Modeling the effects of dispersal and patch size on predicted fisher (*Pekania* [*Martes*] *pennanti*) distribution in the U.S. Rocky Mountains

Lucretia E. Olson [a], Joel D. Sauder [b], Nathan M. Albrecht [c], Ray S. Vinkey [d], Samuel A. Cushman [e], Michael K. Schwartz [a,*]

[a] *Rocky Mountain Research Station, United States Forest Service, 800 E. Beckwith Ave., Missoula, MT 59801, USA*
[b] *Idaho Department of Fish and Game, 3316 16th Street, Lewiston, ID 83501, USA*
[c] *Wildlife Program, Coeur d'Alene Tribe, 401 Anne Antelope Rd., Plummer, ID 83851, USA*
[d] *Montana Fish, Wildlife & Parks, P.O. Box 1066, Philipsburg, MT 59858, USA*
[e] *Rocky Mountain Research Station, United States Forest Service, 2500 S. Pine Knoll Dr. Flagstaff, AZ 86001, USA*

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ABSTRACT

Climate change impacts many species through shifts in habitat. The intensity of this impact will depend on the dispersal rates of the species, the patchiness of the environment, and the velocity of habitat change. Here we examine how dispersal affects projected future habitat availability for a threatened carnivore, the fisher (*Pekania* [*Martes*] *pennanti*). We used non-invasive genetic sampling to detect fisher across their historical distribution in Montana and Idaho. This survey included 4846 non-invasive hair snares, of which 288 identified fishers through mitochondrial DNA analysis. We modeled the distribution of fisher across western Montana and northern Idaho using a suite of vegetative, topographic, and climatic variables. We modeled future distribution using a global climate model and two climate change scenarios (high emissions [A2] or reduced emissions [B2]) and three time steps (2030, 2060, and 2090). We incorporated the effects of dispersal ability and habitat patch size into our model by varying the distance and enforcing a minimum patch size at which newly created habitat could be colonized. We found that the probability of current fisher occurrence was highest given the presence of mesic forest types with tall trees, high annual precipitation, and mid-range winter temperatures. Future predictions show an increase in area of high-probability habitat under most dispersal assumptions. Interestingly, we found a large contrast in results when minimum patch size and species dispersal capabilities were considered. Our distribution model with full dispersal and no limits on patch size predicted a 24.5% increase in fisher habitat by 2090, whereas a dispersal limit of 1 km through non-habitat (agricultural fields and urban zones) and a minimum patch size yielded a loss of 25.8% of fisher habitat under this same scenario. Varying dispersal appears to limit habitat availability more than minimum patch size under most scenarios.

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1. Introduction

As the warming trend in the global climate continues, climate-mediated changes in habitat are predicted to force many species to shift their distributions in order to persist (Chen et al., 2011; Engler et al., 2011; Zhu et al., 2012). Complex interactions between temperature and climatic water balance make the direction of these shifts challenging to predict (Crimmins et al., 2011; Dobrowski et al., 2013), thus requiring careful modeling approaches. One emerging pattern, however, is that different ecosystem types are predicted to shift their distributions at different velocities (Loarie et al., 2009; Burrows et al., 2011). Montane ecosystems, such as temperate coniferous forest and grasslands, have some of the slowest predicted velocities of change, while deserts, mangroves, and flooded grasslands are predicted to shift in response to climate change at the greatest rate (Loarie et al., 2009). For animals that exist exclusively in a given ecosystem, the ability to keep up with the velocity of their changing habitat, or successfully adapt to a new ecosystem, is crucial for their continued survival (Doak and Morris, 2010; Hansen et al., 2012). Species with narrow physiological limits, such as pika, or those that are endemic to a specific habitat type are less likely to be able to keep up with such shifts (McKelvey et al., 2011; Sandel et al., 2011).

The dispersal ability of a species, as well as the degree of fragmentation of future habitat, will likely contribute to a given species' ability to keep up with the pace of climate-mediated habitat

change (Walther et al., 2002). Vagile organisms, those that are easily able to move and disperse, will see an advantage over those that are more sessile, as regional climates are replaced by novel conditions (Araújo and Pearson, 2005). A species' ability to move through what is traditionally considered non-habitat, such as an urban or agricultural matrix surrounding suitable habitat, may also contribute to the success or failure of a species to keep pace with shifting habitat. Thus, we would expect species that are dispersal generalists to persist under rapid climate change as compared to dispersal specialists. In addition, species that currently reside in large contiguous habitats with few topographic breaks (e.g., the boreal forest) may have an advantage over those that reside in habitats that are naturally fragmented (e.g., the intermountain west).

To predict the range changes of an organism under a changing climate, species distribution models are frequently used. Species distribution models (SDMs) use locations at which an animal is known to occur to determine the physical and environmental characteristics most likely to predict species presence. While there are many analytical approaches to create SDMs, one of the most frequently used is a Maxent model (Phillips and Dudík, 2008; Elith et al., 2011), which allows for presence-only occurrence data. A limitation of Maxent and other commonly used SDMs is the lack of ability to realistically incorporate dispersal (but see Engler et al., 2012). Many SDMs are limited to either no dispersal or complete dispersal, neither situation nor species specific.

The importance of incorporating dispersal when investigating the effects of climate change on species persistence has been the subject of much recent research. Pearson et al. (2006) demonstrate the impact of dispersal on predicted gain or loss of suitable habitat for four Proteaceae in the Western Cape of South Africa; under some models the addition of dispersal can increase suitable habitat by greater than 200%, while lack of dispersal reduced habitat. A study by Early and Sax (2011) showed that dispersal ability and population persistence were important predictors of amphibian species' ability to persist in the face of increased climate variability. Schloss et al. (2012) modeled dispersal distances of mammals in the western hemisphere and found that 20% of range contractions in the modeled species would be due to an inability to keep pace with shifting climate. Additionally, the role of connectivity, and indirectly dispersal, between current habitat and patches predicted to be suitable under a changing climate has been examined by Lawler et al. (2013) in vertebrates and Imbach et al. (2013) in plants. Both studies found that movement between suitable habitat patches is crucial for species persistence given a changing climate.

