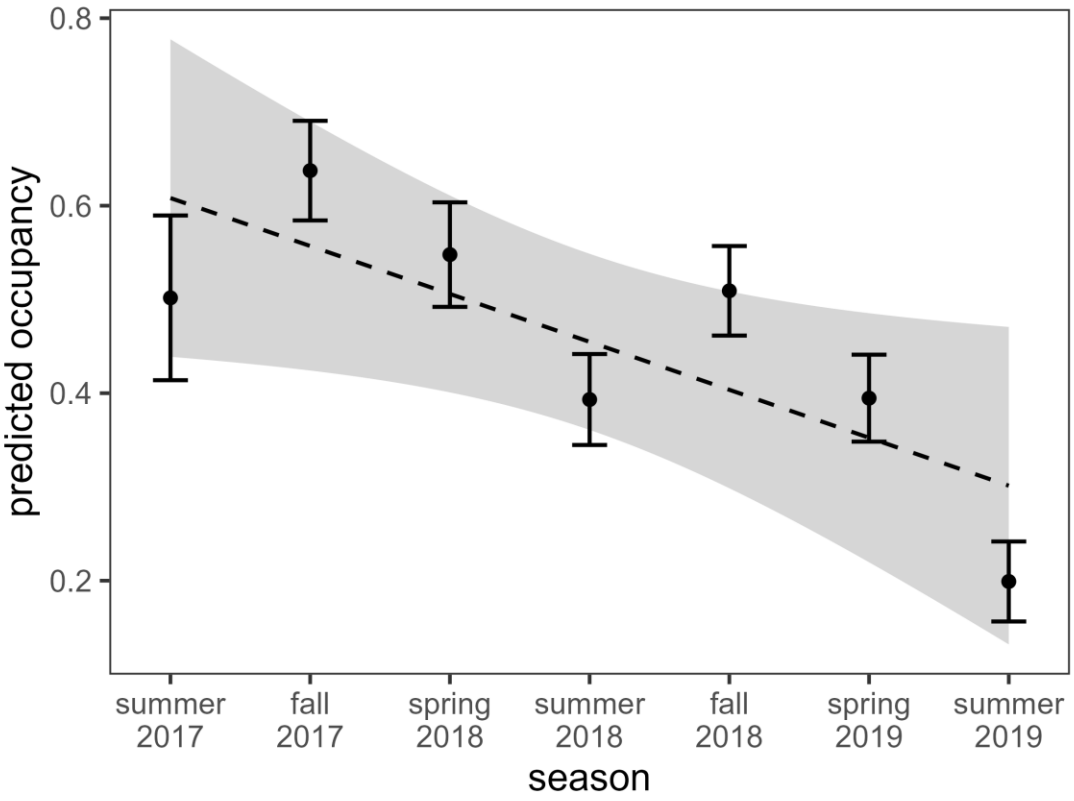

Figure 3.6. Predicted seasonal occupancy ± SE of western spotted skunks in the Willamette National Forest for each season during 2017-2019. Dashed line represents linear regression fit to seasonal occupancy.

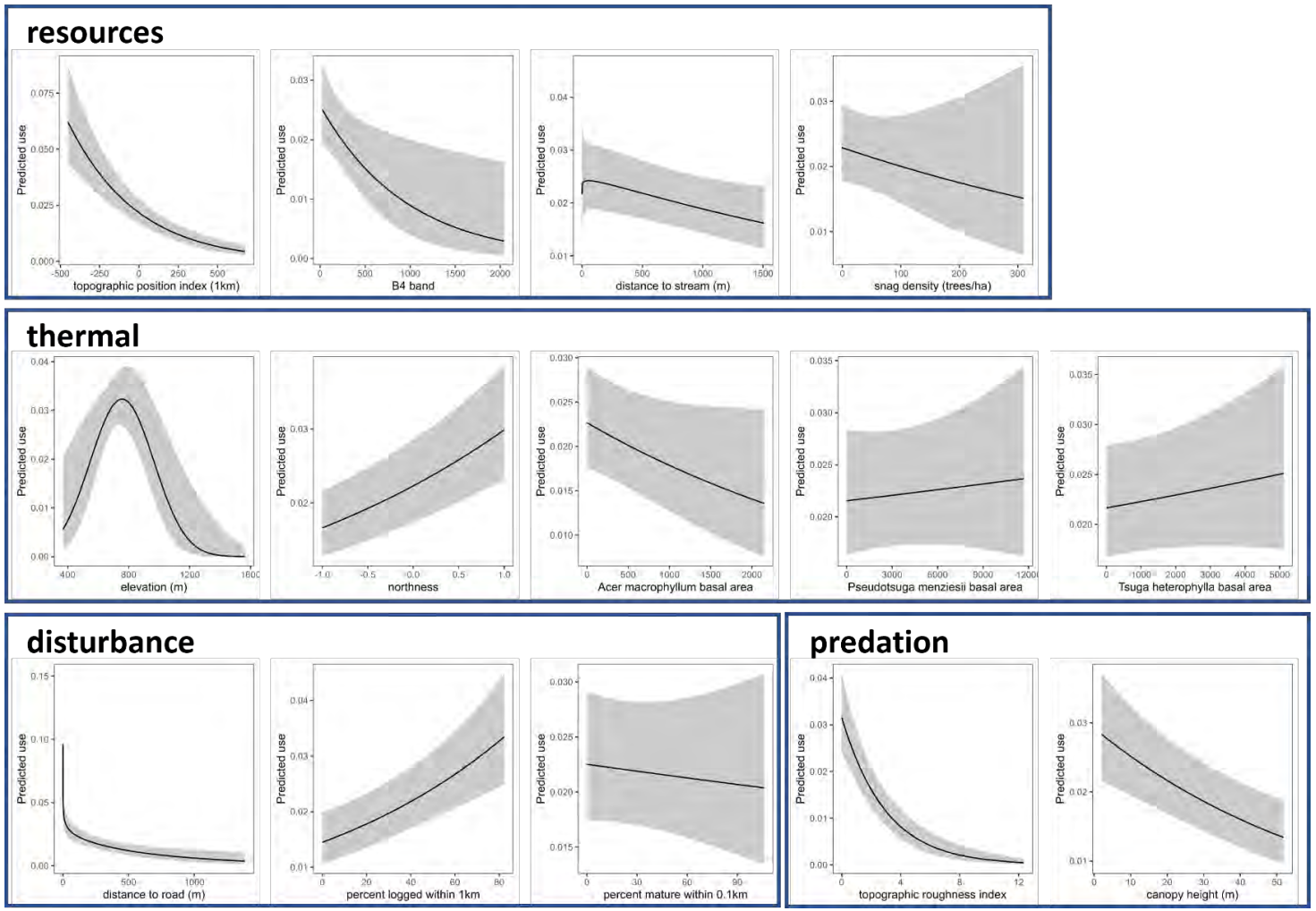

Figure 3.7. Predicted marginal plots for home range level resource selection by western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades from 2017-2019.

CHAPTER 4 – ASSESSING UNMARKED MODELS FOR ESTIMATING DENSITY OF SMALL MAMMALS USING CAMERA TRAPS

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Abstract

Estimating population densities of unmarked animals continues to be a challenge for ecologists. Statistical approaches for calculating density estimates of animal populations have proliferated, but empirical tests on these methods are necessary to show whether these methods are widely applicable. When applying statistical models to empirical data, model assumptions are often violated, especially when using unmarked animal data. Here, we provide a robust analysis at 8 independent sites of 3 small mammal species (deer mouse [*Peromyscus maniculatus*], Townsend's chipmunk [*Neotamias townsendii*], and Humboldt's flying squirrel [*Glaucomys oregonensis*]) with varying life-history traits to thoroughly test a suite of unmarked models (average encounter rates, N-mixture models, time-to-event and space-to-event models, and unmarked spatial capture-recapture models) against multiple marked models (minimum number known alive, Huggins models, and spatial capture-recapture models). All marked models produced density estimates that were positively correlated with one another. Although average encounter rates were the simplest unmarked models we applied to the data, they consistently yielded positively correlated density estimates to spatial capture-recapture density estimates for all 3 small mammal species. In addition, unmarked models generally yielded positively correlated density estimates for chipmunks, but yielded negatively correlated or uncorrelated density estimates for deer mice and flying squirrels. We illustrate that unmarked population estimation models can produce accurate density estimates for species of intermediate density using a sampling scheme that fits the natural history of the species, but not for species with low or high densities. These comparisons provide insight into understanding why a method may or may not produce reliable density estimates under applied conditions where not all assumptions can be met.

Introduction

Animal abundance and population density are fundamental state variables in ecology, conservation, and management, but accurate and precise density estimates are challenging to obtain. Small mammal populations are among the most monitored taxa, in part because of their short generation times and because they are amenable to

mark-recapture live-trapping. Moreover, variation in small mammal abundance can influence a myriad of ecosystem processes such as herbivory (Gedan et al. 2009), seed and fungal spore dispersal (Maser et al. 1978), parasite abundance and disease risk (Ostfeld et al. 2006), or nest predation rates (Schmidt et al. 2001), and can determine the distributions of predatory species because of their value as nutritional resources (Erlinge 1975, Angelstam et al. 1984, Reichel 1991, Forsman et al. 2004, Karanth et al. 2004). Small mammal communities and even some individual species are effective indicators of ecological processes including disturbance and resource abundance (Avenant and Cavallini 2007, Leis et al. 2008, Blois et al. 2010, Rowe et al. 2011). Thus, some small mammal populations have been monitored for many years and have provided valuable insights into drivers of abundance fluctuations and fundamental ecosystem processes leading to valuable development of population ecology theory (Hansen et al. 1999, Boonstra and Krebs 2012, Krebs et al. 2014).

Linkages between small mammal populations and environmental variables allow for understanding broad-scale ecological patterns and ecosystem processes. Small mammal studies historically have relied heavily on mark-recapture methods that are invasive (Delehanty and Boonstra 2009, Bosson et al. 2012), time-intensive, and expensive, which in turn have limited the spatial and temporal extent of inference. Developing a reliable, cost-effective, and non-invasive method to quantify abundance of small mammal populations would facilitate replicated estimates in time and space; small mammal density then could be projected at landscape scales and related to environmental covariates. This would open new avenues of inquiry such as testing the long-term relationships between base and higher trophic levels of terrestrial food webs (Jędrzejewski et al. 1995), predicting disease risk where small mammals are key reservoir hosts for pathogens, or predicting plant and fungus community dynamics where colonization probabilities depend on small mammal abundance.

Camera trapping is a potentially cost-effective and noninvasive alternative method to estimate small mammal abundance. Camera traps can operate continuously, can be left untended for multiple days to weeks at a time, and reduce stress to and mortality of target species from capture and handling. In addition,

camera trapping can lead to a greater understanding of target and non-target species distributions, activity patterns, and other behaviors because likelihoods of detecting cryptic or trap-shy species, multiple individuals per trap per night, and multiple species per trap per night are higher (Karanth and Nichols 1998, Tobler et al. 2008). Thus, camera trapping has become a popular, efficient, cost-effective method for monitoring many wildlife populations (Rowcliffe and Carbone 2008, Burton et al. 2015), but has been an underutilized tool for monitoring small mammals (Cutler and Swann 1999) that is gaining popularity (McCleery et al. 2014, Villette et al. 2016, 2017, Parsons et al. 2021).

Estimating densities of small mammals with camera traps is challenging, however, because most individuals are not individually identifiable in photos, which is a prerequisite for mark-recapture approaches. Previous statistical methods, such as capture mark recapture and spatial capture recapture (SCR) or spatial mark resight (Chandler and Royle 2013), rely on individual identification, which allow researchers to account for imperfect detection, estimate home range size, and estimate variability of these parameters. Nevertheless, advances in statistical modeling have made it possible to estimate the abundance of unmarked populations. In lieu of individual marks, unmarked models make assumptions about independence between sites, geographic closure, and animal movement (e.g., random movement patterns around an activity center), or use auxiliary information (e.g., movement rate, area of detection) to inform estimation of density or abundance. Currently favored models for estimating density of unmarked populations include spatial count (SC; also known as unmarked SCR; Chandler and Royle 2013), time-to-event (TTE) and space-to-event (STE) (Moeller et al. 2018), and random encounter models (REM; Rowcliffe et al. 2008), while N-mixture models, which are still widely used, estimate abundance instead of density (Royle 2004). These models were developed to estimate abundance of various species, such as lions (*Panthera leo*), black bears (*Ursus americanus*), and fisher (*Pekania pennanti*) and other carnivores (spatial count models; Kane et al. 2015, Jiménez et al. 2017, Burgar et al. 2018), elk (TTE and STE models; Moeller et al. 2018), and breeding birds (N-mixture models; Kéry et al. 2005, Kéry 2018). Yet,

even in large-bodied vertebrates, robust tests of model efficacy are rarely conducted (but see Villette et al. 2017, Parsons et al. 2021, Ruprecht et al. 2021).

Robust validation of unmarked models is critical because their assumptions may be challenging to meet in real-world applications (see Gilbert et al. 2021). For example, N-mixture models require that individuals not be double counted or detected at multiple sites (Keever et al. 2017) and the probability of detecting an individual in the population (i.e., detection probability) must be > 0.5 (Dénes et al. 2015, Duarte et al. 2018) for accurate abundance estimates. Spatial count models reverse the assumption of N-mixture models and instead require detections of each individual at multiple sites (Chandler and Royle 2013). TTE, STE, and random encounter models, which were developed specifically for camera trap data, rely on the assumption that encounter rates increase with abundance. Since detection rate, however, depends on abundance and movement rate of the animal, TTE and random encounter models assume that animals move randomly (i.e., cameras are not baited, animals are not aggregated, and animals do not exhibit high fidelity to particular movement paths) and require an approximation of the animal's movement rate through the camera viewshed. STE models, on the other hand, substitute space for time and do not require movement rate estimations, but require synchronous time lapse photos at multiple locations (Moeller et al. 2018).

While past simulations suggest that density estimation for unmarked small mammal populations is feasible (Moeller et al. 2018, Loonam et al. 2021*b*), these methods require robust empirical testing because of challenges in meeting model assumptions. To meet these assumptions, crucial decisions must be made about study design (e.g., duration, use of bait, camera spacing, and how to define a detection) given that many non-invasive methods including camera trapping continuously record data (Gilbert et al. 2021). Another critical consideration when animals are not uniquely identifiable is accounting for multiple detections of the same species at the same site. These could be the same individual, multiple individuals, or simultaneous detections of multiple animals that could be treated as a single detection or separate detections. Depending on these decisions and any violations of assumptions, estimates from the models could differ sharply (Parsons et al. 2021) and the

interpretation can change, such as whether estimates can be treated as absolute abundances or indices of relative abundance. Further, many of these decisions should depend on the life history of the focal species (Gilbert et al. 2021, Parsons et al. 2021).

Here, we test the efficacy of camera traps for estimating small mammal abundance. We compared abundance and density estimates using a suite of unmarked and marked methods for deer mice (*Peromyscus maniculatus*, hereafter mice), Townsend's chipmunks (*Neotamias townsendii*, hereafter chipmunks), and Humboldt's flying squirrels (*Glaucomys oregonensis*, hereafter flying squirrels) on small-mammal trapping grids at 8 separate sites in old-growth coniferous forest within the Oregon Cascades. We estimated small mammal densities on live-trapping grids using SCR, which we used as the standard for testing unmarked models using camera trap data. We first compared SCR density estimates with those obtained by minimum number known alive, traditional Huggins capture-recapture abundance estimators, and unmarked spatial count models to inform 1) the variability in estimates when applying different methods to live-trapping data, 2) to inform the transition from close-capture-recapture models to SCR models, which have rarely been implemented in small mammal trapping studies despite widespread use in other taxa (but see Gerber and Parmenter 2015). We compared SCR density estimate from live-capture data with average detection rates from camera traps (a relative abundance estimator), abundance estimators using N-mixture models, and unmarked density estimators using time-to-event models, space-to-event models, and spatial count models. In each case, we assessed whether the correlation in live-capture and camera-based estimates could be improved by varying both the duration of monitoring (1 – 8 days) and the definition of an 'encounter' by treating each photo as a unique encounter (t = 0 min.) to defining encounters based on increasingly longer time windows between detections (up to t = 1440 min.).

Methods

Study area

We conducted this study at the H. J. Andrews Experimental Forest (HJA), which is located on the western slope of the Cascade Mountains near Blue River, Oregon (Figure 4.1). Elevations range from 410 m to 1,630 m. The maritime climate is typical of the Pacific Northwest region and consists of warm, dry summers and mild, wet winters. Mean monthly temperatures range from 1°C in January to 18°C in July. Precipitation falls primarily as rain, is concentrated from November through March, and averages 230 cm at lower elevations and 355 cm at higher elevations (Greenland 1993, Swanson and Jones 2002). Lower elevation forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Upper elevation forests are dominated by noble fir (*Abies procera*), Pacific silver fir (*Abies amabilis*), Douglas-fir, and western hemlock. The HJA consists largely of old, relatively undisturbed temperate forest (Cissel et al. 1999). Other than timber logging, wildfires are the primary disturbance. Mean fire return interval of partial or complete stand-replacing fires for this area is 166 years and ranges from 20 years to 400 years (Teensma 1987, Morrison and Swanson 1990). Population dynamics of 4 small mammal species (Humboldt's flying squirrel, Townsend's chipmunk, western red-backed voles (*Myodes californicus*), and deer mice) have been studied in old-growth stands at the HJA as part of a long-term study since 2011 (Weldy et al. 2019).

Live trapping

Live trapping occurred at 9 sites (Figure 4.1A) from September to November 2017 according to methods developed for the long-term northern spotted owl prey study (Weldy 2018, Weldy et al. 2019). Sites were chosen to reflect the elevational gradient at the HJA and differed in canopy openness. At each site, we placed 2 Tomahawk traps (201 size; 15.2 cm x 15.2 cm x 48.3 cm; Tomahawk Live Trap, Wisconsin, USA) at 64 stations, arranged in an 8 x 8 grid and spaced 40 m apart. We placed one Tomahawk trap on the ground and secured the other Tomahawk trap 1.5 m from the ground on the nearest tree. We placed an additional 100 Sherman traps (LFATDG model; H. B. Sherman Traps, Florida, USA) arranged in a 10 x 10 grid,

spaced 10 m apart (Figure 4.1B). Each Tomahawk grid was trapped for 2 weeks and each Sherman grid was trapped for 1 week (Figure 4.1C). All traps were pre-baited for 12 days prior to trapping and were baited with a mix of peanut butter, oats, sunflower seeds, molasses, and mealworms. Traps were active for 4 consecutive nights per week and checked in the morning, starting at 0700. Due to snow, low temperatures, and disturbance by non-target species, traps at some grids were closed early (Figure S4.1). During the initial capture, individuals were uniquely marked with an ear tag (Model #1005-1, National Band and Tag Co., Newport, KY, USA). To maintain similar probabilities of capture between live traps, we only analyzed live-capture data from Sherman traps for mice and live-capture data from Tomahawk traps for chipmunks and flying squirrels. All small mammal capture and handling protocols were approved by the Oregon State University Animal Care and Use Committee (Protocol #4959).

Camera trapping

We conducted camera trapping from September to November 2017 at 8 of the 9 live-trapping sites within 2 weeks of live trapping to maximize the likelihood of sampling the same population. At each Tomahawk trap station, we placed remote cameras (TrophyCam models 119676, 119774, 119776, 119836, 119876, Bushnell, Overland Park, KS or Dark Ops BTC-6, Browning, Morgan, UT) approximately 1.5 m away from the bait and 15-20 cm above the ground. We placed an additional 16 cameras (Dark Ops BTC-6, Browning, Morgan, UT) at Sherman trap locations to create a 5 x 5 grid nested within the Tomahawk grid (Figure 4.1). Similar to live-trapping methods, each camera was baited with a mixture of peanut butter, oats, sunflower seeds, strawberry jam, and commercial rabbit food placed within a nylon mesh bag. Bait bags were secured to the ground using garden stakes. We placed a scale bar (1 cm – 5 cm) next to each bait bag to aid in identifying species. We programmed cameras to take 1 photo with a 1-minute time delay between photos to minimize excessive photos of the same individual. Cameras were deployed for at least 7 consecutive nights (De Bondi et al. 2010). To minimize false triggering and ensure unobstructed photos of the animals, we cleared vegetation from the camera's field of view.

We extracted metadata from photos using the *exifr* package in Program R (R Development Core Team 2014). Where possible, we identified animals in photos to species using characteristics such as body shape, head shape, ear morphology, tail length, and size to distinguish between species (Verts and Carraway 1998).

Data analysis

We formatted all data and conducted all analyses in Program R version 3.6.1 (R Core Team 2019). All data for spatial capture-recapture and spatial count models were formatted using the *data2oscr* function in the *oSCR* package (Sutherland et al. 2019). We implemented models in either a maximum likelihood or Bayesian framework. For the Bayesian framework, we ran models using the packages jagsUI (Kellner 2019) or nimble (de Valpine et al. 2021) and used Markov Chain Monte Carlo (MCMC) to draw samples from the posterior distribution for the parameters of interest. We assessed MCMC convergence by visually inspecting trace plots for each monitored parameter and $\hat{R}$ statistics < 1.1 (Gelman and Rubin 1992). We report the posterior mean, mode, standard deviation, and 95% credible interval (CRI).

Density estimation with marked models

Using the capture-mark-recapture data, we calculated abundance and density estimates for each grid using (1) minimum number known alive (MNKA), (2) Huggins closed population mark-recapture models (Huggins 1989, White and Burnham 1999), and (3) SCR models in a Bayesian framework (Royle et al. 2014) (Figure 4.2). We analyzed the capture-recapture data with multiple methods to ensure consistency of estimates and to serve as a baseline for variability in estimates to compare to those of the unmarked models.

Minimum number known alive and Huggins models (non-spatial models)

We calculated MNKA by tabulating the number of individuals that were captured and uniquely marked. Using Huggins closed population mark-recapture models in Program MARK (White and Burnham 1999), we estimated abundances and 95% confidence intervals of target species for each grid using a null model, where we held capture probabilities (p) and recapture probabilities (c) constant (Huggins 1989, White and Burnham 1999). The parameters p and c are computed based on encounter

histories for each captured individual. Since we calculated species abundance based on the null model, abundance (N) can be calculated as:

$$N = \frac{MNKA}{p^*}$$

where p^* is the probability that an individual is captured at least once during the trapping season.

Converting from abundance to density using these models requires an *ad hoc* decision about the size of buffer to use around the trap locations to calculate the area over which animals were trapped. This arbitrary decision can critically influence the absolute density estimates and must be well defined to infer biological meaning to the derived estimates (Karanth and Nichols 1998, Efford 2004). To calculate density, we divided the abundance estimate by an area consisting of the trap locations (Sherman trap grid for mice and Tomahawk grid for chipmunks and flying squirrels) buffered by the mean maximum distance moved (MMDM) and ½ MMDM, as is traditionally calculated to account for the geographic closure assumption. The MMDM was 24.1 m for mice, 86.6 m for chipmunks, and 87.2 m for flying squirrels.

Spatial capture recapture models

We implemented SCR models to estimate spatially explicit densities using spatially referenced individual detections (Royle et al. 2014). These models differ from the MNKA and Huggins models in that these models estimate spatially explicit densities from spatially referenced detections. Each spatially referenced detection is used to calculate a latent activity center (s_i) for each individual animal (i) and a probability of detection (λ) that decreases monotonically with Euclidean distance from the individual activity center by a scaling parameter (σ). For this approach, we used a half-normal function to describe the decrease in probability of detection. Thus, detection of an individual at a trap (j) is a function of the Euclidean distance of the trap from an individual's activity center (d), $\lambda_{i,j} = \lambda_0 * e^{-(\frac{1}{2\sigma})^2 d(s_i, x_j)^2}$, where x_j is the location of trap j and λ_0 is the baseline encounter probability (i.e., the expected rate of detection of an individual given the trap is at the individual's activity center).

We used data augmentation to estimate the number of individuals that were present in the state-space, S, during the sampling session but were not detected during

the study (Royle et al. 2007, Royle and Young 2008). We assigned all augmented individuals with encounter histories consisting of zeros, since individuals were not detected during the sampling period, and used an indicator variable (z_i) to determine whether an augmented individual was a real unobserved individual ($z_i = 1$) or not part of the population ($z_i = 0$; i.e., a structural zero). The indicator variable was modeled as a Bernoulli trial with a probability parameter (ψ) characterizing all trials, $z_i \sim Bernoulli(\psi)$ for $i = 1,2, \ldots M$, where M is the total number of detected individuals and the number of individuals with all zero-encounter histories that were not detected during sampling. We used a Poisson random variable to model encounter histories of each individual at each trap, $y_{i,j}$, to allow for multiple detections, $y_{i,j} \sim Poisson(\lambda_{i,j} \times z_i \times K)$, where K is the number of sampling occasions. The total population size (N) over S is then determined by summing all z_i, $N = \sum_{i=1}^{M} z_i$, and density (D) is calculated by dividing the population size by the area of the state space (A), so that $D = N/A$. We note that the Poisson distribution may not be ideal because counts of detection of each individual is bounded by K occasions since individuals can only be caught at most 1 time during each occasion and only up to 2 individuals can be captured at each trap location (since there are 2 Tomahawk traps at each location). Simulations have indicated, however, that 'single-catch' traps can estimate animal densities when trap saturation is moderate (≤ 86%) even when animals are spatially clustered (Efford et al. 2009).

We used three SCR approaches (Figure 4.2) to estimate densities of mice, chipmunks, and flying squirrels using spatially referenced individual detections (Royle et al. 2014) (code provided in Appendix A). For the first approach (SCR_{sep}), we fit a single SCR model to each site for each species separately (i.e., all sites have distinct estimates for parameters σ and λ_0). For the second approach (SCR_{pool}), we fit the same model to data from all sites for each species but used site as a grouping factor to share data for fitting the detection function (i.e., all sites share the same estimates for parameters σ and λ_0; multi-strata model). Sharing data in this way is expected to improve the precision of estimates (Morin et al. 2018). For the third approach (SCR_{random}), we added a level of hierarchy to the multi-strata approach so that the logarithm of parameters σ and λ_0 for each site are normally distributed with

hyperparameters, Σ and Λ_0 (i.e., σ and λ_0 are allowed to vary among sites but arise from a common distribution and thus are pulled toward the group mean). We used the logarithm of parameters to restrict them to non-negative values. This design allows the model to borrow data from other sites to inform site-specific estimates and allows individuals in more densely populated sites to have more restricted home range sizes with smaller σ values and larger λ_0 values.

For SCR models, we estimated the number of individuals in the state space (*S*) that encompassed all traps within a buffer 5 times the mean maximum distance moved (MMDM), set the maximum number of possible individuals within *S* for each site (*M*) to 10 times the MNKA, and accounted for occasions when traps were non-operational due to weather limitations (Table S1). All SCR models were run in a Bayesian framework in the jagsUI package (Kellner 2019). For each model, we ran 3 chains consisting of 500 iterations for adaptation and 2,500 iterations per chain, where the first 500 iterations were discarded as burn in.

Density estimation with unmarked models

Using camera trap data, we investigated the utility of unmarked models and the effects of the length of encounter window used by repeating analyses with different encounter window lengths (1, 15, 60, 1440 min.). The shortest encounter window (1 min.) treated all photos as separate encounters. Longer encounter windows consolidated multiple photos of the same species (presumably the same animal) into one encounter that occurred for a longer duration. We treated 24-hour intervals as occasions. For nocturnal species (mice and flying squirrels), we counted "days" starting at dusk following bait placement instead of the calendar days.

Average encounter rate

We calculated a simple index of abundance by computing the average number of encounters per camera. This index is also directly proportional to estimates from the random encounter model (Rowcliffe et al. 2008), which simply scales the average number of encounters by a constant that depends on the size of camera viewsheds and the average movement speed of the animal. In addition to exploring the effects of the length of encounter window, we also explored the effect of the number of days cameras were operational on abundance estimates since we expected the number of

detections to decrease because bait was not replaced daily. This method provides information about the relative abundance of each species and a ranking of each grid from lowest to highest abundance by assuming that higher encounter rates result from higher abundance. One of the advantages to this method is that it requires little computational power, no estimation of movement speed, and only assumes that encounters increase with increasing population density.

N-mixture models

Unlike the simple index of abundance, N-mixture models (Royle 2004) incorporate variability in detection probabilities. These models leverage variation in repeated counts at a given site to estimate species abundance over a larger unknown area (Kéry and Royle 2020). Similar to other models, N-mixture models assume population closure and equal detection probability for all individuals in the population, but also require that individuals are not double counted and detections of individuals at each camera are independent (Royle and Nichols 2003, Royle 2004). Cameras can be baited, but N-mixture models are sensitive to assumption violations, so unless assumptions can be verified, estimates should be treated as indices of relative abundance (Duarte et al. 2018, Gilbert et al. 2021).

To implement N-mixture models for each species at each site, we summarized our camera data as a count of encounters ($C_{j,t}$) at trap j on day t on cameras placed on the Sherman grid ($n_{camera} = 25$) for mice and Tomahawk grid ($n_{camera} = 64$) for chipmunks and flying squirrels. We treated each camera station as a replicate and modeled counts of encounter as binomial random variables, $C_{j,t} \sim binomial(N_j, p)$, where p is the probability of detecting an individual, and N_j is the true abundance of the species at trap j. We modeled the unobserved abundance N for each trap j as a Poisson random variable: $N_j \sim Poisson(\lambda)$, where λ is the underlying population density (code provided in Appendix B). Because encounters decreased over time (Figure S4.7), most likely due to a declining amount of bait, and because we used spatial replication instead of temporal replication, we modeled the probability of detection, p, in three ways: first, a single value of p per site per species (N_{base}), second, a different p per trap ($N_{pstation}$) to account for heterogeneity in detection by trap location due to heterogeneity in vegetation structure, camera trap set up, or

camera trap model, and third, an exponentially decaying *p* by day with a different intercept per trap location (N_{pdecay}) to account for decreasing detection over time. We fit N-mixture models in a Bayesian framework using the jagsUI package (Kellner 2019). For each model, we ran 3 chains consisting of 20,000 iterations for adaptation and 20,000 iterations per chain with a thinning rate of 5, where the first 10,000 iterations were discarded as burn in. Finally, we converted abundance to density estimates using the same method as we used for converting MNKA and Huggins by dividing the abundance by the area of the trapping grid buffered by ½ MMDM.

Time-to-event (TTE) and space-to-event (STE) models

TTE and STE models use the time until the first detection of an animal and the amount of area that must be surveyed until the first detection of an animal, respectively, to estimate population density (Moeller et al. 2018). At higher population densities, it is assumed that encounter rates are also higher, reducing the amount of time between encounters. TTE models take advantage of the continuous property of camera trap data and model abundance based on the relationships defined by a Poisson process between the Poisson and exponential distributions. Thus, in these models, $N_{ijk} \sim Poisson(\lambda)$ and $T \sim Exponential(\lambda)$, where N_{ijk} is the number of animals in view at camera *i*, on occasion *j* and period *k*, *T* is the interval between detections, and λ is the average number of animals in view at a camera. TTE models assume that camera trap encounter rate increases as abundance increases, that animal detections are independent in both space and time (i.e., once detected, animals will be less likely to be detected on a neighboring camera and animal will not linger in front of a camera), and that detection is perfect (i.e., if an animal walks in front of the camera, it will be detected) (Gilbert et al. 2021). TTE models, however, rely on estimates of animal movement rate, which can be difficult to obtain. STE models collapse sampling intervals into an instant in time using time-lapse photos, which helps meet the assumption of perfect detection, and model the interval of space, *S*, between detections as an exponential distribution, $S \sim Exponential(\lambda)$.

To implement both TTE and STE models, we followed protocols designed by Moeller et al. (2018). Since TTE and STE models specify that animals should not be attracted or repelled from sampling locations, we only analyzed camera trap data

from days 4-9. By day 4, detections of each species leveled off, indicating that all bait had been consumed and animals were no longer attracted to it (Figure S4.7). We started sampling occasions at sunrise for diurnal species (chipmunk) and at sunset for nocturnal species (mice and flying squirrels). Sunrise and sunset times were obtained from the NOAA Solar Calculator (https://www.esrl.noaa.gov/gmd/grad/solcalc/). We calculated visible camera area based on manufacturer specifications of detection angles (44 degrees for Bushnell Aggressor) and a maximum detection distance of 5 m (approximated from how we positioned our cameras).

For TTE models, we defined the sampling period length as 16 hours (number of night-time hours), sampling frequency (time between each sampling occasion) as 24 hours (each day is a different occasion), and species speed as mean maximum distance moved derived from SCR_{all} models. We chose this value for an hourly speed because small mammals make quick, short distance movements centered around the core area, opposed to long distance movements (Opps et al. 2020). Thus, we assumed that the distance between detections would be similar to distance covered over 1 hour. If no animals were detected during a given sampling occasion, the occasion was represented as NA.

To imitate time-lapse photo data for STE models, we evaluated detections of each species at each camera on the hour (i.e., sampling frequency = 1 hour) and for sampling period lengths of 1, 5, 15, 30, and 60 minutes. In other words, a sampling period length of 1 minute is more representative of time-lapse photos, but longer sampling period lengths could help meet the assumption of perfect detection because if an animal is present, it is more likely to move into the view of the camera with more time. We removed any sampling occasions when species were not expected to be active (i.e., if a species was diurnal, we removed occasions during the night). If no animals were detected during a given sampling occasion, the occasion was represented as NA.

Spatial count models (unmarked SCR)

We ran spatial count (SC) models on both capture-recapture data and camera trap data. First, we tested if unmarked models could recover SCR estimates of abundance from the capture-mark-recapture data by withholding the identity of the

captured individuals and calculated density estimates using spatial count (SC) models in a Bayesian framework (Chandler and Royle 2013). By running SC models on capture-recapture data, we tested whether differences in density estimates were the consequences of the model applied or due to the difference in the data type (live-traps vs. camera traps) and associated differences in detection probability. SC models are similar to SCR models in that they explicitly incorporate spatial information about detections and probability of encounter decreases as a function of Euclidean distance from an individual's activity center, but they do not require the identity of individuals, just spatially correlated count data (Chandler and Royle 2013). Density estimates in SC models are inferred by assuming latent encounter histories ($y_{i,j}$) for individual i at trap j. Unlike in the SCR model, encounter histories are aggregated across all individuals at the trap level and modeled as a Poisson random variable, $N_j \sim Poisson(\Lambda_j * K)$, where N_j represents the number of individuals detected at trap j, $\Lambda_j = \lambda_0 \sum_{i=1}^{M} e^{-(\frac{1}{2\sigma})^2 d(s_i, x_j)^2}$ and represents the probability of the number of detections in a fixed period and location of trap j, and K represents the number of sampling occasions.

We implemented four SC models for capture-recapture data (code provided in Appendix B): first, we estimated density of each species and each site separately with non-informative priors for σ and λ_0 ($SC_{CR,\ noinfo,\ sep}$); second, we built on the $SC_{CR,\ noinfo,\ sep}$ model by adding site as a grouping factor to share data for fitting the detection function for parameters σ and λ_0 ($SC_{CR,\ noinfo,\ pool}$); third, we built on the $SC_{CR,\ noinfo,\ sep}$ model by incorporating parameter estimates for σ and λ_0 that were derived from SCR_{random} models as informative priors ($SC_{CR,info,sep}$); finally, for the fourth model, we built on the $SC_{CR,info,sep}$ model by adding site as a grouping factor ($SC_{CR,info,pool}$). All SC count models using capture-recapture data were run in a Bayesian framework in the nimble package (de Valpine et al. 2021). For each model, we ran 3 chains consisting of 2,500 iterations for adaptation and 10,000 iterations per chain, where the first 2,500 iterations were discarded as burn in. If SC models failed to converge after we augmented models with 2,000 individuals, we concluded that these models did not converge because of limitations with computing memory, computing duration, and computing power.

We implemented SC models for camera trap data using the same structure as the SC models for capture-recapture data. First, we estimated density of each species and each site separately with non-informative priors ($SC_{cam,noinfo,sep}$); second, we built on the $SC_{cam,noinfo,sep}$ model by adding site as a grouping factor ($SC_{cam,noinfo,pool}$); third, we built on the $SC_{cam,noinfo,sep}$ model by incorporating parameter estimates for σ and λ_0 that were derived from SCR_{random} models as informative priors ($SC_{cam,info,sep}$); finally, for the fourth model, we built on the $SC_{cam,info,sep}$ model by adding site as a grouping factor ($SC_{cam,info,pool}$).

Evaluation of model performance and model comparison

We evaluated the performance of models by comparing the density estimates of each species at each site (number of animals per ha), when possible. It was not possible, however, to convert output of all models to density estimates for metrics that had no spatial component such as average encounter rates which are indices of relative abundance.

