

Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context

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Abstract Climate change is likely to alter population connectivity, particularly for species associated with higher elevation environments. The goal of this study is to predict the potential effects of future climate change on population connectivity and genetic diversity of American marten populations across a 30.2 million hectare region of the in the US northern Rocky Mountains. We use a landscape resistance model validated from empirical landscape genetics modeling to predict the current and expected future extent and fragmentation of American marten dispersal habitat under five climate change scenarios, corresponding to climatic warming of between 0.7 and 3.3 °C, consistent with expected climate change by year 2080. We predict the regions of the current and future landscapes where gene flow is expected to be governed by isolation by distance and the regions where population fragmentation is expected to limit gene flow. Finally, we predict changes in the strength and location of predicted movement corridors, fracture zones and the location of dispersal barriers across the study area in each scenario. We found that under the current climate, gene flow is predicted to be limited

primarily by distance (isolation), and landscape structure does not significantly limit gene flow, resulting in very high genetic diversity over most of the study area. Projected climatic warming substantially reduces the extent and increases the fragmentation of marten populations in the western and northwestern parts of the study area. In contrast, climate change is not predicted to fragment the extensive higher elevation mountain massifs in central Idaho, the northern U.S. continental divide, and Greater Yellowstone Ecosystem. In addition, we show locations in the study area that are important corridors in the current landscape that remain intact across the climate change scenarios.

Keywords Climate change · Population connectivity · Gene flow · Genetic diversity · American marten · *Martes americana*

Introduction

Expected climate change over the next century will significantly alter ecological systems, leading to habitat loss, fragmentation and large-scale range shifts. Parmesan and Yohe (2003) documented range shifts averaging 6.1 km per decade towards the poles or climatic equivalent elevation increases across a meta-analysis of 1,700 species. Taxa currently associated with higher elevation environments (Schwartz et al. 2009; McKelvey et al. 2011; Cushman et al. in press) are likely to experience reductions in habitat area and increasing fragmentation and isolation of habitat remnants. As climate warms, it is likely that suitable conditions for most species dependent on current high elevation environments will migrate upslope into smaller and increasingly isolated topographical islands.

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Migration to higher latitudes may frequently be blocked by lower elevation areas of unsuitable habitat, resulting in populations of high elevation species becoming more reduced in extent and fragmented (Opdam and Wascher 2004). The resulting disruptions in population connectivity will likely decrease dispersal (Gibbs 1998; Wasserman et al. 2012), increase mortality (Fahrig et al. 1995) and reduce genetic diversity (Reh and Seitz 1990; Wilson and Provan 2003; Wasserman et al. 2012). Reduction in migration among habitat patches may lead to population declines (Brown and Kodric-Brown 1977; Harrison 1991) and may reduce recolonization following local extinction (Semlitsch and Bodie 1998).

Predictive modeling of climate change effects on population connectivity is an extremely valuable tool to anticipate impacts and guide adaptation strategies. Many researchers have used “bioclimatic envelope” modeling to predict future shifts in the climatic conditions currently associated with species distributions (Iverson et al. 1999; McKenzie et al. 2003; Rehfeldt et al. 2006). However, very few studies have explicitly evaluated effects of climate change on gene flow and genetic diversity. Davis and Shaw (2001) note that rapid climate changes may increase severity of selection and displace populations from environments to which they are adapted. This likely will reduce the potential of populations to migrate to suitable environments or adapt to novel conditions in their former ranges. Thus there is an urgent need to formally link predictions of climate change to predictions of genetic diversity and gene flow to more completely anticipate the population-level effects of climate change, particularly on species inhabiting high elevation environments.

Recent research has indicated that population connectivity of American marten (*Martes americana*) in the U.S. northern Rocky Mountains is controlled by elevation gradients in landscape resistance to gene flow (Wasserman et al. 2010). The optimal resistance model identified in Wasserman et al. (2010) is closely related to areas of high winter snowpack and moist montane forest, which suggests an association with climate. Climate change is predicted to result in large increases in winter temperature in the northern Rocky Mountains (IPCC 2007; Littell et al. 2011). This is likely to result in substantial decrease in the depth of average winter snowpacks (Elsner et al. 2010; Littell et al. 2011) and migration of forest communities upward in elevation. Given the biology of the American marten and its association with high elevation environments, this could result in increased isolation of remnant populations in mountain systems. This suggests that population connectivity of American martens in the northern Rocky Mountains may be highly vulnerable to climate change. However, little is known about the effects climate change is likely to have on the extent, connectivity and genetic

diversity of American marten populations across the full extent of their range in the U.S. northern Rocky Mountains.

Objectives

The goal of this study is to predict the potential effects of future climate change on population connectivity and genetic diversity of American marten populations across a 30.2 million hectare region of the U.S. northern Rocky Mountains. To accomplish this goal, we address four research objectives. *First*, we use a landscape resistance map derived from empirical landscape genetic modeling (Wasserman et al. 2012) to predict the current and expected future extent and fragmentation of American marten dispersal habitat under five climate change scenarios. *Second*, we use regression models, produced by a simulation modeling experiment that evaluated the relationship between habitat configuration and genetic differentiation (Cushman et al. submitted), to predict the regions of current and future landscapes where gene flow is expected to be governed by isolation by distance and the regions where population fragmentation is expected to limit gene flow. *Third*, we use regression models produced from a recent simulation study (Wasserman et al. 2012) to predict genetic diversity across the study area under current and potential future climates. *Fourth*, we predict changes in the strength and location of predicted movement corridors, fracture zones and dispersal barriers across the study area in each scenario.