Here we use Maxent methodology to understand how the distribution of fishers (*Pekania* [*Martes*] *pennanti*) in the northern United States Rocky Mountains (north-central Idaho and western Montana) responds to current and future climatic conditions, while considering the effects of dispersal and minimum patch size. Fishers are a medium-sized mustelid endemic to North America. They are associated with old growth forests that contain ample cover, structure and large diameter trees (Zielinski et al., 2006; Purcell et al., 2009; Aubry et al., 2013; Schwartz et al., 2013). Their historical range spanned the northern portion of the continent from east to west coasts, extending north to the southern Yukon, Canada, with southern extensions into California, Wyoming, and the United States east coast as far south as Kentucky (Lewis and Stinson, 1998). Currently, this range is being recolonized in the eastern and midwestern United States, but remains restricted in the western United States (Montana, Idaho, Washington, Oregon, California) due to historical habitat loss and human influences.

In this study, we model the current distribution of the northern Rocky Mountain population of fishers with data from a non-invasive genetic survey. We then examine predicted changes in the distribution of fishers in response to future climate conditions under two carbon emissions scenarios and at three time steps (2030, 2060, and 2090). To allow prediction of fisher distributions into the future, we created two Maxent models, one that includes vegetation, climate, and topography variables and one that only considers climate and topography variables. Since both future vegetation and climate are uncertain, we use the climate/topography-only model for future predictions of fisher distribution to avoid the uncertainty introduced from modeled vegetation variables. Finally, we expand on standard Maxent models by providing a new approach with which to explore the role of dispersal ability and habitat patch size in allowing fisher to take advantage of shifting habitat as a result of climate change.

2. Methods

2.1. Occurrence data

We used non-invasive genetic sampling to survey for fisher presence across the study area (Zielinski et al., 2006; Kendall and McKelvey, 2008). Several different sampling designs were used to deploy hair snares. The majority of hair snares were deployed across a grid consisting of 5 by 5 mile cells, with approximately 4 snares per grid cell. The choice of grid cell size and number of snares was based on the literature and preliminary data (Zielinski and Kucera, 1995; Squires et al., 2004; Schwartz et al., 2006). We limited the area surveyed to all areas in Idaho and Montana with predicted fisher habitat, as determined by the USGS GAP analysis data. Once the 5 mi² grid was overlaid on all fisher habitat, we limited potential survey grid cells to those with greater than 50% fisher habitat, which resulted in 1689 potential grid cells for survey. From 2007 to 2011, we surveyed 610 of these cells, chosen largely by availability to access during the winter. The remainders of the cells were part of a finer scale survey for fisher lead by the Coeur d'Alene Tribe that deployed similar methodologies. In total we deployed 4846 hair-snares. We sequenced the cytochrome b region of the mitochondrial DNA genome following the methods of Riddle et al. (2003) or Schwartz (2007) to determine the species that deposited the hair collected by the non-invasive snare and obtained 288 genetic samples of fisher DNA (at 279 unique locations). In addition to the non-invasive sampling, we also included harvest data reported by fur trappers in Montana from 1980 to 2010 (N = 47; Vinkey et al., 2006), resulting in a total sample size of 326 fisher locations. To examine the impact of using data collected from individuals that were part of a reintroduction effort, we considered a second dataset that did not include locations from a recent reintroduction of fishers in the Cabinet Mountains of Montana from 1989 to 1991, as defined by Heinemeyer (1993).

Species distribution modeling can be sensitive to the extent of the background chosen; thus, selecting an extent that is overly large or small may influence the predicted distribution (Elith et al., 2011). We chose the extent of the study area based on the minimum hydrologic boundaries that contained all fisher occurrences (Fig. 1). Fisher surveys rarely occurred in wilderness areas; thus, to prevent the use of these areas as background locations in modeling, we used a mask to remove all unsampled wilderness areas, as well as all rivers and lakes, from the study area before running the model.

2.2. Environmental data

We initially considered a suite of vegetative, topographic, and climatic variables potentially important to fisher distribution (Zielinski et al., 2010; Purcell et al., 2009; Raley et al., 2012; Aubry et al., 2013; Table 1). Vegetation data were calculated from land-cover maps produced by LandFire version 1.1 (U.S. Forest Service)
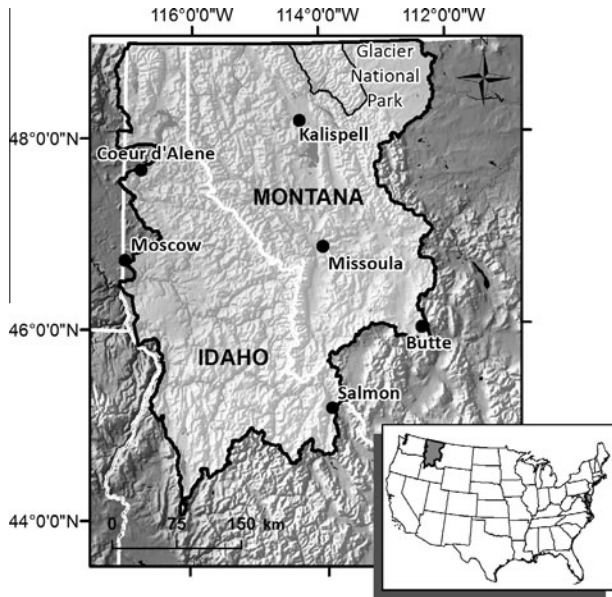
Fig. 1. Geographic extent of the study area, spanning western Montana and northern Idaho; cities and Glacier National Park locations are provided for reference. The inset shows the study area (in dark grey) in relation to the United States.

and satellite imagery obtained from LandsatTM 5. We used the 'Canopy Cover' (CC), 'Canopy Height' (CH), and 'Existing Vegetation Type' (EVT) layers from LandFire. We transformed Canopy Cover, Canopy Height, and Existing Vegetation Type into continuous variables to reduce map inaccuracies. We did this by first simplifying the existing categorical values for each variable. Canopy cover was categorized into Non-Forest, 0–10%, 10–30% cover, 30–60% cover, and 60–100% cover. Canopy height was categorized to Non-Forest, 0–10 m, 10–20 m, and 25–50 m. Existing Vegetation

Type (EVT) was categorized into Other (including urban, agricultural, non-forest, water, rock, and ice), Mixed Conifer (including Dry-Mesic Montane Mixed Conifer, Mesic Montane Mixed Conifer, and Ponderosa Pine Forest), Spruce-Fir (including Subalpine Woodland, Lodgepole Pine, Dry-Mesic Spruce-Fir, Mesic-Wet Spruce-Fir, and Aspen-Mixed Conifer Forest), Riparian (including Montane Riparian, Subalpine/Upper Montane Riparian, and Conifer Swamp), and Douglas Fir (including Montane Douglas-Fir Forest and Douglas-Fir Forest Alliance). Categories for EVT were determined based on visual analysis of the distribution of each existing LandFire category, so that categories that were in close spatial proximity and/or of similar ecological niche were grouped together into a single category. We then converted each newly created category into a binary variable using ArcMap v10, so that at any given location, the value for EVT Mixed Conifer was either 1 (Mixed Conifer present) or 0 (Mixed Conifer absent). This binary variable was than smoothed using a circular 'moving window', so that each 100 m^2 raster cell represented the proportion of each LandFire variable category in a surrounding 900 m radius neighborhood. Thus from three categorical LandFire variables (CC, CH, and EVT), we created 14 indices of the proportion of each variable category in a 900 m neighborhood.

