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RESEARCH ARTICLE

Integrating mechanistic models of landscape change and animal behavior to measure functional connectivity

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Abstract

Context As land-use change and climate change transform landscapes globally, increases in habitat fragmentation and shifts in habitat composition present challenges for the conservation of wildlife. Behavioral approaches to landscape ecology can explore how animal movement across complex landscapes can drive ecological processes like functional connectivity. By integrating mechanisms that link landscape change to animal behavior, simulation models can project how individuals and populations will respond to novel landscapes.

Objectives To understand how dispersal behavior and functional connectivity between populations of American martens respond to changes to the landscape due to land-use and climate. We also seek to demonstrate the explanatory power of integrating mechanistic models of landscape transformation and animal dispersal.

Methods We present a novel investigation of 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).

Results Climate change caused an increase in suitable cover types for martens, but forest diversity is likely to decline. Both land-use and climate change impacted dispersal behavior of martens and functional connectivity between populations. These effects were not consistent across simulations, as dispersal behavior and success were affected by the direction of dispersal (i.e., source population) due to asymmetry in landscape configuration and its interaction with climate and land-use change.

Conclusions This study demonstrates how the integration of behavioral and landscape models can inform conservation in ways that classical modeling cannot and how the use of mechanistic simulation models can produce robust projections about species responses to novel conservation challenges in an uncertain future.

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Keywords American marten · Animal dispersal · Climate change · Functional landscape connectivity · Land use change · Individual-based model

Introduction

Dispersal capacity is integral to the ability of wildlife species to respond to changes in habitat suitability induced by climate change (Pauchard et al. 2016), yet land-use change might impede dispersal and limit species' ability to cope with climate change (Opdam and Wascher 2004; Tucker et al. 2018). Dispersal is also required for populations to maintain connectivity, which is necessary for long-term genetic diversity (Allendorf 1986) and the spread of climate-adaptive alleles (Senner et al. 2018). Connectivity may also be affected by indirect effects of climate change, such as changes in habitat composition or prey availability. To conserve rare or threatened species, conservation planners account for the effects of land-use change and climate change on animal dispersal not only as a means to keep pace with climate, but to maintain connectivity among populations and with climate refugia (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. Approaches are various and include projections of land-use transformation (Tayyebi et al. 2013; Sohl et al. 2014), range shifts in response to climate change (Hargrove et al. 2014; Peters et al. 2020; Potter et al. 2010), process-based simulations of forest succession (Scheller and Mladenoff 2008; Zollner et al. 2008; Thompson et al. 2011; White et al. 2022), and climate envelopes (Hijmans and Graham 2006; McCain and Colwell 2011; Fernandes et al. 2020). Many of these modeling approaches include effects of climate change and/or land-use change on biotic communities from food webs to habitat relationships. However, when considering responses of wildlife to such changes as those to climate and land-use, landscape-scale models tend to omit the role of animal behavior and behavioral plasticity as mechanisms that drive eco-evolutionary processes like population connectivity and adaptation (Muñoz et al. 2015; Hermes et al. 2018; Bocedi et al. 2021). The ability to simulate these processes is needed, as landscape transformation affects the dispersal capabilities of wildlife population's worldwide (Tucker et al. 2018).

The interaction of climate change 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). Potential impacts on behavior such as those driven by changes in landscape composition should not be overlooked when assessing threats to the conservation of rare or threatened species. While behavioral plasticity has been widely documented as a mechanism for species to cope with environmental change, (Berger-Tal et al. 2016) 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 plasticity (Snell-Rood 2013; Beever et al. 2017), and then incorporate those mechanisms (e.g., changes to phenology, microhabitat use, foraging habits) into behaviorally explicit simulation models to reproduce or predict behavioral responses to specific environmental changes (Bocedi et al. 2014; Santini et al. 2016; Schumaker and Brookes 2018). Such models have mostly been applied to answer questions about shifts in species distributions (Brooker et al. 2007; Synes et al. 2015; Santini et al. 2016) rather than connectivity.

We combined a landscape-level simulation model of forest succession (LANDIS; Scheller et al. 2007) with an individual-based model of animal dispersal (SEARCH; Pauli et al. 2013a, b) to evaluate how land-use change and climate change would affect the dispersal and functional landscape connectivity of endangered populations of American martens (*Martes americana;* hereafter martens). We define functional connectivity in terms of the degree to which the landscape facilitates or impedes movement, with consideration for travel costs such as energy use and mortality risk (Belisle 2005). In our study system (Upper Michigan and Wisconsin USA), martens have been repeatedly reintroduced since the 1950s, yet martens remain endangered in Wisconsin (Williams et al. 2007). Functional connectivity and population isolation may play a key role in this slow recovery, as immigration, recruitment, and assortative mating may all contribute to a lack of population growth (Howell et al. 2016; Grauer et al. 2017; Manlick et al. 2017a; Day et al. 2022). These factors may also be interacting with other factors such as inter-specific competition and lack of food availability to limit population connectivity in the region (Carlson et al. 2014; Manlick et al. 2017b; Day et al. 2021). If marten populations in Wisconsin are to persist, understanding how they are likely to respond to land-use change and climate change will be necessary to plan for their conservation. Empirically driven, mechanistic simulation modeling can contribute to the study of such questions because it provides a virtual environment in which to simulate future conditions, test alternative future landscapes, and investigate the consequences of uncertainty in future landscape conditions.

Our goal was to evaluate the behavioral response of martens to landscape transformation as a result of land-use and climate change using a combination of mechanistic simulation modeling approaches. Specifically, we used LANDIS-II (hereafter LANDIS) to simulate forest succession dynamics to project landscape characteristics that are relevant to marten ecology under alternative carbon emissions scenarios. We then used outputs from LANDIS as inputs to an individual-based model (SEARCH) to simulate 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.

Methods

Study system

The study was conducted in territory ceded by the Ojibwe tribes in the treaty of 1842 in northern Wisconsin and the Upper Peninsula of Michigan, USA (Fig. 1). The area is mostly forested but also includes two towns with a population greater than 1,000. Forests in the region are a sub-boreal mixture of deciduous and conifer species. The study area is primarily deciduous forest (53.0% of forested area) interspersed with conifer (7.3%) and mixed (15.7%) stands and is dominated by quaking aspen (*Populus tremuloides*) and the northern hardwood community (e.g., sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*)), although conifers are found in many stands. Roughly one third of the landscape is wetland, most of which is forested with lowland coniferous or lowland hardwood 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, tribal forest, and private industrial and non-industrial forests (Fig. 1).

Martens in the study area require complex forests with vertical structure (Dumyahn et al. 2007; Gilbert et al. 2017). To parameterize habitat suitability inputs for our simulation model, we followed the home-range level habitat selection model of Wright (1999) and Dumyahn et al. (2007) that reported martens selecting for northern hardwoods and sawlog 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). A typical home-range in the study area was composed of at least 70% non-avoided (i.e., either neutral or selected for) habitat types. We note here that this model of habitat selection was developed in the context of present habitat and not with a focus on how this habitat might be affected by future climate change or land-use change.

The goal of the simulations is to evaluate the functional connectivity of a forested corridor that separates reintroduced populations of martens that occupy the east and west end of the corridor, respectively. On the east side of the corridor, the Michigan population has grown large enough to sustain an annual marten trapping season while the Wisconsin population in the west remains state-endangered. The forested habitat in between the two populations is Iron County, WI, which provides the best opportunity for connecting the two populations along the Penokee mountain range. Within the corridor, an asymmetry in landscape configuration 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 developments associated with private lands (Day et al. 2020). Our simulations evaluate functional connectivity across this corridor under alternative scenarios of land-use change and climate change.