Methods

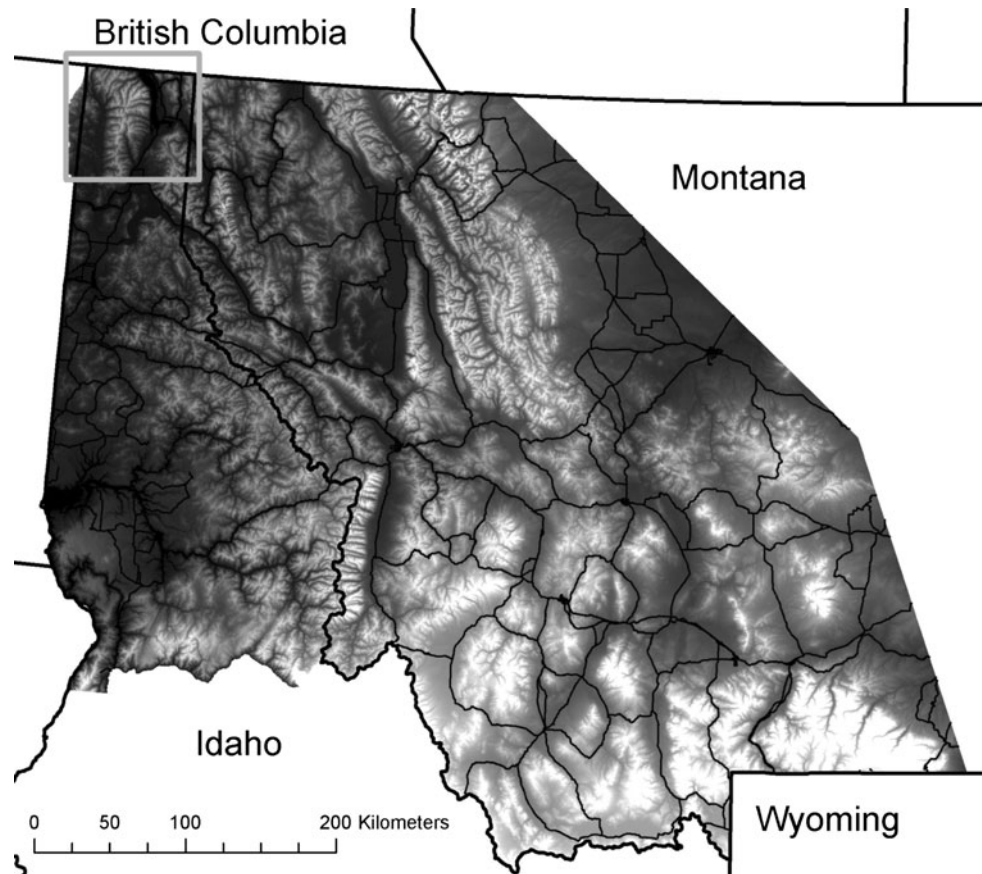
Study area

The study area consists of a 30.2 million hectare area encompassing the United States northern Rocky Mountains in the states of Idaho and Montana (Fig. 1). The topography is diverse, with extensive mountain ranges, large intermountain valleys, and areas of the high plains. Elevation ranges from approximately 700 to 3,500 m.

Climate change scenarios

Projected climate changes in the Pacific Northwest (PNW) and Northern Rockies vary with global climate model (GCM), time frame, season and greenhouse gas emissions scenario. Mote and Salathé (2010) project increases in PNW regional autumn, winter, and spring temperature of about 1.4–2.0 °C by the 2040s and 2.1–3.4 °C by the 2080s (relative to 1970–1999, A1B and B1 emissions scenarios average across 20 and 19 IPCC fourth assessment report (IPCC AR4) GCMs, respectively). Extending methods

Fig. 1 Study area extent is the region covered by the shaded map, and comprises northern Idaho and the western half of Montana, USA, with state boundaries shown in *heavy dark lines*. Major highways are shown in *fine dark lines*. Elevation across the study area is shown in a *gray scale*, from low elevation (*black*) to high elevation (*white*). The *gray box* in the *upper left* is the extent of the Wasserman et al. (2010, 2012) studies upon which the analyses presented in this paper are based



described in Elsner et al. (2010), Littell et al. (2011) and McKelvey et al. (2011), we used a basic spatially-explicit method to downscale monthly PNW and upper Missouri Basin regional projections from the 10 best-ranked GCMs to 1/16th degree ($\sim 5 \times 7$ km) and reported projected climate changes by ecosections (<http://nationalatlas.gov/mld/ecoregp.html>). For the ecosections containing the landscape in this study (all of Bailey M332B, M332C, M333B, M333C, M333D and parts of Bailey M331A, M332A, M332D, M332E, and M333A), the 10 GCM ensemble cool season (Oct.–Mar.) temperature changes are expected to average $+1.8$ °C (ecosection range $+1.75$ to $+1.92$ °C) by the 2040s (2030–2059) and $+3.4$ °C (ecosection range $+3.29$ to $+3.58$ °C) by the 2080s (2070–2099) relative to the 1970–1999 mean of -2.6 °C (ecosection range -4.9 to -0.4 °C).

We assumed a long term average standard environmental lapse rate (rate of decrease in temperature with elevation) of -6.5 °C/km, which is equivalent to an increase in the elevation of current temperatures of approximately 280 m by the 2040s and 520 m by the 2080s (relative to 1970–1999). While lapse rates vary considerably with topography and season in the PNW (e.g., Minder et al. 2010), the standard environmental lapse rate provides

a baseline for future comparison. More importantly, this temperature increase crosses the 0 °C isotherm for the two of the ten ecosections in the landscape by the 2040s and the entire landscape by the 2080s (historical average Oct.–Mar. mean temperature estimated to be -2.6 °C), suggesting a decline in the proportion of winter precipitation falling as snow. Averaged over the all ecosections in the landscape, snowpack is projected to decrease -31 % (ecosection range -10 to -50 %) by the 2040s and -46 % (ecosection range -20 to -72 %) by the 2080s under the 10 GCM ensemble and an A1B emissions scenario (Littell et al. 2011).

We specified five scenarios of climate driven changes to landscape resistance to American marten in the study area. Specifically, we evaluated the effects of upward shift of current temperatures by 100, 200, 300, 400, and 500 m from the current optimum elevation of 1,500 m (Wasserman et al. 2010). This represents a rather conservative range of scenarios, with an upward shift of mean annual temperatures of approximately 500 m expected by the 2080s (Littell et al. 2011). Matching our scenarios with Littell et al. (2011) our $+300$ m scenario approximates expected climatic warming for year 2040, and our $+500$ m approximate warming expected by 2080.

Landscape resistance model

Gene flow in the northern Idaho American marten population is driven by an elevational gradient, where resistance to gene flow is minimized at 1,500 m (resistance value of 1) and resistance maximizes to a value of 10 defined by a Gaussian function of elevation with a 300 m standard deviation (Wasserman et al. 2010). The resistance value in the landscape map represents the cost of crossing each cell relative to the minimum landscape condition (1,500 m). To enable computation of connectivity models across this vast extent, the original resistance map (90 m cell size) was resampled to a 270 m pixel size. This change in grain of the resistance map has very little impact on predictions of connectivity, given that changes in pixel size have been shown to have little effect on the strength and nature of landscape genetic relationships (Cushman and Landguth 2010). This resistance surface is used as the basis for all analyses of current population connectivity and simulation of current landscape genetic structure. It provides a baseline from which predicting future landscape resistance under the five climate change scenarios is used.

Modeling current and future habitat connectivity

We predicted current and future habitat connectivity for American marten using two connectivity modeling approaches. First, we used least-cost resistant kernels (e.g. Compton et al. 2007; Cushman et al. 2010a, b) coupled with landscape pattern analysis with FRAGSTATS (McGarigal et al. 2002) to map and quantify the extent and configuration of habitat connected by dispersal. The resistant kernel approach to connectivity modeling is based on least-cost dispersal from a defined set of sources. The model calculates the expected relative density of American marten in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010a). We wrote an AML script to calculate the resistant kernel (R_k) density. The script uses the ArcGrid COSTDISTANCE (ESRI 2007) function to produce a map of the movement cost from each source up to a specified dispersal threshold. These cost distance grids are inverted and scaled such that the maximum value for each individual kernel is one. Once the expected density around each source cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel. The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. Our objective in the resistant kernel analysis was to predict the extent of occupied and connected habitat. Thus, we used a dispersal threshold of 10,000 cost units, reflecting a dispersal ability of 10 km in uniformly

suitable habitat (i.e., minimum resistance value of 1 for elevation 1,500 m). This threshold is less than the maximum dispersal ability of the species, and reflects the middle of the dispersal probability kernel, which is appropriate for depicting the extent of occupied and connected habitat (Bull and Heater 2001; Broquet et al. 2006). The sources in our case are all cells with landscape resistance less than 3 (Wasserman et al. 2010) and that are forested (Maxwell et al. 2011). This restricts origin cells to locations of relatively high suitability as dispersal habitat for the species (Wasserman et al. 2010).

