

CONSERVATION, CONNECTIVITY, AND COEXISTENCE:
UNDERSTANDING CORRIDOR EFFICACY IN FRAGMENTED LANDSCAPES

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

Fragmentation, the division of landscapes into smaller isolated areas, has transformed the Earth into a complex mosaic of natural and human-modified features (Hobbs et al. 2008). Fragmented landscapes isolate natural patches of land and embed them in a matrix of human land uses that can create significant barriers to dispersal (Crooks et al. 2011; Haddad et al. 2015). Such disruptions to natural ecosystems alter dispersal patterns and increase the risk of inbreeding; resulting in the loss of genetic diversity to genetic drift (Baguette et al. 2013). Today, fragmentation is one of the greatest threats to global biodiversity and challenges in wildlife management (Fahrig 2002; Pereira et al. 2010; Fahrig 2019).

In response to fragmentation, global conservation efforts prioritize landscape connectivity, the degree to which species movement is facilitated or impeded by a landscape. The literature differentiates two types of landscape connectivity (Taylor et al. 1993). Structural connectivity describes the physical linkages connecting two or more patches of similar land cover; regardless of the ability of wildlife to use the linkages. Functional connectivity accounts for the ability of wildlife to use linkages for movement between patches of natural land cover (Tischendorf and Fahrig 2000; Taylor et al. 2006).

An important discrepancy arises in that these two types of connectivity are not mutually exclusive of one another. Functional connectivity can occur in the absence of structural connectivity, and similarly, structural connectivity does not guarantee functional connectivity.

(Mech and Hallet 2000). For instance, populations occupying patches that are not structurally linked can sustain functional populations of species (Hanksi and Simberloff 1997). It is equally likely the quality of habitat within structural linkages is not functional for focal species dispersal among patches (Norton et al. 1995; Hilty et al 2020; Gilbert-Norton et al. 2010).

To facilitate connectivity, conservationists and land managers often depend on structuring ecological networks with conservation corridors (Ferreras 2001; Baguette et al. 2013). Conservation corridors, natural swaths of land connecting patches of similar land cover, are frequently cited and implemented as a preventative or restorative strategy to counteract the consequences of fragmentation (Heller and Zavaleta 2009). As a preventative strategy, swaths of natural land are identified to connect landscape blocks that will support gene flow and demographic stability after the surrounding lands have been converted to human uses (Beier and Gregory 2012). As a restorative strategy, wildlife crossings are developed to connect landscape blocks otherwise fragmented by roads or canals (Clevenger and Huijser 2009).

Corridors are often approached with the mindset *if you build it, they will come*; assuming if a linkage creates structural connectivity that functional connectivity will inevitably follow. However, given functional connectivity can occur in the absence of structural connectivity and structural connectivity does not guarantee functional connectivity, this is not a trivial distinction (Ferreras 2001; Taylor et al. 2006; Baguette et al. 2013).

It is assumed corridors facilitate wildlife movements among patches. Yet, current corridor ecology assesses the functionality of designed and built conservation corridors, such as a wildlife crossing over a highway, or experimental corridor systems. Such designs and systems

are typified as short, straight swaths of homogenous land cover with unambiguous transitions between patches (Figure 1.1). There are few gaps in the connectedness of natural land cover, no pinch points at which edge effects are augmented, and no tortuosity that may affect crossing time or propensity (Beier and Noss 1998). This enables researchers to identify the point easily and accurately at which wildlife traverse patch-corridor transitional areas, estimate the passage time along the corridor to evaluate the influence of species' behavioral mechanisms, and dispersal times on corridor efficacy (Haddad et al. 2000; Legrand et al. 2012).

a Wildlife crossing

Banff National Park in Alberta, Canada



b Experimental corridor system

Savannah River Site in South Carolina, USA



c *De facto* corridor

Kansas, USA



Figure 1.1: Built, experimental, and *de facto* conservation corridors: (a) designed and built wildlife crossing over Trans-Canada Highway Improvement District No. 9 in Banff National Park, Alberta, Canada (Google Earth 2021); (b) experimental corridor system where patches were in a managed forest at the Savannah River Site in South Carolina, United States (Google Earth 2019); (c) *de facto* corridor in public rangelands managed by the Bureau of Land Management in Southern Idaho, United States (Google Earth 2020).

As a result of complex landscape dynamics across large spatial and temporal scales (Bélisle 2005), the majority of connectivity and corridor research has assessed corridor functionality in landscapes at several orders of magnitude smaller scale and embedded in a different landscape context than those for which conservation corridors are designed and implemented (Beier and Gregory 2012). As research has assessed the structural configuration of a landscape independent from a species perspective (Tischendorf and Fahrig 2000; Taylor et al. 2006), studies often overlook the influence landscape heterogeneity and scale has on dispersal mechanisms (Ferreras 2001; Baguette et al. 2013). In addition, species response variables measured are often inadequate to support inferences of long-term persistence (Beier and Gregory 2012; Gregory and Beier 2014). Resultantly, a fundamental knowledge gap in corridor efficacy is how complex mosaics within the structural configuration of a corridor influence corridor functionality long-term. This begs the question: do corridors work?

To address these knowledge gaps in corridor ecology, an ongoing assessment of corridor efficacy is combining field sampling, genetic analyses, and spatial modelling to measure long-term gene flow across 16+ landscapes, internationally (Do Corridors Work 2022). Using *de facto* corridors, natural areas that resemble the design of built conservation corridors but exist as a quirk of human development (Figure 1.1), connectivity is being assessed in the real world in which conservation corridors are designed and built (Beier and Gregory 2012). Specifically, by assessing and understanding the characteristics of corridors that facilitate movement and the species that benefit, we will gain foundational insight into how corridors could be better designed and implemented to ensure a high probability of functionality.

Given the natural occurrence of *de facto* corridors in the real world, they vary in each characteristic that experimental corridors lack variation. Specifically, *de facto* corridors differ in width and tortuosity across varying lengths. They are composed of heterogenous land covers, some of which are not habitats for species utilizing the corridor. In addition, they often have anthropic land uses within and adjacent to them. As such, they are subject to varying degrees of edge effects, further altering the quality of the structural linkage (Beier and Gregory 2012). These characteristics create three conditions differentiating *de facto* corridors from experimental systems.

First, the variation in width and tortuosity results in ambiguous transitions between a corridor and patches; making it difficult to identify the true length of a corridor. Second, the mixture of anthropic land uses within and adjacent to the corridor results in ambiguous delineations; making it difficult to delineate the boundary of the natural land cover from the matrix. Third, the heterogeneity of natural land cover types within the corridor can impact the species utilizing the linkage; making it difficult to measure the degree to which connected patches are structurally linked. These conditions have resulted in two prominent knowledge gaps in the literature.

Firstly, how wide does a corridor have to be to meet conservation objectives (Beier 2018)? This knowledge gap has long been recognized as the most urgent issue land managers must address (Gilbert-Norton et al. 2010; Beier 2018). Yet, implicated in this question is the ability to identify the boundaries of a corridor, the point at which the patch transitions into the corridor, and the point at which the corridor transitions back into the connected patch.

Secondly, how does heterogeneity within the structural configuration of a corridor influence corridor functionality.

The knowledge gap of boundary identification is long recognized, yet seldom modelled or incorporated in corridor designs (Hilty et al. 2020). Corridor literature lacks a unified method for delineating landscape elements, recognizing arbitrary edges of the landscape, identifying the start and end of corridors, and assessing the relationship between measures of structural connectivity and functional connectivity. To allow for meaningful inferences of the conservation value of corridors, it is critical to address these issues.

The focus of my thesis is to address the often-overlooked technical attributes of corridor ecology. Specifically, by developing a robust methodology to test the degree to which various metrics of structural connectivity correlate to functional connectivity using a subset of *de facto* corridors identified by the ongoing assessment of corridor efficacy (Beier and Gregory 2014; Do Corridors Work 2022).

1.2 Terminology and Chapter Descriptions

Given the variation in the terminology used in the field of landscape ecology, I have defined critical terms used throughout this thesis to standardize and clarify definitions (Box 1.1).

Box 1.1: Critical definitions used throughout thesis chapters.

Term	Definition
Boundary	Where environmental gradients change; edge of <i>landscape elements</i>
Composition	Which land cover type is present and amount of each type
Configuration	Spatial arrangement of land cover types
Connectivity	Degree to which landscapes facilitate or impede species movements
Connectivity Modelling	Algorithms to quantify landscape <i>connectivity</i> for <i>focal species</i>
Corridor	Natural swath of land cover connecting patches of similar land cover; composed of <i>focal habitat</i> ; differs from <i>matrix</i>
<i>De facto</i> Corridor	Natural areas that resemble human-made linkages, but exist as a quirk of human development
Focal Habitat	Habitat of interest for <i>focal species</i> ; provides food, water, vegetative cover, and space to hide rest, move about, mate
Focal Species	Specific species being assessed; species of interest
Functional Connectivity	Increases degree of species movement through a <i>landscape</i>
Fragmentation	Natural land cover divided into smaller, disconnected/isolated patches
Heterogeneity	<i>Mosaic</i> of differing land cover types within an area of interest
Interface	Where two systems connect; corridor start/end; patch-corridor-patch
Landscape	Spatially heterogeneous area; spatial <i>patterns</i> interact with <i>processes</i>
Landscape Elements	Number, size, and shape of discrete natural land cover types; <i>boundary of patch</i> or <i>corridor</i>
Landscape Function	Wildlife, plants, nutrients, and energy movement among <i>landscape elements</i>
Landscape Structure	Spatial patterns and connectedness of <i>landscape elements</i>
Matrix	Differing land covers and land uses surrounding <i>focal habitat</i>
Mosaic	Heterogeneous collection of patches spatially arranged; lacks dominance/connectedness
Patch	Natural land cover area composed of <i>focal habitat</i> ; differs from <i>matrix</i>
Pattern	Spatial relationships among <i>landscape elements</i>
Process	Ecological responses to <i>patterns</i>
Species Perspective	Organism's perception of and response to <i>landscape structure</i>

Chapters 2 and 3 are not independent of one another as they continue to build on previous objectives. However, for organizational purposes, I have developed two chapters relative to landscape connectivity. Chapter 2 focuses on structural connectivity across landscapes, while chapter 3 builds upon the results of chapter 2 by modelling functional connectivity within structurally defined linkages and quantifying corridor efficacy using gene flow. There are three major objectives for this research. Objectives 1 and 2 focus on quantifying patterns while objective 3 focuses on identifying processes:

1. Developing a methodology that minimizes the subjectivity and variability in the delineation process of patch-corridor-matrix boundaries.
2. Developing a methodology that reduces the ambiguity in the identification of transitional patch-corridor interfaces.
3. Determine the influences of structural landscape configuration and composition has on functional connectivity and focal species occurrence.

In chapter 2, ‘Using remote sensing to standardize the delineation process of patch-corridor-matrix boundaries across landscape mosaics’, I develop a quantitative and repeatable methodology to standardize the delineation process of patch-corridor-matrix boundaries using remotely sensed data. Specifically, by delineating the boundaries between the focal habitat and the surrounding matrix and identifying a meaningful start and end to corridors. I then quantify habitat quality for focal species within delineated landscape elements to measure the influences structural landscape composition and configurations have on functional connectivity (Box 1.1) in chapter 3.

In chapter 3, ‘Investigating the degree to which the presence of a corridor influences the structural and functional connectivity of small mammal habitats’, I build upon the

methodologies developed in chapter 2 to assess the degree to which the presence of a corridor influences connectivity when compared to intact reference areas and isolates. Rooted in this objective, is measuring the degree to which the presence of a corridor facilitates or impedes focal species dispersal and distribution.

CHAPTER 2

USING REMOTE SENSING TO STANDARDIZE THE DELINEATION PROCESS OF PATCH-CORRIDOR-MATRIX INTERFACES ACROSS LANDSCAPE MOSAICS

2.1 Introduction

Global conservation efforts prioritize landscape connectivity, the degree to which species movement is facilitated or impeded by a landscape. The literature differentiates two types of connectivity (Taylor et al. 1993). Structural connectivity describes the physical linkages connecting two or more patches of similar land cover; regardless of the ability of wildlife to use the linkages. Functional connectivity accounts for the ability of wildlife to use linkages to move between patches of natural land cover (Tischendorf and Fahrig 2000; Taylor et al. 2006). This distinction is important, as most conservation corridors are designed to promote functional connectivity and evaluated based on structural connectivity. It is assumed if structural connectivity exists, functional connectivity will also be achieved. However, this assumption is not true across all landscapes for all species (Taylor et al. 2006).

To facilitate connectivity, conservationists and land managers often depend on structuring ecological networks with conservation corridors (Ferreras 2001; Baguette et al. 2013). Conservation corridors, natural swaths of land connecting patches of similar land cover, are frequently cited and implemented as a preventative or restorative strategy to counteract the consequences of fragmentation (Heller and Zavaleta 2009). Corridors are often approached with the mindset *if you build it, they will come*; assuming if a linkage creates structural connectivity that functional connectivity will inevitably follow. However, an important

discrepancy arises in that these two types of connectivity are not mutually exclusive of one another.

This is not a trivial distinction, given functional connectivity can occur in the absence of structural connectivity and structural connectivity does not guarantee functional connectivity (Ferreras 2001; Mech and Hallet 2000; Baguette et al. 2013). For instance, populations occupying patches that are not structurally connected can sustain functional populations of focal species (Hanksi and Simberloff 1997). Additionally, it is equally likely that the quality of habitat within structural linkages is sufficiently degraded that it is not functional for focal species dispersal among patches (Hilty et al. 2020; Gilbert-Norton et al. 2010).

It is assumed corridors facilitate wildlife movements among patches. Yet, current corridor ecology assesses the functionality of designed and built conservation corridors, such as a wildlife crossing over a highway, or experimental corridor systems. Such designs and systems are typified as short, straight swaths of homogenous land cover with unambiguous transitions between patches (Figure 1.1). There are minimal gaps in the connectedness of natural land cover, no pinch points at which edge effects may be augmented, and no tortuosity that may affect crossing times or propensity (Beier and Noss 1998). This enables researchers to identify the point easily and accurately at which wildlife traverse patch-corridor transitional areas and estimate the passage time along the corridor to evaluate the influence of species' behavioral mechanisms, and dispersal times on corridor efficacy (Haddad et al. 2000; Legrand et al. 2012).

As a result of complex landscape dynamics across large spatial and temporal scales (Bélisle 2005), the majority of connectivity and corridor research has assessed corridor

functionality in landscapes at several orders of magnitude smaller scale and embedded in a different landscape context than those for which conservation corridors are designed and implemented (Beier and Gregory 2012). As research has assessed the structural configuration of a landscape independent from a species perspective (Tischendorf and Fahrig 2000; Taylor et al. 2006), studies often overlook the influences which landscape heterogeneity and scale have on dispersal mechanisms (Ferreras 2001; Baguette et al. 2013). In addition, species response variables measured are often inadequate to support inferences of long-term persistence (Beier and Gregory 2012). Resultantly, a fundamental knowledge gap in corridor efficacy is how complex mosaics within the structural configuration of a corridor influence corridor functionality long-term. This begs the question: do corridors work?

To answer this question, an ongoing assessment of corridor efficacy is combining field sampling, genetic analyses, and spatial modelling to measure long-term gene flow across 16 landscapes, internationally (Do Corridors Work 2022). Using *de facto* corridors, natural areas that resemble the design of built conservation corridors but exist as a quirk of human development (Figure 1.1), connectivity is being assessed in the real world in which conservation corridors are designed and built (Beier and Gregory 2012). Specifically, by assessing and understanding the characteristics of corridors that facilitate movement and the species that benefit, we will gain foundational insight into how corridors could be better designed and implemented to ensure a high probability of functionality.

The larger Corridors Project will address critical knowledge gaps in corridor ecology by combining field sampling, genetic analyses, and spatial modelling to measure demographic

stability and long-term gene flow across 16 landscapes within eight countries on five continents (Do Corridors Work 2022). By assessing large-scale and stable landscapes with *de facto* corridors (Beier and Gregory 2012), connectivity is being assessed in the real world to further our understanding of (1) the structural characteristics of corridors that facilitate movement, (2) the biological traits that determine which species benefit, and (3) how corridors should be designed and implemented with a high probability of functionality.

To assess real world corridors, the project team identified landscapes suitable for the analyses based on the following five criteria (Beier and Gregory 2012):

Landscape criteria

1. Have a full suite of landscape elements present: a *de facto* corridor complex, intact reference, and two isolated patches.
2. A hard-edge defines landscape elements from the surrounding matrix.
3. Similar distances between corridor patches, isolated patches, and the length of the reference.
4. Average corridor widths are greater than 100 m and lengths are greater than 500 m.
5. Maintained a stable landscape configuration for at least 50 years.

Based on the above criteria, a complete landscape configuration is comprised of the following landscape elements: two patches connected by a *de facto* corridor, an intact reference area, and two isolated patches separated by the surrounding matrix (Box 2.1).

Focal species were categorized into two groups based on how they use a corridor: passage species and corridor dwellers. Highly mobile passage species can traverse the length of

a corridor in a discrete event over a few hours or days. Corridor dwellers, species that use a corridor as a habitat, have limited dispersal abilities and require several days for generations for individuals and their genes to move through a corridor (Beier and Loe 1992; Beier 2018). For each landscape, 3-5 focal corridor dwellers and passage species that represent a range of mobility, edge sensitivities, and body size were targeted. The project team identified focal species to be included in the analyses based on the following two criteria (Beier and Gregory 2012):

Focal species criteria

1. A corridor dweller structured by natural landscapes; with 1 or 2 passage species, and
2. have moderate population sizes with less than 1,000 individuals in each area.

Although using *de facto* corridors to study corridor efficacy is a best practice (Gregory and Beier 2012), there are several drawbacks to the ambiguous nature *de facto* corridors when compared to experimental corridor systems (Figure 1.1). Given the natural occurrence of *de facto* corridors in the real world, they vary in each characteristic that experimental corridors were standardized to control for latent effects. Specifically, *de facto* corridors differ in width and tortuosity across varying lengths. They are composed of heterogeneous land covers, some of which are not habitats for species using the corridor. In addition, they often have human land uses within and adjacent to them. As such, they are subject to varying degrees of edge effects, further altering the quality of the structural linkage (Beier and Gregory 2012). These characteristics create three conditions differentiating *de facto* corridors from experimental systems.

First, the mixture of human land uses within and adjacent to the corridor results in ambiguous delineations; making it difficult to delineate the boundary of the natural land cover from the matrix. Second, the variation in width and tortuosity results in ambiguous transitions between a corridor and patches; making it difficult to identify the true length of a corridor. Third, the heterogeneity of natural land cover types within the corridor can impact the species utilizing the linkage; making it difficult to measure the degree to which connected patches are structurally linked. These conditions have resulted in two prominent knowledge gaps in the literature.

Firstly, how wide does a corridor have to be given its length to meet conservation goals (Harrison 1992; Beier 2018)? This knowledge gap has long been recognized as the most urgent issue land managers must address (Gilbert-Norton et al. 2010; Beier 2018). Yet, implicated in this question is the ability to identify the boundaries of a corridor and the point at which a patch transitions into a corridor and the point a corridor transitions back into the connected patch (patch-corridor-patch; Box 2.1). The knowledge gap of boundary identification is long recognized, yet seldom modelled or incorporated in corridor designs (Hilty et al. 2020).

Secondly, how does heterogeneity within the structural configuration of a corridor influence corridor functionality? While some land covers facilitate species movements, others impede wildlife dispersal and fragment patches of species habitat even if all land cover within a corridor is natural vegetation. Species behavior, habitat preferences, and dispersal mechanisms through patches of non-habitat or the matrix influences connectivity (Prevedello et al. 2010).

This research is part of the larger collaborative study to assess conservation corridor efficacy (Do Corridors Work 2022). Using a subset of landscapes, I apply a species perspective approach to spatial modelling to quantify landscape patterns influencing processes for focal species. Specifically, I quantify the configuration and composition of landscape elements and how those patterns influence the ecological responses of focal species to identify processes.

Corridor literature lacks a unified method for delineating landscape elements, recognizing arbitrary edges of the landscape, and identifying the start and end of corridors. This chapter addresses the often-overlooked technical attributes of corridor ecology using a subset of *de facto* corridors (Do Corridors Work 2022). In this chapter I develop a methodology that:

- (1) minimizes the subjectivity and variability in the delineation process of patch-corridor-matrix boundaries,
- (2) reduces the ambiguity in identifying transitional patch-corridor interfaces, and
- (3) allows for the quantification of the composition of species-specific habitats occurring within boundaries of each landscape element (Box 2.1).

2.2 Methods

Spatial analyses were conducted at landscape scales in the United States and Czechia using ArcMap and ArcGIS Pro (ESRI 2019, 2022). Given the spatial extent of the study system, I elected to use remotely sensed data to minimize process error due to the variation in the compilation and classification of regional land cover and land use datasets. All spatial analyses and classifications were executed using 30 m resolution Landsat 8 OLI/TIRS (Landsat 8) imagery and its Universal Transverse Mercator zone spatial reference.

Small mammal trapping was conducted using Sherman traps to collect genetic samples and species occupancy data for each landscape element. For each individual, genetic samples were collected from a 0.02 mm ear tissue notch and stored in Longmire solution until extraction.

Trapping was carried out by local sub-contractors in each landscape following standardized project protocols for field data collection and sampling. All animal handling procedures were approved by the University of North Texas, Institutional Animal Care and Use Committee protocol #200-20. All relevant regional and national wildlife trapping and handling permits, and permissions were acquired and held by local project subcontractors with corridors project staff listed as sub-permittees.

2.2.1 Study Areas and Focal Species

I selected a subset of three landscapes that represent a range of environmental contexts with field and genetic data collection completed. For each landscape, I selected one focal species that covered a wide range of habitats and landscape conditions (Bani et al. 2006) from the sample set that had the highest capture rate at each landscape. Across landscapes, there were a total of five *de facto* corridors, three intact reference areas, three sets of isolated patches (Box 2.1), and three focal species.

Box 2.1: Critical terms used to define the configuration of landscapes.

Term	Definition
Landscape Elements	A complete landscape configuration; corridor complex, intact reference area, and isolated patches
Corridor Complex	Two patches connected by a corridor
<i>De facto</i> Corridor ¹	Natural areas that resemble the design of built conservation corridors, but exist as a quirk of human development
Patch 1	Area where the patch transitions (narrows) into the corridor
Patch 2	Area where the corridor transitions (widens) into the patch
Patch-corridor-patch	Patch 1-corridor-patch 2 configuration delineated from the corridor complex; patches and corridor elements within corridor complex
Reference Area	Intact reference area; encompasses the length of the corridor complex
Isolates	Isolate 1 and 2 separated by the surrounding matrix; at a distance similar to the length of the corridor
Isolate 1	Isolated patch 1; distance to patch 2 similar to length of corridor
Isolate 2	Isolated patch 2; distance to patch 2 similar to length of corridor

¹Beier and Gregory 2014

Kansas

The landscape comprised one *de facto* corridor complex, two isolated patches, and one intact reference area (Figure 2.1). The study area encompassed 116.87 km² in eastern Kansas composed of a mosaic of land cover and land uses of differing suitability. Specifically, grassland pastures and cultivated fields dominated the matrix surrounding the natural gallery forest. The local elevation varied between 312 and 397 m.



Figure 2.1: Study area encompassing 116.87 km² in eastern Kansas, United States comprised of: (a) *de facto* corridor complex, (b) intact reference, (c) isolate one, (d) isolate two.

White-footed mouse (*Peromyscus leucopus*; hereafter, *P. leucopus*) are common throughout eastern United States in dense forests that provide canopy cover at low elevations (Kaufman and Fleharty 1974; Taylor and Hoffman 2014). The species is adaptable to urban and agricultural areas (Wilson and Ruff 1999); with male home ranges recorded up to 15,000 m² (Aguilar 2011). Although habitat generalists, the species prefer complex understory vegetation, with dense ground cover and woody debris. Given the complex habitat preference, abundant populations are found in small forest fragments and edges than interiors (Heske and Rodgers 2022).

Idaho

The landscape was comprised of one *de facto* corridor complex, two isolated patches, and one intact reference area (Figure 2.2). The study area encompassed 4,367 km² in southern Idaho where cultivated fields and irrigated crop circles with a center pivot dominated the matrix surrounding focal rangeland habitat. Rangeland across the study area is public lands used for livestock grazing managed by the Bureau of Land Management. The local elevation varied between 901 and 1540 m.