Since previous studies have indicated the importance of mesic and riparian forest types for fisher habitat in the U.S. Rocky Mountains (Jones and Garton, 1994; Roy, 1991; Schwartz et al., 2013), we also considered single categories of EVTs as possible predictors of fisher presence. For these variables, we used only Dry-Mesic Montane Mixed Conifer, Mesic Montane Mixed Conifer, and Montane Riparian Systems as binary variables, again with a moving window so that each 100 m pixel represented the proportion of a given forest type within a 900 m circular neighborhood.

Aubry et al. (2013) show in a meta-analysis of fisher data from 8 studies conducted on the west coast of North America that both vegetation cover and a heat loading index (a metric that combines aspect, slope, and latitude on temperature accumulation) are

Table 1
Environmental variables considered for use in the model; not all variables were used in the final model.

	Covariate	Resol'n	Source	Description
Vegetation	Gross primary productivity	1 km	MODIS; S. Running	Mean GPP from 2000 to 2006
	Canopy cover	30 m	LandFire	
	Canopy height	30 m	LandFire	
	Existing vegetation type	30 m	LandFire	
	Normalized difference vegetation index	30 m	Landsat 5 TM	Index of vegetation productivity
	Brightness	30 m	Landsat 5 TM	Tasseled cap index, measure of soil
	Greenness	30 m	Landsat 5 TM	Tasseled cap index, measure of vegetation
	Wetness	30 m	Landsat 5 TM	Tasseled cap index, measure of soil and canopy moisture
Topographic	Elevation	100 m	USGS	Originally from 30 m DEM, bilinearly interpolated to 100 m
	Slope	100 m	USGS	Calculated in ArcGIS from elevation using spatial analyst
	Annual potential solar radiation	100 m	USGS	Calculated in ArcGIS using solar analyst
	Topographic position index	100 m	USGS	Measure of terrain variability; positive indicates ridges, negative indicates drainages
Climate	Mean winter precipitation	800 m	PRISM	Average December, January, and February precipitation
	Mean winter minimum temperature	800 m	PRISM	Average December, January, and February minimum temperature
	Mean winter maximum temperature	800 m	PRISM	Average December, January, and February maximum temperature
	Mean summer minimum temperature	800 m	PRISM	Average June, July, and August minimum temperature
	Mean summer maximum temperature	800 m	PRISM	Average June, July, and August maximum temperature
	Annual precipitation	800 m	Moscow FSL	Mean annual precipitation, in mm, 1961–1990
	Degree days less than 0	800 m	Moscow FSL	Average of the summation of the difference between average monthly temp and 0°, 1961–1990
	Growing season precipitation	800 m	Moscow FSL	April to Sept precipitation, 1961–1990
	Mean annual temperature	800 m	Moscow FSL	Mean annual temperature, 1961–1990
	Mean temp in coldest month	800 m	Moscow FSL	Mean temp for the coldest month, 1961–1990
	Mean temp in warmest month	800 m	Moscow FSL	Mean temp for the warmest month, 1961–1990

important for fisher habitat. Thus, we also used Landsat satellite imagery to calculate the tasseled cap vegetation indices. These include brightness, a measure of soil reflectivity, greenness, a measure of green vegetation, and wetness, a measure of moisture in the soil and vegetation (Kauth and Thomas, 1976).

For topographic variables, we used a 30 m digital elevation model (National Elevation Dataset, USGS) and derived slope, annual solar radiation, and topographic position index from this elevation layer using ArcGIS 10.0 (Environmental Systems Research Institute, 2011, Redlands, CA). Annual solar radiation was calculated using the 'Area Solar Radiation' tool, which calculates the total incoming direct, diffuse, and reflected insolation over the space of one year. Topographic position index (TPI) is a measure of terrain variability, with negative values indicating valleys and positive values indicating ridges (Weiss, 2001), and was found to be a significant predictor of fisher distribution in Schwartz et al's (2013) radiotelemetry-based habitat research in Idaho's Clearwater subbasin. We calculated TPI at three scales: 300 m, 1000 m, and 2000 m.

Climatic variables considered included mean annual precipitation, precipitation during the growing season, annual mean temperature, mean temperature during the coldest month of the year, mean temperature during the warmest month of the year, and the number of degree days less than zero. We used climate data compiled by the Moscow Forestry Sciences Laboratory (Rocky Mountain Research Station, U.S. Forest Service). Data was compiled from 1961 to 1990 at an 800 m spatial resolution.

All variables were created in raster format in ArcMap v10, and resampled to 100 m^2 resolution.

2.3. Modeling

To avoid including highly correlated variables in the model, we screened all variables for pairwise correlation using Pearson's correlation coefficient in the statistical package R (R Development Core Team, 2010). We considered variables to be highly correlated if $r \geqslant 0.7$, and kept only the variable that best predicted fisher presence when used as a univariate predictor. This method of variable selection resulted in 18 variables for use in modeling (Table 2).

We ran two models in Maxent version 3.3.3e (Phillips et al., 2006; Phillips and Dudík, 2008), a 'full' model, including all 18 vegetative, topographic, and climatic variables, and a 'climate/topography only' model, including only six topographic and climatic variables (Table 3). We randomly partitioned the data into training

and testing occurrences, with two thirds of the data used to train the model and one third of the data used for testing. We accepted the default values recommended by Maxent for the regularization multiplier (1), a constant supplied by the user which limits model overfitting, and the number of random background locations selected from the study area ($N = 10,000$) for use in constructing the distribution of environmental covariates. To generate measures of model variance, we used k-fold cross-validation (here we used 10-fold), which divides the data into k subsets and runs the model k times, each time using k-1 of the subsets for training, and a different subset for testing. This approach has the advantage of using all of the data for model training, as well as producing estimates of model variation by averaging model results over all k iterations of the model.