To evaluate the performance of marked and unmarked models and their ability to estimate density of each species across all sites, we plotted model density estimates against density estimates derived from SCR_{random} models and fitted linear regressions to each model (SCR_{random} density estimates ~ model density estimates). We extracted the slope, R^2 value, and root mean square error (RMSE) from those linear regressions to characterize the ability of the models to recover absolute density estimates. We also regressed scaled and centered (mean = 0, standard deviation = 1) density estimates from models against scaled and centered density estimates derived from SCR_{random} models and used the same metrics as above to compare model performance. These comparisons between scaled and centered values allowed us to characterize the ability of the models to recover relative density estimates instead of the ability of models to recover absolute density estimates.

The slopes from these linear regressions indicated how well models were able to differentiate sites with low density from sites with high density. Positive slopes (95% confidence interval > 0, $p < 0.05$) indicated that the models were able to differentiate the true relative density of the sites, whereas slopes overlapping 0 indicated that models were not able to differentiate densities of the sites (95%

confidence interval overlapped 0, $p > 0.05$), and negative slopes (95% confidence interval < 0, $p < 0.05$) indicated that models estimated high density for those with low SCR_{random} density and vice versa. A slope of 1 for linear regressions between absolute density estimates represents a special and ideal case where model estimates are perfectly aligned with SCR_{random} density estimates. Again, comparisons between centered and scaled estimates allowed us to compare relative performance of models across different methods. Slope in these linear regressions therefore represented the relationship between 1 SD of unmarked density estimates and 1 SD of SCR_{random} density estimates.

Finally, the R^2 values and RMSE of different models characterized deviations from the SCR_{random} estimates and goodness-of-fit of the linear regression to the data. R^2 values range from 0 to 1, where a value of 1 indicates a perfect fit. RMSE values range from 0 to infinity, where values of 0 indicate a perfect fit (ideal model performance) and larger values indicate larger deviations from values predicted by a linear trendline. We used SCR_{random} as the standard to compare the unmarked models because it incorporates the greatest information available (i.e., encounter histories and spatial distribution of animals) for each species in each site. We compared the performance of marked and unmarked models for each species based on these 3 metrics: slope, R^2 value, and RMSE. We considered models with positive slopes, high R^2 values, and low RMSE to perform better than those with negative slopes, low R^2 values, and high RMSE.

Results

Capture-recapture data analyses

Estimates of abundance from the SCR_{random} models (multi-strata SCR model with hyperparameters for σ and λ_0) ranged from 66 – 316 individuals per grid for mice, 88 – 449 individuals per grid for chipmunks, and 64 – 169 individuals per grid for flying squirrels. This corresponded to density estimates (individuals/ha) that ranged from 13.12 – 62.84 for mice, 1.68 – 8.59 for chipmunks, and 1.14 – 3.02 for flying squirrels (Figure 4.3, Table S4.2). The posterior distributions of SCR_{random} models revealed that there were 3 distinct density (non-overlapping 95% CRI)

estimates of mice, 4 distinct density estimates of chipmunks, but only 2 distinct density estimates of flying squirrels (Figure 4.3, Table S4.3) based on posterior overlap < 0.05. The MMDM ± SD across all grids was 24.80 ± 4.53 m for mice, 78.24 ± 8.58 m for chipmunks, and 85.62 ± 9.64 m for flying squirrels (Figure S4.4).

All models examining the capture-recapture data that incorporated individual identification were able to differentiate between sites with low densities from those with high densities: all models for mice, chipmunks, and flying squirrels had positive slopes (range = 0.92 – 1.68), high R^2 values (range = 0.50 – 1.00), and relatively low root mean squared error (range = 0 – 0.49 and 10.47 for MNKA for mice) when compared to SCR_{random} density estimates (Figure 4.4). When values were scaled and centered, all slopes for regressions overlapped 1 for all 3 species and RMSE ranged from 0 to 0.61 (Figure 4.4). Unsurprisingly, MNKA and Huggins estimates underestimated the SCR_{random} density (slopes > 1), and calculating density for sites separately (SCR_{sep}) increased fit (higher R^2 and lower RMSE values) whereas pooling data across sites (SCR_{pool}) increased variance (lower R^2 and higher RMSE values)

Absolute density estimates were of similar magnitude between Huggins models and SCR_{random} regardless of the buffer size (½ MMDM or MMDM) (Figure S4.5). Confidence intervals and credible intervals of density estimates from Huggins and SCR_{random} models, respectively, overlapped. Post-hoc, we calculated the buffer size relative to the MMDM that would be necessary to yield the same density estimates between the Huggins and SCR_{random} models, using SCR_{random} as the standard since the state-space is explicitly modeled. This ratio value is typically assumed to be 0.5 or 1. In this study, the mean ratio of buffer size to MMDM ± SD was 0.86 ± 0.28 (range: 0.43 - 1.29) for mice, 0.73 ± 0.15 (range: 0.56 - 0.95) for chipmunks, and 0.45 ± 0.06 (range: 0.34 - 0.53) for flying squirrels (Figure S4.6).

When we withheld information about individual identity, many of the SC models applied to the capture-recapture data did not converge without auxiliary information about σ and λ_0 parameters from SCR_{random} models. Convergence issues were greatest for deer mice where we were only able to estimate the density of one site using $SC_{CR,no\ info,sep}$ and $SC_{CR,noinfo,pool}$ and 5 sites each using $SC_{CR,info,sep}$ and $SC_{CR,info,pool}$. We had the least convergence issues for chipmunk and were able to

estimate densities of all 9 sites using both $SC_{CR,noinfo,pool}$ and $SC_{CR,info,pool}$. When models converged, we were able to differentiate the relative densities of all 3 species if auxiliary information about σ and λ_0 parameters were provided ($SC_{CR,noinfo,sep}$ and $SC_{CR,info,sep}$) (slopes: 0.11 – 0.29) (Figure 4.5). In addition, slopes of $SC_{CR,noinfo,pool}$ for chipmunks (slope = 1.52 ± 0.19) and $SC_{CR,noinfo,sep}$ for flying squirrels (slope = 1.42 ± 0.92) were also positive. Generally, SC_{CR} model density values underestimated the density of each species when we used non-informative priors (mice: 1.05 – 3.46 fold, chipmunks: 0.03 – 0.94 fold, and flying squirrels: 0.02 – 0.29 fold) but grossly overestimated the density of each species when we used informative priors (mice: 3.24 – 23.62 fold, chipmunks: 2.87 – 26.50 fold, and flying squirrels: 8.64 – 48.84 fold).

Camera trap data analyses

Overall, we detected deer mice in 16,585 photos, Townsend's chipmunks in 3,935 photos, and Humboldt's flying squirrels in 770 photos from camera traps. Generally, density estimates from unmarked camera trap models were positively correlated with SCR_{random} density estimates for chipmunks, but we had mixed results for mice and flying squirrels where density estimates were positively correlated, not correlated, or negatively correlated for mice and flying squirrels regardless of the analysis (Table 4.2). Unmarked models had relatively low R^2 values and high root mean square error values (R^2 range = -0.45 – 0.87, RMSE range = 0.09– 1.04) compared to the R^2 values and root mean square error of marked models (R^2 range = 0.73 – 1.00, RMSE range = 0 – 0.46).

For all 3 species, the simplest index of abundance, the average encounter rate, was positively correlated with SCR_{random} densities indicating that this metric was able to recover relative density estimates, especially when the consolidation window was short; all slopes of linear regressions were positive or overlapped 0 and there were no concerns about convergence of models (Figure 4.6). All slopes for mice when consolidation times were 0 and 15 minutes, all slopes for chipmunks, and all slopes for flying squirrels when consolidation time was 0 minutes were positive regardless of the number of days on data we used. When we increased consolidation times for

mice and flying squirrels, slopes overlapped 0, particularly when the number of days of data we used increased.

Other unmarked models (N-mixture, TTE, STE, and SC) that we tested on camera trap detections were also generally able to recover relative densities of chipmunks where linear regression slopes were positive (6 of 12 N-mixture, 1 TTE, 5 of 5 STE, and 7 of 16 SC_{cam} models) (Figure 4.7,Figure 4.8, andFigure 4.9). These other unmarked models were only sometimes able to recover relative densities of mice (5 of 12 N-mixture, 1 TTE, 0 of 5 STE, and 7 of 16 SC_{cam} models), and rarely able to recover relative densities of flying squirrels (2 of 12 N-mixture, 0 TTE, 1 or 5 STE, 3 of 16 SC_{cam} models). We experienced convergence issues for more complex models such as N-mixture and SC models, and we were unable to estimate densities at some sites, even for chipmunks. For N-mixture models, we had the most convergence issues when we did not consolidate detections (t = 0) and when detection was held constant across camera traps (N_{base}) (Figure 4.7). The most complex SC models took orders of magnitude longer to run (up to 9 hours to estimate density per site, ~3 weeks to estimate density by pooling data across sites) and had significant model convergence issues (e.g., no models converged for $SC_{cam,noinfo,sep}$ with t = 0). For SC models, including auxiliary information for σ and λ_0 from the SCR_{random} model and pooling data across sites improved convergence rates and improved slope estimates (made them more positive; e.g., $SC_{cam,no.info,sep}$ vs. $SC_{cam,\ info,sep}$ and $SC_{cam,info,sep}$ vs. $SC_{cam,info,pool}$) (Figure 4.9).

We found that unmarked models were sensitive to the consolidation time and the duration of time the camera traps were active. For example, N-mixture model density estimates had slopes closer to 1 when the consolidation time was 15 minutes for mice, but 60 minutes for chipmunks (Figure 4.7). Longer consolidation times, however, decreased the slope of the linear regressions from positive to overlapping 0 in mice when calculating average encounter rates (Figure 4.6) and increased the slope of the linear regression from negative to positive in flying squirrels when calculating densities using space-to-event models (Figure 4.8). Finally, average encounter rates for all three species declined when incorporating more days of data, likely due to decreasing amounts of bait available (Figure 4.6).

Discussion

Although complex statistical models can more accurately reflect the complexities of reality and empirical data collection, we found that the simplest relative abundance index calculated as the average encounter rate per camera trap best captured relative density estimates of 3 small mammal species, which were present at low, intermediate, and high densities. In terms of slope values, R^2 values, and root mean square error values, average encounter rates outperformed the other unmarked models (N-mixture, time-to-event, space-to-event, and spatial count models) that we tested.

A major advantage of this method was that the shortest time frame of monitoring the bait stations of 1 day yielded slopes closest to 1, and this method required the least computational effort since it did not require us to account for imperfect detection, use complex code, or use Bayesian methods. Although relative abundance indices rely heavily on the assumption that detection probability is constant between sites and detection rate has a monotonic relationship to animal abundance (O'Brien 2011) and it has been suggested that this assumption is unlikely to hold true in empirical studies (Harmsen et al. 2010, Sollmann et al. 2013), this metric has shown promising results with small mammal species. Villette et al. (2016) found that average encounter rates standardized by effort based on camera trapping data could estimate relative abundance of deer mice and northern red-backed voles (*Myodes rutilus*), and Parsons et al. (2021) showed similar results with mice, voles, and chipmunks by calculating the proportion of camera trap-nights where a species was detected and the number of independent detections. In this study, this metric may have performed well because all of our sites were located within similar old-growth stands in a single region and mechanisms that may influence detection were similar. Still, these relative abundance indices do not provide absolute values of abundance or density, so a major drawback to this metric is that it is difficult to compare densities between species or between studies (Burton et al. 2015).

It was evident, however, that other unmarked models such as N-mixture models, time-to-event models, and SC models also did not provide accurate absolute density estimates. Other unmarked model estimates were multiple orders of

magnitude larger or smaller than the marked spatial capture-recapture density estimates, so comparisons of these estimates between species or between studies would be impractical. Thus, even though other unmarked models provide density estimate values of each species, they should also be treated as relative density estimates unless there is a way to calibrate the density estimates with another method.

As expected, unmarked models applied to camera trapping data had varying levels of success based on the species and their life history traits (Gilbert et al. 2021). The camera trapping scheme of this study was best suited for the natural history of Townsend's chipmunk, a diurnal species occurring at intermediate densities at these sites and revealed relative densities at each site almost regardless of the method we implemented. Chipmunks had a moderate number of detections (n = 3,935), an intermediate MMDM (78.2 ± 8.6 m) that matched the spacing of the Tomahawk grid (40 m), and 4 differentiable population abundances that may have made it easier for the linear regression to distinguish between grids with low abundance from those with high abundance (Figure 4.3).

The estimates from camera trapping were less ideal for mice and flying squirrels, nocturnal species present at high and low densities, respectively. For these species, we were able to recover the relative densities using some models such as average encounter rates, but for most models, there was no relationship or a negative relationship between SCR_{random} estimates and unmarked model estimates and density estimates were sensitive to the consolidation time used. The number of detections was high for mice (n = 16,585) and low (n = 770) for flying squirrels, which corresponded to high and low density estimates from the live-trapping models. The lack of variation in densities between sites likely also contributed to decreased abilities to differentiate between low- and high-density sites (3 distinct densities for mice and only 2 distinct densities for flying squirrels).

The consequences for differences in life history traits were most evident in the differences in ideal consolidation times by species. For example, longer consolidation times or longer windows of detection improved density estimates for flying squirrels, which are larger bodied animals that occur at lower densities, have slower movement rates, and have larger home range sizes. Therefore, it is likely that multiple detections

of the same species within a short period was the same animal. On the other hand, increasing consolidation times worsened estimates of relative density, especially for the average encounter rate metric, for mice, which are small-bodied animals that occur at higher densities, have fast movement rates, and have smaller home range sizes. For this species, multiple detections of the same species within a short period likely represented different individuals, so consolidating these detections into a single detection misrepresented the number of individuals present. Sensitivity to consolidation times has also been observed by Villette et al. (2016), who found that density estimates changed according to the consolidation time for *Myodes* voles but not mice.

The marked models on the live capture-recapture data yielded density estimates that were highly consistent between methods, regardless of whether they accounted for imperfect detection or were spatially explicit. Densities for each site were within 0.31-fold to 1.33-fold of the SCR_{random} densities and regression lines had slopes close to 1 even without scaling and centering model density estimates. Generally, marked model density estimates were underestimates of the values we chose as the standard (SCR_{random}), indicating that they would provide conservative estimates of the population density. Similar to other comparative studies, we found that spatially explicit methods were superior to non-spatial capture-recapture methods because they can accurately define the area over which the abundance of the population is estimated and estimate variable densities within a site (Blanc et al. 2013).

When individual identity was withheld from capture-recapture data, we found significant issues with convergence in spatial count models, and we were only able to recover relative densities of all 3 species if auxiliary information from SCR_{random} were provided, suggesting that density estimates were sensitive to priors we set for σ and λ_0 parameters. This is consistent with prior simulations that showed that spatial count models have difficulty with reliable convergence because parameters such as σ are not identifiable (Augustine et al. 2019). In some instances, SC models applied to capture-recapture data with non-informative priors were able to recover the relative densities of chipmunks and flying squirrels and showed that SC models could provide

relative densities of species in special cases. These special cases may have yielded accurate relative densities because flying squirrel detections were low, which have been shown to increase the likelihood of convergence (Augustine et al. 2019).

Spatial count models applied to camera trap data had similar results to the spatial count models that were applied to capture-recapture data. When these models were applied to capture-recapture data, slopes were positive or overlapped 0, but when they were applied to camera trap data, slopes were positive, overlapped 0, or negative (Figure 4.9). One of the main differences in these two datasets was that individuals could only be caught once in the live capture data but could be detected multiple times on camera traps. This was more likely when there was fresh bait placed in front of the camera trap that served as an attractant for these species.

Other unmarked methods such as N-mixture, TTE, and STE models, had mixed levels of success for all 3 species. Although Loonam et al. (2021*b*, *a*) found TTE and STE models to produce unbiased and robust density estimates in simulations and with empirical data, we did not find this to be the case. Loonam et al. (2021*b*) suggested that density estimates were sensitive to speed estimations, but when densities were scaled and centered, the regression for flying squirrels produced a negative slope for the time-to-event model, indicating that this model had variable success depending on the species. For TTE and STE models, it is possible that our density estimates were incorrect because we may not have estimated the viewshed area correctly due to heterogeneity in camera trap sensitivity (Moeller et al. 2018). We may have also violated the assumption of perfect detection of animals within the camera trap viewshed, given we use the motion- and heat- triggered camera traps. Still, because we set camera traps at a downward angle and placed bait close to cameras, we believe our estimation of the camera viewshed is fairly accurate and that minimized the occurrence of false negatives in our data.

One of the limitations of this study is that small mammals were camera trapped immediately following the live capture-recapture efforts. As such, many of the small mammals were already habituated and perhaps searching for bait. This could explain why we had such high detection rates of our target small mammal species on the first day that the cameras were deployed (Figure S4.7). The lack of

time between live trapping and camera trapping, however, ensured population closure with both methods. Moreover, this could be considered equivalent to pre-baiting the camera trap sites, which is standard practice with live trapping. It remains undetermined whether pre-baiting is necessary to obtain accurate population estimates.

The use of bait could have altered the behavior of our target species. Individuals can be attracted or repelled from bait depending on the influence of predator avoidance, inter-specific competition, and resource availability on behavior (from Villette et al 2015: Burns 1981, Wolf et al 1983). This could impact both our live capture-recapture estimates and our camera trap estimates. For example, if an animal exhibits a behavior such as food caching, it may generate many camera trap detections of the same individual, resulting in abundance estimates that would be biased high. Still, camera traps detections may be less biased than live-trap captures because an animal may spend considerable amounts of time near a trap, but not get captured due to hesitancy to enter the trap (De Bondi et al. 2010).

The findings of our study support the use of camera traps and relative density indices as a method for answering one of the fundamental questions in ecology, conservation, and management: how many individuals of a species are present at a given time and place? Camera traps continue to be a promising technique to estimate densities of animal populations across larger spatial and temporal scales, but we showed that even methods that produce absolute density estimates require calibration from live-trapping methods to produce reliable density estimates. Through the robust analysis of 8 independent sites of 3 small mammal species, we showed that results of different popular models varied from species to species, but the simplest metric, the average number of detections per camera, was able to recover relative density estimates of all 3 species. Future studies should focus on determining the minimum number of cameras necessary, the correct camera configuration (e.g., distance between cameras), and ideal study design (e.g., random placement of cameras) necessary for accurate density estimates.

Acknowledgments

This publication represents the views of the authors, and any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank B. Doyle, R. Peterson, L. Rivera, D. K. Jakobsma, L. Hodnett, L. Howard, M. Linnell, K. A. Ray, and T. Manning for field support. Funding for this project was provided by the USDA Forest Service, Pacific Northwest Research Station and Oregon State University and USDA National Institute of Food and Agriculture, McIntire Stennis project (1020959). Logistical support was provided by the H. J. Andrews Experimental Forest and the National Science Foundation Long Term Ecological Research Program, which are cooperatively administered by Oregon State University and the USDA Forest Service (Pacific Northwest Research Station and Willamette National Forest).

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Table 4.1. Assumptions for various unmarked models.

Model	Assumptions	Additional information	Underlying distribution	Abundance type	Assumption Violations
Simple index Relative abundance index (RAI)[1]	- Geographic closure of population - Homogenous area, population - Detection probability is constant across individuals and over space - Detection rate increases as abundance increases - Random movement by target species	- Target species home range size - Area sampled - Calibration index	Normal distribution	Relative	
N-mixture[2]	- Individuals only detected at one location - Geographic closure of each plot within each season - Demographic closure within each season - Target species detections are independent of each other		Poisson or Binomial or Beta-binomial observation model	Absolute/Relative (depends on assumption violations)	individuals detected at multiple locations
Random encounter (REM)[3]	- Target species move randomly & independently - Camera are placed randomly - Each detection is independent - Target species are not attracted or repelled (no bait) - Closed population	- Detection zone (radius, angle) - Movement rate of target species	Poisson and Negative binomial	Absolute	
Distance sampling[4]	- Animals distributed independently of transect or point - All animals on transect or at point are detected (perfect detectability at distance=0)	- Detection function	Poisson and Negative binomial	Absolute	

[1] Drennan et al. 1998, Carbone et al. 2001, Conners et al 2005, Harrington et al. 2008, Villette et al. 2015
[2] Royle 2004
[3] Rowcliff et al. 2008
[4] Howe et al. 2017

	- Observation process is a snapshot (observer moves much faster than target species, animals do not move before detected) - Distance measured accurately - Independent detections - Survey is representative of study region			
Time-to-event (TTE)[5]	- Sampling locations distributed randomly - Detection rate increases as abundance increases - Animals are neither attracted or repelled - Geographic closure of study area - Demographic closure - Detections are independent in space and time	- Movement rate of target species - Sampling area	Poisson and exponential distribution	Absolute
Space-to-event (STE)[6]	- Sampling locations are distributed randomly - Detection rate increases as abundance increases - Animals are neither attracted or repelled - Geographic closure of study area - Demographic closure - Detections are independent in space and time	- Sampling area	Poisson and exponential distribution	Absolute
Spatial Count[7]	- Spatial correlation of counts at different sampling locations - Same animal detected at multiple locations		Poisson	Absolute

[5] Moeller et al. 2018
[6] Moeller et al. 2018
[7] Chandler and Royle 2013

Table 4.2. Summary of unmarked model performance and precision in comparison to multi-strata spatial capture-recapture model density estimates (SCR_{random}) for deer mice (*Peromyscus maniculatus*), Townsend's chipmunk (*Neotamias townsendii*), and Humboldt's flying squirrel (*Glaucomys oregonensis*) when density values were centered and scaled. Performance measured by ability of models to differentiate between sites with high and low densities (slope). Precision measured by R-squared value (R^2) and root mean squared error (RMSE) calculated from linear regressions.

Model	Deer mouse	Townsend's chipmunk	Humboldt's flying squirrel
Average encounter rate	Positive slope for shorter consolidation time (t = 0, 15) regardless of number of days active	Positive slopes for all consolidation times and number of days active	Positive slopes for all models
	Medium - high RMSE	Medium RMSE	High RMSE
	Lower RMSE for shorter consolidation times		
	-0.01 < slope < 0.81	0.57 < slope < 0.86	0.07 < slope < 0.51
	0.57 < RMSE < 0.96	0.29 < RMSE < 0.67	0.72 < RMSE < 0.86
N-mixture	Positive slope for models using shorter consolidation times (t = 0, 15)	Positive slope for models using shorter consolidation times (t = 0, 15, 60)	Slopes overlapping 0
	Lower RMSE for base model	Lower RMSE for base model with no consolidation	High RMSE
	-0.2 < slope < 1.25	-0.69 < slope < 0.93	-0.05 < slope < 0.48
	0.19 < RMSE < 0.96	0.09 < RMSE < 0.83	0.74 < RMSE < 0.92
Time-to-event (TTE)	Positive slope	Positive slope	Negative slope
	High RMSE	High RMSE	High RMSE
	Slope = 0.46	Slope = 0.45	Slope = -0.38
	RMSE = 0.86	RMSE = 0.74	RMSE = 0.79
Space-to-event (STE)	Slope negative or overlapping 0	Positive slope for all models	Slope overlapping 0 or positive
			More positive slope for longer encounter windows
	High RMSE	High RMSE	High RMSE
	-0.68 < slope < 0.26	0.46 < slope < 0.59	-0.06 < slope < 0.44
	0.72 < RMSE < 0.96	0.65 < RMSE < 0.74	0.76 < RMSE < 0.90
Spatial count	Positive slopes if data pooled	Positive slopes if data pooled	Mostly slopes negative or overlapping 0
	High RMSE	High RMSE	Medium RMSE

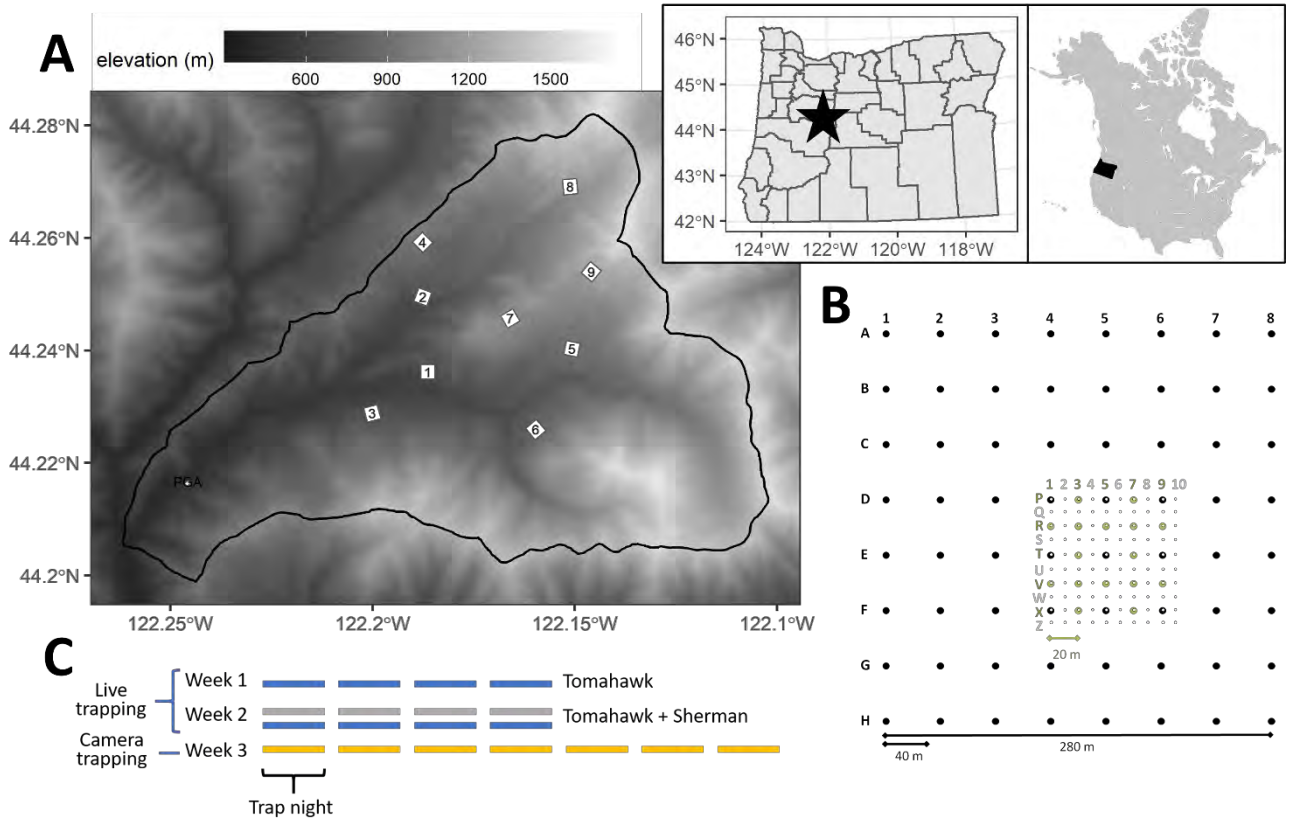

Figure 4.1. Study area, trapping scheme, and trap locations. (A) The H. J. Andrews Experimental Forest on the western slope of the Oregon Cascades within the Willamette National Forest. Squares indicate locations of the 9 sites that were trapped for small mammals using live traps as part of a long-term study on owl prey items from 2011-2022. Sites 1-8 were camera trapped during fall 2017. (B) Configuration of live traps ($n_{Tomahawk}$ = 128 and $n_{Sherman}$ = 100) and camera traps (n = 80) at each small mammal trapping site. Two Tomahawk traps (n = 128) and 1 camera trap (n = 16) were placed at each location in the larger Tomahawk grid (A-H, 1-8; black dots). One Sherman trap was placed at each location in the nested grid (P-Z, 1-10; open circles). One additional camera trap was placed at every other Sherman trap location (P-X, 1-9; n = 16; green dots). (C) Trapping scheme for live traps and camera traps.

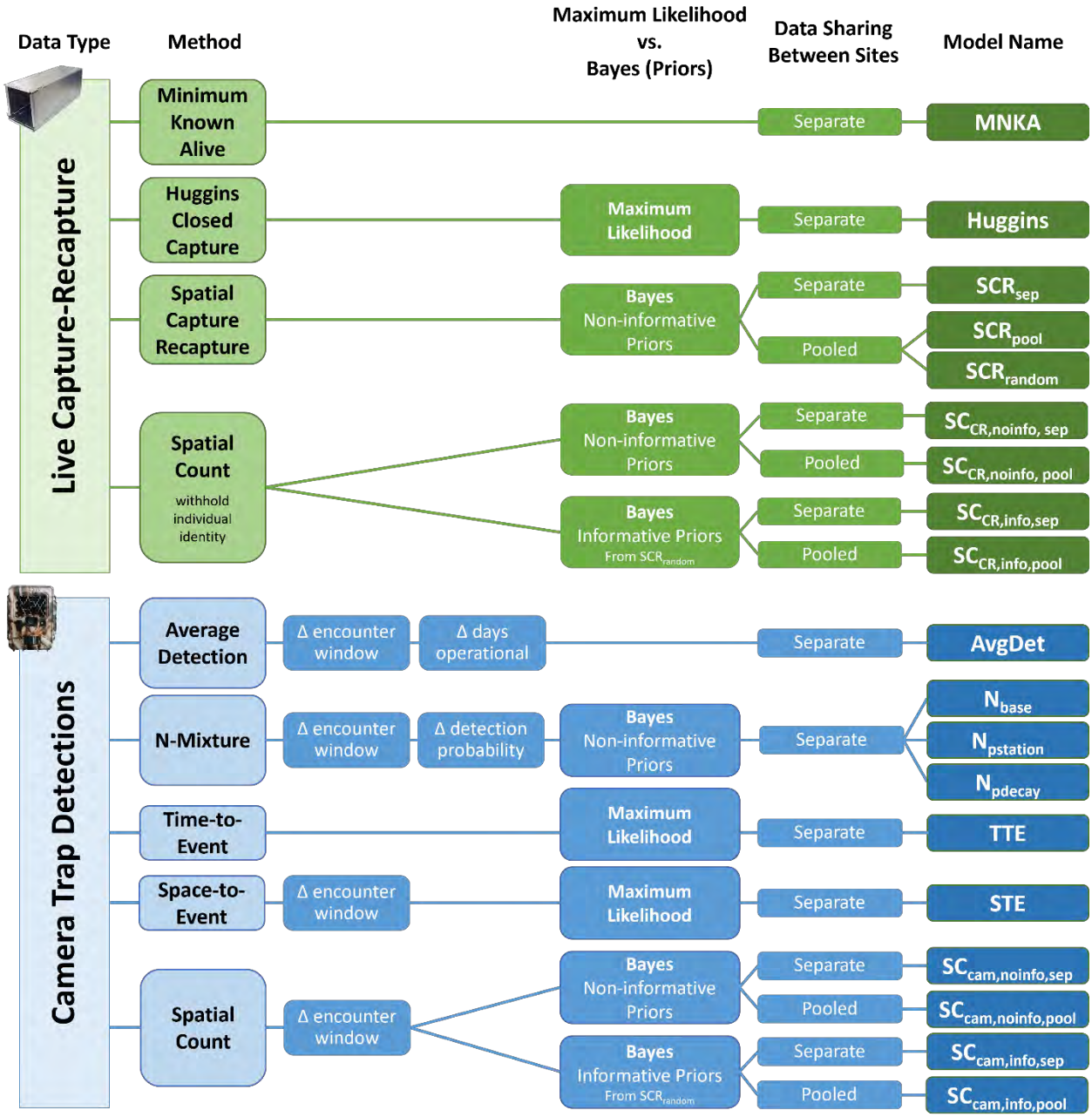

Figure 4.2. Models tested using two types of data: live capture-recapture data (green) and camera trap data (blue).

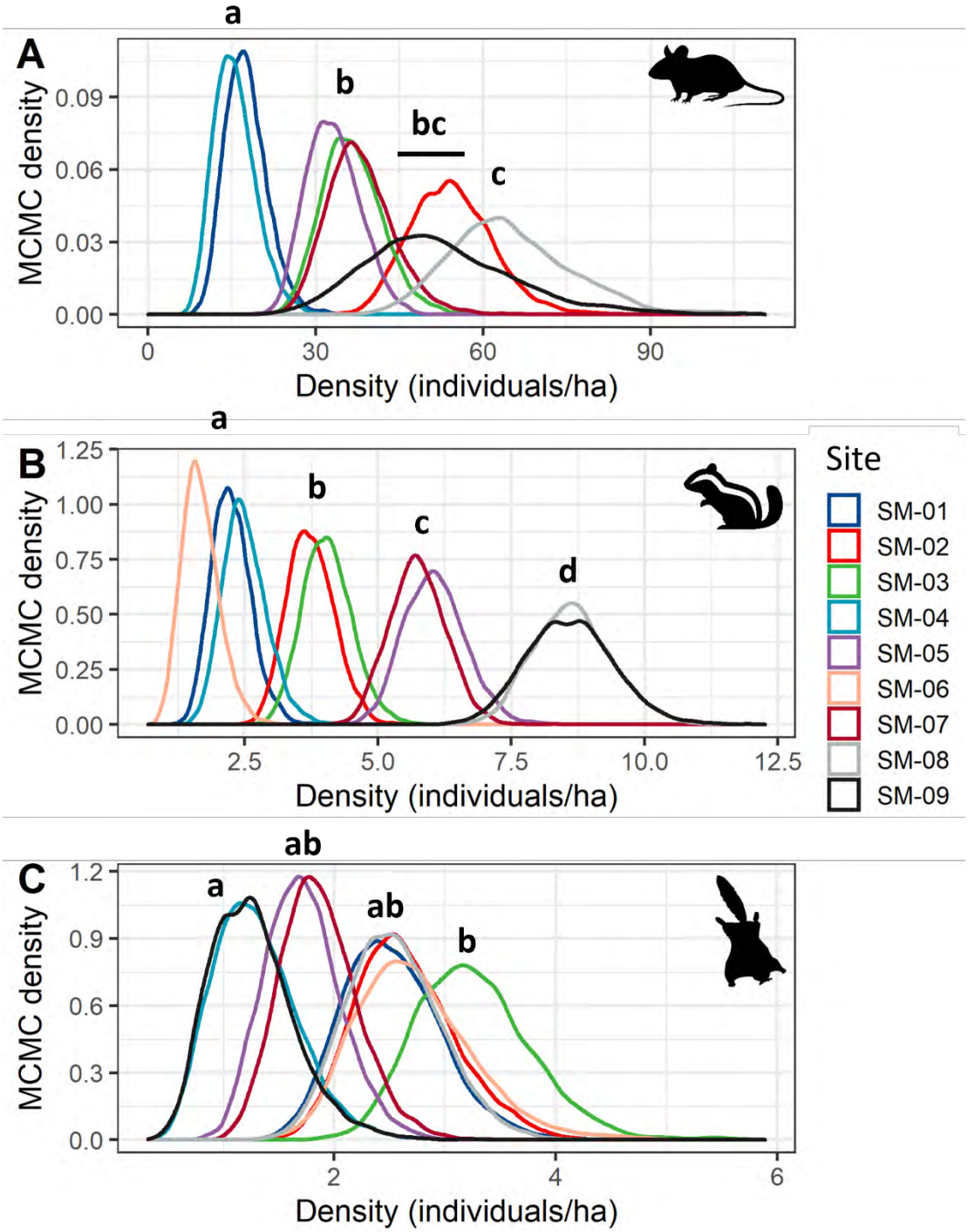

Figure 4.3. Posterior distributions of grid-specific density estimates from multi-strata spatial-capture recapture models (SCR_{random}) for (A) deer mice (*Peromyscus maniculatus*), (B) Townsend's chipmunk (*Neotamias townsendii*), and (C) Humboldt's flying squirrel (*Glaucomys oregonensis*). Different lowercase letters above density curves indicate ≤ 0.05 overlap in posterior distributions (see Table 2).

