MODELING THE BEHAVIORAL LANDSCAPE ECOLOGY OF A REINTRODUCED CARNIVORE

by

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A Dissertation

Submitted to the Faculty of Purdue University
In Partial Fulfillment of the Requirements for the degree of

Doctor of Philosophy

Department of Forestry & Natural Resources
West Lafayette, Indiana
August 2018

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ABSTRACT

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Degree Received: August 2018
Title: Modeling the Behavioral Landscape Ecology of a Reintroduced Carnivore.
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The American marten (*Martes Americana*) is an endangered forest carnivore native to the Upper Midwestern United States and culturally significant to local Ojibwe tribes. In this region, the marten faces a number of potential threats to its persistence, including competition, predation, lack of prey availability, lack of recruitment, and lack of population connectivity. To evaluate how marten behavior affects the conservation and management of this species, I developed an individual-based model to simulate marten dispersal and home range establishment. In Chapter 2, I describe the model and the process of calibrating it to perform comparably to real-world martens. I also demonstrate support for a theoretical hypothesis of animal dispersal, that a dispersing individual should be willing to settle in lower quality habitat over time. In Chapter 3, I apply this model to a nearby landscape in the region to determine how land use change, mortality, and asymmetrical landscape configuration affect the ability of martens to disperse and maintain connectivity between populations. Mortality of dispersing individuals had the greatest effect on connectivity, while landscape configuration had the greatest effect on dispersal metrics. In Chapter 4, I used a dynamic landscape simulation model combined with a model of land transformation to extend my IBM to investigate how 100 years of land use and climate change might affect marten populations. In Chapter 5, I demonstrate how behavioral barriers to mating among reintroduced martens from different source populations may be driving declines in genetic diversity in the region. Ultimately, this work shows how tools such as IBMs and population genetics can be used

to address real-world conservation problems when experimental field methods are limited by factors such as time, cost, and scarcity. At the same time, these applications can be used to ask important questions of theoretical ecology, ultimately serving both pragmatic and paradigmatic purposes.

CHAPTER 1. INTRODUCTION

The American marten (*Martes americana*) is a state and tribally endangered forest carnivore in Wisconsin that is native through much of the Upper Midwestern United States (Williams et al. 2007). The marten is a culturally significant clan animal to local Ojibwe Tribes, serves as an overall indicator of forest health (USDA 2006), and is an economically valuable furbearer where abundant. In Wisconsin, the marten was extirpated in the early 20th century as a result of over-harvest and habitat degradation. Numerous reintroduction projects have been undertaken in the state with the goal of restoring the marten to a portion of its native range (Williams et al. 2007). While martens have persisted in Wisconsin since the initial reintroduction efforts in the 1970s, the species remains state-endangered (Manlick et al. 2017a). Several hypotheses have been investigated as to why population densities have remained low, including competition with fishers, lack of recruitment, lack of suitable habitat, lack of available prey, and lack of population connectivity (McCann et al. 2010, Carlson et al. 2014, Manlick et al. 2017a, Manlick et al. 2017b, Grauer et al. 2017). Martens face additional threats from land-use change and climate change that may limit habitat availability in the future (Carroll 2007, Wasserman et al. 2012, Wasserman et al. 2013).

In 2013, plans were announced for the development of the Gogebic Taconite Mine to be placed in northern Wisconsin's Penokee Hills (Verburg 2014). The mine site in Iron County, WI was located in a potentially vital habitat corridor between two populations of martens: one population reintroduced to the Chequamegon National Forest to the east, and another reintroduced to Michigan's Upper Peninsula to the west. Concerns about interference of the proposed mine with connectivity between the marten populations precipitated the need for a better understanding of habitat use in the matrix between the two reintroduction locations. To address this issue, I developed an individual-based model (IBM) of marten dispersal and home range establishment.

Individual-based modeling is a powerful tool for studying ecosystem processes. The power of the individual-based model (IBMs) comes from its mechanistic approach to simulating ecosystem processes (Grimm 1999, DeAngelis and Mooij 2005). Rather than identifying and reproducing broad-scale patterns, IBMs simulate fine-scale interactions between individual agents in the model and between agents and the environment using simple rules governing behavior (Grimm and Railsback 2005). The goal is for these fine-scale interactions to scale up to reproduce the broad-scale patterns observed in nature from a top-down perspective (Wiegand et al. 2003, Grimm and Railsback 2011). If successful, the result is a model that is robust to changes in the environment in which the individuals are operating, as the mechanistic behaviors respond to the new environment based on first principles (Wiegand et al. 2003). IBMs are therefore ideal tools for studying threatened or endangered species (TES; Letcher et al. 1998, Elderd and Nott 2008). Such species can be difficult to study in the field due to low abundance and sensitivity to disturbance, and thus achieving adequate sample sizes and replicates can be a challenge. In addition, conservation strategies for the recolonization and reintroduction of TES are common (Seddon et al. 2007, Armstrong and Seddon 2008), and models capable of simulating alternative strategies can guide conservation efforts (Jarchow et al. 2016).

I used an IBM to explore questions of marten dispersal for several reasons. First, martens are endangered, and gathering the necessary sample size for a behavioral study on a cryptic, rare species can be difficult. The landscape across which martens disperse is large and dynamic, and I wanted to be able to simulate landscape change over time as well as hypothetical management scenarios. Third, individual animal behavior is extremely difficult to study in the field, and hypotheses of animal behavior can first be evaluated in a simulation environment prior to field testing. Finally, building an IBM from the bottom-up allows for projection of marten behavior under future scenarios while maintaining core behavioral principles. I used the resulting IBM of marten dispersal to evaluate the potential impact of the proposed mine, as well as to investigate population connectivity via population genetics of martens across the landscape. Once the initial IBM was developed and performing according to expectations, I developed additional objectives associated with climate change and land use change to take advantage of the existing IBM framework. To address these questions, I used an existing IBM framework (SEARCH; Spatially Explicit Animal Response to Composition of Habitat (Pauli et al. 2013)) to produce the simulation model of marten dispersal and home range establishment. Using SEARCH, I tested multiple alternative landscapes and hypotheses related to how martens select home ranges and how they might respond to changes in land use and climate.

Development of an IBM is an iterative process and often follows what has been termed “The Modeling Cycle” (Grimm and Railsback 2005). The Modeling Cycle presents model development as a circular process that begins with the simplest possible version of the model and builds in complexity over time. After each iteration of the model, hypotheses are re-evaluated, and a new implementation is produced to address the new hypotheses. Once the model is sufficiently complex to answer the desired questions, model results are then communicated via publication or some other outlet. In developing an IBM of the dispersal behavior of American martens, I followed this cycle of slowly incorporating additional rules to improve the performance of virtual martens relative to data collected from actual martens in the field. As a result, I identified a hypothesis that, once implemented, dramatically improved the performance of the virtual martens. This hypothesis was one I would not have explored without the process of exploring animal dispersal behavior through my own interaction with the model. Ideally, I would have identified this hypothesis *a priori*. However, implementing the modeling cycle aided me in being the first to apply this theoretical hypothesis to vertebrate dispersal behavior.

Another advantage of developing an IBM is that it can aid in identification of critical gaps in knowledge and future research needs. This often occurs as a result of linking mechanisms with processes, or in other words, developing an understanding of the model that allows one to connect results to specific mechanisms in the model (Grimm et al. 2005). Following initial model calibration, I applied my model of marten dispersal to a number of alternative landscapes affected by land-use and climate change. Results were sometimes counter-intuitive, leading to conclusions that conflicted with the prevailing thinking about marten habitat requirements. As one example, in order to model marten response to climate change I simulated habitat conditions under various climate scenarios and modeled marten dispersal across the new landscape of habitat suitability. Despite climate change leading to the simplification and homogenization of forest stands, my model indicated a positive relationship between carbon emissions and habitat suitability for martens. This likely occurred because the habitat suitability model I used did not incorporate factors such as tree species richness or forest structural complexity, because it was originally developed for the present landscape and not for future landscapes subject to climate change. Forest simplification and homogenization was an unexpected effect of climate change, and my subsequent modeling work therefore revealed the need to study how martens respond to such changes in forest composition. Through the modeling process, I ended up providing answers to questions that I did not know needed answers.

With any ecological model, the temptation exists to use the results to make predictions about patterns that arise from ecological processes. However, it is important to emphasize that the insights gained from model development, testing, and exploration can be more valuable than the results themselves. In this way, a model can be thought of as a hypothesis rather than as an accurate representation of reality (Starfield 1997). By exploring a set of hypotheses, the modeler can gain insights about a system that would be impossible to produce given the many constraints associated with studying ecosystem processes and managing natural resources. Results from modeling work are often best viewed as relativistic. In the present work for example, I emphasize the relative effects of various factors on marten dispersal, rather than the actual distance martens traveled in any given scenario. Ecological models can be particularly advantageous when data about a given system are lacking or impossible to collect, as the entire range of parameter space and its effects can be explored using sensitivity analysis or inverse modeling (Wiegand et al. 2003, Cariboni et al. 2007). The tradeoff for all of these advantages is that in any model, simplifying assumptions must be made about real-world processes in order to make the model tractable (Sun et al. 2016). The modeler thus has the responsibility of selecting the key processes required to address the questions of interest.

My work on marten populations and dispersal behavior has likely raised more questions than it has answered. For example, how does the placement versus the size of a mine affect functional connectivity? How will martens respond to effects from climate change such as loss of snow cover and tree species richness? What mechanism is preventing the lack of genetic mixture between subpopulations of martens in Wisconsin and Michigan? These questions represent fulfillment of one of the primary goals of IBM development - to direct future research needs in both the field and within the simulation modeling environment (McLane et al. 2011, Wood et al. 2015). Ideally, feedback between the modeling process and empirically-based field work will provide the foundation to support an adaptive management framework to guide the future of marten conservation in the Upper Midwest (Walters 1986). In the case of martens in Wisconsin, partnerships with agencies such as the Great Lakes Fish and Wildlife Commission, Wisconsin Department of Natural Resources, and the USDA Forest Service have proved invaluable in providing data and support for the development and application of an IBM of marten dispersal, ultimately leading toward achieving solutions to real world problems.

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CHAPTER 2. PLASTICITY IN HABITAT SELECTIVITY EXPLAINS PATTERNS OF DISPERSAL FOR A SOLITARY CARNIVORE

2.1 Abstract

Patterns of dispersal behavior are often driven by the composition and configuration of suitable habitat in a matrix of unsuitable habitat. Interactions between behavior and landscapes can therefore influence population dynamics, population and species distributions, population genetic structure, and the evolution of behavior. Spatially-explicit individual-based models are ideal tools for exploring the effects of landscape structure on dispersal. We developed an empirically-parameterized IBM in the modeling framework SEARCH to simulate dispersal of translocated American martens in Wisconsin, USA. We tested the hypothesis that a time-limited disperser should be willing to settle in lower quality habitat over time. To evaluate model performance, we used a pattern-oriented modeling approach. Our best model matched all empirical dispersal patterns (e.g., dispersal distance) except time to settlement. This model incorporated the mechanism for declining habitat selectivity over time and for a required exploratory phase prior to home range establishment. Finally, we used inverse modeling to identify the rate of movement by dispersing martens, which was critical to successful pattern-matching. The fully calibrated model will be applied to test for effects of factors such as land-use and climate change on marten dispersal and population connectivity. In this sense, our IBM is pragmatic because it addresses a management need for a species of conservation concern. However, our model is also paradigmatic in that it explicitly tests a theory of dispersal behavior. Linking these two approaches to ecological modeling can further the utility of individual-based modeling and provide direction for future theoretical and empirical work on animal behavior.

2.2 Introduction

Interactions between landscape-level patterns and animal decision-making behaviors can regulate important ecological and evolutionary processes for both species and communities (Lima and Zollner 1996). For example, much research has focused on how patterns of animal movement are affected by the composition and configuration of landscapes (Schick et al. 2008). Animals often adjust the speed and/or straightness of their movement as a result of factors such as habitat type (Roshier et al. 2008), disturbance (Anadón et al. 2012), and patchiness (Johnson et al. 2001). These fine-scale effects may ultimately drive major demographic or ecological processes including invasions of non-native species (Holway and Suarez 1999) or spatial and temporal variation in foraging behavior (Johnson et al. 2001; Launchbaugh and Howery 2005). Likewise, interactions between animal movement behaviors and landscape structure can shape the connectivity and distribution of populations through dispersal and settlement (Bowler and Benton 2005; Burgess et al. 2012).

Animal dispersal comprises a complex series of events that begin with emigration from an individual's natal location and end with immigration to a new settlement location. Between emigration and immigration, individuals undergo an exploratory phase wherein they travel between habitat patches in search of a suitable home range (Bowler and Benton 2005). Each of these dispersal events involves adaptive decision-making by individual dispersers that can have significant demographic consequences for animal populations (Bowler and Benton 2005). To explore the consequences of animal decision-making during dispersal, simulation modeling is often used to demonstrate how animal behaviors interact with landscapes to produce population-level patterns of dispersal (Knowlton and Graham 2010). Examples include relationships between landscape structure and population distribution (Vuilleumier and Metzger 2006), resource distribution and mortality risk, energy reserves, and search strategy (Zollner and Lima 1999), and functional grain and movement behavior (Baguette and Van Dyck 2007; Knowlton and Graham 2010). Theoretical simulations have been accompanied by applied simulation models in which dispersers are empirically parameterized (i.e., using field data) and alternative rules for dispersal behavior or habitat selection are tested for their effects on dispersal success (Kanagaraj et al. 2013; Kramer-Schadt et al. 2011; Stenglein et al. 2015). Applied models can then be used as tools to aid in the development of management or conservation plans using case-specific populations, locations, and management scenarios (Pauli et al. 2013).

Spatially explicit, individual-based models (IBM) are commonly used to explore processes of animal behavior and demographics (Johnson et al. 1992), and the use of this technique has been increasing among behavioral and landscape ecologists (DeAngelis and Grimm 2014). IBMs can be “pragmatic” in nature when used as tools for management applications but can also be “paradigmatic” when they explore the underlying theory of ecological questions (Grimm 1999). In either scenario the observed behaviors are a result of external factors combined with underlying cognitive processes and latent behavioral states (Nathan et al. 2008). Thus, it is often more difficult to evaluate and describe the underlying decision-making processes that drive behavior than it is to describe the behavior itself (Lichti et al. 2017). IBMs can be used to test hypotheses and elucidate mechanisms that drive decision-making behaviors at the scale of the individual (e.g., Railsback and Harvey 2002). In a simulation framework, constraints on the breadth of scenarios that can be tested or the number of replicates that can be conducted are usually far less than the constraints on traditional field studies. Therefore, paradigmatic IBMs provide a powerful means for investigating mechanisms driving certain animal behaviors, yet landscape ecologists have often called for more realism and complexity to be incorporated into simulation models (Bonte et al. 2012; Johnson et al. 1992; Lima and Zollner 1996; Travis et al. 2012). In response to such a call, behavioral mechanisms identified from paradigmatic IBMs are applied to more pragmatic models to develop or evaluate plans for the management or conservation of individual populations or species (McLane et al. 2011).

Individual-based models are most commonly evaluated using pattern-oriented modeling (POM; Grimm and Railsback 2011; Wiegand et al. 2003). This approach requires the identification of a number of observed patterns usually derived from empirical data that are then used collectively as a benchmark to assess model performance. As alternative hypotheses and models are tested, they can be retained or rejected until a model is identified that successfully matches the selected patterns. This technique can also be used to calibrate specific uncertain parameters (i.e., inverse modeling) by selecting the parameter values that result in the best model performance (Grimm and Railsback 2011; Wiegand et al. 2003). Since complex systems can rarely be described by a single pattern (Grimm et al. 2005), matching multiple patterns increases the likelihood that the model is reproducing the bottom-up mechanisms that are driving the system – each pattern acting to filter out poor models and ensure that the best performing model is selected.

Models that have been calibrated using POM can be useful for demonstrating interactions between animal dispersal behaviors and landscape structure (Kramer-Schadt et al. 2011). For example, understanding the relationship between the timing of home range establishment and quality of the selected home range has critical implications for the survival, condition, and reproduction of individuals and populations. Early models of dispersal assumed that individuals would distribute themselves in an Ideal Free Distribution, where distribution would be directly correlated with resource availability (Fretwell 1972; Fretwell and Calver 1970). Subsequent work has identified additional factors that affect the quality and timing of home range selection including natal experience (Mabry and Stamps 2008), body size (Stamps 1988), and conspecific attraction (Muller et al. 1997).

Ward (1987) built on the experimental (Knight-Jones 1951, 1953; Wilson 1953) and theoretical (Jaenike 1978; Levins 1968; Levins and MacArthur 1969) work of others to propose a model of dispersal whereby selectivity in habitat selection declines over time for individuals that have a set time period during which they must establish a home range (i.e., time-limited). The probability of selecting habitat for a home range, therefore, is dependent on the likelihood of encountering and accepting similar (or better) habitat in the future. A suboptimal patch of habitat that is initially rejected by the disperser may be accepted at a later time once some threshold of habitat selectivity is reached. Ward's hypothesis has received empirical support from studies on larval marine invertebrates and insects (e.g., Elkin and Marshall 2007). However, the hypothesis lacks support from spatially explicit contexts with more behaviorally complex vertebrates making cognitive decisions in response to physiological and environmental cues.

We developed an empirically-parameterized IBM of dispersal behavior of the American marten (*Martes americana*) in Wisconsin, USA, and tested Ward's prediction of decreasing habitat selectivity with search time. Martens are solitary carnivores that usually leave their natal grounds 4-6 months after birth (Johnson et al. 2009). Their home ranges are associated with increasing canopy cover and complex forest structure, and prey consists primarily of small mammals and leporids. Martens were once abundant in Wisconsin but are currently rare and have been the focus of conservation management programs since the 1970s (Williams et al. 2007). Despite continued efforts, low survival and recruitment in some areas have resulted in a recovery that has been stagnant since the initial reintroduction of martens to northern Wisconsin (Manlick et al. 2017; McCann et al. 2010; Woodford et al. 2005). As dispersal and home range establishment are closely linked to juvenile survival, tools are needed that can be used to evaluate factors that may be influencing dispersal, habitat selection, and home range establishment. Much work has already been done on habitat associations of martens in Wisconsin at multiple scales (Dumyahn et al. 2007; McCann et al. 2014; Wright 1999). Our objective was to identify the behavioral mechanisms that drive those associations. More specifically, are habitat selection requirements static or do they decline over time according to Ward's hypothesis? Is the timing of dispersal dependent only on available resources or on other behavioral rules as well? Answering such questions would improve capabilities for planning for the conservation and management of martens in Wisconsin and throughout their range.

We used the marten IBM to evaluate alternative rules for habitat selection and movement of translocated American martens in northern Wisconsin. Specifically, we had 3 objectives. (1) Parameterize and calibrate an IBM of marten dispersal to match empirical data collected from translocated martens. (2) Evaluate alternative spatial and temporal models of marten habitat selectivity (i.e., perception of habitat suitability) and its effects on dispersal metrics. For this objective, we used alternative submodels to test the effect of minimum time to home range establishment, the proportion of suitable habitat in an area required for home range establishment, and the selectivity of habitat selection over time (Ward's hypothesis). (3) Use inverse modeling to refine an unknown movement parameter – distance moved per time step.

Interactions between landscape-level patterns and animal decision-making behaviors can regulate important ecological and evolutionary processes for both species and communities (Lima and Zollner 1996). For example, much research has focused on how patterns of animal movement are affected by the composition and configuration of landscapes (Schick et al. 2008). Animals often adjust the speed and/or straightness of their movement as a result of factors such as habitat type (Roshier et al. 2008), disturbance (Anadón et al. 2012), and patchiness (Johnson et al. 2001). These fine-scale effects may ultimately drive major demographic or ecological processes including invasions of non-native species (Holway and Suarez 1999) or spatial and temporal variation in foraging behavior (Johnson et al. 2001; Launchbaugh and Howery 2005). Likewise, interactions between animal movement behaviors and landscape structure can shape the connectivity and distribution of populations through dispersal and settlement (Bowler and Benton 2005; Burgess et al. 2012).

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Models that have been calibrated using POM can be useful for demonstrating interactions between animal dispersal behaviors and landscape structure (Kramer-Schadt et al. 2011). For example, understanding the relationship between the timing of home range establishment and quality of the selected home range has critical implications for the survival, condition, and reproduction of individuals and populations. Early models of dispersal assumed that individuals would distribute themselves in an Ideal Free Distribution, where distribution would be directly correlated with resource availability (Fretwell 1972; Fretwell and Calver 1970). Subsequent work has identified additional factors that affect the quality and timing of home range selection including natal experience (Mabry and Stamps 2008), body size (Stamps 1988), and conspecific attraction (Muller et al. 1997).

Ward (1987) built on the experimental (Knight-Jones 1951, 1953; Wilson 1953) and theoretical (Jaenike 1978; Levins 1968; Levins and MacArthur 1969) work of others to propose a model of dispersal whereby selectivity in habitat selection declines over time for individuals that have a set time period during which they must establish a home range (i.e., time-limited). The probability of selecting habitat for a home range, therefore, is dependent on the likelihood of encountering and accepting similar (or better) habitat in the future. A suboptimal patch of habitat that is initially rejected by the disperser may be accepted at a later time once some threshold of habitat selectivity is reached. Ward's hypothesis has received empirical support from studies on larval marine invertebrates and insects (e.g., Elkin and Marshall 2007). However, the hypothesis lacks support from spatially explicit contexts with more behaviorally complex vertebrates making cognitive decisions in response to physiological and environmental cues.

We developed an empirically-parameterized IBM of dispersal behavior of the American marten (*Martes americana*) in Wisconsin, USA, and tested Ward's prediction of decreasing habitat selectivity with search time. Martens are solitary carnivores that usually leave their natal grounds 4-6 months after birth (Johnson et al. 2009). Their home ranges are associated with increasing canopy cover and complex forest structure, and prey consists primarily of small mammals and leporids. Martens were once abundant in Wisconsin but are currently rare and have been the focus of conservation management programs since the 1970s (Williams et al. 2007). Despite continued efforts, low survival and recruitment in some areas have resulted in a recovery that has been stagnant since the initial reintroduction of martens to northern Wisconsin (Manlick et al. 2017; McCann et al. 2010; Woodford et al. 2005). As dispersal and home range establishment are closely linked to juvenile survival, tools are needed that can be used to evaluate factors that may be influencing dispersal, habitat selection, and home range establishment. Much work has already been done on habitat associations of martens in Wisconsin at multiple scales (Dumyahn et al. 2007; McCann et al. 2014; Wright 1999). Our objective was to identify the behavioral mechanisms that drive those associations. More specifically, are habitat selection requirements static or do they decline over time according to Ward's hypothesis? Is the timing of dispersal dependent only on available resources or on other behavioral rules as well? Answering such questions would improve capabilities for planning for the conservation and management of martens in Wisconsin and throughout their range.

We used the marten IBM to evaluate alternative rules for habitat selection and movement of translocated American martens in northern Wisconsin. Specifically, we had 3 objectives. (1) Parameterize and calibrate an IBM of marten dispersal to match empirical data collected from translocated martens. (2) Evaluate alternative spatial and temporal models of marten habitat selectivity (i.e., perception of habitat suitability) and its effects on dispersal metrics. For this objective, we used alternative submodels to test the effect of minimum time to home range establishment, the proportion of suitable habitat in an area required for home range establishment, and the selectivity of habitat selection over time (Ward's hypothesis). (3) Use inverse modeling to refine an unknown movement parameter – distance moved per time step.

2.3 Methods

2.3.1 Study System

We simulated the dispersal and home range establishment of 15 radio-collared martens translocated to the Chequamegon-Nicolet National Forest (CNNF) in north-central Wisconsin in 2010 (Figure 1). This translocation took place on the western portion of the CNNF and was part of a broader program conducted by the Wisconsin Department of Natural Resources, US Forest Service, and Great Lakes Indian Fish and Wildlife Commission that brought a total of 90 martens from Minnesota to the western CNNF from 2008-2010 (Woodford 2010). The releases from 2008-10 were in addition to 139 individuals translocated to the western CNNF in 1987-1990 as well as previous translocations to the eastern CNNF after extirpation of martens from Wisconsin by 1925 (Williams et al. 2007). To calibrate the model, data on mortality, dispersal, and home range establishment for the 15 translocated individuals were collected using radio-telemetry (Woodford et al. 2013) and compared to simulation results.

To define the extent of the simulation area, we buffered marten release locations by 34 km, representing the upper 95% confidence limit of marten dispersal distance measured from martens released during an earlier translocation to the eastern CNNF (Davis 1983). The resulting buffered area was 6,956 km^2 and contained portions of Ashland, Bayfield, Iron, Price, and Sawyer Counties. This area was comprised in large part by the CNNF, but also contained significant portions of county forest, state land, tribal reservations, commercial/residential forested land, and urban/residential areas (Figure 1). Forests in the simulation area were predominantly northern hardwoods dominated by sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and birch (*Betula spp*). Stands of quaking aspen (*Populus tremuloides*) and mixed and conifer stands including balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), northern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*) were common as well. Timber harvest is economically important in the region, and both public and private forests were being actively harvested during the time of the marten translocations. Topography was generally flat, except for where the Gogebic range intersected the northwest portion of the study area, rising in some locations over 150 m to reach elevations greater than 570 m above sea level.

2.3.2 Model Description

To simulate the dispersal and home range establishment of translocated martens, we combined an individual-based model of animal dispersal with habitat suitability modeling (e.g., Kanagaraj et al. 2013; Kramer-Schadt et al. 2011) in the modeling framework Spatially Explicit Animal Response to Composition of Habitat (SEARCH; Pauli et al. 2013). SEARCH has been used previously to explore dispersal of other species such as Burmese pythons (*Python bivittatus*; Mutascio et al. 2017) and northern flying squirrels (*Glaucomys sabrinus*; Trapp et al. unpublished data). In SEARCH, solitary dispersers move across a spatially explicit landscape, querying 4 independent, vector-based spatial layers that govern the following sets of parameters during each time step: food availability, predation risk, movement, and habitat suitability/sociality. Each of these sets of parameters may vary spatially but can be temporally dynamic as well. For example, food availability may vary by habitat, but can also vary daily, seasonally, or annually. Dispersers navigate their environment searching for suitable habitat that is unoccupied by conspecific of the same sex. When an area of contiguous suitable habitat ≥ 10% of the minimum home range size is encountered, the location is added to a list of suitable locations stored in the individual's memory. When the individual decides to attempt home range establishment, it sorts the existing list of stored locations based on a combination of factors including food availability, predation risk, and proximity to present location. The disperser then travels to the top-ranked site and attempts to establish a home range. If the amount of available (i.e., unoccupied) suitable habitat at that site is inadequate to support a home range, the individual either continues searching or reevaluates the list of sites and orients toward the new top priority. This process continues until the individual successfully establishes a home range, dies from predation or starvation, or dies at the end of the dispersal season.

In our application of SEARCH, we simulated a 60-day dispersal period divided into 5,760 time steps of 15-minutes each. Martens actively dispersed for an average of 9.1 hours per day (SD = 0.70), values that corresponded to activity periods in the fall in the same study area (Gilbert et al. 2009). Release locations and sex of the 15 dispersers were chosen based on actual marten releases in 2010. Except where noted, all other parameterizations were derived from data collected from a separate release of martens that were equipped with radio-collars and released in 2009. This allowed us to maintain independence between data used for parameterizing model agents and data used for calibration and pattern-matching. Parameterization of the 4 spatial layers described below followed methods used by McCann (2011).