The second method of connectivity modeling used was a factorial implementation of least cost paths, in which we calculated the least cost paths between all pairs of source cells (e.g., Cushman et al. 2009, 2010b). The purpose of this second connectivity modeling method was to predict the expected pattern and frequency of longer range dispersal. The resistant kernel analysis is intended to map core connected habitat. However, infrequent, long-range dispersal is also important in its influence on population connectivity and genetic diversity. We used UNICOR (Landguth et al. 2012) to predict the locations, density, and strength of least-cost movement paths among the full factorial of all locations in the resistance maps that had near optimal conditions (forested cells with landscape resistance less than 3; Wasserman et al. 2010). We chose a dispersal threshold of 30 km, which is approximately the upper bound of dispersal ability of the American marten. Thus, the UNICOR analysis produces predictions of the locations and importance of locations across the landscape for providing long-distance dispersal connectivity among core habitat patches.

Analysis of connectivity maps

To quantify the extent and connectivity of American marten dispersal habitat, the resistant kernel maps were reclassified into binary form for analysis in FRAGSTATS. Any cell with non-zero kernel density value was classified as connected and all pixels with zero kernel density were classified as non-connected. Cushman et al. (2012) found that the strength of genetic differentiation caused by landscape structure was well predicted by the values of several landscape metrics, including correlation length, patch density and the Clumpy index of aggregation (McGarigal et al. 2002). In addition, Wasserman et al. (2012) found that genetic diversity of American marten in a subsection of our study area was well predicted by the percent of the landscape occupied by connected habitat, the extent of the largest patch of connected habitat and the number of isolated habitat patches. Therefore, we used FRAGSTATS (McGarigal et al. 2002) to calculate the percentage of the landscape (PLAND), correlation length (GYRATE_AM), largest patch index (LPI), clumpy

(CLUMPY) and the density of patches (PD) predicted by the resistant kernel model. PLAND is the simplest metric of landscape composition, and quantifies how much of the study area is covered by potentially occupied habitat for each species and species group. Correlation length, as formulated in a raster implementation, is the area weighted mean patch radius of gyration (GYRATE_AM), and measures the extensiveness of habitat spanning across a landscape. PD of habitat provides an intuitive measure of the degree of fragmentation of the landscape for marten dispersal. When habitat is fully connected there is a single patch, and as habitat becomes progressively fragmented habitat is broken up into successively more isolated patches. The LPI of connected habitat reports the extent of the largest patch of connected core habitat, as a proportion of the size of the study area. CLUMPY is an index of class aggregation that is specifically formulated to report the degree of aggregation controlling for class extent (McGarigal et al. 2002).

Predicting regions of isolation by distance and isolation by resistance

Cushman et al. (submitted) used neutral landscape models and individual-based landscape genetic simulations to evaluate the relationships between habitat area, habitat fragmentation and the strength of genetic differentiation in complex landscapes. They found that correlation length, patch density and clumpy are the most parsimonious set of variables to predict the magnitude of genetic differentiation in complex landscapes. We used the data produced in their simulation to predict the probability of significant effects of landscape resistance on genetic differentiation across the study area (Table 1) under the current and five potential future climates. To do this we developed a logistic regression equation using the variables Cushman et al. (submitted) found to be most influential in driving the strength of landscape genetic effects (Table 1). We then applied the regression equation within moving focal windows of a 9 km radius, producing local predictions of the probability of marten population genetics being structured by landscape resistance (or inversely by isolation by distance).

Predicting genetic diversity

We used data produced in an individual-based, spatially explicit simulation (Landguth and Cushman 2010) of American gene flow (Wasserman et al. 2012) to predict the number of alleles in local populations across the study area (Table 2) under the current and five potential future climates. We evaluated all combinations of PLAND, LPI, and PD as predictor variables in multiple regression and chose the model with the lowest AIC value. This model indicated

Table 1 Parameters of a logistic regression equation predicting probability of significant isolation by landscape resistance effects (independent of isolation by geographical distance) as a function of landscape metrics

	Estimate	Std. Error	z
Intercept	7.43E+00	2.52E+00	2.952
GYRATE_AM	1.72E−03	8.53E−05	20.219
PD	−4.44E+01	2.90E+00	−15.28
CLUMPY	−2.44E+01	2.38E+00	−10.248
R	−2.32E+00	1.08E−01	−21.56
Null deviance	8120.58		
Residual deviance	906.16		
AIC	916.16		

In our model we specified a value of 10 for R, indicating that non-habitat is 10 times as resistant as habitat, which matches the range of resistance contrast found to be supported for marten gene flow by Wasserman et al. (2010)

GYRATE_AM correlation length of habitat; *PD* patch density of habitat; *CLUMPY* clumpy index of aggregation of habitat; *R* relative resistance of non-habitat to habitat

Table 2 Parameters of a multiple regression equation predicting number of alleles at 30 randomly selected microsatellite loci as a function of landscape metrics

	Estimate	Std. Error	t-value
Intercept	−12.75	2.067	−6.17
PLAND	0.915	0.073	12.41
Ln(LPI)	8.287	1.758	4.713
Null deviance	44,955		
Residual deviance	1,968		
AIC	819.8		

LPI is the percentage of the focal landscape occupied by the largest single patch of habitat

PLAND percentage of a focal landscape occupied by habitat; *ln(LPI)* natural logarithm of the LPI

that the number of neutral alleles in a local population is primarily a function of the percentage of the landscape occupied by kernel connected habitat, and the natural logarithm of the largest patch of kernel connected habitat. We applied the regression equation in Table 2 within moving focal windows of the same extent as the Wasserman et al. (2012) study area (25 km radius), producing local predictions of the expected number of alleles in the marten population. Our predictions are of expected number of alleles across 30 randomly selected microsatellite loci.

Identifying corridors, barriers and fracture zones

We evaluated the resistant kernel maps to identify areas that function as corridors between large patches, and areas where breaks in population connectivity produce barriers

isolating portions of the study area. We also identified areas that are predicted to be connected by infrequent long distance dispersal by the UNICOR analysis, but are not connected in the resistant kernel analysis. We termed these latter areas as fracture zones, as they represent areas with limited dispersal between large population patches. We assessed the impacts of climate change on corridors and barriers by (1) identifying those corridors that are robust to climate change and remain intact across all six climate scenarios, (2) identifying those corridors that are broken in one of the climate change scenarios, and (3) identifying barriers that are always predicted to fragment the population across all climate scenarios.