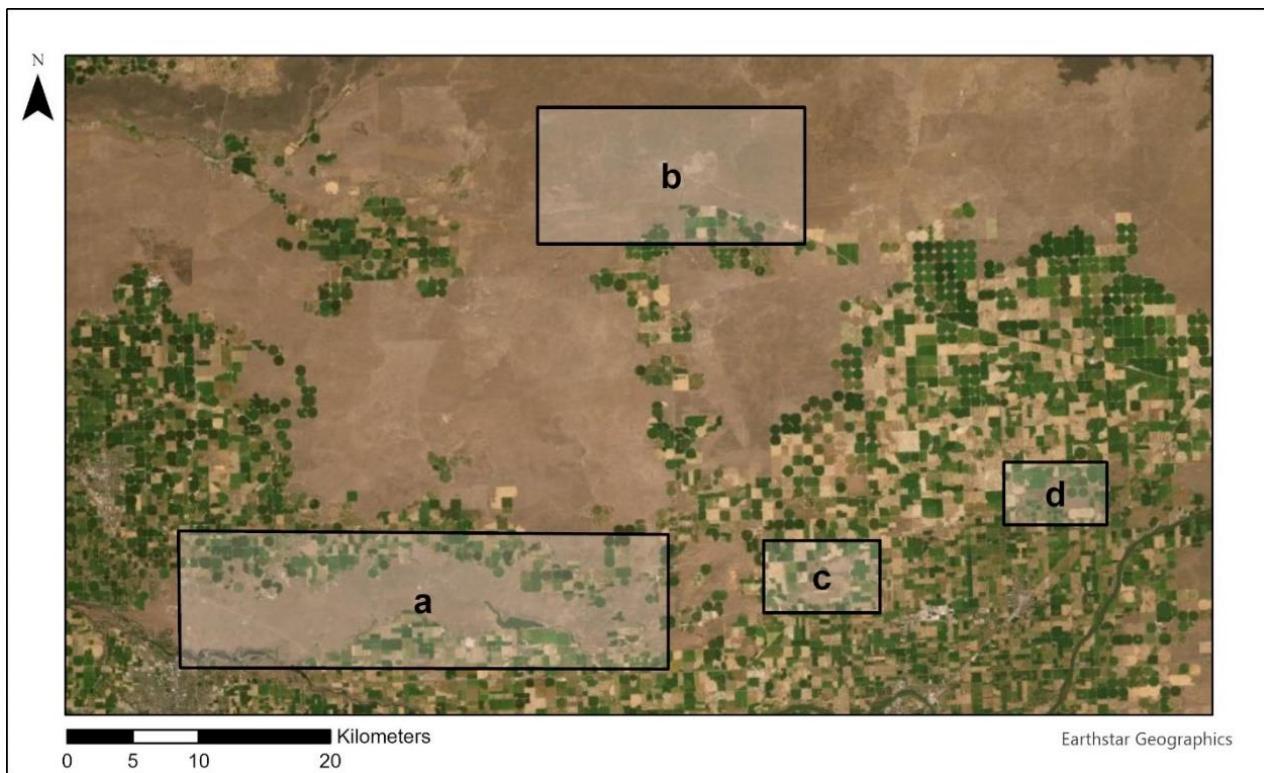


Figure 2.2: Study area encompassing 4,367 km² in southern Idaho, United States comprised of: (a) *de facto* corridor complex, (b) intact reference, (c) isolate one, (d) isolate two.

Western harvest mouse (*Reithrodontomys megalotis*; hereafter, *R. megalotis*) populations are common across the western United States and central Mexico in rangeland, prairies, and deserts with elevations between -77 and 4000 m (Webster and Jones 1982; Ruff

and Wilson 1999). While habitat generalists, *R. megalotis* populations are abundant in rangeland and old fields, as the species require dense vegetative cover and tall grass for foraging, nesting, and protection from predators (Kaufman and Fleharty 1974; Sullivan and Sullivan 2008). Frequently found bordering riparian and agricultural areas and using linear habitats as corridors, the species is not sensitive to edge effects. Over 90% of *R. megalotis* observations have been in proximity to roads and dense populations (Environment Canada 2015); with male home ranges recorded up to 3,525 m² (Konishi 2003).

Czechia

The landscape was comprised of three *de facto* corridor complexes, two isolate patches, and one intact reference area (Figure 2.3). The study area encompassed 3,884 km² that spanned the South Bohemian, Vysočina, and South Moravian regions of Czechia as well as a portion of northern Austria, given the configuration of the reference area. The forests are classified relative to commercial exploitability with high-intensity forest management plans and guidelines in place (Synek et al. 2014). The forest clear-cutting has resulted in a landscape mosaic composed of a high degree of heterogeneity. Surrounding the forests, cultivated fields dominate the matrix. The local elevation varied between 188 and 742 m.

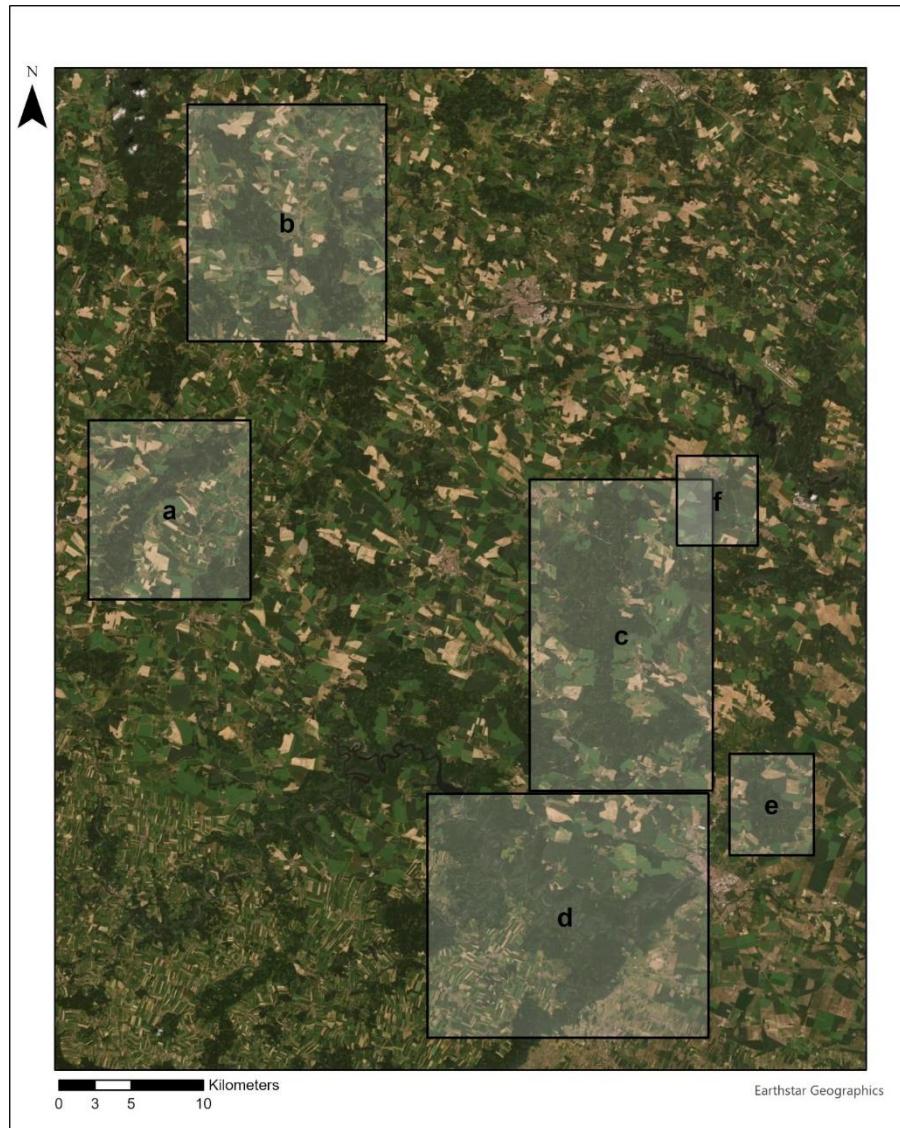


Figure 2.3: Study area encompassing 3,884 km² in the South Bohemian, Vysočina, and South Moravian region of Czechia and northern Austria comprised of: (a) *de facto* corridor complex 1, (b) *de facto* corridor complex 2, (c) *de facto* corridor complex 3, (d) intact reference, (e) isolate one, (f) isolate two.

Yellow-necked mouse (*Apodemus flavicollis*; hereafter, *A. flavicollis*) populations are widely distributed across Europe. The species is semi-arboreal and often associated with forest edges. Populations are most abundant in areas with high canopy cover used for foraging, nesting, predator avoidance, and minimizing interspecific competition (Štěpánková and

Vohralík 2009; Benedek 2021). Given the species' food dependency and tolerance of urban and agricultural areas, *A. flavicollis* are highly mobile (Rico et al. 2007; Bohdal et al. 2016; Benedek 2021); with male home ranges recorded up to 15,500 m² (Schwarzenberger and Klingel 1995).

2.2.2 Minimizing the Subjectivity in the Delineation Process of Patch-Corridor-Matrix

Boundaries

A species perspective was implemented to delineate boundaries to minimize the subjectivity in the identification of arbitrary edges. There is a lack of small mammal dispersal records in the literature (Howard 1960). However, home range areas used for routine travel, foraging, mating, and parental care (Burt 1943) are well-studied, process driven, and influence evolutionary mechanisms (Wayne 2012).

Given males have larger home ranges than females (Burt 1943), male home range estimates were obtained from the literature (Schwarzenberger and Klinkgel 1995; Konishi 2003; Aguilar 2011). Corridor dwellers require more than one generation for individuals and their genes to move among patches and through a corridor (Beier 2018). As such, 3x the home range was implemented to accommodate for home range overlaps where species can mate and reproduce male offspring that disperse.

To achieve a more consistent delineation of patch-corridor-matrix boundaries, landscape elements were delineated by digitizing the boundaries of focal habitat on false composite Landsat 8 imagery. A false color composite was used to enhance the landscape features otherwise invisible to the human eye on natural composites (Assmann et al. 2018). I standardized the delineation process by:

1. Landsat 8 image acquisition dates were selected to be temporally aligned with the biological activity patterns of small mammals as well as the active collection of field data; the same imagery used to classify land cover.
2. A buffer 3x the home range of the male focal species with the largest home range from Sherman trap locations to minimize the subjectivity in delineating arbitrary edges in areas the focal habitat continues without end.
3. At a scale of 1:4,000, landscape elements were digitized using a heads-up approach along the hard edge of the continuous focal habitat to the nearest natural/unnatural pinch point that presents a barrier to movement.
4. Using a false composite of Landsat 8 bands 5, 4, and 3 to enhance the contrast between patch-corridor-matrix boundaries.

Species richness, abundance, and occurrence have been found to have a strong relationship with patch size and edge to area ratio of the landscape element (Turner et al. 2001; McGarigal et al. 2012). Therefore, the boundaries of landscape elements were used to characterize whole-patch metrics including total edge, total patch area, and the edge-area ratio. As the edge-area ratio increases, patch interiors are closer to the edge and have a greater influence on ecological dynamics within the patch.

2.2.3 Reducing the Ambiguity in Identifying Transitional Patch-Corridor Interfaces

Identifying the start and end point of a corridor is an urgent knowledge gap to address given the modelled corridor output will greatly influence the impact of corridor width, length, and tortuosity can have on wildlife movements. As such, it is critical to define meaningful corridor termini within the delineated corridor complex (Majka et al. 2007).

I developed a rigorous process to identify transitional areas to the start and end of the corridor and delineate patch-corridor-patch elements from the corridor complex. Transitional

areas are defined as the inner corridor termini tapered to the outer corridor terminus; the locations at which we expect edge effects to have the strongest influence on species.

First, using the delineated corridor complexes, the centerline through the polygon was identified. Second, points were sampled sequentially along the polygon centerline at equal distances which varied among corridor complexes. The distance at which points were sampled increased for larger corridor complexes to ensure points were sampled linearly along the centerline on a Euclidean distance raster. Third, the distance from the centerline sample points to the nearest polygon edge was measured. Fourth, distance measurements were plotted against the linear distance along the corridor complex centerline from the patch-corridor-patch; where the x-axis represents the polygon length and the y-axis represents the polygon width. Using the distance plots, a breakpoint analysis was used to identify the four points of greatest percent change defined by:

$$\% \text{ Change in Corridor Width} = \left(\frac{w_2 - w_1}{w_1} \right) * 100$$

Where w is equal to width at each sequential sample point; w_1 is equal to the initial point and w_2 the following point.

Specifically, the two points of greatest width and two points of smallest width were identified to represent the widest locations of patches 1 and 2 and the narrowest points within the corridor, respectively. Between the locations at which the patches were of greatest width and two locations at which the corridor width was smallest, four points of greatest percent change in width were identified as transitional areas of patch-corridor interfaces. The negative

percent change on the right side of the graph and positive percent change on the left side were identified given the points were sampled sequentially. As such, points 1 and 2 represent the greatest negative percent change in width where patch one transitions and narrows into the corridor. Points 3 and 4 represent the greatest positive percent change width where the corridor transitions and widens into patch two.

Collectively, the area between the outer and inner start of the corridor (points 1 and 2) and the inner and outer end of the corridor (points 3 and 4) represents the transitional areas from patch to corridor and corridor to patch, respectively. To minimize the subjectivity in delineating arbitrary edges along patch-corridor interfaces, the corridor was delineated from the corridor complex using the inner termini at points 2 and 3 tapered to the outer termini at points 1 and 4 (Figure 2.10 - 2.14). By identifying the four points of greatest percent change in width, I was able to identify transitional zones and define meaningful corridor termini.

Patch-corridor-patch metrics were estimated using the patch-corridor interface boundaries. Patch and corridor metrics included edge, area, and edge-area ratio. Corridor metrics also included length and average width estimated using the outer start and outer end points 1 and 4.

2.2.4 Quantifying Land Cover and Land Use Across Landscape Mosaics

The accuracy of spatial modelling is often highly subjective as it depends on the underlying classification scheme and global land cover layers have low accuracy and high variation among regions (Yu et al. 2019; Tulbure et al. 2022). However, satellite imagery can accurately measure and differentiate the extent and variety of land cover types (Kerr and

Ostrovsky 2003; Majka et al. 2007). Given the uncertainty in the accuracy of global land cover datasets (Yu et al. 2019), the Landsat 8 imagery used to delineate landscape elements was used to classify land cover (Table 2.1) following a modified Anderson Level I classification scheme (Anderson et al. 1976). A supervised classification process was implemented to increase the consistency of land cover layers.

Table 2.1: Modified Anderson Level I classification scheme (Anderson et al. 1976) used to classify landscape mosaics across study areas.

Land Cover	Description
Developed	Urban, residential, commercial, and industrial developments
Agriculture	Cropland, orchards, vineyards, nurseries, confined feeding
Rangeland	Natural grassland and shrubland; includes grazed public lands managed by the Bureau of Land Management in Idaho, United States
Forest	Deciduous and evergreen, and patches and hedgerows >30 m ²
Water	Lakes, reservoirs, rivers, streams, canals, ponds > 30 m ²

Imagery Preprocessing

A false color composite was used to enhance the landscape features otherwise invisible to the human eye on natural composites (Assmann et al. 2018). False color composites of bands 5, 4, and 3 use near-infrared light as red, red light as green, and green light as blue, respectively. Chlorophyll reflects near-infrared light while water absorbs light. The reflectance of a false color composite maximizes the contrast between boundaries of vegetation, development, and water. Vegetation is depicted in various shades of red allowing the user to differentiate areas of healthy vegetation and agriculture (GISGeography 2022). As such, false color composites are particularly useful to identify subtle differences between closely related land cover types such as native grasslands and cultivated wheat grasses (Ali et al. 2016).

Imagery Processing

Training samples were collected using false color composite depictions that reflect land cover types from imagery preprocessing. The supervised classification used pixel characteristics of the training samples for each land cover type to classify the entire Landsat 8 image. As corridor dwellers often depend on steppingstones through landscapes (Majka et al. 2007), land cover areas >30 m² were classified given the 30 x 30 m imagery resolution (Table 2.1).

Image Post-processing

Following imagery processing, Pixel Editor tools were used to reclassify errors in the resultant classified layer to the correct land cover class before the accuracy assessment. An accuracy assessment was conducted using a confusion error matrix. An error matrix uses a cross-tabulation of classified land cover pixels in rows and reference land cover types in columns (Banko 1998). The error matrix was used to estimate errors of commission and omission, and to derive an overall kappa index between the classified land cover and reference.

Errors of commission represented false positives due to the inclusion of pixels in a class; classified as one class but identified as another according to the reference. For example, the classified image identifies a pixel as anthropic while the reference data identifies it as water. Thus, the agriculture class is comprised of misclassified pixels relative to the reference data. Commission errors were calculated from error matrix rows by dividing the number of pixels correctly classified in a class by the total number of pixels within that given class.

Errors of omission represented false negatives due to the exclusion of pixels from a class; omitted as one class and identified as another according to the reference. For example,

the reference data identifies as image as anthropic while the classified image identifies it as water. Thus, there are not enough pixels comprising the anthropic class as reported by the reference data. Omission errors were calculated from error matrix columns by dividing the number of correct pixels in a class by the total number of reference pixels in the class.

The kappa statistic represented the overall accuracy of the classification, indicating an agreement between classified pixels and the reference data. Overall accuracies were calculated from the major diagonal of the error matrix by dividing the total number of pixels correctly classified by the random sample points.

For a consistent assessment, the pansharpened Landsat 8 image was used as a reference as it represented the ground cover on the date the imagery was acquired. As previous studies have found at least 500 random points to accurately assess classification schemes using an error matrix (Czaplewski and Catts 1992; Banko 1998), 500 random sample points buffered at 30 m were used.

2.2.5 Quantifying the Composition of Habitat Within Landscape Element Boundaries

The quantity and quality of habitat across landscapes are the primary drivers of population persistence (Hall et al. 2017). Quality habitat provides wildlife with food, water, vegetative cover, and space to hide, rest, move about, and mate (Yarrow 2009). However, habitat is a species-centric concept and therefore must be quantified relative to focal species resource requirements. The boundaries of landscape elements were used to characterize within-patch metrics including the percent of habitat and non-habitat, core area, and the percent area of high vegetative productivity.

To quantify the percent of habitat and non-habitat within landscape elements, the supervised land cover layer was reclassified as binary to represent habitat areas embedded in a uniform matrix composed of non-habitat. Percentages were calculated by dividing the number of habitat and non-habitat pixel counts by the total number of pixel counts.

To represent the patch area not influenced by edge effects, where adjacent ecosystems abruptly transition (Murcia 1995), the core area was buffered within 30 m of the edge. A 30 m buffer was implemented to account for the majority of the distance light reaches the core area from the edge while minimizing the chance of exceeding the distance abiotic factors influence the core as small mammals often occupy edges due to the structural complexity of vegetation in edge areas (Murcia 1995; Heske and Rodgers 2022).

As an overall estimator of vegetation health, Normalized Difference Vegetation Index (NDVI) measures the primary productivity in an area. NDVI has been found to influence small mammal distributions and species abundances (Pettorelli et al. 2005; McFarland and van Riper 2013; Osman et al. 2022). The overall heterogeneity and quality of landscapes were indexed to quantify areas of high productivity within landscape elements. NDVI was calculated for Landsat 8 imagery acquired for the month with the highest temperature recorded during the year at which landscape elements were delineated and land cover was classified (GloVis, NOAA).

NDVI uses the visible and near-infrared bands of the electromagnetic spectrum. The red band is sensitive to changes in land cover and depicts the greatest contrast between areas of vegetation and soil. The near-infrared band is sensitive to structural leaf area and detects

changes in vegetative cover, plant health, and phenology (Malledgowda et al. 2015). NDVI was derived as:

$$\text{Landsat 8, NDVI} = \frac{(\text{Band 5} - \text{Band 4})}{(\text{Band 5} + \text{Band 4})}$$

The resultant NDVI values range from -1 to 1. Values from 0.1 to 0.3 indicate sparse shrubland or grasslands, values from 0.3 to 0.6 indicate healthy vegetative forest cover, and temperate rainforests value from 0.6 to 0.9 (Weier and Herring 2000). NDVI values were analyzed using the range of values representing focal habitats, forest or rangeland, to estimate the percent area of high vegetative productivity. In addition, the minimum, maximum, range, and average NDVI values were indexed within landscape elements using Zonal Statistics.

2.3 Results

2.2.1 Minimizing the Subjectivity in the Delineation Process of Patch-Corridor-Matrix Boundaries

Kansas

150 *P. leucopus* individuals were captured and sampled. Corresponding to the start of fieldwork, Landsat 8 imagery was acquired for September 19, 2020. Landscape elements were delineated along the hard edge of contiguous forest habitat. In areas of the corridor complex with no distinct forest boundary, topographic or anthropic barriers were used to delineate arbitrary edges at least 3x the home range of *P. leucopus* at 207 m (Figure 2.4a).

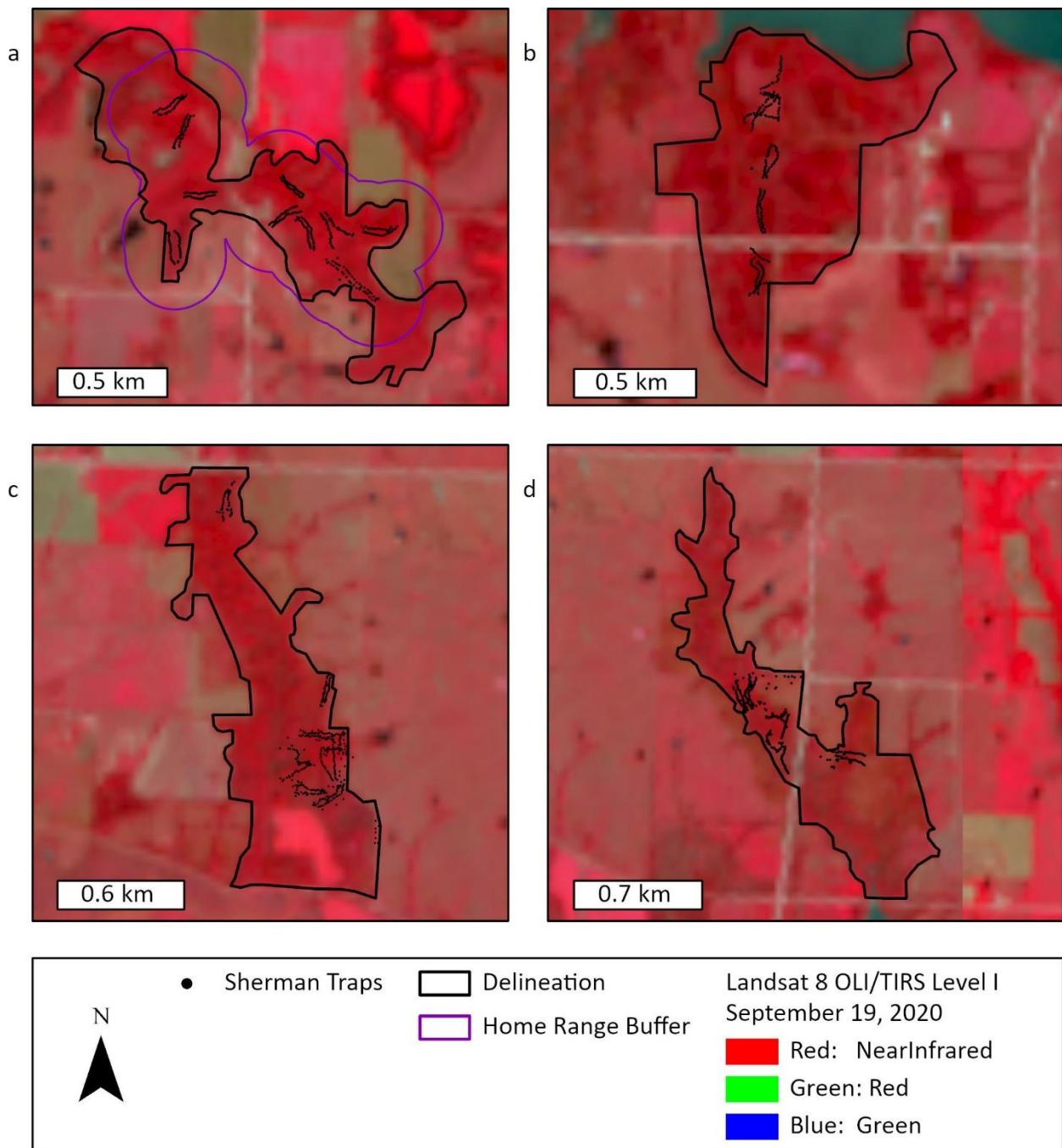


Figure 2.4: Kansas landscape elements sampled and delineated along the edge of contiguous forest using Landsat 8 OLI/TIRS Level I imagery from September 19, 2020: (a) corridor complex, (b) intact reference, (c) isolate one, (d) isolate two. (a) where no forest boundary was distinguishable, topographic or anthropic barriers were used to delineate arbitrary edges at least three times the home range of the white-footed mouse (*Peromyscus leucopus*) at 207 m.