We evaluated model performance using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding and Bell, 1997). This metric plots sensitivity (or true positives) against 1 – specificity (or false positives) for a range of threshold values, with the area under the curve providing a measure of the ability of the model to discriminate between presences and absences. Models with an AUC of 0.5 are no better than random, while an AUC of 1.0 would provide perfect discriminatory ability.

2.4. Future climate scenarios

To predict changes in fisher habitat due to changes in climate, we used future climate variables calculated by the Moscow Forestry Sciences Laboratory (USDA Forest Service, Rocky Mountain Research Station) which are based on 1961–1990 climate normals. We selected a single general circulation model (Hadley Centre Coupled Model, version 3; Collins et al., 2001). Under this model, we selected two emissions scenarios: A2, the more severe scenario, which represents an increasing population and more regional economic development, and B2, the more conservative scenario, which represents continuing but slower population growth and more emphasis on environmental protection (IPCC 2007). We chose these two scenarios to provide a lower and upper bound of projected fisher habitat, from conservative to severe. We also chose three time steps at which to project the model (2030, 2060, and 2090).

Once projected, we converted the future probability habitat maps into binary maps using a threshold value chosen to maximize the sum of sensitivity and specificity (Jiménez-Valverde and Lobo, 2007; Freeman and Moisen, 2008). We compared the percent loss or gain in suitable fisher habitat from current conditions to each future scenario by subtracting current fisher area from future fisher area, dividing by current fisher area, and multiplying by 100.

2.5. Dispersal and patch size

Predicted future distributions may be inapplicable to a species if individuals are not able to physically keep up with the projected pace of a shifting distribution (Zhu et al., 2012). To model the effects of dispersal distance across non-habitat, we used the binary

Table 2
Variables used in full distribution model, ranked by their percent contribution to the model, as determined by Maxent.

Variable	Percent contribution
Canopy height, 25–50 m	19.7
Montane Riparian	16.3
TPI 2000	14.7
Mean annual precipitation	13.3
Mean temp in coldest month	6.3
Canopy height, 0–10 m	4.8
Gross primary productivity	4.4
Spruce/fir and lodgepole	4.2
Annual potential solar radiation	2.9
Wetness	2.7
Slope	2.3
Canopy cover, 10–30%	1.8
Brightness	1.7
Dry-mesic mixed conifer	1.1
Canopy Height, 10–25 m	1.1
NDVI	1
Variation in canopy cover	1
Variation in canopy height	0.6

Table 3
Variables used in climate-only distribution model, ranked by their percent contribution to the model, as determined by Maxent.

Variable	Percent contribution	Permutation importance
Mean annual precipitation	33.9	28.9
TPI 2000	29	21.2
Mean temp in coldest mo	27.3	32.8
Slope	6.2	12.9
Solar radiation	2.1	3.9
Persistent Snow	1.6	0.4

future habitat maps created in the previous section for each time step. We considered anything below this binary threshold non-habitat; this was largely open areas, agricultural valleys, or dry forest. We compared each future time step binary variable to the current distribution in binary form, and grouped future habitat into four categories: unsuitable habitat remaining unsuitable, suitable habitat remaining suitable, unsuitable habitat becoming suitable, and suitable habitat becoming unsuitable. We then used a circular moving window in ArcMap v10 to create buffers of given dispersal distances around all suitable habitat from the current binary distribution. We used the "Extract by Mask" tool in ArcMap v10 to calculate areas in which this buffer and the four category future habitat maps overlapped, and counted only future suitable habitat (either suitable remaining suitable or unsuitable becoming suitable) within a specified dispersal distance as occupiable. We performed this analysis for each future time step and climate scenario, with dispersal distances at 1 km, 1.5 km, 2 km, 4 km, and 10 km, as well as no and unlimited dispersal.

In addition to the ability to physically reach newly suitable habitat, the patch size of the future habitat can also influence whether a species will be able to utilize newly available habitat. We used a patch size of 125 km^2 as the minimum size at which a population of fishers could be maintained, based on an average home range size of 25 km^2 per individual and an arbitrary minimum of five home ranges needed to maintain a population (Reed and Bryant, 2000). We based this home range size on the average between a male home range size of approximately 30–40 km^2 and a female home range of 10–16 km^2 (Arthur et al., 1989; Zielinski et al., 2004). We assume that each home range will have at least one female and potentially one male, as fishers of opposite sexes will tolerate home range overlap (Powell and Zielinski, 1994), as well as several juveniles, for a total population of between 6 and 25 individuals (Powell and Zielinski, 1994). We chose this number as the smallest possible population that could be maintained over the short term to allow long-term population persistence (Reed and Bryant, 2000).

To determine the impact of minimum patch size on future available habitat, we used the same binary habitat maps as were used for dispersal distances, detailed above. We converted each binary habitat raster to polygons using ArcMap v10. Each 100 m^2 raster cell was converted to a polygon, and all adjacent polygons were grouped. Each group of polygons represented one habitat patch. We then performed the same comparison as detailed in the dispersal section between the current binary habitat layer, buffered by various dispersal distances, and each future habitat layer grouped into four habitat suitability categories. In this case, however, the suitable habitat was only considered 'available' if it was within the given buffer distance and part of a patch that was greater than 125 km^2. We then summed all available habitat patches that fit these criteria, and compared this to the amount of currently available habitat in patches greater than 125 km^2 to determine the percent change in available habitat. We again used dispersal distances of 1 km, 1.5 km, 2 km, 4 km, and 10 km, as well as no and unlimited dispersal.

3. Results

3.1. Current fisher distribution

The model showing current fisher distribution produced by Maxent using vegetative, topographic, and climatic variables performed well, with a test AUC of 0.87 (SD = 0.017). When we examined the effect of including animals reintroduced into the Cabinet Mountains on predicted fisher distribution, we found little difference in model outputs: for the model with no reintroduced

locations, the testing AUC was 0.845 (SD = 0.020), the order of variable importance did not change, and the spatial distribution of predicted habitat suitability was visually indistinguishable (map not shown). Therefore, we used the model with both reintroduced and native fisher locations, and did not further consider the model in which Cabinet Mountain reintroduction animals were omitted.