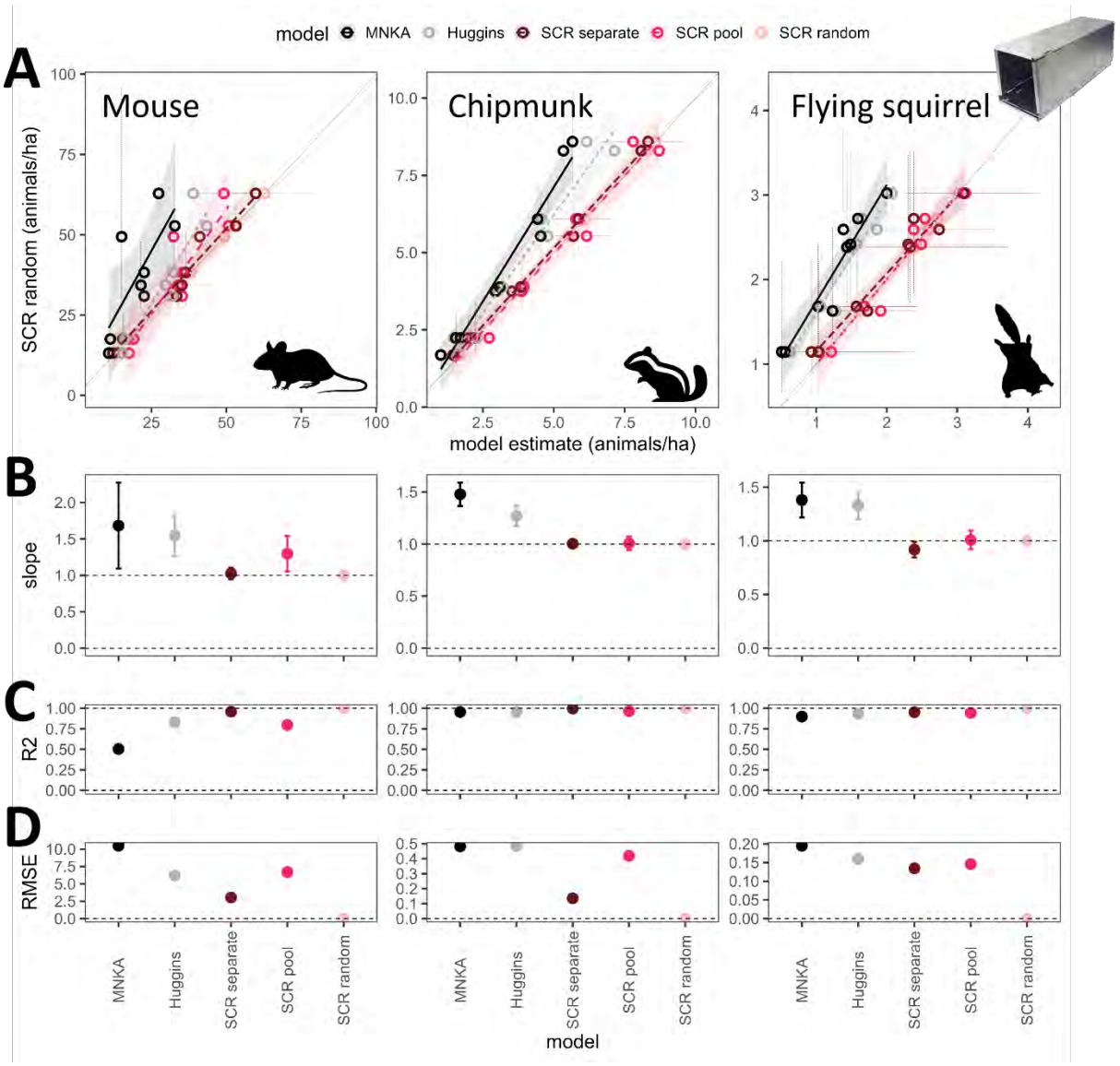

Figure 4.4. Comparison between density estimates calculated with live trapping data that account for individual identity for deer mice (left panels), Townsend's chipmunks (middle panels), and Humboldt's flying squirrels (right panels). Models compared were minimum number of individuals known alive (MNKA; black), Huggins models (Huggins; grey), and spatial capture recapture models in a Bayesian framework (SCR separate, SCR pool, SCR random; shades of red). (A) Model estimates centered and scaled (mean = 0, standard deviation = 1) and compared to SCR random using linear regressions. Grey diagonal line represents 1:1 line. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicate perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression.

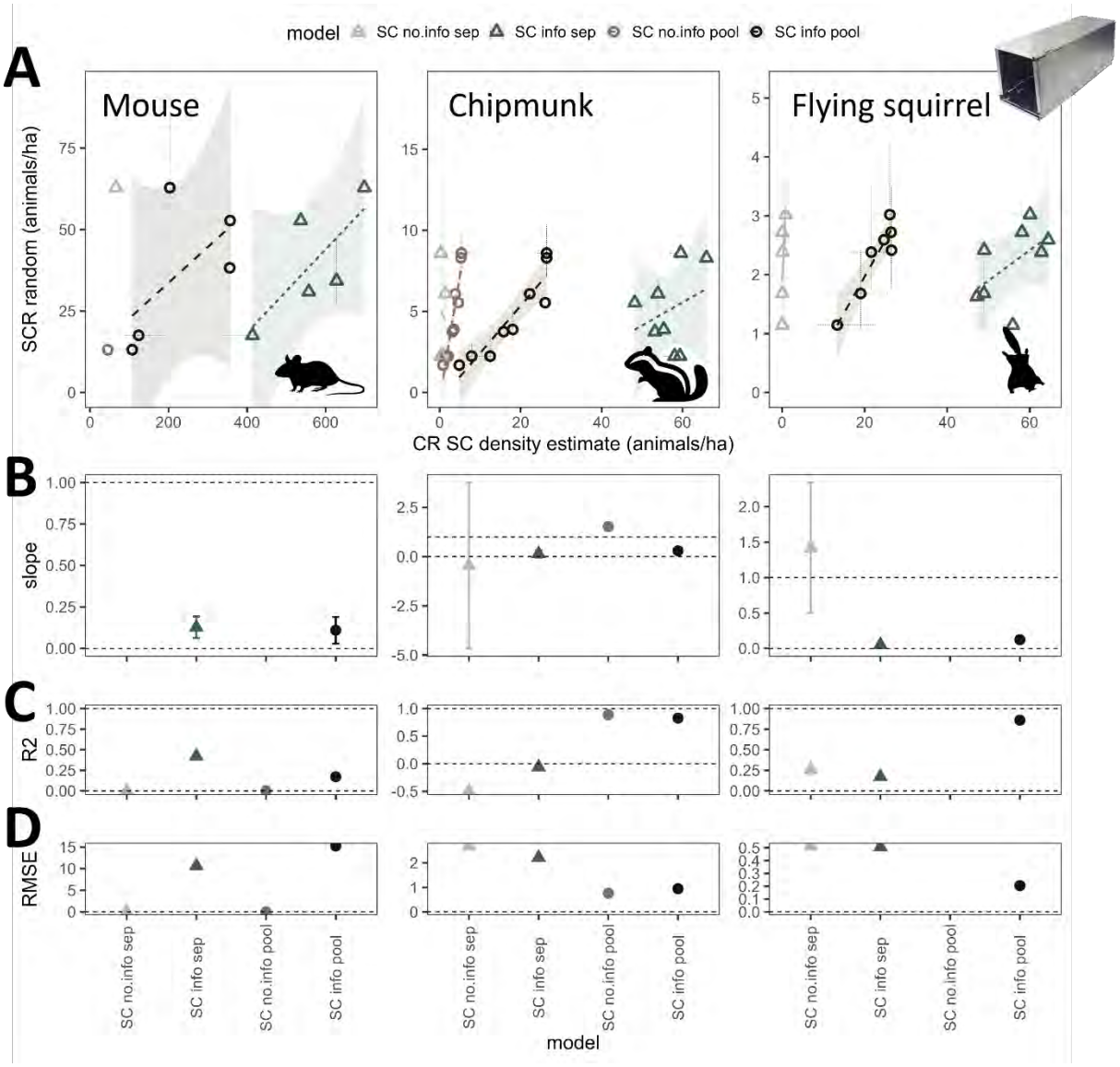

Figure 4.5. Comparison between density estimates from spatial count (SC) models calculated from live trapping data that withheld individual identity and spatial capture-recapture models with random intercepts for each site (SCR random) for deer mice (left panels), Townsend's chipmunk (middle panels), and Humboldt's flying squirrel (right panels). Comparisons made. (A) Model estimates compared to SCR random using linear regressions. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicates perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression. *Note: only estimates from models that converged were included.

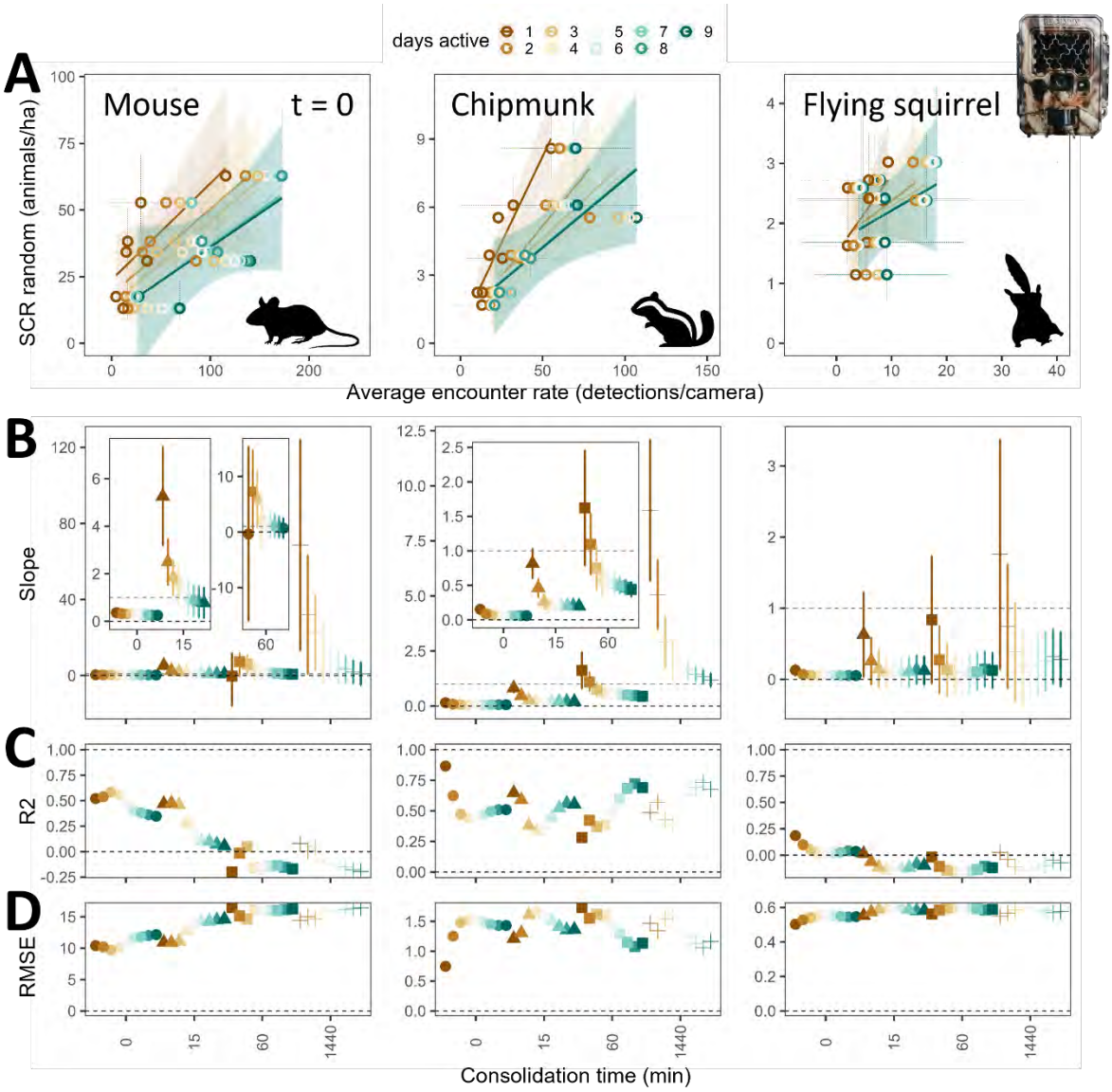

Figure 4.6. Comparison between average encounter rates for camera trap data and multi-strata spatial capture-recapture models with random intercepts for each site (SCR_{random}) for deer mice (left panels), Townsend's chipmunk (middle panels), and Humboldt's flying squirrel (right panels). (A) Model estimates and compared to SCR_{random} using linear regressions. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicates perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared (R2) values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression.

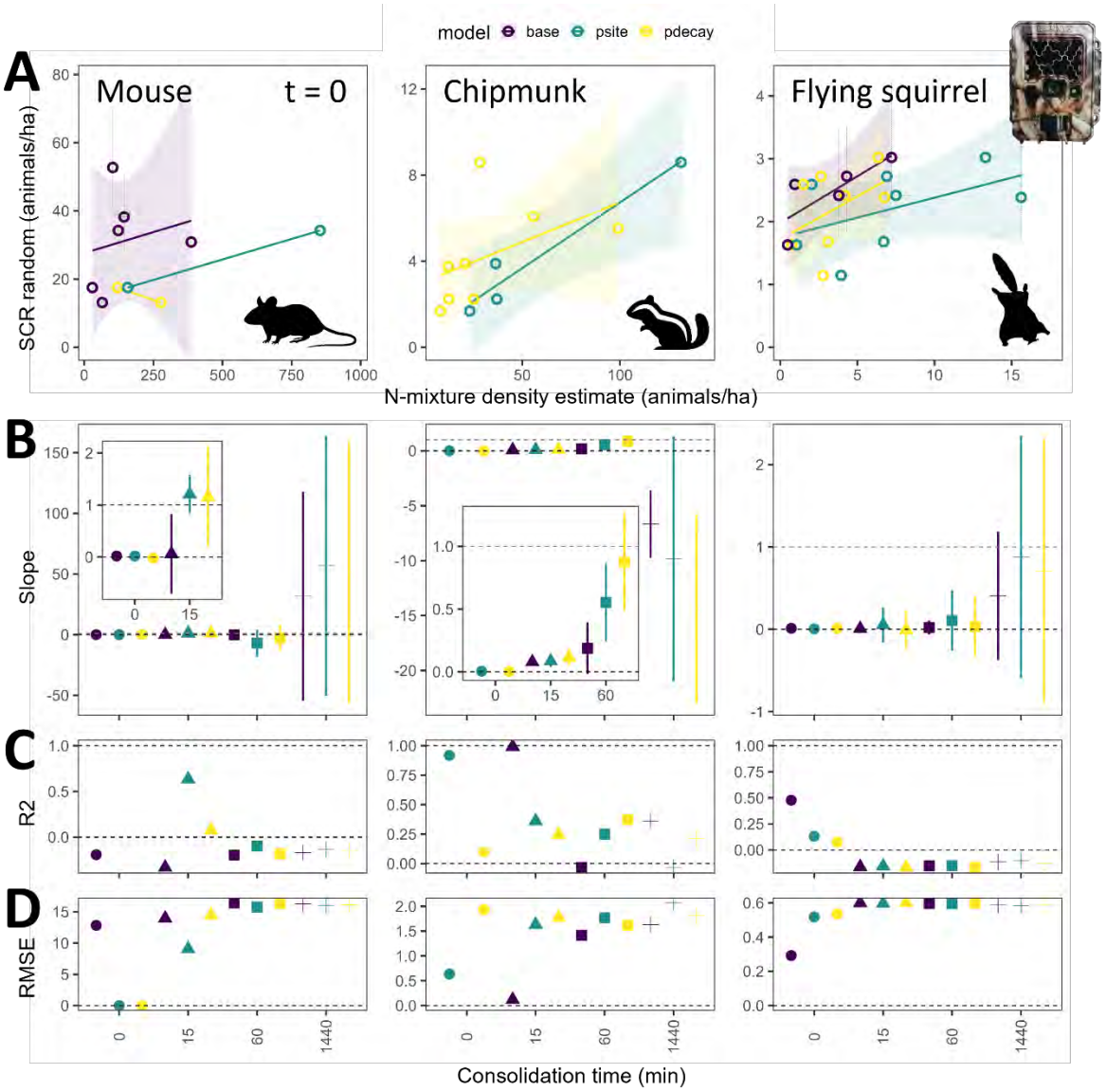

Figure 4.7. Comparison between N-mixture models fitted to camera trap data and multi-strata spatial capture-recapture models with random intercepts for each site (SCR_{random}) for deer mice (left panels), Townsend's chipmunk (middle panels), and Humboldt's flying squirrel (right panels). Abundance converted to density using by dividing abundance by area of trapping grid with ½ mean maximum distance moved (MMDM) for each species derived from the capture-recapture models. (A) Model density estimates compared to SCR_{random} using linear regressions. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicate perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared (R2) values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression. *Note: only estimates from models that converged were included

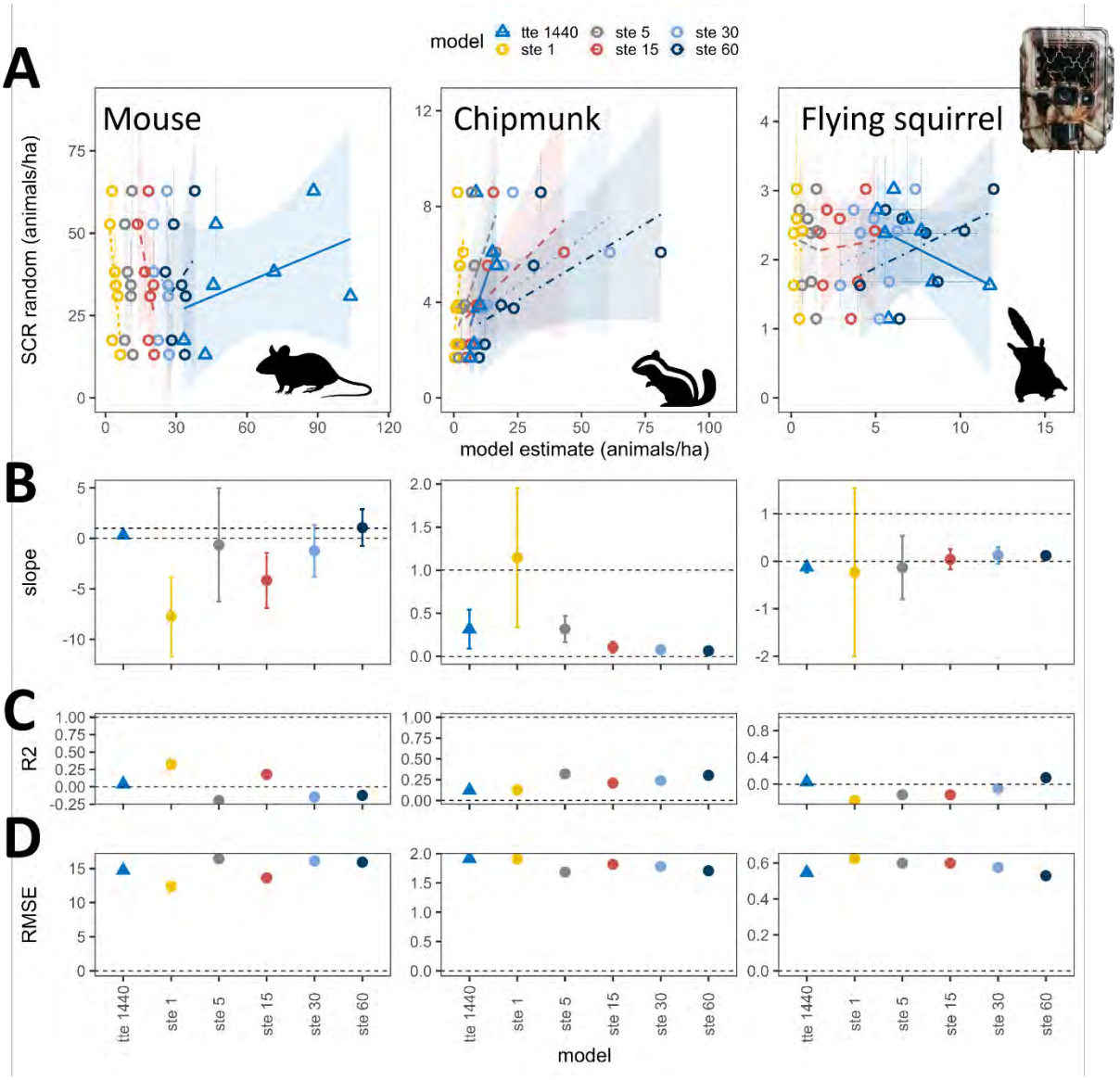

Figure 4.8. Comparison between time-to-event (TTE) and space-to-event (STE) models fitted to camera trap data and multi-strata spatial capture-recapture models with random intercepts for each site (SCR_{random}) for deer mice (left panels), Townsend's chipmunk (middle panels), and Humboldt's flying squirrel (right panels). (A) Model density estimates compared to SCR_{random} using linear regressions. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicates perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared (R2) values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression. *Note: only estimates from models that converged were included

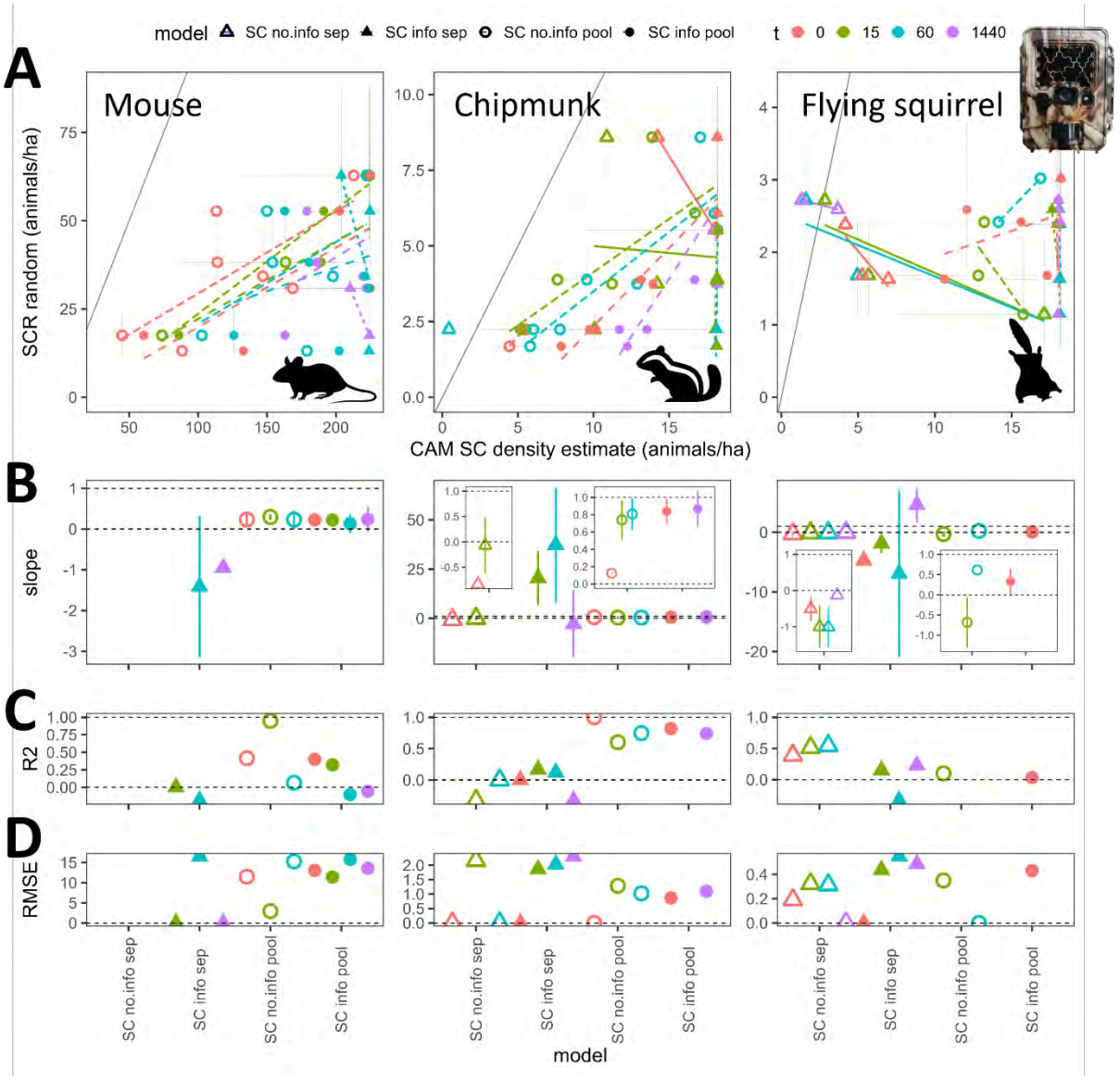

Figure 4.9. Comparison between spatial count (SC) models fitted to camera trap data and multi-strata spatial capture-recapture models with random intercepts for each site (SCR_{random}) for deer mice (left panels), Townsend's chipmunk (middle panels), and Humboldt's flying squirrel (right panels). (A) Spatial count model density estimates compared to SCR_{random} using linear regressions. (B) Slope of linear regression line. Slope of 1 indicates perfect alignment between density estimates whereas slope of 0 indicates no correlation between density estimates, and slope of -1 indicates perfect negative correlation between density estimates. Error bars represent standard error. (C) R-squared (R2) values of linear regression. Values closer to 1 indicate better fit of linear regression. (D) Root mean squared error (RMSE) values for linear regression. Values closer to 0 indicate better fit of linear regression. *Note: only estimates from models that converged were included

CHAPTER 5 – QUANTIFICATION OF THE BIODIVERSITY OF OLD GROWTH TEMPERATE RAINFORESTS ACROSS MULTIPLE TAXA

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Abstract

The majority of terrestrial biodiversity on Earth is supported by forested systems (International Union for Conservation of Nature 2017), but the demand for economic outputs from these areas has resulted in widespread deforestation and forest degradation. Despite growing concerns that we are in "the sixth extinction crisis," we are limited in our ability to stymy this crisis because we still do not understand how species and communities respond to forest age, loss, and degradation. New technologies using next generation natural history methods now allow for linking biodiversity to forest age and structure using landscape-scale biodiversity surveys. We conducted multi-taxa biodiversity surveys across a gradient of forest age and structure inclusive of ancient forests in the Oregon Cascades of the Pacific Northwest during 2017-2019. We used traditional and next generation natural history methods to collect data simultaneously on understory vegetation, overstory trees, fungi, crawling and flying invertebrates, songbirds, and mammals at 96 core biodiversity sites. At 145 additional sites, we collected vegetation and songbird data. From our samples and surveys, we identified 1134 fungal operational taxonomic units (OTUs) from soil cores, 342 invertebrate OTUs from pitfall traps, 891 invertebrate OTUs from Malaise traps, 61 bird species from songbird surveys, and 29 mammal species from camera traps. Using nonmetric multidimensional scaling ordinations (Bray Curtis distance), we identified 2 major gradients, elevation and years since disturbance, that explained differences in community composition. Partial Mantel tests revealed that β-diversity (turnover) was positively correlated with dissimilarity of stand characteristics such as years since disturbance, old growth structural index, canopy height, canopy ruggedness, indicating that species composition in young, recently disturbed forests are distinct from those in old growth forests. Together, we provide an extensive baseline of biodiversity data and an efficient method for surveying multiple taxa simultaneously. With these methods, one can test the efficacy of land-use policies such as the Northwest Forest Plan in providing protection of old-growth associated biota and maintaining biodiversity.

Introduction

Forest loss and degradation have been identified as primary global drivers of biodiversity decline (Betts et al. 2017*b*, 2022) and have contributed to what some call “the sixth extinction crisis" (Ceballos et al. 2015), where population trends across multiple taxa including invertebrates (Hallmann et al. 2017), amphibians (Stuart et al. 2004), birds (Rosenberg et al. 2019), and mammals (Ripple et al. 2014, 2015) show alarming rates of decline during the Anthropocene (Dirzo et al. 2014). Following disturbance, time can be an important mechanism of species accumulation and biodiversity maintenance (Peterken and Game 1984), suggesting that forest age as well as forest loss and forest degradation is likely to affect biodiversity. However, how most species respond to forest loss, degradation, and age is still poorly understood. Given the benefits of biodiversity for ecosystem processes and ecosystem services (Ricketts et al. 2016) and the social values placed on maintaining unique species, knowing these relationships is critical to develop conservation strategies to maintain biodiversity and intact ecosystems.

This relationship between forest age, disturbance, and biodiversity has been studied empirically, but with mixed results. In global analyses of forest loss, risks of species extinction based on IUCN Red List data were predicted to be disproportionately greater for species in relatively intact landscapes (Betts et al. 2017*b*). In the tropics, bird, dung beetle, and leaf-litter ant species richness increased with age and recovery towards old growth forest (Edwards et al. 2014, Owen et al. 2020), but others have observed declines in species richness (Müller et al. 2023). In Canada, even though there was little change in overall forest cover, there were substantial population declines in avian species related to the decline of old growth forests (Betts et al. 2022). Together, these studies indicate that old growth forests may be important for biodiversity maintenance, but this relationship may be location specific.

Some of the oldest and largest trees on Earth occur in the temperate rainforests of the Pacific Northwest, USA. These old growth forests have been presumed to be particularly important for biodiversity maintenance by harboring unique biota. Despite this assumption, the biodiversity response to forest age in this

region is largely unknown, beyond a few flagship species such as a lichen species, *Lobaria oregana* (Sillett et al. 2000), and old-growth obligate bird species, Northern Spotted Owls (Forsman et al. 1984) and Marbled Murrelets (Ralph et al. 1995). Knowing this relationship between age, disturbance, and biodiversity is critical because logging has been a significant cause of forest loss and degradation in this region. Between 1940-1994, timber harvest in the Pacific Northwest accelerated dramatically during and after World War II. In Oregon alone, the extent of timber harvest during this period typically exceeded 8 billion board feet annually (Simmons et al. 2016). The rapid decline of old-growth forests, conservation concerns for Northern Spotted Owl, and growing environmental activism resulted in a period of civil unrest referred to as the "Timber Wars" of the 1980s and early 1990s. With population declines caused by loss of habitat, Northern Spotted Owls were listed under the US Endangered Species Act in 1990 which then resulted in an injunction of timber harvesting on federal lands until a plan was developed that would provide adequate habitat to support population recovery (Lesmeister et al. 2018). The 1994 Northwest Forest Plan was designed to protect and restore old growth forests on approximately 10 million ha of federally administered land to support Northern Spotted Owl recovery, habitat for other old-growth species, and maintain substantial volume of timber production (U.S. Department of Agriculture, Forest Service and U.S. Department of the Interior, Bureau of Land Management [USDA and USDOI] 1994). During this period, much progress was made on identifying the diversity of biota in old growth stands during the USDA Forest Service's Old-Growth Wildlife Habitat Research Program (Ruggiero et al. 1991), and although many old growth stands were protected by the Northwest Forest Plan, protection of these stands was largely motivated by one species following the umbrella-species conservation model (Fleishman et al. 2000, Zacharias and Roff 2001). The degree to which these old-growth stands provide habitat for other biota that specialize in old growth forests is unknown.

Today, timber production still continues to dominate land use in the Pacific Northwest. In Oregon, > 4 billion board feet are harvested annually, producing ~$7 billion in revenue, and supporting > 43,000 jobs (Simmons et al. 2016). Since the

Northwest Forest Plan, conservation concerns for numerous species have continued to grow including the Northern Spotted Owl, Marbled Murrelet (*Brachyramphus marmoratus*), red tree vole (*Arborimus longicaudus*), and Humboldt marten (*Martes americana humboldtensis*), and old growth associated songbirds, indicating that these protections are not enough (Lesmeister et al. 2018, Raphael et al. 2018, Phalan et al. 2019, Heinrichs et al. 2023). Moreover, it still remains unknown 1) if these old growth forests harbor more diversity than younger forests, 2) the extent to which species specialize in old growth forests, and 3) at what scale protection of old growth forests is necessary. Some organisms may need an individual old tree, whereas others may need an old growth dominated stand, landscape, or region (Spies 2004). In addition, even if species are not dependent on old growth forests, *per se*, they may be negatively impacted by the homogenous, even-aged Douglas fir (*Pseudotsuga menziesii*) plantations that are favored by timber harvest and forest management (Lindenmayer et al. 2011).

Until recently, it was difficult to survey biodiversity at a landscape scale across multiple taxonomic groups simultaneously. Surveying multiple taxonomic groups was expensive, labor intensive, and required the integration of many taxa-specific experts, particularly to identify invertebrates and fungal hyphae or spores. Since surveying multiple taxa was demanding, many researchers used indicator, umbrella, or charismatic species as a proxy for biodiversity monitoring and management. These methods, however, have drawn criticism because many co-occurring species are limited by ecological factors that are not relevant to the focal species (Andelman and Fagan 2000, Roberge and Angelstam 2004).

Advances in technology now allow us to survey multiple taxonomic groups simultaneously in detail across broad spatial and temporal extents (Tosa et al. 2021). These advances, including new electronic sensors such as camera traps (Steenweg et al. 2017) and acoustic recorders (Rempel et al. 2005, Sueur et al. 2009), and genetic methods such as DNA metabarcoding (Ji et al. 2013) have enabled researchers to create robust “next-generation natural history” datasets (Tosa et al. 2021). These datasets can then leverage aircraft- and satellite-based remote sensing, which have also improved dramatically, to quantify relationships of biodiversity to environmental

factors and predict biodiversity (Gillespie et al. 2008, Bush et al. 2017, Barsoum et al. 2019). These results can then be utilized for conservation and management.

Here, we used next-generation natural history and traditional methods to implement a rapid biodiversity inventory of plants, fungi, invertebrates, songbirds, and mammals in the Oregon Cascades during 2017-2019. The objective of this study was to quantify the relationships of single species and communities within environmental gradients of elevation and disturbance on federal forests. We predicted that community composition would be strongly driven by the elevation in this mountainous system because it is strongly tied to other conditions critical to species niches including temperature and the amount and type of precipitation (e.g., rain or snow) a site receives. Additionally, we predicted that old growth sites would have higher species diversity because they have had time to accumulate species, provide a diverse number of niches, and provide more area for species to occupy. Quantifying these relationships allowed us to enumerate and identify species that would be lost with the conversion of old growth forests into disturbed forests. We found that a multi-taxa approach was advantageous and necessary because we found evidence for taxon-specific responses to the amount of old growth on the landscape.

Study Area

This study was conducted in the McKenzie River Ranger District of the Willamette National Forest near Blue River, Oregon, which is located on the western slope of the Cascade Mountain Range (Figure 5.1A). Roughly half of the sites were located in the H. J. Andrews Experimental Forest (HJA), a Nation Science Foundation (NSF) Long Term Ecological Research (LTER) site. The HJA was the original study area where northern spotted owls were studied (Forsman et al. 1984). Although monitoring of the northern spotted owl population has continued here, their population has declined dramatically, so much so that it is no longer believed that there are any breeding pairs of northern spotted owls left. The surrounding sites were located on federal lands that are managed for timber production and other objectives by the USDA Forest Service. Elevations range from 410 m to 1,630 m. The maritime climate consists of warm, dry summers and mild, wet winters. Mean monthly

temperatures range from 1°C in January to 18°C in July. Precipitation is concentrated from November through March, and averages 230 cm at lower elevations, mainly as rain, and 355 cm at higher elevations, mainly as snow (Greenland 1993, Swanson and Jones 2002).

Lower elevation forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Upper elevation forests are dominated by noble fir (*Abies procera*), Pacific silver fir (*Abies amabilis*), Douglas-fir, and western hemlock. The understory is variable and ranged from open to dense shrubs. Common shrubs included Oregon grape (*Mahonia aquifolium*), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), vine maple (*Acer circinatum*), Pacific rhododendron (*Rhododendron macrophyllum*), huckleberry (*Vaccinium* spp.), and blackberry and salmonberry (*Rubus* spp.).

Before timber cutting in 1950, 65% of the HJA was covered in old-growth forest. Approximately 30% of the HJA was clear cut or shelterwood cut to create plantation forests varying in tree composition, stocking level, and age. In 1980, the HJA became a charter member of the Long Term Ecological Research network and no logging has occurred since 1985. The Willamette National Forest immediately surrounding the HJA has a similar logging history, but logging continues to occur. Currently, the HJA consists of a higher percentage of old-growth forest than the surrounding Willamette National Forest (approximately 58% in the HJA vs. 37% in the study area) (Davis et al. 2022). Wildfires are the primary disturbance type, followed by windthrow, landslides, root rot infections, and lateral stream channel erosion. Mean fire return interval of partial or complete stand-replacing fires for this area is 166 years and ranges from 20 years to 400 years (Teensma 1987, Morrison and Swanson 1990, Reilly et al. 2017).

Methods

We conducted multi-taxa biodiversity surveys at 96 sites, stratified by elevation and time since disturbance. Sites were also stratified between inside and outside the HJA to capture landscape-scale differences between the long-term

ecological research site where no logging has occurred since 1989 and neighboring sites within a landscape context of continued active management (n_{HJA} = 42, n_{WNF} = 54). At each site, we surveyed vegetation, fungi, invertebrates, songbirds, and mammals (Figure 5.1B). To quantify fungal and invertebrate diversity, we used genetic methods. We conducted all analyses in Program R 4.2.2 (R Development Core Team 2014).