The boundary of the reference area had the lowest edge-area ratio (Table 2.2). The corridor complex had a similar edge-area ratio to both isolates than the reference area. Interestingly, the corridor complex edge-area ratio was similar to isolate 2, which had the highest edge-area ratio (Table 2.2).

Table 2.2: Whole-patch metrics using the boundary of delineated landscape elements to estimate edge, area, and edge to area ratio in Kansas, United States.

	Edge (km)	Area (km ²)	Edge-Area Ratio (km/km ²)
Corridor Complex	8.1	0.86	9.40
Intact Reference	5.1	0.81	6.26
Isolate 1	7.2	0.88	8.18
Isolate 2	8.5	0.89	9.51

Idaho

193 *R. megalotis* individuals were captured and sampled. Corresponding to the start of field work, Landsat 8 imagery was acquired for August 8, 2018. Landscape elements were delineated along the edge of contiguous rangeland habitat (Figure 2.5). In areas of the corridor complex and intact reference with no distinguishable rangeland boundary, topographic or anthropic barriers were used to delineate arbitrary edges at least three times the home range of *R. megalotis* at 101 m (Figure 2.5a, 2.5b).

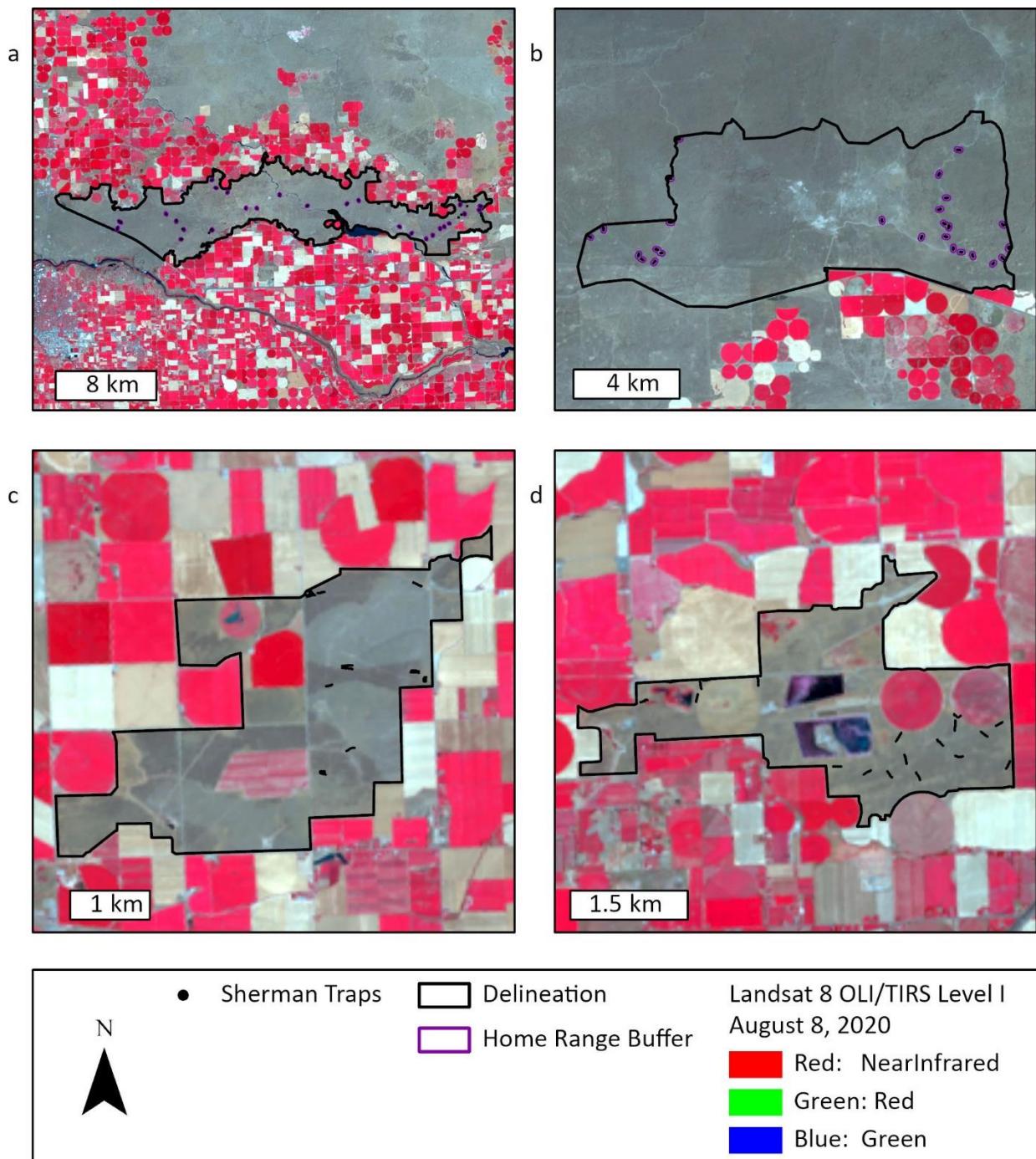


Figure 2.5: Idaho landscape elements sampled and delineated along the edge of contiguous rangeland using Landsat 8 OLI/TIRS Level I imagery from August 8, 2018: (a) corridor complex, (b) intact reference, (c) isolate one, (d) isolate two. (a, b) where no rangeland boundary was distinguishable, topographic or anthropic barriers were used to delineate arbitrary edges at least three times the home range of the western harvest mouse (*Reithrodontomys megalotis*) at 101 m.

The boundary of the reference area had the lowest edge-area ratio (Table 2.3). The corridor complex had an edge-area ratio similar to the reference area than isolates. Isolate 1 and 2 had similar edge-area ratios as one another. However, isolate 2 had the highest edge-area ratio (Table 2.3).

Table 2.3: Whole-patch metrics using the boundary of delineated landscape elements to estimate edge, area, and edge to area ratio in Idaho, United States.

	Edge (km)	Area (km ²)	Edge-Area Ratio (km/km ²)
Corridor Complex	135.7	122.7	1.11
Intact Reference	48.6	81.5	0.60
Isolate 1	21.1	10.4	2.03
Isolate 2	20.4	8.1	2.52

Czechia

455 *A. flavigollis* individuals were captured and sampled. Corresponding to the start of field work, Landsat 8 imagery was acquired for September 9, 2020. Landscape elements were delineated along the edge of contiguous distinct forest habitat (Figure 2.6).

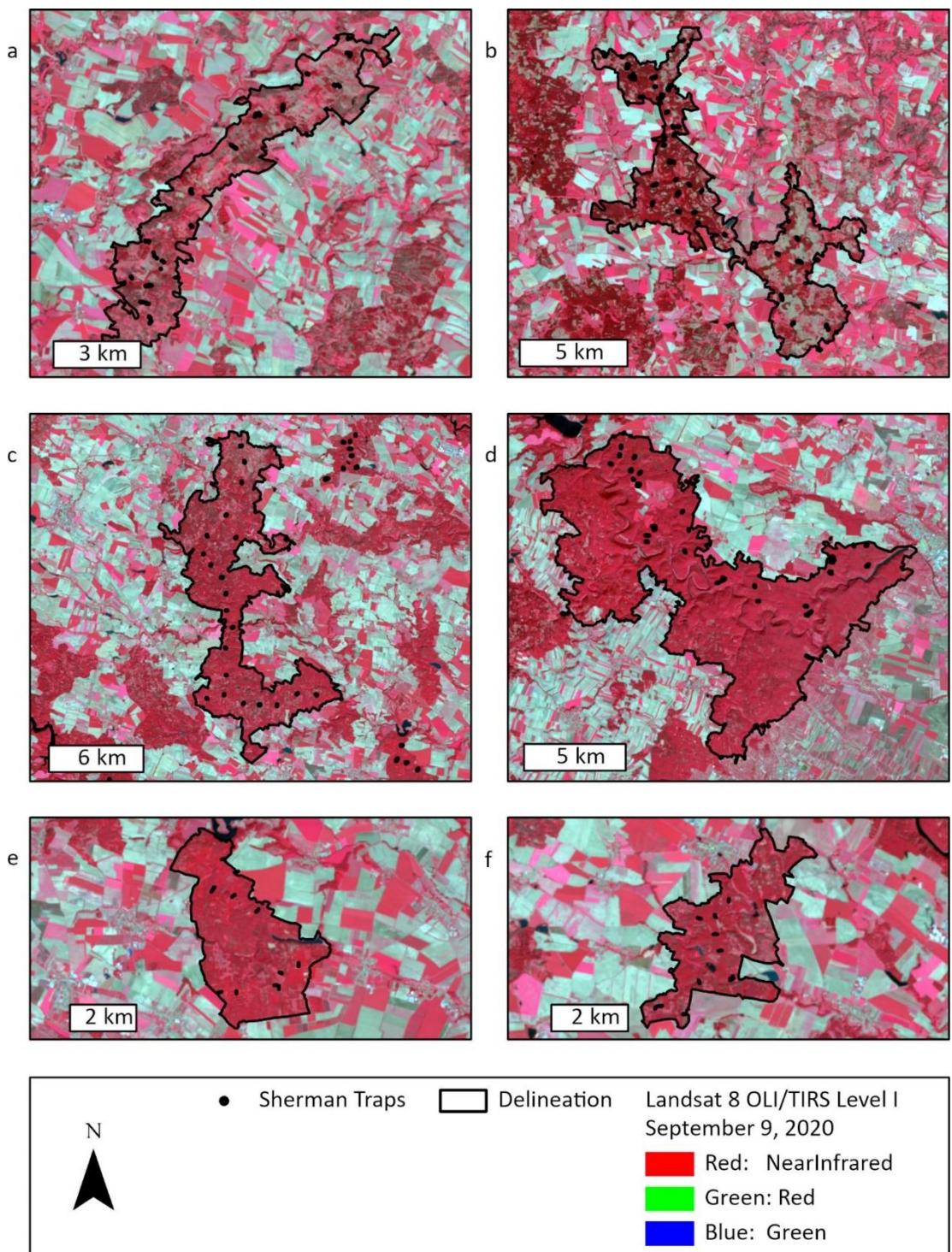


Figure 2.6: Czechia landscape elements sampled and delineated along the edge of contiguous forest using Landsat 8 OLI/TIRS Level I imagery from September 9, 2020: (a) corridor complex 1, (b) corridor complex 2, (c) corridor complex 3, (d) intact reference, (e) isolate one, (f) isolate two.

The boundary of the reference area had the lowest edge-area ratio (Table 2.4). Corridor complex 3 was similar in edge-area ratio to the reference area than it was to corridor complexes 1 and 2. Isolates 1 and 2 were not similar in edge-area ratios; isolate 2 had the highest edge-area. Interestingly, corridor complex 3 was similar to isolate 1 whereas corridor complex 1 was similar to isolate 2 (Table 2.4).

Table 2.4: Whole-patch metrics using the boundary of delineated landscape elements to estimate edge, area, and edge to area ratio in Czechia.

	Edge (km)	Area (km ²)	Edge-Area Ratio (km/km ²)
Corridor Complex 1	59.8	24.3	2.46
Corridor Complex 2	104.9	46.9	2.23
Corridor Complex 3	117.6	77.6	1.51
Intact Reference	119.4	109.9	1.09
Isolate 1	21.3	13.8	1.54
Isolate 2	27.4	9.6	2.86

2.3.2 Reducing the Ambiguity in Identifying Transitional Patch-Corridor Interfaces

The area between the outer and inner start of the corridor (points 1 and 2) and the inner and outer end of the corridor (points 3 and 4) indicates the transitional areas from patch to corridor and corridor to patch, respectively (Figures 2.7-2.11). Total corridor lengths and average widths estimated using the outer start and end points, 1 and 4, varied among landscapes (Table 2.5-2.7). Overall, the outer and inner start of corridor transitional areas were smaller in length than the inner and outer end of the corridor transitional areas.

Across landscapes, the Idaho corridor complex was the largest corridor and with the largest patch areas (Table 2.9). In contrast, the Kansas corridor complex was the smallest corridor and patch areas (Table 2.10). In general, patches had larger areas than isolates with the exception of the Kansas patches and Czechia patches of corridor complex 1.

Kansas

Points were sampled at 10 m intervals along the centerline of the corridor complex.

Total corridor length was 0.45 km with an average width of 0.14 km (Table 2.5; Figure 2.7). The total length of the transitional areas was 0.4 km, with the outer and inner start of the corridor transitional area of 0.02 km smaller than the 0.03 km length from the inner and outer end.

The corridor had a higher edge-area ratio than both patches. Patch 1 had a lower edge-area ratio than patch 2 (Table 2.5). Patches were smaller than isolates (Table 2.2; Table 2.5).

Table 2.5: Patch-corridor-patch metrics delineated from the Kansas *de facto* corridor complex.

	Length (km)	Average Width (km)	Edge (km)	Area (km ²)	Edge-Area Ratio
Corridor	0.45	0.14	0.9	0.05	18.78
Patch 1	-	-	3.3	0.37	8.92
Patch 2	-	-	4.8	0.43	11.21

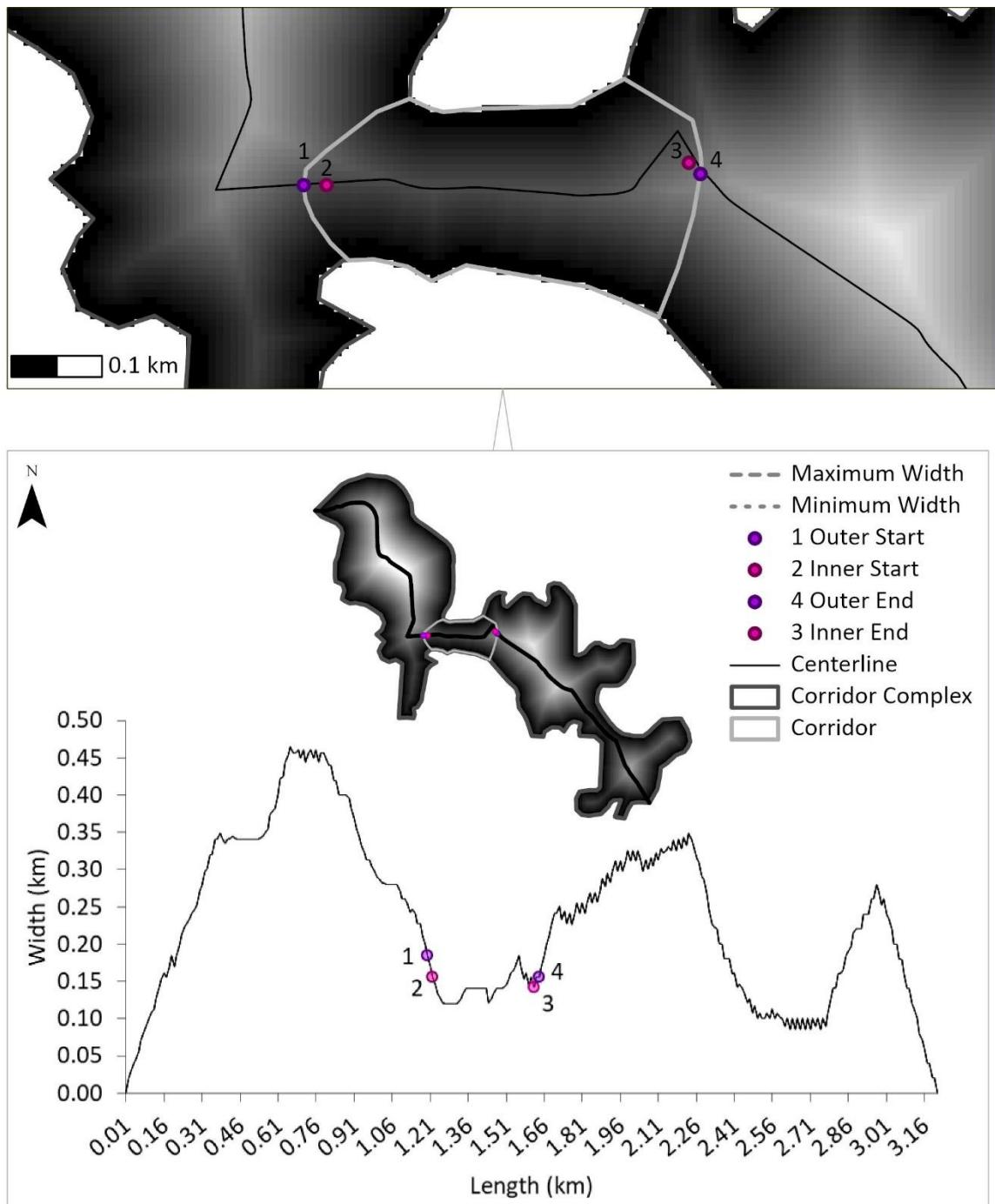


Figure 2.7: Centerline of *de facto* corridor complex in Kansas, United States where the greatest percent change in width was used to identify transitional areas of patch-corridor interfaces between two widest and narrowest points. Point 1 and 2 represent where patch one transitions into the corridor while point 3 and 4 represent where the corridor transitions into patch two. The corridor was delineated from the inner points (2, 3) tapered to the outer points (1, 4).

Idaho

Points were sampled at 90 m intervals along the centerline of the corridor complex. The total corridor length was 4.59 km with an average width of 2.98 km (Table 2.9; Figure 2.8). The total length of the transitional areas was 2.43 km, with the outer and inner start of the corridor transitional area of 0.18 km smaller than the 1.89 km length from the inner and outer end of the corridor.

The corridor had a similar edge-area ratio to both patches; lower than patch 1 but higher than patch 2. Patch 1 had a lower edge-area ratio than patch 2 (Table 2.6). Patches were larger than isolates (Table 2.3; Table 2.6).

Table 2.6: Patch-corridor-patch metrics delineated from the Idaho *de facto* corridor complex.

	Length (km)	Average Width (km)	Edge (km)	Area (km ²)	Edge-Area Ratio
Corridor	4.59	2.98	12.7	9.8	1.30
Patch 1	-	-	50.6	46.3	1.09
Patch 2	-	-	88.3	66.6	1.33

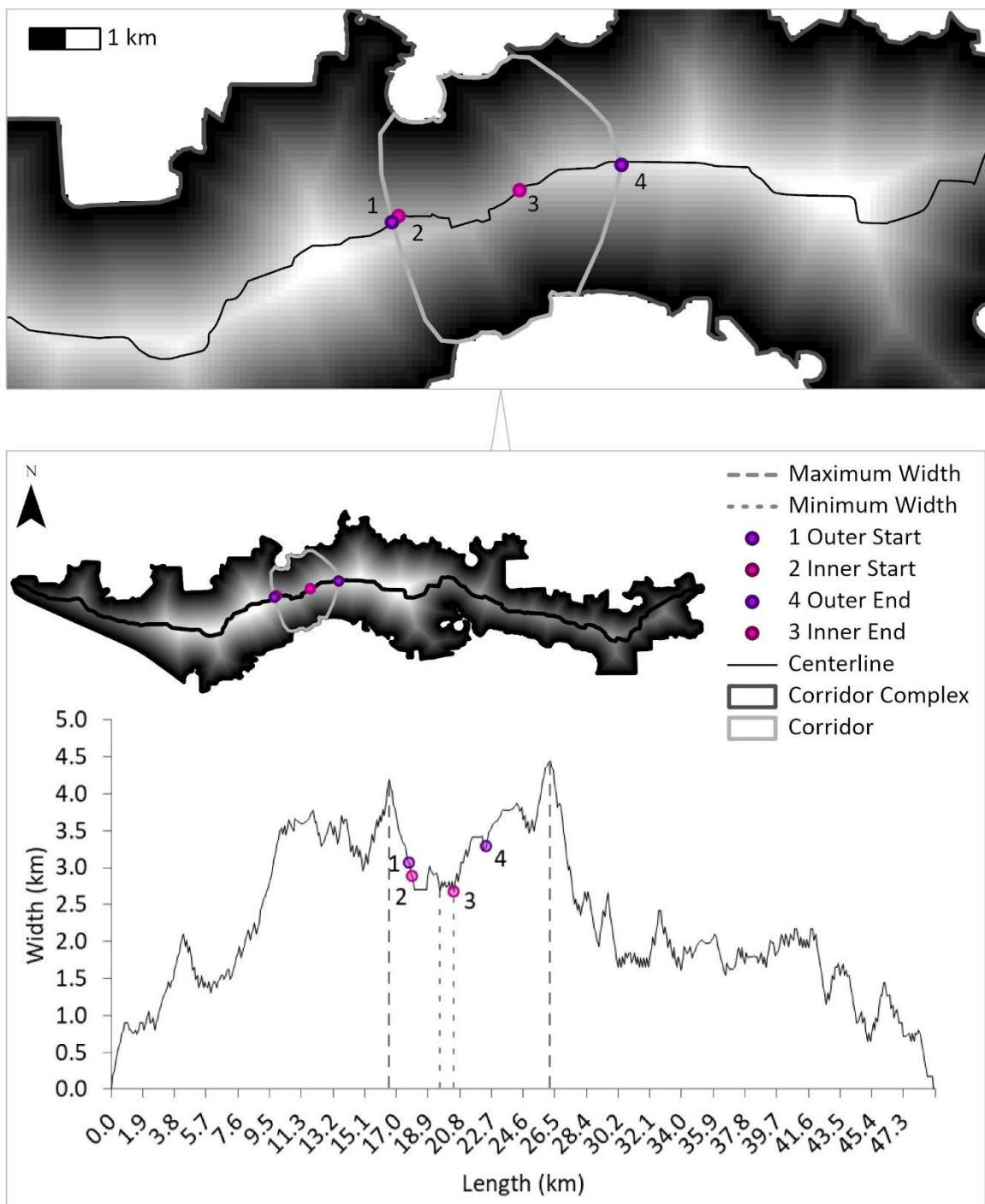


Figure 2.8: Centerline of de facto corridor complex in Idaho, United States where the greatest percent change in width was used to identify transitional areas of patch-corridor interfaces between two widest and narrowest points. Point 1 and 2 represent where patch one transitions into the corridor while point 3 and 4 represent where the corridor transitions into patch two. The corridor was delineated from the inner points (2, 3) tapered to the outer points (1, 4).

Czechia

Points were sampled at 85 m intervals along the centerline of corridor complex 1. The total length of corridor 1 was 3.57 km with an average width of 1.07 km (Table 2.7; Figure 2.9). The total length of the transitional areas was 2.38 km, with the outer and inner start of the corridor transitional area of 0.85 km smaller than the 0.34 km length from the inner and outer end of the corridor.

Corridor 1 had a similar edge-area ratio to both patches. Patch 1 of corridor complex 1 had more edge, greater area, and higher edge-area ratio than patch 2 (Table 2.7). Patches were similar in area with isolates (Table 2.4; Table 2.7).

Points were sampled at 100 m intervals along the centerline of corridor complex 1. The total length of corridor 2 was 3.6 km with an average width of 0.42 km (Table 2.7; Figure 2.10). The total length of the transitional areas was 3.1 km, with the outer and inner start of the corridor transitional area of 0.2 km smaller than the 0.3 km length from the inner and outer end of the corridor.

Corridor 2 had a higher edge-area ratio than both patches. Patch 1 of corridor complex 2 had more edge, greater area, and higher edge-area ratio than patch 2 (Table 2.7). Patches were larger than isolates (Table 2.4; Table 2.7).

Points were sampled at 70 m intervals along the centerline of corridor complex 1. The total length of corridor 3 was 5.39 km with an average width of 1.1 km (Table 2.7; Figure 2.11). The total length of the transitional areas was 3.43 km, with the outer and inner start of the

corridor transitional area of 1.75 km smaller than the 5.39 km length from the inner and outer end of the corridor.

Corridor 3 had a higher edge-area ratio than both patches. Patch 1 of corridor complex 3 had fewer edges, a smaller area, and a higher edge-area ratio than patch 2 (Table 2.7). Patches were larger than isolates (Table 2.4; Table 2.7).

Table 2.7: Patch-corridor-patch metrics delineated from the three Czechia *de facto* corridor complexes.