The variables that contribute the most to fisher habitat suitability are 25–50 m canopy height (19.7%), montane riparian vegetation (16.3%), topographic position index (14.7%), and mean annual precipitation (13.3%; Table 2), as determined by percent contribution to the model, an index created by Maxent based on the increase in model performance with each variable addition. Mean temperature in the coldest month was also a good contributor to the model (6.3%). All other variables had an individual percent contribution to the model of 5% or less (Table 2). Marginal response curves generated by Maxent, which show predicted habitat suitability based on one variable while holding all other variables at their average value (Phillips et al., 2006), show that probability of suitable habitat was highest with greater presence of canopy height of 25–50 m, greater presence of montane riparian landcover, negative values of TPI (drainages), and greater mean annual precipitation. The current distribution of fisher within the study area, as predicted by the model, is shown in Fig. 2(A).

The same model, but without vegetation variables, produced a test AUC of 0.84 (SD = 0.018); variable importance is given in Table 3. In this model, the variables with the greatest percent contribution to the model were mean annual precipitation (33.9%), topographic position index (29%), and mean temperature of the coldest month (27.3%). Based on the marginal response curves, the probability of suitable fisher habitat was highest with greater mean annual precipitation, negative values of TPI, and mid values of mean temperature in the coldest month. The current distribution of fisher within the study area predicted by the climate/topography only model is shown in Fig. 2(B).

Using a threshold criterion of the maximized sum of specificity and sensitivity (0.102), the 'full' model estimated an area of 36,484 km^2 of suitable fisher habitat within the 140,818 km^2 study area. For the climate/topography-only model, the threshold value at which the sum of sensitivity and specificity were maximized was 0.220. Using this threshold, there are an estimated 30,746 km^2 of suitable fisher habitat within the study area. The differences in predicted habitat suitability between the full and the climate only model are shown in Fig. 3.

3.2. Future fisher distribution

Predictions of future fisher distribution were based on the climate/topography-only model. Given the greater fossil-fuel use A2 scenario, fisher habitat is predicted to increase over each time step, with a 12.1% increase from current conditions to 2030, a 21.4% increase from current to 2060, and a 24.5% increase from current to 2090. Under scenario B2, the lower population, lower fossil-fuel use scenario, predicted fisher habitat is expected to undergo a similar, but less pronounced, expansion, with an initial decrease of 10.7% from current conditions to 2030, followed by an increase of 1.6% from current to 2060, and a final increase of 9.2% from current to 2090 (Fig. 4). The location of suitable fisher habitat is also predicted to change, with a greater probability of fisher occurrence in the northern portion of the study area (Fig. 4).

3.3. Dispersal and patch size

The increases in fisher habitat mentioned above under various climate change scenarios assume unimpeded, complete dispersal. If fisher populations are completely unable to track the habitat changes produced by climate change, fisher habitat is expected
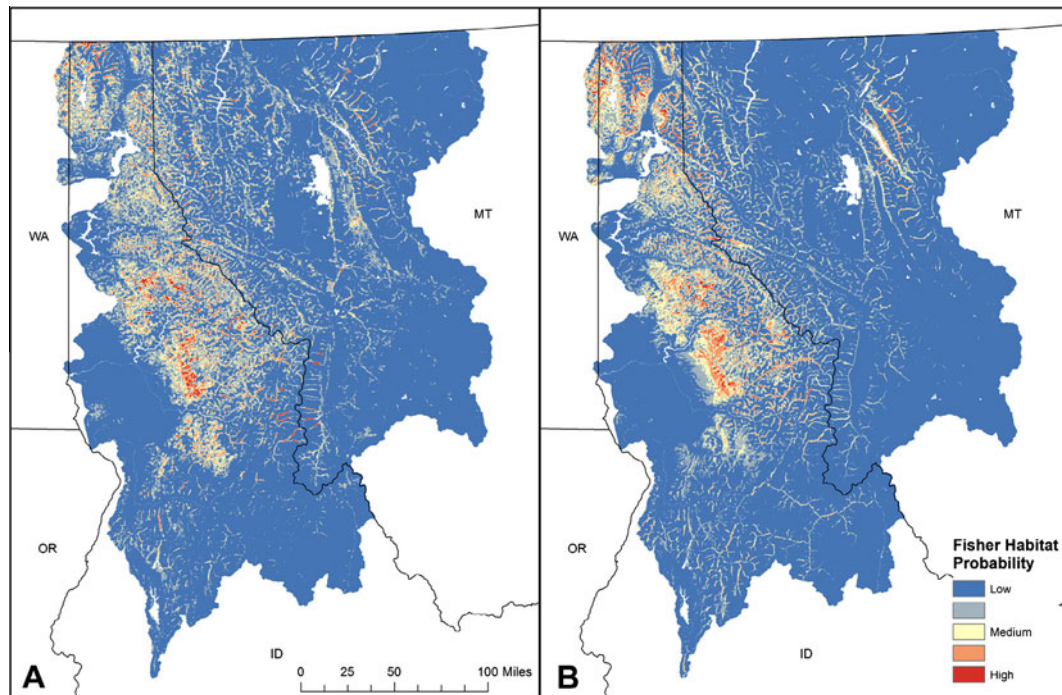
Fig. 2. Current distribution of fishers as modeled with environmental, climate, and topographic variables (A) or climate/topography-only variables (B).
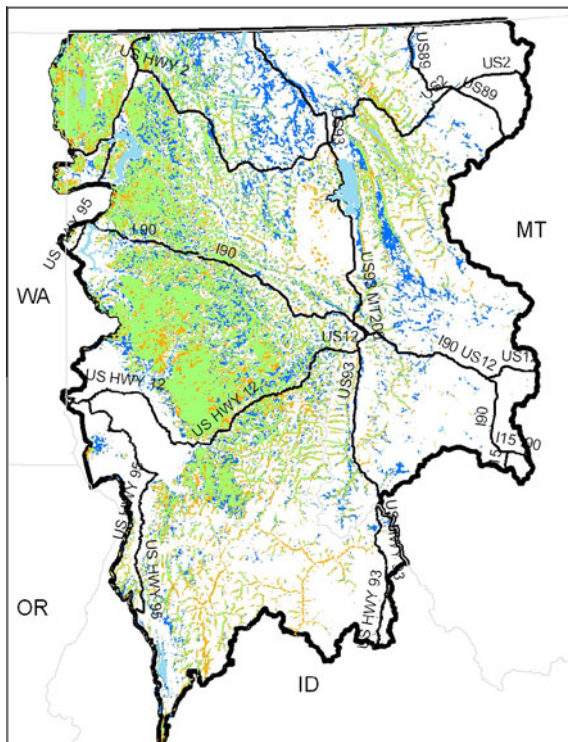