Vegetation Surveys

In 2018, we conducted vegetation sampling according to protocols developed by Kim et al. (2022). Briefly, at each site, we measured vegetation at 500 m^2 subplots (12.6 m radius). Measurements included size of trees (diameter at breast height), vertical structure, ground cover, woody species cover, fern cover, and along one transect, the size and decay class of coarse woody debris. For vegetation-specific analyses, we included 145 additional sites that were surveyed concurrent to our study (Kim et al. 2022). We separated overstory tree communities from understory woody vegetation communities (0-2 m in height) for the purposes of this study.

Fungal Surveys

We collected 5 soil cores (15 cm length x 1.3 cm radius) at each site: 4 samples were taken 10 m from site center in each of the cardinal directions and 1 at site center. We stored samples at -20C until we extracted DNA from soil samples using the FastDNA SPIN Kit for Soil (MP Biomedicals, USA), amplified the ITS1 region from resultant DNA (White et al. 1990, Blaalid et al. 2013), and used DNA metabarcoding to identify operational taxonomic units (OTUs). We sequenced barcode regions of DNA (PE, 150 bp insert size) using the Illumina HiSeq 3000 at the Center for Quantitative Life Sciences at Oregon State University. We assigned taxonomic information to OTUs, when possible, based on the UNITE database (https://unite.ut.ee/). To be conservative with what we considered a species, we removed OTUs that had percent identification < 90%.

Invertebrate Surveys

We collected flying and crawling invertebrate samples using at least 1 Malaise trap and 8 pitfall traps at each site during July and August 2018. Malaise traps were placed at site center. At 32 of the sites, we placed two Malaise traps 20 m in opposite

cardinal directions from site center so that traps were located 40 m apart. Pitfall traps were placed 10 m and 20 m from site center in each cardinal direction. Each pitfall trap consisted of two 475 ml plastic cups (10.0 cm diameter opening, 6.0 cm bottom, 12 cm height). Malaise and pitfall traps were deployed for 7 days. Malaise traps consisted of 100% ethanol and pitfall traps consisted of 150 ml of a 50:50 mixture of propylene glycol and DI water. Pitfall trap samples were pooled at the 10 m and 20 m distances. All samples were transferred to fresh 100% ethanol to store at room temperature until DNA extraction. Prior to DNA extraction, we air-dried and weighed the biomass of all pitfall trap samples to quantify the invertebrate productivity of a site.

We extracted DNA non-destructively by soaking invertebrate samples in 5X lysis buffer (for 50 ml of lysis buffer: 2 ml Tris HCl [1M], 1 ml NaCl [5M], 10 ml SDS [10%], 150 ul $CaCl_2$ [1M], 34.225 ml H_2O) while shaking and incubating at 56C for 60 hours following a protocol described in Ji et al. (2020). For Malaise trap samples, we followed the SPIKEPIPE protocol from Ji et al. (2020) and added a known quantity of invertebrate DNA (not found in the study area) (i.e., internal standard DNA) to help calibrate sequencing data in the downstream bioinformatics pipeline. We shotgun sequenced Malaise trap samples (PE 150, 350 bp insert size) to a mean depth of 29.0 million read pairs (range 21-47) on an Illumina NovaSeq 6000 at Novogene (Beijing, China). We used a custom bioinformatics pipeline to filter reads, assemble sequences, and assigned taxonomic information to OTUs based on the GBIF database (https://www.gbif.org/tools/sequence-id accessed 3 Aug 2021). For pitfall traps, we DNA metabarcoded samples at NatureMetrics (UK) and amplified the COI region using LerayXT primers (Wangensteen et al. 2018). We sequenced barcode regions of DNA using the Illumina MiSeq and used a custom bioinformatics pipeline to filter reads and assign taxonomic information to OTUs based on the NCBI Genbank database. We were conservative in which invertebrate species we included in our analysis by only including those that were assigned to family.

Songbird Surveys

We conducted point count surveys on 3 occasions from 14 May to 9 July in 2018 and from 18 May to 5 July in 2019, corresponding to the arrival and breeding period of most songbird species in the region. Point count surveys followed previously established protocols for long term monitoring of songbirds within the HJA (Frey et al. 2016*b*, Kim et al. 2022). Surveys were conducted during favorable weather conditions between 05:15 and 10:30. Birds heard or seen within a 100 m radius were recorded. For bird-specific analyses, we included 145 additional sites that were surveyed for songbirds concurrent to our study (Kim et al. 2022).

Mammal Surveys

We conducted mammal surveys using remote trail cameras located at the center of each site. Cameras inside the HJA were set in June 2017 and cameras outside the HJA were set in June 2018. Cameras were baited with a can of sardines or cat food, a fresh dead mouse (*Mus musculus*), and a carnivore scent lure and were placed 1.5 – 2 m away from bait. Cameras were visited monthly when accessible, and we replaced baits at this time. We identified species in photos and imbedded tag information in images from camera taps using Picasa 3.9.141 (Google, Inc., 2013) or DigiKam 6.1.0 (KDE, 2019). We used MegaDetector (Beery et al. 2019) to assist in sorting empty photos from those with animals for a subset of photos. After sorting, we manually verified that empty photos were in fact empty and added tags for species if we detected an animal. We extracted metadata information from photos using the *exifr* package (Dunnington and Harvey 2021).

Environmental covariates

We extracted environmental covariates at the site level related to vegetation, forest structure, topography, and anthropogenic features including number of years since disturbance, old-growth structural index (range: 0 to ∞, larger values for more structurally complex stand), elevation (m), canopy height (m), Normalized Difference Vegetation Index (NDVI), Normalized Difference Moisture Index (NDMI), average annual minimum and maximum temperatures (°C), amount of precipitation (inches), distance to roads (m), and distance to stream (m) (Table 5.1). We also calculated

landscape level environmental covariates such as the percentage of area that was logged in the last 100 years, percentage of mature forest (OGSI80), percentage of old growth forest (OGSI200) at various buffer sizes (0.1, 0.5, 1.0, and 5.0 km) using the *landscapemetrics* package (Hesselbarth et al. 2019). In addition, we included variables such as year or season in which the data were collected, management organization (binary WNF = 0, HJA = 1), and whether the site had previously been harvested in the last 100 years (no harvest = 0, harvest = 1). We also classified stand age based on forest succession (0-20 years, 21-40 years, 41-80 years, > 100 years). We log transformed values for number of years since disturbance, distance to road, and distance to stream because the most extreme changes occur immediately after a disturbance and distance variables spanned multiple orders of magnitude.

No single LiDAR acquisition covered our entire study region. Therefore, we derived measures of forest canopy height and cover from data collected during 6 LiDAR acquisitions from 2008 to 2016 that overlapped portions of our study area: H. J. Andrews Experimental Forest (2008), Willamette Valley (2009), Blue River (2011), Lane County (2014), McKenzie River (2016), and Willamette-Sweet Home (2016) acquisitions (downloaded from ftp://lidar.engr.oregonstate.edu; February 2020). Seasonal timing of LiDAR acquisitions varied from June to October, coinciding with the snow-free portion of the growing season. Acquisition details of flights varied (e.g., duration = 2-60 days; minimum flightline overlap = 50% - 100%; maximum scan angle = 14 – 15, sensors included Leica ALS50 Phase II, ALS60 Phase II, ALS70 HP and ALS80), resulting in pulse densities ranging from 8 to 18 pulses m^{-2}. Initial exploration of LiDAR metrics indicated good agreement (coefficient of determination > 0.9) between acquisitions (where overlap was available) for the metrics used in this study: 95^{th} percentile height, cover based on point-cloud density, and cover based on canopy height models. Data delivered by the vendor for each acquisition included (1) 1-m rasters of elevation at the ground surface, (2) 1-m rasters of the elevation of the highest hit (i.e., top of canopy), and (3) x, y, z coordinates of individual classified laser returns (.las or .laz files). All data were reprojected to UTM 10N prior to analysis using the *sp* (Pebesma and Bivand 2005) and *raster* (Hijmans 2022) packages.

Community analysis and non-metric multi-dimensional scaling

We constructed a community matrix consisting of rows representing a site in a particular session or year and columns representing a species or OTU. Values in the matrix were either the number of reads for genetically assigned taxa for a single sampling session, the mean counts of detections across 3 surveys in a single year for songbird surveys, or a standardized count of detections per month for mammal surveys. To simplify interpretation of results and to ensure temporal matching between all taxonomic datasets, we only included songbird data from 2018 and invertebrate data from the first trapping session (July 2018). We fit species accumulation curves for each taxonomic group using the *accumcomp* function in the *BiodiversityR* package (Kindt and Coe 2005) to compare species richness metrics across previously logged sites and sites with no logging history within the last 100 years. Species accumulation curves allowed us to make comparisons between groups with differing numbers of samples. We also calculated species richness for each age class of forest (stand initiation: 0-20, canopy closure: 21-40, stem exclusion: 41-80, and old growth: > 100 years since disturbance) to evaluate differences in taxa at each forest successional stage.

To estimate species turnover (β-diversity), we calculated Jaccard's dissimilarity index to measure species differences between each site and the regional species pool. This metric ranges from 0 (complete overlap in species composition) to 1 (complete mismatch in species composition). We partitioned β-diversity into turnover and nestedness components using the *betapart* package (Baselga and Orme 2012) and then tested for relationships between β-diversity and dissimilarity in site vegetation characteristics (Bray-Curtis distance) using a partial Mantel test (9999 permutations).

To examine differences in community compositions, we conducted non-metric multidimensional scaling (NMDS) ordinations using the *metaMDS* function (distance = bray, k = 3, maxit = 999, trymax = 500) in the *vegan* package (Oksanen et al. 2020). We removed rare species that were present at fewer than 5% of sites (i.e., < 5 sites) to ensure convergence of community analysis models, and we relativized species or OTU abundances by species maxima using the *decostand* function in the

vegan package (Oksanen et al. 2020). Relativization in this way scales all values between 0 and 1 and accounts for differences in abundances due to the year effect and differences in behavior (e.g., flocking vs. solitary). We calculated correlations in community composition with environmental variables using the *envfit* function (perm = 9999). Environmental vector lengths were standardized (range: 0 – 1) to facilitate comparison between taxa. We also overlaid ellipses for each class of years since disturbance at the 50% and 95% confidence limits using the *ordiellipse* function to examine changes in community composition over time. To investigate whether information from one taxon could be applied to other taxa, we repeated this analysis for each taxon.

Generalized linear latent variable models, single species responses, and species traits

Using the main environmental variables with most explanatory power in the NMDS community analyses, elevation and ln(years since disturbance), we fitted generalized linear latent variable models using a negative binomial distribution in the *gllvm* package (Niku et al. 2019) to quantify the strength of response by each species to these variables. To avoid overinterpretation of rare species, we only included species that were detected at more than 10% of sites (> 10 sites). Once models were fitted, we tallied the number of species in each taxon that had 95% confidence intervals that were positive, negative, or overlapped 0. Because songbirds are one of the best studied taxa, especially in North America, we further examined functional relationships between species traits and the environmental gradients using the *gllvm* package (Niku et al. 2019).

Results

We collected 380 pitfall trap samples, 248 Malaise trap samples, and 480 soil core samples, and conducted 96 vegetation surveys, 1,446 songbird surveys, and more than 12 months of camera trapping at all sites. We identified 1,134 fungal OTUs from soil cores, 342 invertebrate OTUs from pitfall traps, 891 invertebrate OTUs from Malaise traps, 61 bird species from songbird surveys, and 29 mammal species from camera traps (Table 5.2). Species accumulation curves revealed that previously logged areas had higher species richness across all taxa surveyed, except for

overstory trees; overstory tree species richness was higher in unlogged stands (Figure 5.2). Trajectories of species accumulation since disturbance, however, varied by taxa (Figure 5.3). Species richness was highest immediately after disturbance in the stand initiation phase, then lowest during the stem exclusion phase, and slowly increased with time for flying invertebrates and songbirds. Overstory tree species richness followed a similar trajectory, but species richness was highest in old growth forests. For mammals, species richness was lowest immediately after disturbance and slowly increased with time and was highest in old growth forests. Woody understory vegetation species richness was highest following disturbance and declined in mature and old growth forests. Species richness of crawling invertebrates and fungi remained relatively constant between years since disturbance classes. Species turnover (β-diversity) was positively correlated with vegetation dissimilarity indices for woody understory species, overstory tree species, fungi, songbirds, and mammals (Figure S5.1).

After removing rare species and OTUs, our final dataset consisted of 9 tree species, 27 understory species, 169 fungal OTUs, 43 pitfall trap species, 188 Malaise trap species, 26 bird species, and 23 mammal classes. NMDS ordinations with the full dataset of all taxa revealed that changes in community composition were most correlated with an elevation-precipitation-temperature gradient and a forest structure gradient (ln(OGSI) and ln(year since disturbance)) (Figure 5.4). Landscape variables and on-the-ground vegetation survey variables had less explanatory power than remotely sensed variables at the local scale.

When NMDS ordinations were performed on each sampling group separately (e.g., Malaise trap species), we consistently found that the elevation-precipitation-temperature gradient (hereafter elevation gradient) had the most explanatory power for differences in community composition (vector lengths for elevation: 0.43 - 0.77; Figure 5.5 and Figure 5.6). The forest structure-disturbance gradient, however, less consistently added explanatory power to the elevation gradient (vector lengths for ln(y): 0.35 - 0.50). For example, the vector for log years since disturbance was almost parallel to the elevation vector for crawling invertebrates, but the vector for log years since disturbance was almost perpendicular to the elevation vector for flying

invertebrates (Figure 5.5). Time since disturbance, number of coarse woody debris, and density of cover between 2 – 4 m were informative variables of fungal communities. Local scale (0.1 km buffer) disturbance variables (percent logged and percent old growth) had the most explanatory power for bird and overstory tree communities, whereas larger landscape scale (5.0 km buffer) variables for amount of mature and old growth forest were more informative for understory vegetation, mammal, crawling invertebrate, and flying invertebrate communities (Figure 5.6). Of note, a binary variable for whether site was inside the HJA, a Long Term Ecological Research site, and the easting of a site had high explanatory power (vector lengths for easting: 0.44 - 0.67; vector lengths for HJA: 0.38 - 0.59). When we overlaid ellipses for classes of years since disturbance, we found community composition overlapped substantially at the 95% confidence limits, but showed separation at the 50% confidence limits between the stand initiation (class 0) and old growth (class 3) for most taxa (Figure 5.7).

The proportion of species that benefitted from longer time since disturbance differed by taxon in the generalized linear latent variable models (Figure 5.8). Nearly half of the songbird (45.9%) and tree species (40%) responded positively to the number of years since disturbance. Only 19.2% of woody understory species (0 - 2 m in height e.g., Devil's club, Pacific yew), on the other hand, responded positively to the number of years since disturbance, but 61.5% of understory species responded negatively to the number of years since disturbance (e.g., snowberry, *Rubus* spp., purshiana).

Functional traits of songbirds and environmental variables were correlated in a predictable manner (Figure 5.9). Frugivorous birds were more abundant in areas that were recently disturbed, and granivorous birds were more abundant at high elevations. Bark foraging and deadwood foraging birds were more abundant in sites that had a disturbance further back in time, and shrub foraging birds were more abundant at low elevation sites.

Discussion

Our analyses of multiple taxa biodiversity across gradients of elevation and disturbance using a combination of next generation natural history methods and traditional methods showed the importance of taking a holistic view of biodiversity and highlighted the complexities of biodiversity conservation. In this temperate rainforest in the Pacific Northwest, we found that previously logged forests had higher species richness than previously unlogged forests. If biodiversity were simply defined by the number of species found at the site level, previously logged forests would be prioritized for conservation. Current definitions of biodiversity, however, account for the greater landscape in which these sites exist, and in this study, we found that species turnover (β-diversity) was associated with differences in vegetation structure at the site and certain species in old growth forests were distinct from those in recently disturbed forest. Even though many species were resilient to disturbance, we found that many others benefited from longer times since disturbance. Moreover, the information gained by studying one taxon was not obviously applicable to other taxa; responses to site-level environmental variables and the relevant scales of landscape-level environmental variables differed by taxa. Finally, the number of species in each taxon varied by orders of magnitude (29 mammalian vs. 1,134 fungal species) and distribution of each species differed greatly (few common, many rare species), which also underscores the difficulty in taking a more holistic view of biodiversity.

In this study, we quantified the relationship between species richness and time since disturbance by substituting space for time. This relationship had only been hypothesized prior to this study (Franklin et al. 2018). As Franklin et al. expected, we observed the highest number of woody understory plant, flying insect, and songbird species with the opening of the canopy and penetration of light into the forest floor, which was followed by a steep decrease in species richness with canopy closure and stem exclusion stages (Figure 5.3). Species richness for these taxa increased with time since stem exclusion, but not to the high levels immediately following disturbance. Species richness of mammals and overstory trees in these sites, however, was lowest

either immediately after disturbance or during the stem exclusion stage and highest in old growth stands. For these taxa, time was necessary to restore high species richness.

These findings are consistent with some studies where total species richness decreased as forests matured (Müller et al. 2023), but contrasted with other studies in forested systems that showed increased species richness, diversity, and abundance as forests became more mature (Owen et al. 2020). Similar to these studies, we also found a trend where older logged stands more closely resembled those of old growth stands (Owen et al. 2020, Müller et al. 2023).

Differences in community composition varied in predictable ways for each taxon surveyed and functional traits of species were predictably related to environmental gradients. Songbirds, which were the most mobile taxon, responded strongest to the elevation gradient and topographic position at the largest scale. Songbirds also had the smallest relative territory sizes and therefore responded strongest to the smallest scale for the amount of area previously logged and amount of old growth. Songbird functional traits related to dead wood were positively related to longer time since disturbance, suggesting that communities are shifting in predictable ways because of changes in resources. Fungal communities were strongly related to the amount of coarse woody debris and the density of understory cover, which provide substrate and a microclimate conducive to fungal growth. Mammal communities were also strongly related to the density of understory vegetation, which may provide cover from predation for small mammals.

We were particularly surprised to find that the binary variable for whether a site was inside or outside the HJA and the east-west gradient were almost as good of a predictor of community composition as the elevation gradient (Figure 5.6). The HJA variable was correlated with the landscape variables such as percentage of mature stands (Pearson's $r = 0.57$) and old growth stands (Pearson's $r = 0.65$), which could be related to legacy effects of human disturbance and differences in current forest management strategies. The east-west gradient was correlated with the elevation gradient (Pearson's $r = 0.61$) but could also represent differences in sites at a larger scale than we examined, such as geophysical or meteorological gradients (e.g., orographic effect).

It must be noted that we conducted our study on public land in the National Forest system that is managed by the USDA Forest Service. As such, the greater landscape that our study area is located within is different from those located within privately managed plantation forests. In addition to a greater area of older forests on federal lands, a larger proportion of these older forests are considered core or core-edge indicating that older forests on federal lands are less fragmented and more contiguous (Davis et al. 2015). We speculate that the forests surrounding each site could be critical in determining the trajectory of the site over time because the surrounding stands could provide biota that could recolonize the stands over time, especially species that are dispersal limited (Leibold et al. 2004).

We were also unable to examine the more nuanced aspects of timber harvest in the Pacific Northwest. Many stands typically received herbicide or pesticide treatments, burned, etc. to increase the volume and speed of growth of merchantable timber and timber harvesting strategies on federal land can be less intense (i.e., thinning or longer plantation rotation cycles from planting to harvest) than the typical clearcutting that occurs on industrial forest land. These practices likely impact the biodiversity that remains after these disturbances and the trajectories of biodiversity accumulation following the disturbance. The discussions on land-sparing vs. land-sharing are relevant to biodiversity conservation in this system (Phalan et al. 2011, 2016, Betts et al. 2021), but we were unable to address these differences in this study.

Next generation natural history methods allowed us to survey numerous taxa at a broad spatial extent and have numerous replicates of sites representing each disturbance class we were interested in. Previous studies that have attempted to survey multiple taxonomic groups were only able to include a few different taxa (e.g., birds, dung beetles, and ants or vegetation, birds, invertebrates, and ungulates) at few sites (n = 18, 32) (Edwards et al. 2014, Kormann et al. 2021). In this study, we were able to replicate our simultaneous biodiversity surveys at 96 sites and leverage data at 145 additional sites for vegetation and songbird communities, but we were not able to survey amphibians, reptiles, and other biota associated with aquatic systems or those located in the forest canopy (e.g., lichens and mosses). Future studies should continue to increase the number of sites surveyed to increase the power to detect statistical

differences in stand types and incorporate repeated sampling at each site to account for differences in detection probabilities of each species. With single sampling occasions, false negative responses may be overpowering our ability to detect changes in community compositions.

Forests, particularly old growth forests, remain an important system for maintaining biodiversity and supporting a variety of taxa. Our study highlights the complexity of biodiversity conservation and the need to take a taxonomically comprehensive approach to biodiversity conservation and valuation of old growth forest. In addition, it is important to keep in mind that old growth stands in the Pacific Northwest are valued for reasons other than biodiversity; old growth stands have societal values for aesthetic and spiritual qualities, and these values were not captured by this study and must be considered when constructing land-use policies (Spies 2004).

Acknowledgments

We thank technicians: B. Doyle, J. Grudens, H. Haeussler, A. Hay, R. Hayes, S. Lundgren, D. Marsh, A. McDonnel, T. Murray, B. Murley, R. Peterson, R. Rich, L. Rivera, K. Slack, S. Sparrow, J. van Arragon, K. Van Nest, M. Yates for field support; C. Boucher, D. Cagle, O. Childress, A. Froelich, N. Griffith, A. Hilger, J. Hedges, R. Mock, A. Saucedo, S. Speirs, H. Thomas for photo tagging and lab work. We also thank J. Allen, and M. Luo for lab support and D. Bell, R. Davis, M. Gregory, and B. McCune for analytical support.

Facilities were provided by the H. J. Andrews Experimental Forest and the Long Term Ecological Research program, which is administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest. Funding for this project was provided by Oregon State University, the USDA Forest Service (16-JV-11261952-047), the National Science Foundation (LTER7 DEB-1440409), the Key Research Program of Frontier Sciences, CAS (QYZDY-SSW-SMC024), the Strategic Priority Research Program of Chinese Academy of Sciences, Grant No. XDA20050202, the State Key Laboratory of Genetic Resources and Evolution (GREKF19-01, GREKF20-01, GREKF21-01) at

the Kunming Institute of Zoology, the University of Chinese Academy of Sciences, and the ARCS Oregon Chapter. This publication represents the views of the authors, and any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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Table 5.1. Biotic and abiotic variables used to examine differences in taxonomic communities from biodiversity surveys conducted during 2017-2019 in the Oregon Cascades.

Variable	Units	Description	Range	Raster Res (m)
Micro-Site Level[+]				
sp.rich	species	Number of woody vegetation species (species richness) 2-4 m in height	1 - 7	NA
canopy start	m	Height at which live canopy begins	2 – 74	NA
num.trees.live	trees	Number of live trees counted with BAF prism	2 – 37	NA
num.trees.broad	trees	Number of broadleaf evergreen trees counted with BAF prism	0 -5	NA
cwd_vol	m^3	Volume of coarse woody debris measured along N-S or E-W transect	0 – 2,057	NA
Site Level				
e	m	Bare earth elevation derived from LiDAR[1]	415 - 1,563	1
mint (maxt)	°C	Average minimum (maximum) annual temperature[2]	1.5 – 4.6 (11.9 – 16.8)	1,000
precip	mm	Average annual precipitation[2]	1,825 - 2,737	1,000
ht	m	Canopy height derived from LiDAR[1]	0 – 75	1
y, logy	years	Years since disturbance[3]	1 – 100	NA
o, logo	NA	Old Growth Structural Index (OGSI) derived from GNN analyses	0 – 85	30
d.road, log(d.r)	m	Distance to road[2]	0 - 941	NA
d.stream, log(d.s)	m	Distance to perennial stream[2]	0 - 1,436	NA
HJA	NA	Binary: site is within the HJA (0) or outside the HJA (1)	0, 1	NA
cover_2m-4m	%	Percent understory cover (2 – 4 m) derived from LiDAR[1]	0 - 0.81	30
cover_4m-16m	%	Percent canopy cover (4 – 16 m) derived from LiDAR[1]	0 – 1.00	30
B1-B11, NDVI, EVI	NA	Landsat band values and values derived from Landsat bands (Normalized Difference Vegetation Index [NDVI], Enhanced Vegetation Index [EVI]) from 17 July 2018	-∞ - ∞	30

Landscape Level				
p.logged	%	Percent logged within the last 100 years at buffer sizes of 0.1, 0.5, 1.0 and 5.0 km	0 - 100	30
p.mature	%	Percent mature forest (> OGSI80) at buffer sizes of 0.1, 0.5, 1.0 and 5.0 km	0 - 100	30
p.old	%	Percent old growth (> OGSI200) at buffer sizes of 0.1, 0.5, 1.0, and 5.0 km	0 - 100	30
TPI		Topographic Position Index (TPI) at buffer sizes of XX, 0.25, 0.5, and 1.0 km	-103 - 132	1

[+] from vegetation surveys

Sources:
[1] LiDAR
[2] Oregon Explorer: https://oregonexplorer.info
[3] USDA Forest Service
[4] LEMMA project: https://lemma.forestry.oregonstate.edu/data/structure-maps

Table 5.2. Summary of taxa identified during biodiversity surveys in the Willamette National Forest in the Oregon Cascades during 2017-2019.

Taxon	Method	Num. Samples	Num. Species	Num. Genera	Num. Families	Num. Orders	Num. Classes	Num. Phyla
Fungus	Soil core	480	499	240	150	84	36	10
Tree	Survey	237	15	10	7	5	2	1
Understory woody plants	Survey	239	55	41	20	15	2	1
Invertebrate	Pitfall trap	380	342	158	114	27	8	4
Invertebrate	Malaise trap	248	891	450	167	18	2	1
Songbird	Point Count Survey	1,446[+]	61	51	25	9	1	1
Mammal	Camera trap	> 12 months	29	28	16	5	1	1

[+]3 point count surveys per year for 2 years at 241 sites

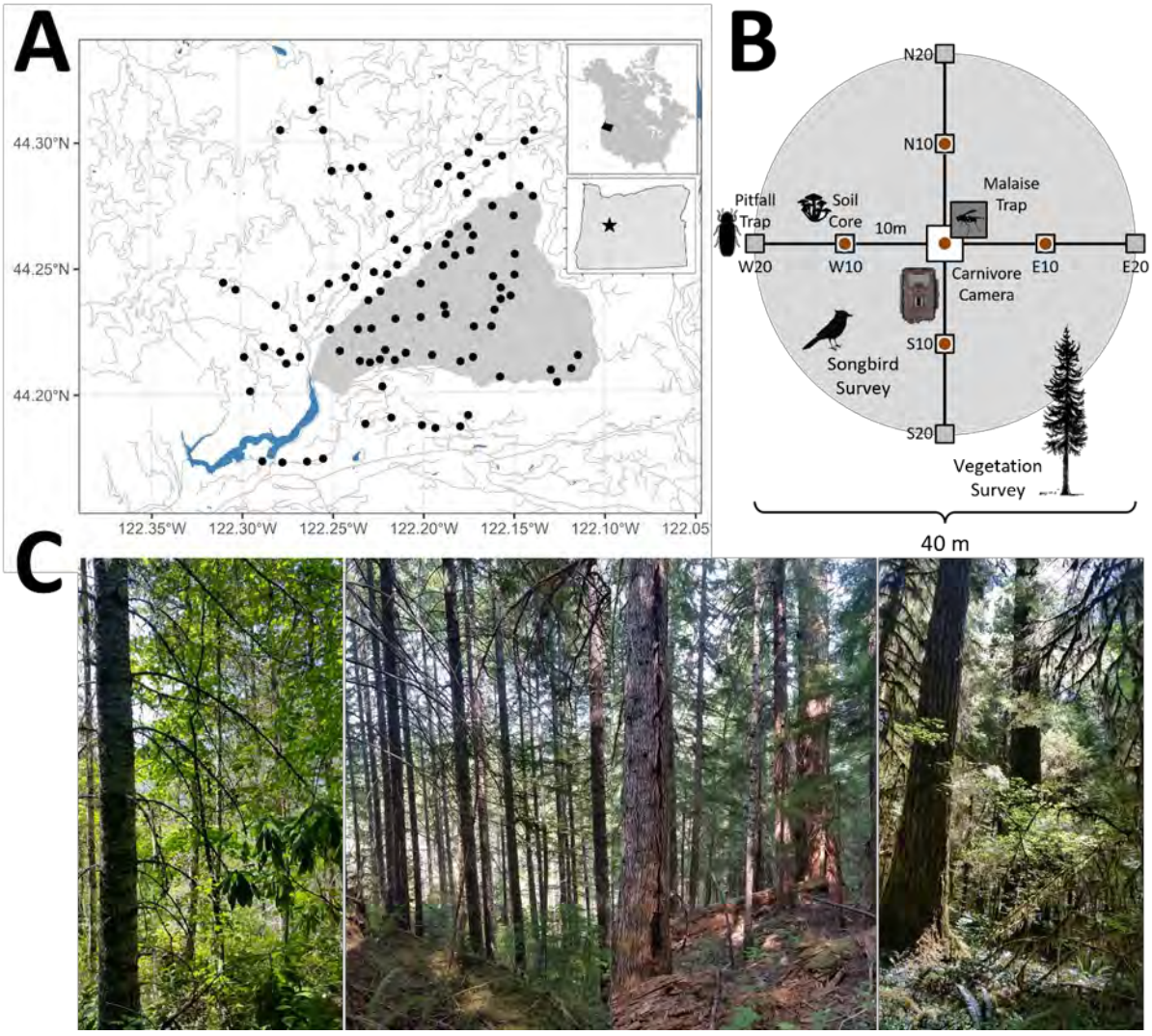


Figure 5.1. A) Study area and multi-taxa biodiversity survey locations (black dots) within the Willamette National Forest in the Cascade Range of Oregon, USA. The H.J. Andrews Experimental Forest shown as gray polygon. B) Multi-taxa survey design at each location. At each location, we surveyed vegetation within a 12.5 m radius plot, fungi using soil cores taken at plot center and in each cardinal direction 10 m apart, ground-dwelling invertebrates using pitfall traps located 10 m and 20 m from plot center in each cardinal direction, flying invertebrates using Malaise traps located at plot center, songbirds using point count surveys from plot center, and mammals using a baited camera trap located at plot center. C) Photographs of young Douglas fir plantation (far left), Douglas fir plantation in stem exclusion phase (center left), mature forest (center right), and old growth forest (far right).

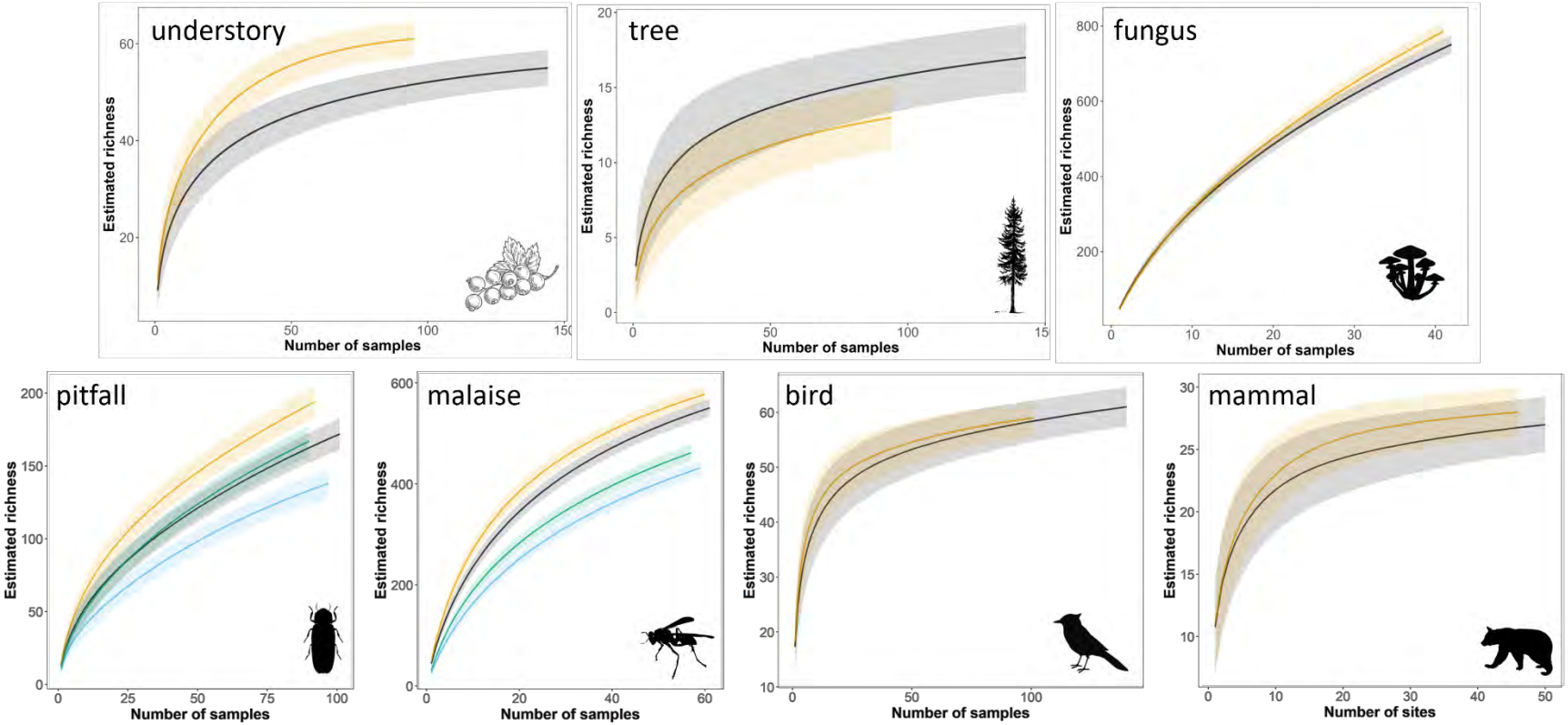


Figure 5.2. Species accumulation curves for all taxa separated by logged (yellow) or not logged within the last century (black). For crawling (pitfall trap) and flying (Malaise trap) invertebrates, second session (August 2018) of sampling shown in green (logged) and blue (not logged within the last century).

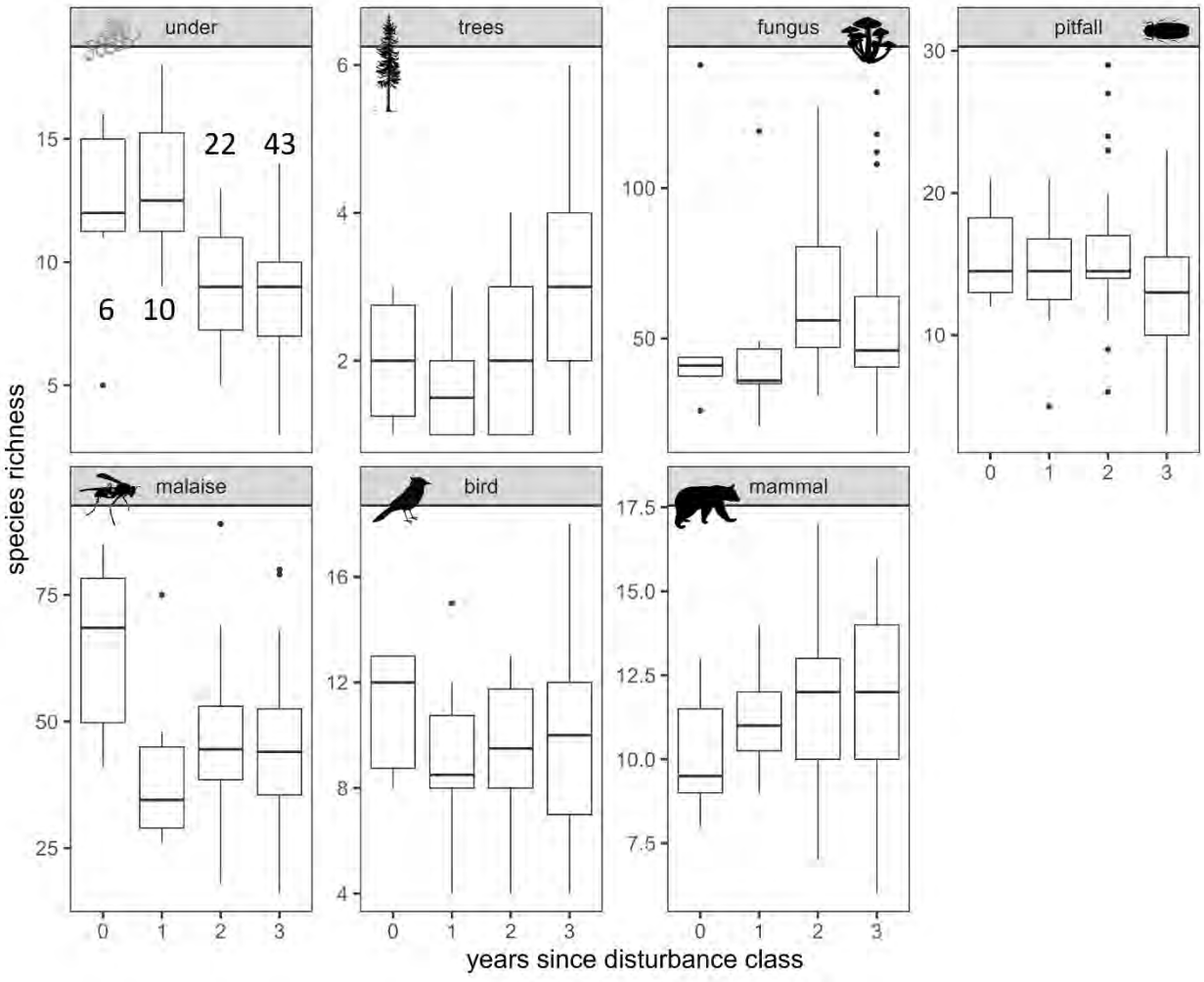


Figure 5.3. Box plots of species richness of each taxon by years since disturbance class (0: 0-20 years, 1: 21-40 years, 2: 41-80 years, 3: > 100 years). Horizontal line in box plot represents the median, box represents 25th and 75th percentiles, and whiskers represent minimum and maximum values or 1.5-fold the inter-quartile range. Outliers (> 1.5-fold the inter-quartile range) shown as black dots.