	Length (km)	Average Width (km)	Edge (km)	Area (km ²)	Edge-Area Ratio
Corridor 1	3.57	1.07	8.3	3.1	2.67
Patch 1	-	-	33.0	12.0	2.74
Patch 2	-	-	24.5	9.1	2.69
Corridor 2	3.60	0.42	9.8	1.9	5.10
Patch 1	-	-	55.4	24.1	2.30
Patch 2	-	-	42.7	20.9	2.04
Corridor 3	5.39	1.10	13.2	5.2	2.55
Patch 1	-	-	42.1	26.4	1.60
Patch 2	-	-	71.2	46.1	1.54

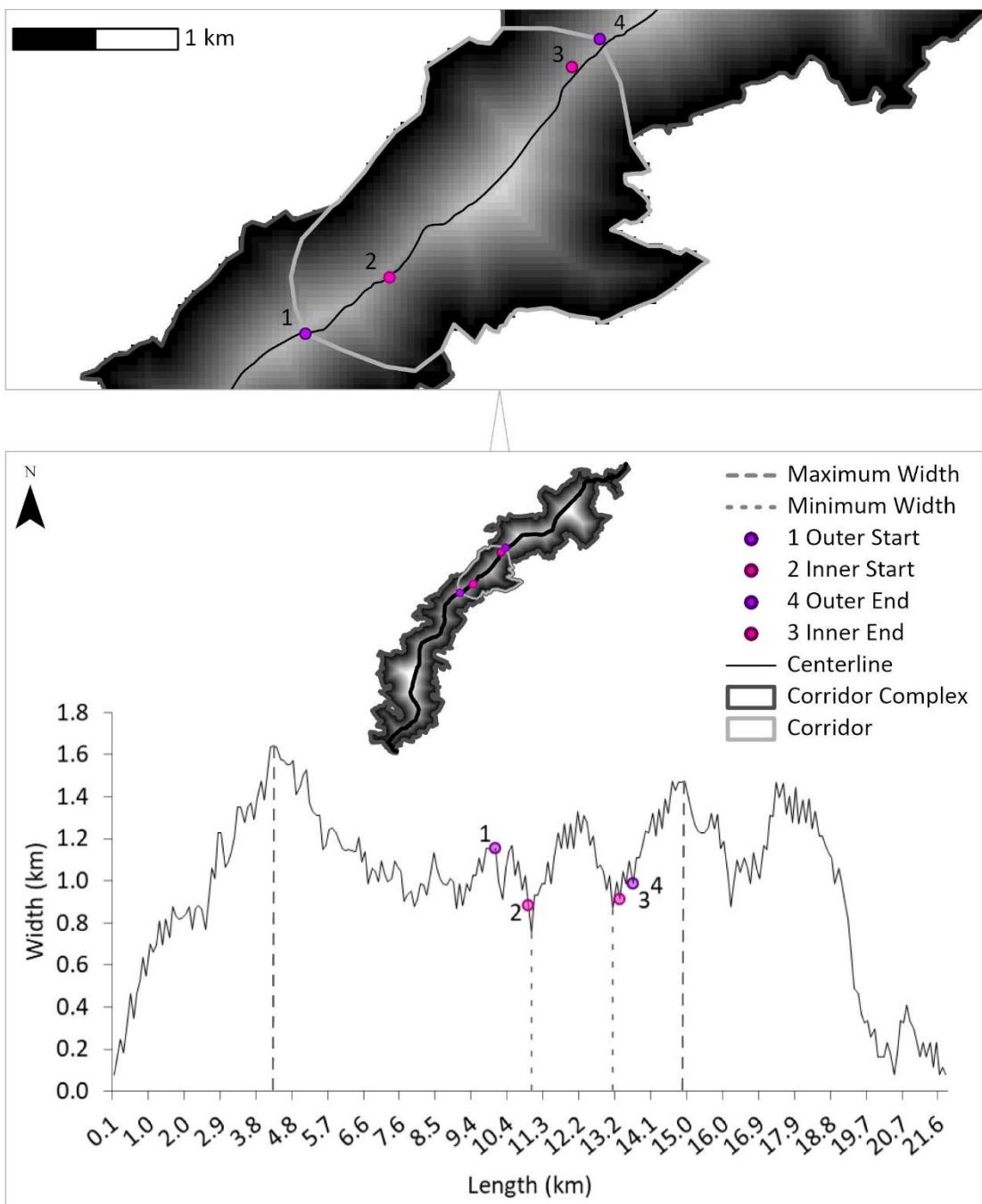


Figure 2.9: Centerline of *de facto* corridor complex 1 in Czechia where the greatest percent change in width was used to identify transitional areas of patch-corridor interfaces between two widest and narrowest points. Point 1 and 2 represent where patch one transitions into the corridor while point 3 and 4 represent where the corridor transitions into patch two. The corridor was delineated from the inner points (2, 3) tapered to the outer points (1, 4).

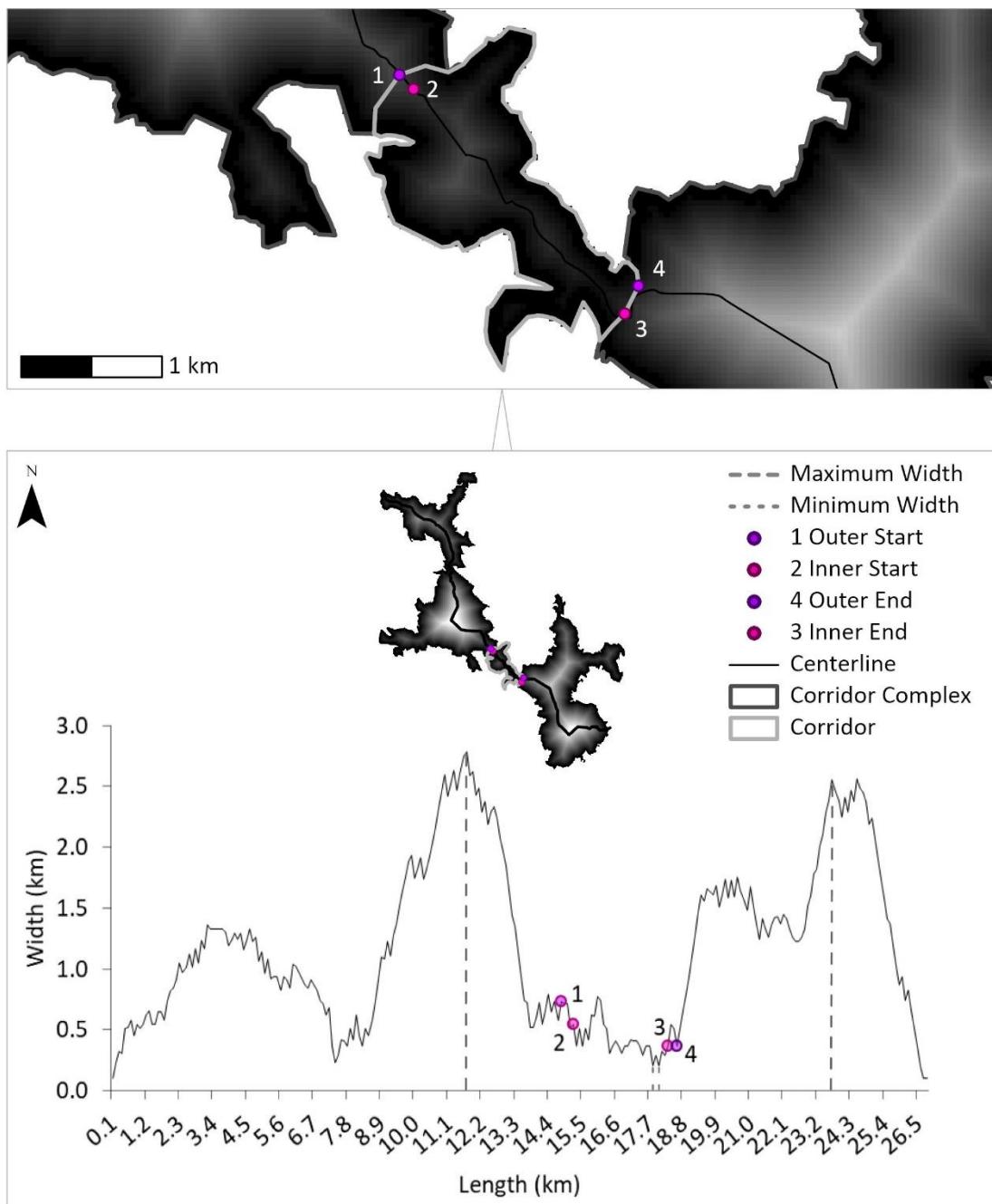


Figure 2.10: Centerline of *de facto* corridor complex 2 in Czechia where the greatest percent change in width was used to identify transitional areas of patch-corridor interfaces between two widest and narrowest points. Point 1 and 2 represent where patch one transitions into the corridor while point 3 and 4 represent where the corridor transitions into patch two. The corridor was delineated from the inner points (2, 3) tapered to the outer points (1, 4).

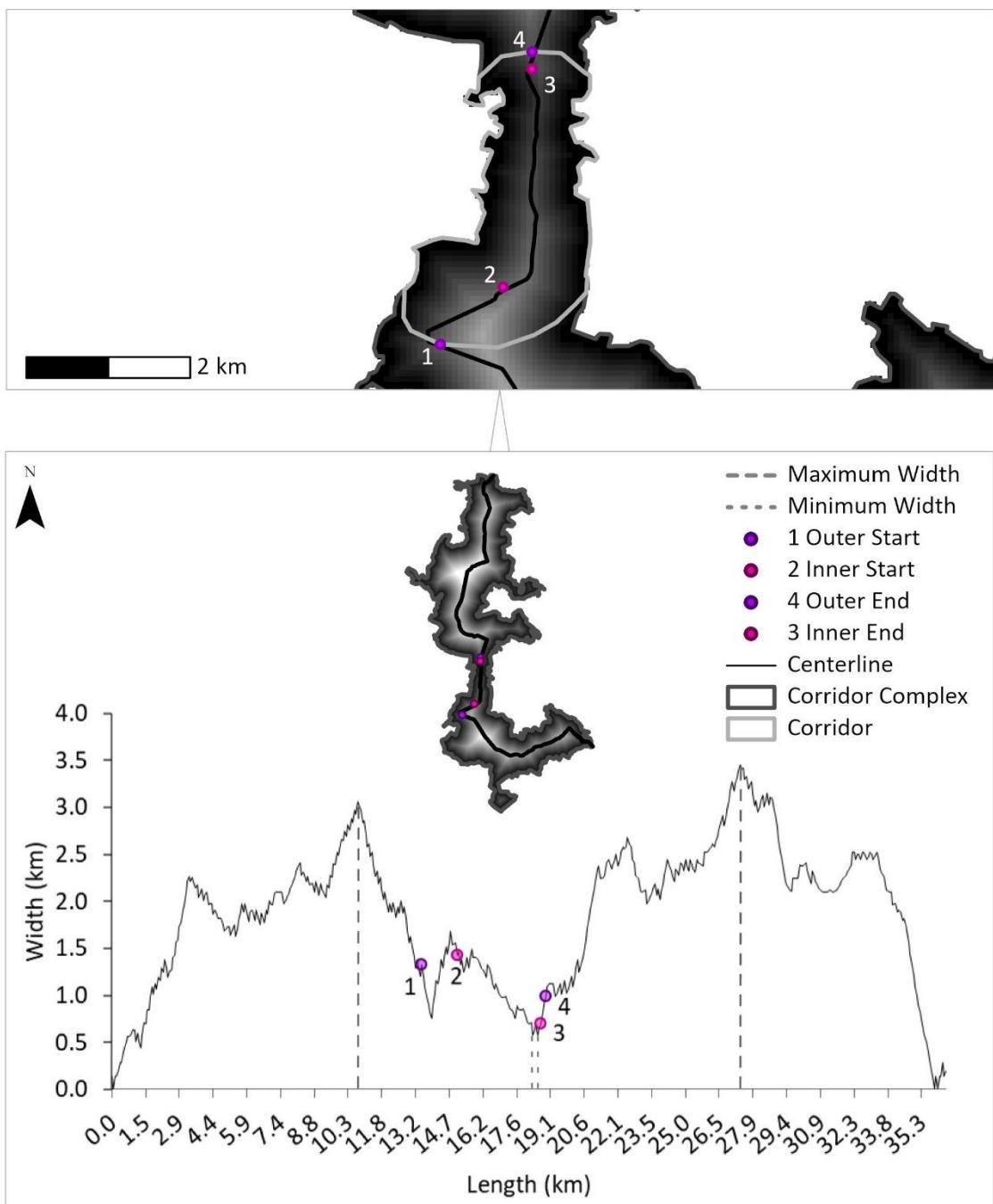


Figure 2.11: Centerline of *de facto* corridor complex 3 in Czechia where the greatest percent change in width was used to identify transitional areas of patch-corridor interfaces between two widest and narrowest points. Point 1 and 2 represent where patch one transitions into the corridor while point 3 and 4 represent where the corridor transitions into patch two. The corridor was delineated from the inner points (2, 3) tapered to the outer points (1, 4).

2.3.3 Quantifying Land Cover and Land Use Across Landscape Mosaics

Overall, the study areas were composed of a high percent of agriculture dominating the matrix (Figure 2.12). Developed areas composed a small percentage of land covers relative to natural land cover types and areas used for agriculture. The Kansas study area was composed of all five land cover classes (Table 2.1). The Idaho study area had no forested areas whereas there was no rangeland in Czechia but both study areas were composed of 1% water (Figure 2.12).

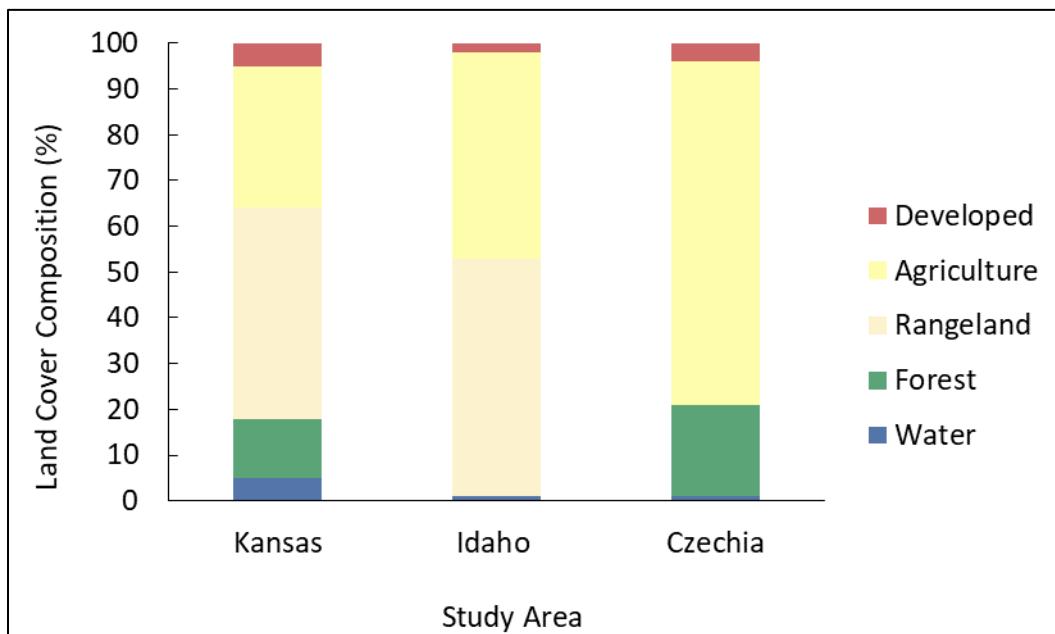


Figure 2.12: Percent land cover composition across study areas in Kansas, Idaho, United States and Czechia.

Kansas

The landscape was classified into five land cover types: developed, agriculture, rangeland, forest, and water. Commission and omission errors were highest for the developed class at 28% (Table 2.8). In contrast, commission errors were lowest for forest focal habitat at

1% while omission errors were lowest for the rangeland class at 5% (Table 2.8). Kappa = 0.92, for an overall 92% classification accuracy.

Table 2.8: Error matrix to assess accuracy of Kansas supervised land cover classification. Major diagonal depicts 461 of 500 accurate pixels, kappa = 0.92 for an overall 92% accuracy.

		Reference						
		D	Ag	R	F	W	Σ	Commission Errors
Classified	Developed (D)	21	1	4	3	0	29	28%
	Agriculture (Ag)	0	130	7	4	1	142	8%
	Rangeland (R)	8	5	219	3	1	236	7%
	Forest (F)	0	0	1	67	0	68	1%
	Water (W)	0	0	0	1	24	25	4%
Σ		29	136	231	78	26	461	
Omission Errors		28%	4%	5%	14%	8%	Kappa	0.92

Forested small mammal habitat composed 13% of the landscape (Figure 2.12). Forests were embedded in a matrix composed of 46% rangeland, 31% agriculture, and 10% other land cover and land uses. Thus, 13% of the landscape composed habitat for focal species with 87% non-habitat encompassing the matrix (Figure 2.12).

Idaho

Using Landsat 8 imagery for August 8, 2018, the landscape was classified into four land cover types: developed, agriculture, rangeland, and water. Commission errors were highest for the water class at 13% while there was no commission error for the developed class. In contrast, omission errors were highest for the developed class at 67% and lowest for rangeland focal habitat at 1% (Table 2.9). Kappa = 0.95, for an overall 92% accuracy.

Table 2.9: Error matrix to assess accuracy of Idaho supervised land cover classification. Major diagonal depicts 476 of 500 accurate pixels, kappa = 0.95 for an overall 95% accuracy.

		Reference				Σ	Commission Errors
		D	Ag	R	W		
Classified	Developed (D)	6	0	0	0	6	0%
	Agriculture (Ag)	9	210	7	0	226	7%
	Rangeland (R)	3	3	253	1	260	3%
	Water (W)	0	0	1	7	8	13%
Σ		18	213	261	8	476	
Omission Errors		67%	1%	3%	13%		
						Kappa	0.95

Rangeland small mammal habitat composed 52% of the landscape (Figure 2.12).

Rangelands were embedded in a matrix composed of 45% agriculture and 3% other land cover and land uses. Thus, 52% of the landscape composed habitat for focal species with 48% non-habitat encompassing the matrix (Figure 2.12).

Czechia

Using Landsat 8 imagery from September 9, 2020, the landscape was classified into four land cover types: developed, agriculture, forest, and water. Commission errors were highest for the agriculture class at 5% while lowest for the water class, as there was no commission error (Table 2.10). In contrast, omission errors were highest for the water class at 67% and lowest for the agriculture class at 1% (Figure 2.15). Forest focal habitat had a 3% commission error and a 12% omission error. Kappa = 0.95 for an overall 95% classification accuracy.

Table 2.10: Error matrix to assess accuracy of Czechia supervised land cover classification. Major diagonal depicts 476 of 500 accurate pixels, kappa = 0.95 for an overall 95% accuracy.

		Reference				Σ	Commission Errors
		D	Ag	F	W		
Classified	Developed (D)	23	1	0	0	24	4%
	Agriculture (Ag)	3	334	16	0	353	5%
	Forest (F)	1	1	118	2	122	3%
	Water (W)	0	0	0	1	1	0%
Σ		27	336	134	3	476	
Omission Errors		15%	1%	12%	67%		
		Kappa				0.95	

Forested small mammal habitat composed 20% of the landscape (Figure 2.12). Forests were embedded in a matrix composed of 75% agriculture and 5% other land cover and land uses. Thus, 20% of the landscape composed habitat for focal species with 80% non-habitat encompassing the matrix (Figure 2.12).

2.3.4 Quantifying the Composition of Habitat Within Landscape Element Boundaries

Across all landscape elements, reference areas were composed of a higher percentage of habitat. In general, isolates had the lowest composition of habitat within their boundaries. However, the exception was Czechia isolates. The percentage of high productivity estimated from NDVI followed a similar trend: where reference areas were composed of a higher percent of productivity compared to corridor complexes and isolates were the lowest. Similarly, the exception to this was the Czechia isolates but also the Kansas corridor complex and isolate 2.

Kansas

The corridor complex and reference area were both composed of 93% forested habitat (Table 2.11; Figure 2.13). Habitat within the corridor itself decreased to 84% with patch

elements both composed of 95% habitat Isolates 1 and 2 had a lower composition of habitat, with isolate 2 being the lowest (Table 2.11; Figure 2.13).

Table 2.11: Within-patch metrics of delineated landscape elements in Kansas, United States.

	Core Area (km ²)	Habitat (%)	High Productivity (%)
Corridor Complex	0.63	93	71
Intact Reference	0.66	93	44
Isolate 1	0.69	90	65
Isolate 2	0.66	83	80
Corridor	0.02	84	59
Patch 1	0.28	95	63
Patch 2	0.30	95	80

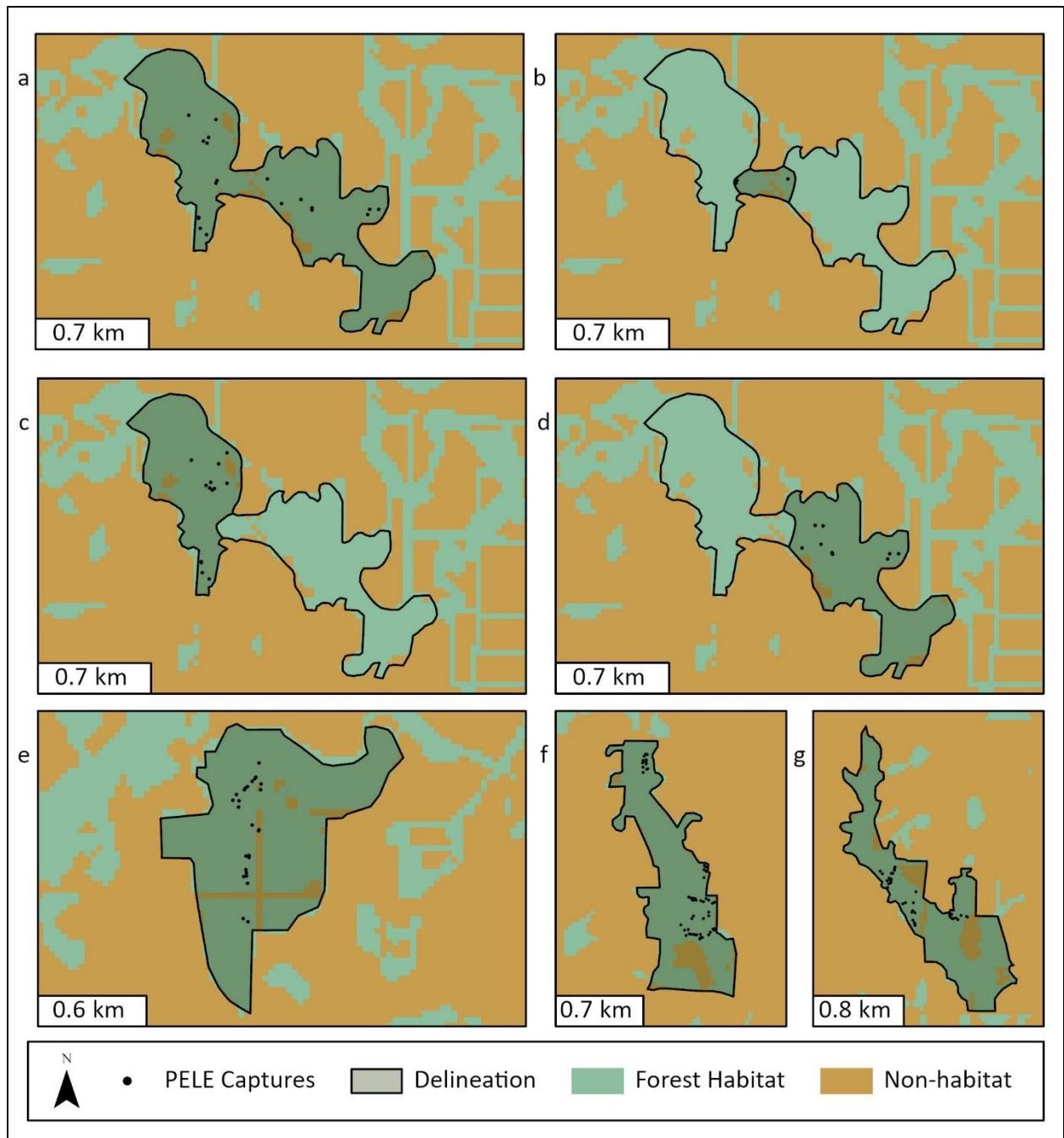


Figure 2.13: Kansas landscape elements composed of forest habitat and white-footed mouse (*Peromyscus leucopus*; PELE) captures. Proportion of individuals captured reported in parentheses from 150 total: (a) corridor complex, 93% habitat, 27 PELE (18%); (b) corridor, 84% habitat, 4 PELE (3%); (c) patch one, 95% habitat, 13 PELE (9%); (d) patch two, 95% habitat, 10 PELE (7%); (e) intact reference, 93% habitat, 26 PELE (17%); (f) isolate one, 90% habitat, 59 PELE (39%); (g) isolate two, 83% habitat, 38 PELE (25%).

The reference area and isolates had similar and greater core areas than the corridor complex (Table 2.11). Patch 1 and patch 2 elements were similar in the core area while the corridor configuration had a smaller core area.

Landsat 8 imagery acquired for June 15, 2020 was used to calculate NDVI across the study area. NDVI values greater than 0.5 were identified as healthy and dense forest with high productivity. Interestingly, the reference area had the lowest forest productivity (Table 2.12). In contrast, isolate 2 had the highest productivity, similar to that of patch 2. Patch-corridor-patch elements varied in their productivity; with patch 2 composed of the highest productivity and the corridor and patch 1 being of similar, moderate productivity (Table 2.11).