Results

Current marten population connectivity and genetic diversity

In the current landscape American marten dispersal habitat is very extensive and well connected (Fig. 2a). Over 70 % of the study area is covered by core connected habitat

(10,000 cost unit dispersal threshold resistant kernel; Fig. 3a) and nearly all core habitat patches are connected through long distance dispersal (30,000 cost unit dispersal threshold factorial least cost paths; Fig. 4a). In the current landscape over 75 % of the extent of the population is predicted to be governed by isolation by distance, in which genetic differentiation is a function of distance between individuals and is not influenced by landscape structure and habitat fragmentation (Fig. 5a). Very high genetic diversity is predicted in these areas, with between 90 and 116 alleles are predicted at 30 neutral loci in the interiors of the large connected patches in the central and eastern parts of the study area (Fig. 6a).

The exception in the current landscape is the far western fringe of the population in Idaho, where deep river valleys (i.e., not suitable dispersal habitat) create complex patch shapes with high edge density. In these areas the local landscape complexity is predicted to result in significant genetic effects arising from the extent and configuration of habitat. A similar pattern is seen along the eastern fringe of the population where the rocky mountains drop into the northern great plains, and also along the edges of large intermountain valleys in southwest and southcentral Montana (Fig. 5a). Reduced genetic diversity (between 45 and

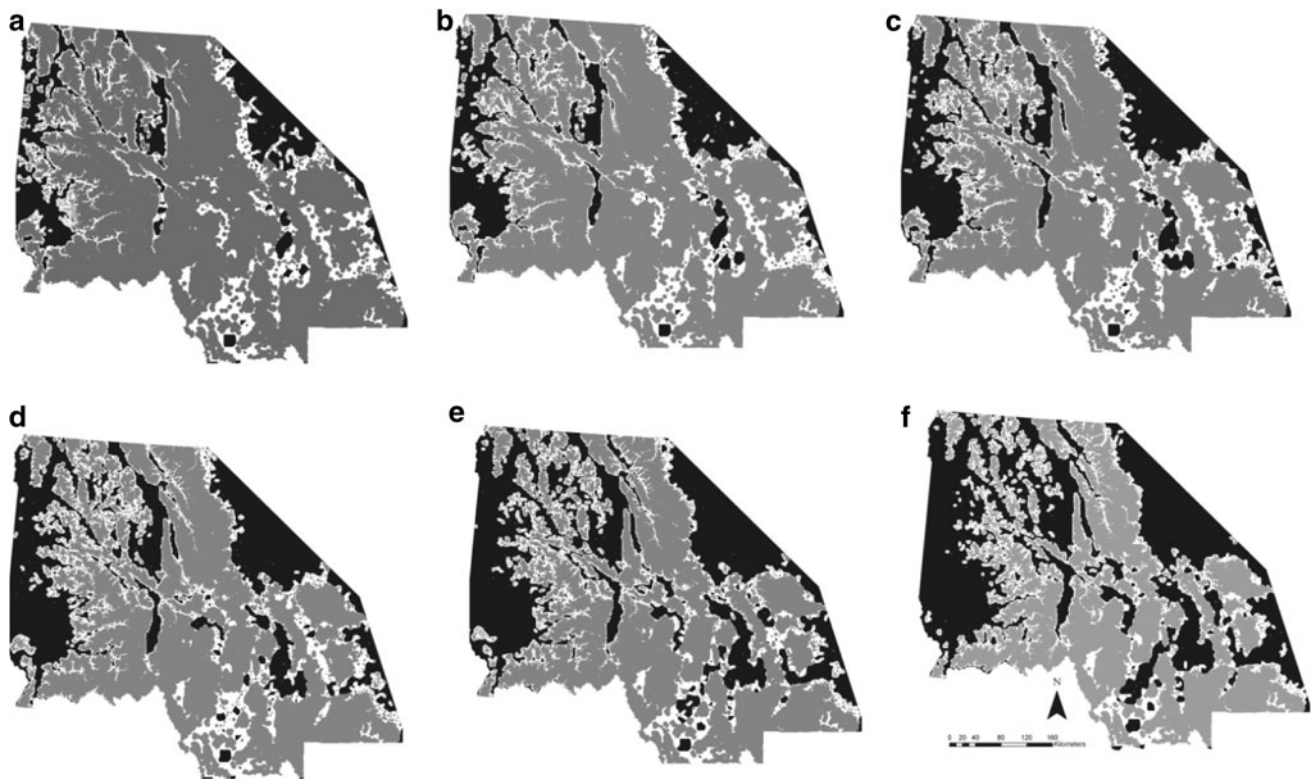
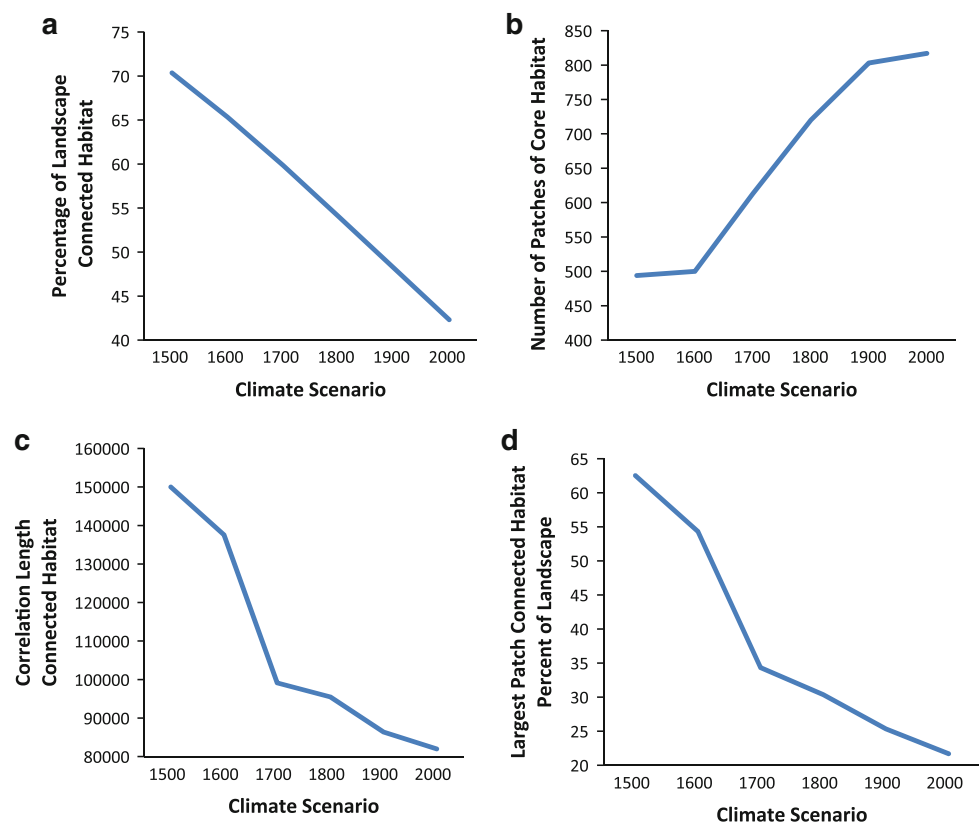