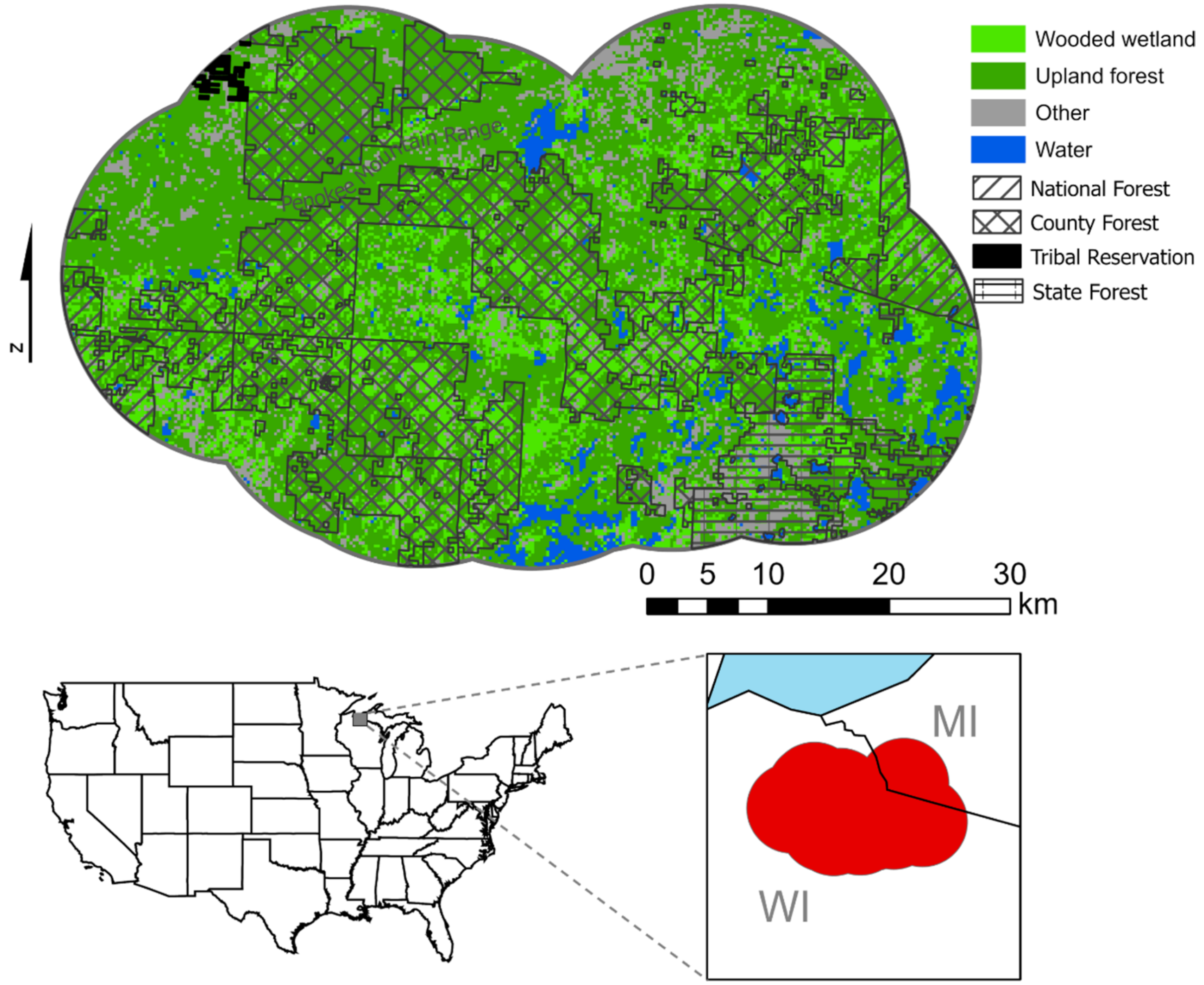

Fig. 1 Patterns of ownership and landcover type within the spatial extent of a simulation study of forest succession and American marten dispersal behavior under alternative climate and land-use change scenarios in the Upper Midwest, USA. The red polygon indicates the forested corridor between the regions where martens were historically introduced from the 1950s to the 2010s in adjacent national forests (Williams et al. 2007)

Study design

This study was carried out in two steps: simulation of forest succession under alternative scenarios of carbon emissions using LANDIS, and simulation of marten dispersal and home-range establishment using the SEARCH modeling framework, informed by outputs of forest composition from the LANDIS simulations and projections of land use change (Sohl et al. 2014). See Fig. 2 for a conceptual framework of the simulation study design.

First, we evaluated forest response to three alternative scenarios of carbon emissions: historical, moderate, and high. To evaluate landscape response to these scenarios, we selected five response variables that were both representative of the effects of climate change on forested habitat and forest diversity, and relevant to marten habitat for both dispersal and home-range establishment. These response variables included (1) total forested biomass, (2) total number of species-age cohorts, (3) species richness per forested cell, (4) age richness per forested cell, and (5) proportion of cover types considered to be non-avoided by martens. Resulting landscapes were converted into habitat suitability maps for the dispersal simulations within SEARCH.

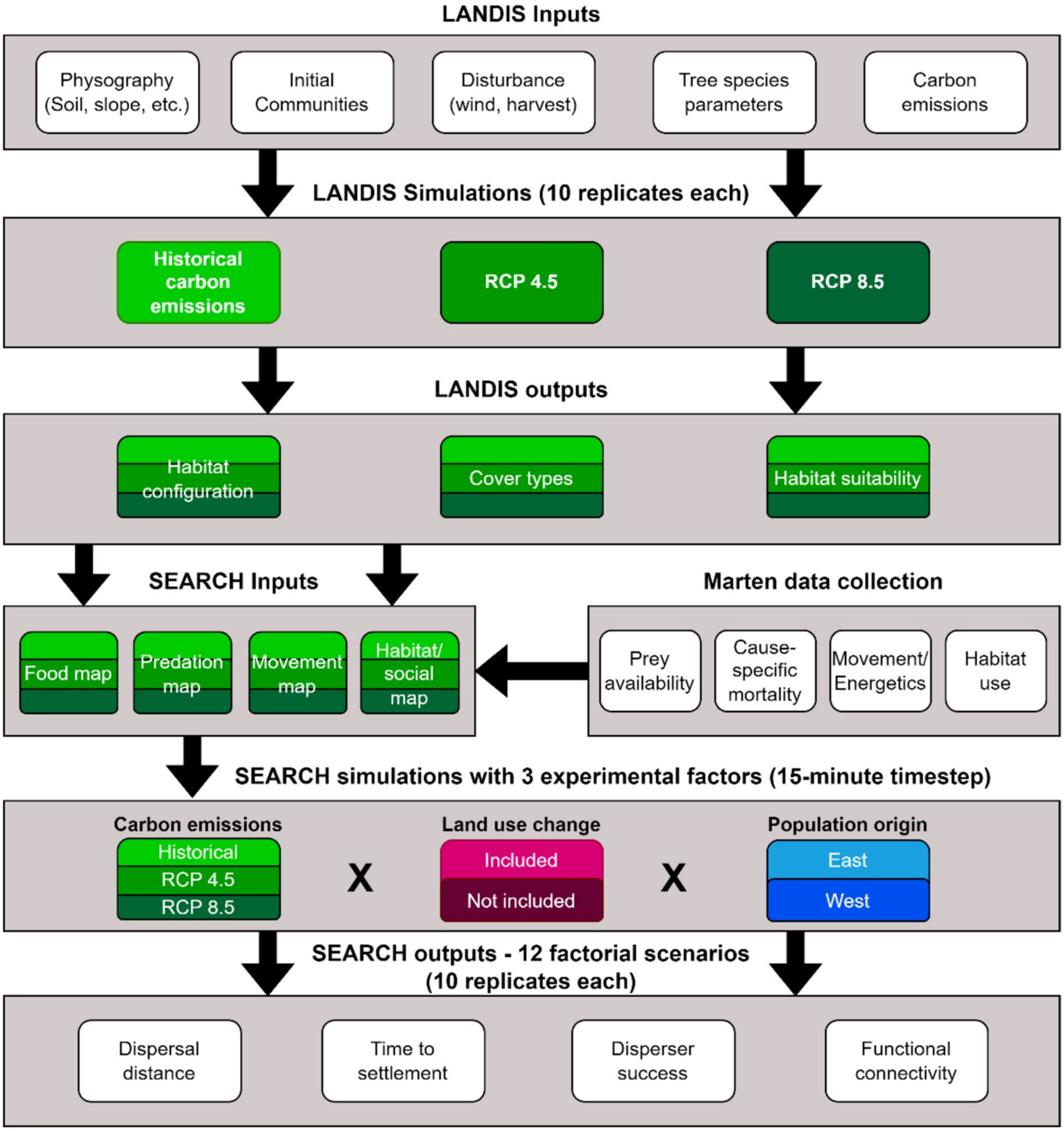

Fig. 2 Flowchart of the overall study design of the integration of a model of forest succession (LANDIS) and a model of American marten dispersal (SEARCH) in northeastern Wisconsin, USA. LANDIS outputs were used as inputs for the SEARCH modeling. Each simulation was run with 10 replicates across all factorial combinations of experimental factors for a total of 30 LANDIS simulations and 120 SEARCH simulations