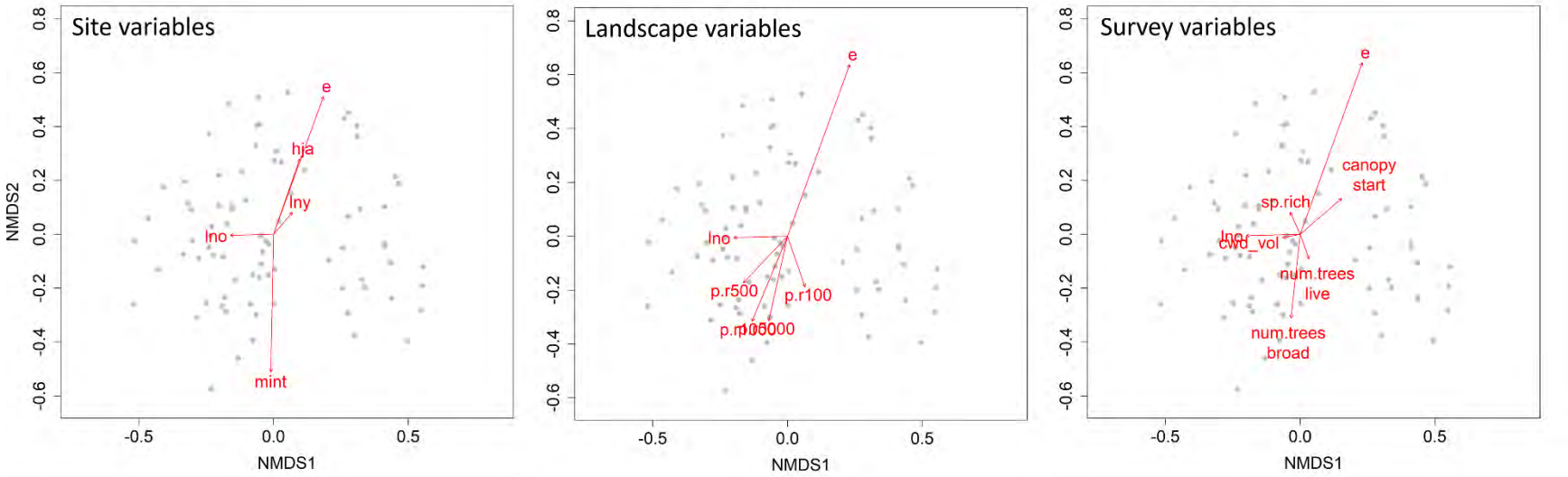


Figure 5.4. Non-metric multi-dimensional scaling (NMDS) ordinations with all taxa included (distance = Bray-Curtis) overlaid with environmental vectors (red arrows). Grey dots represent sampling sites. Site variables, elevation-temperature gradients and natural log of old growth structural index (lno) were best at explaining differences in community composition. Landscape gradients and ground-surveyed variables also overlaid. See Table 5.1 for environmental variable descriptions.

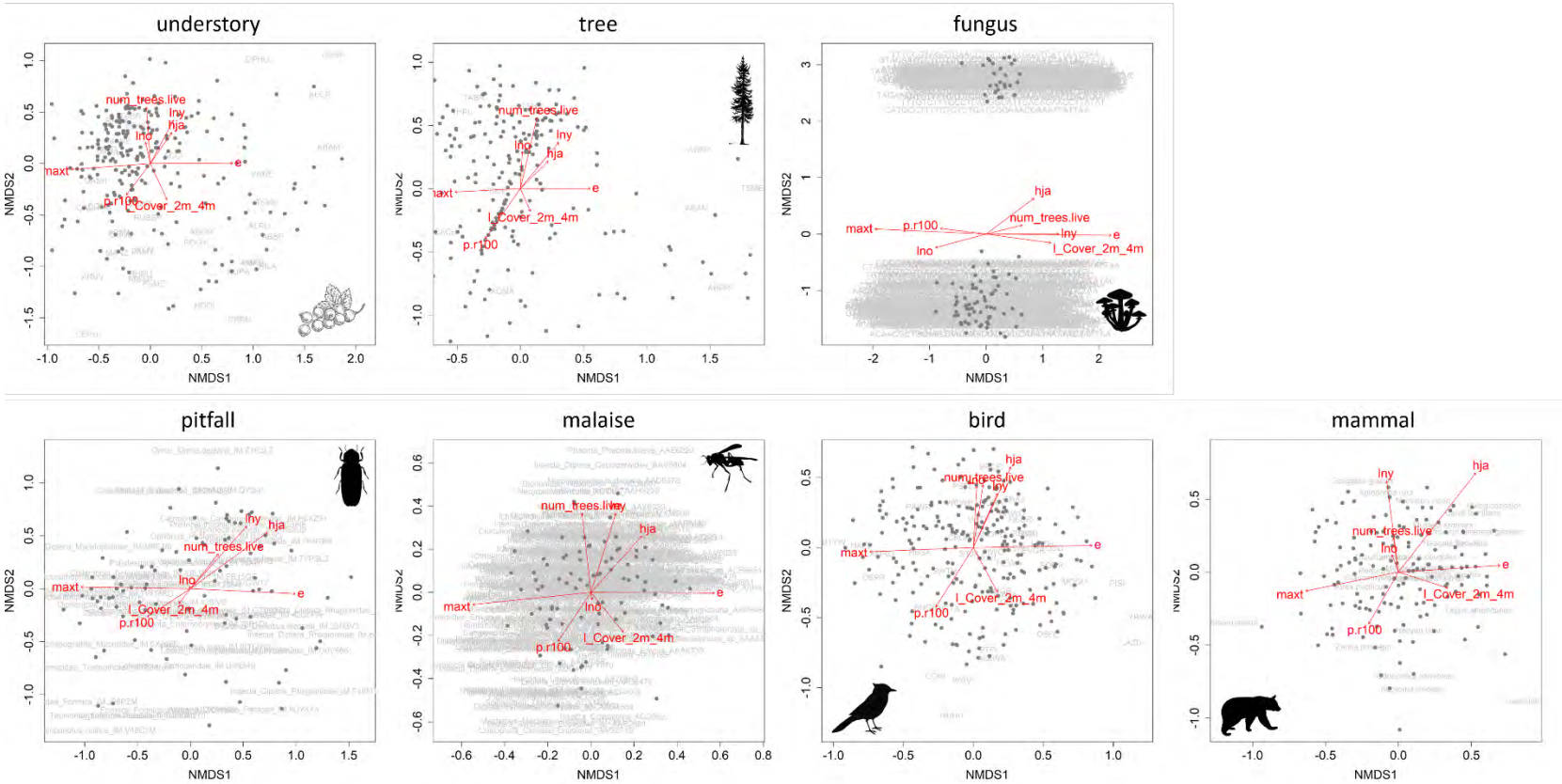


Figure 5.5. Non-metric multi-dimensional scaling (NMDS; distance = Bray-Curtis) with environmental vectors overlaid (red arrows). Grey dots represent sampling sites. Plots rotated to align with elevation (e) vector. Differences in communities of all taxa were strongly correlated to an elevation-temperature gradient and a disturbance-old-growth gradient. See Table 5.1 for environmental variable descriptions.

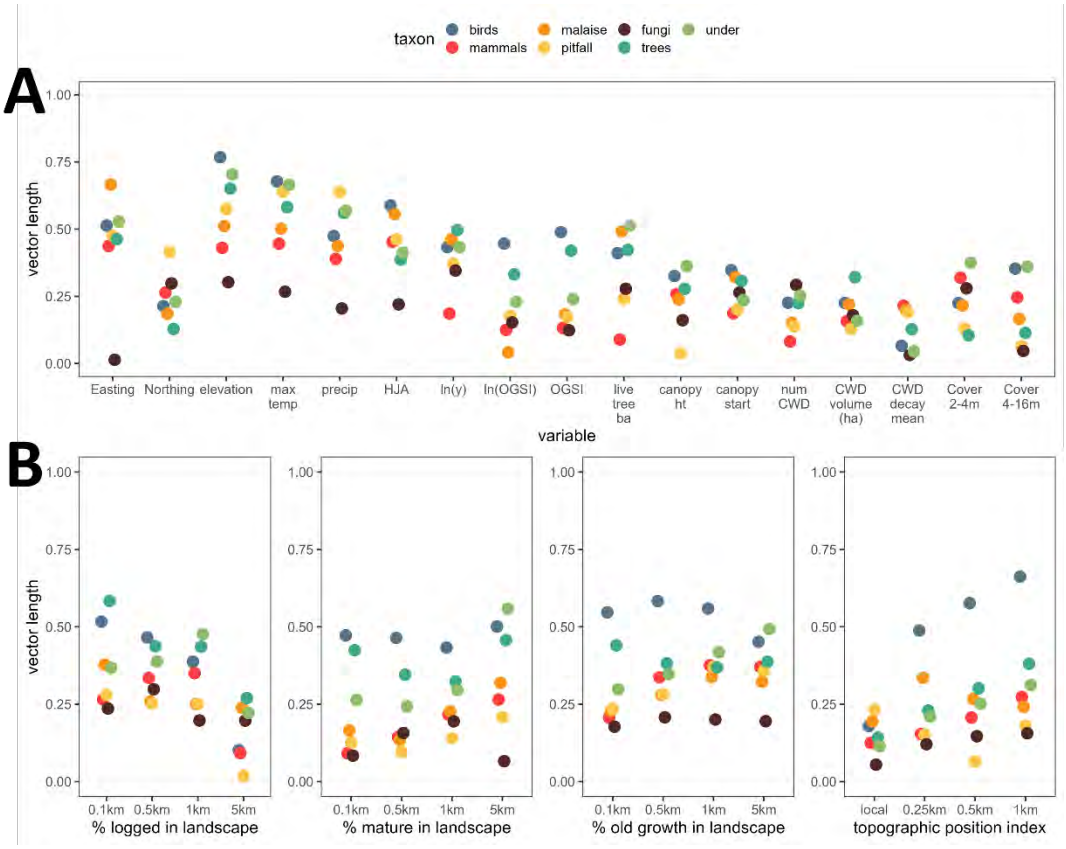


Figure 5.6. Standardized vector length (range: 0-1) of non-metric multi-dimensional scaling (NMDS; distance = Bray-Curtis) with local site environmental variables and landscape level variables at varying buffer sizes (0.1, 0.25, 0.5, 1.0, and 5.0 km). Vector length indicates correlation of variable with site and species dissimilarity. Strongest correlation among all taxa was with elevation. Songbird and tree communities were most strongly correlated to the amount of old growth at the local scale, whereas Malaise invertebrate, pitfall invertebrate, mammal, and understory communities were most strongly correlated to the amount of old growth in the broader landscape scale.

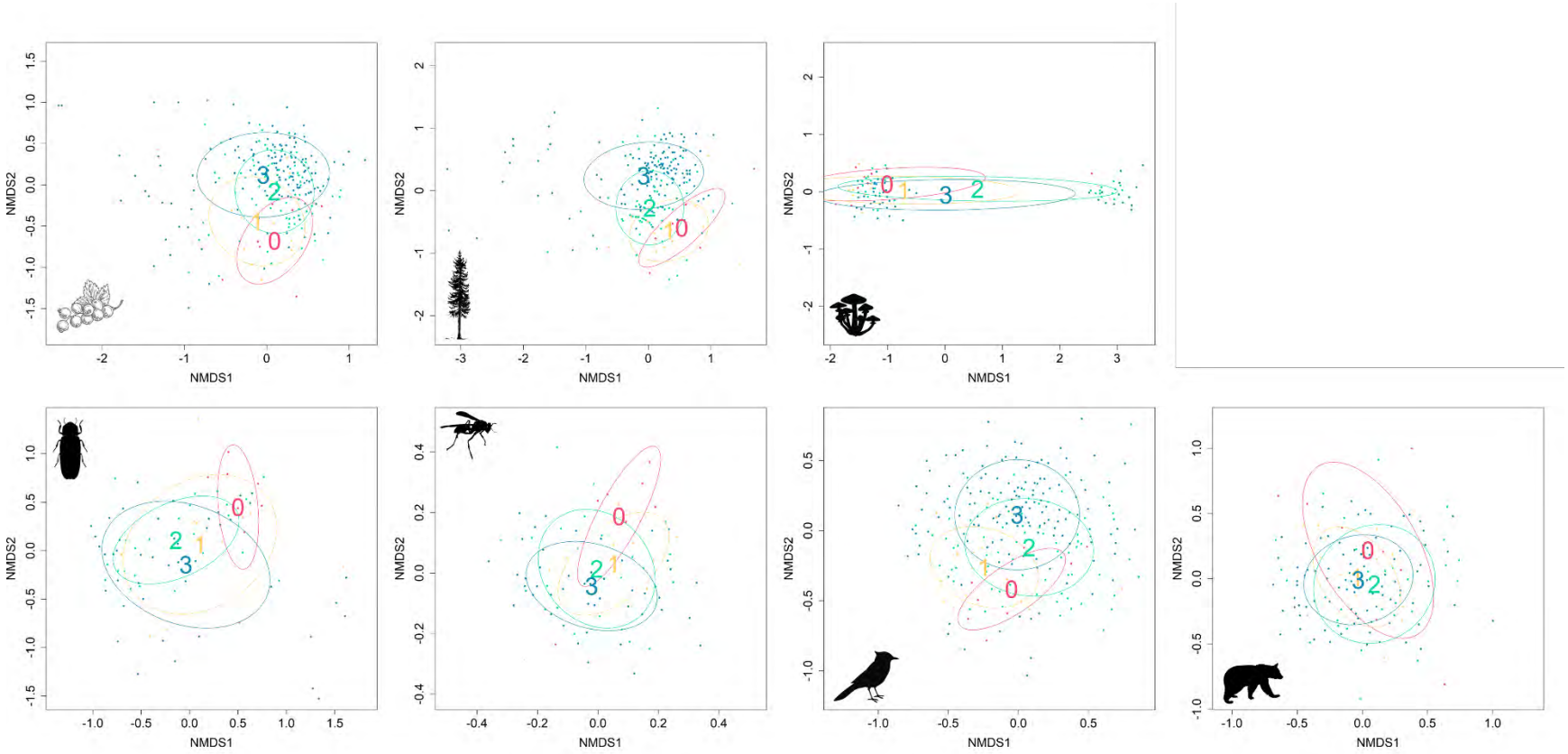


Figure 5.7. Non-metric multidimensional scaling with forest age class ellipses (50% confidence limit; 0 = stand initiation, 1 = canopy closure, 2 = stem exclusion phase, 3 = old growth stand). Substantial overlap in community composition between most classes but some separation between stand initiation and old growth stands for most taxa.

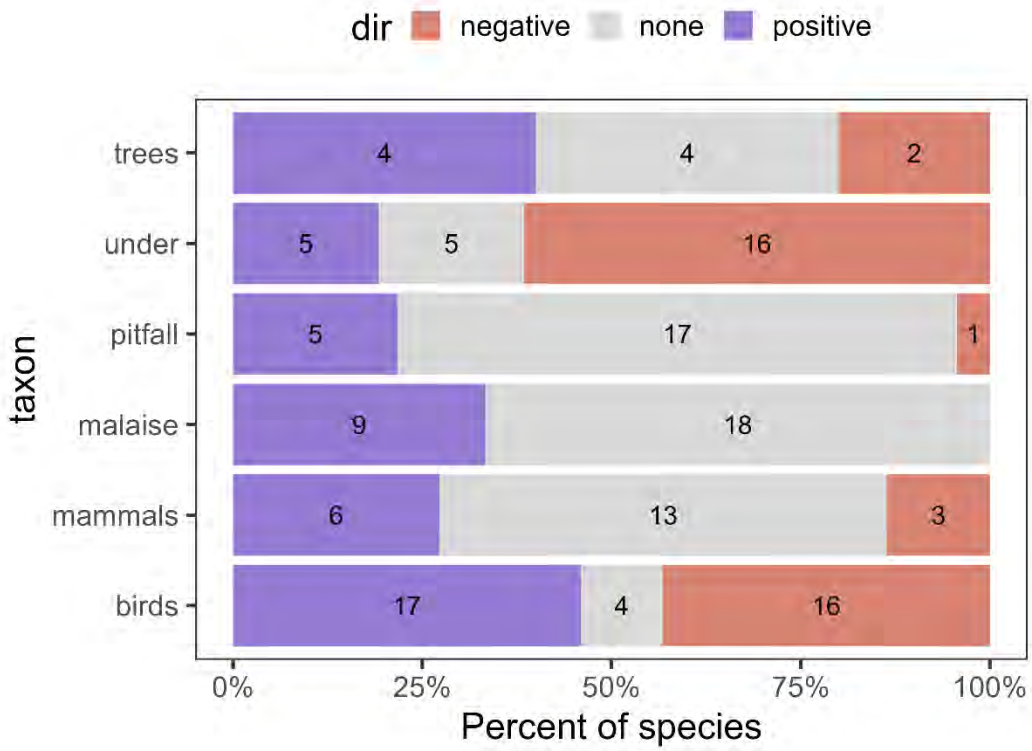


Figure 5.8. Percent of species within each taxon that have a positive (blue), negative (red), or no relationship with number of years since disturbance. Number of species provided within each bar.

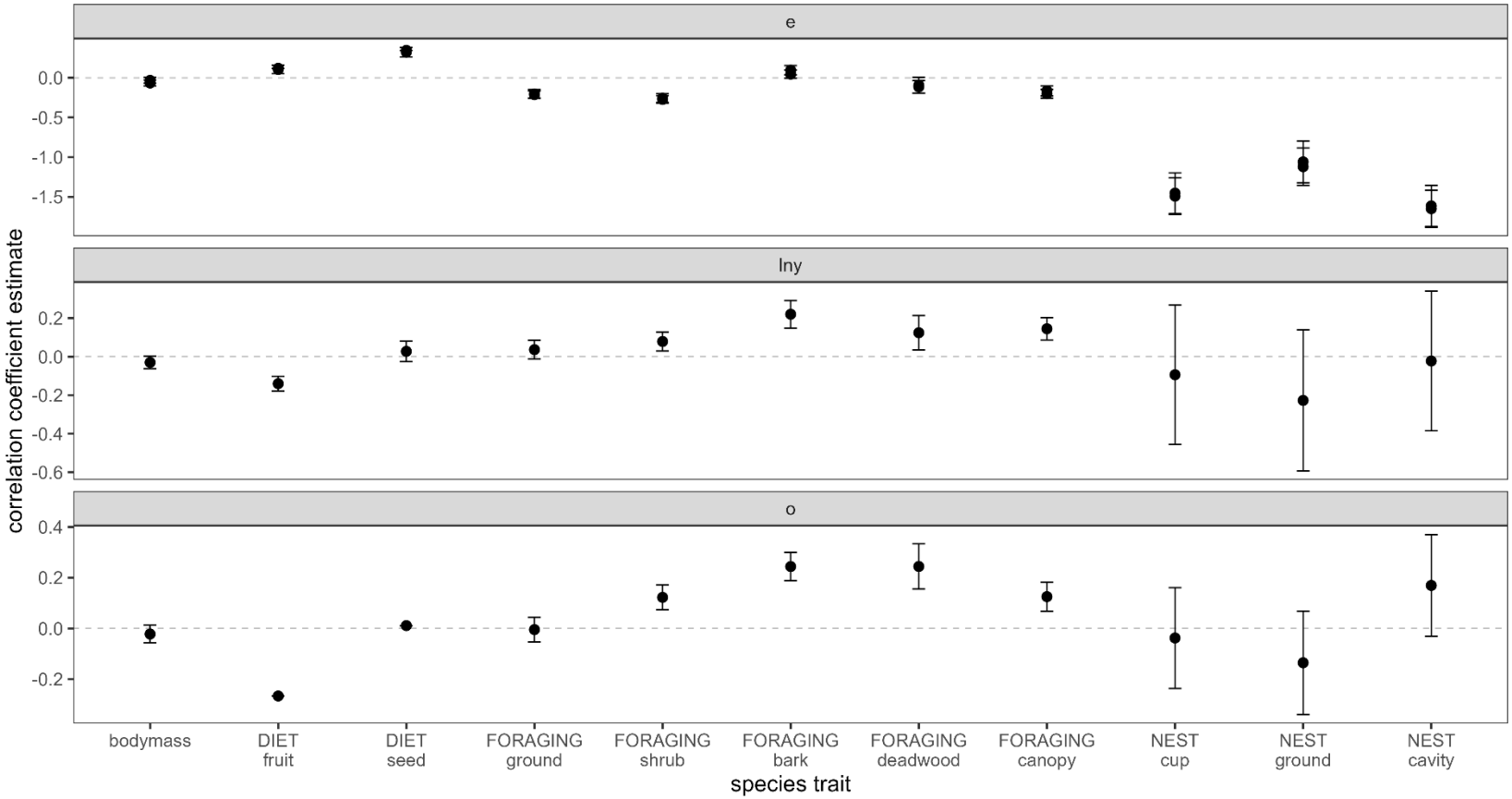


Figure 5.9. Correlation coefficients between environmental variables (e = elevation, lny = log transformed years since disturbance, and o = old growth structural index) and songbird species traits. High elevation sites were associated with seed-eating songbirds, whereas low elevation sites were associated with ground, cup, and cavity nesting species. Recent disturbance and low old growth structural index were associated with fruit-eating songbirds. Evidence of decoupling between number of years since disturbance and dead wood for foraging location and nest structures.

CHAPTER 6 – GENERAL CONCLUSIONS

The temperate rainforests of the Pacific Northwest harbor a great diversity of biota. Previously, conservation and management of this biodiversity had been limited by our ability to study these organisms and their interactions, but next generation natural history methods now allow us to do exactly that. From studying individual organisms to entire communities, we now have better ways to understand the natural world, its response to emerging threats, and the impact that humans are currently having on it. My hope is that the research I conducted in this dissertation has contributed to this knowledge and that it will lead to better coexistence.

In chapters 2 and 3, I focused my efforts on increasing our knowledge concerning the natural history of a single, understudied forest-associated small carnivore, the western spotted skunk. In chapter 2, I used DNA metabarcoding to investigate the foraging ecology of western spotted skunks. I demonstrated that as diet generalists who consumed a wide variety of prey items including vertebrates, invertebrates, and plants, western spotted skunks occupy a key position in the Pacific Northwest food web by providing connections between the arboreal, terrestrial, and aquatic systems. In addition, I showed that western spotted skunks exhibited prey switching behavior between the wet and dry season and their diets were less likely to contain insects when a greater proportion of the landscape surrounding the scat location (1 km buffer) consisted of previously logged forest. Given the high plasticity in their diet, I showed that western spotted skunks may be resilient to disturbance and loss of old growth forest, and they may possess the ability to withstand environmental change that are predicted by climate change with respect to diet.

In chapter 3, I explored the spatial ecology of western spotted skunks by systematically placing camera traps on the landscape and radio-collaring individual animals. As a common species in the temperate rainforests of the Pacific Northwest, western spotted skunks were both widely distributed and highly detectable with bait. At both home range and landscape scales, dynamic occupancy models and resource selection functions revealed that western spotted skunks were more likely to occupy and select for wetter areas and local valleys that are more likely to provide food items

and other resources. At the home range scale, I showed that western spotted skunks likely avoided predation by selecting areas with dense understory vegetation and selected areas surrounded by more previously logged forest (1 km scale). At the population and landscape scale, however, western spotted skunk occupancy was higher at sites that were surrounded by more mature forest (5 km scale). In addition to determining their habitat requirements at the home range and landscape scale, and perhaps more importantly, I showed that western spotted skunks exhibited individualistic habitat selection strategies and have unusually large home ranges compared to other similarly sized carnivores. Because of their large home ranges, western spotted skunks may not require forests of a specific age; instead, they may require large contiguous forest patches. Finally, I showed that western spotted skunk distribution may be limited along the elevational gradient by their sensitivity to cold temperatures and snow accumulation. In the face of climate change, this limitation may be significant because a severe heavy snow event in February 2019, which may be more frequent in the future, caused a large decline in seasonal occupancy rates.

In chapter 4, I explored methods of quantifying the abundance of a single taxonomic group, the small mammal community, in old growth stands. Without methods to accurately estimate the abundance of species, we are limited to treating species as either present or absent and limited in our ability to detect nuanced relationships between species and communities and environmental variables. By pairing capture-recapture data, where individual identities are known, with unmarked camera trap data, where identities of individuals are unknown, I compared the performance of a suite of unmarked methods including average encounter rates, N-mixture models, time-to-event, space-to-event, and unmarked spatial-capture recapture models for estimating densities of deer mice, Townsend's chipmunks, and Humboldt flying squirrels at 8 independent sites. I was able to produce accurate density estimates using multiple unmarked models for Townsend's chipmunks, a species for which the sampling scheme fit its natural history and occurred at medium densities at the sites studied. Despite its simplicity, average encounter rates consistently yielded positively correlated relative density estimates in relation to marked model density estimates for all three species tested. My results suggest that

these simple metrics can distinguish between areas of low and high density with as little as one night's worth of data. These empirical results provide a way forward to rapidly estimate densities of small mammals across large spatial extents with less effort than traditional invasive capture-recapture methods. Without direct measures of small mammal abundance, we are limited to using vegetation structure and composition metrics as a proxy for small mammal abundance, which can vary widely, even within old growth stands. As such, these abundance estimates can be useful for elucidating more direct relationships between multiple taxonomic groups and trophic levels such as interactions between vegetation structure and carnivore populations that depend on small mammals as prey.

Finally in chapter 5, I quantified biodiversity of multiple taxa harbored in temperate rainforest stands and disentangled the effects of elevation and time since disturbance on changes in community composition. I found that sites in previously logged forests generally had higher species diversity across all taxa except for overstory trees, but sites in old growth forests had distinct communities. Even though many species were resilient to disturbance, many species benefited from longer times since disturbance in terms of abundance. Patterns observed in one taxon were not immediately apparent in other taxa and each taxon responded differently to site-level and landscape-level environmental variables, suggesting that studying one species let alone one taxon is not sufficient to make landscape-level conservation or management decisions. The results of this chapter also underscored the importance of single species knowledge, like the knowledge gained in chapters 2 and 3 of this dissertation, can be used to understand the mechanisms for trends and relationships identified in ecosystem and community level response.

Overall, the research constituting this dissertation has provided insights to understanding the complexities of temperate rainforests of the Pacific Northwest. I have contributed knowledge concerning the responses of organisms to disturbances and the role of old growth forests at multiple scales including at the individual, species, taxonomic group, and ecosystem levels. By providing baseline biodiversity data that are efficient, reliable, and replicable, I provided a critical comparison point for future studies. In particular, since collecting the data used in this dissertation, the

H. J. Andrews Experimental Forest and surrounding areas have experienced two large wildfires: the 2020 Holiday Farm Fire and the 2023 Lookout Fire. Approximately half of the sites where we collected biodiversity data have burned at mixed severities. These pre-fire data provide a valuable opportunity to understand the effects of fire and species accumulation processes and generate new testable hypotheses surrounding these concepts. Ultimately, I hope that this research demonstrates the importance of collecting basic ecology and natural history data in advancing our scientific knowledge.

APPENDICES

Appendix 1. Supplementary materials for chapter 2.

Supplemental Text S2.1. PCR specifications and thermocycling programs

Each 12S and trnL PCR was carried out in a total volume of 20 µL using the following reagent mixtures: 10 µL QIAGEN Multiplex PCR Master Mix, 4 µL of forward and reverse primer mix for a final primer concentration of 200 nM, 0.2 µL of bovine serum albumin (BSA), 0.8 µL of water, and 1 µL of DNA template. After 15 minutes of initial denaturation at 95°C, we conducted 40 cycles of 94°C for 30 seconds, 58°C for 90 seconds, 72°C for 90 seconds, and a final extension at 72°C for 10 minutes. Each COI PCR was carried out in a total volume of 20 µL using the following reagent mixtures: 4 µL of GoTaq Flexi Buffer, 1.2 µL of $MgCl_2$, 0.132 µL of GoTaq Polymerase, 0.4 µL of dNTPs, 0.064 µL of BSA, 6.204 µL of water, 4 µL of each primer for a final concentration of 200 nM, and 4 µL of final DNA extract elution. After 2 minutes of initial denaturation at 95°C, we conducted 5 cycles of 94°C for 60 seconds, 45°C for 90 seconds, 72°C for 90 seconds, followed by 40 cycles of 94°C for 60 seconds, 50°C for 90 seconds, 72°C for 60 seconds, and a final extension at 72°C for 7 minutes**.**

Supplemental Text S2.2. Bioinformatics pipeline

1. Pair reads from HiSeq 3000 using PEAR

```
pearrun -f lane8-s001-index-ATCACG-LibA_S1_L008_R1_001.fastq -r lane8-s001-index-
ATCACG-LibA_S1_L008_R2_001.fastq -n 80 -j 12 -o ./PAIRED/SetA.pear.fastq
```

2. demultiplex paired reads and BLAST against NCBI database

```
#!/bin/bash
while read sample lib_index lib f_barcode r_barcode f_primer r_primer locus
do
SampleID=$(echo $sample"_LIB_"$lib"_FBAR_"$f_barcode"_RBAR_"$r_barcode"_LOCUS_"$locus)
        DIR=$(echo "LIB_"$lib)
        [ -d $DIR ] || mkdir $DIR
#Make reverse complements of our primer sets
        f_primer_adj=$(echo $f_primer|sed 's/Y/[CT]/g'|sed 's/W/[AT]/g')
        r_primer_adj=$(echo $r_primer|sed 's/Y/[CT]/g'|sed 's/W/[AT]/g')

        f_search=$f_barcode$f_primer_adj
        rcf_search=$(echo $f_barcode$f_primer_adj|rev|tr ACGT[] TGCA][)
        r_search=$r_barcode$r_primer_adj
        rcr_search=$(echo $r_barcode$r_primer_adj|rev|tr ACGT[] TGCA][)

for i in $2
        do
                grep -oP '(?<='$f_search').*(?='$rcr_search')' $i| sed 's/^/>\n/g' >>
$DIR/$SampleID.fasta
                grep -oP '(?<='$r_search').*(?='$rcf_search')' $i|tr ACGT TGCA| rev | sed
's/^/>\n/g' >> $DIR/$SampleID.fasta

                cat $DIR/$SampleID.fasta | fastx_collapser > $DIR/$SampleID.clust.fasta
if [ "$locus" == "12s" ]
then
        MIDORIDB="/nfs1/FW_HMSC/Levi_Lab/Databases/MIDORIpluslocal_UNIQUE_202006
18_srRNA_SINTAX.fasta"
                VERTMINPROB=0.8
                usearch -threads 1 -sintax $DIR/$SampleID.clust.fasta \
                   -db ${MIDORIDB} -strand plus -sintax_cutoff ${VERTMINPROB} \
                        -tabbedout $DIR/$SampleID.clust.fasta.usearch

                blastn -db /nfs1/FW_HMSC/Levi_Lab/Databases/Marten.Nov2019.Blast.fasta \
                -query $DIR/$SampleID.clust.fasta \
                -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq
sseq" \
                -max_target_seqs 1 -evalue 1e-5 \
                >> $DIR/$SampleID.clust.fasta.assigned

                blastn -db /nfs1/FW_HMSC/Levi_Lab/Databases/nt_12s_eukaryotes \
                -query $DIR/$SampleID.clust.fasta \
                -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq
sseq" \
                -max_target_seqs 1 -evalue 1e-5  \
                >> $DIR/$SampleID.clust.fasta.assigned
```

```
                        awk -F "\t" '$8 > maxvals[$1] {lines[$1]=$0 ; maxvals[$1]=$8}END { for (tag
in lines) print lines[tag] }' $DIR/$SampleID.clust.fasta.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.assigned.bestmatch
elif [ "$locus" == "COI" ]
then
MIDORIDBCOI="/nfs1/FW_HMSC/Levi_Lab/Databases/MIDORI_UNIQUE_20180221_COI_SINTA
X.fasta"
        INVERTMINPROB=0.8
        usearch -threads 1 -sintax $DIR/$SampleID.clust.fasta \
           -db ${MIDORIDBCOI} -strand plus -sintax_cutoff ${INVERTMINPROB} \
              -tabbedout $DIR/$SampleID.clust.fasta.usearch

                        blastn -db /nfs1/FW_HMSC/Levi_Lab/Databases/nt_COI_eukaryotes \
                        -query $DIR/$SampleID.clust.fasta \
                        -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq
sseq" \
                        -max_target_seqs 1 -evalue 1e-5  \
                        >> $DIR/$SampleID.clust.fasta.assigned

                        cat $DIR/$SampleID.clust.fasta.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.assigned.bestmatch

elif [ "$locus" == "ITS" ]
then
ITS="/nfs1/FW_HMSC/Levi_Lab/Databases/sh_general_release_dynamic_s_02.02.2019.fasta"
        ITSMINPROB=0.8
        usearch -threads 1 -sintax $DIR/$SampleID.clust.fasta \
           -db ${ITS} -strand plus -sintax_cutoff ${ITSMINPROB} \
              -tabbedout $DIR/$SampleID.clust.fasta.usearch


                        blastn -db
/nfs1/FW_HMSC/Levi_Lab/Databases/sh_general_release_dynamic_s_02.02.2019.fasta \
                  -query $DIR/$SampleID.clust.fasta \
                  -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq sseq" \
                  -max_target_seqs 1 -evalue 1e-5  \
                  >> $DIR/$SampleID.clust.fasta.assigned

        cat $DIR/$SampleID.clust.fasta.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.assigned.bestmatch

elif [ "$locus" == "trnL" ]
then
                        blastn -db /nfs1/FW_HMSC/Levi_Lab/Databases/trnL_Kwhite.fasta -task
blastn-short \
                        -query $DIR/$SampleID.clust.fasta \
                        -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq
sseq" \
                        -max_target_seqs 1 -evalue 1e-5 \
                        >> $DIR/$SampleID.clust.fasta.ALASKA.assigned
        cat $DIR/$SampleID.clust.fasta.ALASKA.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.ALASKA.assigned.bestmatch


                        blastn -db /nfs1/FW_HMSC/Levi_Lab/Databases/trnLsequences_nospace.fasta -
task blastn-short \
```

```
                        -query $DIR/$SampleID.clust.fasta \
                        -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue bitscore qseq
sseq" \
                        -max_target_seqs 1 -evalue 1e-5 \
                        >> $DIR/$SampleID.clust.fasta.trnLnew.assigned
        cat $DIR/$SampleID.clust.fasta.trnLnew.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.trnLnew.assigned.bestmatch

else
                        blastn -db nt \
                        -query $DIR/$SampleID.clust.fasta \
                        -task blastn -outfmt "6 qseqid sseqid sscinames staxids pident qcovs evalue
bitscore qseq sseq" \
                        -max_target_seqs 1 -evalue 1e-5 \
                        >> $DIR/$SampleID.clust.fasta.assigned

        cat $DIR/$SampleID.clust.fasta.assigned | sort -nk1 >
$DIR/$SampleID.clust.fasta.assigned.bestmatch

fi
          done
done<$1
```

Figure S2.1. Weekly climate values for Lane County, Oregon during 2017 – 2019. (A) Values indicating the percentage of county in drought categories of abnormally dry (D0), moderate drought (D1), severe drought (D2), extreme drought (D3) and exceptional drought (D4). (B) Mean temperature difference (°C) compared to mean monthly temperature calculated from data from 1901 – 2000.