2.3.3 Spatial Layers

The movement layer regulates distance moved per time step (Mean Step Length, MSL), average turning angle per time step (expressed as Mean Vector Length, MVL; Benhamou, 2004), perceptual range, and probability of crossing between habitat types. We calculated MSL and MVL for each cover type by snow-trailing martens on the study area during winters 2008-9 and 2009-10 (see McCann et al. 2014 for a full treatment of these data). These values differed by cover type and by sex (Moriarty et al. 2016). Females averaged shorter MSL and sharper turning angles than males, and the female-male ratio was 0.9 for MSL and 0.97 for MVL. We set perceptual distance at 100 m for all cover types (Gardner and Gustafson 2004). We assumed that dispersing martens crossed freely between forested cover types, but rarely (i.e., with a 1% probability) crossed into unforested cover types (e.g., clearcuts, lakes, urban areas) (Chapin et al. 1998; Hargis et al. 1999; Moriarty et al. 2016).

The food availability layer regulates probability of prey capture by cover type and mean (±SD) energy acquired given a successful predation event. We calculated probability of prey capture and species of prey acquisition from the previously described snow-trailing data (McCann et al., 2014). Mean energy acquired (kJ) from a predation event was derived from estimates reported by Cumberland et al. (2001). Martens began each simulation with an initial energy reserve of 5,491 kJ, calculated by multiplying the average mass of a marten by the fraction of a marten composed of fat. Martens expended 10.5 kJ of energy per time step (1,006 kJ/day (Gilbert et al. 2009). Individuals died from starvation after energy reserves reached 0 kJ.

The predation risk layer regulates probability of mortality due to predation. We calculated this probability per time step based on mortality data collected from an earlier translocation during which martens were monitored for an average of 70 days on the CNNF (Davis 1983). We allocated risk to each cover type based on indices of relative abundance of the primary predators of martens (i.e., fishers, *Pekania pennanti*, and owls) and to unknown causes (McCann et al. 2010). We calculated these indices based on the presence of fisher tracks (McCann et al. 2014) and owl calls (PAZ unpublished data) in each cover type. We distributed unknown causes of mortality equally across all cover types.

In SEARCH, habitat suitability is represented as a binary layer of suitable/unsuitable habitat. Previous work in our study area demonstrated that at least 70% of marten HRs were composed of preferred or neutral (i.e., non-avoided) habitat types (Bissonette et al. 1997; Dumyahn et al. 2007; Wright 1999). Suitability was dependent on both cover type and size of the trees (i.e., Diameter at Breast Height) in each stand. To determine cover type and tree size for public lands on our study area, we retrieved all available stand-level data within the simulation extent from the Wisconsin Forest Inventory and Reporting System (WisFIRS), the CNNF, and the Bad River Band of the Lake Superior Chippewa Tribe. These data included both the primary cover type and size of the stand (i.e., seedling/sapling, pole, saw log). We then converted each of these stands to preferred, neutral, or avoided habitat types based on Wright's (1999) classification. For the proportion of the landscape in which we lacked stand data (48.8%), we used the remotely sensed Wisconsin Land Cover Data set (Wiscland) Level III. These data provided cover type but not size data. Habitat suitability is dependent on tree size however, so rather than assign binary habitat suitability values to these cover types, we assigned habitat suitability values according to the proportions of the corresponding stand-level data that were considered preferred or neutral. For example, 17% of aspen on public lands were suitable (i.e., saw log class), therefore pixels with the aspen cover type from Wiscland received a suitability value of 0.17. After assigning suitability values, we used the Focal Statistics tool in ArcGIS 10.3 (Esri, Redlands, CA, USA) to identify pixels where 70% of the surrounding area in a 1 km^2 buffer represented non-avoided cover types. However, we varied the 70% rule to test for responses in dispersal patterns based on habitat selectivity. The resulting rasters were then converted to vector as a binary habitat suitability layer in SEARCH (Figure 2).

To produce maps of conspecific HRs, we started with an unoccupied landscape and populated it with 22 known HRs based on 100% minimum convex polygons (JH Gilbert unpublished data; Dumyahn et al. 2007). To populate the rest of the landscape, we simulated the release and home range establishment of an additional 78 martens based on a total pre-translocation population estimate of 100 martens for the study area (Figure 2). We distributed release locations randomly throughout suitable habitat and allowed individuals to establish a home range immediately. We conducted these randomized establishment runs for each alternative model of habitat suitability.

2.3.4 Study Design

To investigate how martens select habitat, we tested 9 combinations of alternative rules for habitat suitability and home range establishment against the empirical data set. First, we tested 3 versions of a static habitat suitability map using a 50%, 60%, and 70% non-avoided habitat type criterion for home range establishment (see Habitat Suitability section and Figure 2). In these scenarios, martens were allowed to establish a home range immediately, with no exploratory period (Static scenarios). Second, we tested these same scenarios but required individuals to undergo an exploration phase of 2 weeks prior to attempting home range establishment (Delay scenarios). We chose 2 weeks because that matched the minimum time to home range establishment from our empirical data set. Third, we used a dynamic rule for habitat suitability, in which the selectivity criterion for habitat selection was relaxed over time (Dynamic scenarios). Using this dynamic model of habitat suitability, we tested 2 progressions of home range criteria rules: (70% to 60% to 50%) and (80% to 70% to 60%). In each of these 2 scenarios, the 3 separate home range criteria rules were distributed in equal periods throughout the 60-day dispersal period (i.e., 70% rule for 20 days, then 60% rule for 20 days, etc.). For the latter progression, we also tested 2 alternative timing scenarios: one in which the timing for changing habitat suitability maps started immediately, and one in which timing initiation was delayed until after the 2-week exploratory phase.

For each scenario tested, we conducted 5 replicates. For each set of replicates, we also tested 3 values for distance moved per time step (MSL) since it is impossible to derive speed of movement from snow-trailing data. Thus, we used inverse modeling (Wiegand et al. 2003) to identify distance moved per time step by martens. We selected 3 distances for MSL that corresponded to 10, 20, or 30 bounds per minute for each sex (McCann et al. 2017). Therefore, we ran a total of 27 sets of simulations comprising 9 alternative home range establishment criteria crossed with 3 alternative values for MSL.

2.3.5 Data Analysis

We used a pattern-oriented modeling approach to evaluate model calibration success (Grimm and Railsback 2011; Grimm et al. 2005). We analyzed data collected from translocated individuals that were radio-collared and radio-tracked during dispersal (Woodford et al. 2013) and identified 9 empirical patterns to match as a result of our analysis (Table 1). Seven patterns were matched to an empirical estimate and the other 2 incorporated binary matching criteria. Because pattern-matching methods vary widely across studies, we used multiple pattern-matching methods to evaluate which simulation scenarios matched empirical patterns, including a pass/fail, weighted pass/fail, rank-sum, weighted rank-sum, Total Indicator (TI) based on root mean square deviation, and a multi-variate measure (Mahalanobis Distance, D^2). Using multiple methods allowed us to assess the level of corroboration for our model selection across a variety of methods used in the POM literature, and to assess the effect of the selection of a pattern-matching method on model selection results. To select the best model, we ranked all models according to each ranking method and summed their totals (Table 2, Appendix S1).

For the pass/fail method, we established matching criteria for the numerical patterns based on 1.96 times the standard error of the mean value from empirical data, as 95% of population means should fall within that range (i.e., 95% confidence interval; Bauduin et al. 2016). We could not calculate empirical standard errors for population-level patterns (i.e., mortality, days to home range establishment SD, dispersal distance SD), therefore we bootstrapped empirical data using the ‘asbio’ package in Program R to estimate 95% confidence intervals and compare to simulation results (Aho 2016). To penalize models that failed to represent differences in dispersal behavior between males and females, we included 2 patterns associated with timing of and distance to home range establishment by sex. To match these patterns of males dispersing farther and taking more time to settle than females, all 5 replicates of a scenario/bound combination had to reproduce the pattern. After all patterns were evaluated, we ranked models based on the number of patterns matched out of 9. We used the same process for the weighted pass/fail method, except that we assigned an importance value of low, medium, or high to each pattern, corresponding with a score of 1, 2, or 3 points (Stenglein et al. 2015). After evaluating the models for each pattern, we assigned scores corresponding to the pattern's importance value which we then summed across all patterns.

For the rank-sum method we ranked each model scenario based on its accuracy in reproducing the observed pattern, and then summed the ranks across all patterns. For the weighted rank-sum, we used the same weighting system as previously described, and then summed the resulting ranks across all patterns for each scenario. We calculated the Total Indicator (TI) measure (Piou et al. 2007; Semeniuk et al. 2012) by calculating the root mean square deviation (RMSD) for each pattern:

$$\mathrm{RMSD} = \sqrt{\frac{\sum_{\mathrm{r}=1}^{\mathrm{N_{rep}}}(\mathrm{Obs} - \mathrm{Sim})^2}{\mathrm{N_{rep}}}}$$

where r is the replicate, N is the number of replicates, Obs is the observed mean, and Sim is the simulated mean. We then calculated the TI for each model scenario by summing the ratio of each RMSD to the RMSD of the best performing scenario:

$$\mathrm{TI} = \sum_{\mathrm{p}=1}^{\mathrm{n}} \frac{\mathrm{RMSD_p}}{\mathrm{RMSD_{best}}}$$

where p represents each pattern. Finally, we calculated the mean Mahalanobis distance (D^2; Mahalanobis 1936) across replicates between each model scenario and observed data using the pooled covariance matrix (S; Legendre and Legendre 2012).

$$\mathrm{D}^2 = \mathrm{d_{obs,sim}} \cdot \mathrm{S}^{-1} \cdot \mathrm{d'_{obs,sim}}$$

Here d represents the vector of differences between the means of the observed and simulated data for each pattern. Unlike the other approaches used, this approach accounts for covariance among patterns. We ranked models based on D^2 in ascending order.

After pattern-matching and calibration were complete and we had selected our best model, we evaluated that model for its ability to reproduce the general distribution of dispersal distance kernels ($k_d(r)$; Nathan et al. 2012). For martens and across most taxa, dispersal distance kernels are generally leptokurtic and fat-tailed due to occasional long-distance dispersal events (Broquet et al. 2006; Nathan et al. 2012). We evaluated our model for these characteristics by fitting the dispersal distances across all replicates from our top model to a Weibull distribution using a maximum likelihood estimator (Paradis et al. 2002). We then conducted the Anderson-Darling Goodness-of-Fit test to measure how well our simulated results matched the theoretical distribution. We selected the Anderson-Darling statistic because it gives equal weight to the tails and main body of the distribution (D'Agostino and Stephens 1986).

2.4 Results

We completed 135 simulation runs of 15 dispersing martens each. Of the 9 combinations of home range establishment rules we evaluated, the scenario that included the 2-week delay to home range establishment (i.e., exploratory phase) and dynamic habitat selectivity (i.e., Ward’s hypothesis) was consistently the top-ranked model across all methods used to evaluate pattern-matching (Table 2). The longer delay in timing of map swapping (Dynamic 80 (2)) also outperformed the scenario with no delay (Dynamic 80 (1); Table 2). All 6 pattern-matching methods consistently selected the 2-week delay in settlement over the same scenarios with no delay in settlement. For bounds per minute of 20 and 30, the dynamic habitat selectivity scenarios performed best (Table 2). However, for 10 bounds per minute, the 70% static habitat scenario performed best (Table 2). Across both dynamic and static habitat selectivity rules, the scenarios with higher habitat selectivity (i.e., more selective martens) performed better than the scenarios with lower habitat selectivity (e.g., 80, 70, 60 percent rules over the same scenarios with 70, 60, 50 percent rules; Table 2).

Our best-performing model matched 7 of 9 pass/fail patterns, failing to match mean time to home range establishment and male > female time to settlement (4 of 5 replicates reproduced this pattern). Simulations matched patterns to varying degrees (Figure 3). Mean dispersal distance of actual martens (13.92±13.25 km) was 3.86 km greater than simulated martens (10.06±7.09 km), and mean time to establishment of actual martens (37.27±10.33 d) was 17.69 days greater than simulated martens (19.58±7.98 d). One long-distance dispersal outlier from the actual martens dispersed 46.7 km, and pattern-matching greatly improved with this outlier removed from the empirical data set (Figure 3). While our simulations did not produce any dispersal distances greater than 46.7 km, we did record simulated dispersal events up to 36.6 km (Figure 4). Based on the pass/fail criteria, mean time to establishment was the only pattern not matched by any model scenarios. The dispersal distances produced by our model also fit the Weibull distribution ($A^2 = 0.40$, $P = 0.84$), indicating the dispersal distance kernel was both leptokurtic and fat-tailed.

Results from inverse modeling indicated that dispersing martens were more likely to move an average of 30 bounds per minute than 10 or 20 bounds per minute in our study area (Figure 5). All pattern-matching methods except D^2 selected 30-bound simulations as the 2 best performing model scenarios (Table 1). D^2 was more likely to select 10-bound simulations as its top performing model scenarios.

2.5 Discussion

We found support for the hypothesis proposed by Ward (1987) that a time-limited disperser's selectivity for suitable habitat declines over time. To our knowledge, this is the first demonstration of support for this hypothesis for behaviorally complex vertebrates. Without this mechanism of dynamic habitat selectivity included, simulations failed to match empirical dispersal data. When testing static maps with low selectivity, dispersers established HRs too closely and too quickly. On static maps with high selectivity, they exhibited an unrealistic rate of failure to settle before the end of the dispersal period. Thus, allowing individuals to be temporally plastic in their perception of habitat suitability resulted in simulations that best matched empirical data. Matching empirical patterns also required an imposed 2-week exploratory phase prior to home range establishment. We note here that our support for these hypotheses is based primarily on simulation work, and that additional field work to test our conclusions is an important avenue for further research.

Others have explored how search costs (e.g., mortality risk), body condition, and time available for search affect the timing of home range establishment. As a result, Stamps et al. (2005) concluded that longer search times should be accompanied by higher selectivity rather than lower. For example, an individual with more energy reserves should be able to search longer, and thus be more selective. Our simulated martens did not change behavior with risk of mortality, began with equal energy reserves, and had a set timeframe for dispersal, so we were unable to test for these effects. However, these questions represent additional questions for future empirical and simulation work.

Our results have implications for the conservation of martens and other time-limited, solitary dispersers. Martens disperse in the fall and are thus time-limited because they face starvation and increased exposure to weather and predators if they are unable to locate a home range with suitable resources prior to the onset of winter (Bull and Heater 2001; Johnson et al. 2009). Our results suggest that in poor habitat conditions, martens will disperse farther distances and for longer periods of time, ultimately settling for a tradeoff between habitat quality and risk of mortality. Johnson et al. (2009) demonstrated that as natal dispersal distance of martens increased, mortality risk also increased. This effect was amplified for martens dispersing through poor habitat and may be further amplified for translocated individuals that are unfamiliar with the local environment and the conditions that maximize fitness. This phenomenon may provide some explanation as to why carnivore reintroduction programs have often been unsuccessful (Breitenmoser et al. 2001), since individuals released into inadequate or unfamiliar habitat may have longer search times and are thus subject to greater mortality risk (Stamps and Swaisgood 2007). Such factors should be taken into consideration when planning reintroductions or translocations (Pérez et al., 2012; Seddon et al. 2007).

Overall, our IBM performed well at reproducing empirical patterns of marten dispersal. In addition to the patterns matched during calibration, we also tested our output for its ability to match a classic distribution of dispersal distances (Figure 4). This was an important test to conduct outside of model calibration because it provided independent verification that the fine-scale, individual-based mechanisms of our IBM accurately represented those processes driving patterns of marten dispersal (Martin et al. 2013). Some deviations from empirical patterns may be attributed to the low frequency of long-distance dispersal (LDD) events during simulations. LDD can play an important role in a variety of eco-evolutionary processes including population expansion, population connectivity, gene flow, and response to disturbance (Nathan et al. 2012) so it is important to capture LDD events. Our simulations did produce LDD (Figure 4), but not at the frequency or distance exhibited by the actual marten population. Our empirical field data included one long-distance disperser that traveled farther than any simulated long-distance disperser. With this outlier removed, discrepancies between empirical and simulated patterns were greatly reduced

(Figure 3), though it’s possible that our small sample size overrepresented the effect of LDD in the empirical data.

The pattern that our models deviated from most was mean time to home range establishment, as simulations underperformed relative to empirical data. Model output did match the standard deviation of time to home range establishment, however. For our pragmatic purposes, we were more interested in matching spatial patterns, since spatial patterns have greater implications for population connectivity, gene flow, and conservation. However, this result also demonstrates that our model may not capture all the fine-scale mechanisms required to accurately reproduce marten dispersal behavior, and further investigation is warranted. It is also possible that subjectivity in the analysis of timing of home range establishment affected pattern-matching, as criteria used to define establishment can vary widely in reporting the amount of time individuals explore prior to settlement (McCann 2011; Woodford et al. 2013).

Pattern-oriented modeling is becoming the standard for evaluating ecological IBMs, but the methods used to assess matching vary across studies (Bauduin et al. 2016; Chudzinska et al. 2016; Stenglein et al. 2015). Ultimately, individual-based ecology may benefit from an algorithmic framework by which one would select the appropriate method(s) to assess a model’s ability to match empirical patterns (Grimm and Railsback 2011). In our case, we used 6 different techniques (e.g., pass/fail, rank sum, root mean square deviation, and Mahalanobis distance) to evaluate matching because a consensus across alternative methodologies would provide additional support for the best model. We did identify a consensus in model selection across all 6 methods in terms of habitat selection rules, but the pass/fail methods were less discriminatory than other methods and often resulted in tied rankings among models (see Table 2, Figure 3). In addition, Mahalanobis Distance (D^2) selected a different bound rate than all other methods (though D^2 could only evaluate

4 of 9 patterns). This result likely occurred because D^2 inherently accounts for covariance among patterns (Mahalanobis 1936), and therefore uncorrelated patterns carry relatively more weight. In our model the time to home range establishment pattern was the least correlated with all other patterns, and lower bound rates led to longer and more accurate dispersal times. Time to home range establishment was also the one pattern our models failed to match, giving greater weight to better performing scenarios. D^2 and other multi-variate statistics may be quite useful in pattern-matching analyses, particularly when researchers want to control for covariance and maintain independence among patterns. In our case, however, we chose several patterns that were likely to be somewhat correlated to give more weight to the spatial rather than the temporal component of model results. Our findings demonstrate the need for careful selection of one's methods for assessment of pattern-matching, and that the objectives of the study and format of the data should be considered when selecting a method.

In addition to POM for model selection, we used inverse modeling (i.e., indirect parameterization) to determine that dispersing martens were more likely to move an average of 30 bounds per minute than 10 or 20 bounds per minute (Figure 5). Because our movement data were collected while following marten snow tracks, they lacked a fine-scale temporal component, and therefore mean step length was an unknown parameter in the model. However, all of our competing model scenarios and pattern-matching analyses except D^2 agreed that the 30-bound version of the model produced the most accurate dispersal patterns. This use of pattern-matching to calibrate unknown parameters is often used on a suite of parameters simultaneously e.g., (Kanagaraj et al. 2013), and is used less often to target a single unknown parameter e.g., (Rossmanith et al. 2007). We demonstrate here that when an abundance of empirical data is available, inverse modeling can be used effectively to derive information about uncertain or unknown parameters related to demographics or behavior (Wiegand et al. 2003).

Our study highlights the power of spatially explicit IBMs to both reproduce empirical patterns and to test specific behavioral hypotheses. In our case, fine scale parameterizations (e.g., 15-minute time steps) were able to reproduce broad-scale patterns. Such individual-based models have been commonly used in both pragmatic (i.e., associated with management goals) and paradigmatic (i.e., associated with underlying theory) contexts (DeAngelis and Grimm 2014). While our model is essentially pragmatic because it addresses a management need for an endangered carnivore, it is paradigmatic in that it explicitly tests a theory of animal behavior. Grimm (1999) called for an increased focus on theory in individual-based ecology, and we add to that call the need for more pragmatic models to test ecological theory produced by both individual-based models and traditional ecological models. In this way pragmatic IBMs can maintain their role as important tools for the management and conservation of wildlife populations (Aben et al. 2016; McLane et al. 2011; Wood et al. 2015), while simultaneously advancing underlying ecological theory (Railsback and Harvey, 2002).

Our application of the SEARCH modeling framework can be used in a number of future applications of both the pragmatic and paradigmatic variety. For example, future work may include pragmatic questions associated with the response of martens to land-use and climate change, or to explore the role of long-distance dispersal events in population connectivity. Theoretical applications may include the effects of energy reserves and deferred costs on dispersal patterns, which could have important implications for marten populations. Ultimately, researchers do not have to choose whether their IBM application will be entirely pragmatic or paradigmatic, but should take advantage of opportunities to address questions of both management and theory in their use of individual-based models in ecology.

2.6 Acknowledgments

We thank the Wisconsin DNR, J. Schmidt and the Chequamegon-Nicolet National Forest, Iron County Forestry and Parks, and the Bad River Band of Lake Superior Chippewa Tribe for providing forest inventory data. We thank B. Cummings, B. Pauli, E. Gustafson, and the Purdue Envision Center for development and management of SEARCH software. We thank many that contributed to the field work that supported parameterization of the IBM, including T. Aldred, J. Dumyahn, J. Parisian, R. Parisian, S. Roepke, S. Sveiven, J. Woodford, and M. Worland. Funding and logistical support for this study and for field work used in parameterization of the model was provided by the Great Lakes Indian Fish and Wildlife Commission, the Department of Forestry and Natural Resources at Purdue University, the Wisconsin Department of Natural Resources, the US Forest Service, and a Presidential Early Career Award for Scientists and Engineers (PAZ). We also thank The McIntire-Stennis Cooperative Forestry Research Program for their financial support.

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2.8 Tables

Table 2.1: Patterns evaluated for calibration of a model of American marten dispersal following a translocation in northern Wisconsin in 2010. An ‘x’ in the last four columns indicates whether a given pattern was evaluated using that column’s method for pattern-matching analysis. All patterns were derived from empirical data from translocated martens in northern Wisconsin. Hierarchical level indicates whether the pattern was averaged across individuals or was a characteristic of the population. Weight indicates the importance of each pattern as assigned by the authors. Pass/Fail represents a binary matching criterion and assigned points to a model based on whether a given pattern was successfully matched. Rank-sum ranked each model according to its ability to match each pattern and then summed the resulting ranks. TI (Total Indicator) ranked models based on their root mean square deviation from empirical patterns. D^2 (Mahalanobis distance) ranked models based on a multi-variate measure that accounts for covariance among patterns.

Pattern	Hierarchical level	Weight	Observed pattern	Pass/Fail	Rank-sum	TI	D^2
Dispersal distance mean	Individual	High	13.9 km	x	x	x	x
Dispersal distance SD	Population	Medium	13.2 km	x	x	x	
Days to HR establishment mean	Individual	Medium	37.3 days	x	x	x	x
Days to HR establishment SD	Population	Medium	10.3 days	x	x	x	
Average neighbor distance mean	Population	High	26.4 km	x	x	x	x
Nearest neighbor distance mean	Individual	Medium	11.5 km	x	x	x	x
Mortality rate	Population	Low	0.17	x	x	x	
M:F Dispersal distance	Population	Low	M > F	x			
M:F Days to establishment	Population	Low	M > F	x			

2.9 Figures

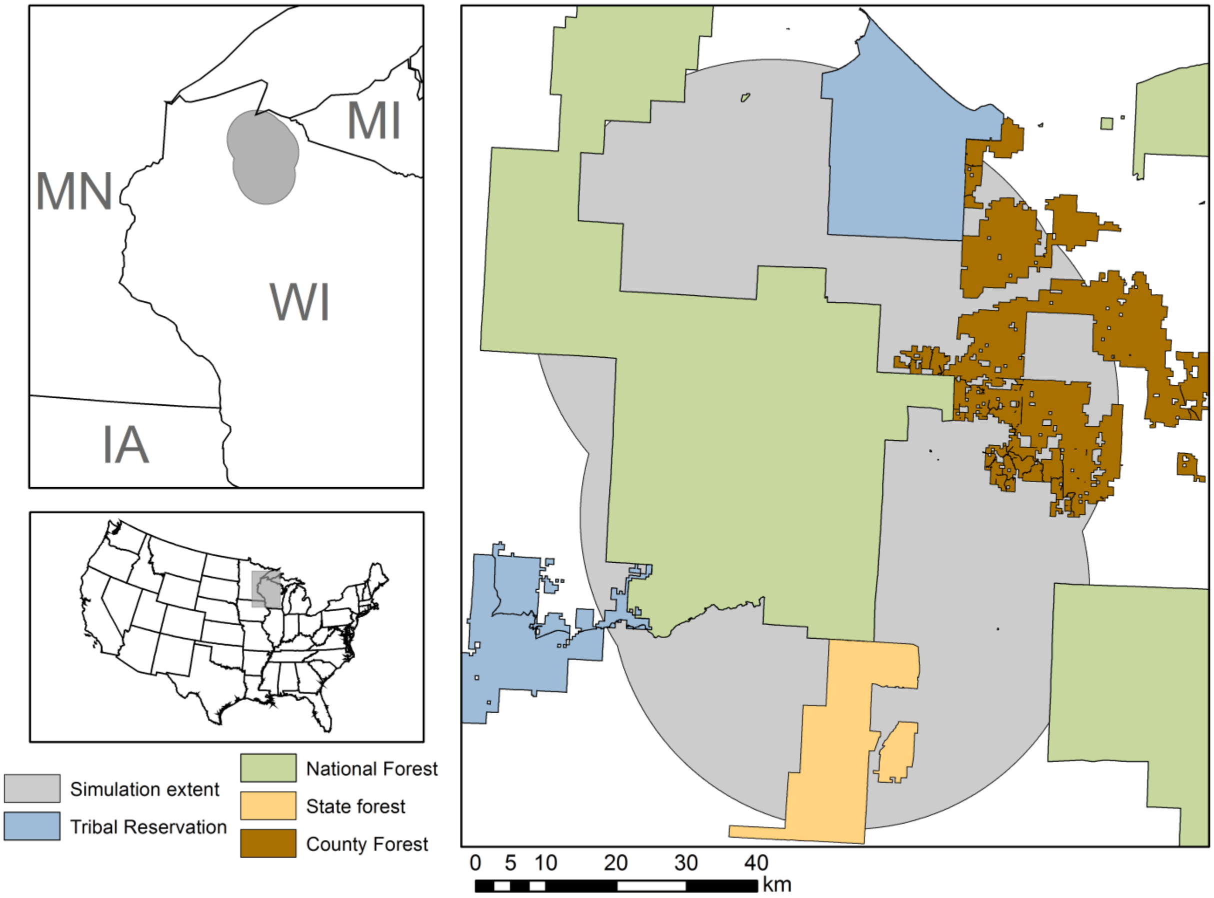

Figure 2.1: Study area in northern Wisconsin, USA, on which we simulated the dispersal of 15 translocated American martens in 2010.

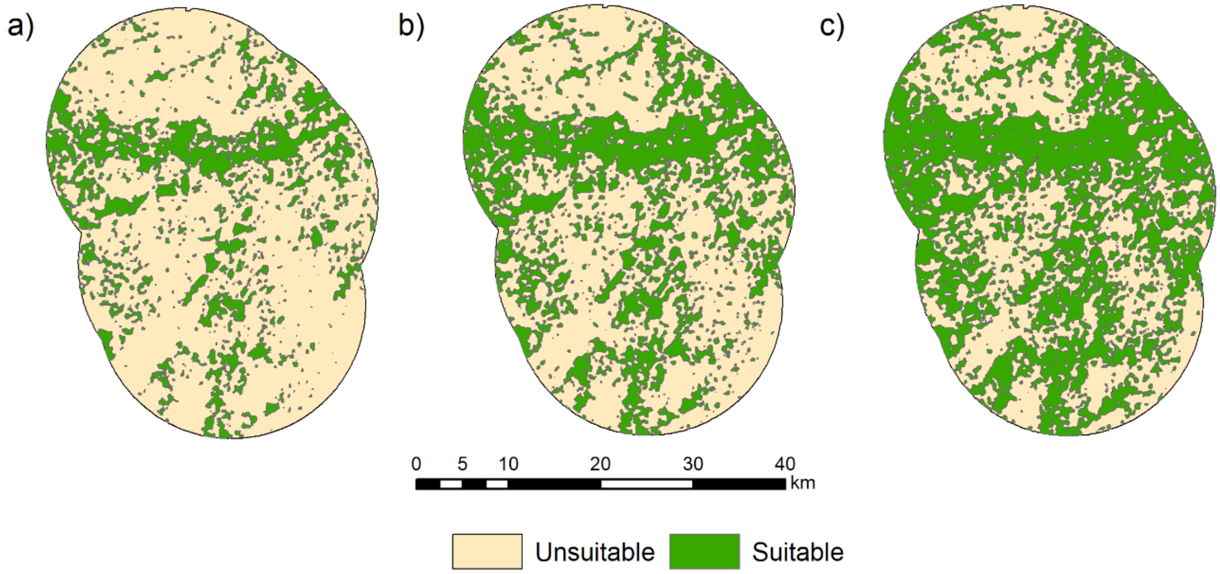

Figure 2.2: Examples of alternative rules used for habitat suitability in SEARCH modeling of American marten dispersal in northern Wisconsin. Panels illustrate the dynamic progression of habitat selectivity over time from the 70% (a), to the 60% (b), to the 50% (c) threshold rules. Percentages represent the proportion of an area around a pixel in the cover type data that must be represented by non-avoided cover types to be classified as suitable. Therefore, as the percentage decreases over time, martens perceive an increasing proportion of the landscape as suitable.