For animal dispersal modeling, we implemented a factorial simulation experiment across three factors: (1) carbon emissions (historical, moderate, high) as implemented in LANDIS, (2) land use change (present/absent), and (3) source population (east/west). We replicated each of the 12 unique combinations of factors within SEARCH (i.e., model scenarios) 10 times, for a total of 120 simulation runs. Outputs from 10 LANDIS runs per carbon emissions scenario were used to provide unique landscape inputs for each of the 10 SEARCH replicates. For each combination of model scenario and replicate, we simulated 5 generations of dispersers, with each generation producing 10 new dispersers for a total of 50 dispersal events per replicate (6000 dispersal events total). For the source population factor, we simulated dispersing animals originating from the Michigan population (east) or from the Wisconsin population (west). This allowed us to evaluate the effects of directional asymmetry in dispersal due to landscape configuration on landscape connectivity (Day et al. 2020), as well as any interactive effects between source population and other experimental factors. We evaluated each factor's effect on functional connectivity between the two populations, as well as effects on local dispersal metrics including dispersal distance, time to settlement, and probability of successful home-range establishment.

We conducted SEARCH simulations on all three carbon emissions scenarios: historical, moderate (Representative Concentration Pathway (RCP) 4.5), and high (RCP 8.5 (IPCC 2013)). We converted the LANDIS species-age cohort output at year 100 to cover types and size classes that matched those of a local model of marten habitat suitability (Wright 1999; Dumyahn et al. 2007) using the reclass extension in LANDIS (Scheller and Mladenoff 2004). This allowed us, for example, to spatially delineate the simulated landscapes in terms of marten habitat selection (i.e., selected, avoided, or non-avoided) or food availability. In this way, we used the results from LANDIS describing cover type and tree size to generate spatial input layers for the SEARCH model (described below).

For the land-use change treatment (Fig. 3), we produced two complete sets of inputs for each carbon emission scenario to be implemented in the SEARCH model. One set was based on a temporally static landscape (i.e., no land-use change over time), and another set incorporated land-use change for the region projected out to the year 2100 (Sohl et al. 2014; Fig. 3). The primary changes in land-use that affected the SEARCH maps included forested habitat converted to pasture, agriculture, or urban areas. Below, we provide details for parameterization and development of the LANDIS simulations, followed by the SEARCH simulations.

Simulating landscape dynamics

We used the LANDIS (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 is a raster-based, spatially explicit modeling framework that simulates processes of forest succession (growth, mortality, regeneration,

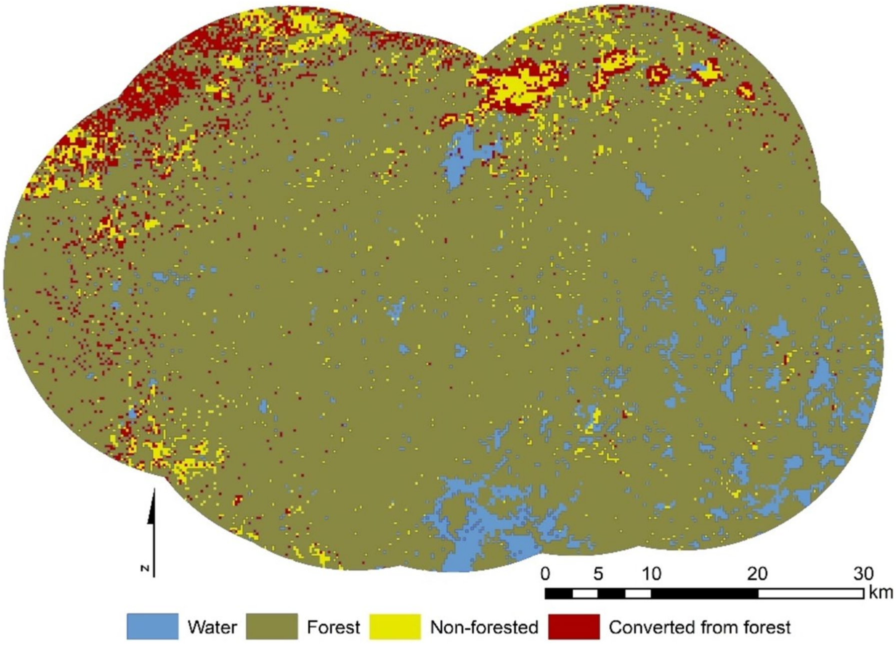

Fig. 3 Land-use change projections from the United States Geological Survey (Sohl et al. 2014) comparing land-use between the years 2006 and 2100. Yellow polygons indicate non-forested areas in 2006, and red polygons indicate projections of forest conversion to urban areas, agriculture, and pasture by the year 2100

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; Gustafson et al. 2023) 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 (seed dispersal and contagious disturbances) 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 the methodology from Day et al. (2020), buffering known marten locations from the study area by 14 km, equal to the mean dispersal distance of martens translocated to the study area 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 (4439 sq km), divided into 90×90 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 disturbances 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 and associated increases in atmospheric CO2 (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 from 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).

Initial communities—To create a base map of initial forest cover we used publicly available land cover data sets (WDNR 2016; MDNR 2001) in combination with the Landscape Builder software (Dijak 2013) and Forest Inventory Analysis Database (FIA; Miles et al. 2001). We selected 19 tree species (Table 1) for simulation (Scheller and Mladenoff 2005; Dumyahn et al. 2007) and produced a set of species-age cohorts for each included FIA plot. These communities were then randomly assigned to matching cover types across the landscape (Table 2), and this process was repeated 10 times to produce 10 landscape replicates. For more information on how initial communities were created, see Appendix S1.

Physiographic regions—We defined ecoregions in the study area based on soil type, soil depth, and slope using data available from the Soil Survey Geographic Database (SSURGO; Soil Survey Staff 2017) available from the USGS Geo Data Portal (https://cida.usgs.gov/gdp/). We assigned a unique ecoregion type to each combination of soil type, depth, and slope, for a total of 38 ecoregions. For more detail on how these physiographic regions were developed, see Appendix S1.

Carbon emissions and climate—We derived future climate scenarios (minimum and maximum temperature and precipitation) from a single Global Climate Model (GCM, GFDL-ESM2G; Delworth et al. 2006) using two Representative Concentration Pathways (RCP 4.5, 8.5) from the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC 2013). We also incorporated monthly solar irradiation (Kittel et al. 2000) and atmospheric CO2 concentrations (Meinhausen et al. 2011). We simulated a historical climate and carbon emissions scenario based on 50 years of monthly weather data from 1950 through 1999 (Daly and Gibson 2002) and annual values of atmospheric CO2 (Institute for Atmospheric and Climate Science, http://www.iac.ethz.ch). For additional detail, see Appendix S1.