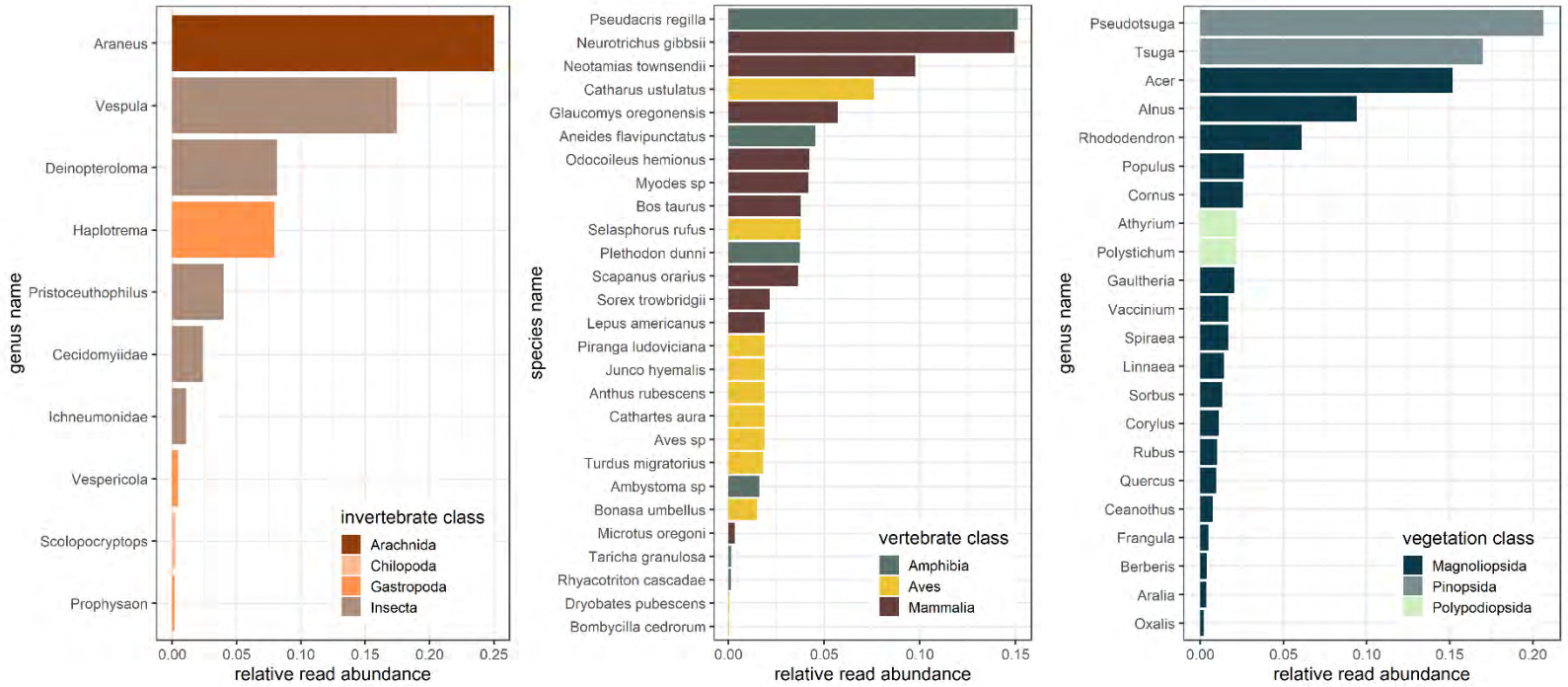


Figure S2.2. Relative read abundances of (A) invertebrates, (B) vertebrates, and (C) plants in western spotted skunks (*Spilogale gracilis*) diets during 2017-2019 in the Willamette National Forest near Blue River, Oregon. Note figure only represents diet items identified through DNA metabarcoding.

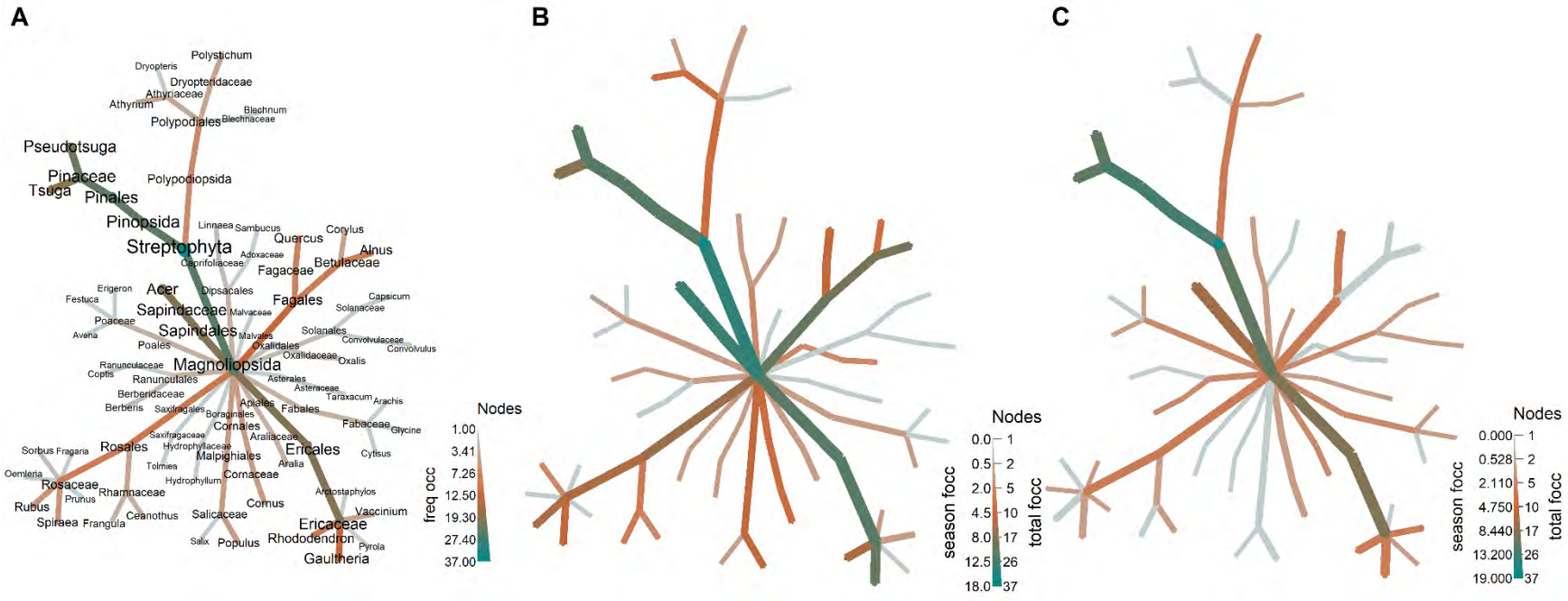


Figure S2.3. Plant diet of western spotted skunks (*Spilogale gracilis*) identified through DNA metabarcoding. (A) Plant identified in all scats collected from 2017-2019 (n = 37), (B) plants identified in scats collected during the dry season (n = 18), and (C) plants identified in scats collected during the wet season (n = 19) in the Willamette National Forest.

Appendix 2. Supplementary materials for chapter 3.

Table S3.1. Relocation counts, home range size, and core area for each western spotted skunk (*Spilogale gracilis*) captured between August 2017 – August 2019 in the Willamette National Forest, Oregon. Values in parentheses represent 95% confidence intervals of home range and core area size.

Animal ID	Sex	Capture Date	Total Length (cm)	Initial mass (g)	Total Locations	Home Range (km^2)	Core Area (km^2)
SG-001_1	M	12-Oct-2017	41.1	550	85	11.83 (9.29 - 14.67)	2.72 (2.14 - 3.37)
SG-001_2	M	10-May-2018	41.1	550	92	10.57 (7.64 - 13.96)	2.05 (1.48 - 2.71)
SG-002	M	12-Oct-2017	42.0	760	21	33.85 (14.95 - 60.33)	9.31 (4.11 - 16.59)
SG-003	M	12-Oct-2017	40.8	475	48	22.92 (16.20 - 30.80)	3.89 (2.75 - 5.23)
SG-004	M	13-Oct-2017	43.5	675	21	12.46 (7.49 - 18.67)	2.59 (1.56 - 3.88)
SG-005	F	14-Oct-2017	38.0	385	58	11.22 (8.45 - 14.37)	2.55 (1.92 - 3.27)
SG-006	M	18-Oct-2017	43.1	615	166	37.13 (31.56 - 43.15)	6.32 (5.37 - 7.34)
SG-007	F	25-Oct-2017	37.0	365	30	18.99 (9.89 - 31.01)	4.89 (2.55 - 7.98)
SG-008	F	09-Feb-2018	39.4	435	139	8.27 (6.91 - 9.74)	1.89 (1.58 - 2.23)
SG-009	F	25-Mar-2018	37.2	325	219	8.73 (7.31 - 10.27)	2.34 (1.96 - 2.76)
SG-010	M	16-Apr-2018	39.3	390	100	12.67 (7.72 - 18.82)	2.22 (1.35 - 3.29)
SG-011	M	18-Apr-2018	43.5	555	114	35.38 (24.93 - 47.63)	7.58 (5.34 - 10.20)
SG-012	M	05-Sep-2018	44.0	585	13	12.96 (5.14 - 24.34)	3.18 (1.26 - 5.98)
SG-013	M	08-Sep-2018	44.3	610	42	27.44 (16.15 - 41.69)	5.51 (3.24 - 8.37)
SG-014	M	16-Sep-2018	43.0	495	31	19.73 (12.10 - 29.21)	4.28 (2.62 - 6.34)
SG-015	F	17-Sep-2018	37.5	385	70	5.55 (4.29 - 6.96)	0.94 (0.72 - 1.17)
SG-016	F	18-Sep-2018	40.3	445	12	29.62 (14.77 - 49.54)	6.04 (3.01 - 10.10)
SG-017	F	27-Sep-2018	39.3	345	31	9.73 (6.30 - 13.91)	1.94 (1.25 - 2.77)
SG-018	F	03-Oct-2018	36.5	445	31	7.51 (4.10 - 11.92)	2.11 (1.15 - 3.35)

SG-019	M	06-Oct-2018	43.9	640	121	23.42 (16.01 - 32.20)	6.01 (4.11 - 8.27)
SG-020	F	10-Oct-2018	40.0	395	40	2.97 (1.96 - 4.18)	0.89 (0.59 - 1.26)
SG-021	M	11-Oct-2018	43.3	545	22	27.56 (17.05 - 40.55)	6.77 (4.19 - 9.96)
SG-022	M	19-Oct-2018	43.0	685	17	20.02 (11.32 - 31.16)	5.16 (2.92 - 8.03)
SG-023	M	23-Apr-2019	47.0	625	5	75.56 (20.58 - 165.61)	19.47 (5.3 - 42.67)
SG-024	M	24-Apr-2019	39.5	555	3	NA	NA
SG-025	M	04-Jul-2019	42.3	685	5	36.18 (9.86 - 79.30)	9.28 (2.53 - 20.34)
SG-026	M	20-Aug-2019	40.3	455	3	NA	NA
SG-027	F	20-Aug-2019	35.7	355	3	NA	NA
SG-028	M	20-Aug-2019	39.1	415	2	NA	NA
SG-029	F	23-Aug-2019	35.4	350	1	NA	NA
SG-030	M	23-Aug-2019	38.5	500	3	NA	NA
SG-031	F	27-Aug-2019	35.7	405	1	NA	NA

Table S3.2. Comparison of hypothesis models from dynamic occupancy analysis of camera trap detections of western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
psi.resource	6	5389.77	0	0.57	0.57	-2688.48
psi.thermal	5	5391.91	2.15	0.19	0.76	-2690.67
psi.disturbance	5	5392.82	3.06	0.12	0.89	-2691.13
psi.predation	5	5393.51	3.74	0.09	0.97	-2691.47
null	4	5396.01	6.24	0.03	1.00	-2693.82

Table S3.3. Coefficients for final dynamic occupancy model of western spotted skunks in the Oregon Cascades during 2017-2019.

Parameter	Variable	Category	β estimate	95% CI	SE
	BAIT	Temporal	-0.09	(-0.12--0.07)	0.01
	SPRING	Temporal	-0.56	(-0.75--0.36)	0.10
	SUMMER	Temporal	-1.03	(-1.22--0.83)	0.10
	2018	Temporal	0.25	(0.09-0.4)	0.08
Detection	2019	Temporal	0.36	(-0.09-0.82)	0.23
	P_MATURE.5KM	Disturbance	0.99	(-0.33-2.3)	0.67
Initial	B4	Resource	-1.23	(-3.57-1.1)	1.19
occupancy	TOPO POS.1KM	Resource	-0.71	(-1.58-0.17)	0.45
	TRI	Predation	0.25	(-0.14-0.64)	0.20
	B6	Resource	-0.69	(-1.2--0.19)	0.26
	SPRING	Temporal	-1.05	(-2.76-0.66)	0.87
	SUMMER	Temporal	1.70	(0.7-2.69)	0.51
Colonization	ABAM	Thermal	-0.53	(-1.16-0.1)	0.32
	LOG(YRSSINCEDIST)	Disturbance	-1.47	(-3.27-0.33)	0.92
	P_MATURE.5KM	Disturbance	-0.40	(-0.8--0.01)	0.20
	YRSSINCEDIST	Disturbance	0.88	(-0.61-2.37)	0.76
	TOPO POS.500M	Resource	0.45	(0.07-0.83)	0.19
	SPRING	Temporal	1.10	(0.25-1.95)	0.43
	SUMMER	Temporal	-0.39	(-1.29-0.52)	0.46
	2018	Temporal	1.04	(0.35-1.72)	0.35
	ABAM	Thermal	0.65	(-0.26-1.55)	0.46
	ELEVATION	Thermal	-5.14	(-8.13--2.15)	1.53
Extinction	ELEVATION^2	Thermal	5.76	(2.48-9.04)	1.67

Table S3.4. Comparison of hypothesis models from home range level resource selection analysis of camera trap detections of western spotted skunks (*Spilogale gracilis*) in the Oregon Cascades.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Disturbance	6	12336.3	0	1	1	-6162.2
Predation	4	12409.4	73.1	< 0.001	1	-6200.7
Resources	8	12434.5	98.2	< 0.001	1	-6209.3
Thermal Tolerance	8	12469.8	133.5	< 0.001	1	-6226.9
null	2	12551.9	215.6	< 0.001	1	-6273.9

Table S3.5. AICc table comparing western spotted skunk resource selection functions including a term for random intercept by individual and random slope for one environmental variable by individual.

model name	model	delta AICc	K
glob.random10	global + (elevation + elevation^2|animal ID)	0	24
glob.random2	global + (p.logged.1km|animal ID)	43.4	21
glob.random7	global + (dist.waterbody|animal ID)	67.4	21
glob.random6	global + (TPI.1km|animal ID)	108.8	21
glob.random13	global + (PSME|animal ID)	117.4	21
glob.random8	global + (snag density|animal ID)	117.9	21
glob.random11	global + (northness|animal ID)	118.3	21
glob.random	global + (TRI|animal ID)	118.6	21
glob.random5	global + (p25|animal ID)	124.0	21
glob.random3	global + (p.mature.0.1km|animal ID)	124.8	21
global	global	130.1	19
glob.random4	global + (dist.road|animal ID)	131.8	21
glob.random14	global + (TSHE|animal ID)	133.0	21
glob.random9	global + (B4|animal ID)	133.5	21
glob.random12	global + (ACMA|animal ID)	133.8	21
null	null	590.8	2

Table S3.6. Coefficients for resource selection model without random slope variable of western spotted skunks in the Oregon Cascades during 2017-2019.

Category	Variable	β Estimate	Std. Error	*P*
	INTERCEPT	-2.81	0.31	< 0.001
Disturbance	DIST.ROAD	-0.15	0.06	0.01
	LOG(DIST.ROAD)	-0.15	0.03	< 0.001
	P_LOGGED.R1000	0.17	0.03	< 0.001
	P_MATURE.R100	-0.02	0.03	0.56
Predation	TRI	-0.22	0.03	< 0.001
	P25	-0.13	0.03	< 0.001
Resource	TPI.1000M	-0.29	0.04	< 0.001
	DIST.STREAM	-0.06	0.05	0.22
	LOG(DIST.STREAM)	0.02	0.05	0.67
	STPH	-0.03	0.03	0.35
	B4	-0.12	0.04	0.01
Thermal	ELEV	-0.004	0.04	0.93
	ELEV^2	-0.01	0.03	0.68
	NORTHNESS	0.28	0.04	< 0.001
	ACMA	-0.08	0.03	0.02
	PSME	0.02	0.03	0.57
	TSHE	0.03	0.03	0.38

Table S3.7. Coefficients for final resource selection function model with random slopes for elevation by individual of western spotted skunks in the Oregon Cascades during 2017-2019.

Category	Variable	β Estimate	Std. Error	*P*
	INTERCEPT	-2.76	0.32	< 0.001
Disturbance	DIST.ROAD	-0.14	0.06	0.01
	LOG(DIST.ROAD)	-0.15	0.03	< 0.001
	P_LOGGED.R1000	0.17	0.04	< 0.001
	P_MATURE.R100	-0.02	0.03	0.62
Predation	TRI	-0.22	0.03	< 0.001
	P25	-0.13	0.03	< 0.001
Resource	TPI.1000M	-0.29	0.04	< 0.001
	DIST.STREAM	-0.10	0.05	0.06
	LOG(DIST.STREAM)	0.02	0.05	0.72
	STPH	-0.03	0.03	0.37
	B4	-0.10	0.04	0.02
Thermal tolerance	ELEV	0.02	0.15	0.87
	ELEV^2	-0.39	0.13	< 0.001
	NORTHNESS	0.30	0.04	< 0.001
	ACMA	-0.06	0.03	0.07
	PSME	0.01	0.03	0.65
	TSHE	0.03	0.03	0.35

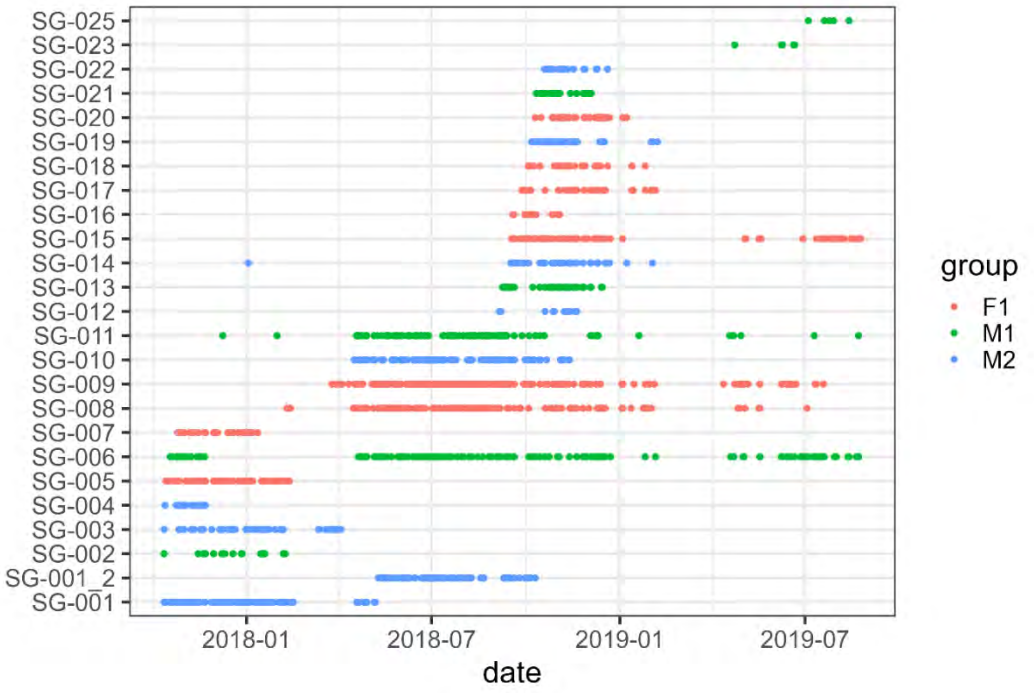


Figure S3.1. Distribution of western spotted skunk (*Spilogale gracilis*) location data by date. Colors indicate home range size group (F1 = small female, M1 = large male, M2 = small male).

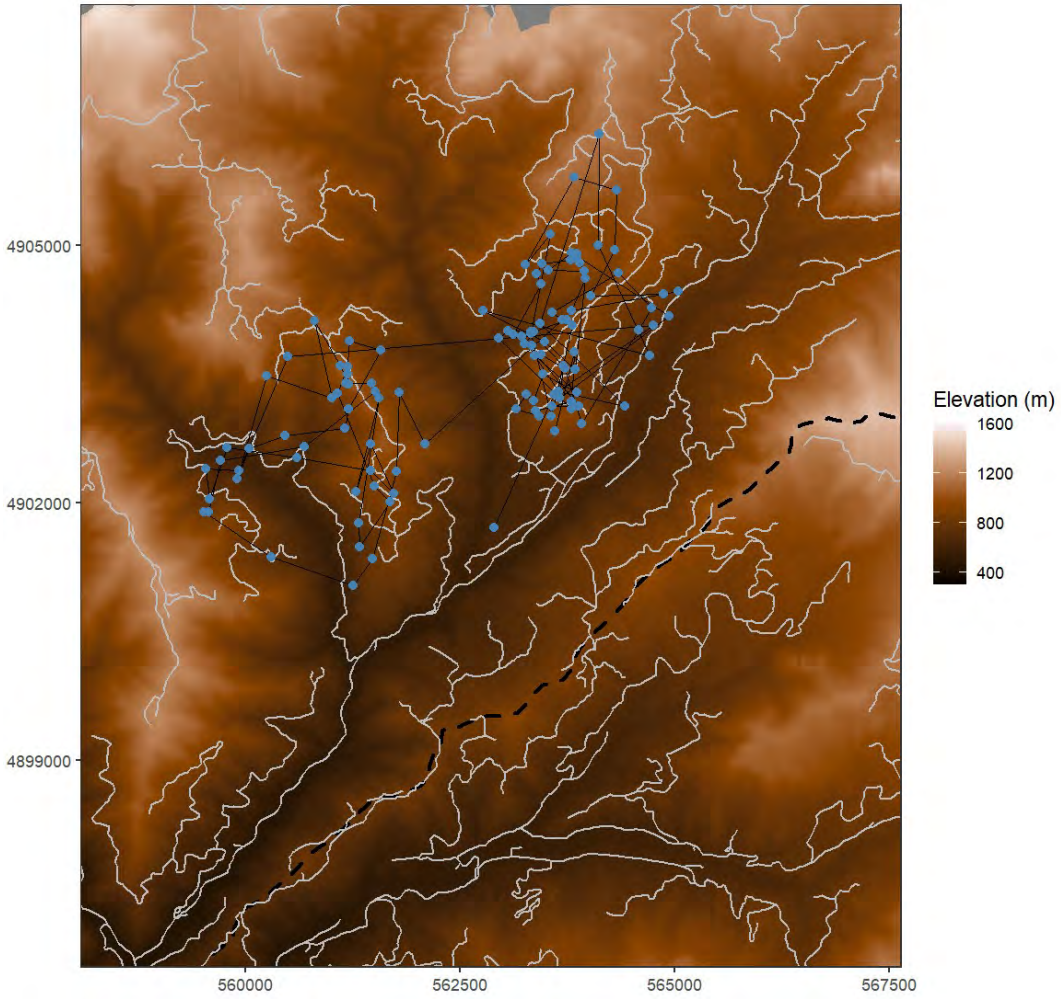


Figure S3.2. Locations of male western spotted skunk (SG-019) fitted with GPS collar programmed to take swift fix locations (blue points). Consecutive GPS locations connected with black line. Dashed line represents boundary of the HJ Andrews Experimental Forest.

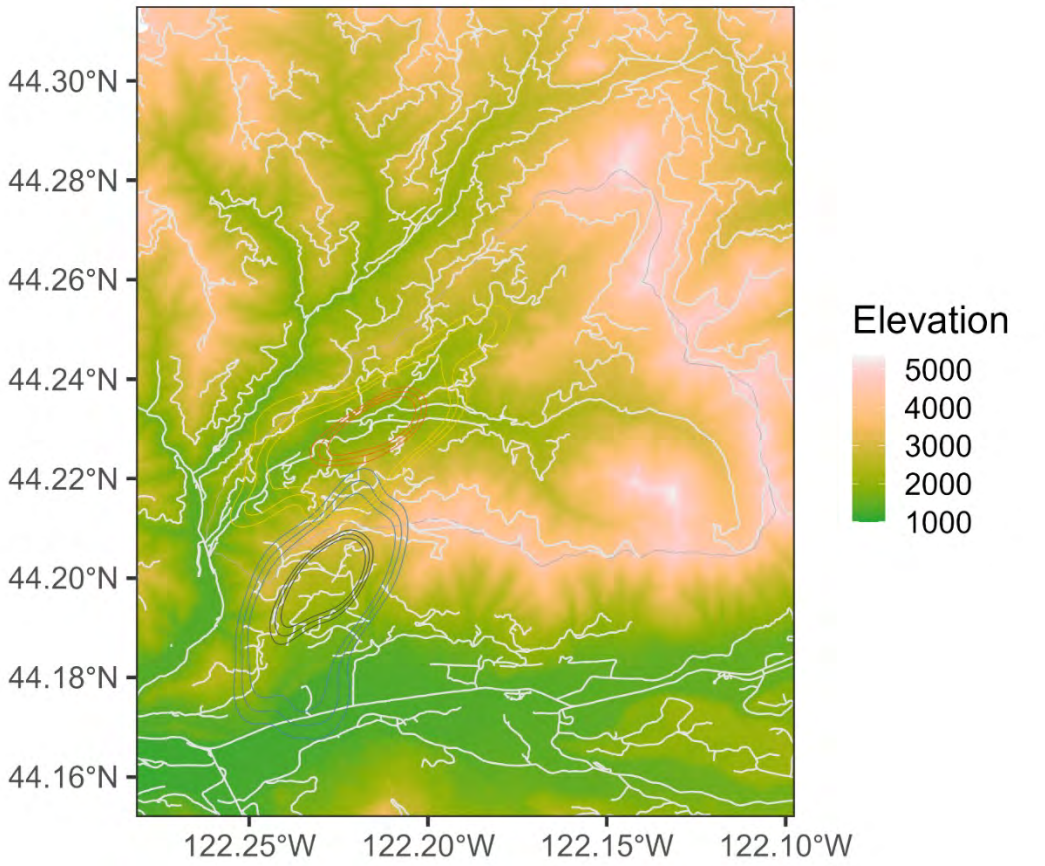


Figure S3.3. Core areas (darker) and 95% isopleth home ranges (lighter) of western spotted skunk (SG-001) before (blue) and after dispersal (orange). Dispersal movement occurred between 07 May 2018 and 10 May 2018.

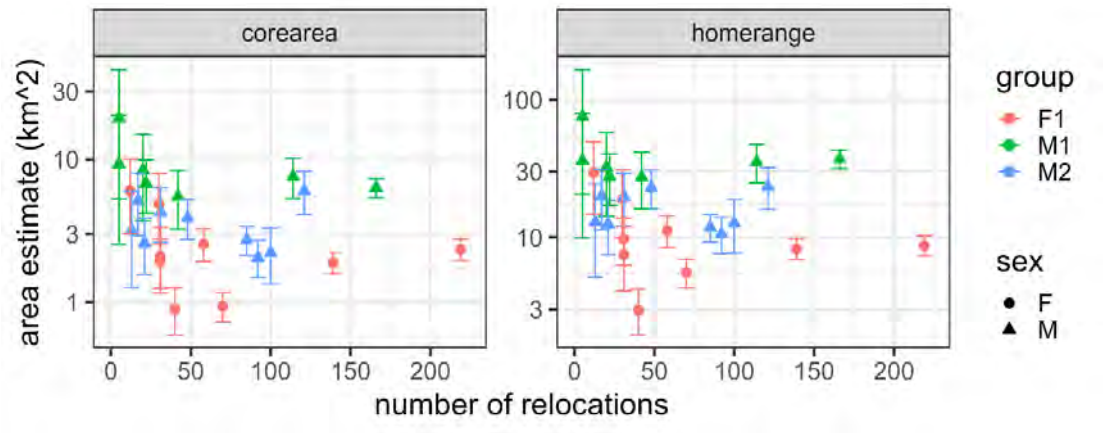


Figure S3.4. Number of locations used to estimate area of core area (50% utilization distribution) and home range (95% utilization distribution) of western spotted skunks in the Willamette National Forest in the Oregon Cascades.

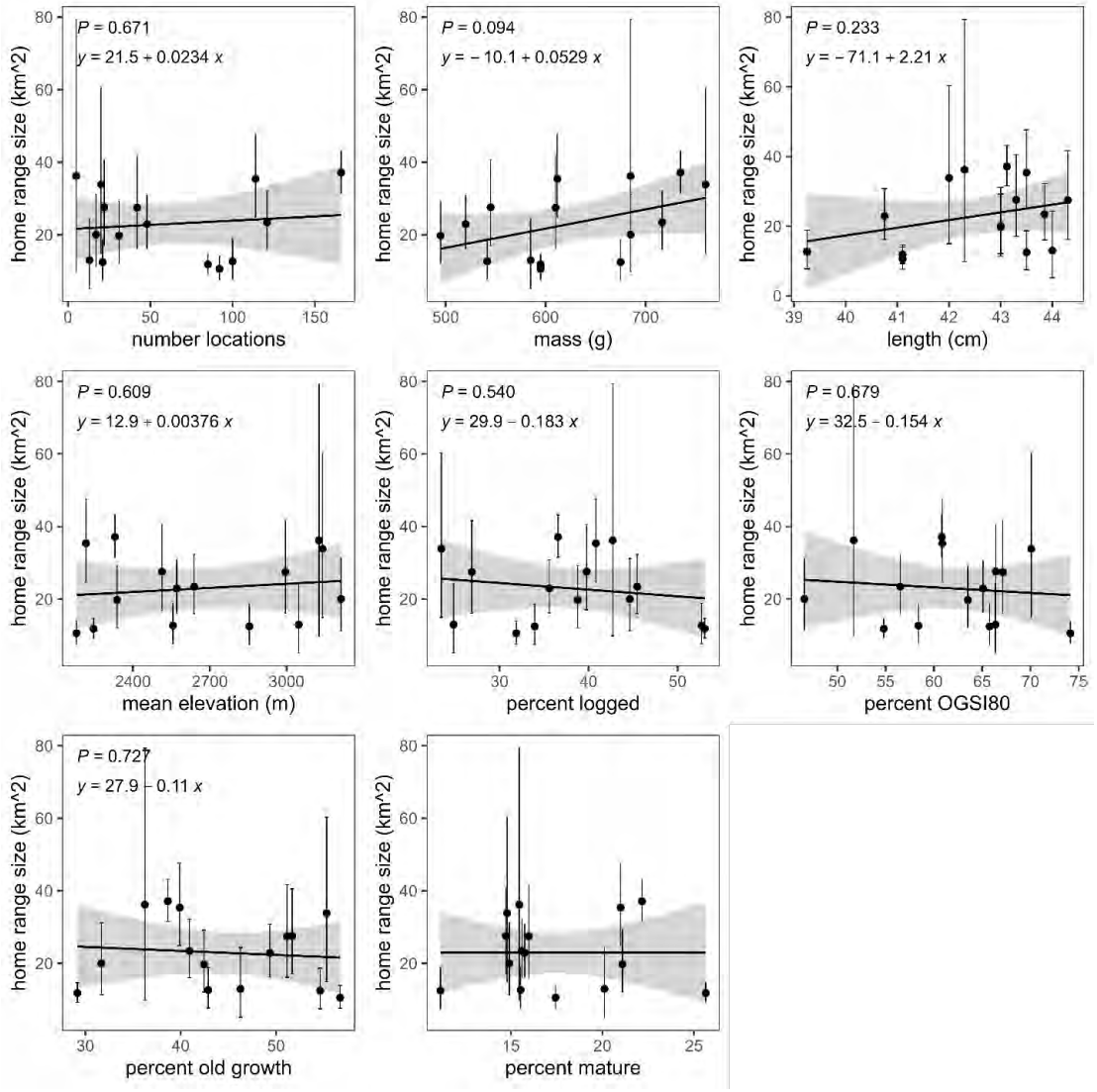


Figure S3.5. Comparison between male western spotted skunk (*Spilogale gracilis*) home range size (km^2) and various individual and environmental factors. Lines and shaded area represent linear regressions and confidence intervals. Equation for linear regression and p-value provided for each variable in each panel.

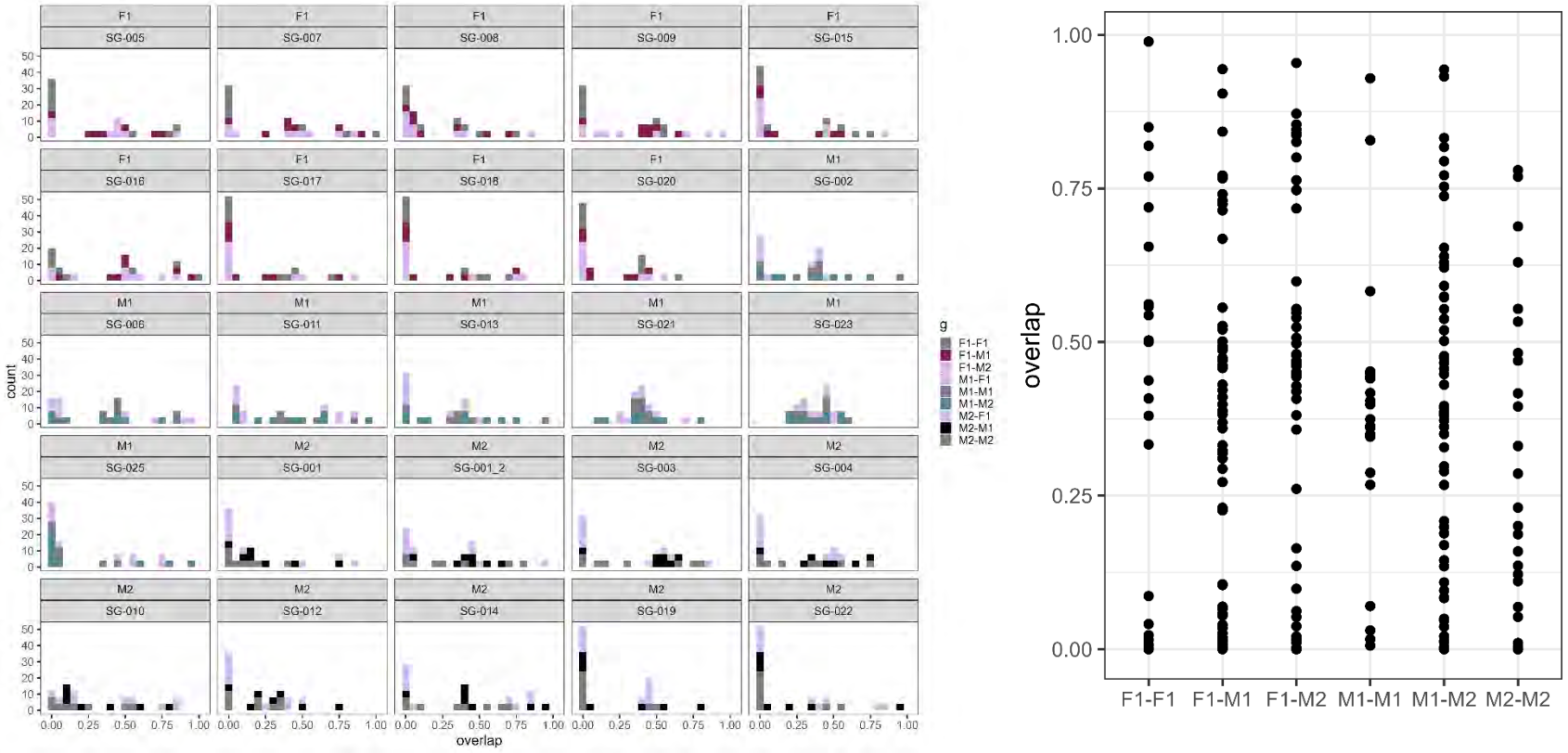


Figure S3.6. Histogram of home range overlap between western spotted skunks and their neighbors. Overlap of 1 indicates complete home range overlap whereas overlap of 0 indicates no home range overlap.