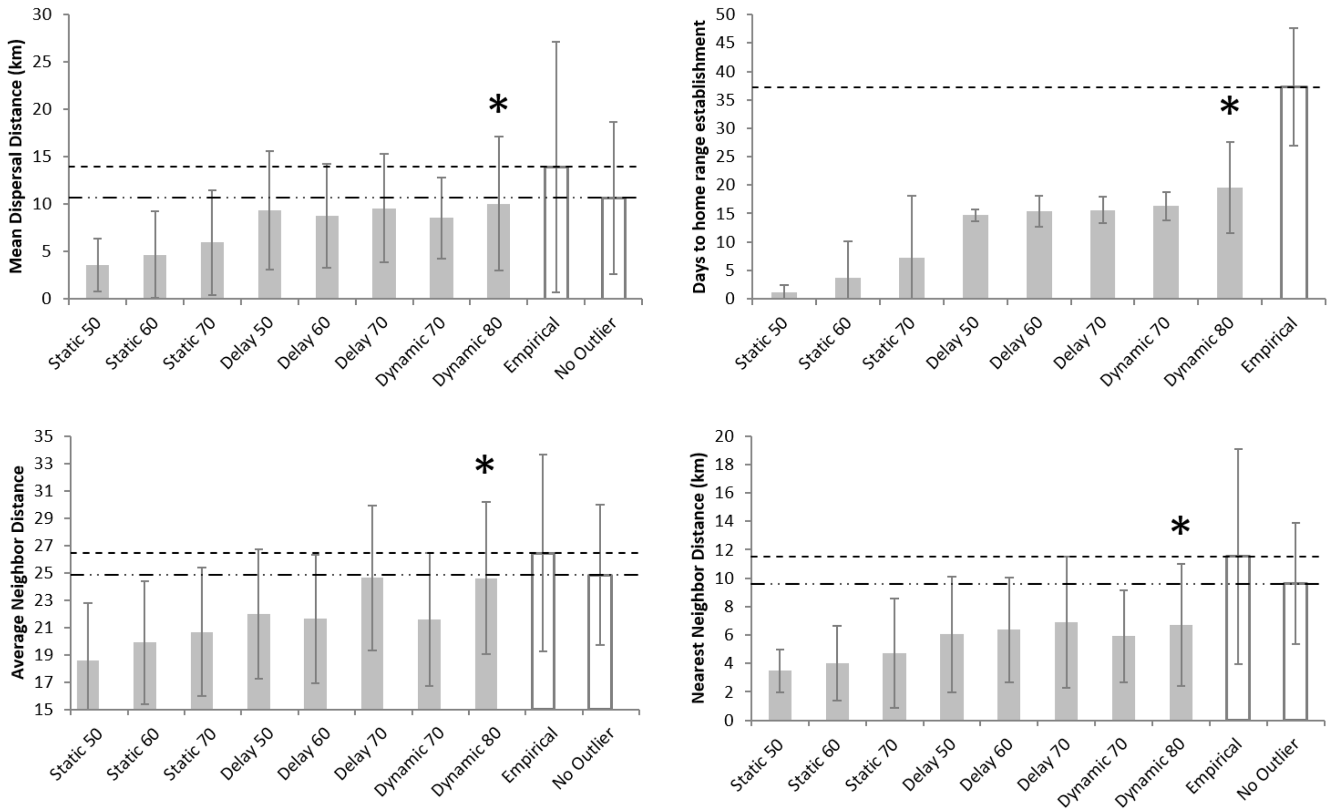

Figure 2.3: Performance of the best-performing model from each presented configuration in matching empirical patterns of dispersal by 15 martens translocated to northern Wisconsin in 2010. Asterisks denote the top performing model overall. Patterns matched that are displayed here include dispersal distance mean and SD, time to home range establishment mean and SD, mean average neighbor distance, and mean nearest neighbor distance. Dashed lines represent empirical means, while dashed-dotted lines represent empirical means with one outlier removed (time to home range establishment had no outlier). Means and standard deviations from actual martens with and without a single outlier included are represented by hollow bars. For model simulations, the mean of means and mean standard deviations across 5 replicates are presented. Static and Delay scenarios incorporated a single habitat suitability map with the 50, 60, or 70 % habitat suitability rule. Delay represents an imposed 2-week exploratory phase prior to settlement. Dynamic scenarios incorporated the 2-week delay as well as a progression of habitat suitability maps over time ([70, 60, 50 % rules] or [80, 70, 60 % rules]) to represent a decline in habitat selection selectivity by the disperser. Bound rates are not displayed here because only the overall best performing bound rate for each scenario is presented

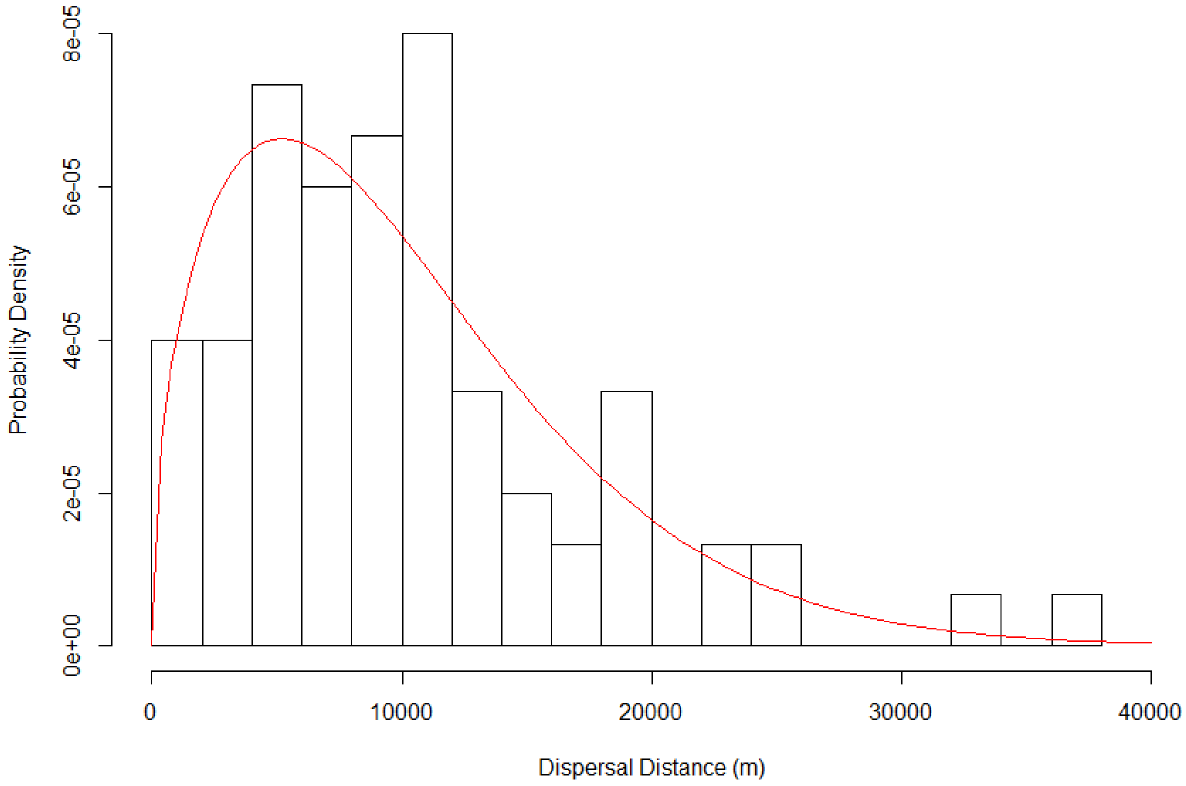

Figure 2.4: A histogram of dispersal distances across 5 replicates of our top-performing model of American marten dispersal. These data are fitted to a Weibull dispersal distance kernel plotted as the probability density function of the distribution of distances traveled by dispersing martens away from their natal grounds.

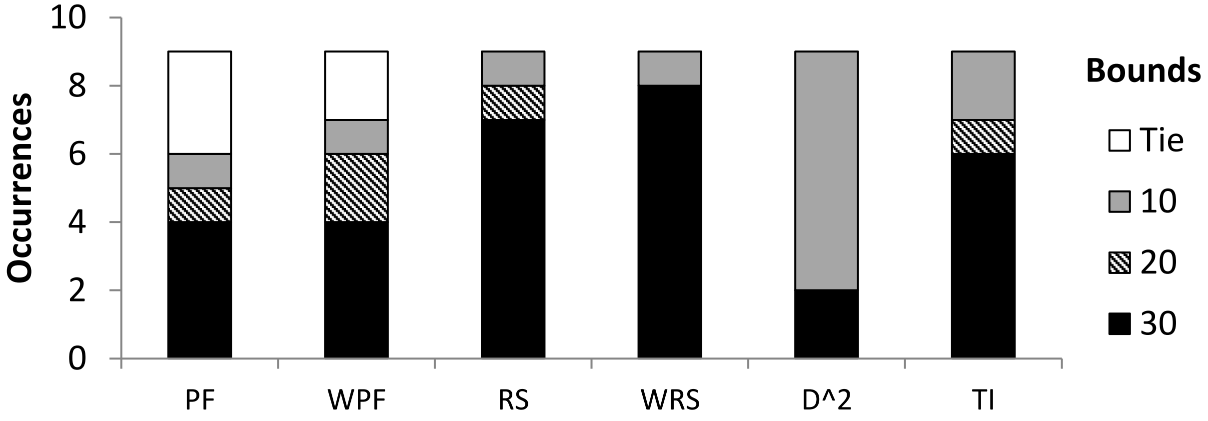

Figure 2.5: Number of times each of the three values tested for number of bounds per minute (i.e., mean step length) was selected as the best performing model by each method used to evaluate pattern-matching. Models simulated American marten dispersal of translocated individuals released in northern Wisconsin in 2010. PF = Pass/Fail, WPF = Weighted pass/fail, RS = Rank-sum, WRS = Weighted rank-sum, D^2 = Mahalanobis distance, and TI = Total Indicator.

CHAPTER 3. EFFECTS OF MORTALITY, LAND USE CHANGE, AND ASYMMETRICAL LANDSCAPE CONFIGURATION ON FUNCTIONAL LANDSCAPE CONNECTIVITY OF AMERICAN MARTENS

3.1 Abstract

Functional landscape connectivity is vital for the conservation of rare or threatened wildlife species, when these species occur in small, isolated groups. While the definition of functional landscape connectivity has proven to be nebulous, it is generally accepted that evaluations of this metric should go beyond structural landscape configuration to account for factors such as animal behavior and dispersal costs. One solution to this problem has been to develop individual-based models of animal movement that incorporate animal behavior and adaptive decision-making in real time. Resulting population-level patterns of animal dispersal can then be used to assess landscape connectivity among alternative simulated environments. We applied this methodology to evaluate factors that might affect landscape connectivity for the American marten, a state-endangered carnivore in Wisconsin, USA. Specifically, we evaluated how mortality, land use change, and asymmetrical landscape configuration affected the ability of martens to disperse between two reintroduced populations. Results indicated that mortality due to predation and starvation had the greatest impact on the ability of martens to successfully traverse the landscape and establish a home range. Land use change and landscape configuration also affected functional landscape connectivity, but primarily only when mortality was off and only for the subset of individuals that traveled furthest into the matrix of dispersal habitat. Additionally, local dispersal metrics displayed different relationships with each of the three factors than did functional landscape connectivity. We suggest that to preserve connectivity between wildlife populations, prey availability and predation risk within the dispersal habitat should be considered along with the suitability of

breeding habitat. We also demonstrate how local dispersal metrics such as average movement rates or distances are not necessarily synonymous with functional landscape connectivity. We encourage the continued development of individual-based models to explore questions of wildlife conservation that require the explicit incorporation of both the spatial variation of habitat and its relationship with complex animal behavior.

3.2 Introduction

Threatened or endangered animal populations often occur in small, isolated groups of individuals. As habitat quality decreases and isolation from neighboring populations increases, the probability of extinction also increases (Hanski 1998, Prugh et al. 2008). Extinction risk can be mitigated by a landscape that connects isolated populations to one another, or to a larger source population (Hess 1996). Such a landscape facilitates the successful dispersal of individuals into nearby populations, followed by recruitment and reproduction. Thus, functionally connected animal populations are able to exchange genetic information and contribute to the demographic viability of vulnerable populations (Coulon et al. 2004, Lowe and Allendorf 2010).

Given the importance of functional landscape connectivity to the health and survival of animal populations, understanding the factors affecting connectivity can be vital to the success of conservation planning efforts (Gardner and Gustafson 2004, Prugh et al. 2008, La Morgia et al. 2011). However, describing the relationships between landscape-scale patterns of connectivity and the process that govern them is a challenging task, for several reasons. One reason is that the variables that contribute to a functionally connected landscape are unique to each species and location and vary based on habitat requirements, behavior, demography, and landscape configuration (King and With 2002, Bélisle 2005, Elliot et al. 2014). Additionally, ecological processes occur at multiple scales, and the relevant scales must be identified and considered when evaluating the landscape in terms of connectivity (Levin 1992). Furthermore, landscapes are rapidly changing, and this dynamic presents challenges when considering the long-term conservation of rare or threatened species (Pressey et al. 2007, Schloss et al. 2012).

A variety of approaches have been developed to address the problem of measuring the connectivity of a landscape. In a review by Correa-Ayram et al. (2016), the authors identified 23 different methods for evaluating landscape connectivity in papers published between 2000 and 2013. The most common methods involved the identification of landscape variables that either facilitate or impede animal movement (Tischendorf and Fahrig 2000). These relationships are then applied to a spatial representation of the landscape that is used to identify habitat corridors or critical conservation areas. For example, in least cost path and circuit theory analyses, a resistance surface is developed and used to identify probable movement corridors between locations (Nowakowski et al. 2015, Merrick and Koprowski 2017). In graph theory analysis, populations or locations (i.e., nodes) are connected by edges whose length represents the functional distance between them (Bunn et al. 2000, Urban and Keitt 2001). One common element among these analyses is that they approach the problem of connectivity from a top-down perspective of the landscape or the population, rather than from the bottom-up perspective of the individual disperser. As a result, landscape connectivity studies may fail to incorporate certain factors that influence functional connectivity such as individual variation in animal behavior, mortality risk, food availability, or perceptual range (Lima and Zollner 1996).

Individual-based modeling (IBM) is an approach that can provide a bottom-up perspective to the patterns observed in ecological systems, though IBMs have not been used often in the context of landscape connectivity (Correa Ayram et al. 2016). The objective of individual-based simulation modeling is to produce broad-scale observable patterns that emerge from simple mechanisms governing the behavior of and interaction between individuals (Grimm and Railsback 2005). In spatially explicit IBMs, individuals also interact with landscape features that affect decision-making in real time (e.g., Pauli et al. 2013, Schumaker 2013). In this framework, landscape connectivity can be evaluated using a model that has been calibrated by matching simulated patterns to empirical patterns of animal movement (Wiegand et al. 2004, Grimm et al. 2005, Allen et al. 2016). Thus, landscape-level patterns emerge from simple mechanisms rather than being imposed on model processes. In this way, IBMs simulate the basic principles, or underlying mechanisms driving landscape-scale patterns, making simulations more readily applicable to alternative scenarios or contexts (Baguette and Van Dyck 2007). Results from such efforts can be used in conservation planning (McLane et al. 2011). Potential applications include assessing landscapes for their suitability for a reintroduction (Kramer-Schadt et al. 2004) or evaluating alternative strategies to improve connectivity between populations (Kanagaraj et al. 2013).

We developed an IBM of American marten (*Martes americana*) dispersal to evaluate factors that may affect landscape connectivity between two reintroduced populations in the Upper Midwestern United States. The American marten is a small (<1.3 kg), semi-arboreal carnivore that was functionally extirpated from the states of Wisconsin and Michigan in the first half of the 20th century due to over-harvest and habitat degradation (Berg 1982). Several translocations were carried out in both states between 1955 and 2010 in an effort to restore the species to a portion of its native range (Williams et al. 2007). While reintroductions in Michigan have resulted in established populations, the marten remains endangered in Wisconsin. One possible factor contributing to the lack of population growth is that functional connectivity among populations may be limited, and therefore the protection and improvement of movement corridors was included as a management goal in Wisconsin’s 2011 marten conservation plan (Woodford and Dumyahn 2011).

Our objective was to use a previously calibrated IBM of marten dispersal applied to a new landscape to evaluate the role of three factors affecting functional landscape connectivity between two populations of reintroduced American martens. First, we compared connectivity of the existing landscape to the same landscape under alternative scenarios of land use change due to mining activities. Second, we evaluated the effect of asymmetry in landscape configuration, and whether functional connectivity was greater in the direction of one population than the other. Third, we investigated the role of mortality as it affects functional landscape connectivity, specifically mortality due to starvation or predation during dispersal events. Ultimately, our goal is to use the results from this simulation modeling work to contribute to future conservation plans for the American marten by providing insights into factors that may be limiting marten dispersal and landscape connectivity.

3.3 Methods

3.3.1 Study System

Our study area incorporated portions of both northeastern Wisconsin and the western portion of the Upper Peninsula of Michigan, USA (Fig. 1). This area is mostly forested but also includes the adjoining towns of Hurley, WI and Ironwood, MI, whose combined population size is approximately 6,500 people (figure 1a). Forested areas were primarily deciduous and composed of stands dominated by the northern hardwood community (e.g., sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*)) and quaking aspen (*Populus tremuloides*). Wetlands composed roughly one third of the landscape, most of which consisted of lowland coniferous and deciduous forest. The landscape was a mosaic of ownership types, with roughly half of the land owned by private entities and half owned publicly as county, state, tribal, and national forests (Fig. 1b). Land use change in the area occurs as a result of management for recreational activities and extractive industries and has a significant impact on ecosystem structure and function (Schulte et al. 2007). In 2010, plans were announced for the development of an iron mine along Highway 77 in the Penokee Hills of the Gogebic mountain range. The proposal was for an open pit iron ore mine with a footprint of 27.2 km^2 situated in the western portion of the study area.

The simulation extent represented a potential habitat corridor between two reintroduced populations of American martens in the Chequamegon-Nicolet National Forest (CNNF) in Wisconsin, and the Porcupine Mountains Wilderness State Park in Michigan. We defined the extent of the simulation area by buffering known locations of American martens identified from previous work using hair snares and remote cameras (Chapter 4). We buffered these locations by 14 km, which was equal to the mean dispersal distance of martens translocated to the CNNF in 2010 (Chapter 1). The resulting polygon was 2,502 km^2 and approximately 40 km from north to south and 70 km from east to west. The elongated shape of the simulation extent encompassed the known north-south distribution of martens in the area and was bounded on these sides by habitat unsuitable for marten occupancy.

3.3.2 Model Description

To simulate the movement of martens across the landscape, we used the spatially-explicit, individual-based modeling framework SEARCH (Spatially-Explicit Animal Response to Composition of Habitat) (Pauli et al. 2013, Mutascio et al. 2017). For a full ODD description (Overview, Design concepts, and Details, Grimm et al., 2006) of SEARCH, see Pauli et al. (2013). For the major components of the Wisconsin marten application, see the Chapter 1 model description. Below, we provide a general overview of SEARCH and describe key processes of our application of the model.

In SEARCH modeling, the primary processes center around the dispersal of individuals in search of a location that is both suitable for home range establishment and is unoccupied by a member of the same sex. To begin simulations, dispersing individuals are either released from user-defined locations or are a result of reproduction by an existing resident population. During dispersal, individuals respond to and make decisions based on four vector-based, spatially-explicit maps that regulate movement, food availability, predation risk, and habitat suitability. While searching for suitable home range locations, movement takes place at fine temporal resolutions (e.g., 15 minutes), and is guided by a correlated random walk that varies by habitat type. As dispersers move through the landscape, they maintain a memory map of habitat suitability for the area they have visited on the landscape. The extent of the memory map depends on the user-defined perceptual range of the species, which dictates how far from an individual’s present location they are capable of perceiving habitat suitability. As potentially suitable home range locations are encountered, dispersers add them to a list of potentially suitable home range locations in their memory. At some user-defined point in the simulation, dispersers switch out of search mode and begin orienting toward a specific potential home range location. At this point, the list of potential sites is sorted and ranked based on a user-defined criterion and the individual orients toward the top-ranked site and attempts to establish a home range. If home range establishment fails, the disperser either reorients toward the next site on the list, or (if no more sites are stored in memory) goes back to searching for new suitable home range locations.

For our application of SEARCH, we followed the parameterization from our previously-calibrated model of marten dispersal described in detail in Chapter 1. That model was calibrated using a pattern-oriented modeling approach to match dispersal patterns of actual martens from the nearby translocations on the CNNF in 2010 (Woodford et al. 2013). The best performing model from calibration and applied to the current application included an initial 2-week exploratory phase prior to allowing attempts at home range establishment. It also included a dynamic habitat suitability map that represented a decline in the selectivity of habitat selection by dispersers over time. This mechanism allowed individuals to settle for progressively lower quality habitat to avoid failing to establish a home range. For the current application, we collected forest stand data, including primary forest type and tree size, from the following sources: Bad River Band of Lake Superior Chippewa Tribe Natural Resources Department, Chequamegon-Nicolet National Forest, Gogebic County Forestry and Parks, Iron County Forestry and Parks, Ottawa National Forest, and the Wisconsin Forest Inventory and Reporting System (WisFIRS). For private forests, we mosaicked raster cover type data from the remotely sensed Wisconsin Land Cover Data set (Wiscland 2) Level III and the Michigan IFMAP/GAP Upper Peninsula Land Cover data set (2001).

3.3.3 Study Design

Prior to modeling dispersal, we simulated a baseline density of resident martens on the study area following the method described in Chapter 1. We released martens at random locations in suitable habitat and allowed them to establish a home range immediately. Because we conducted 10 replicates per scenario, we created 10 unique configurations of resident home ranges. This was important because in SEARCH, dispersing animals are unable to occupy a location already occupied by an individual of the same sex.

To investigate the effects of each of the three explanatory variables on marten dispersal, we conducted 10 replicates of 10 dispersers for each unique combination of factors. Each simulation was run consecutively for 5 generations for a total of 600 simulation runs and 6,000 dispersal events. To initiate the simulation, all 10 martens were released from either the east (Wisconsin population) or the west (Michigan population) end of the study area and allowed to disperse for up to 60 days, or until they died or established a home range. By only simulating dispersal from one direction at a time, we were able to evaluate the effects of asymmetrical landscape configuration on patterns of dispersal. We ran simulations for 5 consecutive generations. Upon completion of a given generation of dispersal, those martens that succeeded in establishing a home range produced a single offspring to disperse the following year. Using this simplified model of reproduction, we were able to simulate connectivity based on a chain of consecutive parent-offspring dispersal events. If a marten died or failed to establish a home range during dispersal, it was replaced in the following generation by a marten released from the original release location at the east or west end of the landscape. These replacement individuals represented a new migrant into the habitat corridor that replaced the failed migrant. Thus, there were always 10 dispersers at the start of each generation.

To evaluate the effect of the proposed mine on marten dispersal, we developed 3 alternative land-use scenarios. One scenario represented the current landscape condition and excluded the proposed iron mine, one scenario included the mine as a single contiguous patch of deforested (i.e., unsuitable) habitat, and a third included the mine plus a 2 km buffer of unsuitable habitat (as perceived by the marten). The length of the buffer approximated the diameter of a marten home range, and the buffer simulated the potential effect of mining activity on the willingness of a marten to utilize the area and establish a home range nearby (Tigner et al. 2015). Within the footprint of the mine, food availability and predation risk were set equal to that of urban areas and forest clearcuts. Probability of crossing into the mine area from a forested area was 1 %, equal to the probability of crossing from forested habitat into an urban area.

Finally, we tested for effects of disperser mortality on functional connectivity between marten populations. To accomplish this, we created two different parameterizations with respect to mortality. The first scenario included all potential sources of mortality: predation, starvation, and exposure as a result of failing to establish a home range after 60 days. For the second scenario, we removed the possibility of mortality due to predation or starvation, so that failure to locate suitable habitat as a result of landscape structure was the only possible cause of dispersal mortality. All three factors tested during simulations (directionality, land use change, mortality) were implemented in a fully crossed design.

3.3.4 Data Analysis

The primary metric we used to evaluate landscape connectivity was the proportion of the landscape traversed between the two populations by individual martens. In other words, for individuals released in the eastern portion of the study area we measured how far west across the east-west gradient they traveled, and vice versa. After dispersal, individuals were assigned a connectivity value on a continuous scale from 0 to 1 (e.g., 0 if they established a home range within their original release area, 0.5 if they established a home range half way between the 2 populations, and a value of 1 if they established a home range on the side of the landscape opposite their release location).

Because we were primarily interested in functional connectivity, we examined percentiles of the ‘proportion traversed’ data set, including values above the 0th (i.e., all data included), 75th, 90th, and 99th percentiles. As the percentile threshold increased, analyses therefore included the more distal portion of the tail of the distribution of dispersal across the landscape. We considered the leading edge of dispersal to be more representative of functional connectivity, since maintaining connectivity between populations is often accomplished by relatively few migrants (Mills and Allendorf 1996). We used the package “rpart” in Program R to conduct regression tree analyses (R Core Team 2017, Therneau et al. 2017) and to determine what factors affected the ability of individuals to traverse the landscape. To determine the relative importance of explanatory variables, we used random forests analysis (“randomForest” package, number of trees = 10,000; (Liaw and Wiener 2002)) to calculate the percent increase in Mean Standard Error (scaled by standard error) after permutation of a given explanatory variable.

We calculated other dispersal metrics for each disperser including dispersal distance, time to home range establishment, dispersal success, and tortuosity (total distance traveled / dispersal distance). To compare these dispersal metrics across model scenarios, we used t-tests and Analysis of Variance. Where data failed to meet parametric test assumptions, we used the non-parametric Mann-Whitney U test, the Kruskal-Wallis test, and the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Scheirer et al. 1976). To examine landscape usage among scenarios, we used the Point Density tool to create heat maps of landscape usage in ESRI ArcGIS version 10.4 (Redlands, CA, USA).

3.4 Results

Regression tree results indicated that the factors affecting landscape connectivity (i.e., distance traversed across the landscape) varied with the percentile of data analyzed (Figure 2). However, mortality due to starvation and predation represented the root node for all percentiles. As the percentile threshold increased, the number of factors that significantly affected connectivity also increased. When data from all dispersers were included (i.e., 0th percentile threshold), mortality from starvation and predation was the only factor that affected connectivity, and connectivity increased when mortality was turned off in the model. For the 75th percentile threshold, inclusion of the mine effectively increased landscape connectivity when mortality was turned off, but not when mortality was included. Directionality in dispersal was significant for the 90th and 99th percentile thresholds, with animals traversing farther across the landscape in the east-to-west direction.