Disturbance—To simulate timber harvest on the landscape, we obtained copies of forest management plans from six management agencies representing each county, state, and national forest within the study area. We then developed harvest prescriptions for each of the six management agencies, and target

Table 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	Longevity age (years)	Age at maturity (years)	HalfSat (µmol/ m2/ sec)	Effective seed dispersal (m)
Abies balsamea	0.9	225	0.25	150	25	105	30
Acer rubrum	2.2	60	1	200	10	111	100
Acer saccharum	2.1	47	1	300	40	105	100
Betula alleghaniensis	2.2	50	1	300	40	105	100
Betula papyrifera	2.4	75	1	130	20	100	200
Fraxinus americana	2.5	60	1	200	30	111	70
Fraxinus nigra	2.6	65	1	150	20	100	100
Larix laricina	2.7	60	1	180	35	105	50
Picea glauca	1.1	225	0.25	200	25	111	30
Picea mariana	1	200	0.25	200	30	111	80
Pinus banksiana	1.3	245	0.3333	100	10	118	30
Pinus resinosa	1.5	230	0.3333	250	25	118	12
Pinus strobus	1.8	220	0.5	300	40	111	30
Populus tremuloides	2.5	85	1	90	15	100	500
Prunus serotina	2.5	70	1	150	30	111	30
Quercus rubrum	2.6	60	1	200	25	111	30
Thuja occidentalis	1	130	0.5	400	30	111	45
Tilia americana	2.5	50	1	200	30	111	30
Tsuga canadensis	1.4	105	0.3333	450	30	105	30

LMA Leaf Mass Area, *HalfSat* regulates shade tolerance and indicates half saturation intensity of radiation for photosynthesis (De Bruijn 2014)

Table 2 Species groupings and corresponding model of habitat selection by American martens, reproduced from Wright (1999) and Dumyahn et al. (2007)

Cover type	Species	Selected	Avoided	Neutral
Aspen	*Betula papyrifera*, *Populus tremuloides,*	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	*Larix laricina*, *Picea mariana*, *Thuja occidentalis*	–	All	–
Upland conifer	*Abies balsamea*, *Picea glauca*, *Tsuga canadensis*	–	–	All
Pine	*Pinus banksiana*, *Pinus resinosa*, *Pinus strobus*	–	–	All

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)

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

cutting acreages for each prescription based on past and projected timber harvest activity (Table 3). 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

Table 3 Harvest regime implemented in LANDIS-II modeling of forest succession in the Upper Midwest, USA under alternative climate scenarios

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
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

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

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 in each 10-year time step, 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 for the forest type and time step 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 produce a linear pattern, 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).

Animal dispersal model

American martens are solitary, territorial carnivores that display sexually dimorphic patterns of juvenile dispersal and average home range size (males = 4.3 km^2, females = 2.3 km^2) within the study area (Dumyahn et al. 2007). To simulate marten dispersal across the Iron County habitat corridor, we built upon previous applications of the SEARCH modeling framework (Spatially Explicit Animal Response to Composition of Habitat) implemented for the same region and species (Day et al. 2019, 2020). Dispersal behavior in the original model was calibrated using pattern-oriented modeling to match dispersal patterns of actual martens from translocations on the CNNF in 2010 (Woodford et al. 2013). These patterns included, for example, dispersal distance mean (13.9 km) and standard deviation (13.2 km), mean days to home-range establishment (37.3 days), and disperser mortality rate (0.17). Following, we describe the general processes and key parameters of our SEARCH application. For a full ODD description (Overview, Design, 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 an individual of the same sex. To initialize our SEARCH runs, we first simulated the establishment of marten home-ranges on the study area for each combination of landscape replicate (10 per carbon emissions scenario output by LANDIS), carbon emissions scenario, and land-use scenario to generate a map of existing resident home-ranges (Day et al. 2019). To do this, we simulated the release of virtual martens reflecting the 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 maps of resident home-ranges were used as the initial marten occupancy map for each combination of experimental factors simulated by SEARCH (Fig. 2).

SEARCH simulates the fine-scale animal dispersal and home-range establishment or mortality of individual animals across spatially explicit landscapes. During dispersal in SEARCH, martens made decisions at 15-min time steps, responding to their location within four independent, vector-based maps that defined habitat suitability and availability, movement, food availability, and predation risk (See Figure S1 for an example of each map type). For each combination of landscape scenario and replicate, we created a unique set of these four maps derived from the LANDIS output. Generation of the spatial configuration of these maps was based on landscape characteristics associated with cover type and tree size classes derived from cohort age and biomass in LANDIS (Day et al. 2019, 2020). For the habitat suitability map, we converted LANDIS output to a binary layer of avoided and non-avoided cover types (Table 2). 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 (Ward 1987). This mechanism allowed individuals to settle for progressively lower habitat quality when population density was high or to mitigate potential failure to locate and establish a home-range (Day et al. 2019).

Map layers defining disperser movement behavior, food availability, and predation risk all varied by cover type and followed previous applications of the marten SEARCH model (Day et al. 2019, 2020). The movement map was generated with values derived from a snow-trailing study near the simulation extent (McCann et al. 2014), including sex-specific values for distance moved per time step, mean turning angle per time step, and probability of crossing between cover types. Perceptual distance, or the radius of the area that an individual was able to perceive the suitability of surrounding habitat, was 100 m for all cover types (Gardner and Gustafson 2004). Food availability, or species-specific probabilities of prey capture per time step, were derived from the snow-trailing study (McCann et al. 2014). Successful prey capture provided energy reserves for dispersing martens (Gilbert et al. 2009), and failure to maintain energy reserves resulted in starvation. Predation risk similarly varied by cover type, and probability of mortality per time step was derived from a study of mortality of dispersing martens (Davis 1983) combined with relative abundance of predators (i.e., fishers [*Pekania pennanti*] and owls; McCann et al. 2014, PAZ unpublished data).

Disperser movement while searching for suitable home-range locations was simulated by a correlated random walk at 15-min time steps. Based on previous simulations calibrating SEARCH behavior to empirical data (Day et al. 2019), simulated martens were required to undergo a two-week exploration phase prior to being allowed to establish a home-range. As dispersing martens moved through the simulated landscape, they maintained a memory map of habitat suitability for the areas they visited. The extent of the memory map was a function of perceptual range, or the distance from an individual's location at which they are capable of perceiving suitable habitat. As potentially suitable home-range locations were encountered, dispersers added them to a list of potentially suitable home-range locations in their memory. If sufficient suitable habitat was observed following the 2–week exploration phase, 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 available suitable habitat was insufficient for home-range establishment, the marten either reoriented toward the next site on the list, or (if no more sites were stored in memory) returned to searching for new suitable home-range locations. This pattern of searching for a suitable home-range continued until either settlement was achieved or 60 days passed, at which point the individual suffered mortality. Successful dispersers produced a single offspring that then dispersed the following year, repeating the cycle of dispersal for up to five generations per combination of LANDIS replicate and landscape scenario.

Data analysis

Forest composition—To evaluate landscape response to the alternative scenarios of carbon emissions (LANDIS output), we conducted analysis of variance for each of the five response variables (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 response variables to provide a visual representation of trends over time for each carbon emissions scenario.

Local dispersal—To evaluate marten behavioral responses to the carbon emissions and land-use change treatments (SEARCH output), we measured three variables associated with marten dispersal in the simulations. These three response variables—straight-line dispersal distance, time from release until home-range establishment, and proportion of dispersers that were successful (i.e., survived and established a home-range)—were local dispersal metrics that were not considered indicative of functional connectivity per se, but provide information about how factors affecting all dispersal behavior differ from those affecting behavior that are indicative of functional connectivity (Day et al. 2020).

To evaluate the role of the experimental factors on these local dispersal outcomes, we developed a set of general linear models (GLMs), evaluated using Akaike's Information Criterion (AIC) in an information theoretic approach (Akaike 1974; Burnham and Anderson 2002). 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 factors, we developed a new GLM to test for interactions among variables and compared the resulting AIC value to the best additive model. 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 response variable.

Functional connectivity—We compared functional connectivity across landscape scenarios based on outputs of the simulated dispersal behavior of the individuals in the SEARCH model using machine learning analyses. To measure functional connectivity, we developed a metric to evaluate landscape effects following the method from Day et al. (2020). This metric was a measure of net directional displacement of an individual from the original release site, expressed as a fraction of the distance traversed between the two population origins. For example, if an individual originating in the east established a home-range in the western release area, the landscape received a connectivity value of 1. An individual that settled halfway between the two release sites would contribute a connectivity value of 0.5. This metric assumes that greater movement between populations in the controlled simulation environment is an indicator of functional connectivity of the landscape, accounting for both the structural elements of the landscape and the travel costs incurred by the landscape (Belisle 2005; Day et al. 2020).