NDVI values within the reference area and the corridor had the same coefficient of variation with the corridor complex being slightly lower. Patch 2 had the lowest coefficient of variation, similar to isolate 2 (Table 2.12). In contrast, isolate 2 had the highest variation, similar to patch 1 (Table 2.12).

Table 2.12: NDVI values within delineated landscape elements; including patch-corridor-patch elements in Kansas, United States.

	Minimum	Maximum	Range	Average	Variation (%)
Corridor Complex	0.23	0.60	0.37	0.52	12
Intact Reference	0.27	0.58	0.30	0.48	13
Isolate 1	0.16	0.60	0.44	0.49	17
Isolate 2	0.10	0.60	0.50	0.52	11
Corridor	0.33	0.58	0.25	0.50	13
Patch 1	0.23	0.60	0.37	0.51	15
Patch 2	0.28	0.59	0.32	0.53	9

Idaho

The corridor complex and patch-corridor-patch elements had high habitat compositions similar to the reference area (Table 2.13; Figure 2.14). The reference area was entirely composed of rangeland habitat. Isolates 1 and 2 had a lower composition of habitat, with isolate 2 being the lowest (Table 2.13; Figure 2.14).

Table 2.13: Within-patch metrics of delineated landscape elements in Idaho, United States.

	Core Area (km ²)	Habitat (%)	High Productivity (%)
Corridor Complex	118.7	96	80
Intact Reference	80.0	100	95
Isolate 1	9.7	82	70
Isolate 2	7.5	61	35
Corridor	9.4	95	58
Patch 1	44.8	96	88
Patch 2	64.0	95	77

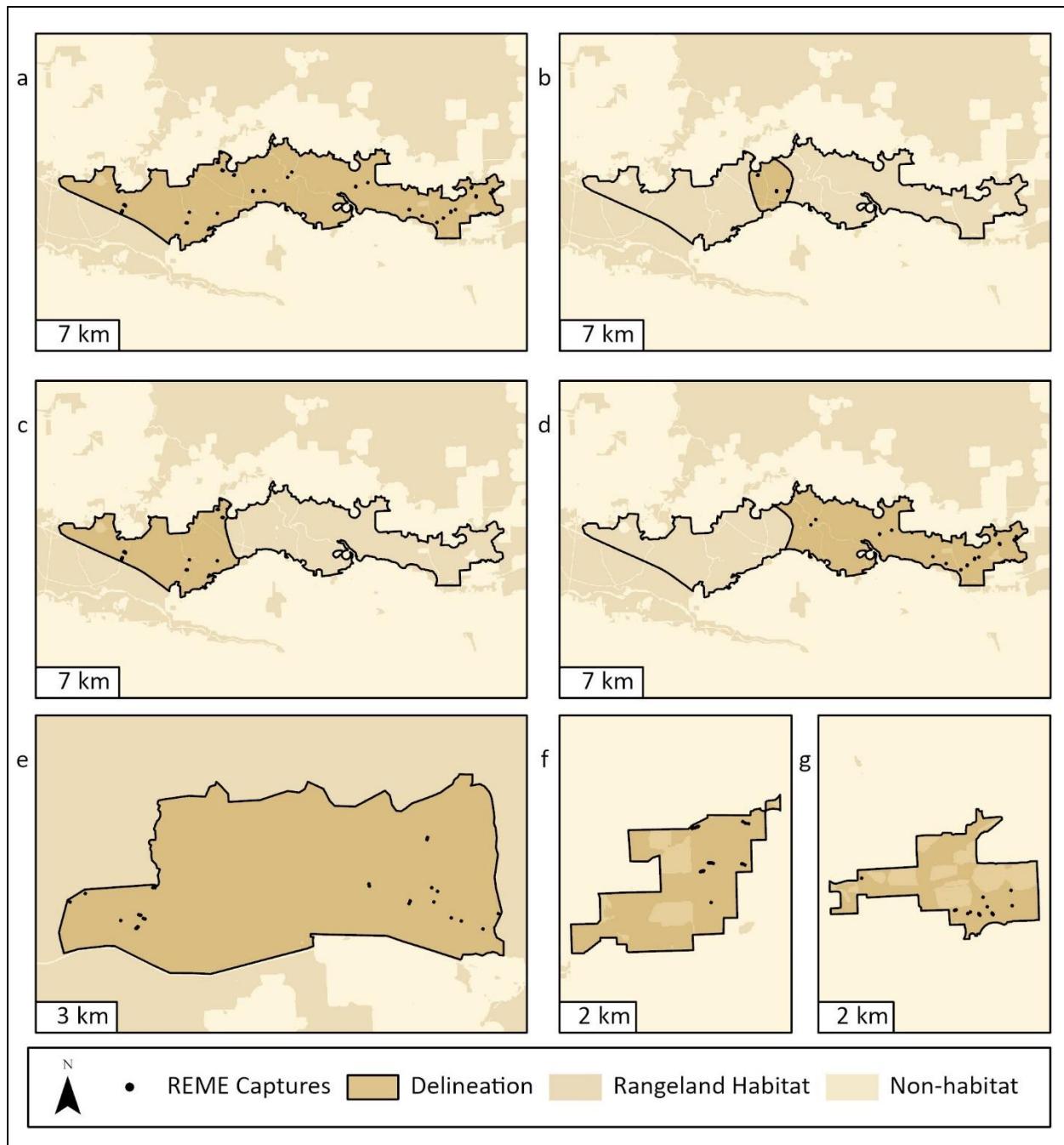


Figure 2.14: Idaho landscape elements composed of rangeland habitat and western harvest mouse (*Reithrodontomys megalotis*; REME) captures. Proportion of individuals captured reported in parentheses from 193 total: (a) corridor complex, 96% habitat, 93 REME (48%); (b) corridor, 95% habitat, 11 REME (6%); (c) patch one, 96% habitat, 46 REME (24%); (d) patch two, 95% habitat, 36 REME (19%); (e) intact reference, 100% habitat, 40 REME (21%); (f) isolate one, 82% habitat, 37 REME (19%); (g) isolate two, 61% habitat, 23 REME (12%).

The corridor complex had the greatest core area (Table 2.13). Isolates 1 and 2 were similar in core area to the corridor.

The same Landsat 8 imagery acquired for August 8, 2018 used to classify land cover and delineate landscape elements was used to calculate NDVI across the study area (Table 2.14).

NDVI values ranging from 0.1 - 0.15 were identified as healthy and dense rangeland with high productivity. The reference area had the highest percent of productivity. In contrast, isolate 2 had the lowest productivity. The corridor complex was composed of high productivity. However, 60% of the corridor was composed of high productivity (Table 2.13).

NDVI values within the reference area had the lowest coefficient of variation (Table 2.14). The patches of the corridor complex had similar variation of the corridor complex. In contrast, isolates 1 and 2 had the highest variation of NDVI values (Table 2.14).

Table 2.14: NDVI values within landscape elements; including patch-corridor-patch elements in Idaho, United States.

	Minimum	Maximum	Range	Average	Variation (%)
Corridor Complex	-0.13	0.60	0.73	0.14	26
Intact Reference	0.06	0.25	0.18	0.11	8
Isolate 1	-0.14	0.59	0.74	0.17	57
Isolate 2	-0.14	0.52	0.66	0.18	50
Corridor	-0.05	0.37	0.43	0.15	10
Patch 1	-0.07	0.50	0.58	0.13	29
Patch 2	-0.13	0.60	0.73	0.14	25

Czechia

Corridor complex 1 had a similar habitat composition to the reference and isolates (Table 2.15; Figure 2.15, 2.16). In contrast, corridor complexes 1 and 2 had a high composition of non-habitat (Table 2.15).

Table 2.15: Within-patch metrics of delineated landscape elements in Czechia.

	Core Area (km ²)	Habitat (%)	High Productivity (%)
Corridor Complex 1	22.5	59	50
Corridor Complex 2	43.8	61	34
Corridor Complex 3	74.2	80	51
Intact Reference	106.4	89	72
Isolate 1	13.2	88	75
Isolate 2	8.8	80	76
Corridor 1	2.9	56	44
Patch 1	11.1	65	36
Patch 2	8.4	51	42
Corridor 2	1.6	63	38
Patch 1	22.4	69	25
Patch 2	18.7	54	41
Corridor 3	4.8	90	58
Patch 1	25.1	82	61
Patch 2	44.0	77	44

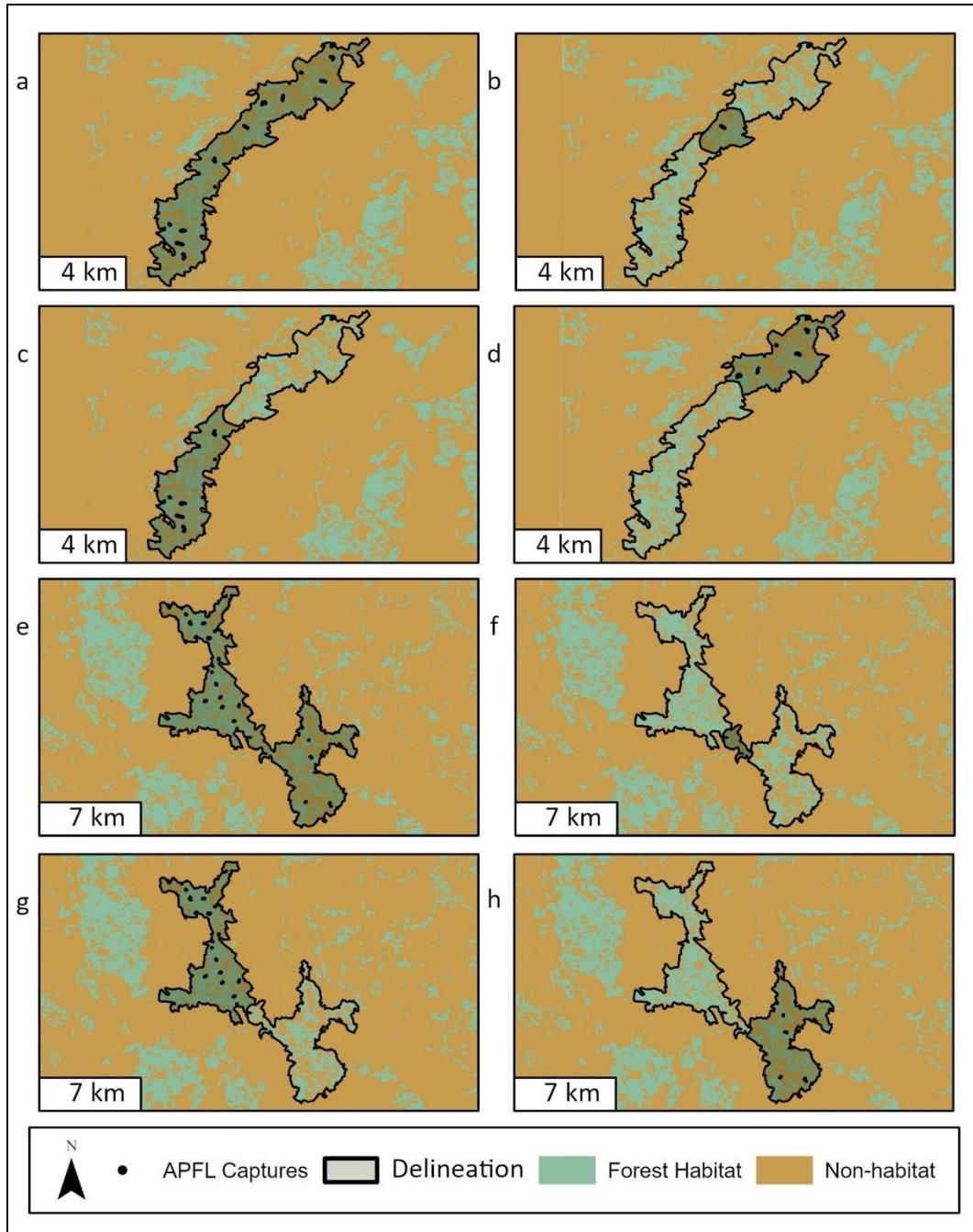


Figure 2.15: Czechia landscape elements composed of forest habitat and yellow-necked mouse (*Apodemus flavicollis*; APFL) captures. Proportion of individuals captured reported in parentheses from 455 total (see also Figure 2.16): (a) corridor complex 1, 59% habitat, 217 APFL (48%); (b) corridor 1, 56% habitat, 16 APFL (4%); (c) patch one, 65% habitat, 135 APFL (30%); (d) patch two, 51% habitat, 66 APFL (15%); (e) corridor complex 2, 61% habitat, 63 APFL (14%); (f) corridor 2, 63% habitat, 0 APFL (0%); (g) patch one, 59% habitat, 51 APFL (11%); (h) patch two, 54% habitat, 12 APFL (3%).

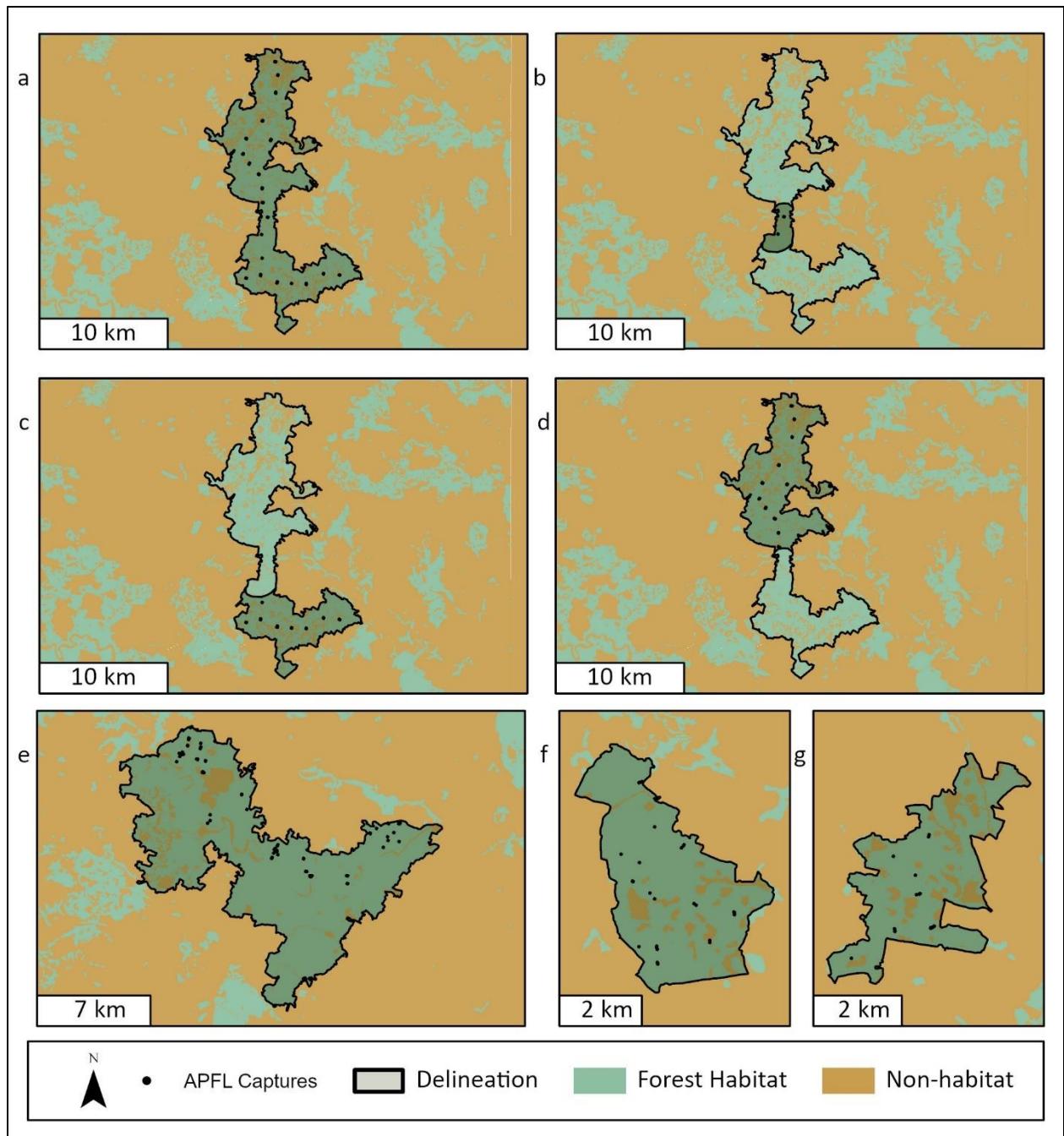


Figure 2.16: Czechia landscape elements composed of forest habitat and yellow-necked mouse (*Apodemus flavicollis*; APFL) captures. Proportion of individuals captured reported in parentheses from 455 total (see also Figure 2.15): (a) corridor complex 3, 80% habitat, 71 APFL (16%); (b) corridor 3, 90% habitat, 4 APFL (1%); (c) patch one, 82% habitat, 19 APFL (4%); (d) patch two, 77% habitat, 48 APFL (11%); (e) intact reference, 89% habitat, 55 APFL (12%); (f) isolate one, 88% habitat, 24 APFL (5%); (g) isolate two, 80% habitat, 25 APFL (5%).

The reference area had the greatest core area (Table 2.15). Isolates 1 and 2 were similar in the core area to corridor complexes 1 and 2 patches but the corridor of corridor complex 3.

Landsat 8 imagery acquired for July 30, 2020 was used to calculate NDVI values across the study area. NDVI values ranging from 0.24 – 0.37 were identified as healthy and dense forest with high productivity. Isolate 2 had the highest composition of productive forest (Table 2.15). In contrast, corridor complex 2 and patch-corridor-patch elements were composed of the lowest productivity. Corridor complexes 2 and 3 and both their patch-corridor-patch elements were moderately composed of productive vegetation (Table 2.15).

NDVI coefficient of variation values within the reference area were the same as corridor complex 3 (Table 2.16). Corridor complexes 1 and 2 were similar in variation and had the highest values excluding patch-corridor-patch elements. Patch-corridor-patch elements of corridor complex 2 were the highest, with similar variations to patch-corridor-patch elements of corridor complex 1. Patches 1 and 2 of corridor complex 3 were similar to isolates 1 and 2 (Table 2.16).

Table 2.16: NDVI values within Czechia landscape elements; including patch-corridor-patch elements.

	Minimum	Maximum	Range	Average	Variation (%)
Corridor Complex 1	-0.08	0.57	0.64	0.34	23
Corridor Complex 2	-0.11	0.56	0.66	0.30	26
Corridor Complex 3	-0.08	0.58	0.66	0.37	16
Intact Reference	-0.16	0.61	0.77	0.40	16
Isolate 1	-0.08	0.56	0.64	0.40	15
Isolate 2	-0.10	0.58	0.68	0.37	17
Corridor 1	0.12	0.56	0.44	0.33	26
Patch 1	-0.04	0.57	0.61	0.34	21
Patch 2	-0.08	0.54	0.61	0.33	24
Corridor 2	-0.11	0.52	0.62	0.29	34
Patch 1	-0.09	0.54	0.63	0.30	24
Patch 2	0.07	0.56	0.48	0.30	28
Corridor 3	-0.08	0.54	0.63	0.38	14
Patch 1	-0.07	0.58	0.65	0.38	15
Patch 2	-0.06	0.57	0.63	0.36	17

2.4 Discussion

A critical component to understanding the efficacy of conservation corridors is the ability to identify corridor termini. However, rooted in this knowledge gap is the ability to delineate the boundaries of landscape elements. I'm hopeful the methodologies I've developed to delineate corridor boundaries and identify patch-corridor interfaces will ignite conversations among researchers and conservationists to continue to address critical issues.

The majority of research fails to adequately define and measure the extent of edges and arbitrarily defining the edge of habitat within a fixed distance is insufficient (Murcia 1995, Klein and Cameron 2012). The distance at which abiotic and biotic factors influence an interior habitat varies from 5 to 50 m from edge into the core area (Murcia 1995). Thus, natural land cover is characterized by gradients of change from edge to core which influences the

delineation of edge areas (Klein and Cameron 2012). The technical definition of core area is defined by the edge depth criterion of the user and represents the patch area not influenced by edge effects (McGarigal 1995). As core areas are frequently used by species as their home range and are expected to be composed of dependable resources (Samuel et al. 1985), future research should implement a species perspective, or multispecies perspective, to quantify core areas with vegetation indices indicative of quality habitat.

Changes in environmental conditions influence the composition of habitat within landscape elements. For example, since 2004 in Czechia, the spread of emerald ash borer (*Agrilus planipennis*), has threatened ash trees across Europe. In recent years, the invasive species has resulted in the dramatic decline of tree species within corridor complex 2. As such, the corridor complex was vastly different at the start of field collection whereas now, the patch has been clear-cut.

While a species perspective was implemented to minimize the subjectivity in the delineation of the boundaries of landscape elements, a single species approach may have limitations. Species have varying sensitivities to edges and during certain life stages species may be willing to cross through the matrix. For example, Keeley et al. (2017) found that kinkajou (*Potos flavus*) movements within their home ranges were highly structured by forest interiors but during natal and breeding dispersal events, could willingly move through highly inhospitable anthropic landscape matrices. Consequently, delineating rigorous boundaries may restrict spatial models from quantifying or predicting critical ecological processes that influence ecosystem functioning and metapopulation dynamics. However, even if we accept that hard

boundaries may not restrict all species movements in all seasons, researchers still must identify a method for minimizing subjectivity when bounding study systems for spatial modelling.

Whether the species in question is willing to cross the matrix or not, the ability to delineate matrix from habitat for focal species is a critical first step in identifying the propensity for that species to cross the matrix in the first place.

Although the goal of identifying corridor termini using transitional areas was to reduce the ambiguity, it has increased the lexical complexity used to identify corridors. Specifically, as natural landscape elements start to transition into corridors at areas in which species are observed to be influenced by edges. As such, quantifying the variation in potential transitional areas could have critical implications for species that are edge sensitive. To the best of my knowledge, there have been few studies to observe this tendency and quantify its effects.

In terms of structural landscape patterns that influences species processes, these findings suggest that corridor management plans should consider extending management into patches. A recent evaluation of best management practices for corridors noted it was critical to manage for edge effects along corridor and patch boundaries but failed to identify transitional areas of patches into corridors as potential areas where special management actions ought to be taken (Gregory et al. 2021). It is critical for future research to continue to quantify and assess these patterns and processes within transitional areas to determine if we need to manage corridors distinctly from patches or if we should extend management plans into patches to promote corridor efficacy.

The structural configuration and heterogeneity in composition within real world corridors is more complex than experimental corridor systems. Assessing the efficacy of real-world corridors is critical as conservation corridors are designed and built in the world and species will respond to the complex heterogeneity of the landscape.

CHAPTER 3

INVESTIGATING THE DEGREE TO WHICH THE PRESENCE OF A CORRIDOR INFLUENCES THE STRUCTURAL AND FUNCTIONAL CONNECTIVITY OF SMALL MAMMAL HABITATS

3.1 Introduction

Global conservation efforts prioritize landscape connectivity, the degree to which species movement is facilitated or impeded by a landscape. The literature differentiates two types of connectivity (Taylor et al. 1993). Structural connectivity describes the physical linkages connecting two or more patches of similar land cover; regardless of the ability of wildlife to use the linkages. Functional connectivity accounts for the ability of wildlife to use linkages to move between patches of natural land cover (Tischendorf and Fahrig 2000; Taylor et al. 2006).

To facilitate connectivity, conservationists and land managers often depend on structuring ecological networks with conservation corridors (Ferreras 2001; Baguette et al. 2013). Conservation corridors, natural swaths of land connecting patches of similar land cover, are frequently cited and implemented as a preventative or restorative strategy to counteract the consequences of fragmentation (Heller and Zavaleta 2009). Such conservation measures aim to enhance demographic stability, gene flow, or patch recolonization and occupancy (Haddad and Tewksbury 2006). Thus, connectivity facilitates dispersal mechanisms, strengthens metapopulation dynamics, and conserves biodiversity (Thrall et al. 2000; Baguette et al. 2013; Dutta 2016).

Corridors are often approached with the mindset *if you build it, they will come*; assuming if a linkage creates structural connectivity that functional connectivity will inevitably

follow. However, an important discrepancy arises in that these two types of connectivity are not mutually exclusive of one another. This is not a trivial distinction, given functional connectivity can occur in the absence of structural connectivity and structural connectivity does not guarantee functional connectivity (Ferreras 2001; Mech and Hallet 2000; Baguette et al. 2013). For instance, populations occupying patches that are not structurally linked can sustain functional populations of focal species (Hanksi and Simberloff 1997). Additionally, it is equally likely that the quality of habitat within structural linkages is sufficiently degraded that it is not functional for focal species dispersal among patches (Hilty et al. 2020; Gilbert-Norton et al. 2010).