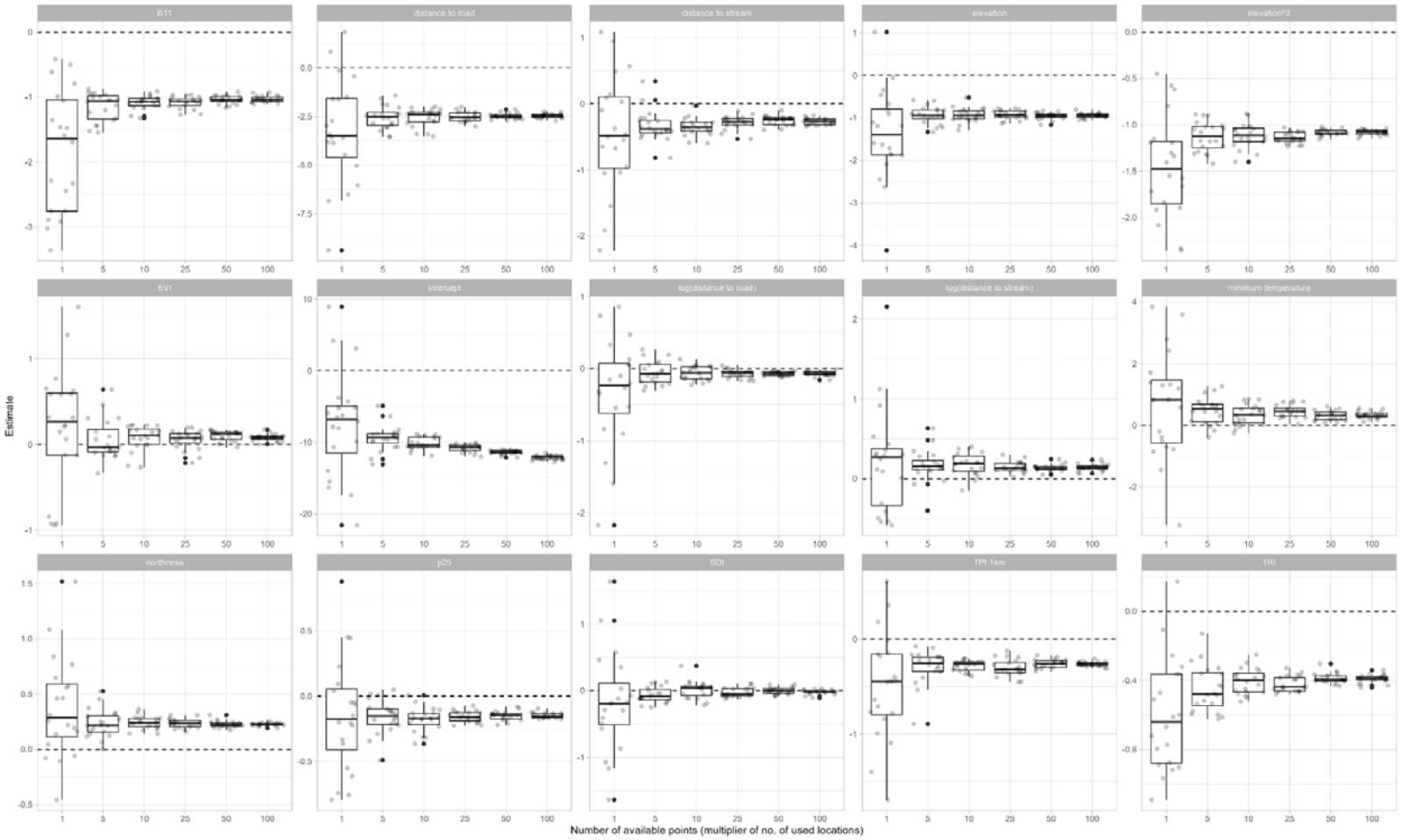


Figure S3.7. Example of exploration of the number of available locations to use for resource selection analysis using the amt package.

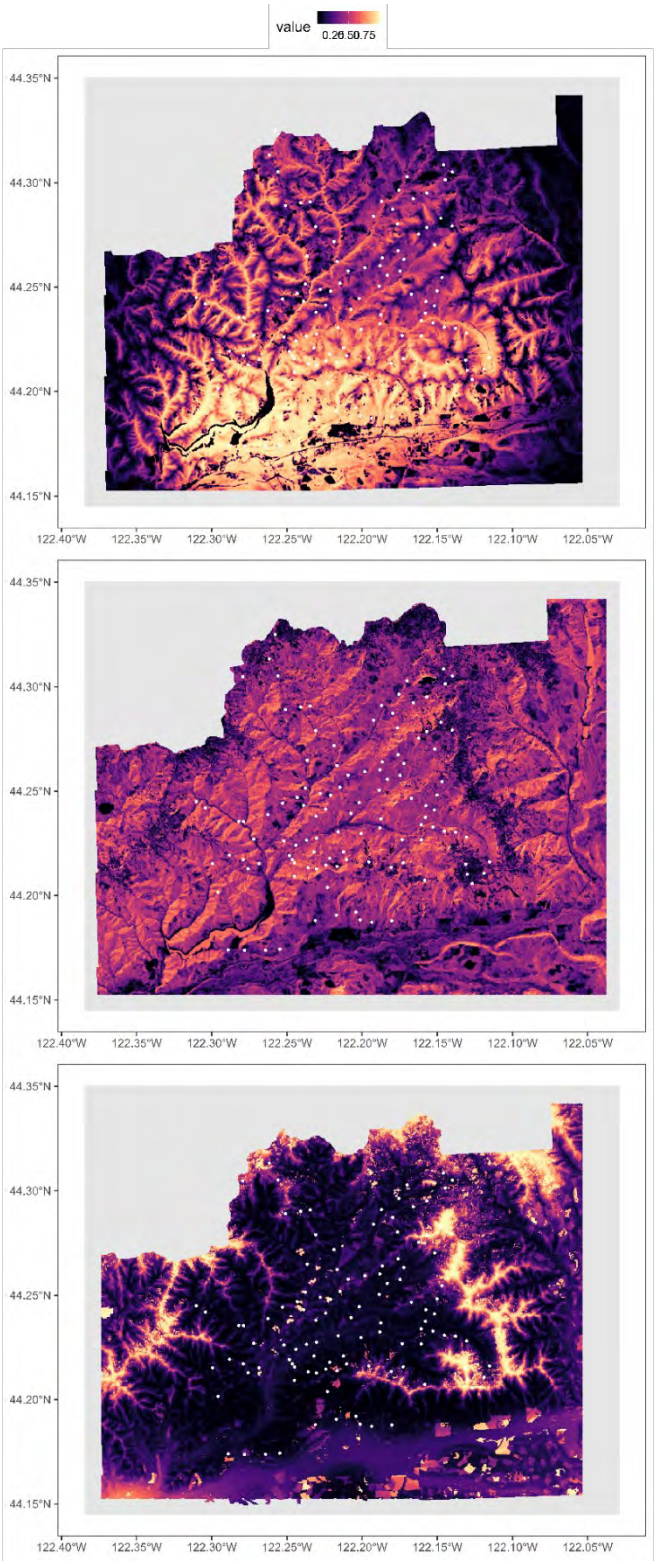


Figure S3.8. Predicted (A) initial occupancy, (B) colonization, and (C) extinction probabilities of western spotted skunks (*Spilogale gracilis*) across the study area in the Oregon Cascades from the final annual occupancy model.

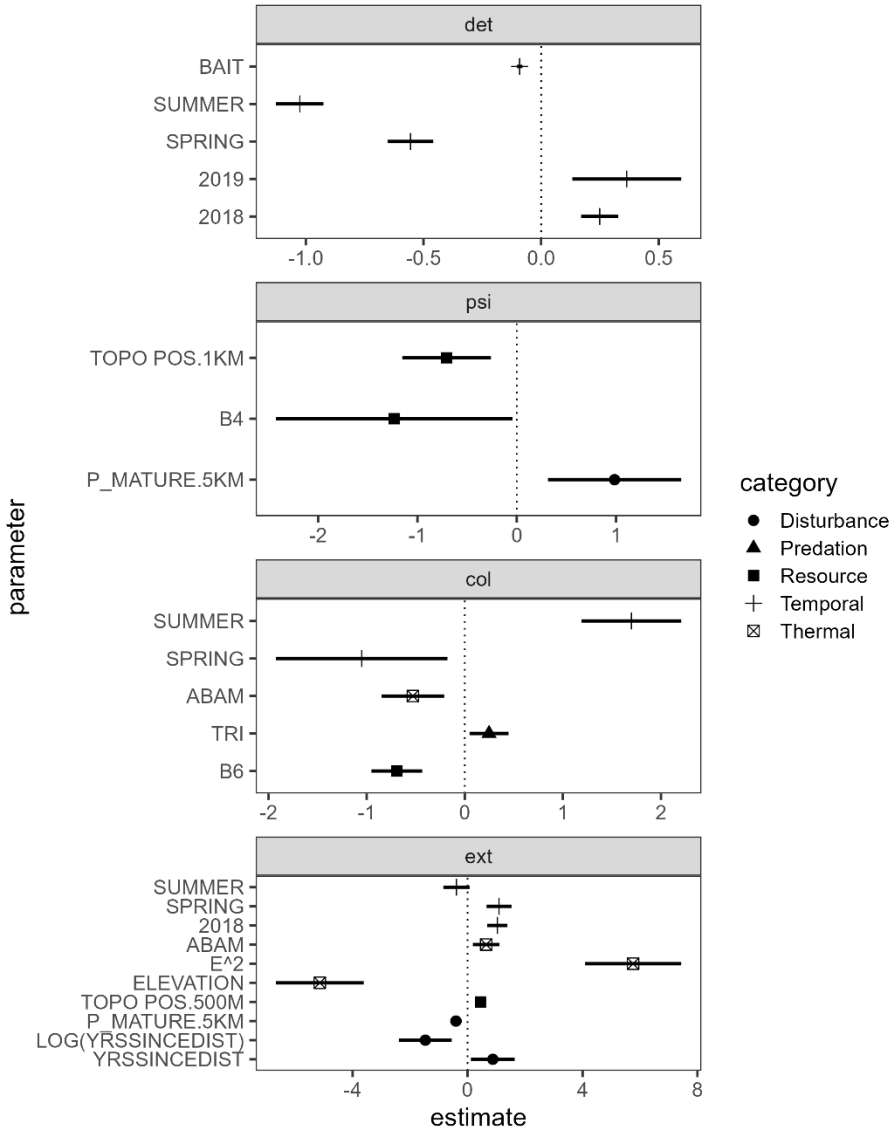


Figure S3.9. Coefficient estimates and standard errors of variables included in global model for multi-season occupancy of western spotted skunks in the Oregon Cascades during 2017-2019.

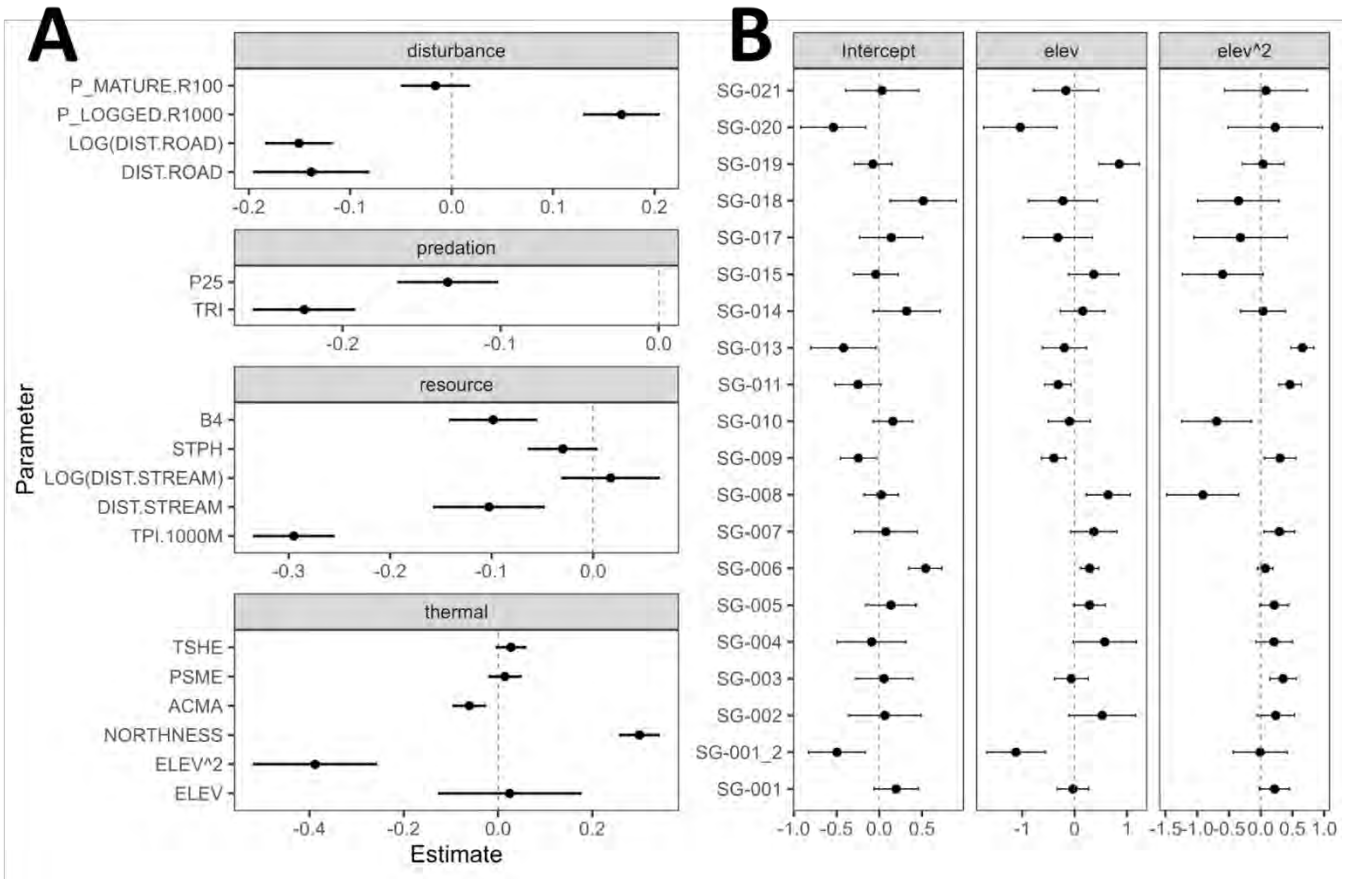


Figure S3.10. Estimates of coefficients for environmental variables included in home range level 2nd order resource selection by western spotted skunks in the Oregon Cascades. A) β-coefficient estimates for fixed effects. B) β-coefficient estimates for random effects (random intercept + random slope).

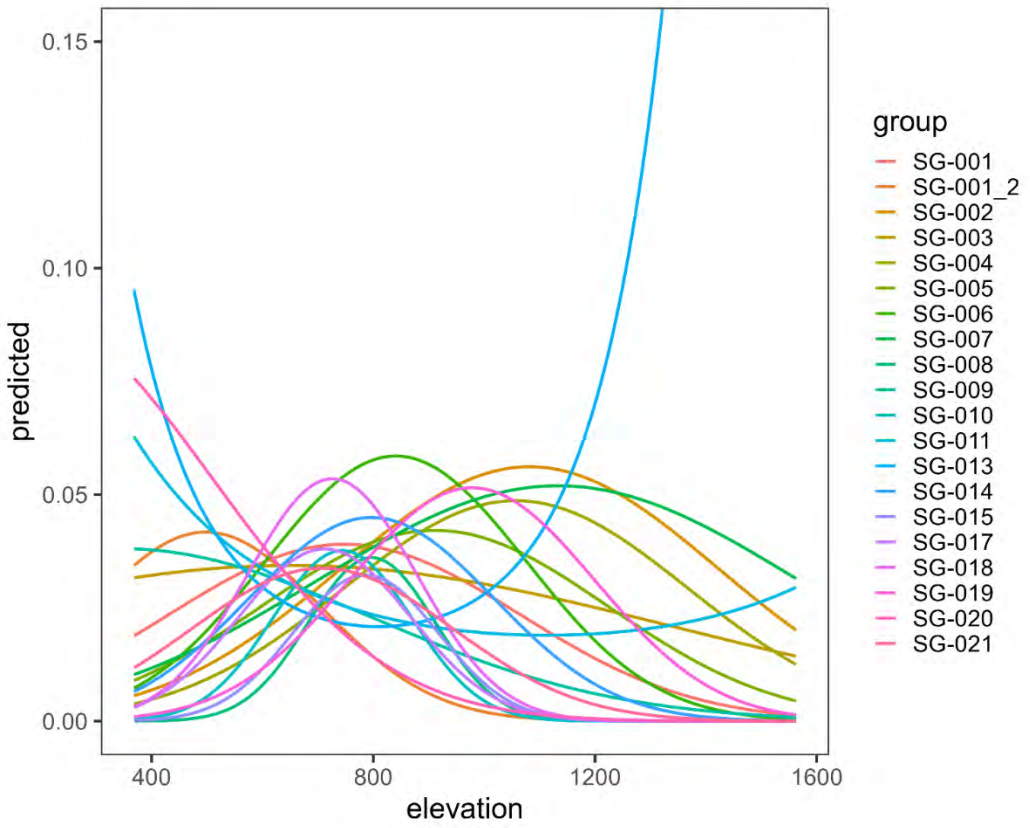


Figure S3.11. Marginal plot of individual responses to elevation from the global resource selection function model for western spotted skunks. Each colored line represents a response by an individual western spotted skunk to elevation.

Appendix 3. Supplementary materials for chapter 4.

Models for marked individual data

Basic Spatial Capture Recapture models (SCR_{sep})

```
cat("
    model
    {
        #uninformative priors
        lam0~dunif(0,5) #
        sigma~dunif(0,100) #smoothing parameter
        psim~dunif(0,1)

        #### model for marked individuals
        for (i in 1:mmax) #individual i
        {
            zm[i] ~ dbern(psim)
            S[i,1] ~ dunif(xlims[1], xlims[2]) #activity center x coord
            S[i,2] ~ dunif(ylims[1], ylims[2]) #activity center y coord

            for(j in 1:J) #location j
            {
                #pythagorian theorem, distance to activity center
                D2[i,j] <- (S[i,1]-X[j,1])^2 + (S[i,2]-X[j,2])^2
                #lambda accounting for distance from activity center
                lam[i,j] <- lam0*exp(-D2[i,j]/(2*sigma^2))
                #model accumulated counts across K occasions for marked individuals
                and add for whether a camera is functioning or not
                y[i,j]~dpois(lam.effm[i,j]*K[j])
                lam.effm[i,j] <- lam[i,j]*zm[i] #lambda accounting for existence of
        individual
            }
        }
        N <- sum(zm[1:mmax])
        D <- N/S.Area*10000 #adjust to density per ha
    }
",fill = TRUE
```

Spatial Capture Recapture models sharing parameters across grids (SCR_{pool})

```
cat("
    model
    {
        #### priors across grids
        lam0~dunif(0,5)
        sigma~dunif(0,100) #smoothing parameter

        for (g in 1:n.sess) #for each grid
        {
            #### priors for each grid
            psim[g]~dunif(0,1)

            #### model for marked individuals
            for (i in 1:mmax) #individual i
            {
                zm[g,i] ~ dbern(psim[g])
                S[g,i,1] ~ dunif(xlims[1], xlims[2]) #activity center x coord
                S[g,i,2] ~ dunif(ylims[1], ylims[2]) #activity center y coord

                for(j in 1:J) #location j
                {
                    D2[g,i,j] <- (S[g,i,1]-X[j,1])^2 + (S[g,i,2]-X[j,2])^2 #pythagorian
                    theorem, distance to activity center
                    lam[g,i,j] <- lam0*exp(-D2[g,i,j]/(2*sigma^2)) #lambda
                    accounting for distance from activity center
                    y[g,i,j]~dpois(lam.effm[g,i,j]*K[g,j])  #model accumulated counts
                    across K occasions for marked individuals and add for whether a
                    camera is functioning or not
                    lam.effm[g,i,j] <- lam[g,i,j]*zm[g,i] #lambda accounting for
                    existence of individual
                }
            }
        }

        for (g in 1:n.sess)
        {
            N[g] <- sum(zm[g,1:mmax])
            D[g] <- N[g]/S.Area*10000
        }
    }
    ", fill = TRUE, file="SCR_multigrid.txt")
```

Multi-Strata Spatial Capture Recapture models with grid as random effect (SCR_{random})

```
cat("
    model
    {
    #### priors across grids
    #use log normal so all values are positive
    #mean sigma across all grids on log scale
    mu.log.sigma ~ dnorm(log(40), 1/(log(100)^2))
    allgrids.mu.sigma <- exp(mu.log.sigma) #put on real scale
    sd.log.sigma ~ dunif(0,100) # sd of sigma on log scale
    tau.log.sigma <- pow(sd.log.sigma,-2) # precision of sigma on log scale

    # mean lam0 across all grids on log scale (here, mean=0.1, sd=0.1 on real scale)
    mu.log.lam0 ~ dnorm(log(0.1), 1/(log(0.1)^2))
    allgrids.mu.lam <- exp(mu.log.lam0) #put on real scale
    sd.log.lam0 ~ dunif(0,5) # sd of lam0 on log scale
    tau.log.lam0 <- pow(sd.log.lam0,-2) # precision of lam0 on log scale

    for (g in 1:n.sess) #for each grid
    {
        #### priors for each grid
        log(sigma[g]) <- log.sigma[g] # take log sigma, note: now you cannot provide
        initial values for sigma
        log.sigma[g] ~ dnorm(mu.log.sigma, tau.log.sigma) # random effect on sigma
        for each grid
        log(lam0[g]) <- log.lam0[g] # take log lam0, note: now you cannot provide
        initial values for lam0
        log.lam0[g] ~ dnorm(mu.log.lam0, tau.log.lam0) #random effect on lam0 for
        each grid

        psim[g]~dunif(0,1)

        #### model for marked individuals
        for (i in 1:mmax) #individual i
        {
            zm[g,i] ~ dbern(psim[g])
            S[g,i,1] ~ dunif(xlims[1], xlims[2]) #activity center x coord
            S[g,i,2] ~ dunif(ylims[1], ylims[2]) #activity center y coord

            for(j in 1:J) #location j
            {
                D2[g,i,j] <- (S[g,i,1]-X[j,1])^2 + (S[g,i,2]-X[j,2])^2 #pythagorian
                theorem, distance to activity center
                lam[g,i,j] <- lam0[g]*exp(-D2[g,i,j]/(2*sigma[g]^2)) #lambda
                accounting for distance from activity center
```

```
                y[g,i,j] ~ dpois(lam.effm[g,i,j]*K[g,j])  #model accumulated counts
                across K for marked individuals and add for whether a camera is
                functioning or not
                lam.effm[g,i,j] <- lam[g,i,j]*zm[g,i] #lambda accounting for existence
                of individual
            }
        }
    }

    for (g in 1:n.sess)
    {
        N[g] <- sum(zm[g,1:mmax])
        D[g] <- N[g]/S.Area*10000
    }
}
", fill = TRUE, file="SCR_multigrid_randomeffect.txt")
```

Models for unmarked data

Base N-mixture model (N_{base})

```
model
{
	for (i in 1:Nsites) #for each site
	{
		N[i]~dpois(lambda) #state model

		#likelihood
		for (j in 1:Nreps)
		{
			y[i,j]~dbinom(p,N[i]) #observation model
		}
	}

	#priors
	#p~dbeta(1,1)
	p~dunif(0,1) #uniform
	lambda~dgamma(0.001,0.001) #underlying density

	sumN <- sum(N[])/Nsites #calculate average
}
```

N-mixture model with different detection rate by trap location ($N_{pstation}$)

```
model
{
	for (i in 1:Nsites) #for each site
	{
		p[i]~dunif(0,1)
		N[i]~dpois(lambda) #state model

		#likelihood
		for (j in 1:Nreps)
		{
			y[i,j]~dbinom(p[i], N[i]) #observation model
		}
	}

	#priors
	lambda~dgamma(0.001,0.001)
	sumN <- sum(N[])/Nsites #calculate average
}
```

N-mixture model with heterogeneity in detection by trap location and decay in detection over occasions (N_{pdecay})

```
model
{
        for (i in 1:Nsites) #for each site
        {
                det[i]~dunif(0,1)
                N[i]~dpois(lambda) #state model

                #likelihood
                for (j in 1:Nreps) #for each obs
                {
                        p[i,j] <- det[i]*exp(d0*(j-1))
                        y[i,j]~dbinom(p[i,j], N[i])
                }
        }
        #priors
        d0~dunif(-10,0)
        lambda~dgamma(0.001,0.001)
        sumN <- sum(N[])/Nsites #calculate average, derived parameters
}
```

Spatial count models (SC)

```
cat("
    model
    {
        #uninformative priors
        lam0~dunif(0,5)
        sigma~dunif(0,100)
        psi~dunif(0,1)

        #informative priors
        lam0~dgamma(", pars[pars$sp == sp.cr & pars$g == g,]$lam0,",",
pars[pars$sp == sp.cr & pars$g == g,]$lamsd,")
        sigma~dgamma(",pars[pars$sp == sp.cr & pars$g ==
g,]$sigma,",",pars[pars$sp == sp.cr & pars$g == g,]$ssd,")

        ####model for unmarked individuals
        for (i in 1:M)
        {
            z[i]~dbern(psi)
            Su[i,1]~dunif(xlims[1], xlims[2])
            Su[i,2]~dunif(ylims[1], ylims[2])
            for(j in 1:J)
            {
                D2u[i,j] <- (Su[i,1]-X[j,1])^2 + (Su[i,2]-X[j,2])^2
                lamu[i,j] <- lam0*exp(-D2u[i,j]/(2*sigma^2)) * z[i] * K[j]
                yu[i,j]~dpois(lam.eff[i,j])
                #add in whether camera was funtioning or not
                lam.eff[i,j]<-lamu[i,j]*z[i] #*Eff[j,k]
            }
        }

        for (j in 1:J)
        {
            bigLambda[j] <- sum(lam.eff[,j])
            n[j] ~ dpois(bigLambda[j])
        }

        N <- sum(z[1:M])
        D <- N/S.Area*10000
    } #end model description
",fill = TRUE, sep="")
```

Table S4.1. Number of days Sherman and Tomahawk traps were operational for capture-mark-recapture on each site.

Site	Sherman Traps	Tomahawk Traps
1	4	8
2	4	8
3	4	8
4	4	4
5	4	8
6	0	6
7	4	8
8	3	7
9	2	4

Table S4.2. Density estimates (D; individuals/ha) and 95% confidence intervals or credible intervals derived from capture-recapture data of deer mice, Townsend's chipmunk, and Humboldt's flying squirrel. Minimum known number alive (MNKA) and Huggins model estimates converted from abundance to density using a buffer size of 1 mean maximum distance moved (MMDM).

Species	Site	MNKA	Huggins	SCR_{sep}	SCR_{pool}	SCR_{random}
	1	11.29	16.03 (13.13 - 23.51)	15.49 (10.74 - 24.48)	19.11 (12.54 - 27.08)	17.52 (11.34 - 25.88)
	2	32.80	43.51 (36.67 - 58.11)	53.24 (40.83 - 67.45)	50.80 (42.41 - 65.90)	52.75 (41.41 - 70.67)
	3	21.51	29.77 (24.86 - 40.86)	35.16 (26.62 - 45.39)	34.02 (26.68 - 45.39)	34.26 (27.08 - 47.78)
	4	10.76	15.27 (12.48 - 22.54)	12.15 (7.20 - 20.25)	17.51 (12.14 - 26.08)	13.12 (9.16 - 23.09)
	5	22.59	32.06 (26.83 - 43.74)	33.47 (24.30 - 41.48)	35.26 (27.67 - 47.58)	30.89 (24.49 - 43.20)
	6	NA	NA	NA	NA	NA
	7	22.59	32.06 (26.83 - 43.74)	36.44 (27.05 - 47.11)	35.41 (27.87 - 47.58)	38.24 (27.87 - 50.77)
	8	36.57	38.93 (32.73 - 52.37)	59.78 (45.97 - 78.91)	49.20 (40.02 - 65.10)	62.84 (44.79 - 87.80)
Deer mouse	9	30.11	NA	41.15 (28.64 - 84.52)	32.38 (24.69 - 49.97)	49.38 (29.86 - 95.96)
	1	1.55	1.48 (1.41 - 1.77)	1.99 (1.67 - 2.84)	2.09 (1.51 - 2.82)	2.24 (1.59 - 3.01)
	2	2.94	3.02 (2.90 - 3.39)	3.53 (2.92 - 4.37)	3.87 (3.14 - 4.88)	3.75 (2.93 - 4.65)
	3	3.10	3.19 (3.06 - 3.57)	3.84 (3.20 - 4.67)	3.94 (3.35 - 5.11)	3.88 (3.22 - 5.11)
	4	3.42	2.28 (1.99 - 2.88)	2.23 (1.71 - 2.94)	2.72 (2.01 - 3.71)	2.24 (1.78 - 3.37)
	5	4.43	4.56 (4.39 - 4.99)	5.87 (4.91 - 7.01)	5.78 (4.88 - 7.01)	6.09 (5.02 - 7.32)
	6	1.35	1.57 (1.28 - 2.21)	1.45 (1.06 - 2.46)	1.51 (0.98 - 2.09)	1.68 (1.07 - 2.47)
	7	4.54	4.79 (4.61 - 5.23)	5.69 (4.62 - 6.60)	6.16 (5.04 - 7.28)	5.54 (4.81 - 6.99)
Townsend's	8	6.47	6.16 (5.88 - 6.74)	8.32 (7.13 - 9.67)	7.80 (6.62 - 9.19)	8.59 (7.26 - 10.24)
chipmunk	9	10.68	7.14 (6.47 - 8.20)	8.08 (6.97 - 9.62)	8.71 (7.16 - 10.30)	8.30 (7.12 - 10.36)
	1	1.44	1.49 (1.45 - 1.72)	2.33 (1.86 - 3.71)	2.33 (1.66 - 3.24)	2.38 (1.74 - 3.51)
	2	1.59	1.65 (1.60 - 1.89)	2.38 (1.89 - 3.50)	2.54 (1.88 - 3.49)	2.72 (1.84 - 3.51)
Humboldt's	3	2.00	2.07 (2.02 - 2.34)	3.09 (2.29 - 4.01)	3.12 (2.42 - 4.17)	3.02 (2.36 - 4.28)
flying	4	1.13	0.63 (0.54 - 0.96)	1.03 (0.56 - 2.04)	1.22 (0.72 - 2.20)	1.14 (0.68 - 2.18)
squirrel	5	1.03	1.06 (1.03 - 1.27)	1.57 (1.10 - 2.40)	1.68 (1.09 - 2.43)	1.68 (1.09 - 2.42)

6	1.85	1.86 (1.58 - 2.47)	2.74 (1.77 - 3.91)	2.38 (1.77 - 3.53)	2.59 (1.79 - 3.79)
7	1.23	1.28 (1.24 - 1.50)	1.73 (1.18 - 2.39)	1.91 (1.38 - 2.83)	1.63 (1.29 - 2.61)
8	1.70	1.57 (1.51 - 1.85)	2.3 (1.68 - 3.40)	2.49 (1.81 - 3.44)	2.42 (1.75 - 3.47)
9	1.03	0.63 (0.54 - 0.96)	0.93 (0.56 - 2.38)	1.04 (0.68 - 2.04)	1.15 (0.66 - 2.20)

Table S4.3. Amount of overlap between grid-specific density curves (area under the curve =1) created from posterior distributions of abundance estimates from the multi-strata spatial capture-recapture models (SCR_{random}) of (A) deer mice (*Peromyscus maniculatus*), (B) Townsend's chipmunk (*Neotamias townsendii*), and (C) Humboldt's flying squirrel (*Glaucomys oregonensis*). Sites where overlap ≤ 0.05 are bolded to indicate distinct densities of animals.

A.

Site	1	2	3	4	5	6	7	8
2	**0.00**							
3	**0.04**	0.17						
4	0.79	**0.00**	**0.02**					
5	0.07	0.08	0.75	**0.04**				
6	-	-	-	-	-			
7	**0.03**	0.22	0.91	**0.02**	0.66	-		
8	**0.00**	0.56	0.07	**0.00**	**0.03**	-	0.10	
9	**0.02**	0.70	0.37	**0.02**	0.26	-	0.43	0.52

B.

Site	1	2	3	4	5	6	7	8
2	0.07							
3	0.04	0.74						
4	0.75	0.15	0.08					
5	**0.00**	**0.02**	**0.05**	**0.00**				
6	0.42	**0.01**	**0.00**	0.27	**0.00**			
7	**0.00**	**0.04**	0.09	**0.00**	0.78	**0.00**		
8	**0.00**	**0.00**	**0.00**	**0.00**	**0.05**	**0.00**	**0.02**	
9	**0.00**	**0.00**	**0.00**	**0.00**	0.07	**0.00**	**0.03**	0.95

C.

Site	1	2	3	4	5	6	7	8
2	0.90							
3	0.45	0.53						
4	0.13	0.10	**0.03**					
5	0.31	0.24	0.07	0.54				
6	0.85	0.93	0.59	0.11	0.24			
7	0.41	0.33	0.10	0.42	0.84	0.32		
8	0.96	0.92	0.46	0.13	0.29	0.86	0.39	
9	0.13	0.10	**0.03**	0.97	0.51	0.10	0.39	0.12

Table S4.4. Density estimates (D; individuals/ha) and 95% credible intervals derived from capture-recapture (CR) data using unmarked models (spatial count [SC]) for deer mice, Townsend's chipmunk, and Humboldt's flying squirrel. Only models that converged are reported.

Species	Site	$SC_{CR,noinfo,separate}$	$SC_{CR,info,separate}$	$SC_{CR,noinfo,pool}$	$SC_{CR,info,pool}$
Deer mouse	1				123.90 (87.96 - 193.48)
	2				
	3		627.72 (432.90 - 675.73)		
	4				107.45 (72.20 - 159.44)
	5				
	6	NA	NA	NA	NA
	7				
	8		698.12 (500.71 - 698.26)		355.83 (245.61 - 356.86)
	9				
Townsend's chipmunk	1	0.92 (0.66 - 3.77)	59.34 (55.39 - 59.78)	1.53 (0.86 - 2.55)	7.90 (5.99 - 10.29)
	2		53.17 (48.90 - 53.18)	3.13 (2.24 - 5.23)	15.81 (13.34 - 20.24)
	3		55.35 (52.31 - 55.35)	3.51 (2.41 - 5.78)	18.04 (15.50 - 23.27)
	4	0.35 (0.17 - 2.73)		2.09 (1.34 - 3.58)	12.47 (9.06 - 16.40)
	5		53.90 (50.43 - 53.91)	3.86 (2.68 - 6.39)	
	6			0.85 (0.44 - 1.67)	4.84 (3.24 - 6.61)
	7		48.18 (45.68 - 48.21)	4.61 (3.21 - 7.35)	26.06 (21.44 - 26.34)
	8		59.54 (56.86 - 59.57)	5.38 (3.72 - 8.39)	26.42 (24.17 - 26.43)
	9			5.24 (3.95 - 8.51)	26.42 (24.21 - 26.41)
Humboldt's flying squirrel	1		62.87 (55.20 - 62.91)		
	2	0.09 (0.06 - 2.24)			26.41 (20.96 - 26.46)
	3		60.07 (55.75 - 60.37)		26.11 (22.41 - 26.50)
	4		55.89 (47.59 - 55.88)		
	5	0.07 (0.07 - 11.57)	48.93 (42.44 - 48.99)		

6		24.68 (19.49 - 26.16)
7		
8	48.96 (45.60 - 49.04)	
9		13.37 (8.53 - 22.73)

Table S4.5. Density estimates (D; individuals/ha) and standard deviations, 95% confidence intervals, or 95% credible intervals derived from camera-trap data using unmarked models for deer mice, Townsend's chipmunk, and Humboldt's flying squirrel.