Because long-distance dispersal events are often critical to maintaining connectivity between populations, we followed Day et al. (2020) and examined four percentile subsets of the functional connectivity metric based on those individuals that had traveled furthest in the direction of the population opposite their source population. These included all individuals above the 0th (all data included), 75th, 90th, and 95th percentiles. The larger the percentile, the further that individuals included in the analysis traveled across the landscape between populations. In this way, we evaluated the relative influence of each experimental factor on the subsets of individuals that contributed most to population connectivity while omitting those with strong site fidelity. To describe the relationship between each factor and the connectivity metric, we used the "rpart" package in Program R to conduct ordinary regression tree analyses (R Core Team 2017; Therneau et al. 2017). Pruning of regression trees was conducted by limiting the number of splits in a tree such that the cross-validated error was <0.01. Because regression trees can be subject to overfitting, we also used the R package "dismo" (Hijmans et al. 2021) to conduct boosted regression tree analysis to determine the relative importance and effect of each of the three factors in describing landscape connectivity (Elith et al. 2008). In order to identify the combination of parameters for this analysis that minimized residual deviance in model fit, we conducted a grid search across all combinations of three values for three different regression tree parameters: tree complexity (maximum number of node splits), learning rate (weight applied to individual trees), and bag fraction (portion of the data used to construct each tree). The optimal number of trees for each combination of parameter values was determined using the "gbm.step" function in the "dismo" package.

Results

Forest landscape dynamics

Each of our LANDIS response variables varied according to carbon emissions scenario by year 100 (Figs. 4 and 5). In general, total biomass increased with carbon emissions, while forest diversity declined. The three forest diversity metrics (species richness, age richness, and total cohorts) all followed similar trends in response to carbon emissions (Fig. 4b–d). All three variables were greatest under historical carbon emissions 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 other two emissions scenarios. Total cohorts and age richness showed dramatic declines under climate change, while remaining relatively constant under the historical scenario.

Despite declines in overall forest diversity, the proportion of the forested landscape considered non-avoided by martens (i.e., selected for or neutral) increased with carbon emissions (Fig. 5, Table 2).

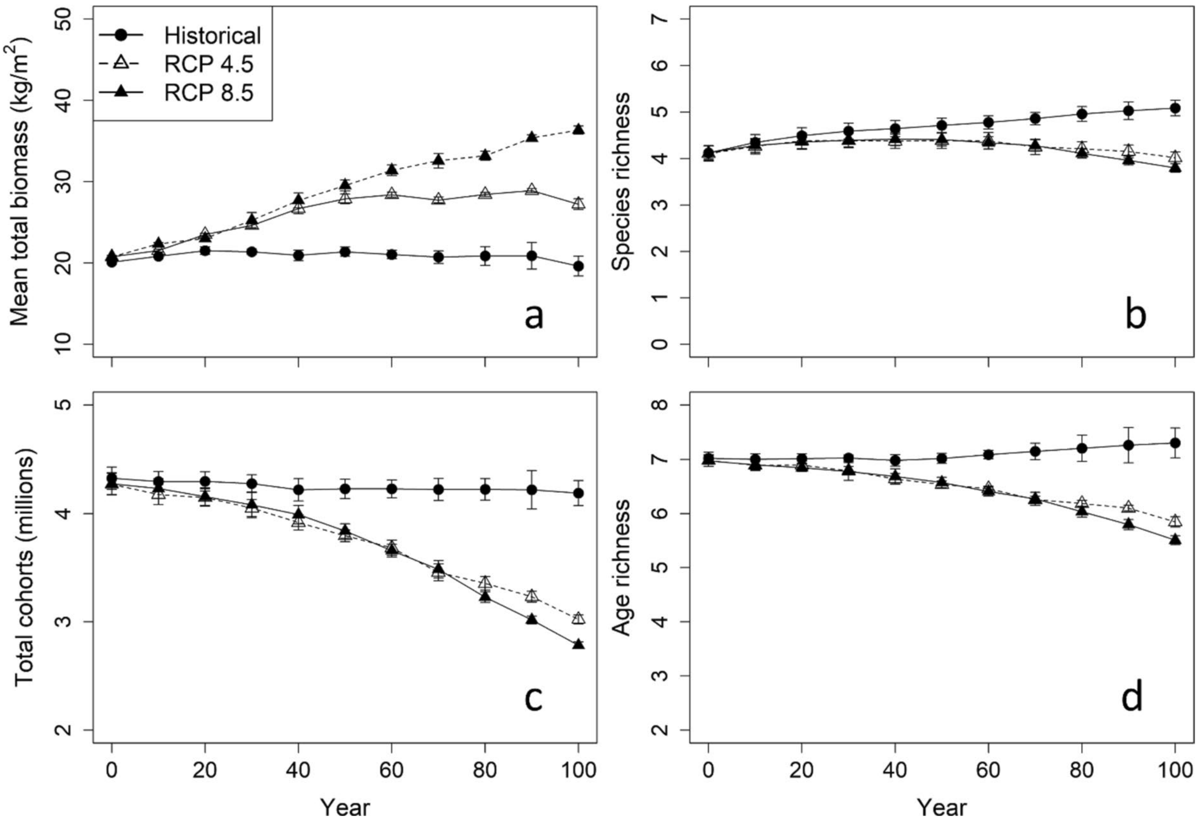

Fig. 4 Forest response to alternate carbon emissions scenarios based on LANDIS-II simulations from the year 2006 through 2106 in the Upper Midwest, USA. Two representative concentration pathways (RCP) for carbon emissions are presented, along with a historical emissions scenario based on the years 1950 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 scenario

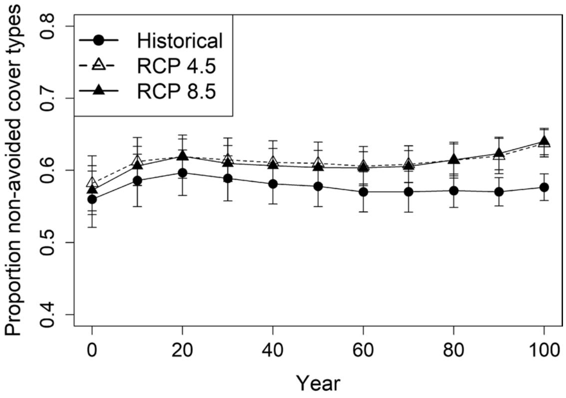

Fig. 5 Mean proportion of forested landscape composed of cover types that are not avoided by American martens when selecting home-ranges. Results represent output from LANDIS-II modeling of forest succession in the Upper Midwest, USA under two climate scenarios based on two alternate representative concentration pathways (RCP) for carbon emissions and one historical scenario (1950 – 1999). Error bars represent one standard deviation among 10 replicates for each scenario

Under historical emissions, 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 ($F_{1,18} = 30.76$, $p < 0.001$). While the proportion of non-avoided cover types at year 100 increased with carbon emissions, no significant difference could be detected among the three carbon emissions scenarios with 10 simulation replicates ($F_{2,27} = 2.52$, $p = 0.099$).

SEARCH results—animal dispersal

The top competing models describing variation in the three dispersal metrics (disperser success, dispersal distance, and time to settlement) included all three experimental factors (carbon emissions, land-use change, source population; Table 4). Overall, increased carbon emissions had a positive effect on dispersal, resulting in greater disperser success and

Table 4 Model-based inference of three response variables characterizing simulated dispersal behavior through a habitat corridor in the Upper Midwest, USA

Response variable	Model	k	AIC	ΔAIC	ωτ	R^2
Disperser success	**Direction*Land-use + Climate**	6	2304.2	0	0.785665	0.175
	Direction + Climate + Land-use	5	2306.8	2.6	0.214119	0.17
	Direction + Land-use	3	2320.6	16.4	< 0.001	0.148
	Direction + Climate	4	2351	46.8	< 0.001	0.106
	Direction	2	2363.5	59.3	< 0.001	0.084
	Climate + Land-use	4	2363.8	59.6	< 0.001	0.086
	Land-use	2	2376	71.8	< 0.001	0.064
	Climate	3	2403.8	99.6	< 0.001	0.022
Dispersal distance	**Direction + Climate**	4	11,501	0	0.36004	0.032
	Direction + Climate + Land-use	5	11,501	0	0.36004	0.032
	Direction*Climate + Land-use	7	11,502	1	0.218375	0.034
	Direction	2	11,506	5	0.029554	0.02
	Direction + Land-use	3	11,506	5	0.029554	0.021
	Climate	3	11,512	11	0.001471	0.011
	Climate + Land-use	4	11,513	12	< 0.001	0.012
	Land-use	2	11,518	17	< 0.001	< 0.001
Time to settlement	**Direction + Climate + Land-use**	5	9468	0	0.721106	0.411
	Direction*Climate + Land-use	7	9469.9	1.9	0.278881	0.41
	Direction + Land-use	3	9490	22	< 0.001	0.387
	Direction + Climate	4	9527.1	59.1	< 0.001	0.349
	Direction	2	9546.6	78.6	< 0.001	0.325
	Climate + Land-use	4	9731.8	263.8	< 0.001	0.084
	Land-use	2	9744.6	276.6	< 0.001	0.061
	Climate	3	9769.8	301.8	< 0.001	0.023