It is assumed corridors facilitate wildlife movements among patches. Yet, current corridor ecology assesses the functionality of designed and built conservation corridors, such as a wildlife crossing over a highway, or experimental corridor systems. Such designs and systems are typified as short, straight swaths of homogenous land cover with unambiguous transitions between patches (Figure 1.1). There are minimal gaps in the connectedness of natural land cover, no pinch points at which edge effects may be augmented, and no tortuosity that may affect crossing times or propensity (Beier and Noss 1998). This enables researchers to identify the point easily and accurately at which wildlife traverse patch-corridor transitional areas and estimate the passage time along the corridor to evaluate the influence of species' behavioral mechanisms, and dispersal times on corridor efficacy (Haddad et al. 2000; Legrand et al. 2012).

As a result of complex landscape dynamics across large spatial and temporal scales (Bélisle 2005), the majority of connectivity and corridor research has assessed corridor

functionality in landscapes at several orders of magnitude smaller scale and embedded in a different landscape context than those for which conservation corridors are designed and implemented (Beier and Gregory 2012). As research has assessed the structural configuration of a landscape independent from a species perspective (Tischendorf and Fahrig 2000; Taylor et al. 2006), studies often overlook the influence landscape heterogeneity and scale has on dispersal mechanisms (Ferreras 2001; Baguette et al. 2013). In addition, species response variables measured are often inadequate to support inferences of long-term persistence (Beier and Gregory 2014).

Resultantly, a fundamental knowledge gap in corridor efficacy is how complex mosaics within the structural configuration of a corridor influence corridor functionality long-term. This begs the question: do corridors work?

To answer this question, an ongoing assessment of corridor efficacy is combining field sampling, genetic analyses, and spatial modelling to measure long-term gene flow across 16 landscapes, internationally (Do Corridors Work 2022). Using *de facto* corridors, natural areas that resemble the design of built conservation corridors but exist as a quirk of human development (Figure 1.1), connectivity is being assessed in the real world in which conservation corridors are designed and built (Beier and Gregory 2012). Specifically, by assessing and understanding the characteristics of corridors that facilitate movement and the species that benefit, we will gain foundational insight into how corridors could be better designed and implemented to ensure a high probability of functionality.

The larger Corridors Project will address critical knowledge gaps in corridor ecology by combining field sampling, genetic analyses, and spatial modelling to measure demographic stability and long-term gene flow across 16 landscapes within eight countries on five continents (Do Corridors Work 2022). By assessing large-scale and stable landscapes with *de facto* corridors (Beier and Gregory 2012), connectivity is being assessed in the real world to further our understanding of (1) the structural characteristics of corridors that facilitate movement, (2) the biological traits that determine which species benefit, and (3) how corridors should be designed and implemented with a high probability of functionality.

To assess real world corridors, the project team identified landscapes suitable for the analyses based on the following five criteria (Beier and Gregory 2012; Do Corridors Work 2022):

Landscape criteria

1. Have a full suite of landscape elements present: a *de facto* corridor complex, intact reference, and two isolated patches.
2. A hard-edge defines landscape elements from the surrounding matrix.
3. Similar distances between corridor patches, isolated patches, and the length of the reference.
4. Average corridor widths are greater than 100 m and lengths are greater than 500 m.
5. Maintained a stable landscape configuration for at least 50 years.

Based on the above criteria, a complete landscape configuration is comprised of the following landscape elements: two patches connected by a *de facto* corridor, an intact reference area, and two isolated patches separated by the surrounding matrix.

Focal species were categorized into two groups based on how they use a corridor: passage species and corridor dwellers. Highly mobile passage species can traverse the length of a corridor in a discrete event over a few hours or days. Corridor dwellers, species that use a corridor as a habitat, have limited dispersal abilities and require several days to generations for individuals and their genes to move through a corridor (Beier and Loe 1992; Beier 2018). For each landscape, 3-5 focal species that represent a range of mobility, edge sensitivities, and body size were targeted. The project team identified focal species to be included in the analyses based on the following two criteria (Beier and Gregory 2012; Do Corridors Work 2022):

Focal species criteria

1. A corridor dweller structured by natural landscapes; with 1 or 2 passage species, and
2. have moderate population sizes with less than 1,000 individuals in each area.

Although using *de facto* corridors to study corridor efficacy is a best practice (Gregory and Beier 2012), there are several drawbacks to the ambiguous nature *de facto* corridors when compared to experimental corridor systems (Figure 1.1). Given the natural occurrence of *de facto* corridors in the real world, they vary in each characteristic that experimental corridors lack variation. Specifically, *de facto* corridors differ in width and tortuosity across varying lengths. They are composed of heterogeneous land covers, some of which are not habitat for species utilizing the corridor. In addition, they often have human land uses within and adjacent to them. As such, they are subject to varying degrees of edge effects, further altering the

quality of the structural linkage (Beier and Gregory 2012). These characteristics create three conditions differentiating *de facto* corridors from experimental systems.

First, the mixture of human land uses within and adjacent to the corridor results in ambiguous delineations; making it difficult to delineate the boundary of the natural land cover from the matrix. Second, the variation in width and tortuosity results in ambiguous transitions between a corridor and patches; making it difficult to identify the true length of a corridor. Third, the heterogeneity of natural land cover types within the corridor can impact the species utilizing the linkage; making it difficult to measure the degree to which connected patches are structurally linked. These conditions have resulted in two prominent knowledge gaps in the literature.

Firstly, how wide does a corridor have to be given its length to meet conservation goals (Harrison 1992; Beier 2018)? This knowledge gap has long been recognized as the most urgent issue land managers must address (Gilbert-Norton et al. 2010; Beier 2018). Yet, implicated in this question is the ability to identify the boundaries of a corridor and the point at which a patch transitions into a corridor and the point a corridor transitions back into the connected patch. The knowledge gap of boundary identification is long recognized, yet seldom modelled or incorporated in corridor designs (Hilty et al. 2020).

Secondly, how does heterogeneity within the structural configuration of a corridor influence corridor functionality? While some land covers facilitate species movements, others impede wildlife dispersal and fragment patches of habitat. Species behavior, habitat

preferences, and dispersal mechanisms through patches of non-habitat or the matrix influences connectivity (Prevedello et al. 2010).

Dispersal, whether natal or breeding, from an individual's home range is non-random and dependent on internal and external information (Clobert et al. 2009) resulting from species behavioral interactions with their habitat and the quality of the landscape as habitat for the species (Smith 1993). Dispersal influences the complex structuring of ecosystems as it impacts population distributions and local abundance. It is considered a central concept in ecology and evolutionary biology as dispersal influences gene flow within and among local populations (Coulon et al. 2004).

The variation in the structural composition and configuration of a landscape determines dispersal pathways and influences demographic stability (Atkins et al. 2019; Weins 2002). While successful dispersal is critical for ecological processes, it is difficult to assess in the real world (Roffler et al. 2016). Recent advances in spatial modelling and statistics have enabled researchers to address this latent knowledge gap as it pertains to dispersal mechanisms (Fattebert et al. 2015). An extension of spatial modelling that integrates population genetics and landscape ecology is the relatively recent advanced field of Landscape Genetics (Manel et al. 2003; Manel and Holderegger 2013), which has resulted in an unparalleled increase of our understanding of how landscape structure influences landscape function within and among populations.

Landscape Genetics considers how composition, configuration, and quality of the matrix influence gene flow and genetic variation. Thus, it is an efficient tool to understand the

functional connectivity of landscapes (Storfer et al. 2007). Using response variables such as gene flow to assess species responses to landscape heterogeneity resulting from human land use and conservation efforts provides insight into corridor efficacy (Epps et al. 2007; Gregory and Beier 2014).

This research is part of the larger collaborative study to assess conservation corridor efficacy (Beier and Gregory 2012; Do Corridors Work 2022). Using a subset of landscapes and species population genetic data, I apply a species perspective approach to spatial modelling to quantify landscape patterns influencing processes for focal species. Specifically, I quantify the configuration and composition of landscape elements and how those patterns influence the ecological responses of focal species to identify processes.

Corridor literature lacks a unified method for delineating landscape elements, recognizing arbitrary edges of the landscape, and identifying the start and end of corridors. This chapter addresses this often-overlooked technical aspect of corridor ecology using a subset of *de facto* corridors (Beier and Gregory 2012; Do Corridors Work 2022) delineated in the methodologies developed in chapter 2. In this chapter, I will build upon the quantification of the configuration and composition of landscape elements from chapter 2 and identify how those patterns influence the ecological responses of focal species to identify processes. Understanding and predicting the effects of landscape structure on movement and gene flow, and identifying areas important to conserve, requires models that relate landscape structure to movement processes (McRae et al. 2008).

The analyses in this chapter apply a more sophisticated approach to the spatial modelling of corridors. Specifically, by assessing the degree to which *de facto* corridors influence the movement of focal species when compared to an intact reference area and isolates using spatial modelling and gene flow.

3.2 Methods

Spatial analyses were conducted at landscape scales in the United States and Czechia using ArcMap and ArcGIS Pro (ESRI 2019, 2022). Given the spatial extent of the study system, I elected to use remotely sensed data and global datasets to ensure conformity and minimize process error due to the variation in the compilation of regional datasets. All spatial analyses and reclassifications were executed using 30 m resolution datasets. For each landscape, all datasets were projected to its Universal Transverse Mercator zone (UTM) to match the datasets generated in chapter 2 to measure shapes, areas, and distances with a higher precision. To summarize the data generated in chapter 2 that will be implemented in this chapter:

1. The boundaries of landscape elements were delineated on false composite Landsat 8 imagery using male home range estimates to implement focal species perspectives.
2. Corridor termini were identified as the inner corridor terminus tapered to the outer corridor terminus.
3. Land covers were classified following a modified Anderson Level I classification scheme (Table 2.1).
4. The composition of habitat within landscape elements was quantified for the percent of habitat and non-habitat, core area, and the percent of productivity.

Small mammal trapping was conducted using Sherman live-traps to collect genetic samples and species occupancy data for each landscape element. For each individual, a genetic sample was collected via a 0.02 mm ear tissue notch. Tissue samples were stored and stored in Longmire's solution until extraction.

Trapping was carried out by local sub-contractors in each landscape following standardized project protocols for field data collection and sampling. All animal handling procedures were approved by the University of North Texas, Institutional Animal Care and Use Committee protocol #200-20. All relevant regional and national wildlife trapping and handling permits, and permissions were acquired and held by local project subcontractors with corridors project staff listed as sub-permittees.

3.1.1 Study Areas and Focal Species

I selected a subset of three landscapes that represent a range of environmental contexts with field and genetic data collection completed in Kansas and Idaho, United States and Czechia. For each landscape, I selected one focal species that prefer one habitat type but tolerate various broad environmental conditions and landscape conditions (Bani et al. 2006) from the sample set that had the highest capture rate at each landscape (Table 3.1). Across landscapes, there were a total of five *de facto* corridors, three intact reference areas, three sets of isolated patches, and three focal species. The definitions of landscape configurations are defined in Box 2.1 in this thesis.

Overall, the study areas were composed of a high percent of agriculture dominating the matrix (Figure 2.12). Developed areas composed a small percentage of land covers relative to

natural land cover types and areas used for agriculture. The Kansas study area was composed of all five land cover classes (Table 2.1). The Idaho study area had no forested areas whereas there was no rangeland in Czechia (Figure 2.12).

Table 3.1: Total number of individuals captured within landscape elements across study areas: 150 white-footed mouse (*Peromyscus leucopus*; PELE), 193 western harvest mouse (*Reithrodontomys megalotis*; REME), and 455 yellow-necked mouse (*Apodemus flavicollis*; APFL) captures.

	Corridor Complex 1	Corridor Complex 2	Corridor Complex 3	Reference	Isolate 1	Isolate 2
PELE	27	-	-	26	59	38
REME	93	-	-	40	37	23
APFL	217	63	71	55	24	25

Kansas

The landscape comprised one *de facto* corridor complex, two isolated patches, and one intact reference area (Figure 2.1). The study area encompassed 116.87 km² in eastern Kansas composed of a mosaic of land cover and land uses of differing suitability. Specifically, grassland pastures and cultivated fields dominated the matrix surrounding the natural gallery forest. The local elevation varied between 312 and 397 m.

Peromyscus leucopus (hereafter, *P. leucopus*) are common throughout eastern United States in dense forests that provide canopy cover at low elevations (Kaufman and Fleharty 1974; Taylor and Hoffman 2014). The species is adaptable to urban and agricultural areas (Wilson and Ruff 1999); with male home ranges recorded up to 15,000 m² (Aguilar 2011). Although habitat generalists, the species prefer complex understory vegetation, with dense ground cover and woody debris. Given the complex habitat preference, abundant populations are found in small forest fragments and edges than interiors (Heske and Rodgers 2022).

Idaho

The landscape was comprised of one *de facto* corridor complex, two isolated patches, and one intact reference area (Figure 2.2). The study area encompassed 4,367 km² in southern Idaho where cultivated fields and irrigated crop circles with a center pivot dominated the matrix surrounding focal rangeland habitat. Rangeland across the study area is public lands used for livestock grazing managed by the Bureau of Land Management. The local elevation varied between 901 and 1540 m.

Reithrodontomys megalotis (hereafter, *R. megalotis*) populations are common across the western United States and central Mexico in rangeland, prairies, and deserts with elevations between -77 and 4000 m (Webster and Jones 1982; Ruff and Wilson 1999). While habitat generalists, *R. megalotis* populations are abundant in rangeland and old fields, as the species require dense vegetative cover and tall grass for foraging, nesting, and protection from predators (Kaufman and Fleharty 1974; Sullivan and Sullivan 2008). Frequently found bordering riparian and agricultural areas, using linear habitats, the species is not sensitive to edge effects. Over 90% of *R. megalotis* observations have been in proximity to roads and dense populations (Environment Canada 2015); with male home ranges recorded up to 3,525 m² (Konishi 2003).

Czechia

The landscape was comprised of three *de facto* corridor complexes, two isolate patches, and one intact reference area (Figure 2.3). The study area encompassed 3,884 km² that spanned the South Bohemian, Vysočina, and South Moravian regions of Czechia as well as a portion of northern Austria, given the configuration of the reference area. The forests are

classified relative to commercial exploitability with high-intensity forest management plans and guidelines in place (Synek et al. 2014). The forest clear-cutting has resulted in a landscape mosaic composed of a high degree of heterogeneity. Surrounding the forests, cultivated fields dominate the matrix. The local elevation varied between 188 and 742 m.

Apodemus flavicollis (hereafter, *A. flavicollis*) populations are widely distributed across Europe. The species is semi-arboreal and often associated with forest edges. Populations are most abundant in areas with high canopy cover used for foraging, nesting, predator avoidance, and minimizing interspecific competition (Štěpánková and Vohralík 2009; Benedek 2021). Given the species' food dependency and tolerance of urban and agricultural areas, *A. flavicollis* are highly mobile (Rico et al. 2007; Bohdal et al. 2016; Benedek 2021); with male home ranges recorded up to 15,500 m² (Schwarzenberger and Klingel 1995).

3.1.2 Developing Expert Literature-based Models for Focal Species

Given the technical terminology used for connectivity modelling, I have defined critical terms used throughout chapter 3 in this thesis (Box 3.1).

Box 3.1: Critical terms used for modelling landscape connectivity.

Term	Definition
Factor	<i>Pixel</i> attribute made up of classes/categories
Functional Connectivity	Increases degree of species movement through landscapes
Structural Connectivity	Physical land cover linking patches; ignores species' responses
Pixel	Smallest area in GIS raster (30 x 30 m); contains a value comprising its landscape attributes
Raster	<i>Pixel</i> grid of rows and columns (30 x 30 m); comprised of <i>pixels</i>
Resistance	Value represents the difficulty of a species to move through a <i>pixel</i> based on its attributes; scaled 0 to 10, 10 is the highest resistance
Resistance Raster	Represents cost of movement for focal species to traverse a landscape

Resistance-based connectivity modelling is frequently used to assess a species response to the structural heterogeneity of landscapes (Bélisle 2005; Zeller et al. 2012). Connectivity models compute the ecological costs for a species to traverse a landscape. Landscapes are represented by a resistance raster where pixel values are reclassified to reflect the hypothesized difficulty for a species to traverse through that land cover or land use class. Values are assigned based on species habitat preference and behavioral mechanisms. Thus, resistance represents the degree to which the structural composition and configuration of a landscape facilitates or impedes species movements (Adriaensen et al. 2003).

To model connectivity, a resistance raster representative of the cost for focal species to traverse the landscape was created using expert literature-based models (Clevenger et al. 2002; Spear et al. 2010). The resistance surface was comprised of environmental factors known to influence small mammal movements and patch occupancy: land cover, roads, distance to water, and elevation (Benedek et al. 2021). Classes or categories were reclassified as numerical scores representing the resistance or cost associated with movement across a land cover class or category based on species-specific behavioral mechanisms and habitat requirements (Zeller et al. 2012; Majka et al. 2007; Etherington 2016). Scores were assigned on a scale of 1-10, where 1 is the lowest resistance and 10 is the highest resistance. An important caveat of these scores is that they are relativistic and scalable to the species of interest (Spear et al. 2010). As such, I've provided biological interpretations of threshold values for habitat suitability (Majka et al. 2007): a score of 1 indicates highest suitability; 5 indicates minimal suitability; and 10 indicates no suitability.

Land cover represents habitat preference as it relates to canopy cover and food availability. Moreover, the land cover and land uses surrounding focal habitat represents the matrix and varying levels of human disturbance (Majka et al. 2007); which creates significant barriers to dispersal (Crooks et al. 2011; Haddad et al. 2015). Using the land cover layers classified in chapter 2 of this thesis, land cover classes were scored independently for each focal species (Table 3.2; Figure 3.1, 3.2, 3.2).

Table 3.2: Scores reclassified (cost) for focal species *Peromyscus leucopus* (PELE), *Reithrodontomys megalotis* (REME), and *Apodemus flavicollis* (APFL) to traverse land cover classes assigned a weight of 4.

Species	Class	Cost	Weight	Weighted Cost	Justification	Source
PELE	Developed	8	4	32	Limited cover, foraging; movement barrier	Merriam et al. 1989; Howell et al. 2017
REME		8	4	32	Limited cover, foraging; movement barrier	Merriam et al. 1989; Howell et al. 2017
APFL		5	4	20	Human and building tolerant; increased foraging	Reutter et al. 2003; Benedek et al. 2021
PELE	Agriculture	5	4	20	Limited but some cover, foraging	Merriam et al. 1989; Howell et al. 2017
REME		7	4	28	Cattle grazing; roads between crop irrigation	Merriam et al. 1989; Howell et al. 2017
APFL		4	4	16	Some cover, foraging; wheat corridors	Sozio et al. 2013; Michał and Rafał 2014
PELE	Rangeland	3	4	12	Some cover, foraging	Kaufman and Fleharty 1974; Verts 1957
REME		1	4	4	High cover, foraging	B.C. Ministry of Environment 2014
APFL		-	-	-	-	-
PELE	Forest	1	4	4	High cover, foraging	Merriam et al. 1989; Burt 1940; Kaufman and Fleharty 1974
REME		-	-	-	-	-
APFL		1	4	4	High cover, foraging	Benedek et al. 2021
PELE	Water	10	4	40	Dispersal barrier	Klee et al. 2004; Carter and Merritt 1981; Root et al. 2003
REME		10	4	40	Dispersal barrier	Root et al. 2003; Landry and Lapointe 1999
APFL		10	4	40	Dispersal barrier	Gortat et al. 2003

Roads are a barrier to movement for small mammals given their low mobility that genetically fragment and isolate populations (Gortat et al. 2021). Earlier research suggests small mammals avoid crossing a road surface itself but use roadside vegetation as habitat to move parallel along roads (McGregor et al. 2008, Bissonette and Rosa 2009, Galantinho et al. 2022).

As such, roads were rasterized as a binary layer to represent the presence and absence of roads. To ensure road coverage within landscape elements and between isolates, road discontinuities were reconnected using the Global Roads Inventory Project (Meijer et al. 2018) on Landsat imagery. Roads were rasterized at 30 m; except for the highway in Idaho that was rasterized at 60 m (Table 3.3; Figure 3.1, 3.2, 3.2).

Table 3.3: Scores reclassified (cost) for focal species *Peromyscus leucopus* (PELE), *Reithrodontomys megalotis* (REME), and *Apodemus flavicollis* (APFL) to traverse the presence or absence of roads assigned a weight of 3.

Species	Category	Cost	Weight	Weighted Cost	Justification	Source
PELE		9	3	27	Unwilling to cross; barrier; avoid pavement	Merriam et al. 1989; Oxley et al. 1974; McGregor et al. 2008
REME	Roads	9	3	27	Barrier; avoid pavement; unwilling to cross	Kozel and Fleharty 1979; McGregor et al. 2008; Kuykendall and Keller 2011
APFL		7	3	21	No cover, increased predation risk; food dependent, mobile; insufficient barrier	Mader 1984; Bąkowski and Kozakiewicz 1988; Gortat et al. 2003; Rico et al. 2007
PELE		1	3	3		
REME	No Roads	1	3	3		
APFL		1	3	3		

Distance to water influences small mammal abundances (Benedek et al. 2021). They frequently use riparian vegetation as habitat to facilitate movement, increasing diversity (Mahan and O'Connell 2005; Hamilton et al. 2015). Riparian areas, adjacent to a river or stream, provide small mammals with the water, food, and canopy cover resources they require

(Hamilton et al. 2015). As such, distance to water was reclassified using focal species home ranges (Table 3.4; Figure 3.1, 3.2, 3.2).

Table 3.4: Scores reclassified (cost) for focal species *Peromyscus leucopus* (PELE), *Reithrodontomys megalotis* (REME), and *Apodemus flavicollis* (APFL) to traverse within distances to water and weighted 2.

Species	Category	Cost	Weight	Weighted Cost	Justification	Source
PELE	Distance to Water	0 – 1	5	2	10	Water bodies
		1 – 70	1	2	2	Within one HR distance
		70 – 207	3	2	6	Within 3x HR distance
		> 207	5	2	10	> 3x HR distance
REME	Distance to Water	0 – 1	5	2	10	Water bodies
		1 – 35	1	2	2	Within one HR distance
		35 – 101	3	2	6	Within 3x HR distance
		> 101	5	2	10	> 3x HR distance
APFL	Distance to Water	0 – 1	5	2	10	Water bodies
		1 – 70	1	2	2	Within one HR distance
		70 – 211	3	2	6	Within 3x HR distance
		> 211	10	2	20	> 3x HR distance

Elevation influences land cover, thermal environments, and precipitation (Beier et al. 2007). Slope, derived from elevation, increases soil erosion which decreases ground vegetation. Ground vegetation provides small mammals with food and cover resources and is considered a key factor influencing populations (Lee et al. 2020). As such, a digital elevation model, 30 m Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global was used to derive the inclination and steepness of slope (USGS Earth Explorer). Specifically, by measuring percent slope, where it identifies the maximum height change from each cell (Table 3.5; Figure 3.1, 3.2, 3.2).

Table 3.5: Scores reclassified (cost) for focal species (*Peromyscus leucopus*, *Reithrodontomys megalotis*, and *Apodemus flavicollis*) to traverse slope inclinations assigned a weight of 1.

Species	Category	Cost	Weight	Weighted Cost	Justification
PELE	0 – 10	1	1	1	Flat
	10 – 15	3	1	3	Slight incline
	15 – 20	5	1	5	Moderate incline
	REME Slope	20 – 25	7	1	Moderately steep incline
	APFL	25 – 40	8	1	Steep incline
		40 – 60	9	1	Extreme incline
		60 – 1000	10	1	Reaches infinity

The four reclassified layers were combined and weighted based on their influence on small mammal populations. Weights were standardized across landscapes for statistical comparisons and determined based on their relative importance for small mammals and impacts on habitat suitability and dispersal. Using the weighted sum, the four reclassified layers were weighted to total sum of 10. Land cover was considered the most important factor and weighted 4. Roads were weighted 3 given the strong barriers they present for small mammals. Distance to water was weighted 2 and slope was weighted 1. Scores were multiplied by the assigned weight to develop resistance values for each pixel. The resultant resistance raster was used as the input raster for connectivity modelling using cost distance and circuit theory.