Random forests analysis confirmed that mortality was the most important variable for explaining variation in functional connectivity across all percentile thresholds (Figure 3). For the 0th percentile threshold, random permutations of the mortality variable resulted in a 1.75 times greater increase in MSE relative to permuting directionality, and 2.42 times greater relative to permuting the mine scenario. For the opposite extreme (99th percentile threshold), permutations of mortality resulted in a 2.83 and 2.67 times increase in MSE over directionality and the mine, respectively.

In contrast to evaluating landscape connectivity, we also evaluated local dispersal and how it was affected by each factor that we tested. Most movement and home range establishment took place within or near the initial release populations (i.e., local dispersal; Figure 4). Barriers to movement such as lakes (Figure 5, b) or the mine footprint (Figure 4, 5a) resulted in an increased concentration of locations near the barrier during simulations. Events where individuals successfully traversed the landscape and established home ranges in the opposite release polygon were rare, occurring 9 times out of 6,000 total dispersal events (Figure 4) and only 2 times with mortality turned on. Incorporating the mine into west-to-east simulations funneled dispersers around the mine, resulting in greater space use to both the north and the south (Figure 5a). Incorporating mortality into east-to-west simulations resulted in a greater proportion of space use in the southeast (lake area), and less space use to the west, away from the release area and toward the opposite population of martens (Figure 5b).

Mean dispersal distance and mean time to establishment per simulation run (Figure 6) were both greater during simulations with mortality turned off ($t = 13.64$, $p < 0.001$; $t = 10.881$, $p < 0.001$). There was an interaction effect between directionality and dispersal distance, however, with west-to-east dispersal distances being greater than east-to-west dispersal distances only when mortality was off ($F = 25.68$, $p < 0.001$; Figure 6). Across mine scenarios, there was no difference in dispersal distance ($F = 0.722$, $p = 0.486$) or time to establishment ($F = 0.374$, $p = 0.688$) in either direction, but time to establishment was greater from east to west ($t = 25.65$, $p < 0.001$) than from west to east. Dispersal success (i.e., the number of individuals that successfully established home ranges per simulation) was not different among mine scenarios (Kruskal-Wallis $\mathrm{X}^2 = 2.37$, $p = 0.307$) but there was an interaction between mortality and direction, as when mortality was incorporated, dispersers released from the western population were more successful ($H = 24.11$, $p < 0.001$; Figure 6). Mean tortuosity was likewise not different among mine scenarios (Kruskal-Wallis $\mathrm{X}^2 = 3.801$, $p = 0.145$) but was greater with mortality turned on ($\mathrm{W} = 34019$, $p < 0.001$) and for individuals released from the eastern population ($\mathrm{W} = 67802$, $p < 0.001$).

3.5 Discussion

3.5.1 Functional Landscape Connectivity

In our model of American marten dispersal, mortality due to predation and starvation had a greater impact on functional landscape connectivity than habitat configuration or land use change. This result demonstrates the importance of the quality of the matrix habitat (i.e., habitat situated between suitable patches) and associated travel costs when managing for the conservation of isolated or reintroduced populations. Risk of mortality is rarely incorporated explicitly into models of landscape connectivity (Zeller et al. 2012), even though it has been demonstrated that mortality due to predation or anthropogenic disturbance can be the primary limiting factor (Ruckelshaus et al. 1997, Kramer-Schadt et al. 2004, Baggio et al. 2011). Dispersing animals are often also forced to make a tradeoff between foraging efficiency and minimizing predation risk (Zollner and Lima 2005, Cushman et al. 2011). Thus, if prey availability is a limiting factor in the habitat matrix, incorporating both energetics and predation risk are likely important for understanding factors that limit connectivity between populations (Bélisle 2005, Wilkinson et al. 2013, Carlson et al. 2014). Additionally, while dispersal models often assume that the habitat matrix is homogeneous, this is rarely the case. In SEARCH, travel costs associated with movement, predation risk, and food availability are each regulated by an independently parameterized spatial layer. Therefore, the composition and configuration of the matrix itself – and not just the configuration of suitable habitat patches – can affect functional landscape connectivity.

Land use change (i.e., introduction of an iron mine) and asymmetrical landscape configuration also affected functional landscape connectivity. These factors were only significant for the individuals that made up the leading edge of dispersers across the landscape. This is because most individuals dispersed short distances, contributing relatively little to connectivity between the two marten populations. Additionally, land use change and landscape configuration were a factor primarily when mortality was excluded in the model. When mortality was included, no difference in connectivity was detected for all but the 99th percentile. In this context, efforts to improve the health of Wisconsin marten populations may need to focus not only on the restoration of breeding habitat, but on reducing the risk of predation and starvation for dispersers traveling through the matrix.

For the percentile of dispersers for which direction of travel significantly affected landscape connectivity, individuals moving from east to west traveled farther across the landscape on average than individuals moving from west to east. This was an unexpected result, as the eastern half of the landscape was more fragmented than the western half. Based on such a result, it may seem that increasing habitat fragmentation would facilitate rather than impede movement between populations (Tischendorf and Fahrig 2000, Bélisle 2005). Again, however, this result is negated by the inclusion of mortality on the landscape, further illustrating how neglecting to account for disperser mortality could lead to misinterpretation of results as they relate to functional connectivity (Ruckelshaus et al. 1997).

Landscape corridors between populations in our model were rather diffuse and difficult to detect based on visualizations (Gustafson and Gardner 1996; Figure 4). Barriers to movement, such as bodies of water, were more readily apparent, and individuals often became trapped in highly fragmented areas on the landscape (Kanagaraj et al. 2013), particularly in the east. While some effect of the mine on marten space use could be detected funneling individuals to the north and south, the mine had a relatively minor effect on functional landscape connectivity. With mortality incorporated into simulations, the mine was not identified by our analysis as having a significant effect on dispersers' ability to cross the habitat matrix. This probably occurred because the mine was placed in a location of relatively low fragmentation and high habitat quality. This provided the counter-intuitive result that despite maximum habitat loss, the mine had a minimal effect on connectivity. Had the mine been placed in the more fragmented eastern portion of the study area, it's possible that less total habitat would have been lost, but the reduction in functional connectivity would have been greater.

For most species, relatively few individuals have the greatest impact on the maintenance of functional connectivity between populations (Koenig et al. 1996, Mills and Allendorf 1996, Trakhtenbrot et al. 2005). This was the case in our simulations, as after 5 generations of dispersal less than 1% of dispersers successfully established a home range in the territory of the opposite population. As a result, understanding functional connectivity requires the evaluation of how landscape variables affect those few long-distance dispersers that are the most influential in connecting populations. Neglecting to do so and evaluating dispersal metrics for all dispersers may lead to very different results. Based on common dispersal metrics (excluding functional connectivity) from all dispersers in our simulations such as dispersal distance, time to home range establishment, dispersal success, and tortuosity of movement paths, one might conclude that the landscape's asymmetrical configuration had the greatest impact on connectivity (Figure 5) rather than mortality or land use change. For example, tortuosity and time to home range establishment were significantly lower for individuals originating from the more fragmented eastern portion of the landscape, regardless of mortality. Thus, while this factor did have strong effects on local dispersal, it was the least important variable in terms of functional connectivity (Figure 3). Similarly, land use change had no effect on the mean dispersal metrics of all dispersers, but did have an effect on functional connectivity in the absence of mortality (Figure 2). Therefore, when assessing connectivity between populations, it is important to carefully select metrics that represent functional connectivity rather than assume that greater rates of movement or faster times to establishment are synonymous with greater connectivity between populations (Bélisle 2005).

3.5.2 IBMs and Connectivity

Our application of the SEARCH modeling framework to evaluate landscape connectivity builds on the work of others in several important ways. For example, it is common for IBMs of animal dispersal to incorporate a single mode of movement during a given simulation, such as a non-oriented correlated random walk (Schippers et al. 1996, Lookingbill et al. 2010). In presenting a framework for the unification of individual behavior and population distributions, Mueller and Fagan (2008) called for the integration of non-oriented, oriented, and memory-based movement mechanisms that vary based on the animal's behavioral state. SEARCH accomplishes this by using a non-oriented correlated random walk during the exploration phase, and then combines spatial memory with oriented movement while individuals are homing to a potential home range location. The integration of these mechanisms mimics the behavioral complexity of dispersal and facilitates the incorporation of effects of behavior on landscape connectivity (Lima and Zollner 1996, Baguette and Van Dyck 2007).

SEARCH incorporates other important behavioral complexities into its mechanisms of animal dispersal. Perceptual range, which has been shown to affect functional landscape connectivity (Graf et al. 2007), is key to building the memory map that is used by dispersers to sort and select potential home range sites. SEARCH also simulates interactions between individual dispersers. Rather than assume connectivity if a disperser is capable of moving between patches of suitable habitat (Morzillo et al. 2011), animals must also identify locations that are unoccupied by members of the same sex (Kramer-Schadt et al. 2011). In our marten model, habitat availability was limited by the resident adult population, and each time a disperser established a home range it precluded another individual of the same sex from also establishing in that location. Thus, search time, dispersal distance, home range quality, and landscape connectivity were affected not only by habitat composition and configuration, but also by population density (Mitchell and Powell 2004). Finally, SEARCH allows for spatially and temporally dynamic resource maps (Mueller and Fagan 2008). In our application, we used this functionality to simulate the decline of habitat selectivity over time, so that the quality of habitat that constituted a suitable home range declined over the course of the simulation (Chapter 1; Ward 1987). Without this mechanism included, dispersal distances and times were much lower than the observed empirical patterns.

Despite the progress made in the application of IBMs to evaluate functional landscape connectivity, methods such as least cost path analysis and graph theory are more widely used. This may be because IBMs often require unique data (e.g., fine-scale movement) that can be difficult to collect, or because the development and implementation of a simulation model is more technical and labor intensive than a statistical landscape analysis. Additionally, no IBM application incorporates all of the potential factors that might influence dispersal and connectivity. For example in our marten model, demography of resident individuals was simplified and assumed to be constant over time. Yet others have demonstrated that functional connectivity can be greatly affected by the demographic status of the metapopulation (Revilla and Wiegand 2008, Schumaker et al. 2014). Our simulations were also restricted by the number of dispersers and size of the landscape, a tradeoff for modeling at fine scales. While we simulated a total of 6,000 dispersal events, simpler models operating at coarser scales have been capable of simulating millions of dispersers over thousands of years (Mueller et al. 2011).

3.5.3 Management Implications

Our simulation model of dispersal represents an additional tool that may be used to support the ongoing conservation efforts for American martens in the Upper Midwest and elsewhere. Because our results indicate that disperser mortality may be the limiting factor for dispersal success between populations, future work may prioritize investigating the roles of prey availability and predation risk in the dispersal matrix and the resulting interaction with juvenile survival and recruitment. Increasing dispersal success between populations might ultimately improve recruitment rates, which are likely contributing to lack of population growth despite multiple translocations to augment the population (Carlson et al. 2014, Manlick et al. 2017). Additionally, our model can be used to explore an unlimited number of future scenarios of land-use change, climate change, or management strategies and their effects on functional landscape connectivity. Such flexibility is necessary as landscapes continue to undergo rapid transformation.

Our simulation modeling approach is also generally applicable to reintroduction and translocation projects of terrestrial wildlife. Despite their common use, particularly for carnivores, reintroductions have often resulted in failure or have had no evaluation due to a lack of post-release monitoring (Breitenmoser et al. 2001, Seddon et al. 2007). Since functional landscape connectivity is vital to the success of translocations, the use of a simulation model can improve estimates of connectivity (Coulon et al. 2015) and improve planning and feasibility assessments (McLane et al. 2011) while accounting for factors that limit reintroduction success (Allen et al. 2016). Such factors often include those identified in the present study, such as mortality due to predation or starvation (Kramer-Schadt et al. 2004, Day et al. 2013, Pires 2017). As IBMs continue to become more accessible and more widely used, they can become an integral tool for using behavioral landscape ecology to evaluate species' responses to changing landscapes (Lima and Zollner 1996, Knowlton and Graham 2010).

3.6 Acknowledgments

We thank the Wisconsin Department of Natural Resources for providing access to forest stand data via the WisFIRS database. We also thank the Bad River Band of the Lake Superior Tribe of Chippewa Indians, the Chequamegon National Forest, J. Schmidt, Gogebic County Forestry and Parks, Iron County Forestry and Parks, and the Ottawa National Forest for providing forest stand data. This study was funded in part by grant no. 2017-67011-26040 from the United

States Department of Agriculture, and by the Great Lakes Indian Fish and Wildlife Commission. We also thank The McIntire-Stennis Cooperative Forestry Research Program for their financial support.

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3.8 Tables

Table 3.1: Factors varied for simulation scenarios of American marten dispersal in a fully orthogonal design. All scenarios were replicated 10 times.

Factors	Levels	Notes
Generations	1-5	Generations were not independent, but were linked from parent to offspring following successful home range establishment
Landscape scenario	No mine Mine Mine + buffer	Length of the mine buffer = diameter of an average marten home range
Directionality	East to west West to east	This factor represented movement between two reintroduced marten populations through the simulated habitat corridor
Mortality	Predation, starvation, and exposure Exposure only	Mortality due to exposure was simulated as a result of failure to locate and establish a home range after the 60-day dispersal period

3.9 Figures

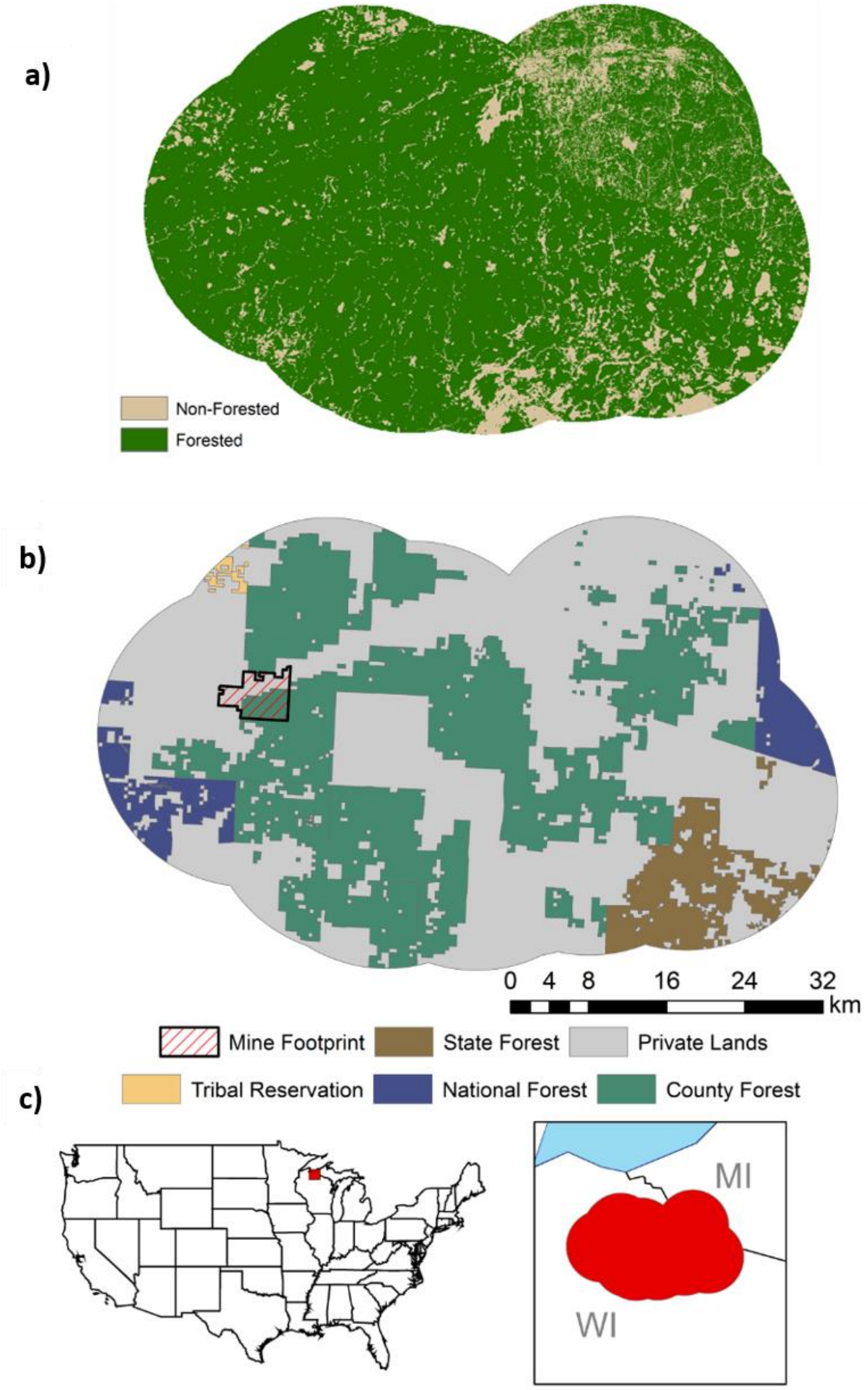


Figure 3.1: Extent of simulations indicating (a) forested and non-forested habitat, (b) land ownership and (c) location of a proposed mine.

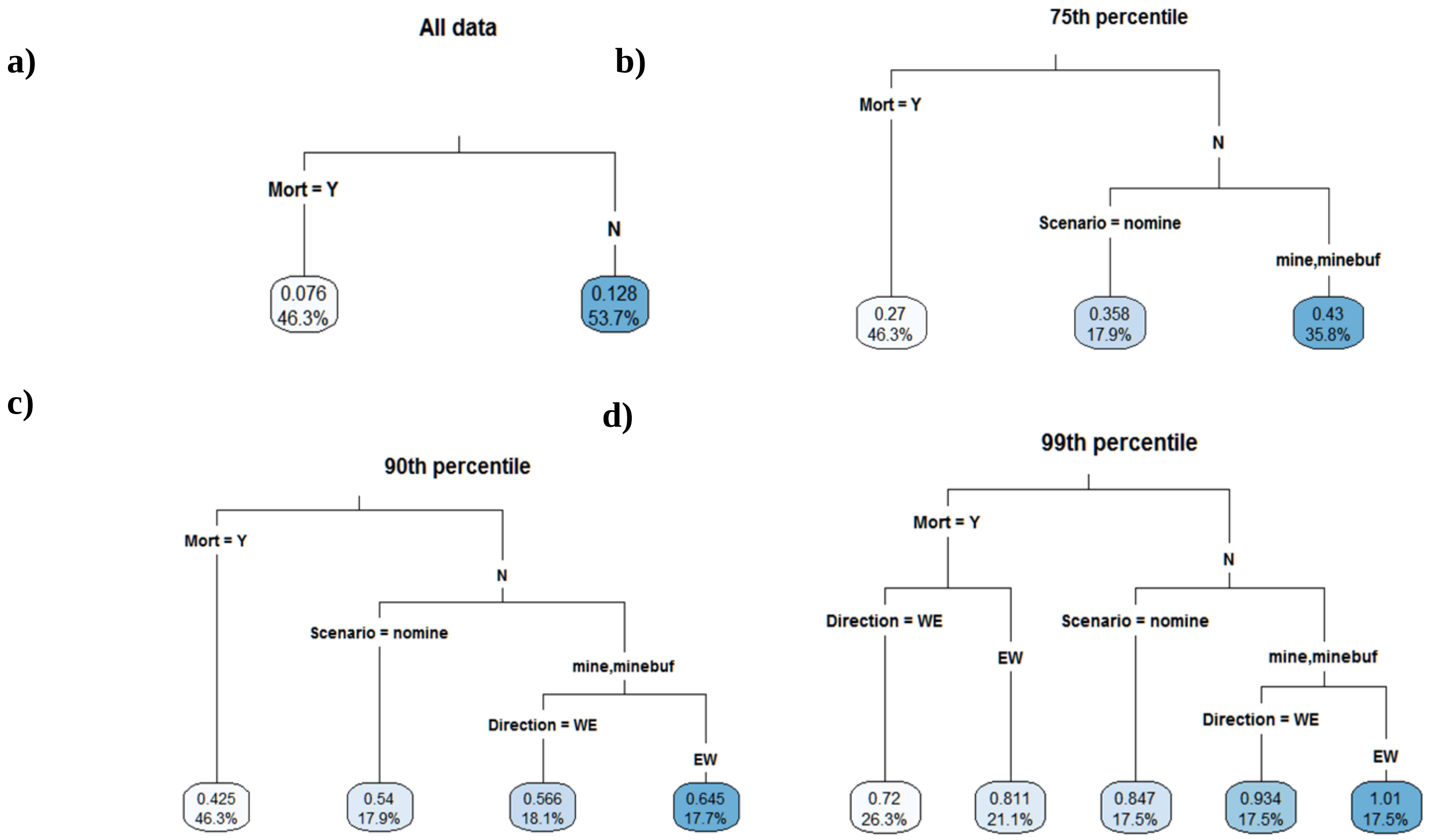


Figure 3.2: Regression trees indicating factors affecting the distance across the landscape traversed by martens across all simulations. Panel a displays the resulting tree when data from all dispersers were included. The remaining panels (b, c, d) display results when data from a portion of dispersers were included based on how far they had traveled between the two populations. Percentiles represent the threshold above which data were included in the analysis. Factors varied included mortality due to starvation and predation, direction traveled, and land use change (no mine, mine included, mine plus buffer around the mine). Values in the terminal leaf-nodes indicate the mean value and percentage of data included in that node.

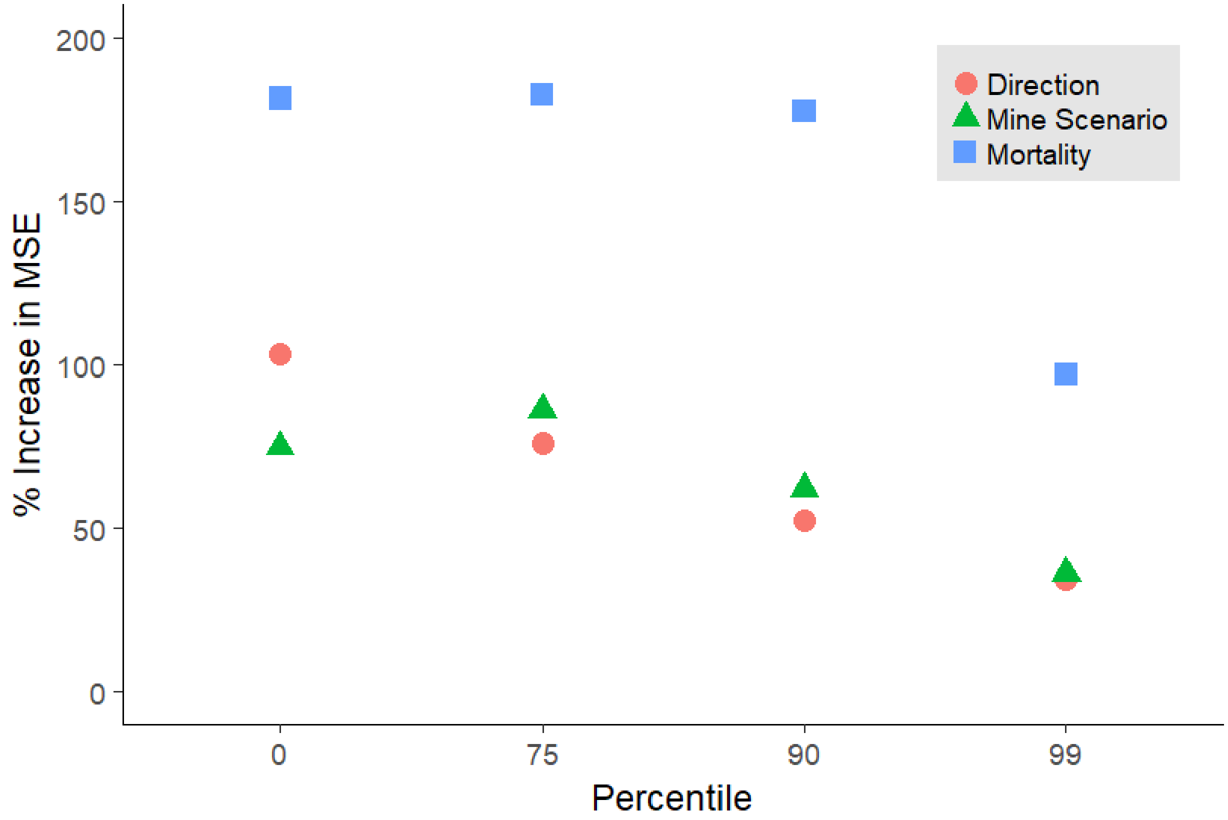


Figure 3.3: Relative importance of variables tested for their ability to explain variation in functional landscape connectivity between two reintroduced populations of American martens in the Upper Midwest. Plotted values represent the percent increase in mean squared error (MSE), scaled by standard error, when values of explanatory variables were permuted during random forest analysis (number of trees = 10,000). A greater value for a given variable indicates a greater decrease in the model's ability to capture the variation in the data when that variable's values are randomly shuffled. Percentiles represent the threshold above which data were included for lateral distance traversed across the landscape between populations.

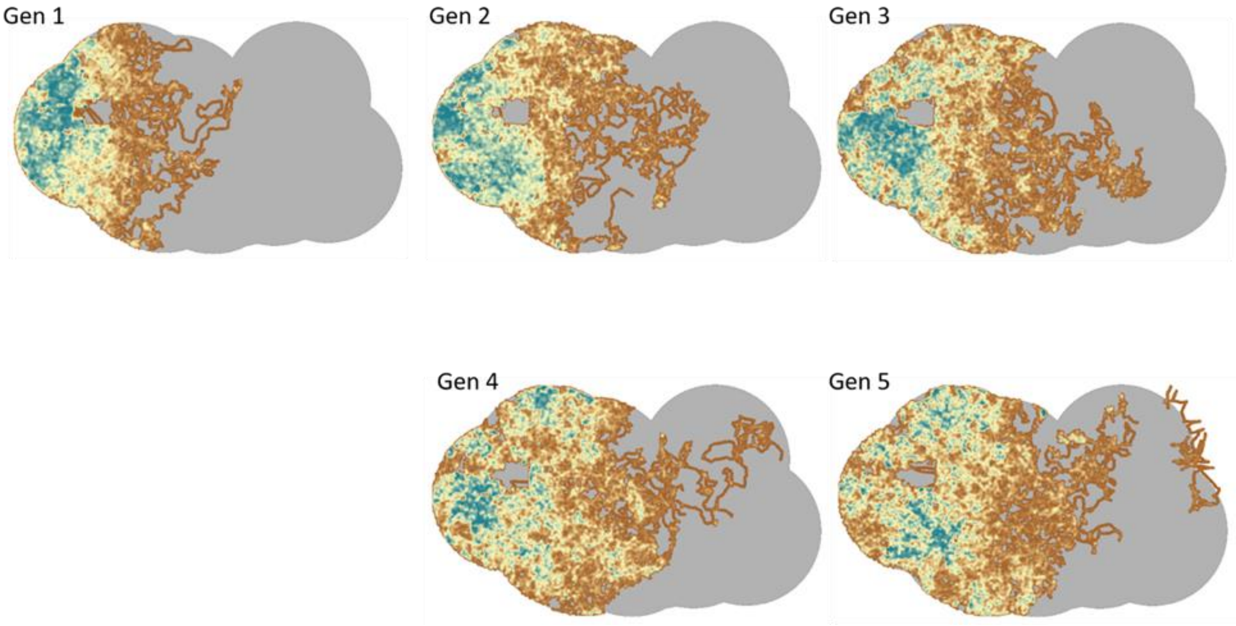


Figure 3.4: A series of point density maps of marten locations during simulated dispersal events that demonstrates the progression of dispersal across the landscape over time. The scenario displayed here includes no mortality and a simulated open-pit mine, with all dispersers in generation 1 being released from the western population.

