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Expansion of American marten (*Martes americana*) distribution in response to climate and landscape change on the Kenai Peninsula, Alaska

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Rapidly changing environmental conditions are influencing distributions of wildlife species in Alaska. Due to strict physiological requirements, the distribution of American martens (*Martes americana*) is theorized to be driven by changing habitat, climate, and other anthropogenic conditions. We aimed to quantify marten distributions on the Kenai Peninsula, Alaska, and compared historic and contemporary occurrence records. To illustrate changing distribution patterns, we developed predictive niche models for 2 decades and investigated patterns by relating environmental trends with predicted distributions. Museum and trapping records, supplemented by aerial videography detections for martens on the Kenai over the past century, served to train RandomForests-based niche models for 1988–2001 and 2002–2010. Change-detection analyses revealed an ongoing westward expansion of likely marten distribution on the Kenai Peninsula since at least 1988, and historic records indicated longer-term growth. Top predictors in the models included soil ecotype, landcover, distance to trails, and distance to recreation sites. Our research suggests that on the Kenai Peninsula, marten distribution is responding to a combination of landscape and climate effects that have contributed to expanding marten distributions over the past century.

Key words: aerial digital videography, climate change, landscape ecology, niche modeling, RandomForests, snow

Alaska is undergoing climatic warming at least twice the global rate, resulting in shifting biomes, changing ecological functions, and a redistribution of species (Lawler et al. 2009; IPCC 2013; Vihma 2014). Average annual temperatures in Alaska over the past 60 years have increased by more than 2°C, minimum winter temperatures have increased by almost 4°C, and the growing season has been extended by more than 10 days (Hughes 2000; Stafford et al. 2000; Berg 2005; Yom-Tov and Yom-Tov 2005; Euskirchen et al. 2006; Wendler and Shulski 2009; Wendler et al. 2014). An increase in precipitation has been documented for much of Alaska (National Assessment Synthesis Team 2014) and an increase in the amount of rainfall at the expense of snowfall has been a predominant trend for the western United States over the past 60 years (Knowles et al. 2006).

The Kenai Peninsula, in subarctic Alaska, has emerged at the forefront of issues related to climate change (e.g., NFWPCA Partnership 2012:16). Like the rest of the state, the Kenai has experienced average winter temperatures that have warmed by 3 times as much as temperatures in summer, and the number of very warm nights has doubled since 1977 (Berg 2006). Documented responses to these rapidly changing conditions include rising shrub- (2.8 m/year) and tree-lines (1.1 m/year—Dial et al. 2007, 2016), drying wetlands (Klein et al. 2005; Ives et al. 2013), decreasing fire return intervals (Berg and Anderson 2006; Morton et al. 2006), and damaging spruce bark beetle (*Dendroctonus rufipennis*) outbreaks (> 420,000 ha—Berg et al. 2006; Boggs et al. 2008), among others. As the climate continues to warm, and changing precipitation regimes shift biomes, we can expect wildlife distributions to move in unexpected and synergistic ways that will challenge current paradigms of community arrangement (Williams and Jackson 2007; Urban et al. 2012; Baltensperger and Huettmann 2015a, 2015b). Determining how to effectively manage wildlife populations

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within this context is becoming a paramount issue for wildlife agencies (Fritts et al. 2006; Czech et al. 2014; ADFG 2015).

American martens (*Martes americana*) have strict physiological requirements in winter (Buskirk et al. 1988; Buskirk and Harlow 1989; Taylor and Buskirk 1994). Deep snow, which insulates the subnivean zone, buffers martens from below-freezing ambient temperatures while resting under snow (Marchand 1982; 1987; Buskirk 1984; Taylor and Buskirk 1994; Brainard et al. 1995). As the density of snow increases, particularly after thaw or winter rain events, the minimum snow depth required to insulate the subnivean space may exceed 30 cm (Formozov 1965; Marchand 1982, 1987; Halfpenny and Ozanne 1989). Insulating snow cover is also crucial for the survival of subnivean-dwelling prey such as voles (Subfamily Arvicolinae) and shrews (*Sorex* spp.—Formozov 1965; Mellander et al. 2005; Pauli et al. 2013).