Experimental factors included direction (i.e., source population—east or west), climate scenario (historical, RCP 4.5 RCP 8.5), and land-use change (included or excluded). The top competing models (in bold) describing each response variable were identified using Akaike's Information Criterion (AIC) and associated model weights (ω) shorter dispersal times (Fig. 6). Land use change had the opposite effect, resulting in lower disperser success and longer time to settlement. Source population had the strongest effect on dispersal events, with individuals from the more fragmented east having lower success and longer dispersal times than individuals originating in the west. Dispersal distance appears unaffected by the 3 experimental factors, as the ability of the best-performing regression model describing dispersal distance was poor ($R^2 = 0.032$).The legend for figure 4 got split with part of its content being included in a row at the bottom of the table rather than being incorporated as part of the legend. The text that ended up incorporated in the last row of the table rather than in the the table caption clarifies that bold text indicated most competitive models according to AIC

Including an interaction between source population and land-use change for the disperser success model significantly improved model performance ($F_1 = 4.58$, $p = 0.032$; Fig. 6). Land use change resulted in lower disperser success for both populations, but the effect was stronger on individuals from the more contiguous west than the more fragmented east. Including interaction effects did not improve performance for models describing dispersal distance or time to settlement, though these are considered competing models ($\Delta\mathrm{AIC} < 2$).

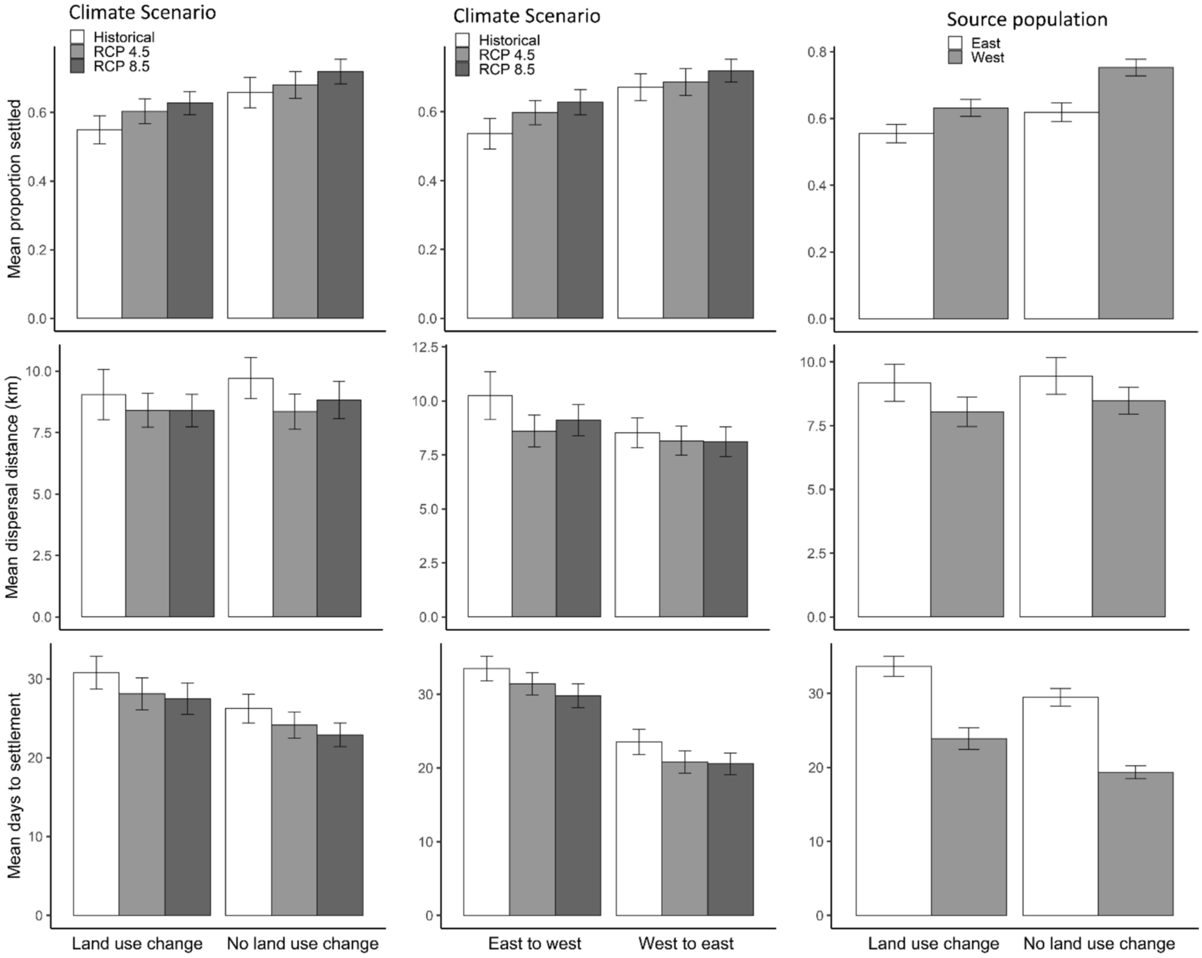

Fig. 6 Interaction between American marten dispersal behavior and 3 experimental factors: carbon emissions scenario, land use change, and direction (i.e., source population). Results are based on individual-based modeling of dispersal behavior through a habitat corridor situated between two reintroduced marten populations in the Upper Midwest, USA. Means and standard errors are displayed across replicates each representative of 10 simulated dispersal events

SEARCH results—functional landscape connectivity

Based on boosted regression tree analyses, functional connectivity was lower from west (more contiguous) to east (more fragmented) and also declined with land-use change (Fig. 7, S2). The effect of emissions scenario was not consistent across data subsets. Connectivity was generally higher in the highest emissions scenario (RCP 8.5) and especially for the longer-distance dispersal, but the middle emissions scenario (RCP 4.5) produced lower connectivity than historical in the 0th and 75th percentiles of functional connectivity. Across all variables, the magnitude of the effect of the variable on connectivity increased as the subset of long-distance dispersers was more limited (e.g., strongest effect for 95th percentile; Figure S2).

When including data from all dispersing martens (0th percentile), the standard regression trees identified no significant effects on functional connectivity from the three experimental factors. For long-distance dispersers represented by percentile subsets of data (75th, 90th, and 95th), the regression trees identified source population (east vs west) of individual martens as the most important factor affecting functional connectivity, followed by emissions scenario and then land-use change (Fig. 7). Boosted regression trees confirmed the relative importance of experimental factors, except for the 75th percentile in which emissions were most important followed by land use and source population (Fig. 8).

Across subsets of dispersers, differences occurred between animals originating from different source populations. For martens released in the east, both emissions scenario and land-use change had significant effects on connectivity across all subsets. For animals released in the west, land-use only affected the 95th percentile and emissions affected only the 90th and 95th percentiles. Interaction also occurred between source population and climate scenario. Connectivity consistently increased with carbon emissions for animals originating from the west, whereas for animals from the east the historical carbon emissions scenario often resulted in higher connectivity than other emissions scenarios (Fig. 7).