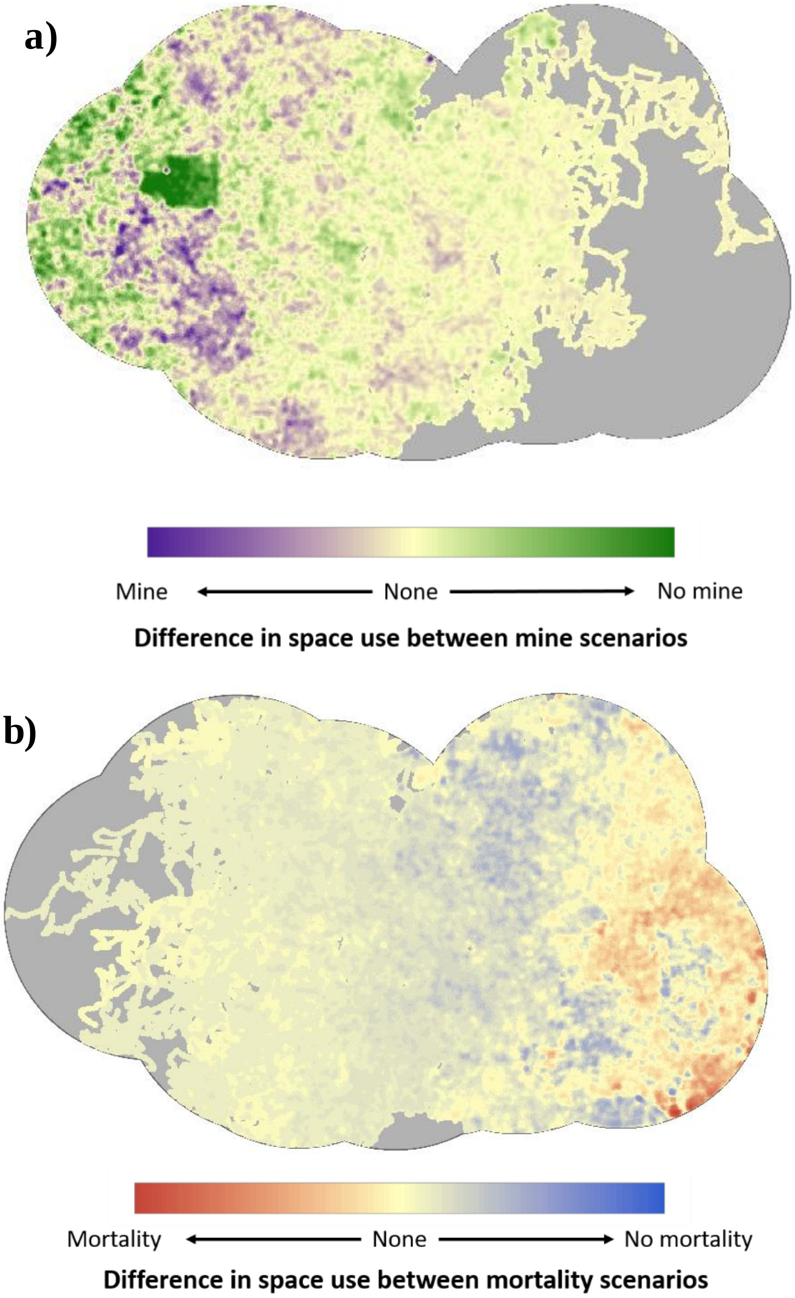
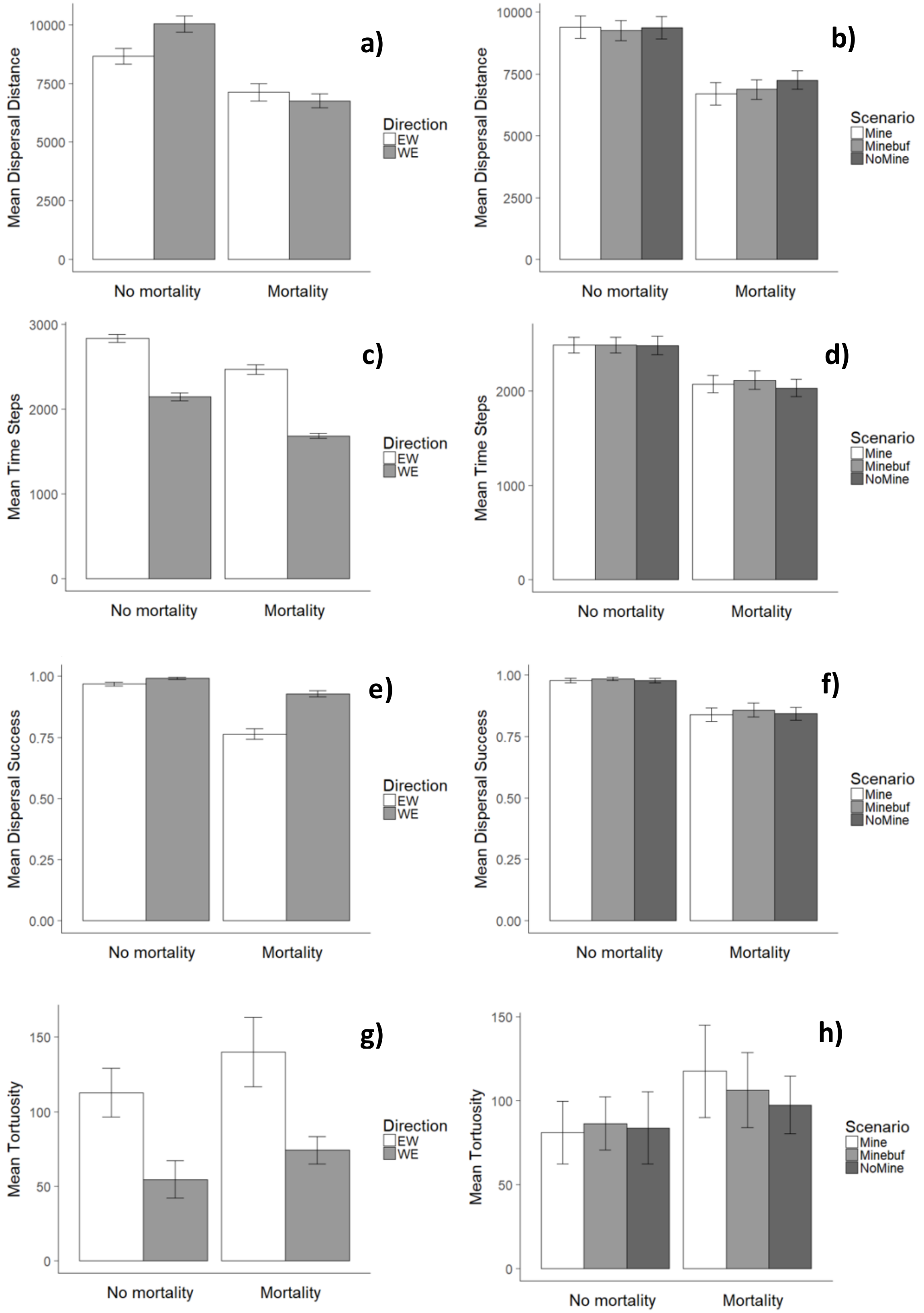


Figure 3.5: Comparison of space use for different simulation scenarios represented by the difference in density of locations used by simulated martens across the landscape. Panel a displays locations for martens released from the west where space use was greater with the mine included (purple) and excluded (green). Panel b displays locations for martens released from the east where space use was greater with predation and starvation included (red) and excluded (blue). Locations represented in each panel include those from all individuals from all replicates and generations for each respective scenario. Point density rasters were first created for each scenario based on the proportion of point locations per cell, and then subtracted to produce the current figures.

Figure 3.6: Mean (± 95% confidence interval) dispersal distance (a, b), time to home range establishment (c, d), dispersal success (e, f), and tortuosity (g, h) by martens that established home ranges during simulations. Factors displayed include mortality due to predation and starvation, direction of movement from the source population to the destination (e.g., EW = east to west), and land-use scenario (No mine, mine included, mine with 2 km buffer of unsuitable habitat).


a)
Mean Dispersal Distance
0
2500
5000
7500
10000
No mortality
Mortality
Direction
EW
WE
b)
Mean Dispersal Distance
0
2500
5000
7500
10000
No mortality
Mortality
Scenario
Mine
Minebuf
NoMine
c)
Mean Time Steps
0
1000
2000
3000
No mortality
Mortality
Direction
EW
WE
d)
Mean Time Steps
0
1000
2000
No mortality
Mortality
Scenario
Mine
Minebuf
NoMine
e)
Mean Dispersal Success
0.00
0.25
0.50
0.75
1.00
No mortality
Mortality
Direction
EW
WE
f)
Mean Dispersal Success
0.00
0.25
0.50
0.75
1.00
No mortality
Mortality
Scenario
Mine
Minebuf
NoMine
g)
Mean Tortuosity
0
50
100
150
No mortality
Mortality
Direction
EW
WE
h)
Mean Tortuosity
0
50
100
150
No mortality
Mortality
Scenario
Mine
Minebuf
NoMine

CHAPTER 4. FROM INDIVIDUALS TO LANDSCAPES: MEASURING FUNCTIONAL CONNECTIVITY UNDER LAND USE AND CLIMATE CHANGE

4.1 Abstract

Land-use change and climate change continue to rapidly transform landscapes worldwide. The resulting increases in habitat fragmentation and shifts in habitat composition present numerous challenges for the conservation of wildlife, particularly for rare or sensitive species with specific habitat requirements. Behavioral approaches to landscape ecology can be used to explore how species will respond to projected changes in landscape composition and configuration. By incorporating mechanisms that drive animal behavior, simulation models can project how individuals and populations will respond to novel landscapes. However, this approach also requires the ability to project changes to the environment occupied by the target species. In this study, we present a novel method to investigate behavioral responses to land-use and climate change by linking a landscape-level simulation of forest succession (LANDIS-II) with an individual-based model of animal behavior (SEARCH). We applied this method to answer questions about the dispersal behavior and functional connectivity between two populations of American martens (*Martes americana*), a state-endangered carnivore at the southern edge of its range in the Upper Midwestern United States. Our results show that climate change may result in an increase in available cover types suitable for martens, but that overall forest diversity is likely to decline. We also found that both land-use and climate change impacted dispersal behavior of martens and the functional connectivity between populations. However, these effects were not consistent across all simulations, as asymmetrical landscape configuration interacted with climate and land-use change to affect individual behavior and dispersal success. Our case study demonstrates how behavioral

landscape ecology can identify conservation issues that more traditional modeling cannot. We present this example as a template for how to use knowledge of animal behavior to improve projections about species responses to conservation challenges such as land-use and climate change.

4.2 Introduction

Landscapes and ecosystems worldwide continue to undergo rapid transformation due to land-use and climate change (Newbold et al. 2015, Pecl et al. 2017). Land-use change due to anthropogenic development often results in landscape fragmentation, which restricts the ability of terrestrial animals to move across landscapes (Tucker et al. 2018). The realization of climate change further complicates this issue, as increases in temperature create a need for species to migrate to cooler latitudes and elevations to counteract the effects of a warming climate (Pauchard et al. 2016). These two forces are in opposition to one another, as land-use change restricts the ability of species to use dispersal movements to cope with climate change (Opdam and Wascher 2004). Furthermore, landscape fragmentation limits the ability of animal populations to maintain functional connectivity, which is necessary for long-term genetic diversity and population viability (Allendorf 1986). Indirect effects of climate change, such as shifts in habitat composition, may likewise affect connectivity. In considering the conservation of rare or threatened species, conservation planners must account for the effects of land-use and climate change on animal dispersal not only as a means to keep pace with climate, but to maintain connectivity between populations and with climate refugia as well (Nuñez et al. 2013).

Landscape-scale models of changes to the composition and configuration of habitats have been widely developed to improve understanding of potential impacts from climate change and land-use change. For example, projections of land transformation have been developed to predict land-use change for the entire United States (Tayyebi et al. 2013, Sohl et al. 2014). Models such as the ForeCASTS project (https://www.geobabble.org/ForeCASTS/resources.html) attempt to predict how the ranges of tree species might shift in response to climate change (Potter et al. 2010). More fine-scale frameworks, such as LANDIS, model the effects of climate change and land-use change using mechanistic first principles to simulate forest succession and wildlife habitat (Scheller and Mladenoff 2008, Zollner et al. 2008, Thompson et al. 2011, Duveneck and Scheller 2016). Species distribution models such as climate envelopes, in which future potential ranges are predicted based on climate projections, are commonly used to predict how wildlife species might shift their range in response to changing climate (Hijmans and Graham 2006, McCain and Colwell 2011). These kinds of models have far-reaching effects for biotic communities from food webs to habitat relationships. However, when considering responses of wildlife to landscape change, landscape-scale models tend to ignore the role of animal behavior and behavioral plasticity from the mechanisms driving model results (Muñoz et al. 2015, Hermes et al. 2018).

Behavioral plasticity (i.e., flexibility) has been widely documented as a mechanism for coping with environmental change, including changes due to land-use and climate (Berger-Tal et al. 2016). However, the majority of reported examples have been observational (reviewed in Beever et al. 2017) and predicting behavioral responses to environmental change remains a challenge (Muñoz et al. 2015). One solution is to identify the mechanisms that allow for behavioral flexibility (Snell-Rood 2013, Beever et al. 2017), and then incorporate those mechanisms into simulation models to reproduce or predict behavioral responses to environmental change (Santini et al. 2016). Behaviorally-explicit, individual-based modeling is a promising avenue for the development of such applications (Bocedi et al. 2014, Schumaker and Brookes 2018). When these models of species' responses to climate change have been behaviorally explicit, they have often focused on shifts in species distributions (Brooker et al. 2007, Synes et al. 2015, Santini et al. 2016). However, the interaction of climate and land-use change will also affect animal movement and landscape connectivity in places other than at the margins of a species range (Hannah 2011). Such impacts should not be overlooked when assessing threats to the conservation of rare or threatened species.

We combined a landscape-level simulation model of forest succession with an individual-based model of animal dispersal to evaluate how changes in land-use and climate would affect the dispersal and functional landscape connectivity of endangered populations of American martens (*Martes americana;* hereafter martens). The ability to simulate these processes is particularly relevant as landscape transformation is affecting the dispersal capabilities of declining wildlife populations worldwide (Tucker et al. 2018). In our study system martens have been repeatedly reintroduced to the Upper Midwestern USA since the 1950s, yet martens remain endangered in Wisconsin (Williams et al. 2007). Functional landscape connectivity and population isolation may be playing a key role in this slow recovery, as immigration, recruitment, and assortative mating may all contribute to a lack of population growth (Grauer et al. 2017, Manlick et al. 2017a; Chapter 2). These factors may also be interacting with other factors such as competition with fishers (*Pekania penannti*) and lack of food availability to limit population connectivity in the region (Carlson et al. 2014, Manlick et al. 2017b; Chapter 4). If marten populations in Wisconsin are to persist, understanding how they might respond to land-use and climate change will be necessary to plan for their conservation. Such an undertaking would also provide an example of how simulation modeling at multiple ecological scales can be used to synthesize species responses to changing landscapes.

Our overall goal was to evaluate the behavioral response of martens to landscape transformation as a result of land-use and climate change using a mechanistic simulation modeling approach. Specifically, we used LANDIS-II to develop a simulation model of forest succession to project landscape characteristics in terms of marten ecology under alternate climate scenarios. We used output from LANDIS-II as input for an individual-based model of animal dispersal and home range establishment of martens under each scenario. Our specific objectives were to use these simulation models to evaluate 1) the effects of climate change on forest composition and habitat suitability and 2) the effects of climate change and land-use change on marten dispersal and functional landscape connectivity.

4.3 Methods

4.3.1 Study System

Our study area is located in northern Wisconsin and the western Upper Peninsula of Michigan, USA (Fig. 1). The area is mostly forested but also includes the adjoining towns of Hurley, WI and Ironwood, MI, whose joint population size is approximately 6,500 people. Forests in the region are primarily deciduous and composed of stands dominated by quaking aspen (*Populus tremuloides*) and the northern hardwood community (e.g., sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*)). Roughly one third of the landscape is wetland, most of which is forested with lowland coniferous and deciduous species. Timber harvest is economically important in the region (Iron County 2006), and the landscape is a mosaic of ownerships, including three county forests, one state forest, two national forests, and private industrial and non-industrial forests (Fig. 1).

Martens in our study area require complex forests with vertical structure and tend to select home ranges with >70% non-avoided (i.e., neutral or selected for) cover types (Gilbert et al. 2017).

Reports of home-range cover type selection have varied somewhat across studies. In order to parameterize habitat suitability inputs for our simulation model, we followed the habitat selection model of Wright (1999) and Dumyahn et al. (2007) that reported martens selecting for northern hardwoods and saw-log aspen, while selecting against lowland conifers, sapling lowland hardwoods, sapling\pole aspen, and non-forested cover types. All other cover types were considered neutral (i.e., neither selected nor avoided).

The study area consists of a forested habitat corridor situated between two reintroduced populations of martens. On the east side of the corridor, the Michigan population has flourished while the Wisconsin population in the west remains state-endangered. In between the two populations is Iron County, WI, which is mostly forested and provides the best opportunity for connecting the two populations along the Penokee mountain range. Within the corridor, an imbalance exists from west to east, with the western portion being more forested and containing more contiguous suitable habitat than the eastern portion which is more fragmented by lakes, wetlands, and urban areas.

4.3.2 Simulating Landscape Dynamics

We used the LANDIS-II (v 6.2; Scheller et al. 2007) forest landscape model to simulate 100 years (2006 - 2106) of forest succession and disturbance in the study area. LANDIS-II (hereafter LANDIS) is a raster-based, spatially-explicit modeling framework that simulates processes of forest succession (growth, mortality, regeneration, seed dispersal, and establishment of species-age cohorts) and disturbance. LANDIS has been widely used to simulate forest succession in the Upper Midwest (Scheller et al. 2011, Gustafson and Sturtevant 2013) under alternative scenarios of climate change and disturbance (Xu et al. 2007, Duveneck et al. 2014), as well as to predict patterns of wildlife habitat (Radeloff et al. 2006, Zollner et al. 2008). In LANDIS, each cell on the landscape contains an assemblage of species-age cohorts that compete and interact with surrounding cells to produce dynamics of forest succession that are output as a time series of forest attribute maps that can be used to predict marten habitat suitability. The physiographic features of the landscape are represented as ecoregions delineated by soils and landform.

To define the extent of the LANDIS simulations, we followed our methodology from Chapter 2, buffering known marten locations from the study area by 14 km, equal to the mean dispersal distance of martens translocated to the CNNF in 2010. We further buffered the resulting extent by an additional 5 km, a distance equal to the maximum seed dispersal distance of tree species simulated in LANDIS. This resulted in a 53.5 by 82.9 km raster (4,439 sq km), divided into 90 x 90 m cells. Using a 10-year time step, we used the PnET-Biomass Succession Extension (v2.0; de Bruijn et al. 2014) to simulate succession and the Biomass Harvest Extension (v3.2; Gustafson et al. 2000) and Linear Wind Extension (v1.0; Gustafson et al. 2015) to simulate the primary disturbance structuring the landscape. We used PnET-Succession because its mechanistic use of first principles to simulate the competition of cohorts for light and water is well-suited to model novel situations such as climate change (Gustafson 2013). Soil water availability is determined by precipitation inputs, loss to evaporation and runoff, soil porosity, and consumption by species cohorts. Access to light depends on canopy position, leaf area and shade tolerance. Each species responds to temperature as a function of departure as optimal temperature for photosynthesis, coupled with temperature effects on vapor pressure deficit, respiration and evapotranspiration rates. Thus, in PnET-Succession, growth rates vary monthly by species and cohort as a function of precipitation and temperature, which directly affects competition and ultimately successional outcomes. A more detailed description of the model can be found in De Bruijn et al (2014).

4.3.3 Initial Communities

Prior to running LANDIS, the study area was populated with a map of species-age cohorts of tree species or groups of species. We selected 19 tree species for simulation based on their abundance in the study area and relevance to marten ecology (Dumyahn et al. 2007, Scheller and Mladenoff 2005). Individual species parameters (Table 1) were calibrated for previous applications of PnET-Succession in northern Wisconsin (Gustafson and Sturtevant 2013, Gustafson and Shinneman 2015). To create a map of initial forest composition and age we used the publicly available land cover data sets WISCLAND 2.0 (Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data, Level 3; WDNR 2016) and IFMAP (Integrated Forest Monitoring, Assessment, and Prescription; MDNR 2001). These data contained information on forest cover type, but not tree size. To produce initial communities throughout the study area, we used the Landscape Builder software (Dijak 2013) to impute plot inventory data from the Forest Inventory Analysis Database (FIA; Miles et al. 2001) across cover types. For our application, Landscape Builder utilized 233 FIA plots and produced a set of species-age cohorts for each FIA plot based on the number and sizes of trees for each species present. Based on the included land cover data, Landscape Builder assigned cohorts to landscape cells based on a randomly selected FIA plot that matched the cover type of the forested cell. We identified 6 primary cover types from land cover data including aspen, oak, upland conifer, upland hardwoods, lowland conifer, and lowland hardwoods (Table 3). Because this process was randomized, we produced 10 replicates of initial communities that were used to initialize 10 replicates of each LANDIS climate scenario.

4.3.4 Physiographic Regions

We defined ecoregions in the study area based on soil type, soil depth, and slope. To obtain each of these parameters, we used the Soil Survey Geographic Database (SSURGO; Soil Survey

Staff 2017) available from the USGS Geo Data Portal (https://cida.usgs.gov/gdp/). We calculated soil types based on percent composition (i.e., clay, sand, silt) to match the default soil types available in the PnET extension. Soil depths of 0 were considered inactive (i.e., bedrock). We binned slope and depth values based on natural histogram breaks using Jenks' optimization method (Jenks 1967) in ArcGIS (Redlands, CA). We then assigned a unique ecoregion type to each combination of soil type, depth, and slope, for a total of 38 ecoregions. For each of these ecoregions, we calculated the proportion of precipitation runoff that does not enter the soil as a function of slope.

4.3.5 Climate

Our future climate scenarios were derived from a single Global Climate Model (GCM) using three Representative Concentration Pathways (RCP 2.6, 4.5, 8.5) from the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC 2013). Our objective was to simulate a broad range of climate futures without attempting to identify the most likely future. We used down-scaled climate futures from the Geophysical Fluid Dynamics Laboratory GCM (GFDL-ESM2G; Delworth et al. 2006), specifically monthly values of minimum temperature, maximum temperature, and precipitation. We selected the GFDL GCM because it is commonly used in North America and has performed well relative to other GCMs in this region (Winkler et al. 2012, Duveneck et al. 2014, Demaria et al. 2016). We used future monthly values of solar irradiation from the Vegetation-Ecosystem Modeling and Analysis Project (VEMAP 2; https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=567; Kittel et al. 2000). For carbon dioxide, we retrieved yearly atmospheric values from each RCP and its corresponding Extended Concentration Pathways based on future estimates of greenhouse gas emissions (Meinshausen et al. 2011).

We also simulated a baseline climate scenario based on 50 years of historical data from 1950 through 1999. Monthly weather data from this period were retrieved from the PRISM Climate Group (Daly and Gibson 2002), and global yearly values for atmospheric carbon dioxide were retrieved from the Institute for Atmospheric and Climate Science, Switzerland (http://www.iac.ethz.ch). During LANDIS simulations, yearly historical data sets were randomly selected for each simulated future year.

4.3.6 Disturbance

To simulate timber harvest on the landscape, we obtained copies of forest management plans from each county, state, and national forest within the study area. We then developed harvest prescriptions for each of the 6 management agencies, and target cutting acreages for each prescription based on past and projected timber harvest activity. Spatial boundaries of forest stands were delineated based on spatial stand inventory data provided by each management agency. Stand boundaries were not available for private and commercial forests, so we delineated an arbitrary grid of 9 ha stands on those lands. Based on the USDA Forest Service Woodland Owner Survey (Brett Butler, unpublished data), we assumed that 40% of the private industrial and private non-industrial forests are not currently under active timber management, and randomly assigned 40% of private stands as unmanaged (no timber harvest allowed). We developed harvest prescriptions for the remaining 60% of private forests that were comparable to those for county forests. For each prescription on each ownership, the Harvest extension ascertained the eligibility of each stand according to age and composition criteria, and eligible stands were cut in order of decreasing stand age (age of oldest cohort) until the target acreage was reached or until no eligible stands remained.

For wind disturbance, we used the linear wind extension (Gustafson et al. 2015) which simulates cohort mortality due to blowdown as a result of wind events that occur linearly, such as tornadoes and derechos. Frequency, intensity, and directionality of wind events are user defined, and the severity of cohort mortality is dependent on the age of the affected cohorts (older cohorts experience greater severity). Wind intensity is greatest along the primary axis of the wind event and declines with distance from the axis. We parameterized this extension based on multiple sources that reported on the frequency and intensity of wind events in the region (Johnson and Miyanishi 2010, Peterson et al. 2016, Corfidi et al. 2017, NOAA 2017).

4.3.7 Animal Dispersal

To simulate marten dispersal across the Iron County habitat corridor, we built upon a previous application of the SEARCH modeling framework (Spatially Explicit Animal Response to Composition of Habitat) implemented for the same study area and species (see Chapter 2). This application was based on the previously calibrated model of marten dispersal described in detail in Chapter 1. That model was calibrated using a pattern-oriented modeling approach to match dispersal patterns of actual martens from translocations on the CNNF in 2010 (Woodford et al. 2013). Following, we describe the general processes and key parameters of our SEARCH application. For a full ODD description (Overview, Design concepts, and Details) of the SEARCH framework, see Pauli et al. (2013a).

In SEARCH modeling, the primary processes center around the dispersal of individuals in search of a location that is both suitable for home-range establishment and is unoccupied by a member of the same sex. Prior to initiating SEARCH runs, we simulated a baseline density of resident martens on the study area following the method described in Chapter 1. For each combination of replicate, climate scenario, and land-use scenario, we released a specified number of martens based on estimated marten density in the region. These individuals were released at random locations across suitable habitat polygons and were allowed to establish a home-range immediately. The resulting landscapes of resident home-ranges were then used to represent existing marten occupancy for each combination of climate scenario, land-use scenario, and replicate of marten dispersal.

During dispersal, martens interacted with and made decisions based on 4 independent, vector-based, spatially explicit maps that regulated movement, food availability, predation risk, and habitat suitability/sociality. For each combination of scenario and replicate, we created a set of unique maps based on output from LANDIS modeling. Parameterization of these maps was based on cover types and size classes and followed methods from Chapters 1 and 2. For the habitat suitability map, we converted LANDIS output to a binary layer of avoided and non-avoided cover types (Table 3). We then used focal statistics in ArcGIS (ESRI, Redlands, CA) to determine which cells were considered suitable (i.e., the surrounding 1 sq km was composed of ≥70% non-avoided cover types). While 70% is considered the baseline rule for marten habitat selection, our application also included a dynamic habitat suitability map that implemented a decline in habitat selectivity by dispersers over time. This mechanism allowed individuals to settle for progressively lower habitat quality to prevent failure to establish a home-range (see Chapters 1 and 2).

Disperser movement while searching for suitable home-range locations was guided by a correlated random walk at 15-minute time steps. Mean step lengths and mean vector lengths of the correlated random walk varied by habitat type. As dispersing martens moved through the simulated landscape, they maintained a memory map of habitat suitability for the areas which they visited. The extent of the memory map was based on perceptual range of 100 m (Gardner and Gustafson 2004), or the distance from an individual’s location at which they are capable of perceiving habitat suitability. As potentially suitable home-range locations were encountered, dispersers added them to a list of potentially suitable home-range locations in their memory. After 2 weeks of dispersal (see Chapter 1), martens switched out of search mode and began orienting toward a specific potential home-range location. At this point, the list of potential home range sites was ranked and sorted based on proximity, food availability, and predation risk, and the martens oriented toward the top-ranked site and attempted to establish a home-range. If home-range establishment failed, the marten either reoriented toward the next site on the list, or (if no more sites are stored in memory) returned to searching for new suitable home-range locations. Throughout the simulation, martens were subject to variation in habitat type that dictated risk of predation, food availability, and movement parameters.