Fig. 2 Resistant kernel and least-cost path connectivity maps for each of the six climate change scenarios. **a** 1,500 m optimal elevation, **b** 1,600 m optimal elevation, **c** 1,700 m optimal elevation, **d** 1,800 m optimal elevation, **e** 1,900 m optimal elevation, and **f** 2,000 m optimal elevation. The *gray shaded areas* are patches predicted to be

connected by dispersal by the resistant kernel maps. They represent core occupied habitat. The *white areas* are areas predicted to be connected by long range dispersal (up to 30,000 cost units) using UNICOR. These represent fracture zones of infrequent occupancy that connect core population patches

Fig. 3 Change in four FRAGSTATS metrics quantifying the extent and fragmentation of the American marten population in the United States northern Rocky Mountains across the six climate change scenarios. The metrics are **a** PLAND percentage of the landscape occupied by patches of connected populations, **b** number of isolated patches of habitat, **c** correlation length of habitat, and **d** the extent of the largest patch of connected habitat. The climate change scenarios reflect different optimal elevations for American marten gene flow and dispersal (1500, 1600, 1700, 1800, 1900, and 2000 m; Wasserman et al. 2010, 2012). The 1,500 m scenario reflects the current climate and each 100 m increment corresponds to warming of approximately 0.65 °C



80 alleles) is predicted in these areas due to habitat fragmentation effects (Fig. 6a).

Effects of climate change on population connectivity and genetic diversity

Climate change was predicted to dramatically reduce the extent and connectivity of dispersal habitat across scenarios (Fig. 2b–e). The extent of dispersal habitat is reduced by over 40 % between the 1,500 and 2,000 m scenario, corresponding to a climatic warming of +3.3 °C (Littell et al. 2011), to 42 % of the study area (Fig. 3). The largest patch of connected habitat decreases by 65 % (from 62 to 22 % of the study area) between the 1,500 and 2,000 m scenario (Fig. 3). Long distance dispersal is still predicted to maintain a level of gene flow among the core populations in the central and eastern parts of the study across all climate change scenarios (Fig. 4b–e), but many of the remnant core habitat patches in the northwestern part of the study area are predicted to become genetically isolated by the 1,900 m scenario (Fig. 5b–e). As a result of this increasing fragmentation, large portions of the study area are predicted to express significant isolation by landscape resistance, and genetic diversity is predicted to decrease dramatically in the northwestern parts of the study area between scenarios 1,600 and 2,000 m (Fig. 6b–e). By scenario 2,000 m (+3.3 °C) genetic diversity in all subpopulations in the northwestern

quarter of the study area is predicted to be reduced to very low levels. In contrast, climate change is not predicted to substantially reduce genetic diversity in the large patches of habitat in central Idaho, the northern continental divide, southwest Montana and the Greater Yellowstone Ecosystem (Fig. 2a–e). These areas are predicted to remain suitable as marten dispersal habitat across all climate change scenarios, and as a result genetic diversity is predicted to remain high (Fig. 6a–e).

Corridors, barriers and fracture zones

There are relatively few locations in the study area that are important corridors in the current landscape that also remain intact across the climate change scenarios (Fig. 7). We identified only five such locations (Table 3). Conversely, we identified seven locations that were always a barrier (based on resistant kernel predictions) across all climate scenarios (Table 3). There were 19 locations that were predicted to function as corridors in the current landscape that become barriers by scenario 2,000 m (Table 3).

Discussion

Climate change is affecting populations by changing the distribution of suitable ecological conditions (niche

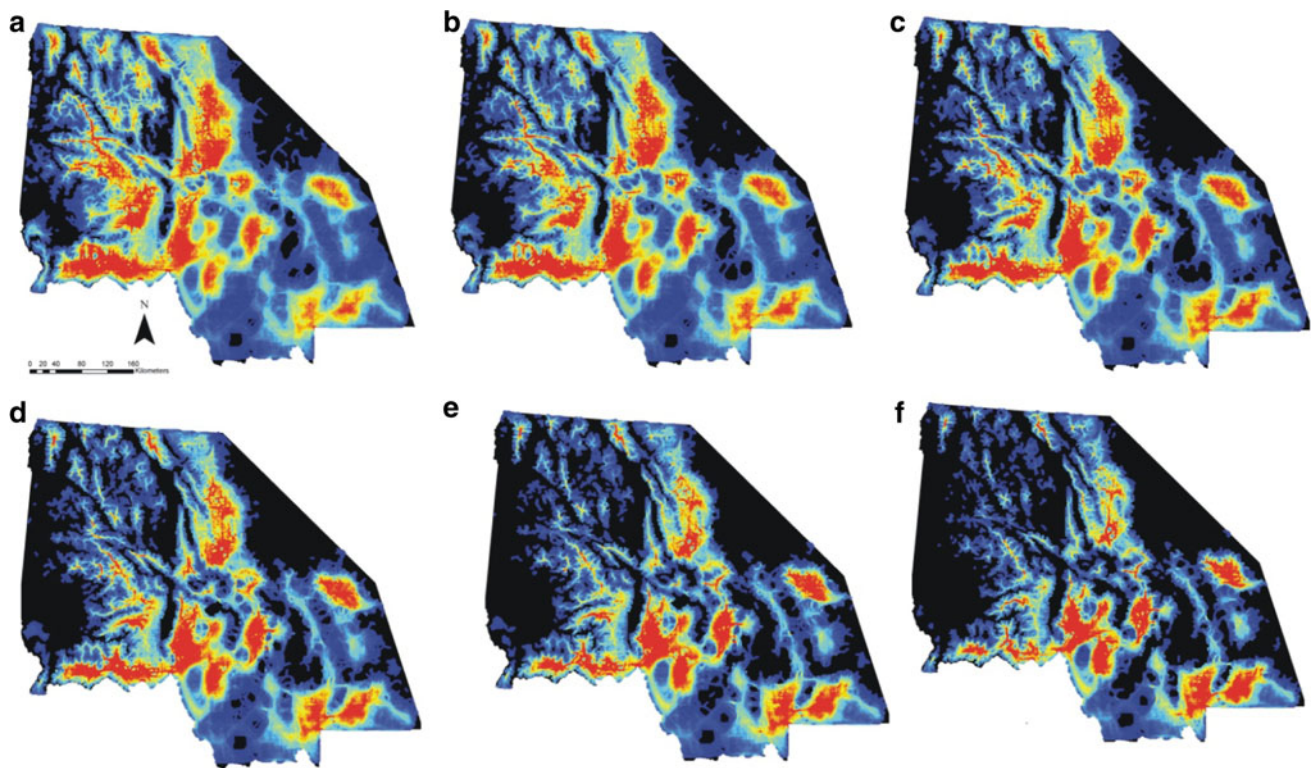


Fig. 4 Predicted density of least cost paths connecting all pixels of optimal marten habitat at a 30,000 unit cost distance dispersal threshold for each of the six climate change scenarios. **a** 1,500 m optimal elevation, **b** 1,600 m optimal elevation, **c** 1,700 m optimal elevation, **d** 1,800 m optimal elevation, **e** 1,900 m optimal elevation,