Because of their physiological sensitivity to environmental conditions, martens represent one of the most proximate mammalian sentinel species of climate change (Zielinski et al. 2005; Yom-Tov et al. 2008). American martens are distributed throughout the boreal and montane forests of North America but continental populations are believed to have declined over the past century as a result of habitat loss and over-trapping (Reid and Helgen 2008). Currently, martens in Alaska are not considered vulnerable, but the effects of climate change and local over-harvest on population size, persistence, and distributions have not yet been adequately considered, especially in the context of long-term conservation (Fritts et al. 2006). Simulations of shifts in distribution have predicted that species living near their upper physiological limits both in the Arctic and in the Tropics are the most threatened by climate change (Deutsch et al. 2008; Tewksbury et al. 2008; Somero 2010). Conversely, those species living near the lower limits of their thermodynamic envelope, like martens in Alaska (Buskirk and Harlow 1989), should stand to benefit from increased temperatures, at least over the short term.

Other processes that are inversely related to rising temperatures may, however, counteract some of these climate change benefits. Elevated winter temperatures and more frequent rain-on-snow events on the Kenai Peninsula may result in more frequent thaws, increasing the density of an already shallow snowpack (Liston and Hiemstra 2011; McAfee et al. 2014), reducing its ability to insulate subnivean species such as martens and their prey (Merritt 2001; Solonen 2006; Pauli et al. 2013). Because of their dependence on subnivean access points and thermal cover, martens may be confined to habitat that meets certain minimum standards for available forest cover, coarse woody debris (CWD), midden piles, and snow cover (Spencer 1987; Schumacher et al. 1989; Carroll 2007). The combination of a physiologically sensitive furbearer species inhabiting an area undergoing rapid environmental change provides an opportunity to evaluate the associations among a changing climate, a growing human population, and shifting wildlife distributions and to address impacts of climate change with effective conservation policy.

In some of the 1st research on martens on the Kenai Peninsula, Schumacher et al. (1989) concluded that a large population of martens inhabited the eastern side of the peninsula, but martens were considered extremely rare west of the Kenai Mountains. In 2002, the capture of a juvenile male marten in the Kenai Lowlands first suggested the possibility that martens may have expanded into areas where they were not known to occur. Our research marks the subsequent response to investigate and map the potentially shifting distribution of martens on the Kenai Peninsula. We used an aerial digital videography (ADV) survey (Fig. 1) and other field and museum data to create species niche models to compare the historic and contemporary distributions of martens on the Kenai Peninsula. Spatial analyses highlight regions of distribution change and we present potential drivers to explain patterns observed in the models (e.g., Baltensperger and Huettmann 2015a, 2015b). We believe this approach may serve as a useful template for collating disparate occurrence records, predicting ecological niche spaces, and detecting early distributional changes in understudied furbearers as they respond to a rapidly changing climate throughout the circumpolar Boreal Forest.

Materials and Methods

Study area.—Our study area was the 24,000-km^2 Kenai Peninsula in south-central Alaska (Fig. 1), with most field work conducted on the 805,000-ha Kenai National Wildlife Refuge (KENWR). Forested vegetation on the western Kenai Peninsula is largely dominated by black spruce (*Picea mariana*) especially in the Kenai Lowlands, whereas white spruce (*P. glauca*) and small stands of western hemlock (*Tsuga heterophylla*) are found in more xeric, upland sites (Schumacher et al. 1989; Reynolds 1990). The western peninsula is characterized by colder, drier winters. Monthly winter temperatures at the nearby Kenai Airport (10 m elevation) ranged from average lows of −14.7°C in January to average highs of 0°C in March between 1949 and 2007 (Ashby 2008). Maximum yearly snow depths are highly variable and range from 0 to 152 cm at an elevational range of 0–100 m above sea level (McClure 2006; Ashby 2008; Baltensperger 2009).