The best-performing model from calibration and applied to the current application included an initial 2-week exploratory phase prior to allowing attempts at home-range establishment. It also included a dynamic habitat suitability map that implemented a decline in habitat selectivity by dispersers over time (Chapter 1).

4.3.8 Study Design

For SEARCH modeling, we implemented a fully factorial simulation experiment across three explanatory variables: climate change, land use change, and release location (east/west). For each combination of levels among factors, we conducted 3 replicates of 10 dispersers each. Inputs for each of the 3 replicates for each climate scenario were based on output from each of 3 unique LANDIS simulations.

For the climate scenarios, we limited SEARCH modeling to historical climate, RCP 4.5, and RCP 8.5. The historical climate provided a baseline reference scenario while the 2 climate change scenarios represented moderate and high carbon emissions scenarios. Given the intermediate results returned from the RCP 2.6 LANDIS modeling (Figure 3), we determined that the 3 selected climate scenarios were sufficient to represent the range of impacts that climate is likely to have on dispersal results. We converted the LANDIS species-age cohort output at year 100 to cover types and size classes that matched those used in the habitat suitability model from Chapters 1 and 2 (Table 3; Wright 1999, Dumyahn et al. 2007). We then used the resulting layer of cover type and tree size to parameterize each of the 4 SEARCH input layers (Chapters 1 and 2).

For the land-use change variable, we produced two sets of SEARCH maps. One set was based on a temporally static landscape (i.e., no land-use change over time), and another in which land-use change in the region was projected out to the year 2100 (Sohl et al. 2014; Figure 2). We incorporated these land-use change projections into all 4 of the SEARCH maps for this scenario (Figure 2). The primary changes in land-use that affected the 4 input maps in our application included forested habitat converted to pasture, agriculture, or urban areas. Finally, we conducted separate simulations for dispersing animals originating from the Michigan population (east) and from the CNF population (west). This allowed us to evaluate the effects of asymmetrical landscape configuration on landscape connectivity (Chapter 2), as well as any interactive effects between release location and other explanatory variables.

4.3.9 Data Analysis

For the LANDIS output, we selected 5 response variables that were both representative of the effects of climate change on forested habitat and relevant to marten dispersal habitat. These response variables included total forested biomass, total number of species-age cohorts, species richness per forested cell, age richness per forested cell, and proportion of cover types considered to be non-avoided by martens. We produced plots of each of these variables to provide a visual representation of trends over time for each climate scenario. We used analysis of variance to determine if outcomes for climate scenarios differed from one another.

For SEARCH output, we selected 4 additional response variables to evaluate the effects of climate change and land-use change on functional landscape connectivity and marten dispersal behavior. We developed a surrogate metric for functional landscape connectivity, described below. The other three response variables – dispersal distance, time to settlement, and proportion of successful dispersers – were all metrics of dispersal outcomes that were independent of their role in connecting the two populations. To evaluate the role of climate change, land-use change, and release location on these dispersal outcomes, we developed a set of general linear models that we evaluated using Akaike's Information Criterion (AIC) in an information theoretic approach (Akaike 1974, Burnham and Anderson 2002). To do this, we first developed a full suite of additive models for each response variable and identified the best model using AIC. If the top-performing model included multiple explanatory variables, we developed a new GLM to test for interactions among variables and compared the resulting AIC value to the best additive model. Due to substantial differences in the composition of suitable habitat on the east and west portions of the study area, we conducted additional analyses to determine if the effects of land use and climate change varied according to release location. To accomplish this, we repeated the model selection process for data sets restricted to individuals originating from a single source population. Following model selection, we used analysis of variance to determine if the variables in each of the top models had a significant effect on the chosen dispersal metrics.

To evaluate landscape effects on functional landscape connectivity, we followed the method from Chapter 2 to develop a metric of net directional displacement from the original release site, expressed as a fraction of the distance traversed between the two origin points. For example, if an individual originating in the east established a home-range in the western release area, it received a displacement value of 1. An individual that moved half way between the two release locations received a displacement value of 0.5.

Because landscape connectivity is often driven by long-distance dispersal events, we examined subsets of the displacement metric based on those individuals that had traveled furthest in the direction of the population opposite their release location. These included all individuals above the 0th (i.e., all data included), 75th, and 90th percentiles. To evaluate how each explanatory variable affected this displacement metric, we used the "rpart" package in Program R to conduct ordinary regression tree analyses (R Core Team 2017, Therneau et al. 2017). Pruning was conducted by limiting the number of splits to that associated with the lowest cross-validated error. We also used random forest analysis (number of trees = 10,000) to determine the relative importance of each of the three explanatory variables in describing landscape connectivity (Liaw and Wiener 2002).

4.4 Results

4.4.1 Landis Results

Each of our response variables varied according to carbon emissions scenario by year 100 (Figures 3 and 4). Across 10 replicates, mean total aboveground biomass increased with increasing carbon emissions (Figure 3a). Biomass for the historical climate scenario remained relatively steady throughout simulations, while increasing under the highest carbon emissions scenario (RCP 8.5). The 2 moderate emissions scenarios (RCP 2.6 and 4.5) both increased in biomass through year 50 and then leveled off through year 100. The 3 diversity metrics (species richness, age richness, and total cohorts) all responded to carbon emissions in a similar fashion (Figure 3 b-d). All 3 variables were greatest under historical climate and generally declined as carbon emissions increased. Species richness per forested cell (mean ± SD) increased from 4.12 ± 0.16 to 5.08 ±

0.17 under the historical scenario, but remained steady under the 3 climate change scenarios. Total cohorts and age richness showed dramatic declines under climate change, while remaining relatively constant under the historical climate scenario.

The proportion of the forested landscape that we considered non-avoided (i.e., selected for or neutral) by martens increased with carbon emissions (Figure 4, Table 3). Under historical climate, the mean proportion of non-avoided cover types increased slightly from 0.56 ± 0.039 at year 0 to 0.58 ± 0.019 at year 100 ($F_{1,18}$=2.13, p=0.162), while under RCP 8.5 this proportion increased from 0.57 ± 0.034 to 0.64 ± 0.018 ($F_{1,18}$=30.76, p<0.001). However, while the proportion of non-avoided cover types at year 100 increased with carbon emissions, no significant difference could be detected among the 3 three RCP scenarios ($F_{2,27}$=2.52, p=0.099).

4.4.2 SEARCH Results – Animal Dispersal

The best models describing variation in disperser success (i.e., proportion of individuals to establish a home range) across all simulations included all 3 explanatory variables (climate, land-use change, release location; $F_{4,175}$=11.12, p<0.001), and also indicated an interaction effect between land-use change and release location ($F_{5,175}$=9.35, p<0.001; Figure 5, top row; Table 4). When we evaluated disperser success for each release location, climate was the best descriptor of success for martens originating in the east ($F_{2,87}$=5.43, p=0.006) while land-use was the best descriptor for martens from the west ($F_{1,88}$=13.54, p<0.001). Overall, disperser success increased with carbon output, decreased with land-use change, and was higher from the west than from the east.

The best model describing variation in dispersal distance included only release location as an explanatory variable ($F_{1,178}$ =7.61, p=0.006; Figure 5, middle row; Table 4), and was greater for individuals originating from the eastern end of the study area. For time to settlement, the best model included all 3 variables and an interaction effect between climate and release location ($F_{6,173}$=30.84, p<0.001; Figure 5, bottom row; Table 4). When evaluating data separately for each release location, the best model was an additive model including land-use and climate for both east ($F_{3,86}$=4.19, p=0.008) and west ($F_{3,86}$=9.49, p<0.001) data sets. Overall, time to settlement decreased with carbon output, increased with land-use change, and was higher for individuals originating from the east.

4.4.3 SEARCH Results – Functional Landscape Connectivity

Across all data subsets, functional landscape connectivity was best explained by the release location (east vs west) of individual martens, followed by climate scenario and land-use change (Figure 6). However, differences occurred between animals originating from different release locations. For martens released in the east, climate scenario and land-use change had minimal effect on connectivity. For animals released in the west, connectivity was strongly affected by both variables. Random forests analysis confirmed the relative importance of these variables, with origin of release resulting in the greatest percent increase in Mean Squared Error across all data subsets, followed by climate and land-use.

4.5 Discussion

Simulation modeling can be a valuable tool in planning for the conservation of American martens and other species of conservation concern (Lacy and Clark 1993, Starfield 1997). We show how combining dynamic models of landscape change with individual-based models of animal behavior can be used to explore how the interface at behavioral and landscape ecology will affect wildlife populations in a changing world (Knowlton and Graham 2010). Results from our study indicate that marten habitat and behavior are likely to be affected by future climate and land-use change, and that present landscape configuration may have an important role in behavioral and demographic responses (Chapter 2). Future conservation planning for martens in our study area would benefit from accounting for potential effects from these factors.

Climate change in our simulations had a clear impact on marten habitat, dispersal behavior, and functional landscape connectivity, even on a time scale of only 100 years. Although we detected a relatively minor increase in non-avoided cover types with increasing carbon emissions, this result translated into a 19% increase in disperser success (i.e., rates of home range establishment) and 41% shorter search times following the two-week exploration phase, with no effect on dispersal distance. Climate change also resulted in increased functional landscape connectivity (ability of dispersers to move between populations), though only in the west to east direction. Taken together, these results indicate that climate change may provide benefits to marten conservation. Other LANDIS simulations in the region have likewise reported similar increases in total biomass as well as the biomass of tree species commonly selected for by martens (Scheller and Mladenoff 2005, Thompson et al. 2011).

While forest habitat conditions may improve under climate change based on our present model of marten habitat suitability (Dumyahn et al. 2007), we note that the habitat selection model we used was developed in the context of present habitat rather than future climate change. This has made the model ideal for present applications (Zollner et al. 2008; Chapters 1 and 2) yet unable to foresee potential habitat needs in the context of climate change. For example, while forest biomass increased in our climate change simulations, species richness and age richness each declined with increasing carbon emissions, potentially signaling a loss of forest resistance and resilience (Duveneck and Scheller 2016). It is unknown how martens might respond to general declines in tree species diversity, but they do require forests with complex structure and a mix of coniferous and deciduous species (Gilbert et al. 1997, Gilbert et al. 2017). Further, the homogenization of forests in the Great Lakes region has been ongoing for more than a century and is likely accompanied by a decline in overall biodiversity (Schulte et al. 2007). Such a decline would limit the diversity of prey available to martens, promoting competition with fishers (Manlick et al. 2017b). In addition to biodiversity factors, future snow cover has the potential to affect the survival and landscape connectivity of marten populations. Deep snow cover in winter both facilitates marten movement (Moriarty et al. 2015) and impedes fisher movement, potentially mitigating competitive interactions (Manlick et al. 2017b, Suffice et al. 2017). Each of the above factors, while omitted from the present habitat model, has the potential to override gains in structural habitat and shift the overall effect of climate change on marten conservation. These factors therefore represent important avenues for future work on the response of martens and other forest carnivores to habitat transformation due to climate change.

Land-use change is another force projected to result in the significant fragmentation and loss of forested habitat (Sohl et al. 2014) in ways that are likely to impact functional connectivity for martens (Hargis et al. 1999). Incorporating land-use change in dispersal simulations resulted in a 12% decrease in disperser success, a 4.9% increase in dispersal distance, and a 14% increase in search times following the imposed exploration phase. And while less impactful than climate, land-use change also produced an increase in functional connectivity, though that result of animals dispersing farther was offset by the increase in disperser mortality (Chapter 2; Johnson et al. 2009). Again, these results interacted with release location, as land-use change had no effect on connectivity in the east-to-west direction. Overall, these results concur with general predictions of the effects of land-use change on connectivity and dispersal, particularly for carnivores (Crooks et al. 2011, Howell et al. 2016). However, these predictions can be strengthened if they explicitly consider the effect of asymmetry on the flow of dispersal across the landscape.

The asymmetrical configuration of the study landscape played a major role in our simulations, as all results associated with dispersal behavior and functional connectivity exhibited interactions with the original release location of the dispersers. This was likely a result of the imbalance of fragmentation and available suitable habitat between the two ends of the habitat corridor (see Chapter 2). The ability of individuals originating from the east to settle in the west was not affected by climate or land-use scenario. Individuals from the west, however, were more successful traversing the landscape to settle in the east as available suitable habitat on the landscape increased. In other words, fragmentation and lack of available suitable habitat in one portion of the landscape may have acted as a directional barrier from the west, while forcing martens from the east to venture further into the corridor. Mortality acted to offset the effects of landscape configuration, as disperser success was lower for animals from the east (Chapter 2), despite increases in individual connectivity values. These asymmetrical effects of landscape configuration are likely widespread among similar species that disperse long distances, especially as landscapes continue to become more fragmented (Schippers et al. 1996, Ferreras 2001).

Identifying barriers to connectivity due to landscape configuration is common in the field of landscape genetics (Landguth et al. 2010, Storfer et al. 2010), though this analysis requires the collection of genetic samples and prohibits the analysis of future landscape scenarios. Other landscape-level approaches such as least cost path or circuit theory analyses require prior assumptions about resistance to movement, and do not traditionally address asymmetry in landscape configuration (Zeller et al. 2012). Our approach, in which functional connectivity is derived from an individual-based model and emerges from the interaction of individuals with landscape features at a fine scale, is a powerful and flexible means of identifying barriers and evaluating the connectivity of alternative landscapes (Chapter 2). Because of its mechanistic nature, this approach can be used to project functional connectivity under novel and future conditions such as landscapes affected by climate change. As our results demonstrate, this ability is important because asymmetry in functional connectivity may have wide-reaching conservation implications for the future of rare or isolated populations.

An underappreciated utility of simulation modeling is assistance in identifying gaps in knowledge that may be needed for conservation planning (Starfield 1997). For example, the effects of climate on forest structure in our model revealed the need to investigate how martens respond to measures of forest diversity such as age richness and species richness in order to better understand how they might respond to climate change. More work is also needed to understand how changing snow cover will affect the movement capabilities and conservation of martens in a warming climate (Pauli et al. 2013b). Finally, our application would benefit from an improved habitat selection model that accounts for home range selection at multiple grains, as the present model may be too coarse to identify important conifer stands occurring within larger hardwood stands (McCann et al. 2014). These are all research needs made more apparent by the process of model testing and development, as well as by combining models of landscape and behavior to evaluate alternative future landscape scenarios.

Since Lima and Zollner's (1996) introductory paper on behavioral landscape ecology, much progress has been made integrating animal behavior and landscape features to address ecological questions. Yet researchers continue to call for the collection of empirical behavioral data as model development outpaces the availability of data needed for model parameterization (Knowlton and Graham 2010, Urban et al. 2016). Our simulation model was developed and parameterized based on a long history of ecological investigation into martens in this system (e.g., Chapters 1, 2, and 4, Gilbert et al. 1997, Gilbert et al. 2009, McCann et al. 2010, McCann et al. 2014, Manlick et al. 2017a), and represents a template for how a long-term empirical study of one species can be used to develop a complex model of behavioral landscape ecology whose properties emerge from fine-scale processes (Breckling et al. 2005). For example, in our application from Chapter 1 we were able to reproduce dispersal distance distributions that matched general empirical patterns, including occasional long-distance dispersal. The behavioral plasticity apparent in these long-distance dispersal events was not imposed, but emerged from the same basic behavioral rules followed by all dispersers. With this mechanistic approach, natural behavioral responses can emerge even when modeling novel or future landscapes, especially when combined with a dynamic landscape simulation model such as LANDIS. These modeling approaches are needed if conservation biology is to better understand how species will functionally respond to the continuation of rapid land transformation due to land-use and climate change.

4.6 Acknowledgments

We thank Brian Miranda, Bill Dijak, Nicholas McCann, and Hannah Panci for their valuable contributions to the parameterization of simulation models and climate scenarios. This study was funded in part by grant no. 2017-67011-26040 from the United States Department of Agriculture, and by the Great Lakes Indian Fish and Wildlife Commission. We also thank The McIntire-Stennis Cooperative Forestry Research Program for their financial support.

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4.8 Tables

Table 4.1: Key species parameters included in the LANDIS-II simulation model of forest succession in the Upper Midwest, USA under alternative climate scenarios.

Species	Foliar nitrogen (%)	Maximum LMA (gm-2)	Annual foliage turnover	Maximum age (years)	Age at maturity (years)	Shade tolerance (units)	Maximum seed dispersal (m)
Abies balsamea	0.9	225	0.25	150	25	4	160
Acer rubrum	2.2	60	1	200	10	4	200
Acer saccharum	2.1	47	1	300	40	5	200
Betula alleghaniensis	2.2	50	1	300	40	4	400
Betula papyrifera	2.4	75	1	130	20	2	5000
Fraxinus americana	2.5	60	1	200	30	3	140
Fraxinus nigra	2.6	65	1	150	20	2	200
Larix laricina	2.7	60	1	180	35	1	200
Picea glauca	1.1	225	0.25	200	25	3	200
Picea mariana	1	200	0.25	200	30	3	200
Pinus banksiana	1.3	245	0.3333	100	10	1	100
Pinus resinosa	1.5	230	0.3333	250	25	2	275
Pinus strobus	1.8	220	0.5	300	40	3	120
Populus tremuloides	2.5	85	1	90	15	1	5000
Prunus serotina	2.5	70	1	150	30	1	200
Quercus rubrum	2.6	60	1	200	25	3	100
Thuja occidentalis	1	130	0.5	400	30	3	60
Tilia americana	2.5	50	1	200	30	4	120
Tsuga canadensis	1.4	105	0.3333	450	30	5	100

Table 4.2: Harvest regime implemented in LANDIS-II modeling of forest succession in the Upper Midwest, USA under alternative climate scenarios. Numerical values indicate the percentage of forest for each ownership cut per decade under each prescription. Values of N\A indicate either that no management plan was in place for a given cover type or the complete absence of that cover type from the ownership. ALSF = American Legion State Forest; CNNF = Chequamegon Nicolet National Forest; ONF = Ottawa National Forest.

Forest type	Prescription	Ashland County	Iron County	Gogebic County	ALSF	CNNF	ONF	Private
Upland hardwoods	Uneven aged	9	5.5	9.5	3.5	9	9.5	10.5
Lowland hardwoods	Shelterwood	0.55	0.12	0.55	N\A	N\A	N\A	N\A
Aspen	Clearcut	1.5	1.25	0.5	1.7	1.65	1.2	0.5
Oak	Shelterwood	N\A	0.02	N\A	N\A	N\A	N\A	N\A
Red/white pine	Select	N\A	N\A	N\A	1.6	N\A	N\A	N\A
Red/white pine	Clearcut	0.025	0.05	0.01	0.32	0.05	0.75	0.6
Upland conifer	Clearcut	1.4	1.2	0.16	0.05	0.33	0.25	2.35
Forested area (ha)		14,570	57,850	11,031	14,701	12,638	12,158	102,803

Table 4.3: Species groupings and corresponding model of habitat selection by American martens, reproduced from Wright (1999) and Dumyahn et al. (2007). Species groupings were used to impute initial communities for LANDIS-II modeling and parameterize SEARCH input layers based on LANDIS-II output. Values for habitat selection* indicate how martens select home ranges based on the size class of the corresponding cover type (sapling, pole, saw log).

Cover type	Species	Selected	Avoided	Neutral
Aspen	*Betuala papyrifera, Populus tremuloides, Populus grandidentata*	Saw	Sapling/Pole	-
Oak	*Quercus rubrum*	-	-	All
Lowland hardwood	*Acer rubrum, Fraxinus nigra*	Saw/pole	Sapling	-
Upland hardwood	*Acer saccharum, Betula alleghaniensis, Fraxinus americana, Prunus serotina, Tilia americana*	All	-	-
Lowland conifer	*Betula alleghaniensis, Larix laricina, Picea mariana, Thuja occidentalis, Tsuga canadensis*	-	All	-
Upland conifer	*Abies balsamea, Picea glauca*	-	-	All
Pine	*Pinus banksiana, Pinus resinosa, Pinus strobus*	-	-	All

*Dashes indicate where none of the three size classes fall under the corresponding selection category.

Table 4.4: Model-based inference of 3 response variables characterizing simulated dispersal behavior through a habitat corridor in the Upper Midwest, USA. Explanatory variables included direction (i.e., release location – east or west), climate scenario (historical, RCP 4.5 RCP 8.5), and land-use change (included or excluded). The best model describing each response variable was identified using Akaike's Information Criterion (AIC) and associated model weights (ω).

Response variable	Model	k	AIC	□AIC	□$_t$
Disperser success	Direction*Land-use + Climate	6	706.34	0	0.503
	Direction + Climate + Land-use	5	706.41	0.07	0.486
	Direction + Climate	4	715.06	8.72	0.006
	Direction + Land-use	3	715.83	9.49	0.004
	Direction	2	723.73	17.39	0
	Climate + Land-use	4	724.13	17.79	0
	Climate	3	731.7	25.36	0
	Land-use	2	732.2	25.86	0
Dispersal distance	Direction	2	3413.1	0	0.489
	Direction + Land-use	3	3414.3	1.2	0.268
	Direction + Climate	4	3415.6	2.5	0.14
	Direction + Climate + Land-use	5	3416.8	3.7	0.077
	Land-use	2	3419.8	6.7	0.017
	Climate	3	3421.2	8.1	0.009
	Climate + Land-use	4	3422.4	9.3	0.005
Time to settlement	Direction*Climate + Land-use	7	2788.2	0	0.873
	Direction + Climate + Land-use	5	2792.2	4	0.118
	Direction + Land-use	3	2802	13.8	0.001
	Direction + Climate	4	2805.1	16.9	0
	Direction	2	2813.8	25.6	0
	Climate + Land-use	4	2897.4	109.2	0
	Land-use	2	2901.1	112.9	0
	Climate	3	2903.7	115.5	0

4.9 Figures

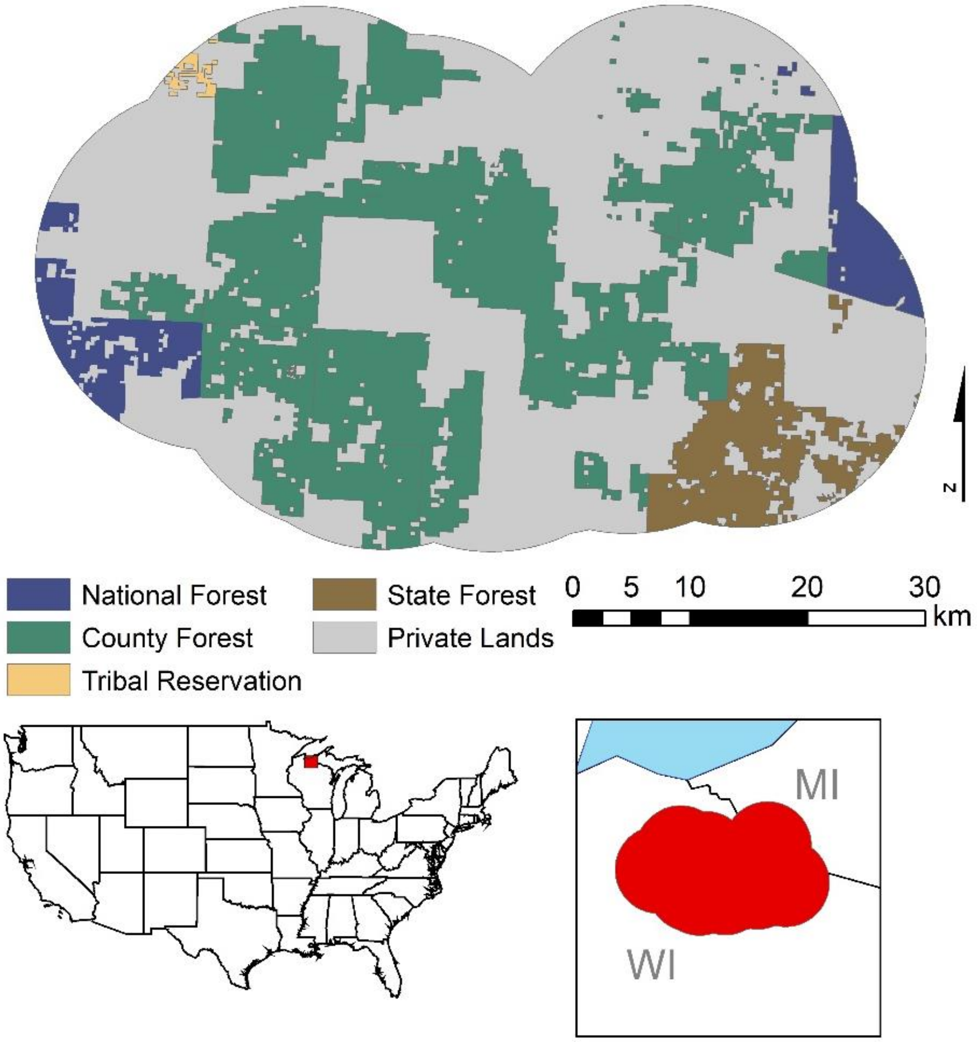


Figure 4.1: Patterns of ownership within the spatial extent of a simulation study of forest succession and American marten dispersal behavior under alternative climate and land-use change scenarios in the Upper Midwest, USA.

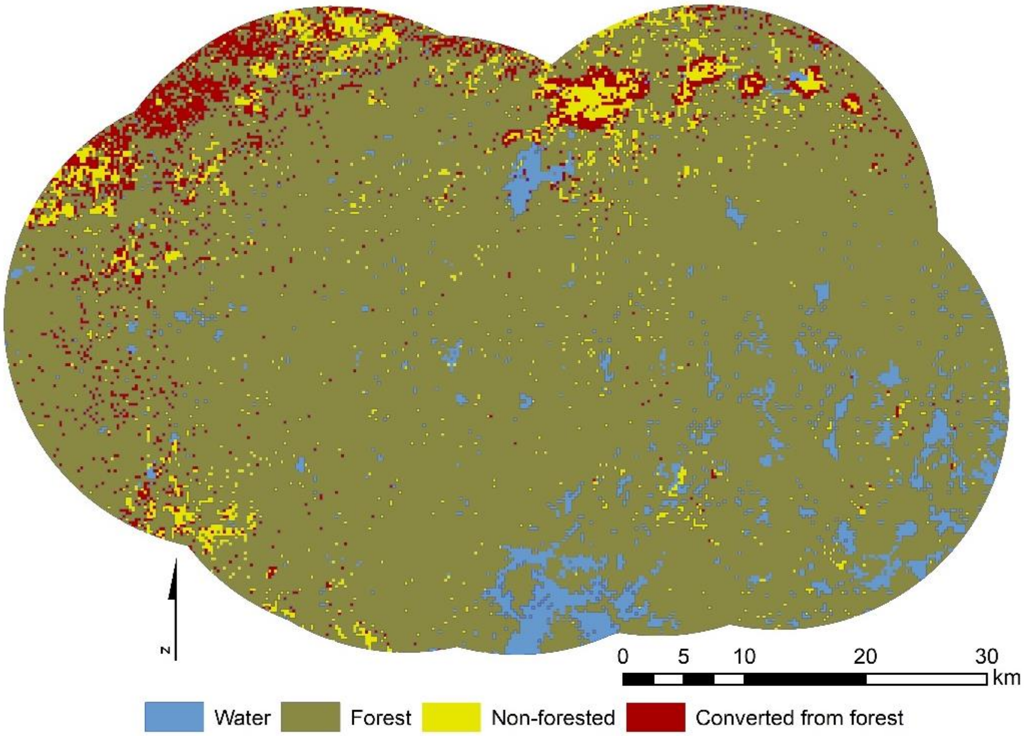


Figure 4.2: Land-use change projections from the United States Geological Survey (Sohl et al. 2014) comparing land-use between the years 2006 and 2100. Yellow polygons indicate non-forested areas in 2006, and red polygons indicate projections of forest conversion to urban areas, agriculture, and pasture by the year 2100. These projections were incorporated into the simulation modeling of American marten dispersal in the Upper Midwest, USA.