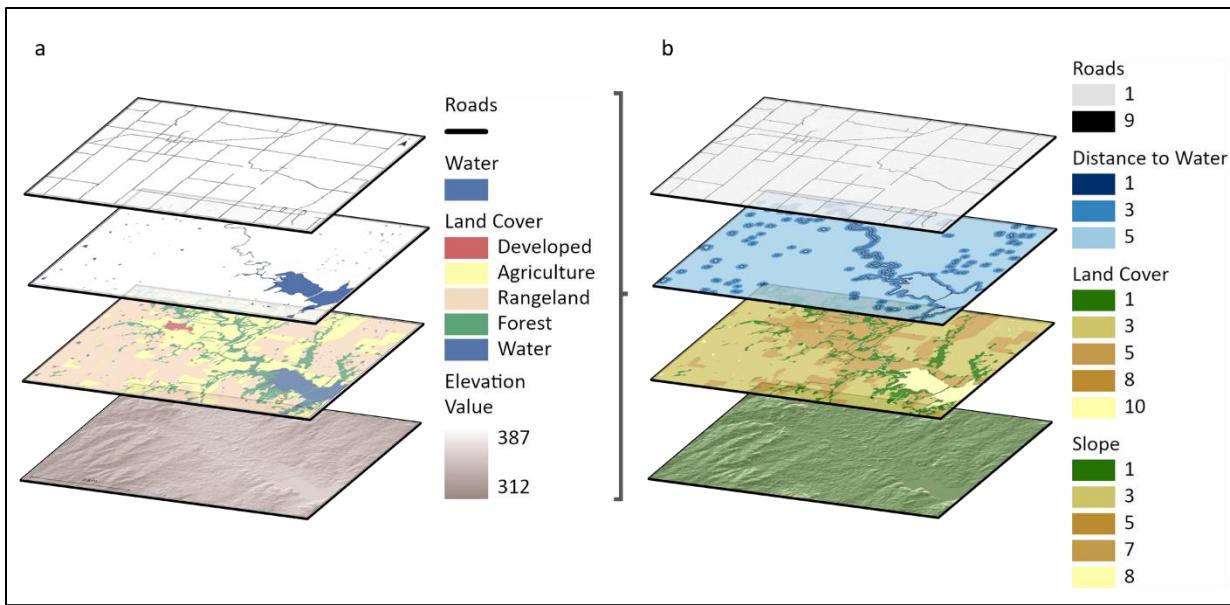


Figure 3.1: Reclassification process of Kansas study area for the white-footed mouse (*Peromyscus leucopus*) to develop a resistance raster: (a) environmental layers known to influence small mammals and (b) reclassified layers representing resistance (or cost) associated with movement across a class or category. Scores assigned 1-10, 1 lowest and 10 highest.

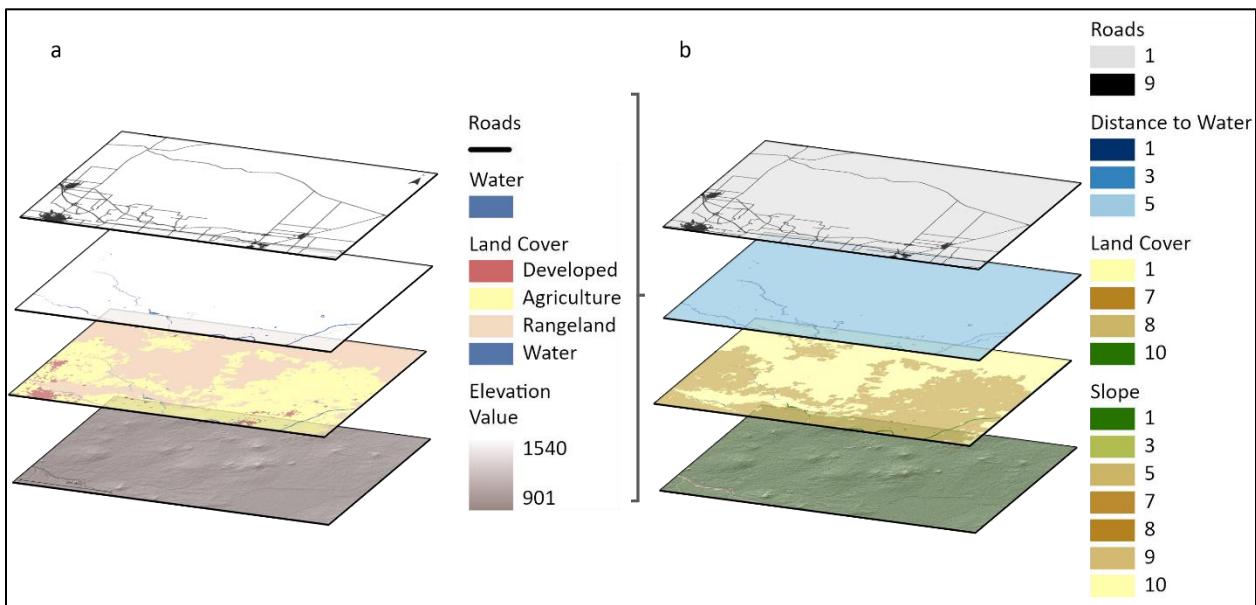


Figure 3.2: Reclassification process of Idaho study area for the western harvest mouse (*Reithrodontomys megalotis*) to develop a resistance raster: (a) environmental layers known to influence small mammals and (b) reclassified layers representing resistance (or cost) associated with movement across a class or category. Scores assigned 1-10, 1 lowest and 10 highest.

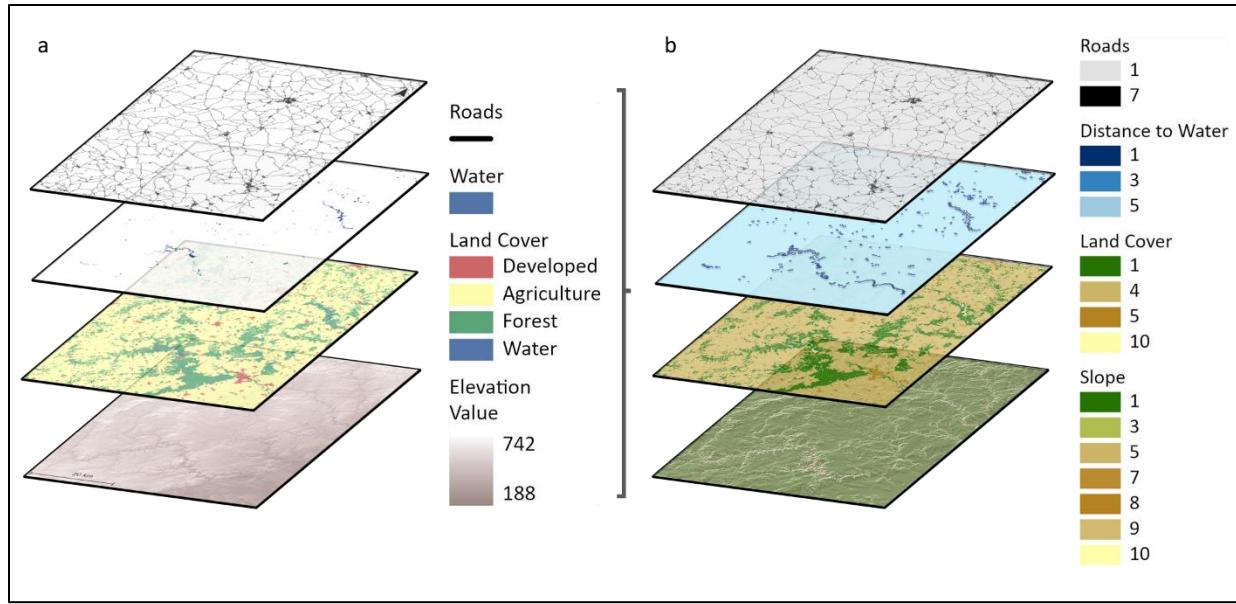


Figure 3.3: Reclassification process of Czechia study area for the yellow-necked mouse (*Apodemus flavicollis*) to develop a resistance raster: (a) environmental layers known to influence small mammals and (b) reclassified layers representing resistance (or cost) associated with movement across a class or category. Scores assigned 1-10, 1 lowest and 10 highest.

3.1.3 Quantifying Landscape Connectivity with Resistance-based Modelling

Euclidean distances between patches are critical to understanding structural connectivity as it relates to patch proximity (Etherington 2016). However, some landcovers function as barriers to movement while others allow species to move freely. As such, considering the landscape mosaic is critical to model connectivity as species behavior, life-history traits, and willingness to disperse through non-habitat patches or the matrix influences connectivity on heterogenous landscapes (Prevedello et al. 2010). Moreover, linear structures are rare in natural ecosystems and edges are often tortuous.

In heterogenous landscapes, tortuosity is critical for dispersal success as it may affect crossing times or propensity (Beier and Noss 1998; Nams 2014). Species life-history traits and

perception of the matrix to move between patches influences tortuosity of movements. Such effects present movement barriers to smaller animals (Prevedello et al. 2010).

As opposed to assuming uniform permeability of the matrix, resistance-based modelling will account for landscape heterogeneity. Spatial and landscape ecologists commonly implement cost distance and current flow models to model the influences of structural connectivity on functional connectivity (Bélisle 2005; Zeller et al. 2012). Both models use a resistance surface raster developed in Geographic Information Systems (GIS) to represent the heterogeneity of a landscape and identify areas of low resistance to species movement. However, the algorithms and assumptions of each model varies in terms of species perception and movement.

Cost distance models, such as the least cost path, is an algorithm that identifies the optimal path of lowest cost between patches of habitat for focal species. The least-cost path assumes an individual has complete knowledge of the surrounding landscape and relates total cumulative resistances to movement or gene flow through that single path (Adriaensen et al. 2003). Cost distance models have been the most implemented framework for connectivity modelling (Knaapen et al. 1992; Dickson et al. 2019). However, one downfall of the least cost path is that it does not consider the potential of several dispersal pathways on overall landscape connectivity (McRae 2006).

Alternatively, current flow models, based on circuit theory, is an algorithm that identifies a network of all possible paths between patches of habitat for focal species (McRae et al. 2008; Wade et al. 2015). The model assumes an individual has no knowledge of the

surrounding landscape and predicts species dispersal and gene flow to some degree across all potential connectivity paths as a function of the relative resistance to movement across a particular land cover type that an individual might experience while attempting to disperse. (McRae 2006; Dickson et al. 2019). As such, flow analysis implements dynamic movements opportunities into species responses to structural landscape patterns that drive processes.

Both modelling approaches provide important and complementary measures of landscape connectivity. Least-cost paths are informative to identify biologically meaningful connections between sample locations (Spear et al. 2010). In contrast, circuit theory models are useful to implement gene flow across landscapes using several pathways (McRae 2008).

The Euclidean distance was estimated between the outer corridor termini, patches 1 and 2 maximum, the entire corridor complex, the intact reference area, and isolates. The distance between these termini is critical to compare to the resultant least cost and cumulative resistance values as it can indicate the quality of habitat between termini with a simplistic linear measurement as it relates to more complex connectivity models.

Tortuosity through corridors was estimated using Euclidean distances divided by the length of the centerline from chapter two. Resultant tortuosity values equal to 1 represent straight lines. The higher the degree of tortuosity, the values increase greater than 1.

In GIS, the least-cost path was used to identify the tortuous corridor within the structural configuration of the delineated corridor. The least-cost path was used to identify the optimal path of lowest cost-weighted distance between outer corridor termini, patches 1 and 2 maximum, the entire corridor complex, the intact reference area, and isolates. The

resultant cost values were used to compare the average cost to traverse among landscape elements points.

Single, narrow paths are less likely suitable habitat for species than several, wider paths (McRae and Beier 2007). Circuit theory models predict several paths across heterogenous landscapes while accounting for swaths of structural habitat (Koen et al. 2014). The model links terminus regardless of landscape resistance; indicating all patches are of equal value (McRae 2006; McRae et al. 2008). In *Circuitscape*, current flow was used to identify the cumulative resistance values to move between all potential paths, where the cumulative current density map predicts functional connectivity. Specifically, between outer corridor termini, patches 1 and 2 maximum, the intact reference area, and isolates.

Two separate analyses of resistance among landscape elements were conducted using two current flow models. First, the potential paths identified by the flow model was restricted and the algorithm calculated flow along a linear route between isolates. The simulated route was of similar width as each corridor that corresponded to corridor width(s) on that landscape. This approach assumed that animals would preferentially choose the most direct (shortest Euclidean distance) route to disperse regardless of the relative cost or inhospitable matrix. This model mimics how most land managers perceive landscapes when designing corridors and implementing strategies (Beier et al. 2008). Second, a landscape perspective was implemented which allowed the flow model to identify the best set of paths across the landscape connecting isolates. In this instance, the flow model was given room to run through the matrix and identify paths that used patches of habitat as steppingstones. While this may have increased the

Euclidean distance traveled, it decreased the total cumulative resistance of dispersal through the matrix (McRae et al. 2008).

Defining these two separate analyses in this manner, allowed for a specific ecological question to be tested: is measuring landscape resistance between isolates as a function of the linear matrix distance between isolates meaningful, or is evaluating total landscape connectivity potentially a better model to predict species movements on complex landscapes?

3.1.4 Investigating the Degree to Which the Presence of a *De facto* Conservation Corridor Influences Connectivity

Raincloud plots were developed using the *R* package *ggplot2* (Kay 2021) to compare the average and variation of cost and cumulative resistance values between sampled landscape elements. Specifically, to investigate the degree to which the presence of a corridor influences the structural and functional connectivity between patches when compared to intact reference areas and isolated patches where focal species traverse the matrix.

Available genetics data were used to analyze the efficacy of corridors in Kansas and Idaho for two focal species: *P. leucopus* in Kansas and the North American deer mouse (*Peromyscus maniculatus*; hereafter *P. maniculatus*) in Idaho. Genetic microsatellite data were provided for use in this analysis by the Corridors Project (Beier and Gregory 2012). The method used by project personnel to obtain these data were as follows:

Genomic DNA was extracted from tissue using a modified Qiagen DNeasy Blood & Tissue Kit. DNA quantity and quality were measured via small volume spectrophotometry and DNA concentrations were standardized to 15ng/ μ L prior to PCR amplification. PCR reactions were set

up using a three-primer system, in 15 µL PCR cocktails containing GoTaq® G2 Colorless Master Mix (Promega Corp., Madison, WI), 15 ng of template DNA, 0.12 µM of a reverse primer and 0.2 µM of a fusion of the forward primer and the M13 universal primer (Schulke 2000).

Descriptive statistics of genetic diversity were calculated for each loci and each species using GenAIEx 6.5 (Peakall & Smouse 2012). Descriptive statistics included Hardy-Weinberg exact tests, Probability of Identity (PI), and the Probability of Identity among Siblings (PI-Sibs) (Raymond and Rousset 1995; Evett & Weir 1998). Genetic differentiation was measured between individuals and populations using pairwise Nei's genetic distances (Nei 1978).

Nei values were used to calculate a corridor success index (CSI) and evaluate corridor efficacy (Gregory and Beier 2014). Pairwise estimates were averaged for landscape elements and calculated using the equation:

$$CSI = \frac{GS_{corridor} - GS_{isolates}}{GS_{reference} - GS_{isolates}}$$

Where $GS_{corridor}$ is equal to the genetic distance between corridor-connected patches, $GS_{isolates}$ is equal to the genetic distance between isolates, and $GS_{reference}$ is equal to the genetic distance between sampling locations in the intact reference area (Gregory and Beier 2014). CSI values close to 0 indicate a failed corridor, intermediate values indicate relative corridor success, CSI values close to 1 or >1 indicate a successful corridor.

For both Kansas and Idaho, the *R* package *vegan* (Okanese et al. 2016), was used to implement a redundancy analysis (RDA). The RDA ordinated Nei's genetic distance among small mammal demes sampled at each landscape element by the associated environmental

attributes of landscape elements. Environmental variables were standardized to allow for comparisons with the same units of measurements. The most explanatory variables influencing genetic diversity used for the RDA included: edge, area, edge-area, core area, and the percent of habitat composition.

3.3 Results

3.3.1 Developing Expert Literature-based Models for Focal Species

Overall, the Idaho study area had the highest resistance surface raster (Figure 3.5). The Kansas and Czechia study areas had similar resistance values (Figure 3.4; Figure 3.6). In general, *A. flaviollis* had a higher tolerance to a variety of land cover types than either *P. leucopus* or *R. megalotis* (Table 3.4). Moreover, the presence of roads can be an insufficient barrier to movement as they are food dependent and mobile (Table 3.5).

Kansas

The resistance values for *P. leucopus* surface raster ranged from 10-78 across the study area (Figure 3.4).

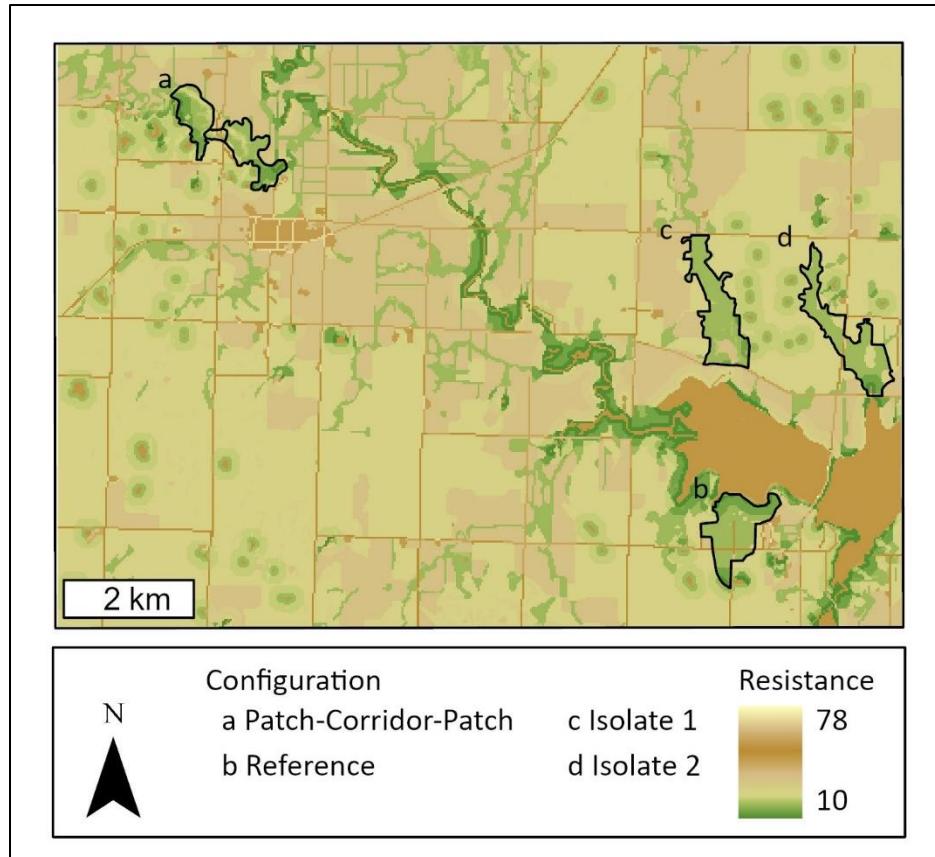


Figure 3.4: Resistance raster of Kansas study area developed using an expert literature-based model for the white-footed mouse (*Peromyscus leucopus*).

Idaho

The resistance values for *R. megalotis* surface raster ranged from 9-259 across the study area (Figure 3.5).

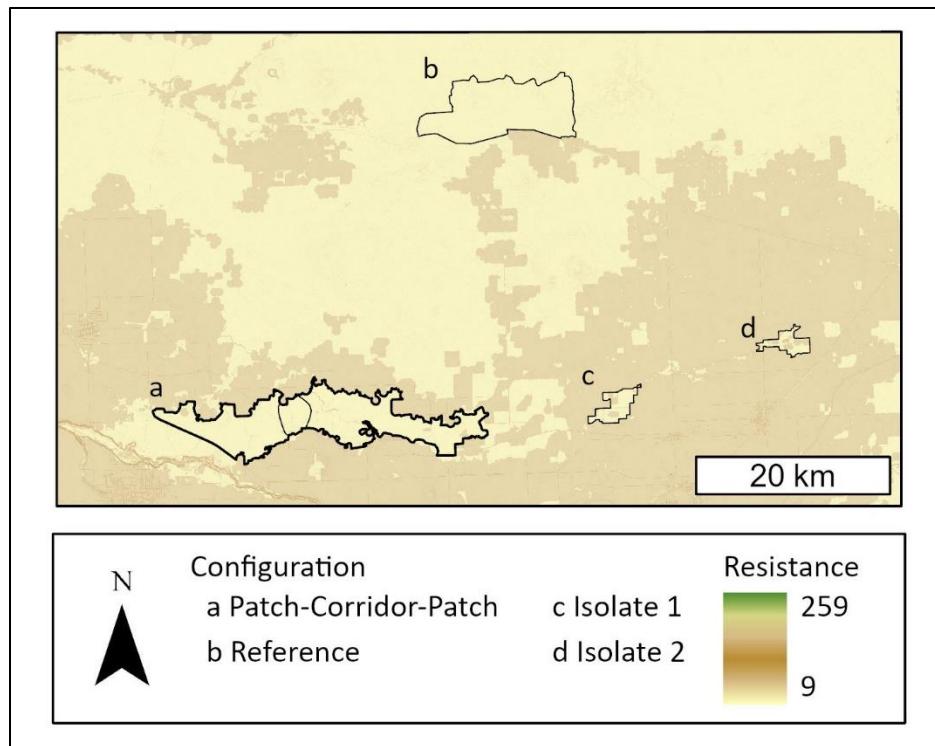


Figure 3.5: Resistance raster of Idaho study area developed using an expert literature-based model for the western harvest mouse (*Reithrodontomys megalotis*).

Czechia

The resistance values for *A. flavicollis* surface raster ranged from 10-79 across the study area (Figure 3.6).

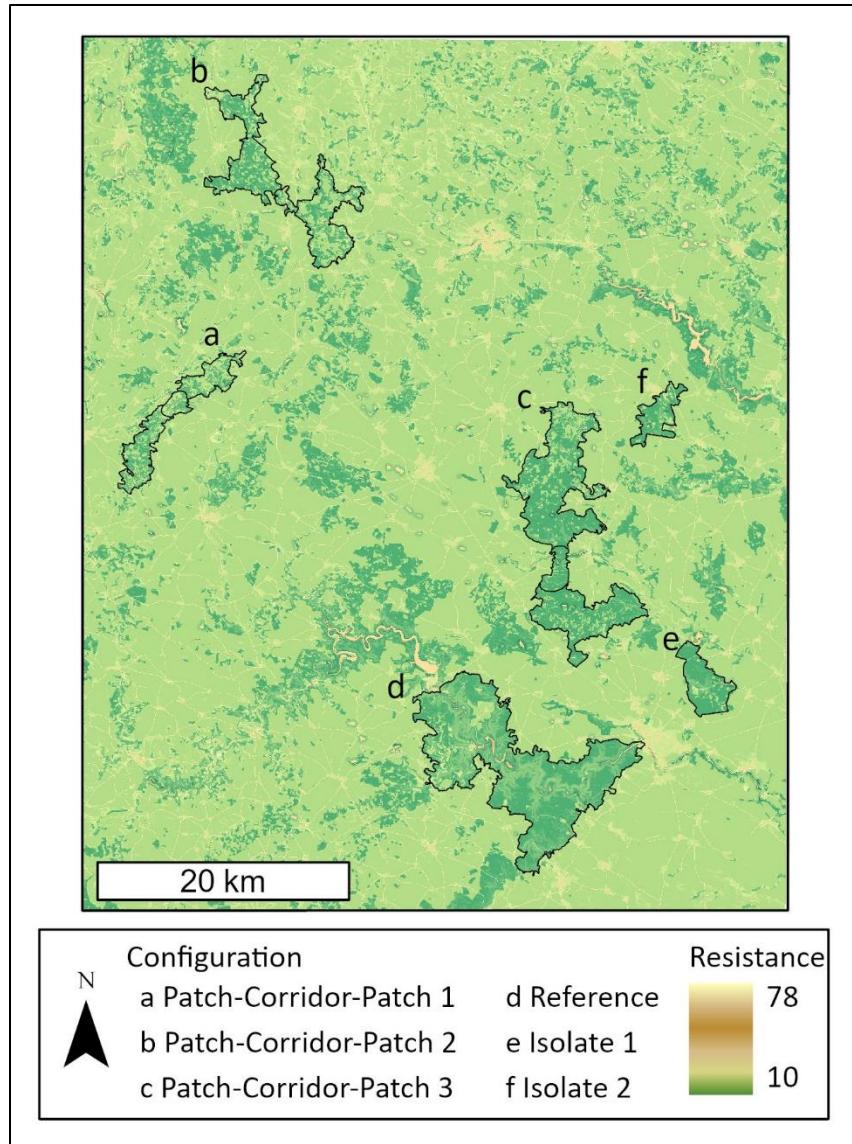


Figure 3.6: Resistance raster of Idaho study area developed using an expert literature-based model for the yellow-necked mouse (*Apodemus flavicollis*)

2.1.2 Quantifying Landscape Connectivity with Resistance-based Modelling

Overall, the linear distance between outer corridor termini, patches 1 and 2 maximum, through the reference area, and between isolates varied across landscapes. Across landscape elements, the distance through the reference areas was the highest.