and **f** 2,000 m optimal elevation. *Black areas* are predicted to have zero density of least cost paths and are expected to have zero occupancy. The *color gradient* from *dark blue* to *red* reflects increasing density of least cost paths connecting optimal habitat, with red areas having very high density of least-cost paths

migration), the ability of populations to migrate from current to future suitable habitat conditions, and ability to maintain connectivity within populations as these changes in the landscape occur (Parmesan and Yohe 2003). Thomas et al. (2004) found that mid-range climate-warming scenarios for 2050 may commit between 15 and 37 % of species to extinction because of inability to track climate change with range shifts. Species associated with high elevation habitats may be particularly at risk given these populations tend to exist in isolated habitat islands that grow increasingly small and further isolated with climate change (Thomas et al. 2004). For example, Schwartz et al. (2009) demonstrated gene flow is restricted in areas of the landscape without spring snow and facilitated along corridors and stepping stones of high elevation habitat. McKevley et al. (2011) projected the extent and pattern of likely future spring snowpack and modelled changes in extent of suitable wolverine habitat and population connectivity. They found that expected climate change by 2080 would dramatically reduce the extent of suitable habitat and population connectivity for wolverine across their range in the lower 48 states.

American marten is also a species associated with relatively high elevations and extensive snow pack in the

western United States. Our analysis suggests that as suitable habitat area is reduced and fragmented by climatic warming, gene flow will likely become attenuated across the landscape, greatly reducing genetic diversity, particularly in areas of relatively low elevation, and with many local populations predicted to become fully isolated or be eliminated altogether.

Current population connectivity and genetic diversity

Our prediction of current isolation by distance and high genetic diversity within large unfragmented habitat patches is similar to results of landscape genetic studies of American marten in other parts of their range. For example, Broquet et al. (2006) found that American marten in northwestern Ontario had very weak correlation between genetic distance and geographic or ecological distance across large spatial extents. Koen et al. (2012) found significant support for isolation by distance in a genetic study of American marten across Ontario, with no independent support for isolation by increased landscape resistance resulting from logging. The above studies are from boreal landscapes where elevation, climate and major vegetation types are constant across large extents.

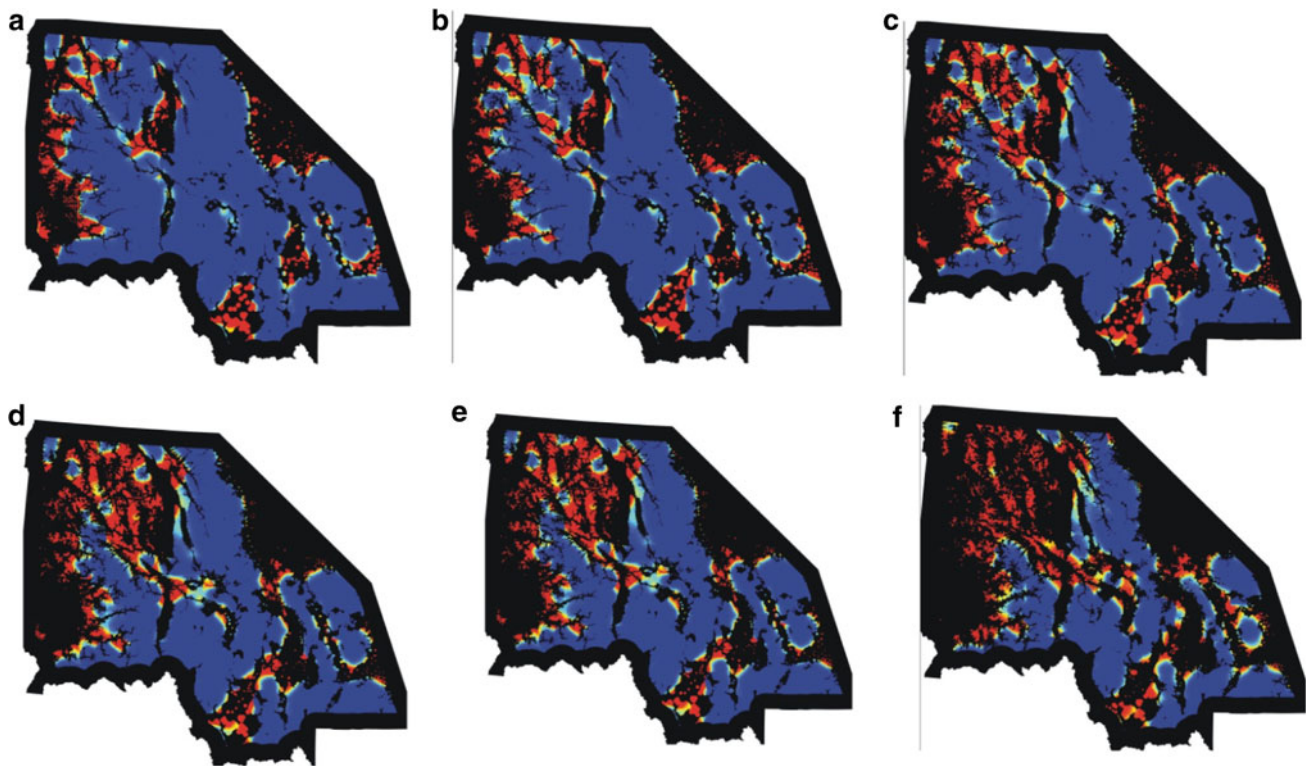


Fig. 5 Predictions of the probability of the genetic structure in the local population (62,500 ha) being significantly affected by population fragmentation (independent of distance) across all six climate scenarios. **a** 1,500 m optimal elevation, **b** 1,600 m optimal elevation, **c** 1,700 m optimal elevation, **d** 1,800 m optimal elevation, **e** 1,900 m optimal elevation, and **f** 2,000 m optimal elevation. Red areas are

predicted to have 100 % probability of significant influence of landscape fragmentation on genetic differentiation. Blue areas are predicted to have no significant effect of landscape fragmentation, and reflect areas of isolation by distance. The gradient from blue to red is of increasing probability of significant landscape fragmentation effects

Notably, climatic conditions are uniform or change gradually over long geographical distances. Cushman et al. (submitted) showed that one would not expect to detect significant isolation by landscape resistance in such uniform environments.