Fig. 3. Comparison between binary predictions for the full model (blue), the climate only model (orange), and the areas in which the models agree (green).

to decrease under both emissions scenarios despite the overall net increase in predicted suitable habitat. Scenario A2 shows a more pronounced loss (47.0%) than scenario B2 (27.7%; Fig. 5A and C). However, the natural history of a habitat specialist with adequate dispersal abilities suggests that neither a full dispersal nor a no-dispersal model is appropriate. Fig. 5 shows the percent increase in

habitat associated with improvements in dispersal ability through non-habitat (e.g., agricultural valleys, cities, etc.). The most pronounced change occurred in the last time step of the A2 scenario climate model, where a change in dispersal from 1 km to 10 km increased available habitat by 37.3% (Fig. 5A).

When a minimum patch size of 125 km^2 is considered, the climate/topography-only model predicted approximately 23,895 km^2 of suitable fisher habitat under current conditions (a 22% decrease from the model with no patch size restrictions). The predicted future percent habitat gain is lower under both A2 and B2 scenarios, with a maximum gain of 20.2% by 2090 for the A2 scenario under unlimited dispersal (Fig. 5B), as compared to 24.5% with no patch size limit (Fig. 5A). Though decreased, habitat gains are still seen for three of the dispersal distances (unlimited, 10 km, and 4 km) by 2090 under the A2 climate scenario (Fig. 5B). Climate scenario B2 never results in a habitat gain when a minimum patch size is enforced, and instead incurs a habitat loss of 1.2% by 2090 under unlimited dispersal ability, and a loss of 41.7% with no dispersal ability (Fig. 5D).

4. Discussion

The most important finding from this study is the contrast in results that occurs when species distribution models are used without regards to minimum patch size and species dispersal capabilities. Projecting our climate-only model under the more severe climate change scenario with full dispersal and no limits on patch size shows a 24.5% increase in predicted fisher habitat by 2090. Limiting dispersal to 1 km of movement through non-habitat (agricultural fields and urban zones) and enforcing a minimum patch size requirement results in a loss of 25.8% of available fisher habitat under this same scenario, despite the overall increase in suitable habitat. In general, varying dispersal appears to limit habitat availability more than minimum patch size, although there is an interaction between the two. This change is readily apparent when considering the change between the large, contiguous block of habitat predicted currently versus the more fragmented pieces of habitat predicted by 2090, as seen in
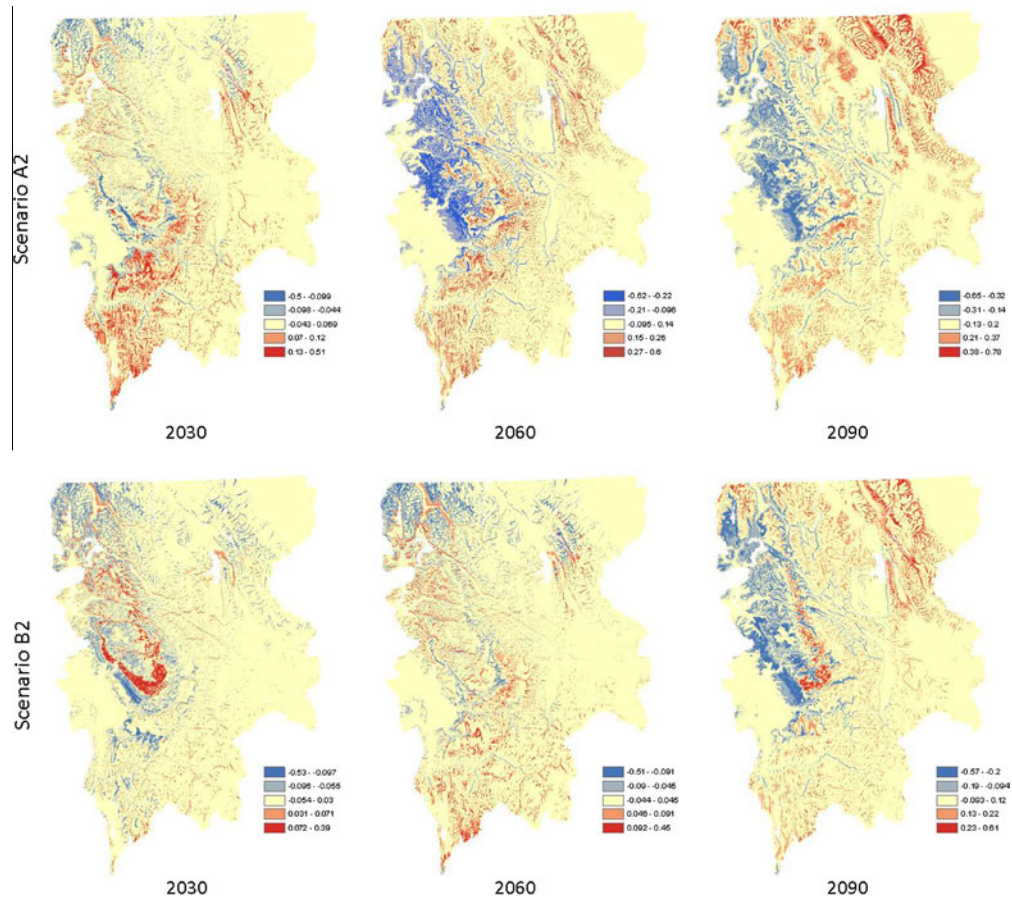
Fig. 4. The percent gain or loss of fisher habitat as predicted by two emissions scenarios (A2 and B2), and at three time steps (2030, 2060, 2090). Cool colors represent habitat loss, warm colors represent habitat gain, and yellow is neutral.

Supplemental Fig. 1. While total area increases between these time steps, the amount of contiguous habitat decreases. We discuss these findings below in relation to the habitat variables that define the fisher species distribution model.