The Kansas corridor had the lowest degree of tortuosity (Table 3.6). In contrast, corridor 3 in Czechia had the highest degree of tortuosity. The tortuosity through corridors was similar among the configurations in Czechia.

Table 3.6: Euclidean distances between landscape element termini used for connectivity modelling for the white-footed mouse (*Peromyscus leucopus*), western harvest mouse (*Reithrodontomys megalotis*), and yellow-necked mouse (*Apodemus flavicollis*) including tortuosity through *de facto* corridors.

	Termini	Euclidean Distance (km)	Length (km)	Tortuosity
Kansas	Corridor	0.35	0.44	1.26
	Patches	1.01	-	-
	Reference	2.71	-	-
	Isolates	0.94	-	-
Idaho	Corridor	3.34	4.59	1.37
	Patches	7.50	-	-
	Reference	16.44	-	-
	Isolates	12.39	-	-
Czechia	Corridor 1	2.52	3.57	1.41
	Corridor 1 Patches	2.27	-	-
	Corridor 2	3.74	-	-
	Corridor 2 Patches	7.65	3.60	1.59
	Corridor 3	8.20	-	-
	Corridor 3 Patches	10.42	5.39	1.44
	Reference	17.99	-	-
	Isolates	15.80	-	-

In Kansas, the Euclidean distance of 0.35 km between outer corridor termini was the lowest (Table 3.6). In contrast, the distance through the reference area of 2.71 km was highest. The distance between patches 1 and 2 maximum was similar to the distance between isolates. Path tortuosity of the corridor was 1.26 (Table 3.6).

In Idaho, the linear distance of 3.34 km between outer corridor termini was the lowest (Table 3.6). In contrast, the distance through the reference area of 16.44 km was highest. The

distance between patches 1 and 2 maximum was most similar to the distance between isolates.

Path tortuosity of the corridor was 1.37 (Table 3.6).

In Czechia, the linear distance of 2.52 km between outer corridor 1 termini was the lowest (Table 3.6). In contrast, the distance through the reference area of 17.99 km was highest. The distance between corridor 3 termini and patch maximums was the highest of the corridor systems. Distances between isolates were most similar to the reference area. The tortuosity of corridor 2 was highest among corridors at 1.59 whereas it was lowest for corridor 1 (Table 3.6). The degree of tortuosity was similar between corridors 1 and 2.

3.3.3 Investigating the Degree to Which the Presence of a *De facto* Corridor Influences Connectivity

Overall, for focal species to traverse between isolates, the least-cost path (Figure 3.7) and cumulative resistance values of the simulated current flow analysis were highest (Figure 3.8a). Across a network of paths for both current flow analyses, cumulative resistance values were lowest through corridors (Figure 3.8a, 3.8b). However, from a landscape perspective, resistance to traverse the matrix among isolates were more similar to corridor resistance values (Figure 3.8b).

The average cost values for focal species to traverse a single path was lowest through reference areas (Figure 3.7). In contrast, traversing through the matrix between isolates was highest. Traversing a single path through corridors was lower than patches but of similar values.

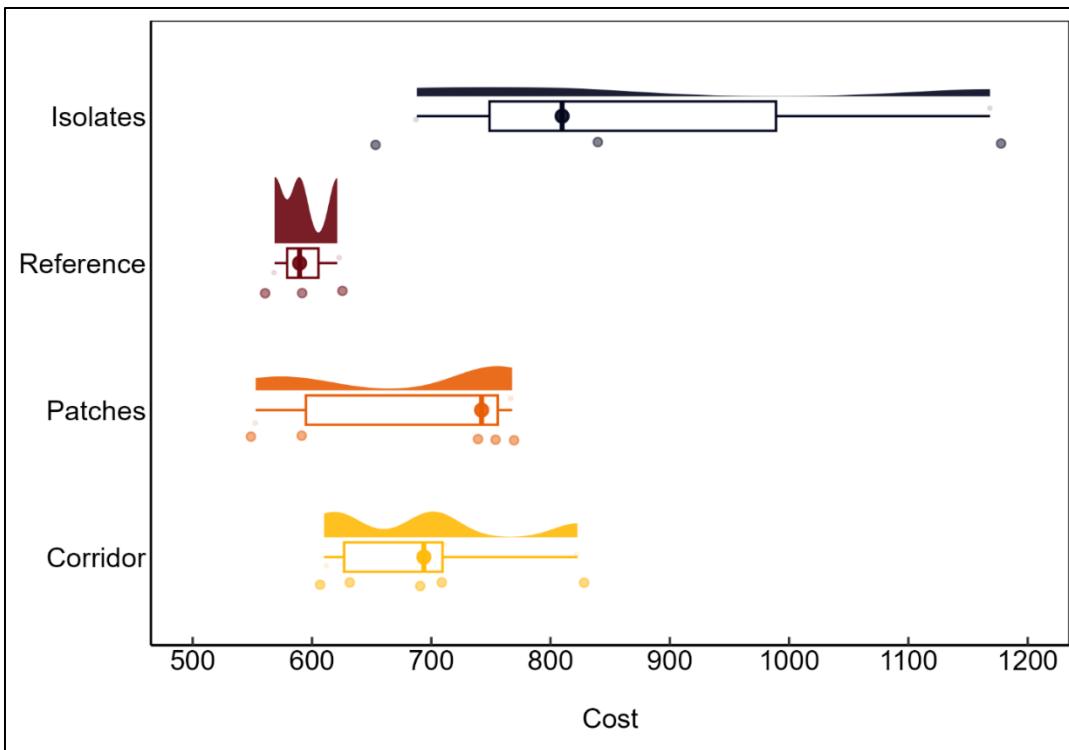


Figure 3.7: Boxplots depicting the average and variation of cumulative resistance values for white-footed mouse (*Peromyscus leucopus*) in Kansas, western harvest mouse (*Reithrodontomys megalotis*) in Idaho, and yellow-necked mouse (*Apodemus flavicollis*) to traverse between outer corridor termini, patches 1 and 2 maximum width, through an intact reference, and between isolates through a matrix.

Similar to the least-cost path, traversing the matrix among isolates had the highest cumulative resistance along simulated routes equivalent to corridor widths (Figure 3.5a).

Cumulative resistance was lowest for focal species to traverse a network of paths through corridors. Resistance between patches and reference areas had similar values.

In contrast, when current flow was modelled from a landscape perspective, the resistance values between isolates through the matrix were more similar to those of the corridors, which had the lowest resistance values (Figure 3.8b). Traversing through the matrix

had lower resistance values than those of patches and reference areas. Resistance values were highest to traverse through reference areas from a landscape perspective.

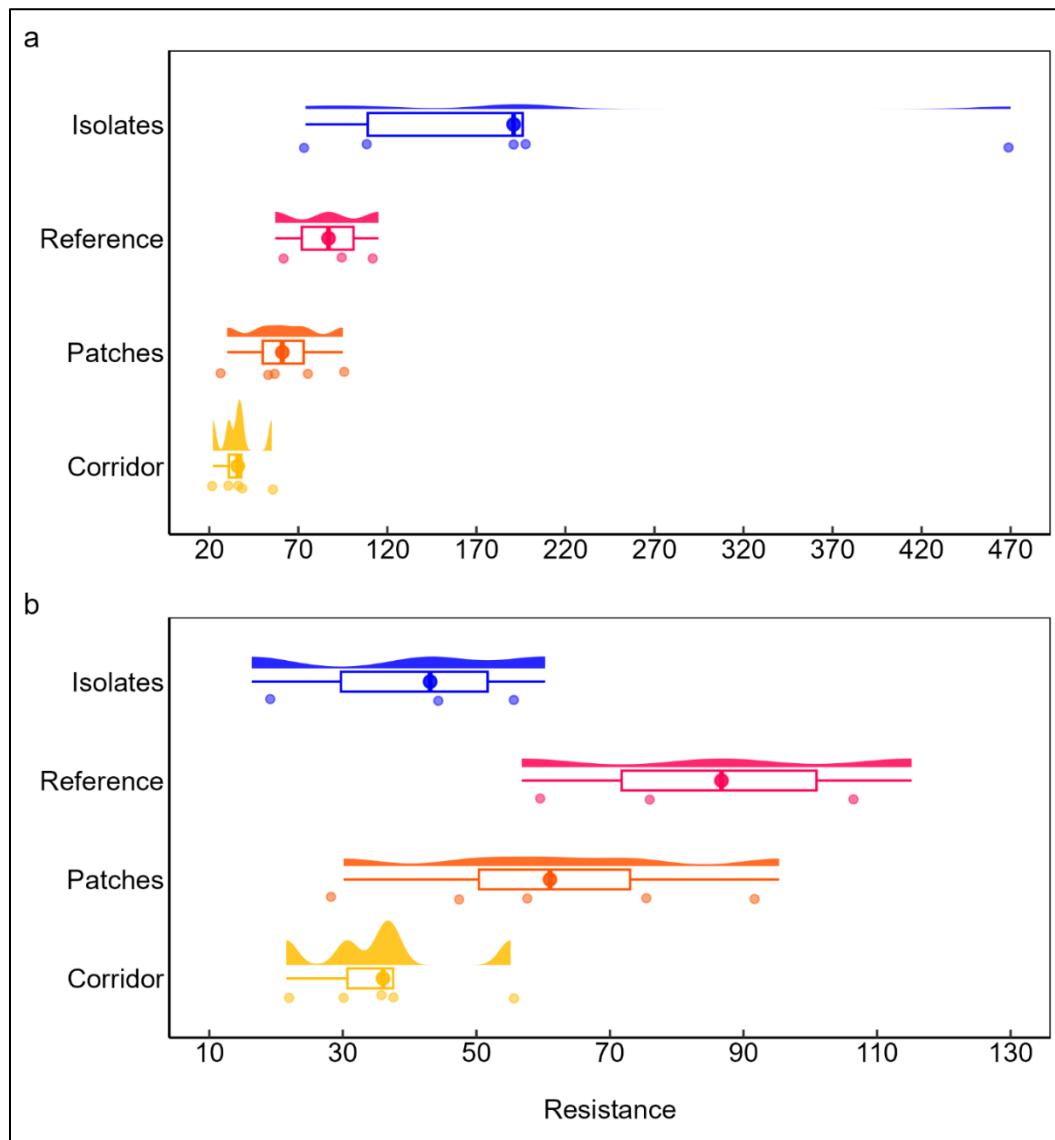


Figure 3.8: Boxplots depicting the average and variation of cumulative resistance values for white-footed mouse (*Peromyscus leucopus*) in Kansas, western harvest mouse (*Reithrodontomys megalotis*) in Idaho, and yellow-necked mouse (*Apodemus flavicollis*) in Czechia to traverse between outer corridor termini, patches 1 and 2 maximum width, through an intact reference, and between isolates through a matrix. Current flow was modelled (a) between isolates through a simulated linear route equivalent to corridor width(s) on each landscape and (b) from a landscape perspective where current flowed through the matrix between isolates.

In terms of the genetic results, for *P. leucopus* in Kansas, 9 microsatellites were used for 153 samples; 1 of which was not in Hardy-Weinberg equilibrium ($P < 0.05$). Genetic diversity was high ($H_o = 0.73 \pm 0.03$; $H_e = 0.79 \pm 0.014$; AR = 8.17) and the power to detect differentiation was moderate ($PI = 7.2 \times 10^{-16}$). Using pairwise Nei's genetic distance values among spatially structured sampling points within each landscape element, the CSI value for the Kansas corridor was CSI = 1.86, a successful corridor (Table 3.7).

Across five RDA axis, a total of 94.4% of variance was explained. The constrained values of the RDA analysis in Kansas were greater than the unconstrained values (constrained = 0.94351; unconstrained = 0.05649). RDA 1 and RDA 2 explained a total of 85.56% of the variance in the genetic distance among sampled landscape elements (Figure 3.6a). RDA 1 was strongly influenced by positive associations with percent of habitat in the corridor and negatively associated with edge-area (Table 3.8; Figure 3.6a). RDA 2 was strongly influenced by positive associations with core area and area in patches, reference area, and isolates and negatively associated with habitat amount.

For *P. maniculatus* in Idaho, 3 microsatellites were used for 44 samples; 2 of which were not at Hardy-Weinberg equilibrium ($P < 0.001$). Genetic diversity among samples was high ($H_o = 0.712 \pm 0.074$; $H_e = 0.941 \pm 0.009$; AR = 25), but the power of the analysis with only three markers was weak ($PI = 2.5 \times 10^{-7}$). The CSI value for the Idaho corridor calculated using pairwise values of Nei's genetic distance was CSI = 1.29, also a successful corridor (Table 3.7).

Across five RDA axis, a total of 94.6% of variance was explained. The constrained values of the RDA analysis in Idaho were greater than the unconstrained values (constrained =

0.94586; unconstrained = 0.05414). RDA 1 and RDA 2 explained a total of 78.94% of the variance in the genetic distance among sampled landscape elements (Figure 3.6b). RDA 1 was strongly influenced by negative associations with percent of habitat and edge in the corridor and isolates (Table 3.8; Figure 3.6b). RDA 2 was strongly influenced by positive associations with core area and area in the isolates and reference area and negatively associated with edge-area.

Table 3.7: Nei's genetic distances between landscape elements (Nei 1978) for the white-footed mouse (*Peromyscus leucopus*; PELE) in Kansas and North American deer mouse (*Peromyscus maniculatus*; PEMA) in Idaho.

Landscape	Species	Landscape Elements	Neis Modified Genetic Distance
Kansas	PELE	Corridor Connected Patches	0.499
		Isolates	0.154
		Reference	0.339
Idaho	PEMA	Corridor Connected Patches	0.684
		Isolates	1.844
		Reference	0.943

Table 3.8: Factor loading scores from constrained environmental variables associated with the first two redundancy analyses ordinating Nei's genetic distances for the white-footed mouse (*Peromyscus leucopus*; PELE) in Kansas and North American deer mouse (*Peromyscus maniculatus*; PEMA) in Idaho.

Landscape	Species	Environmental Variable	RDA1	RDA2
Kansas	PELE	Edge	0.4795	-0.08662
		Area	0.7509	0.08992
		Edge-Area	-0.8973	0.32910
		Core	0.8313	0.07296
		Habitat (%)	0.4926	-0.65396
Idaho	PEMA	Edge	-0.02960	0.1102
		Area	0.38271	0.5361
		Edge-Area	-0.07463	-0.8341
		Core	0.38967	0.5429
		Habitat (%)	-0.21854	0.7279

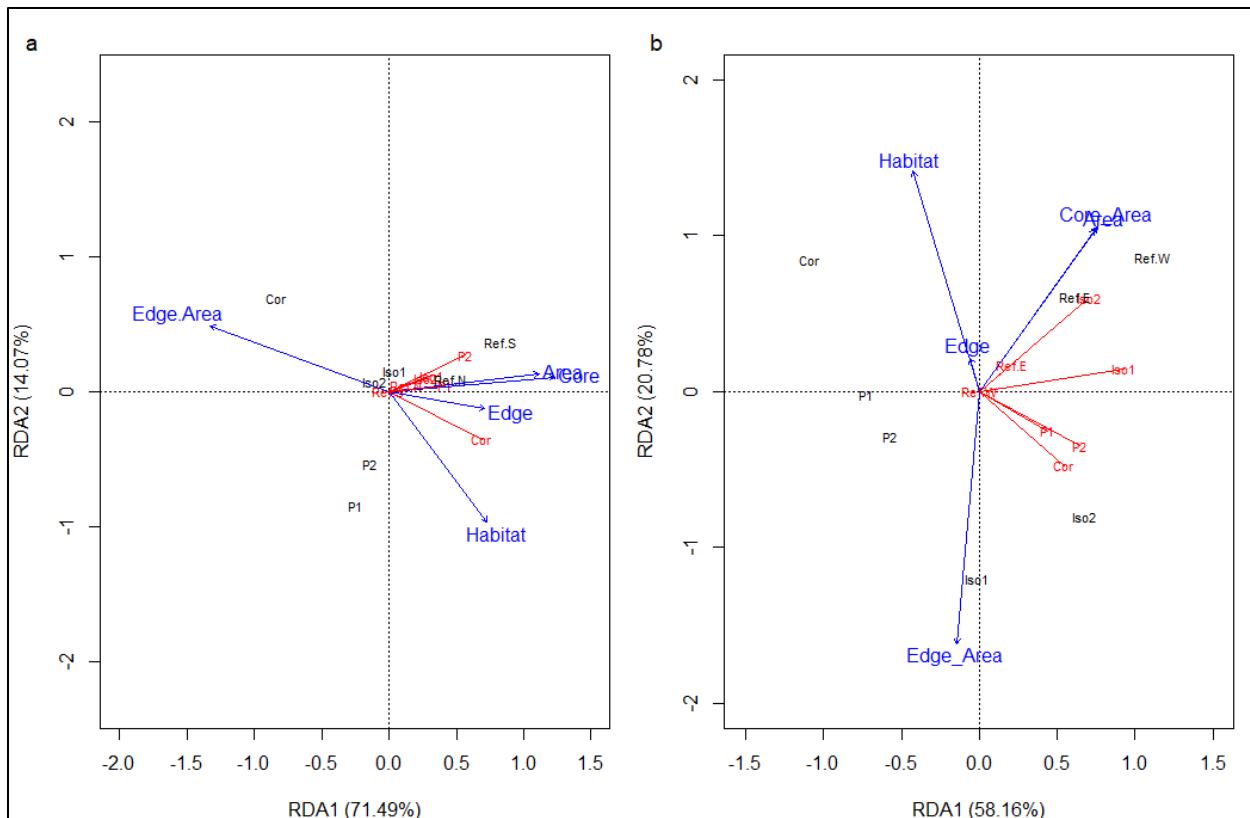


Figure 3.9: Redundancy analysis ordinating Nei's genetic distances for (a) the white-footed mouse (*Peromyscus leucopus*) in Kansas and (b) North American deer mouse (*Peromyscus maniculatus*) in Idaho by the associated with environmental variables measured for each landscape element.

3.4 Discussion

As expected, the least-cost path for focal species to traverse a single path through the reference area was the lowest across landscape elements. However, the Euclidean distance through the reference area termini was the greatest. This suggests intact reference areas are composed of suitable habitat for focal species. Interestingly, from a landscape perspective, when a network of several paths was identified using current flow, the cumulative resistance was higher in reference areas than corridors, patches, and isolates.

From a landscape perspective, for focal species to traverse a network of paths, cumulative resistance among isolates was most similar to corridors and lower than patches and intact reference areas. However, the cumulative resistance values were highest to traverse among isolates along simulated routes. This suggests in the absence of structural connectivity, the permeability or stepping stones throughout the matrix provides functional connectivity for focal species in the absence of structural connectivity.

These finding suggests short matrix crossings among stepping stones in the landscape could be as effective a connectivity strategy as establishing or protecting a continuous swath of natural vegetation between focal patches. This could argue landscape connectivity might arise due to irreducibly complex ecological interactions and direct focused movement between focal landscape elements. Thus suggesting, the amount of available habitat for a species on a landscape could be more important for conserving animals than the relative habitat connectivity (Fahrig 2017). When there is limited habitat availability on landscapes (10-30%), Moore et al. (2022) found that landscape configuration may be critical for connectivity. My findings support this and suggest that there is a dynamic interaction between landscape intactness and the value of these corridors. More empirical and simulation work is needed on this dynamic to identify where such critical thresholds may exist (Horan et al. 2011).

Such findings support the idea that patches that are not structurally linked can sustain functional populations (Hanksi and Simberloff 1997) for these small mammal populations. However, it is important to recognize that these small mammals are corridor dwellers and

therefore often require more than one generation for individuals and their genes to move among patches and through a corridor (Beier 2018).

Both the Kansas and Idaho corridors had CSI values > 1 , indicating high functionality of these structural linkages for *P. leucopus* and *P. maniculatus*. The constrained values of the RDA analyses in both Kansas and Idaho were greater than the unconstrained, suggesting that the majority of the variance in Nei's modified genetic distance among sample groups was explained by the environmental variables. Genetic distances were negatively associated with edge-area ratios, indicating genetic diversity decreased edge-area decreased. In contrast, genetic distances among sample groups were positively associated with core area and area, indicating genetic diversity increased with larger patch interiors and patches. This suggests core areas, which contain home ranges and reliable resources (Samuel et al. 1985), are used more frequently by *P. leucopus* and *P. maniculatus*. As such, the amount of core area and area for *Peromyscus* species is critical for the functionality of corridors.

Interestingly, the same structural composition and configuration of landscapes had similar but opposite influences on genetic distance for both *Peromyscus* species. Genetic distances in Kansas were positively associated with edge and percent of habitat whereas they were negatively associated with these variables in Idaho. This supports previous findings with Moore et al. (2022) where configuration of landscapes was critical with limited habitat availability. Specifically, as the Kansas landscape was composed of less habitat (13%) for focal species than the Idaho landscape (52%).

Given the Kansas corridor is 0.45 km long and 0.14 km wide (Table 2.5) and the Idaho corridor is 4.59 km long and 2.98 km wide (Table 2.5), these findings suggest with smaller corridor configurations, the amount of available habitat is critical for genetic diversity. Specifically, for corridor dwellers in this case, which use a corridor as habitat and require several days to multiple generations for individuals or their genes to disperse through a corridor (Beier and Loe 1992; Beier 2018).

This research has advanced the field of corridor ecology by developing methodologies to further our understanding of complex patterns and processes in the real-world that we don't have a foundational understanding of. Future research further assessing the functionality of corridors using gene flow will continue to further our understanding of conservation corridors. In addition, researchers should continue to assess landscape heterogeneity for focal species.

A critical component to understanding the efficacy of conservation corridors is the ability to identify corridor termini. However, rooted in this knowledge gap is the ability to delineate the boundaries of landscape elements. The methodologies developed to delineate corridor boundaries and identify patch-corridor interfaces was intended to ignite conversations among researchers and conservationists to continue to address critical issues.

The structural configuration and heterogeneity in composition within real world corridors is more complex than experimental corridor systems. Assessing the efficacy of real-world corridors is critical as conservation corridors are designed and built in the world and species will respond to the complex heterogeneity of the landscape.

CHAPTER 4

SUMMARY

The purpose of this research was to advance the field of corridor ecology by addressing critical knowledge gaps in our understanding of corridor efficacy. The structural configuration and heterogeneity in composition within real world corridors is more complex than experimental corridor systems. Assessing the efficacy of real-world corridors is critical as conservation corridors are designed and built in the world and species will respond to the complex heterogeneity of the landscape.

The most urgent issue land managers must address (Gilbert-Norton et al. 2010) is how wide does a corridor have to be given its length to meet conservation goals (Harrison 1992; Beier 2018)? Identifying meaningful corridor termini is a critical component in understanding the efficacy of conservation corridors. Yet, implicated in the question of corridor width and length is the ability to identify the boundaries of a corridor. Given this long recognized knowledge gap that is seldom modelled or incorporated in corridor designs (Hilty et al. 2020), I'm hopeful the methodologies I've developed with a spatial modelling approach to delineate corridor boundaries and identify patch-corridor interfaces will ignite conversations among researchers and conservationists to continue to address critical issues.

In chapter 2, 'Using remote sensing to standardize the delineation process of patch-corridor-matrix boundaries across landscape mosaics', I developed a quantitative and repeatable methodology to standardize the delineation process of patch-corridor-matrix boundaries using remotely sensed data. Specifically, by delineating the boundaries between

focal habitat and the surrounding matrix and identifying a meaningful start and end to corridors.

Moreover, how does heterogeneity within the structural configuration of a corridor influence corridor functionality? While some land covers facilitate species movements, others impede wildlife dispersal and fragment patches of habitat. Species behavior, habitat preferences, and dispersal mechanisms through patches of non-habitat or the matrix influences connectivity (Prevedello et al. 2010). The quality of the matrix influences ecological dynamics in fragmented landscapes (Fahrig 2007). As such, considering the landscape mosaic is critical to model connectivity as species behavior, life-history traits, and willingness to disperse through non-habitat patches or the matrix influences connectivity on heterogeneous landscapes (Prevedello et al. 2010).

In chapter 3, ‘Investigating the degree to which the presence of a corridor influences the structural and functional connectivity of small mammal habitats’, I built upon the methodologies developed in chapter 2 to assess the degree to which the presence of a corridor influences connectivity when compared to an intact reference area and isolated patches. Rooted in that objective, was measuring the degree to which the presence of a corridor facilitates or impedes the dispersal and distribution of corridor dwelling *Peromyscus* species. The configuration of landscapes is critical for maintaining the genetic diversity among these species when habitat availability is low.

As such, the structural configuration of corridors is critical for assessing their functionality for focal species. Implementing a species perspective to define the spatial extent at which we evaluate connectivity may provide a useful starting point for spatial modelling.

Conservation corridors remain frequently cited and we invest limited conservation resources and funds toward designing and building such structures. Yet, if we evaluate connectivity across a landscape versus patch elements, we are not necessarily left with the question of do corridors work, but do corridors matter?

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