The eastern side of the Kenai Peninsula is dominated by the Kenai Mountains, where forests are comprised of Sitka spruce (*P. sitchensis*) and Lutz spruce (*P.* × *lutzii*) at low to mid elevations, whereas mountain hemlock (*T. mertensiana*) stands generally form the tree-line (250–700 m above sea level—Schumacher et al. 1989; Reynolds 1990). Near tree-line, stands of subalpine shrubs, especially alder (*Alnus* spp.) and willow (*Salix* spp.), are common (Schumacher et al. 1989; Reynolds 1990). Alpine tundra generally dominates above 750 m (Schumacher et al. 1989). The Kenai Mountains typically receive more precipitation and exhibit less daily temperature variation in winter than the lowlands. Monthly winter temperatures in the mountains at Moose Pass ranged from average lows of −14°C in January to average highs of 2°C in March between 1952 and 2004 (Ashby 2008). Yearly maximum snow depths have ranged between 88 and 207 cm above 300 m elevation since 1951 (McClure 2006; Ashby 2008).

Potential prey in both regions include red-backed voles (*Myodes rutilus*), root voles (*Microtus oeconomus*), singing voles (*M. miurus*), northern bog-lemmings (*Synaptomys*

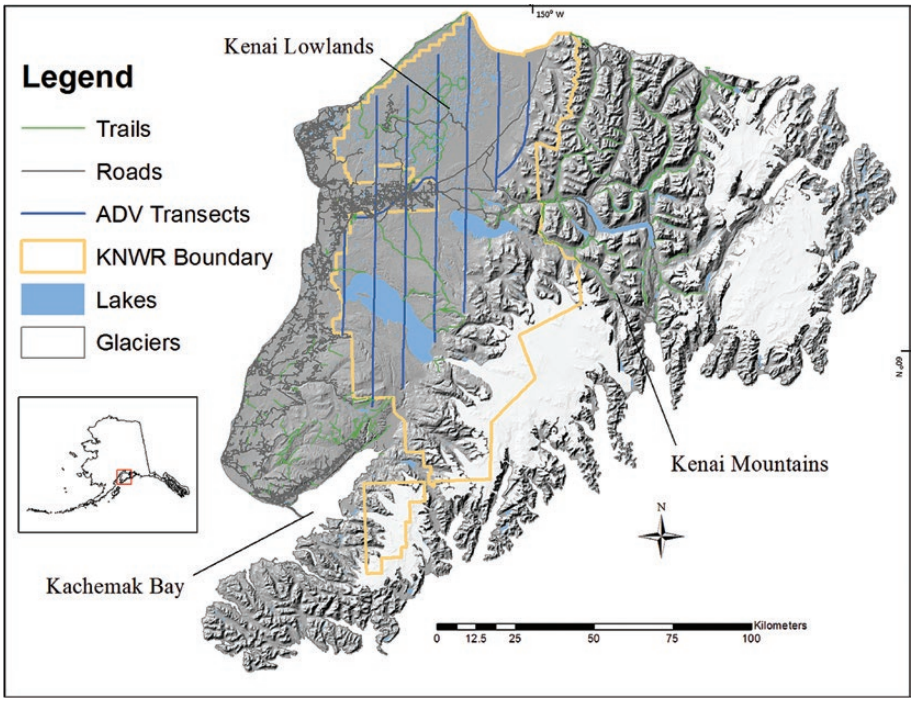

Fig. 1.—Study area map depicting the location of the Kenai National Wildlife Refuge, area roads, trails, and aerial digital videography (ADV) transects flown in 2006 on the Kenai Peninsula, Alaska.

borealis), cinereus shrews (*Sorex cinereus*), montane shrews (*S. monticolus*), red squirrels (*Tamiasciurus hudsonicus*), and snowshoe hares (*Lepus americanus*—MacDonald and Cook 2009; Baltensperger and Huettmann 2015a).