Fisher distribution within our study area is characterized by drainages with riparian-type habitat, tall trees (correlated with mixed mesic habitat types), higher mean annual precipitation, and mid-range temperatures during the winter. This finding is in agreement with what is currently known about fisher habitat in other areas of its range, such as Oregon and Washington along the west coast (Raley et al., 2012; Schwartz et al., 2013; Aubry et al., 2013).

Previous work on west coast populations of fishers found that dense forest canopy was one of the most consistent predictors of fisher habitat. Weir and Corbould (2010) found that fishers selected stands with greater than 30% canopy cover, Purcell et al. (2009) found canopy cover to be the most important variable at predicting fisher resting sites, and Zielinski et al. (2004) showed that higher average canopy cover was critical for predicting fisher resting habitat. In fact, Purcell et al's (2009) study, based on radio-telemetry data, recommended the maintenance of stands with at least 61% canopy cover to maintain fisher habitat. Our results concur with this finding, although we modeled the response to canopy height, a variable which was highly correlated ($r = 0.85$) with dense canopy cover. We found that the proportion of canopy consisting of trees between 25 and 50 m tall (the largest tree height category), was the most important predictor of fisher occurrence in the northern Rocky Mountains, based on percent contribution to the full model. Tree height was also highly correlated with mesic and dry-mesic montane mixed conifer forest ($r = 0.80$), a habitat layer

that we expected to be significant based on our radio-telemetry studies. In univariate comparisons, however, tree height was the better predictor of fisher habitat; thus, we did not include mixed mesic forests in the model.

Another important predictor of fishers' occurrence in the full model was the presence of montane riparian vegetation, as characterized by landcover data from LandFire. This landcover type occurs across a wide range of elevations, from 900 m to 2800 m, and consists of a variety of tree-dominated communities and an assortment of shrubs found along rivers and canyons (NatureServe, 2008). The importance of riparian vegetation for the presence of fishers has been shown in studies conducted in British Columbia, the southern Sierra Nevada in California, and northwestern Montana (Zielinski et al., 2004). This preference for a landcover type that has a variety of trees and shrubs of various sizes may reflect a previously demonstrated fisher preference for a variety of forest structures, successional stages, and plant communities, which is thought to maximize hunting opportunities and provide cover from predation (Lofroth et al., 2010; Schwartz et al., 2013).

Across both the full model and the climate/topography-only model, we found that fishers were more likely to occur in areas with higher mean annual precipitation, mid-range minimum winter temperatures, and topography in the form of drainages or valleys. These abiotic factors indicate a fisher preference for wetter, milder climates, such as those found in fisher habitat along the west coast in Oregon and California, and along parts of New England. Interestingly, one of the locations within our study area in the Rocky Mountains with the greatest fisher abundance is the Clearwater subbasin in Idaho, an area considered a glacial refugia, with a current pacific maritime climate (Brunsfeld and Sullivan, 2005;
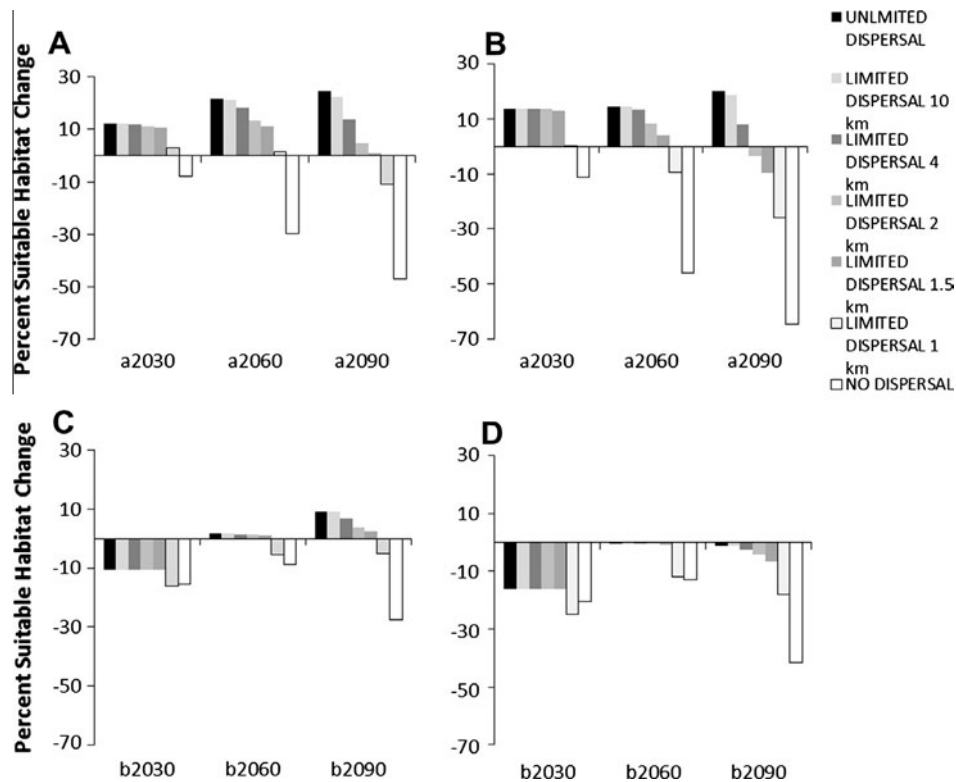
Fig. 5. Percent changes in amount of suitable habitat available to fishers. The top row shows the more severe climate scenario A2 with no patch restrictions (A) and when a minimum patch size of 125 km² is considered (B). The bottom row shows the more conservative climate scenario B2, with no patch restrictions (C) and with patch size restrictions (D).

Shafer et al., 2010). Fisher have also been shown to avoid dry habitat types, which in the west are frequently dominated by ponderosa (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*) and lack understory cover, needed for protection from predators and to provide habitat for prey (Jones and Garton, 1994; Schwartz et al., 2013). Our model found no support for fisher selection for dry forests.

Deep snow pack is also largely avoided by fishers (Raine, 1983; Krohn et al., 1995, 2005). Krohn et al. (2005) suggest that fisher foot loading is greater than 2 times that of martens, which makes travel through deep snow energetically inefficient. Carr et al. (2007) show that snow depth limits fisher dispersal in Ontario, Canada among five populations. These results are consistent with our finding that fisher prefer locations not only with precipitation, but also precipitation in milder climates.