Discussion

Measuring functional connectivity

Our approach to measuring functional connectivity, in which functional connectivity is derived from an individual-based model and emerges as many fine-scale movements scale up to population-level patterns (Suraci et al. 2020), is a powerful and flexible means of evaluating the connectivity of alternative landscape futures (Day et al. 2020; Hunter-Ayad and Hassall 2020). Mechanistic methods to measure functional connectivity are needed as landscapes are increasingly impacted by anthropogenic activity (Van Moorter et al. 2021). Identifying barriers to connectivity due to landscape configuration can be done using techniques of landscape genetics (Landguth et al. 2010; Storfer et al. 2010), though landscape genetics requires the collection of genetic samples and limits the ability to evaluate future landscape scenarios. Other landscape-level analytical approaches such as least cost path or circuit theory analyses require prior assumptions about resistance to movement and an individual's awareness of the whole landscape, and do not typically address directional asymmetry in dispersal due to landscape configuration (Zeller et al. 2012; Rinnan 2018). Because of its mechanistic nature, our approach can be used to project functional connectivity under novel and future conditions such as landscapes affected by climate change and is well-suited for application to other populations (Radchuk et al. 2019). As we discuss below, our results demonstrate that this ability is important because directional asymmetry in functional connectivity may have substantial conservation implications for the future of rare or isolated populations.

Simulation modeling can be a valuable tool in planning for the conservation of American martens and other motile species of conservation concern (Lacy and Clark 1993; Starfield 1997). We have demonstrated how combining dynamic models of landscape change with individual-based models of animal behavior can be used to explore how pattern and process can affect wildlife populations in a rapidly changing world (Knowlton and Graham 2010; da Rocha et al. 2021). Results from our study indicate that future climate and land-use change interact to impact marten habitat and their use of that habitat, and that the interactions can readily be

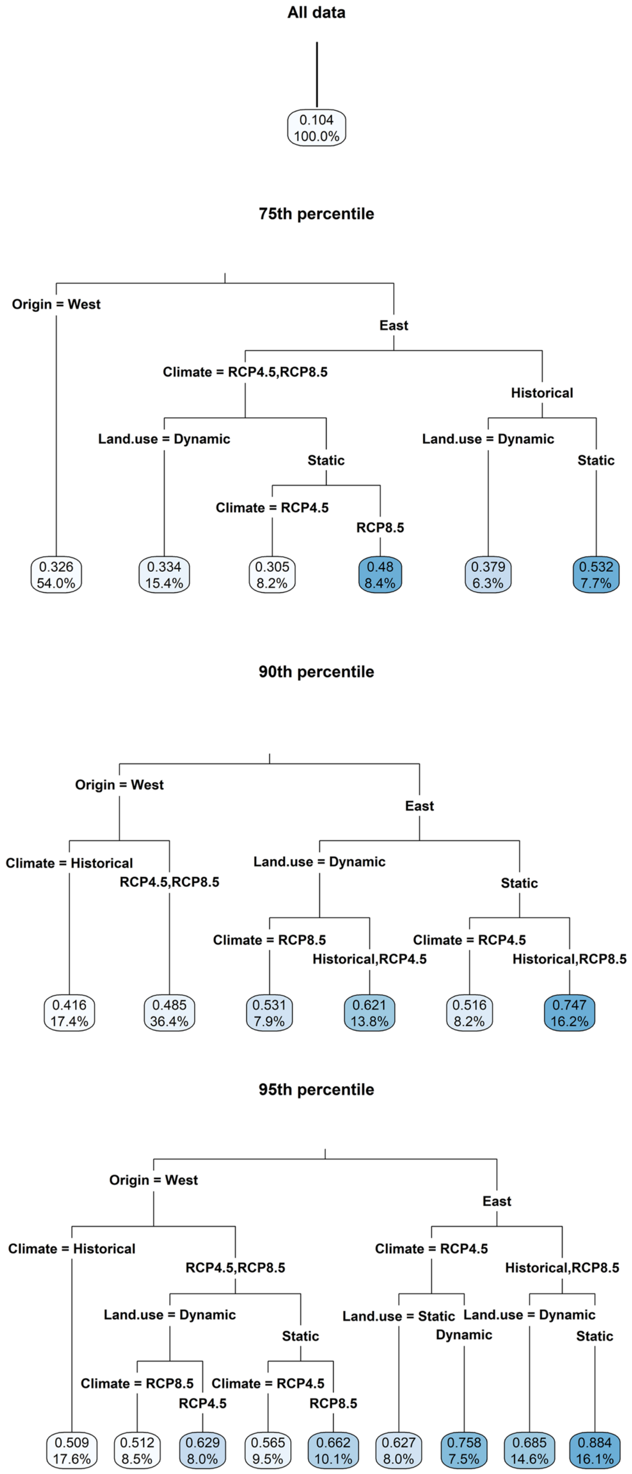

Fig. 7 Regression trees (left column) and relative influence plots (right column) indicating factors affecting the functional connectivity (net directional displacement of dispersers presented as a fraction) between two reintroduced populations of American martens in the Upper Midwest, USA. Factors varied included origin of release (east or west population), carbon emissions 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). Percentiles associated with each tree indicate the threshold above which data were included in the analysis. 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 color represents a greater proportion of the data. Relative influence plots were produced using boosted regression trees optimized for number of trees, learning rate, tree complexity, and bag fraction

estimated with process-based models. Such interactions can be particularly difficult to identify empirically, given that studies across large landscapes are usually limited to a single replicate with no opportunity to experimentally manipulate factors of interest. When an ecological model has previously