We predict that the northwestern portions of the current landscape are sufficiently fragmented to produce isolation by landscape resistance and the resulting reductions in genetic diversity. Consistent with our predictions, Wasserman et al. (2010) found relatively strong patterns of genetic differentiation as a function of elevation, independently of geographical distance in the northwestern part of our study area. Similar results have been reported for other species. For example, Short Bull et al. (2011) also found that landscape structure only significantly affects gene flow in American black bear (*Ursus americanus*) in regions with high heterogeneity in landscape resistance.

Climate change and connectivity in the northern Rocky Mountains

We predict that climate change will result in a transition from genetic isolation by distance to isolation by landscape

resistance throughout the western and northwestern U.S. northern Rocky Mountains, resulting in substantial local reductions in genetic diversity. Genetic diversity is expected to be reduced when populations are fragmented into disjunct patches or along the edges of complex patches (Shirk and Cushman 2011). The isolation of remnant marten populations in northwest Montana and the Idaho Panhandle predicted by 2080 may dramatically reduce genetic diversity, with most loci predicted to be fixed at a single allele. American marten populations in the western and northwestern portions of the study area may suffer severe demographic and genetic consequences. The dramatic reduction of habitat area will likely be accompanied by large decreases in local population size, increasing likelihood of local extinction due to demographic or environmental stochasticity (Stacey and Taper 1992) or Allee effects (Dennis 2002). We predict that many of the remnant habitat patches will be isolated thus cannot benefit from demographic rescue or experience recolonization after local extinction. The very low genetic diversity predicted in these small isolated patches increases the likelihood of fixation of deleterious recessive alleles (Willi et al. 2006) and decreases in fitness due to inbreeding depression

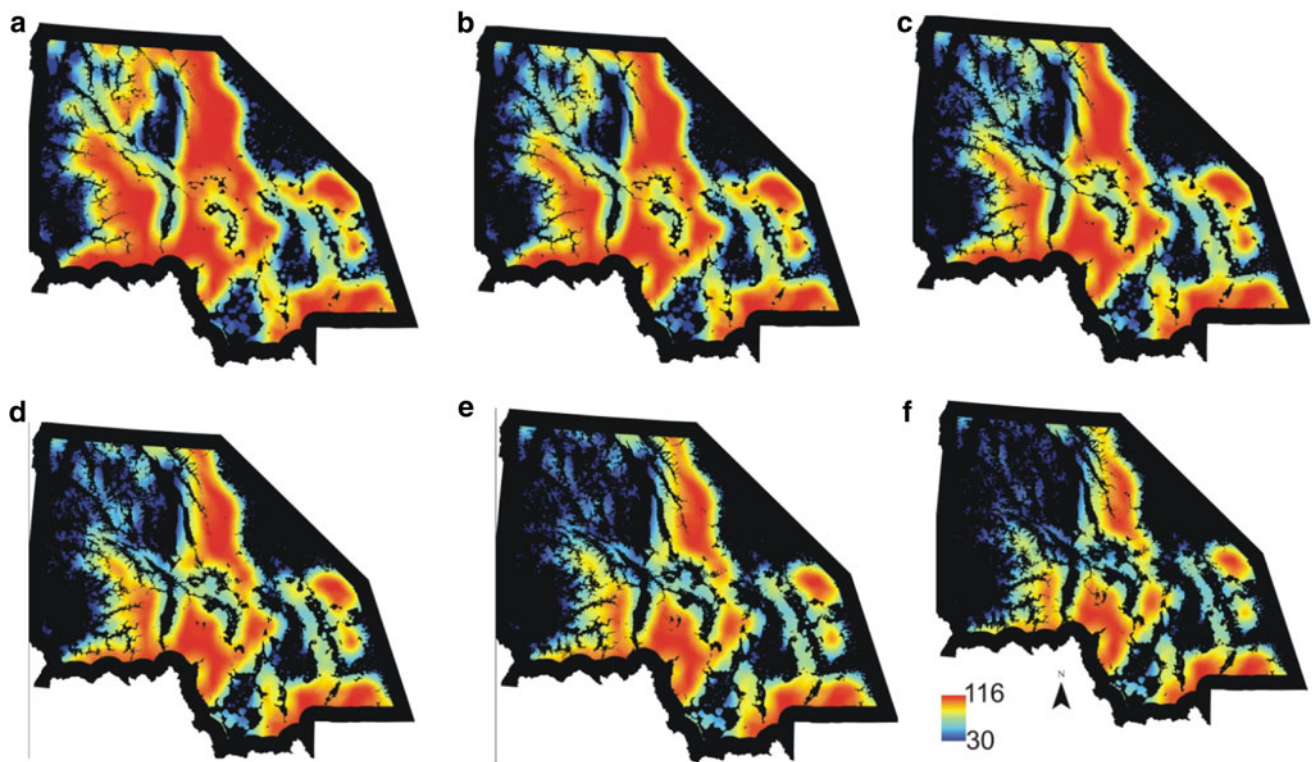


Fig. 6 Predicted number of alleles in the local American marten population (within a 62,500 km extent) across all six climate scenarios. **a** 1,500 m optimal elevation, **b** 1,600 m optimal elevation,

c 1,700 m optimal elevation, **d** 1,800 m optimal elevation, **e** 1,900 m optimal elevation, and **f** 2,000 m optimal elevation. The prediction is the expected number of alleles across 30 microsatellite loci

(Brook et al. 2002; Crnokrak and Roff 1999; Hedrick and Kalinowski 2000; O’Grady et al. 2006; Tanaka 2000).

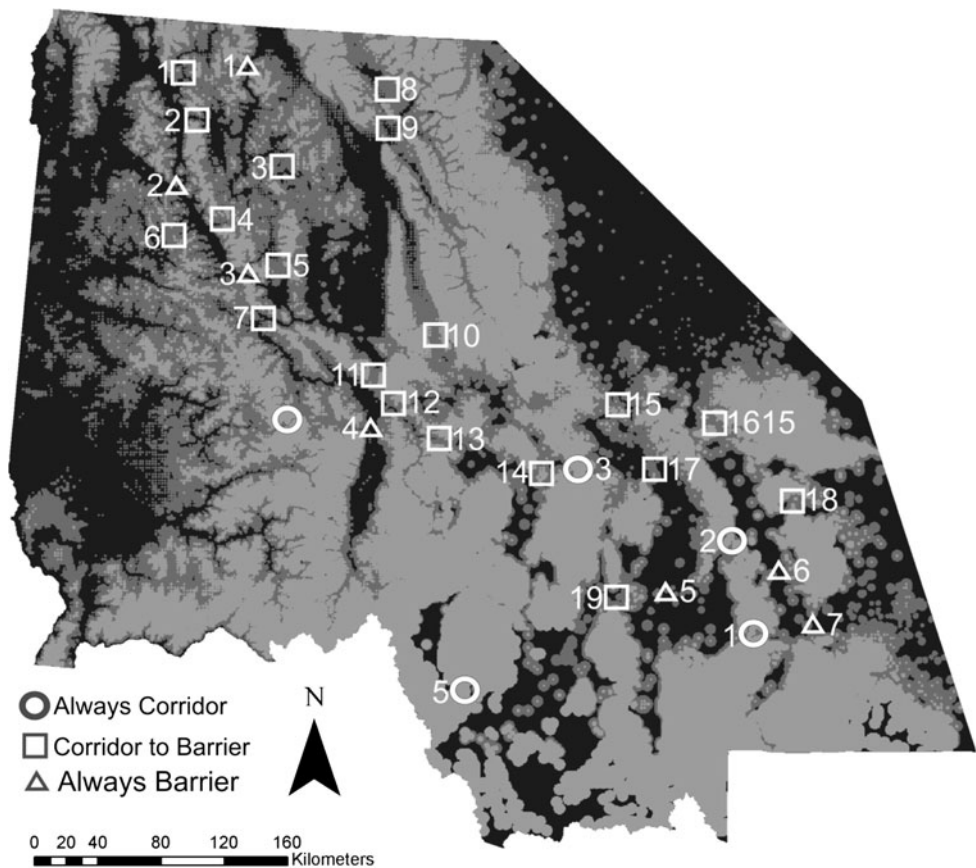
In contrast, the degree of climate change expected by 2080 we predict will not fragment the large population core areas in the central and eastern portions of the study area. These areas are characterized large extents of high elevation forest that are predicted to remain suitable as marten dispersal habitat across all climate change scenarios. As a result, gene flow is predicted to remain governed by isolation by distance with retention of high levels of genetic diversity.