Both the full model including vegetative covariates and the climate/topography-only model were good predictors of fisher locations, with very similar test AUC values (0.87 and 0.84, respectively). Frequently, climate-only models are criticized for ignoring covariates such as landcover or remotely sensed vegetative indices, since this may lead models to miss important biological factors such as the presence of food resources or protective cover (Pearson and Dawson, 2003). Our results show little difference between the predicted distributions when only climate and topography variables were used and when landcover variables were included. The main differences, based on the binary division of the models into suitable and unsuitable habitat, appear to be in the south of the study area, where the climate/topography-only model tends to predict suitable habitat in lower elevation and wet areas; and the north of the study area, where the full model predicts suitable habitat in older forests with large trees. The climate/topography-only model relies more strongly on annual

precipitation and TPI than does the model which includes landcover variables, resulting in a predicted distribution more likely to include river and valley bottoms.

Based on our climatic projection results, fisher distribution in the study area will likely shift north and east over time, and will show an increase in total area of suitable, although not necessarily contiguous, habitat. This shift is similar in direction to the shift observed between 1916 and 2005 for minimum temperature in this region (Dobrowski et al., 2013). Under the more severe emissions scenario (A2), the habitat shift is marked by a loss of suitable habitat near the center of the fisher distribution, in northern Idaho south of Moscow, ID, and a gain of suitable habitat in the mountainous areas of Glacier National Park and areas south of Kalispell, MT (Fig. 4). The more conservative emissions scenario (B2) also shows this pattern, but does so at a later time step. As global temperatures rise, the climate of the Rocky Mountains is projected to become more similar to the Pacific Northwest, with warmer, wetter winters (Littell et al., 2011). This change in regional climate is likely to favor species like the fisher, which appear to prefer wet, maritime-like forests and lower snowpack.

Species affected by climate change must be able to follow shifts in suitable habitat in order to persist. Fishers are capable of large dispersal distances (Schwartz et al. 2013), with males generally moving farther than females. In an Oregon study, juvenile males were found to disperse an average of 29 km, while females dispersed an average of 6 km (Aubry and Raley, 2006). Since juvenile fishers primarily disperse during winter (Arthur et al., 1993) and fisher dispersal may be limited by snow (Carr et al., 2007), a climatic shift that results in less snow may actually assist juvenile fisher dispersal. Adult fishers are also capable of long distance movements, with a study by Aubry and Raley (2006) showing that adult males during the breeding season frequently make

extra-territory explorations of 7–30 km before returning to their original territory.

Movement through non-habitat between suitable habitat patches at a large scale, however, can be challenging due to increased vulnerability to predators, increased exposure to anthropogenic factors, and decreased food availability between patches (Greenwood, 1980; Van Vuren and Armitage, 1994; Yoder et al., 2004). The success of dispersing individuals in surviving the journey and establishing a territory in a new location is not assured. A study in British Columbia found that 55% of transient fishers (those with no established home range) died (Weir and Corbould (2010)). Additionally, anecdotal evidence based on two populations of fishers in Oregon separated by approximately 20 km of non-habitat (valley bottom and developed land) indicates that no dispersal between the two populations has taken place in approximately 10 generations of fishers (Swiers et al., Submitted). Thus, while fishers may be capable of the dispersal movements required to keep pace with their changing habitat, the challenges posed by moving through non-favorable habitat may prevent them from adequately doing so. The northern U.S. Rocky Mountains have been shaped by erosion and glaciation, and can be characterized by a series of mountain ranges separated by large intermountain valleys. Many of these valleys are semi-arid, naturally dominated by grasses and shrubs, and often highly developed. While our maximum dispersal distance of 10 km is within the dispersal capability of fishers in high quality fisher habitat, these uninhabitable valleys are predicted by our model to remain a barrier at all future timesteps (see Supplemental Fig. 1) and may limit fishers' ability to colonize new habitat. In this case, the results of our dispersal simulation show a large disparity between the amounts of suitable habitat available to fishers if they are capable of successful long-distance dispersal versus if they are unable to disperse.

The fragmented distribution of potentially suitable habitat may also prevent fishers from taking advantage of all newly available areas. The areas in which future habitat is predicted to occur under both climate scenarios are steeply mountainous, such as the Lewis Range in Glacier National Park, the Purcell Mountains in northwest Montana, and the Selkirk Mountains in the northern tip of Idaho (Fig. 4, time step 2090). These mountain ranges have a wide range of elevation and topography, resulting in a variety of climatic conditions and 'islands' of suitable habitat as the climate changes. The areas that are predicted to become less suitable, such as the Clearwater Mountains in Idaho, are more uniform in elevation and climate, resulting in a large loss of contiguous habitat as climate changes. A study on marten (*Martes americana*), a close relative of fisher, showed that marten distribution in the northern Rocky Mountains would also become increasingly fragmented under a warming climate (Wasserman et al., 2012).

With a minimum patch size, the total amount of future habitat gain for fishers is reduced when dispersal distance is less than 4 km per time step. However, the amount of available fisher habitat is still projected to increase by 2090 under the more severe climate scenario, A2, if fishers have dispersal abilities between 4 and 10 km per time step. Thus, though predicted future habitat is more fragmented, the overall increase in suitable habitat is such that fishers may still incur a net gain, given moderate dispersal abilities. The predicted future habitat under climate scenario B2, however, which is based on reduced emissions, predicts markedly different future habitat availability. This scenario predicts less pronounced climate and precipitation changes, which results in less area converting to suitable fisher habitat (Fig. 5C) Newly gained habitat is less contiguous, as well, resulting in a small to considerable (41%) future habitat loss (depending on fisher dispersal ability) when only patches greater than 125 km^2 are considered (Fig. 5D). Our model shows that the more extreme climate scenario will convert more land into suitable habitat, indicating that fisher may benefit from climate warming. Since climate scenarios B2 and A2 are similar in direction but differ in magnitude, the loss of habitat under the more conservative scenario (B2) suggests that the response of fisher habitat to increases in temperature and precipitation is not linear. Further work to identify an upper limit of climate warming, at which fisher habitat would cease to be favorably impacted, would be a valuable contribution.

The results of our model incorporating dispersal into shifting distributions highlight the importance of considering the maintenance of dispersal for fisher conservation. While our model predicts an expanded fisher distribution under future climate warming scenarios, if fishers are unable to achieve regular dispersal distances greater than 4 km through unsuitable habitat, the total area of available habitat will likely decline over time.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.10.022.

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