Species	Site	Average Detections Per Camera (t = 1 day 1)	N-mixture (P_{decay}, t = 15)	Space-to-event (t = 60)	Time-to-event (t = 1440)	$SC_{cam,info,pool}$ (t = 1)
Deer mouse	1	4.42 ± 6.86	15.80 (10.93 - 22.32)	28.06 (21.90 - 35.96)	33.22 (29.20 - 37.79)	60.59 (46.34 - 77.61)
	2	29.60 ± 44.26	22.13 (16.90 - 29.77)	28.89 (22.63 - 36.88)	46.76 (41.19 - 53.09)	202.73 (169.29 - 217.88)
	3	14.83 ± 20.67	33.27 (24.20 - 45.68)	32.29 (25.35 - 41.13)	45.69 (40.77 - 51.21)	-
	4	11.68 ± 15.15	22.18 (16.19 - 30.66)	33.6 (26.42 - 42.73)	42.26 (38.01 - 46.98)	132.78 (110.80 - 156.69)
	5	35.96 ± 41.36	20.54 (16.00 - 26.87)	33.99 (26.63 - 43.39)	103.83 (93.50 - 115.31)	224.97 (211.59 - 224.97)
	6	13.88 ± 15.03	15.36 (11.30 - 21.29)	28.23 (22.08 - 36.10)	43.77 (39.03 - 49.10)	99.25 (81.67 - 121.94)
	7	16.20 ± 16.52	25.67 (18.96 - 35.75)	25.4 (19.70 - 32.74)	71.47 (63.69 - 80.19)	-
	8	115.60 ± 64.35	28.72 (21.37 - 38.67)	37.84 (29.76 - 48.11)	88.19 (79.07 - 98.36)	224.75 (219.24 - 224.97)
Townsend's chipmunk	1	10.33 ± 18.39	0.82 (0.67 - 0.99)	12.03 (8.77 - 16.50)	7.96 (6.65 - 9.52)	10.16 (8.50 - 12.42)
	2	25.55 ± 21.59	1.22 (1.04 - 1.43)	23.46 (17.90 - 30.75)	9.35 (8.01 - 10.92)	13.94 (12.30 - 17.06)
	3	17.62 ± 17.65	0.88 (0.72 - 1.07)	18.52 (13.94 - 24.62)	10.14 (8.71 - 11.81)	13.14 (11.41 - 16.39)
	4	13.48 ± 18.28	0.54 (0.44 - 0.66)	12.14 (8.88 - 16.58)	7.82 (6.56 - 9.32)	9.73 (7.85 - 11.70)
	5	32.13 ± 31.43	1.40 (1.17 - 1.66)	81.07 (62.17 - 105.72)	15.16 (13.47 - 17.05)	18.19 (17.21 - 18.21)
	6	13.12 ± 19.00	0.41 (0.33 - 0.49)	9.86 (7.06 - 13.77)	6.39 (4.94 - 8.25)	7.87 (6.34 - 10.44)
	7	23.02 ± 15.30	3.41 (2.76 - 4.19)	31.26 (23.59 - 41.42)	16.82 (14.54 - 19.44)	18.21 (17.85 - 18.21)
	8	55.05 ± 30.85	1.64 (1.38 - 1.95)	34.05 (26.18 - 44.30)	8.67 (7.68 - 9.79)	18.2 (17.28 - 18.21)
Humboldt's flying squirrel	1	8.48 ± 15.09	0.36 (0.29 - 0.44)	7.95 (5.77 - 10.95)	5.54 (4.26 - 7.21)	18.2 (17.27 - 18.21)
	2	5.85 ± 12.21	0.25 (0.19 - 0.31)	5.58 (3.87 - 8.05)	5.1 (3.63 - 7.16)	18.02 (14.35 - 18.16)
	3	9.38 ± 13.49	0.32 (0.26 - 0.40)	11.96 (8.98 - 15.95)	6.06 (5.08 - 7.24)	18.21 (17.53 - 18.21)
	4	3.50 ± 7.51	0.35 (0.28 - 0.44)	6.4 (4.49 - 9.13)	5.76 (4.62 - 7.19)	-
	5	5.52 ± 11.79	0.24 (0.19 - 0.30)	8.67 (6.35 - 11.85)	8.37 (6.56 - 10.68)	17.31 (14.21 - 18.02)

	6	2.05 ± 6.35	0.13 (0.10 - 0.17)	6.57 (4.63 - 9.32)	6.87 (5.35 - 8.82)	12.06 (10.16 - 15.84)
	7	2.00 ± 5.11	0.12 (0.09 - 0.16)	4.07 (2.69 - 6.15)	11.75 (8.70 - 15.87)	10.63 (8.17 - 12.66)
	8	5.87 ± 12.98	0.21 (0.17 - 0.27)	10.24 (7.55 - 13.88)	7.7 (6.31 - 9.39)	15.61 (13.05 - 17.51)

Table S4.6. Species detected by live-capture and camera trapping at the H. J. Andrews Experimental Forest, Blue River, Oregon during the fall of 2017.

Species	Scientific name	Camera trapping	Live-capture
Shrew	*Sorex spp.*	X	
Deer mouse	*Peromyscus maniculatus*	X	X
Pacific jumping mouse	*Zapus trinotatus*	X	X
Townsend's chipmunk	*Neotamias townsendii*	X	X
Humboldt's flying squirrel	*Glaucomys oregonensis*	X	X
Douglas squirrel	*Tamiasciurus douglasii*	X	X
Hare	*Lepus spp.*	X	
Vole	*Microtus spp.*, *Clethrionomys californicus*	X	X
American pika	*Ochotona princeps*	(X)	X
California ground squirrel	*Otospermophilus beecheyi*	(X)	X
Coast mole	*Scapanus orarius*		X
Bushy-tailed woodrat	*Neotoma cinerea*	X	X
Short-tailed weasel	*Mustela erminea*	X	X
Long-tailed weasel	*Mustela frenata*	X	X
Western spotted skunk	*Spilogale gracilis*	X	X
Bobcat	*Lynx rufus*	(X)	
Black bear	*Ursus americanus*	(X)	
Varied Thrush	*Ixoreus naevius*	X	
Steller's Jay	*Cyanocitta stelleri*	X	X
Gray Jay	*Perisoreus canadensis*		X

(X) - could identify, but did not have any

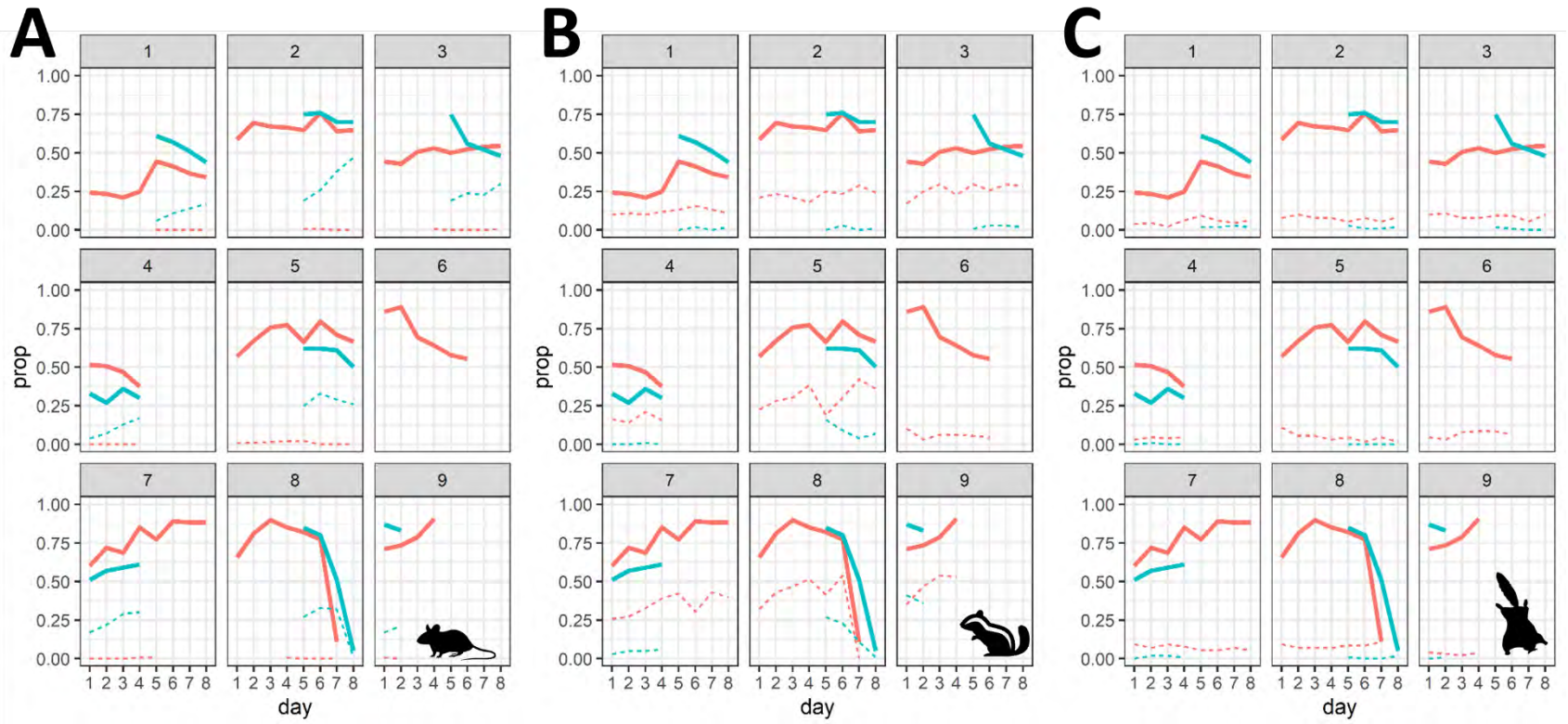


Figure S4.1. Percentage of Tomahawk traps (pink lines) and Sherman trap (blue lines) closed by grid number during each trap night for any reason (solid lines) in comparison to percentage of traps filled due to capture of each species (dashed lines): (A) deer mice, (B) Townsend's chipmunks, and (C) Humboldt's flying squirrels.

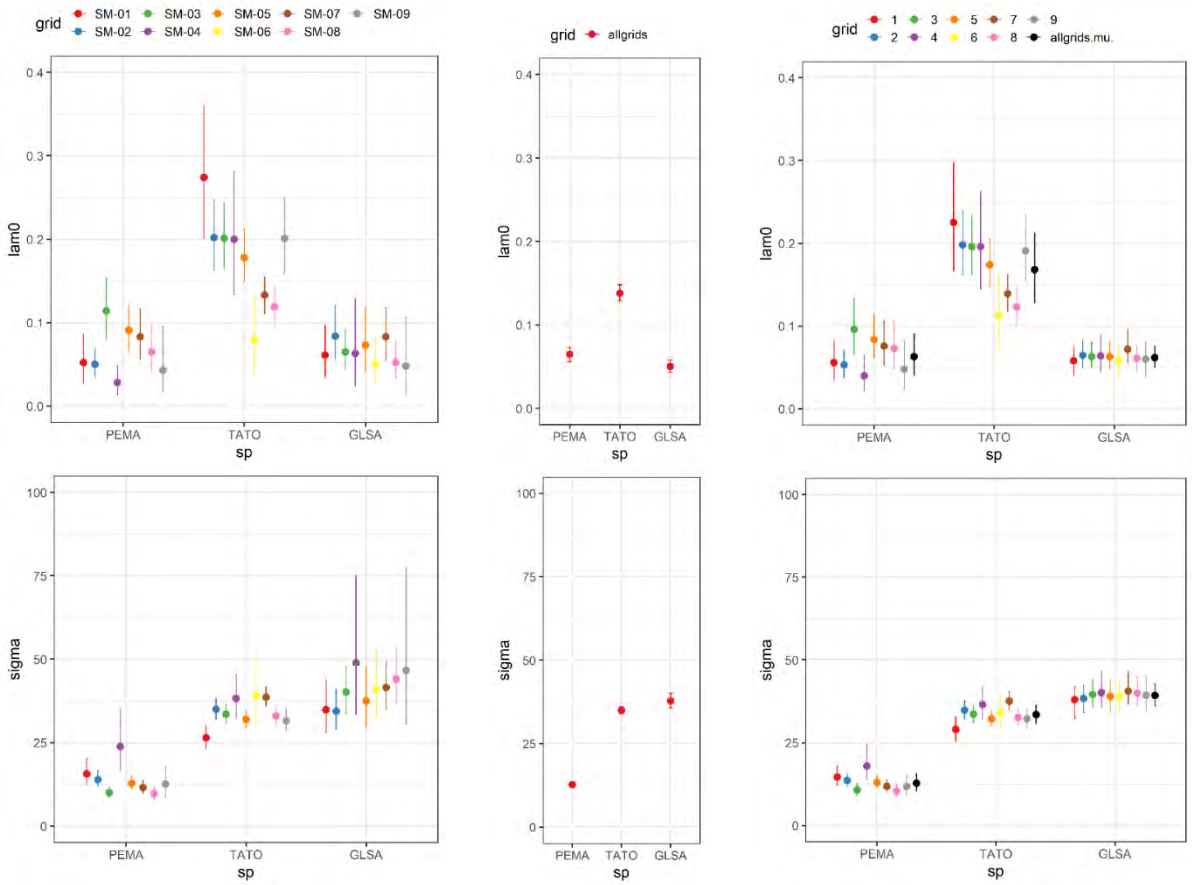
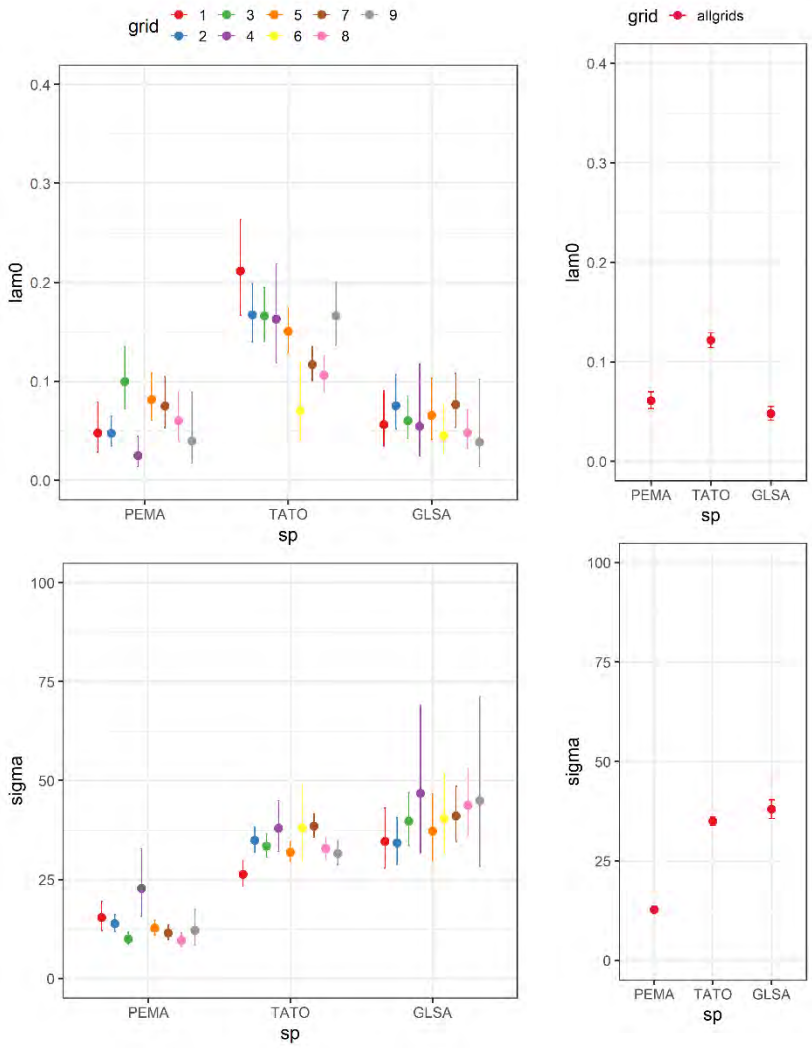


Figure S4.2. Lambda$_0$ (lam0) and sigma estimates for spatial capture recapture (SCR) models in a Bayesian framework when modeling each grid separately (SCR$_{sep}$; left column), modeling all grids together sharing parameters λ_0 and σ across grids (SCR$_{pool}$; middle column), and modelling all grids together with a random effect of grid (SCR$_{random}$; right column). SCR density estimates calculated for 3 species: deer mice (PEMA), Townsend's chipmunks (TATO), and Humboldt's flying squirrel (GLSA).



Separate grids Pooled grids

Figure S4.3. Lambda$_0$ (lam0) and sigma estimates for spatial capture (SCR) models applied to capture-recapture data in a maximum likelihood framework when modeling each grid separately (oSCR; left column) and modeling all grids together sharing parameters λ_0 and σ across grids (oSCR$_{pool}$; right column).

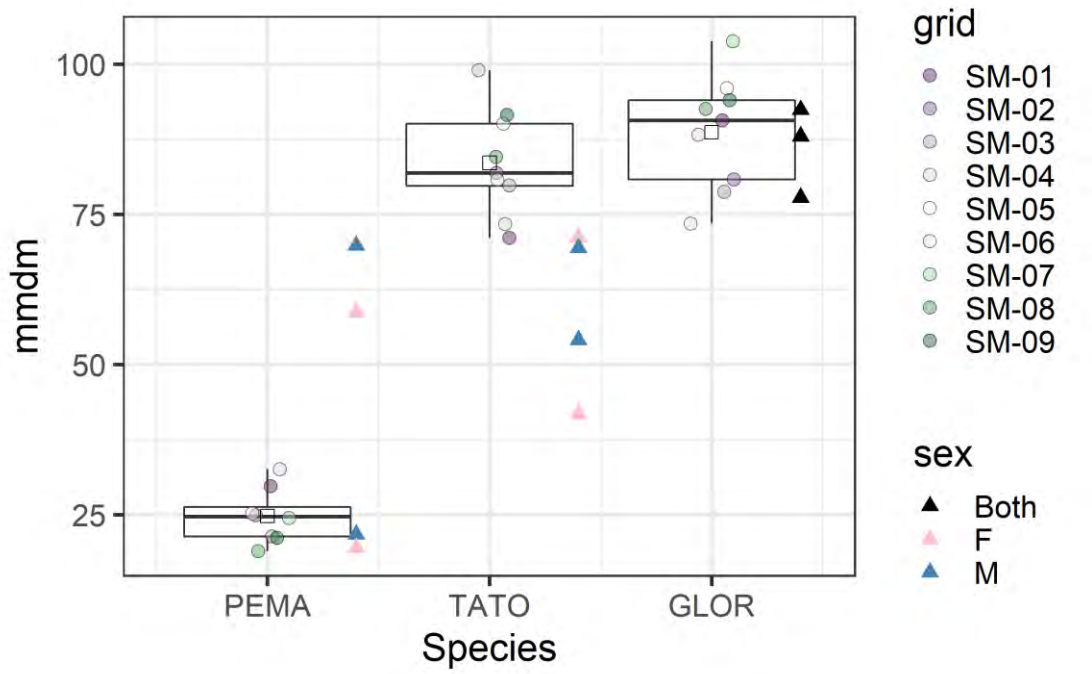


Figure S4.4. Mean maximum distance moved (MMDM) estimated per grid and mean of MMDM for all grids from the live capture-recapture data for deer mouse (PEMA), Townsend's chipmunk (TATO), and Humboldt's flying squirrel (GLOR). Triangles represent estimates from the peer-reviewed literature black for male and female, blue for male, and pink for female specific estimates. PEMA estimates from Feldhammer 1979 and Larson 2002, TATO estimates from Hayes et al. 1995 and Larson 2002, GLOR estimates from Rosenberg and Anthony 1991 and Rosenberg et al. 2003.

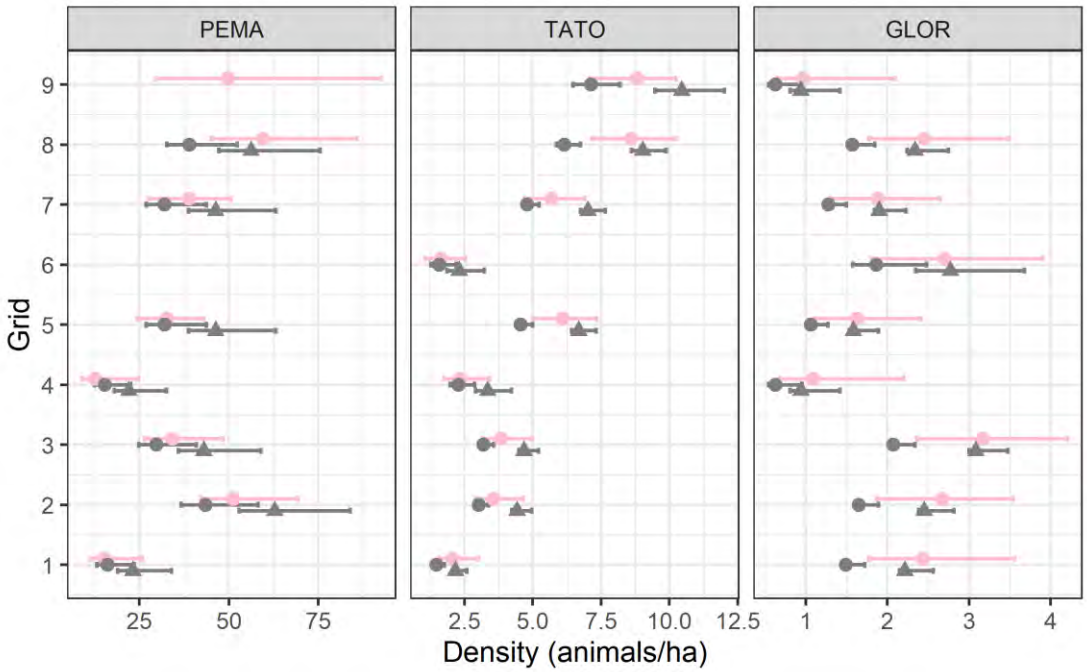


Figure S4.5. Density estimates of deer mouse (PEMA), Townsend's chipmunk (TATO), and Humboldt's flying squirrel (GLOR) estimated from capture-recapture data at each grid using hierarchical spatial capture-recapture (SCR_{random}; pink circle) and Huggins closed capture models (grey). Density estimates for Huggins models were calculated using a buffer size equal to mean maximum distance moved (MMDM; grey circle) and ½ MMDM (grey triangle). Error bars for SCR_{random} represent 95% credible intervals, error bars on Huggins estimates represent 95% confidence intervals.

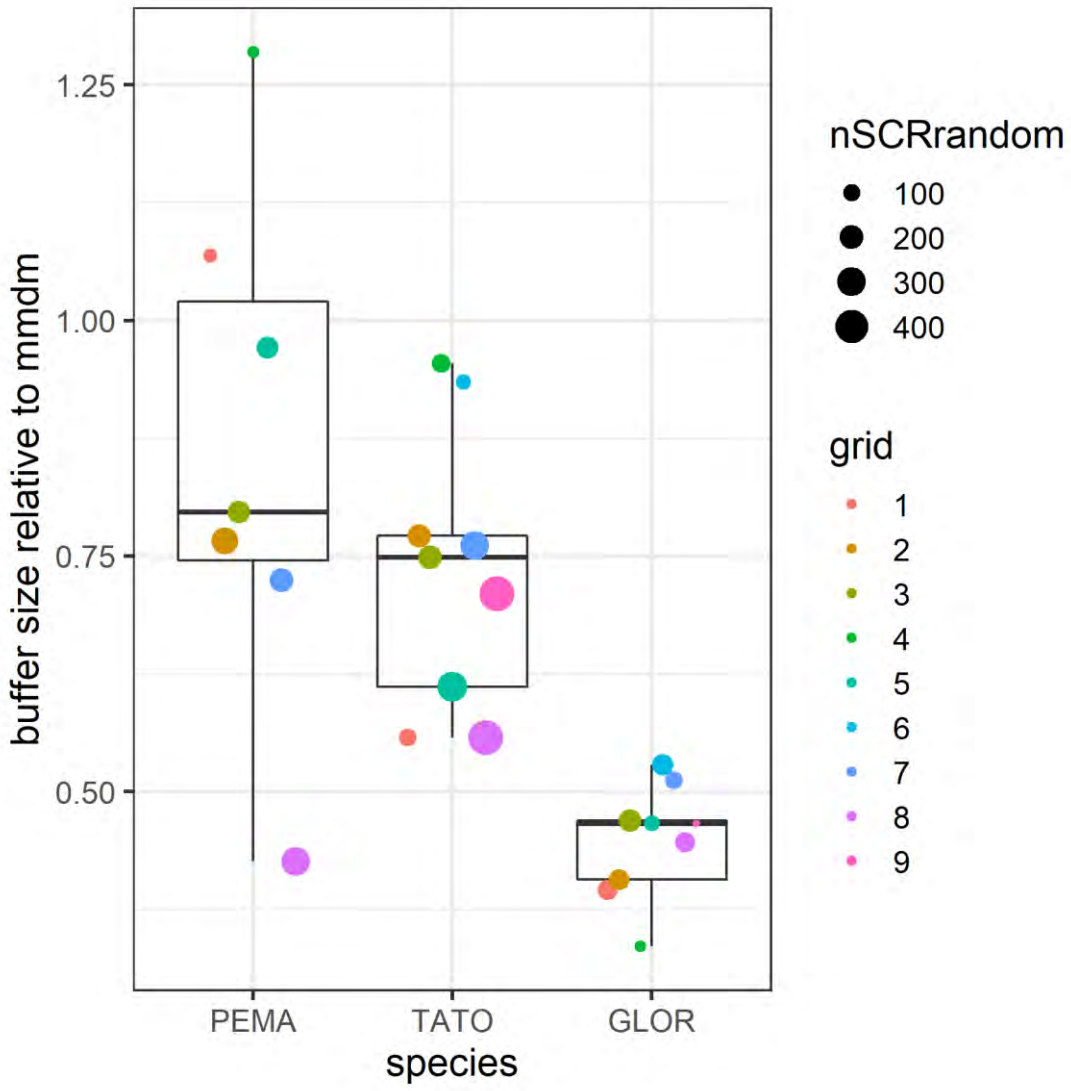


Figure S4.6. Buffer sizes relative to mean maximum distance moved (MMDM) of each species in order for Huggins model abundance estimates (Huggins) to yield the same densities as those derived from the hierarchical spatial capture-recapture models (SCR_{random}). Typically, MMDM or ½ MMDM is used to calculate densities from non-spatially explicit models.

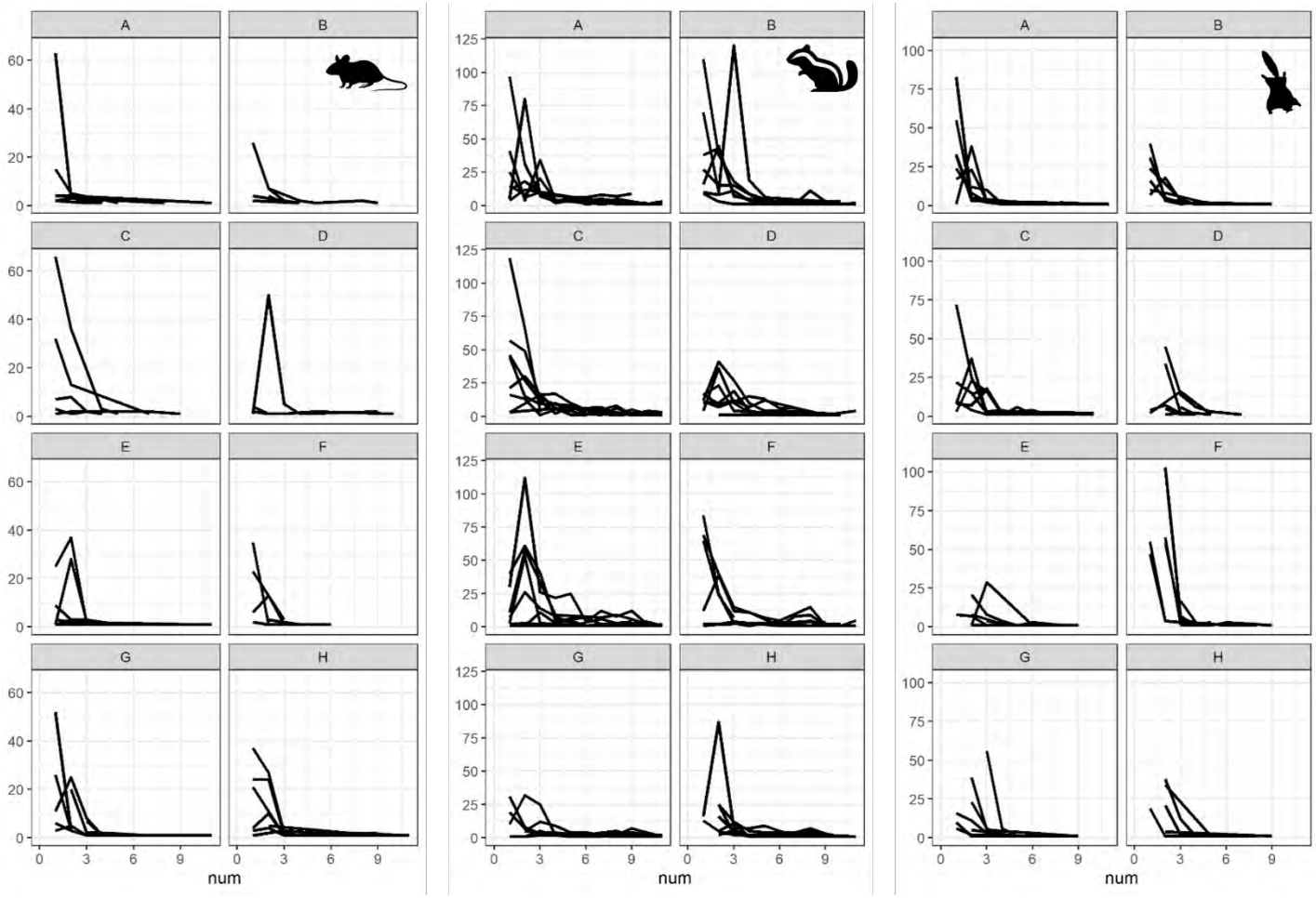


Figure S4.7. Example of reduction in detections over time at a site of (A) deer mice, (B) Townsend's chipmunk, and (C) Humboldt's flying squirrel on trail cameras by day or night number. Note that the number of detections were particularly high during the first 3 days following camera deployment due to the presence of bait.

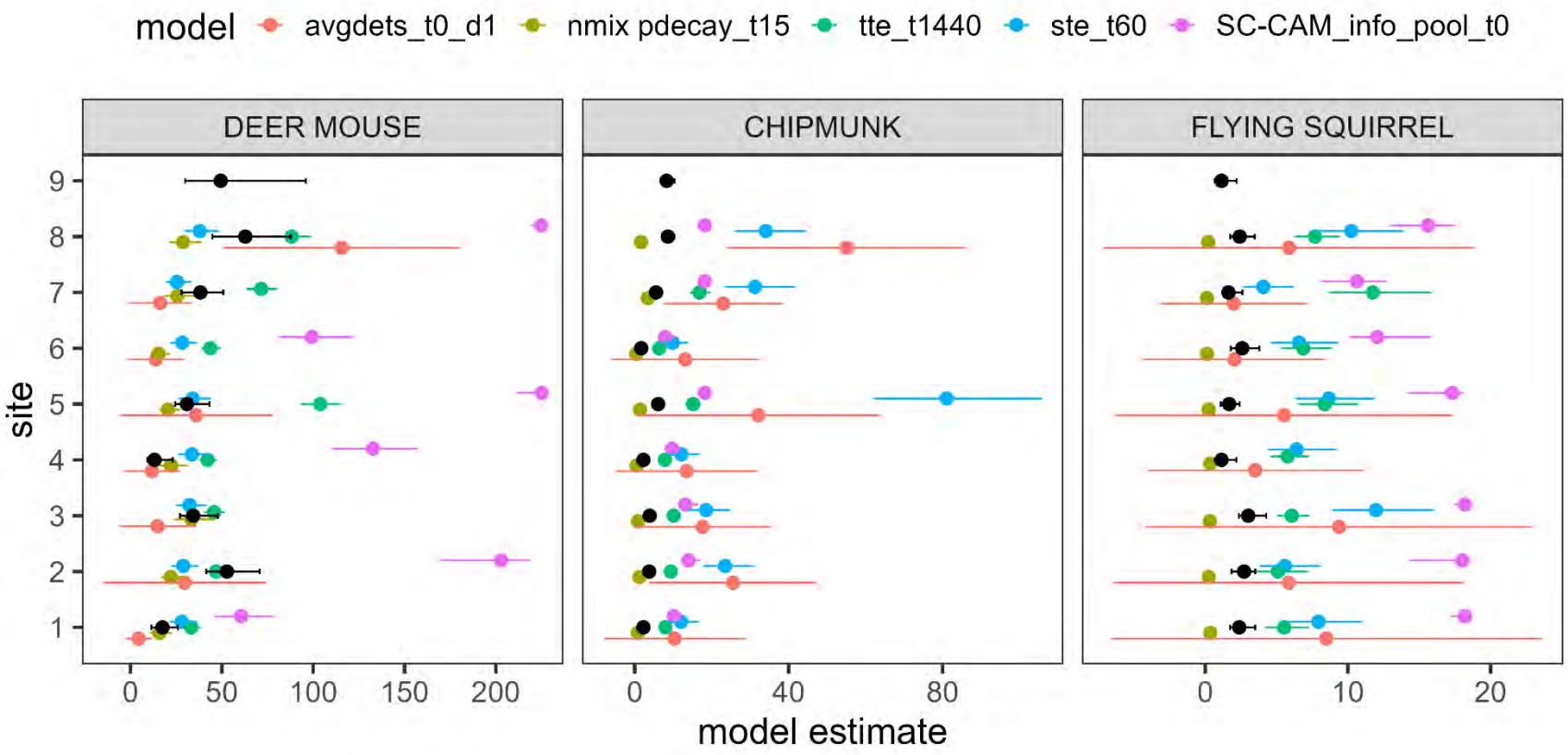


Figure S4.8. Estimates from unmarked methods compared to SCR density estimates from capture-recapture data (black circles).

Appendix 4. Supplementary material for chapter 5.

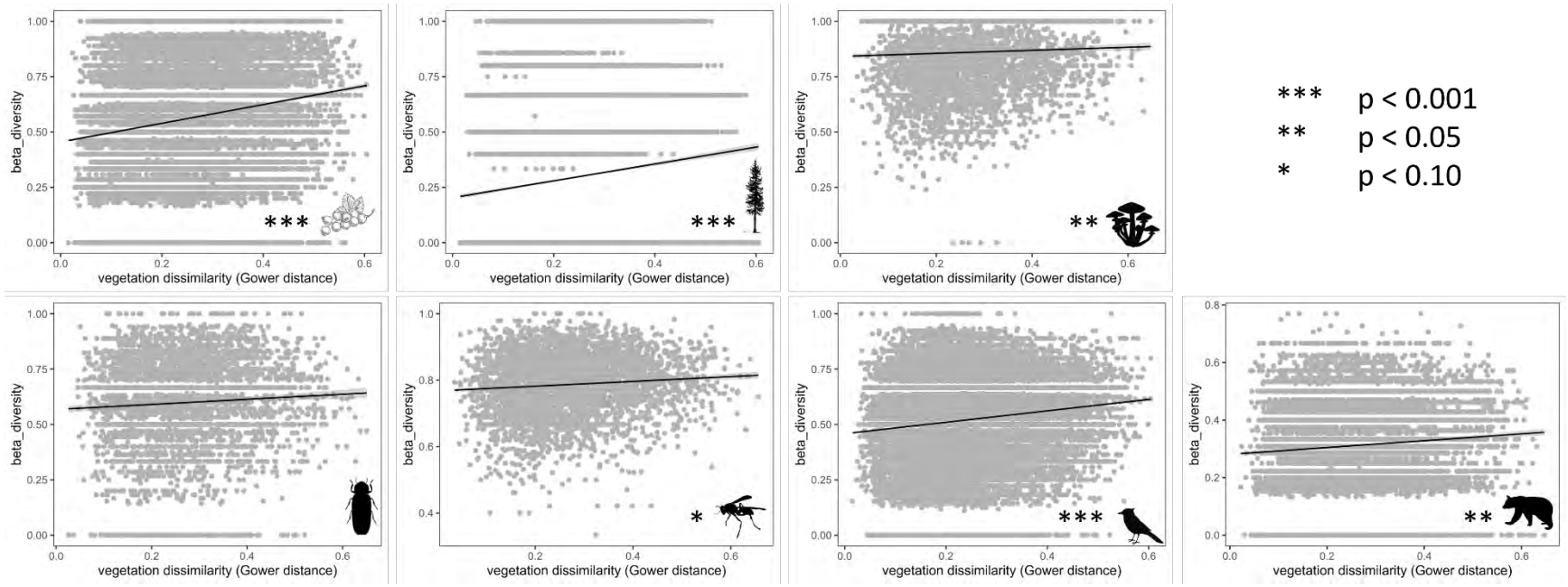


Figure S5.1. Partial Mantel test statistics reveal correlation between β-diversity (turnover) and vegetation structure dissimilarity across most taxa.