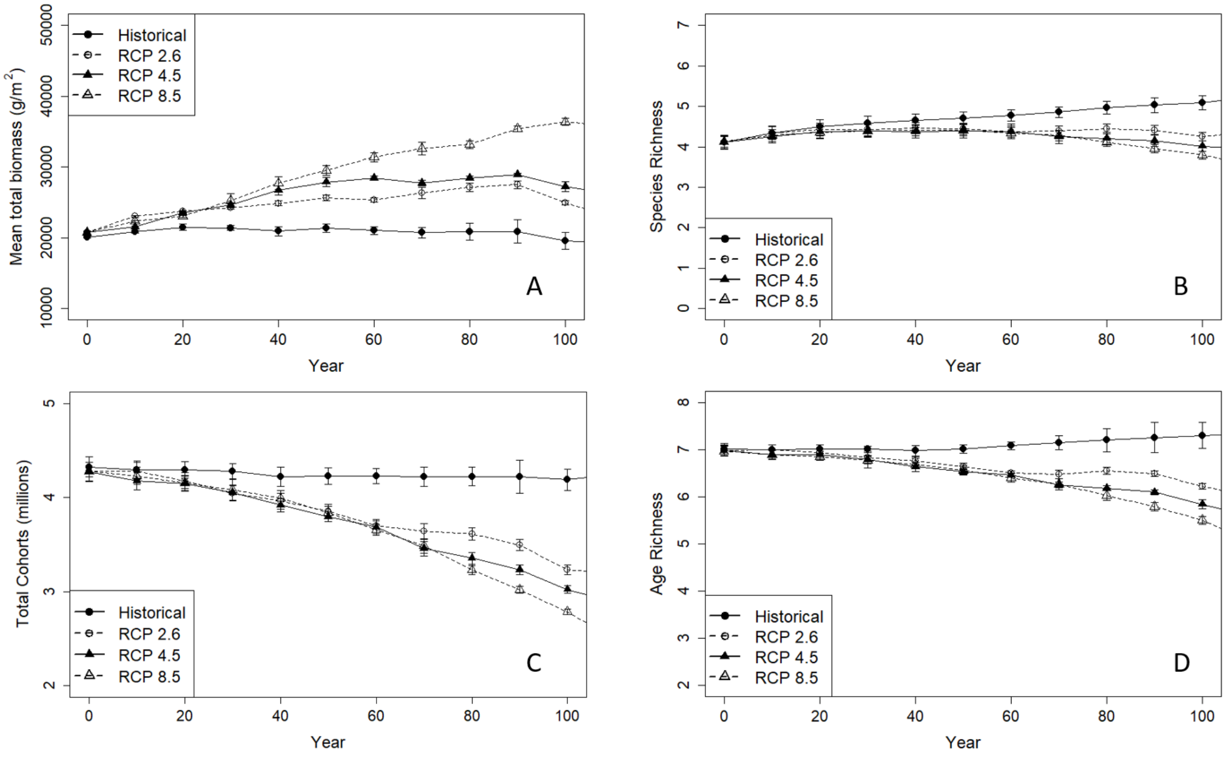


Figure 4.3: Forest response to alternate climate scenarios based on LANDIS-II simulations from the year 2006 through 2106 in the Upper Midwest, USA. Three representative concentration pathways (RCP) for carbon emissions are presented, along with a historical climate scenario based on the years 1950 to 1999. Panel b indicates the mean number of species present per forested cell, panel c indicates the total number of species-age cohorts on the landscape, and panel d indicates the number of 10-year age classes present per cell across all species. Error bars represent one standard deviation among 10 replicates for each climate scenario.

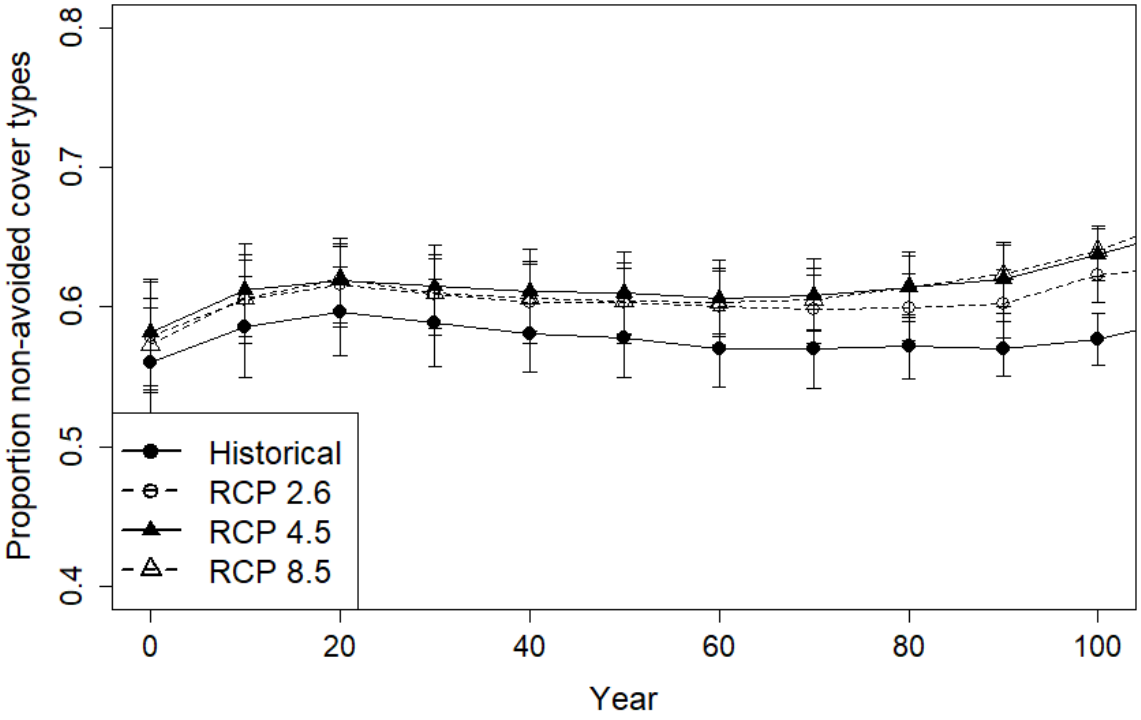
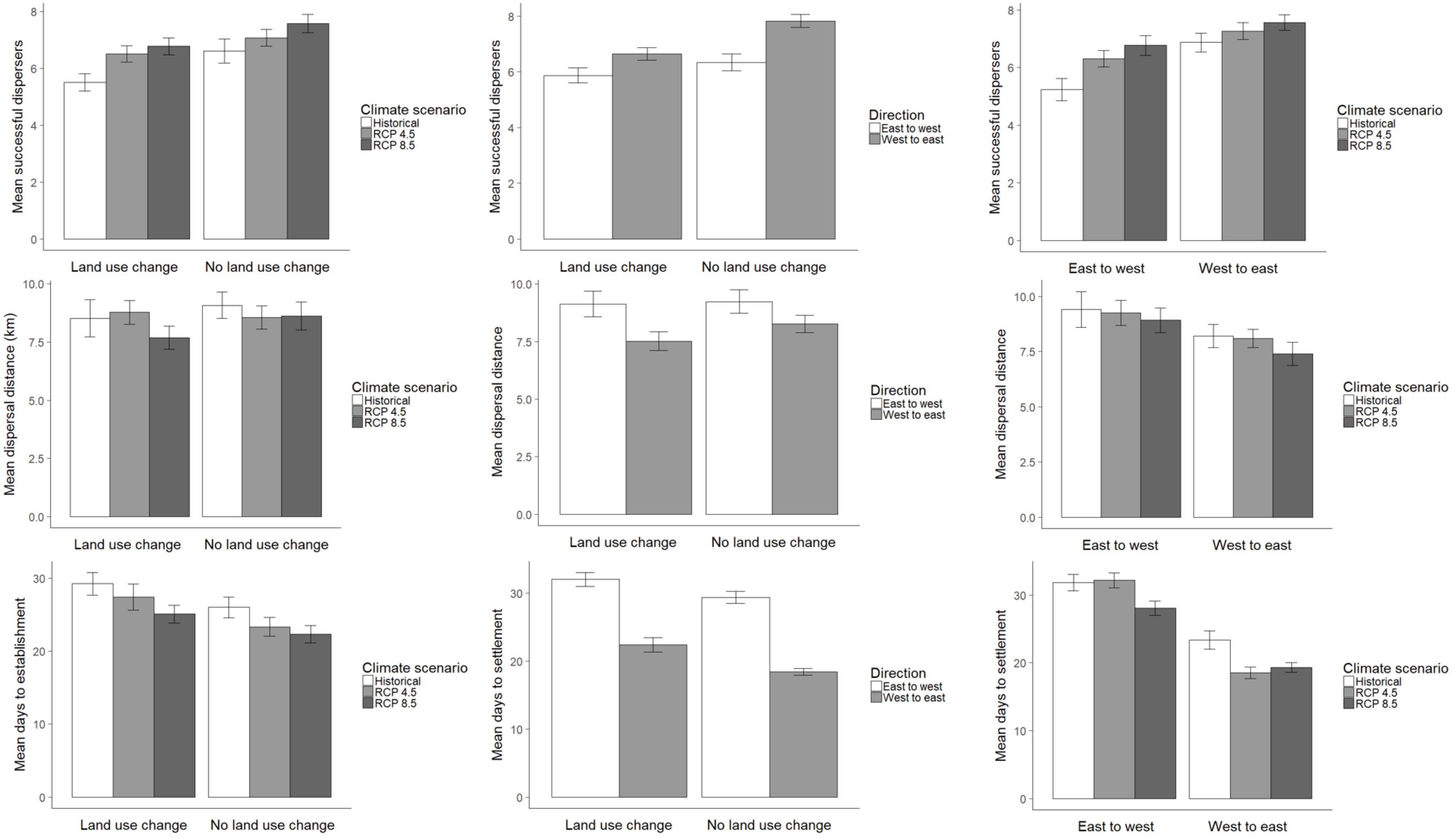


Figure 4.4: Mean proportion of forested landscape composed of cover types that are not avoided by American martens when selecting home ranges. Results represent output from LANDIS-II modeling of forest succession in the Upper Midwest, USA under 3 climate scenarios based on 3 alternate representative concentration pathways (RCP) for carbon emissions and one historical climate scenario (1950 – 1999). Error bars represent one standard deviation among 10 replicates for each climate scenario.

Figure 4.5: Interaction between American marten dispersal behavior and 3 explanatory variables: climate scenario, land use change, and direction (i.e., release location). Results are based on individual-based modeling of dispersal behavior through a habitat corridor situated between two reintroduced marten populations in the Upper Midwest, USA. Displayed are means and standard errors across replicates each representative of 10 simulated dispersal events.


Mean successful dispersers
Mean dispersal distance (km)
Mean dispersal distance
Mean days to establishment
Mean days to settlement
Land use change
No land use change
East to west
West to east
Climate scenario
Historical
RCP 4.5
RCP 8.5
Direction
East to west
West to east
0
2
4
6
8
0.0
2.5
5.0
7.5
10.0
0
10
20
30

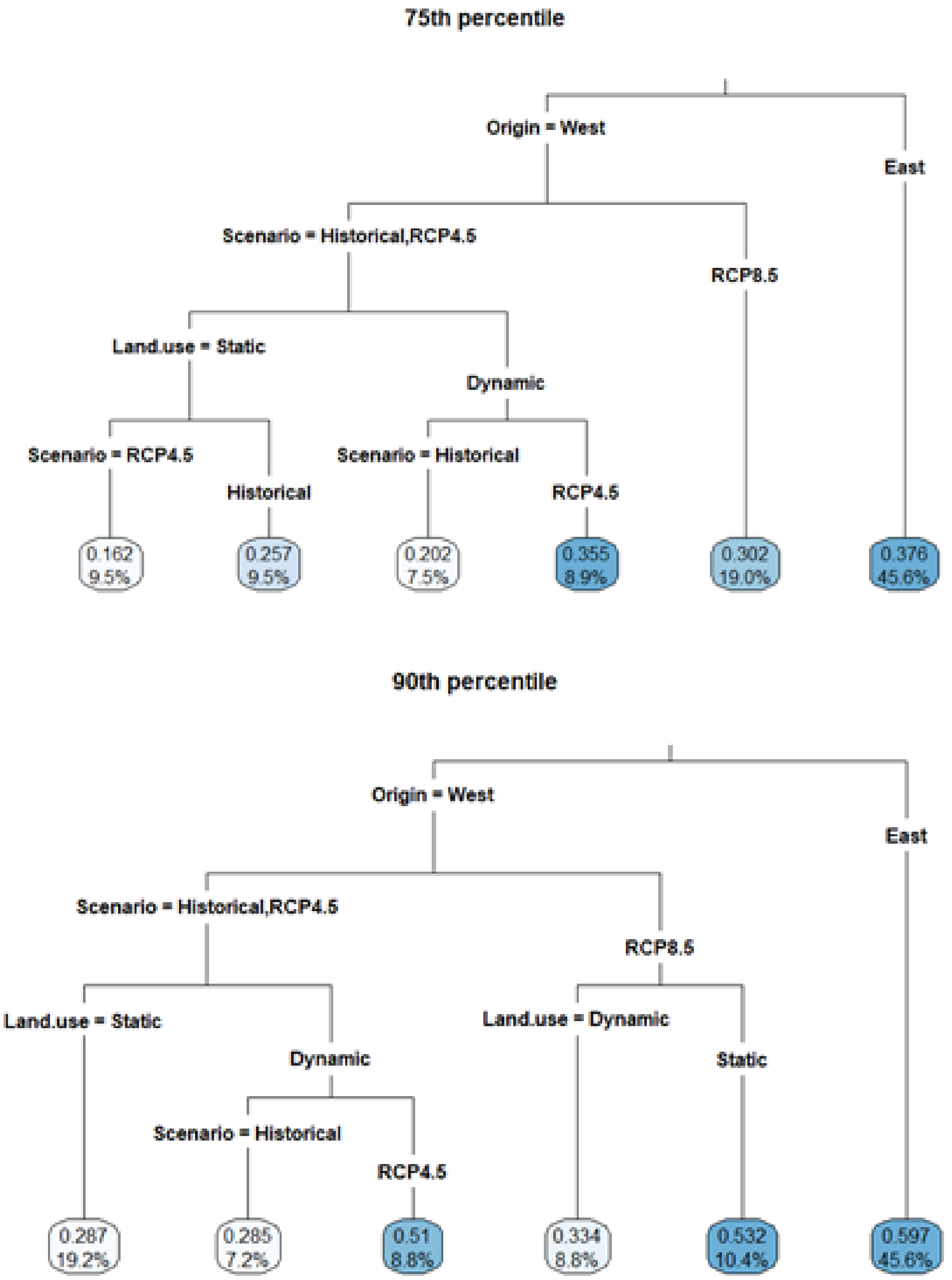


Figure 4.6: Regression trees indicating factors affecting the functional connectivity (net directional displacement of dispersers presented as a fraction) between two reintroduced populations of American martens in the Upper Midwest, USA. Percentiles associated with each tree indicate the threshold above which data were included in the analysis. Factors varied included origin of release (east or west), climate scenario (Historical, RCP 4.5, or RCP 8.5), and land-use change (static indicates no land-use change, dynamic incorporated land-use change through the year 2100.). Values in the terminal leaf-nodes indicate the mean net displacement between populations for the corresponding subset of simulations as well as the percentage of the total data used to calculate those means. The relative number of data points included in each terminal node is represented by color shading, so that darker blue represents a greater proportion of the data.

CHAPTER 5. TEMPORAL AND SPATIAL EFFECTS OF ASSORTATIVE MATING ON A REINTRODUCED CARNIVORE

5.1 Abstract

Threats to the long-term survival of reintroduced populations can be mitigated by releasing animals into a functionally connected landscape. Populations connected by habitat corridors often maintain elevated rates of migration relative to populations that occur in more fragmented landscapes. Such increases in migration are more likely to result in gene flow among populations, ultimately mitigating the effects of genetic drift and allele fixation and improving long-term population viability. However, behavioral barriers to reproduction such as assortative mating can limit the genetic benefits of migration between populations and reduce the likelihood that genetic diversity will be maintained. We investigated the role of landscape connectivity and reproductive behavior in the population genetics of reintroduced American martens in the Upper Midwestern United States. Using genetic samples collected during two time periods separated by 10-15 years, we evaluated the effects of genetic drift, a potential habitat corridor, and assortative mating on the spatial and temporal genetic structure of martens spread across four spatial locations. Our results indicate that both inbreeding and genetic structure have increased for these marten populations over time. Genetic clustering analysis suggests that cluster membership probabilities have also increased over time (i.e., decline in admixture), possibly due to assortative mating among individuals from different source populations. While the potential habitat corridor does appear to be linking otherwise geographically separated populations, assortative mating may be limiting the genetic benefits of the corridor's presence. Thus, despite achieving population connectivity among reintroduced populations, long-term viability may be declining due to assortative mating and its genetic ramifications. Future management of this and other reintroduced animal populations

should plan for long-term genetic monitoring in order to better assess the temporal trajectory of the population genetics of the species. We encourage any future reintroduction or translocation projects to carefully balance the need for genetic diversity with the risk of assortative mating among disparate source populations.

5.2 Introduction

Species reintroductions often result in the failure of the reintroduced species to establish a self-sustaining population (Fischer and Lindenmayer 2000, Breitenmoser et al. 2001). The failure or success of a reintroduction may be influenced by factors such as habitat quality, emigration, mortality rates, inter-specific interactions, number and sex ratio of animals released, and genetic diversity (Griffith et al. 1989, Fischer and Lindenmayer 2000, Powell et al. 2012). Reintroductions of carnivore species (order Carnivora) may be particularly susceptible to failure given that carnivores occur at naturally low densities, require large amounts of space, are often sensitive to human disturbance, and have the potential to create human-wildlife conflict (Breitenmoser et al. 2001). Experimental approaches to reintroductions combined with post-release monitoring are important not only to evaluate the outcome of the reintroduction, but to determine what factors likely contributed to its failure or success (Seddon et al. 2007).

Ensuring connectivity between the reintroduced population and a network of suitable habitat and/or other extant or reintroduced populations has the potential to mitigate reintroduction failures (Richardson et al. 2015). Despite this, reintroduction biology has focused primarily on more immediate threats to population persistence such as habitat suitability, emigration, and predation (Armstrong and Seddon 2008, Ewen 2012). Only recently have studies begun to incorporate explicit models and evaluations of landscape connectivity for reintroduced populations (Kramer-Schadt et al. 2004, La Morgia et al. 2011, Cianfrani et al. 2013, Richardson et al. 2015, Jarchow et al. 2016, Torres et al. 2017). The evaluation of landscape connectivity is important because isolated populations are more susceptible to demographic stochasticity and genetic drift than connected populations that experience regular immigration (Allendorf 1986, Frankham 1998). Ensuring demographic connectivity promotes the exchange of genetic information between populations, offsetting the effects of genetic drift and mitigating inbreeding and allele fixation. In the absence of such connectivity, small populations in particular may become more susceptible in the long-term to deleterious alleles, disease outbreaks, and extinction (Frankham 2005, Jamieson and Lacy 2012). Thus demographic and genetic connectivity can be vital to the long-term success of species reintroductions.

The development and maintenance of habitat corridors between animal populations has been a common method used to promote connectivity between isolated populations (Beier and Noss 1998). A habitat corridor generally consists of suitable dispersal habitat that connects two or more otherwise isolated populations occupying larger areas of suitable habitat. Although the general effectiveness of corridors has long been debated (Simberloff et al. 1992, Beier and Noss 1998), it is clear that for certain taxa, including carnivores, habitat corridors can yield a significant increase in movement between populations (Gilbert-Norton et al. 2010). This additional movement may in turn yield an increase in gene flow among populations that are otherwise genetically isolated.

However, linking populations via animal dispersal does not always guarantee genetic connectivity. Behavioral or physiological barriers to mating may still prevent effective reproductive and genetic contributions by immigrants. One such behavioral barrier, assortative mating, is a behavioral phenomenon in which pairs of individuals that share similar traits are more likely to breed than would be expected in a random mating system. Assortative mating can play an important role in the genetic status of reintroduced populations. Often, multiple translocations over time may be sourced from different populations, sub-species, or even species (Raesly 2001, Slade et al. 2014, Grauer et al. 2017). This practice can potentially result in assortative mating among genetically similar individuals, causing further genetic isolation for individual clusters.

The American marten (*Martes americana*), a small (<2 kg) semi-arboreal species of the family Mustelidae, has been widely reintroduced in North America (Powell et al. 2012). Between 1950 and 2010, at least 10 major translocations involving the release of more than 700 individuals have occurred in Michigan and Wisconsin, USA (Williams et al. 2007). The goal of these translocations was to produce self-sustaining populations that would restore the species to portions of its former range as well as sustain an annual furbearer harvest. As a result, Michigan reinstated a marten trapping season in the Upper Peninsula in 2000 (Frawley 2002). In Wisconsin, however, the marten remains state- and tribe-endangered, and abundance has remained low despite additional releases to augment the populations (Woodford 2010, Manlick et al. 2017).

We used genetic data collected during two time periods separated by 10-15 years to evaluate the genetic success of reintroductions in northern Michigan and Wisconsin, USA. Our specific objectives were to (1) evaluate changes in genetic diversity and structure in marten populations over time, (2) evaluate the role of assortative mating in genetic structure, and (3) evaluate the role of the matrix between reintroduced marten populations in maintaining functional landscape connectivity. We developed the following hypotheses related to each objective. (1) Because marten abundance in Wisconsin has remained low since the initial reintroduction, genetic diversity within populations would decline and genetic structure between populations would increase over time. (2) The landscape situated between the Wisconsin and Michigan populations would serve as a habitat corridor connecting the reintroduced populations. (3) As a result of multiple translocations from several different source populations, assortative mating would be an important factor contributing to lack of genetic diversity and admixture in the region. The evaluation of these hypotheses provides insights into how to maximize the likelihood of success of carnivore reintroduction projects.

5.3 Methods

5.3.1 Study Area

We conducted sampling from north-central Wisconsin, USA, east through the western portion of Michigan's Upper Peninsula (Figure 1). The study area was bounded on the north by Lake Superior, and its southern border represents the southernmost distribution of martens in Wisconsin. The Penokee-Gogebic Range runs east to west through the study area and rises to elevations > 550 m above sea level. This region is primarily forested with both coniferous and deciduous forests common. It contains two national forests (the Chequamegon-Nicolet National Forest and the Ottawa National Forest), one tribal forest (Bad River Tribe), several county forests, one state forest (the American Legion State Forest), and both private industrial and private non-industrial forest. The primary forest types in the region are characterized by northern hardwood communities, lowland conifer communities, and aspen stands (*Populus spp.*). Timber harvest and recreation are both economically important industries in the region.

5.3.2 Sample Collection

We categorized samples into 4 primary populations based on spatial location across two time periods: historic and contemporary. Historic samples included those collected between 2000 and 2004, and contemporary samples included those collected between 2012 and 2016. The 4 locations were the Chequamegon National Forest (CNF), the Nicolet National Forest (NNF), the

Ottawa National Forest (ONF), and Iron County, Wisconsin (IC). We collected samples for each of these groups in both the historic and contemporary time periods. However, due to a lack of samples from the historic period for the IC location, we supplemented this data set with samples collected from 2007 to 2009. For some analyses, we also included samples from individuals translocated from Minnesota (MNT; Minnesota translocate) to the CNF from 2008 to 2010 (Woodford et al. 2013).

Contemporary samples for CNF (2012 – 2014 (Manlick et al. 2017)), NNF (2015 – 2016 (Grauer et al. 2017)), and IC (2014) were collected during winter using non-invasive hair-snare techniques (Pauli et al. 2008, Manlick et al. 2017). Hair snares consisted of a 38 cm long section of 10 cm PVC pipe with wire steel brushes inserted through the center of the cross-section at each end of the pipe. Bait (e.g., beaver (*Castor canadensis*) meat) was then secured inside the snare so that any animal retrieving the bait would necessarily rub against the brushes and leave behind a hair deposit. Using this method, baits were usually completely consumed or removed from the snare, preventing additional captures of martens or other non-target species. In addition to the bait, we also used crayfish oil and Caven’s Gusto Lure (Minnesota Trapline Products, Pennock, MN) as long-distance scent lures. We placed snares in suitable marten habitat along accessible roads and snowmobile trails and revisited them within 1-2 weeks. We then collected hairs from the brushes and stored them in a freezer until DNA extraction. We collected contemporary UP samples from harvested individuals with assistance from local agencies as described by Grauer et al. (2017). All samples except for the contemporary IC samples were included in previously published studies. The IC sample collection followed protocols established through the Purdue Animal Care and Use Committee (Protocol #1309000955) and followed the guidelines established by the American Society of Mammalogists for the use of mammals in research (Sikes et al. 2016).

We obtained historic CNF samples through partnership with the Great Lakes Indian Fish and Wildlife Commission (GLIFWC). Martens were live-trapped on the CNF from 2001 to 2004 in wire box traps (Tomahawk Trap Company, Tomahawk, WI), and blood was collected for DNA extraction (Gilbert et al. 2009). Historic NNF samples collected from 2004 to 2005 were obtained through partnership with the Wisconsin Department of Natural Resources (Woodford et al. 2005). Historic UP samples were obtained through partnership with the Michigan Department of Natural Resources from harvested individuals from 2000 to 2004 (Williams and Scribner 2010).

5.3.3 Laboratory Methods

We performed DNA extraction using DNeasy Tissue Kits (QIAGEN, Inc., Venlo, Netherlands). For all historic samples and the CNF and IC contemporary samples, we genotyped the following 14 microsatellite loci: Gg3, Gg7, Ma1, Ma2, Ma5, Ma7, Ma8, Ma11, Ma14, Ma19, Tt4, Mer022, Mer041, and Mvis072 (Davis and Strobeck 1998, Fleming et al. 1999). For the contemporary NNF and UP samples, we excluded 4 loci that provided little explanatory power based on previous studies: Ma7, Ma8, Ma19, and Mer022 (Grauer et al. 2017). We used the Gg3 locus to screen samples for differentiation between martens, fishers, and mink (Davis and Strobeck 1998, Williams et al. 2009). For PCR and genotyping methods for contemporary IC and CNF samples, see Manlick et al. (2017). For PCR and genotyping methods for contemporary NNF and UP samples, see Grauer et al. (2017). For PCR and genotyping methods for historic samples, see Williams and Scribner (2010).

5.3.4 Data Analysis

To determine differences in genetic diversity and structure between historic and contemporary marten populations, we conducted separate analyses for each of these two time periods. In addition to temporal stratification, we stratified the samples spatially and conducted analyses for four sub-populations from the following spatial locations: the Chequamegon National Forest (CNF), the Nicolet National Forest (NNF), the Ottawa National Forest (ONF), and Iron County, Wisconsin (IC; Figure 1).

Prior to conducting genetic analyses, we used the program Cervus 3.0.7 to identify and censor samples from identical individuals in those data that were collected from hair or scat samples (see Manlick et al. 2017). We used the "gstudio" package (Dyer 2016) in program R (R Core Team 2017) to calculate allelic diversity, allele frequencies, observed and expected heterozygosity, Wright's inbreeding coefficient (F_{IS}; (Wright 1949), and genetic structure (G'_{ST}; (Hedrick 2005). To test for deviation from Hardy Weinberg Equilibrium (HWE) and linkage disequilibrium (LD) among loci, we used the program Genepop (Rousset 2008) and applied the Holm-Bonferroni correction for statistical tests (Holm 1979). For all Genepop analyses, we used a dememorization value of 10,000 and ran 100 batches with 5,000 iterations per batch.

We assessed whether our sampled populations displayed any effects of a population bottleneck. To do this, we used the software Bottleneck v. 1.2.02 (Cornuet and Luikart 1996) to test for excess heterozygosity relative to allelic diversity. We used the Wilcoxon signed-rank test for both the stepwise mutation model (SMM) and the two-phased mutation model (TPM), with 90% of mutations as single-step and the remaining 10% as multi-step (Piry et al. 1999, Williams and Scribner 2010).