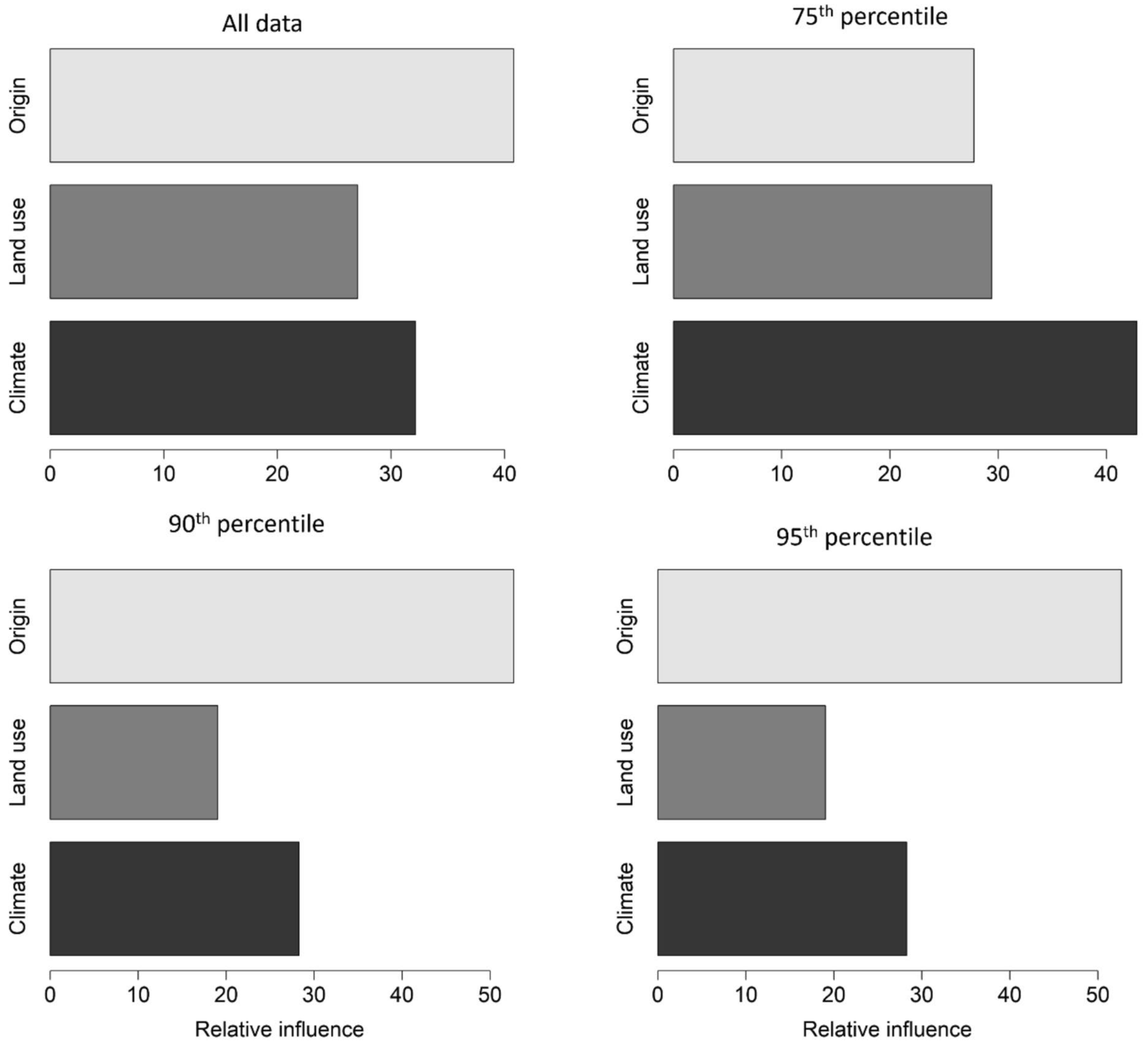

Fig. 8 Relative influence plots indicating factors affecting the functional connectivity (net directional displacement of dispersers presented as a fraction) between two reintroduced populations of American martens in the Upper Midwest, USA. Factors varied included origin of release (east or west population), carbon emissions 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). Relative influence plots were produced using boosted regression trees optimized for number of trees, learning rate, tree complexity, and bag fraction

been calibrated to match observed empirical patterns as is the present case, emergent results from subsequent simulation experiments are more robust to alternative and future scenarios that are a challenge to study empirically (Radchuk et al. 2019).

Climate change

Climate change in our simulations had a significant impact on habitat, dispersal behavior, and functional landscape connectivity, on a time scale of only 100 years. As a result of the increase in non-avoided cover types with increasing carbon emissions, martens exhibited a 12% increase in disperser success (i.e., rates of home-range establishment) and 23% shorter search times following the two-week exploration phase, with little effect on straight line dispersal distance. Results for effects of climate change on functional connectivity were less clear, as there was not always a clear trend with increasing carbon emissions (see Figure S2). For example, functional connectivity was generally higher under climate change for individuals originating from the west, but this trend was not as clear for individuals from the more fragmented eastern portion of the landscape. Increased functional connectivity with carbon emissions was also more apparent for the 90th and 95th percentile dispersers, but only under the maximum carbon emissions scenario. Taken together, these results suggest that changes in habitat due to high carbon emissions could be beneficial for marten population connectivity. Other LANDIS simulations in the region have 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 become more suitable for martens under climate change based on our present model of 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; Day et al. 2020) yet unable to foresee potential habitat needs in the context of climate change. For example, while forest biomass increased in the climate change simulations, species richness and age richness each declined as carbon emissions increased, potentially signaling a loss of forest resistance and resilience (Duveneck and Scheller 2016). It is unknown how martens might respond to 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, 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

Land-use change is another driver 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 of landscapes occupied by martens (Hargis et al. 1999). Incorporating land-use change in dispersal simulations resulted in a 14% decrease in disperser success and a 42% increase in search times, despite having little effect on straight line dispersal distance. In other words, martens experience higher risk and more effort to ultimately disperse the same distance. Land-use change also caused a decrease in functional connectivity, though it was the least impactful of the three factors. This decrease was likely affected by the increase in disperser mortality in the land-use change scenarios (Johnson et al. 2009; Day et al. 2020). Again, these results interacted with source population, because land-use change had a stronger effect on individuals originating from the east. 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). Such predictions, however, can be strengthened if they explicitly consider the effect of disperser mortality (Day et al. 2020) and directional asymmetry (Rinnan 2018) on the flow of dispersal across the landscape.

Landscape configuration

The asymmetrical configuration of the study landscape played a major role in the simulations, as most results associated with dispersal behavior and functional connectivity exhibited interactions with the source population 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 (Day et al. 2020). Functional connectivity from east to west was affected by both carbon emissions scenario and land-use across all subsets of dispersers. These individuals from the east, however, were more successful traversing the landscape as available suitable habitat on the landscape increased. In other words, fragmentation and a lack of habitat in the eastern portion of the landscape may have acted as a directional barrier for individuals dispersing from the west, while funneling martens from the east to venture further into the corridor between populations. Mortality acted to offset these effects of landscape configuration (Day et al. 2020), as disperser success was lower for animals from the east despite greater connectivity values. These asymmetric effects of landscape configuration are likely widespread among similar species that disperse long distances, especially as landscapes become more fragmented (Ferreras 2001; Rinnan 2018; Schippers et al. 1996).

Conservation implications

For the American marten, these results have significant conservation implications, and for the Ojibwe people on whose ceded territories this work was conducted, significant cultural implications. Previous work has shown that the viability of isolated marten populations increases dramatically with just a single immigration event per year (Mills and Allendorf 1996; Grauer et al. 2017; Manlick et al. 2017a). For the region being considered in the present study, it is critical that individuals from the more established population in Michigan are able to disperse west into the smaller, endangered population in Wisconsin. While martens in the region have been observed moving from the western to the eastern population (JHG personal observation), similar movements have yet to be observed from east to west. Thus, it is important to understand how landscape configuration interacts with changing environments to drive asymmetry in dispersal, thereby mediating gene flow and potential demographic rescue. The Ojibwe tribes in the region are using results from studies such as this to develop landscape-scale habitat projects that are designed to enhance corridors and connectivity among subpopulations. These efforts are consistent with the Ojibwe view that plans should be made thinking about the Seventh Generation into the future (Marvin Defoe, Red Cliff Tribal Historic Preservation Offices).

The role of simulation modeling

An underappreciated utility of simulation modeling is in how it helps to identify gaps in knowledge that may be needed for conservation planning (Starfield 1997). For example, the effects of carbon emissions 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). Our application would also benefit from an improved habitat selection model that accounts for home-range selection at multiple scales, as the present model did not identify lowland conifer stands that are important at the within-home-range scale (McCann et al. 2014). These are all research needs made apparent by the process of model testing and development, as well as by combining models of landscape processes and animal behavior to evaluate alternative future landscape scenarios.

Since Lima and Zollner's (1996) seminal 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 dispersal simulation model was developed and parameterized based on a long history of ecological investigation into martens in this ecosystem (e.g., Day et al. 2019, 2020, 2022; Gilbert et al. 1997, 2009; McCann et al. 2010, 2014; Manlick et al. 2017a), and represents an example of how long-term empirical study of one species can be used to develop a complex model of behavioral landscape ecology. In a previous application, Day et al. (2019) used SEARCH to reproduce marten dispersal distance distributions that emerged from fine-scale processes (Breckling et al. 2005), including occasional long-distance dispersal. The behavioral plasticity apparent in these long-distance dispersal events was not imposed, but emerged from basic behavioral rules followed by all dispersers.

With such a mechanistic approach, natural behavioral responses can emerge even when modeling novel or future landscapes (Radchuk et al. 2019), especially when combined with a dynamic landscape simulation model such as LANDIS. Such modeling approaches are needed to help conservation biologists to better understand how species will functionally respond to rapidly changing landscapes in an uncertain future. References 'Demaria et al. (2016), Liaw and Wiener (2002), Newbold et al. (2015), Pecl et al. (2017), Winkler et al. (2012).' are given in list but not cited in text. Please cite in text or delete them from list.

Acknowledgements We gratefully acknowledge the traditional ceded territories of the Indigenous People upon which our fieldwork was conducted. We honor and appreciate the Ojibwe People who are the original Indigenous caretakers. This study was conducted with their permission and endorsement. We thank Brian Miranda, Bill Dijak, Nicholas McCann, and Hannah Panci for their valuable contributions to the parameterization of simulation models and carbon emissions 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 Project IND90024786MS for their financial support of PAZ.

Author contributions All authors conceptualized the study, curated the data, developed the methodology, and contributed to review and editing. CCD conducted formal analysis, investigation, validation, visualization, and writing of the original draft. CCD, PAZ, and JHG contributed to funding acquisition. PAZ, JHG, and EJG contributed supervision and resources.

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Data availability The data that support the findings of this study are available on github at https://www.github.com/cday41/martensims_data.

Declarations

Conflict of interest The authors declare no competing interests.

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