The observation of dramatically different potential responses to climate change within a single species in one geographical region has a number of potentially important implications. First, it shows that the consequences of climate change for population connectivity and genetic diversity are highly dependent on how the ecology of the particular species interacts with the degree and nature of ecological change that climate change brings to the landscape. American marten are not likely to have a single, monotonic response to climate change. In the warmer and lower elevation northwestern parts of the United States northern Rocky Mountains climate change is expected to rapidly push the landscape past fragmentation thresholds resulting in dramatic reductions in habitat area and genetic

diversity, while in the higher and colder central and eastern parts of the range climate change is predicted to not push the landscape past connectivity thresholds and the marten populations are expected to remain in large, well connected and genetically diverse patches, at least within the next seven decades. This highlights the importance of evaluating species vulnerability to climate change based on clear understandings of the drivers of population connectivity and gene flow, and how a given degree of climatic warming will interact with current landscape conditions.

Our connectivity modeling identified numerous places where current landscape linkages connecting population core areas are predicted to be broken by climate change. Given that the connectivity model for this species is driven by climate (Wasserman et al. 2010), it would seem there may be relatively little that can be done to mitigate these effects other than global scale efforts to reduce greenhouse gas emissions. However, even though the formal connectivity model that is most empirically supported based on genetic differentiation is climate driven, there may be landscape-scale conservation and restoration strategies that might enhance the viability of local core populations and connectivity among them. Habitat suitability of American marten in the study area is highly related to canopy cover, road density and extent of late-seral forest at broad

Fig. 7 Climate change impacts on corridors and barriers. The *light gray areas* are predicted to be connected populations at the 2,000 m scenario. The *dark gray areas* are predicted to be connected in the 1,500 m scenario. Circles represent corridors that are robust to climate change and remain intact across all scenarios. *Squares* are locations that are corridors in the 1,500 m scenario, but that are broken and no-longer connected in the 2,000 m scenario. The *triangles* are areas that are predicted to be barriers to dispersal in all scenarios. The number correspond to the order in Table 3



landscape extents (Wasserman et al. in press). Landscape-level habitat suitability of marten could be enhanced by management strategies that reduce road densities, increase average canopy cover within watersheds, and protect late seral forests. Increased habitat suitability might result in denser populations and a larger number of dispersing individuals in each core population, which could partly balance the effects of increased isolation on successful inter-core dispersal.

To implement such an approach most effectively, managers should prioritize corridors in the current landscape based on their importance to maintaining network connectivity, and evaluate the importance of corridors as climate change progresses. Our predictions of current and future corridor locations could guide this prioritization. Once key corridor locations are identified, conservation and restoration efforts should be focused in these areas and the adjacent population core areas to enhance habitat quality by reducing road density, increasing canopy closure and protecting late seral forest.

Limitations of the analysis

Our results should be interpreted within the scope and limitations of our analysis. We use a landscape resistance model developed in the northwestern quarter of the study

area for the entire extent of the Northern Rocky Mountains. It is untested whether this model applies to the full study area. Cushman et al. (2009) extrapolated a landscape resistance model for Black bear (*U. americanus*) developed in the same northwestern study area to the full Northern Rocky Mountains. Subsequently, Short Bull et al. (2011) confirmed through a meta-replicated landscape genetic study that the Cushman et al. (2006) resistance model used in Cushman et al. (2009) applied robustly to the full Northern Rocky Mountains. The resistance model used here is a single variable model (elevation) suggesting that it is more likely to be generalizable than complex multivariate models (such as Cushman et al. 2006). Thus, while the assumption of spatial stationarity of our resistance model is untested, we think it is very likely.

Ideally, we would have simulated genetic diversity explicitly in each of our six climate scenarios across the full study area. However, individual-based landscape genetic simulations require that every individual in the simulated population be represented. The expected number of individual martens in our 30.2 million hectare study area is in the tens to hundreds of thousands. It is intractable with current simulation models and computing technology to conduct full individual-based, spatially-explicit simulation modeling on such a large and broadly distributed population. Accordingly, we used the relationships identified by

Table 3 Locations of predicted corridors and barriers across climate change scenarios

Climate robust corridors	
1	Beartooth to Bridger
2	Bridger to Big Belt
3	Nevada to Lewis and Clark
4	Northern to southern central Idaho mountains
5	Beaverhead to Pioneer
Climate vulnerable corridors	
1	W to E Purcell
2	Purcell to Cabinet
3	N to S Salish
4	W to E Cabinet
5	Salish to Cabinet
6	W to E Coeur D'Alene
7	Coeur D'Alene to Reservation Divide
8	Whitefish to Livingston
9	Whitefish to Apgar
10	Mission to Swan
11	Reservation Divide to Rattlesnake
12	Rattlesnake to Garnett and Saphire
13	Garnet to John Long
14	Garnet to Boulder
15	Nevada to Big Belt
16	Big Belt to Little Belt
17	Big Belt to Elkhorn
18	Castle to Crazy
19	Tobacco Root to Bolder
Consistent barriers	
1	Purcell to Salish
2	Cabinet to Coeur D'Alene 1
3	Cabinet to Coeur D'Alene 2
4	Bitterroot to Saphire
5	Tobacco Root to Big Belt
6	Bridger to Crazy
7	Crazy to Absaroka

Names reflect the mountain ranges separated by the barrier/corridor (e.g., Beartooth to Bridger corresponds to a climate robust corridor between the Beartooth and Bridger Mountain Ranges). The locations of these corridors and barrier are shown in Fig. 7

Wasserman et al. (2012) between genetic diversity and landscape configuration to predict local genetic diversity across our study area in each of our scenarios.

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