To further examine the genetic structure of marten populations, we conducted Principal Components Analysis (PCA) in gstudio and Discriminant Analysis of Principal Components (DAPC) using the R package "adegenet" (Jombart 2008, Jombart et al. 2010). We used DAPC because all populations in the contemporary period had some loci that were out of Hardy-Weinberg equilibrium, and HWE is not a requirement for DAPC. DAPC requires individuals to be grouped into genetic clusters prior to discriminant analysis. We conducted this *a priori* clustering using both spatial and aspatial approaches. For the spatial analysis, we designated clusters based on the spatial location of the sampled individual (Figure 1). For the aspatial analysis, we used a K-means clustering algorithm to determine the optimal number of clusters following a PCA. After initial clustering, we selected the number of principal components to retain for each discriminant analysis via alpha-score optimization. We used cluster membership probabilities resulting from DAPC to evaluate admixture among genetic clusters. We considered any individual with no membership probability ≥0.5 to be admixed.

To assess isolation by distance, we used the 'mantel' function in the R package "vegan" (Oksanen et al. 2013), which returned a Mantel *r* score based on Pearson's correlation. We computed significance values of this score via the permutation of rows and columns in the distance matrices. We conducted this analysis for each population in each time period, as well as for all populations grouped for each time period.

5.4 Results

We incorporated 164 genetic samples from the historic period, and 132 samples from the contemporary period. Allelic richness was higher for all contemporary populations (R_a = 11.86 alleles per locus) than historic populations (R_a = 6.57). However, observed heterozygosity was lower for all contemporary populations, and the inbreeding coefficient was higher. From the contemporary to the historic time period, F_{IS} increased from 0.018 to 0.311. For a complete list of genetic diversity summary statistics, see Table 1.

For historic populations, only one locus from one of the four populations deviated from Hardy-Weinberg equilibrium (ONF; Ma1a). For the contemporary period, all populations had at least 5 loci out of HWE (CNF, 5; IC, 9; ONF, 7; NNF, 9). Historic samples also had two pairs of loci in linkage disequilibrium. However, when each local population was tested, this association was only present in the ONF population. Contemporary samples also had one locus in linkage disequilibrium, but this association was not significant for any of the local populations.

Bottleneck analysis on the aspatial genetic clusters indicated that for the historic populations, 3 of 4 clusters exhibited heterozygote deficiency relative to allelic diversity, but none exhibited heterozygote excess. The one cluster without heterozygote deficiency was made up of individuals primarily from ONF and along with several from NNF. For the contemporary populations, 2 of 4 clusters exhibited significant heterozygote deficiency, while 1 exhibited heterozygote excess, indicating a possible bottleneck (p = 0.0015). Only the contemporary population made up primarily of ONF individuals showed no signs of heterozygote imbalance.

The first two principal components from the PCA that included all samples captured 17.2% of the total variation common among loci (Figure 2). The first principal component loading represented variation in genotype due to the period in which samples were collected. We developed a linear model for PC1 using period as the explanatory variable, and the resulting model explained 62% of the variation in PC1. With the Minnesota translocates removed from analysis, this proportion improved to 69%.

The aspatial K-means clustering algorithm indicated that the optimal number of genetic clusters for both the historic and contemporary time periods was 4 (Figure 3), which matched the number of spatial locations used in the spatial analysis. When we included the Minnesota translocates in the contemporary analysis, the algorithm found no difference in likelihood between 4 or 5 clusters as optimal. As expected, DAPC results for both time periods indicated that individuals in the spatially informed clusters were reassigned to a different cluster more often than the aspatial clusters. For example, the contemporary spatial DAPC reassigned 27 individuals to clusters other than their original spatial location (mean assignment success per population = 0.754), while the aspatial DAPC reassigned 4 individuals (0.973). Probabilities for posterior cluster membership, which are indicative of admixture, were also different across analyses, as aspatial analyses averaged greater membership to clusters than spatial analyses (Table 2; Figure 3). In addition, spatial membership probabilities were higher for historic than contemporary samples (t=4.35, p<0.001), while aspatial membership probabilities were higher for contemporary (t=2.48, p=0.014; Figure 3). Overall, historic samples had one more (5) admixed individual than contemporary samples (4). Following DAPC analyses, we recalculated G'_{ST} for the aspatial populations. As a result of placing individuals in aspatial clusters, G'_{ST} increased from 0.195 to 0.263 for the contemporary populations and decreased from 0.149 to 0.123 for the historic populations.

Across all DAPC analyses a distinct genetic cluster was associated with the ONF population (Figure 3). For the spatially informed analyses, clusters appeared to align well with the previously designated spatial locations. Both historic and contemporary spatial analyses resulted in greater overlap in multi-dimensional space than the aspatial analyses (Figure 3), corresponding with membership probabilities. For the historic aspatial analysis, one cluster is split between ONF and NNF, while the remaining two clusters are split among all 4 spatial locations. For the contemporary aspatial analysis, one cluster aligns well with CNF and NNF, another with CNF and IC, and a third that is split among CNF, IC, and NNF. In evaluating the role of IC as a corridor based on the spatial analysis, 4 CNF and 4 NNF individuals were reassigned to the IC cluster, while 5 IC individuals were reassigned to NNF.

We found evidence for isolation by distance for both historic and contemporary periods, and results suggested that the effects of isolation by distance were stronger for contemporary samples (Table 3, Figure 4). For individual historic populations, only IC displayed significant isolation by distance. For contemporary populations, IC was the only location that failed to exhibit isolation by distance, possibly as a result of recent immigration. For all other populations, the Mantel *r* statistic increased from the historic period to the contemporary period.

5.5 Discussion

Overall, our results support our first hypothesis as genetic diversity (i.e., heterozygosity, inbreeding) appears to be declining moderately and genetic structure increasing over time for all reintroduced populations of American martens that we evaluated. It is unclear exactly what may be causing these shifts in diversity. Genetic drift is likely a contributor, as population size can be a good predictor of genetic diversity (Frankham 1996) and Wisconsin marten population levels have remained low since initial reintroductions (Woodford et al. 2005, Williams et al. 2007). The decline may also be related to the influx of martens translocated to the CNF from 2008 to 2010, during which 90 martens were released. Because the translocated individuals have made little contribution to the resident population in terms of demographics (Manlick et al. 2017), their presence may be artificially inflating values for expected heterozygosity, and therefore inbreeding. However, larger populations (e.g., ONF) that remain genetically distinct from the translocated individuals (Grauer et al. 2017) are experiencing declines in overall genetic diversity as well.

Assortative mating provides one likely explanation for the observed trends in the genetic structure of these reintroduced marten populations. From the 1950s through the 2000s, at least 7 major reintroduction/translocation events took place in the area, with animals sourced from multiple regions including Ontario, CA and Colorado, Michigan, and Minnesota, USA (Williams et al. 2007). Indeed, previous analyses of these reintroductions and resulting populations have found no evidence of admixture among distinct genetic clusters that were closely related to their source populations (Williams and Scribner 2010, Grauer et al. 2017). Our results provide further support that assortative mating is likely driving genetic diversity in the system. In particular, cluster membership probabilities were extremely high for the contemporary populations and have increased since the historic time period. Furthermore, clusters were not tightly linked to the spatial distribution of the sampled populations in either time period. In other words, genetic clusters were dispersed among geographic populations, but membership probabilities remained high even though landscape features do not seem to be preventing movement through the region.

Results from Iron County samples highlight the issue of assortative mating. Most of Iron County, WI is made up of county and private forests that are situated between the three national forests that house the reintroduced marten populations. For these three populations to be genetically connected, Iron County forests would likely need to serve as a habitat corridor for dispersing and resident animals. Although the ONF appears to be genetically isolated from the Iron County martens, our results suggest that Iron County is providing a functional corridor between the CNF and NNF populations, but that little admixture is taking place. The populations seem to be connected geographically, but not genetically. Furthermore, it is not clear how recently movement between populations occurred. Our results show that the historic populations were more inter-dispersed than the contemporary populations. The contemporary results may therefore not be a result of present connectivity, but rather the remaining signature of earlier long-distance dispersal between populations. Such events are often associated with the reintroduction and translocation of carnivores, including martens (Davis 1983, Fritts et al. 1984, Proulx et al. 1994, Spinola et al. 2008, Woodford et al. 2013).

The current status of marten populations in our study area is indicative of the challenges associated with the maintenance of long-term genetic diversity and population viability, which has become a fundamental issue in reintroduction biology. While many reviews have emphasized the value of planning for long-term genetic viability (Sarrazin and Barbault 1996, Jamieson and Lacy 2012, Richardson et al. 2015), long-term genetic studies of reintroduced populations are rarely conducted (Seddon et al. 2007, Taylor et al. 2017). In cases where results have been reported, numerous mechanisms have been hypothesized including having only a few dominant breeders (Koelewijn et al. 2010), inbreeding (Hillman et al. 2017), having sourced from captive or inbred populations (Rhodes and Fike 2008), and assortative mating among populations originating from different sources (Bradley et al. 2014, Slade et al. 2014, Ranke et al. 2017). Effects of these mechanisms can be exacerbated by the fact that most reintroductions comprise relatively few individuals, and reintroduced populations often show signs of a population bottleneck.

Currently, the Michigan marten populations show no signs of a bottleneck (Williams and Scribner 2010), though some loci from Wisconsin populations do. Wisconsin population sizes have also remained relatively small, which Armstrong and Seddon (2008) have pointed out may necessitate continued management toward population persistence. However, any continued management in Wisconsin would require a delicate balance between adding more individuals that would not compound the problem of assortative mating, but would also introduce genetic diversity. This was the goal of the recent 2008 translocation, yet the result has not been able to counteract the effects of drift and assortative mating. Probably most important, however, is that the genetics of the reintroduced marten populations continue to be monitored. While some results (e.g., heterozygosity, allelic richness) are not yet alarming, the trajectories indicate overall declines in genetic diversity and increases in fine-scale genetic structure. Without continued monitoring, managers will be unable to make informed decisions about the future of martens in the region.

5.6 Acknowledgments

We thank the Great Lakes Indian Fish and Wildlife Commission and the Department of Forestry and Natural Resources at Purdue University for providing funding and logistical support for this study. We thank the University of Wisconsin-Madison, Michigan State University, the Chequamegon-Nicolet National Forest, the Wisconsin Department of Natural Resources, and the Michigan Department of Natural Resources for providing genetic samples and data sets. We thank Zach Wilson for his genetic sample contributions and for his invaluable knowledge of local marten ecology. We also thank The McIntire-Stennis Cooperative Forestry Research Program for their financial.

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5.8 Tables

Table 5.1: Statistics summarizing the genetic diversity and population structure of American martens in northern Wisconsin and the western Upper Peninsula of Michigan, USA. Historic samples were collected between 2000 and 2005 and contemporary samples were collected between 2012 and 2016. The translocation of animals from Minnesota to CNF occurred from 2008 to 2010. CNF = Chequamegon National Forest; IC = Iron County, WI; ONF = Ottawa National Forest; MNT = martens translocated from Minnesota to the CNF; NNF = Nicolet National Forest.

Location	Period	N	R_a	F_{IS}	Ho	He	G'_{ST}
CNF	Historic	27	4.86	-0.0753	0.588	0.547	
CNF	Contemporary	30	7.43	0.176	0.545	0.661	
IC	Historic	15	4.43	-0.0664	0.450	0.638	
IC	Contemporary	21	5.71	0.436	0.360	0.676	
ONF	Historic	90	6.07	-0.0127	0.620	0.613	
ONF	Contemporary	41	8.8	0.134	0.558	0.608	
Nicolet	Historic	32	5.07	0.0103	0.602	0.608	
Nicolet	Contemporary	40	10.2	0.323	0.539	0.855	
MNT	Translocation	68	6.71	0.111	0.551	0.621	
All	Contemporary	132	11.86	0.311	0.512	0.748	0.195
All	Historic	164	6.57	0.0178	0.608	0.619	0.149
All		365	12.21				

Table 5.2: Mean (± standard deviation) membership probabilities of individual American martens to genetic clusters derived through discriminant analysis of principal components. Spatial analyses included spatial location information prior to DACP, whereas aspatial analyses did not. Results from t tests are also displayed comparing membership probabilities between spatial and aspatial analyses for each time period. Historic data represent genetic samples collected from martens between 2000 and 2005, and contemporary samples were collected between 2012 and 2016.

Analysis	Period	$\bar{x}$	*SD*	*t*	*p*
Spatial	Historic	0.865	0.155		
Aspatial	Historic	0.907	0.137	2.60	0.001
Spatial	Contemporary	0.780	0.176		
Aspatial	Contemporary	0.946	0.132	8.67	<0.001
Spatial	All	0.827	0.169		
Aspatial	All	0.924	0.136	7.69	<0.001

Table 5.3: Isolation by distance as evaluated by a simple Mantel test using Pearson's correlation coefficient to compare physical distance matrices with genetic distance matrices. Genetic distance was calculated using the distance metric from analysis of molecular variance (AMOVA). The significance of the statistic was determined by permuting rows and columns of the two matrices. All samples were collected from American martens in Wisconsin and the Michigan Upper Peninsula. Historic samples were collected between 2000 and 2005, and contemporary samples were collected between 2012 and 2016. CNF = Chequamegon National Forest; IC = Iron County, WI; ONF = Ottawa National Forest; MNT = martens translocated from Minnesota to the CNF; NNF = Nicolet National Forest.

Location	Period	*N*	Mantel *r*	*p*
CNF	Historic	27	0.086	0.213
CNF	Contemporary	30	0.106	0.057
IC	Historic	15	0.404	0.009
IC	Contemporary	21	0.175	0.115
ONF	Historic	90	0.066	0.158
ONF	Contemporary	41	0.457	<0.001
Nicolet	Historic	32	0.104	0.092
Nicolet	Contemporary	40	0.233	0.020
All	Historic	164	0.134	0.002
All	Contemporary	132	0.233	<0.001

5.9 Figures

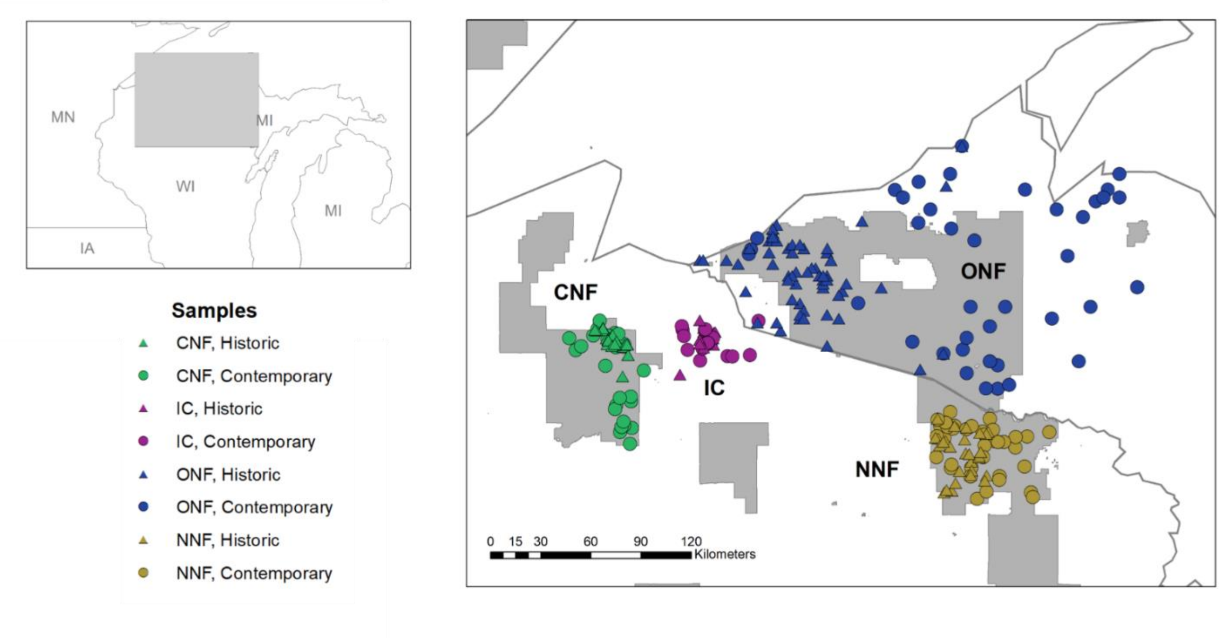


Figure 5.1: Study area and locations of American martens sampled in Wisconsin and Michigan, USA. Historic samples were collected between 2000 and 2005, and contemporary samples were collected between 2012 and 2016.

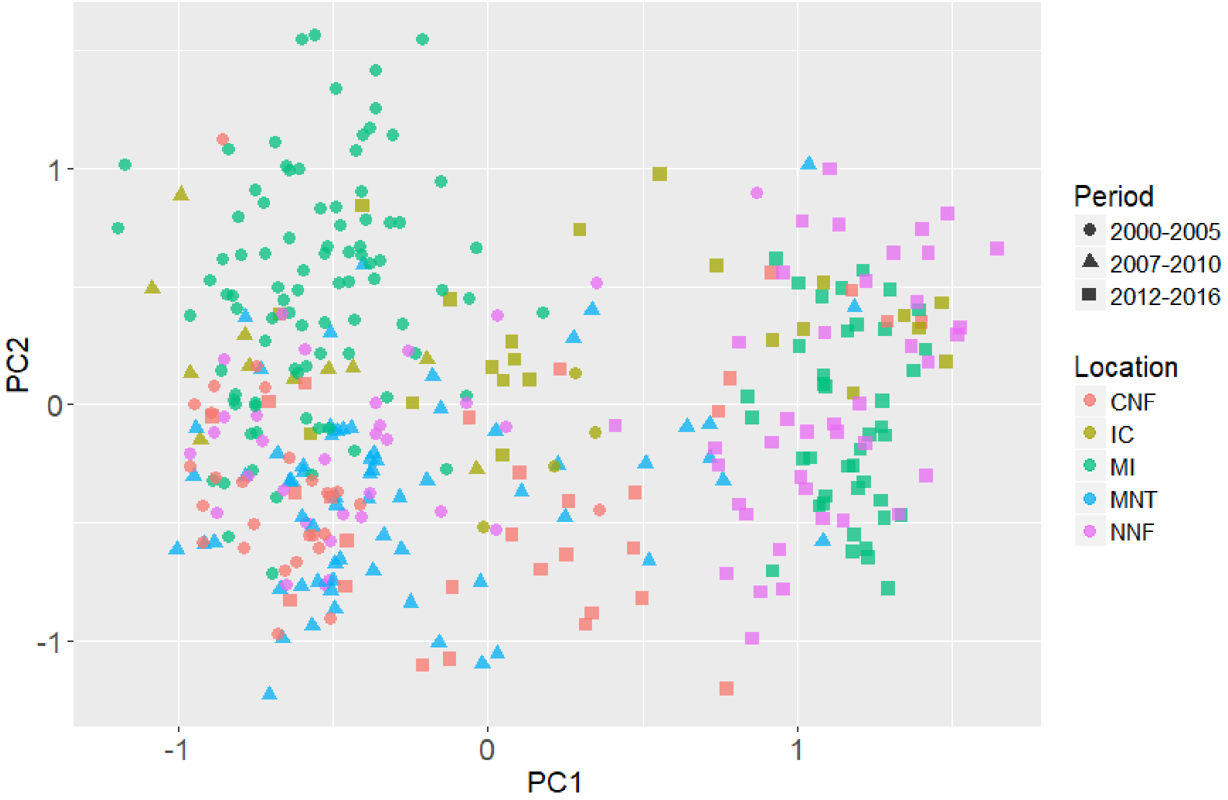
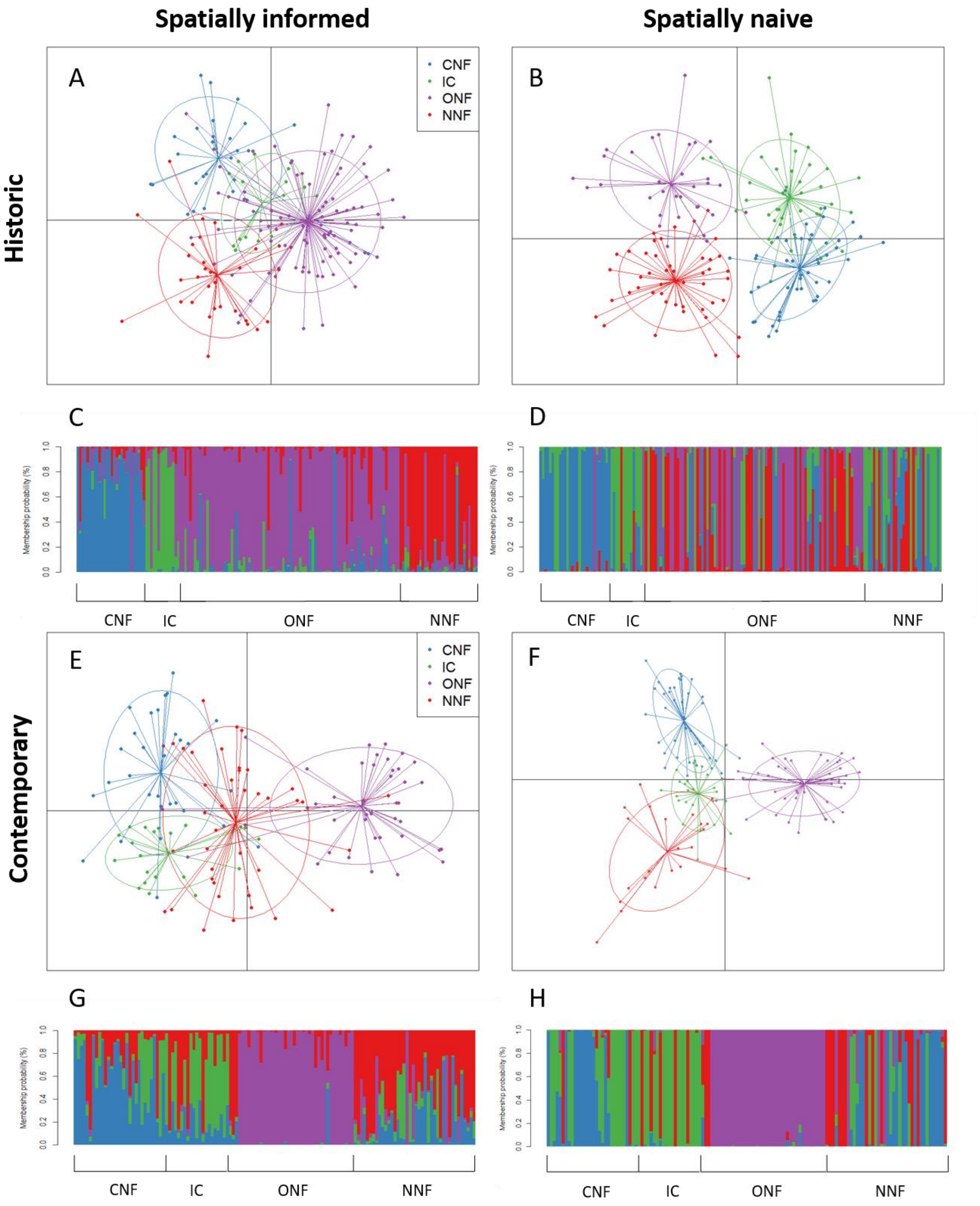


Figure 5.2: Results from a principal components analysis of genetic scores from American martens in northern Wisconsin and the Upper Peninsula of Michigan over time. CNF = Chequamegon National Forest; IC = Iron County, WI; ONF = Ottawa National Forest; MNT = martens translocated from Minnesota to the CNF; NNF = Nicolet National Forest.

Figure 5.3: Results of discriminant analysis of principal components (DAPC) conducted on genetic samples from American martens in northern Wisconsin and the Upper Peninsula of Michigan. Independent results are displayed for samples collected during the historic period (2000 – 2005; panels A through D) and the contemporary period (2012 – 2016; panels E through H). Clustering prior to DAPC was done both spatially (i.e., informed by spatial location; left column) and aspatially (i.e., informed by K-means clustering; right column). CNF = Chequamegon National Forest; IC = Iron County, WI; ONF = Ottawa National Forest; NNF = Nicolet National Forest.


Spatially informed
Spatially naive
Historic
Contemporary
A
B
CNF
IC
ONF
NNF
C
D
Membership probability (%)
0.0
0.2
0.4
0.6
0.8
1.0
CNF
IC
ONF
NNF
E
F
G
H
CNF
IC
ONF
NNF

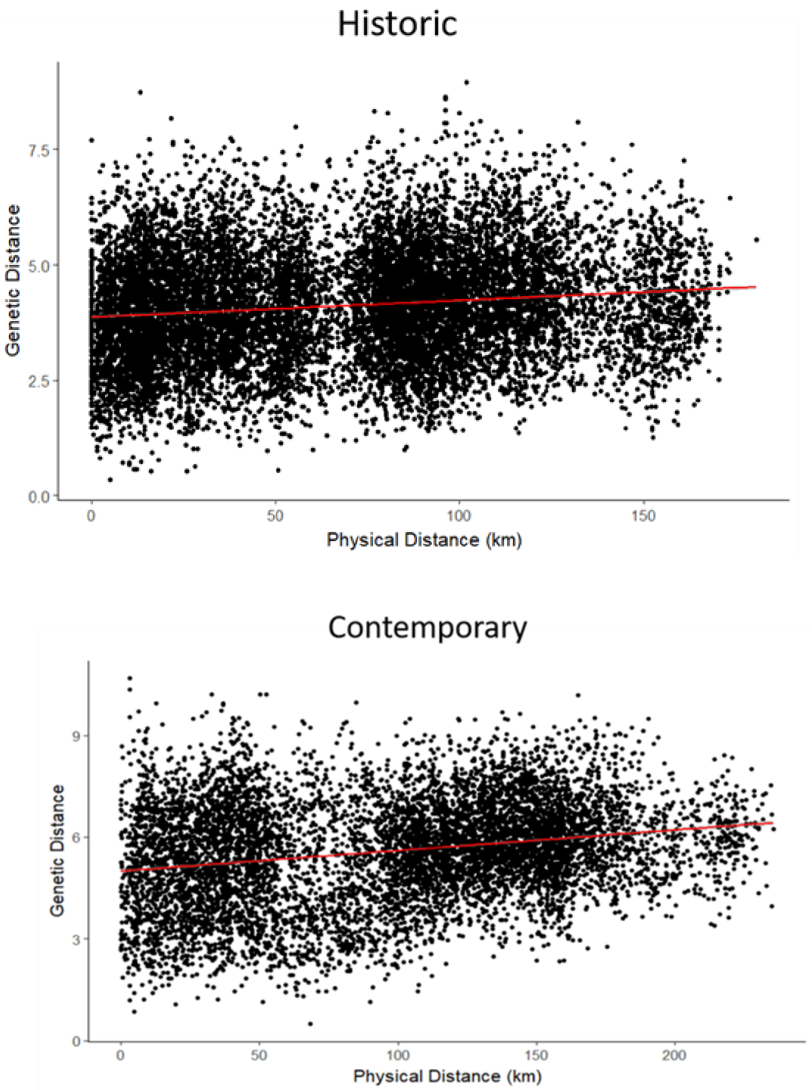


Figure 5.4: Isolation by distance results for samples collected from American martens during historic (2000 – 2005) and contemporary (2012 – 2016) time periods. Samples were collected from the Chequamegon National Forest, Nicolet National Forest, and Iron County in Wisconsin, and from the Ottawa National Forest and surrounding lands in the Upper Peninsula of Michigan. Both time periods displayed effects of isolation by distance, but the Mantel score for the contemporary period (Mantel $r = 0.233$, $p < 0.001$) was greater than the Mantel score for the historic period (Mantel $r = 0.134$, $p = 0.002$).