Records of marten occurrence.—We compiled records of marten occurrences between 1906 and 2010 from a variety of sources including museum records, Alaska Department of Fish and Game (ADFG) "sealing records" (verified pelts), KENWR furbearer records and surveys, interviews with local trappers, a 1989 research project on martens (Schumacher et al. 1989), a 2006 ADV survey, and winter field trapping conducted between 2007 and 2008 (Baltensperger 2009; for details see Supplementary Data SD1). We reviewed museum collections from the University of Alaska Fairbanks and the University of California Berkeley and recorded dates and locations of martens harvested and observed on the Kenai Peninsula since 1906. Locations prior to 1988 were accurate to at least 50 km (and were thus excluded from model analyses), while subsequent records used in models were within 1 km accuracy, and most within 10 m. We also obtained sealing records for martens on the Kenai Peninsula between 1988 and 2010. Because ADFG unfortunately does not require the reporting of exact harvest locations or trapping effort, sealing records were identified only to minor drainage units (Uniform Coding Unit; UCU) in which martens were harvested. For modeling purposes, points were randomly plotted within the forested portions of UCUs ($n = 43$, $\bar{x}_{\text{UCU area}} = 66.5$ km^2, $\sigma = 94.6$) using ArcGIS 10.2.

A program to purchase marten carcasses was also instituted by the KENWR in 2006 to identify additional detections of martens, whereby trappers were paid $50 for each marten carcass and detailed locational information pertaining to captures. Personal interviews with area trappers between January 2007 and April 2008 supplemented a trapper survey conducted in 1980 (Bailey 1986) and provided additional locations (1 km accuracy) of martens harvested on the Kenai Peninsula, especially within the KENWR. While some anecdotal observations can be spurious, donated marten carcasses provided proof of correct species identification, and in-depth discussions and field verification with trappers yielded exact point locations of harvests on topographic maps. Skull dimensions, corpora lutea, and tooth cementa analyses were used to determine morphology, fertility rates, and age demographics, respectively, for these individuals (Matson Laboratory LLC, Missoula, Montana; Supplementary Data SD2). Methods for capturing, handling, and studying martens were reviewed and approved by Colorado State University's Animal Care and Use Committee (protocols 06-097A-01, 06-097A-02). Skulls and carcasses were donated to the University of Alaska Museum of the North for permanent archival.

Aerial digital videography.—Seven transects, spaced 10 km apart, were flown using a ported Piper Super Cub aircraft at 150 m altitude over the KENWR on 13 March 2006 for the purpose of detecting general mammalian and snow machine tracks in snow (Fig. 1). Following a significant snowfall, weather conditions on the KENWR were cold, calm, and clear for 3 days preceding the survey, so that tracks were allowed to accumulate with minimal structural degradation. The ground was filmed with a Sony video camera linked to a GPS unit and laptop computer that recorded times and locations of video frames into a spreadsheet.

Approximately 323,240 video frames were recorded at a rate of 30 frames per second so that every 5th video frame (11.6 m wide) represented a unique image and a sampled subset. All video frames were reviewed individually using Adobe Premier

video editing software and frames containing potential marten tracks were saved for further analysis. A set of 109 georeferenced video frame images containing potential marten tracks was then reviewed by 2 technicians, and a subset of tracks identified as marten was also confirmed by an ADFG furbearer biologist. Of species that may produce tracks similar to martens, fishers (*Martes pennanti*) and long-tailed weasels (*Mustela frenata*) are not present in Alaska (MacDonald and Cook 2009), and mink (*Neovison vison*) tracks are smaller and primarily occur near water (Elbroch 2003). As such, tracks located within 50 m of open water were excluded from the set of potential marten tracks.

The difficulty of accessing remote areas in Alaska precluded us from conducting independent ground observations to estimate consistent detection rates (O'Connell et al. 2006). Instead, we assumed equal detectability across all frames, but we recognize that ADV likely underestimates detections of tracks in forests with dense canopies. Detections of martens on the KENWR therefore represent a minimum, presence-only data set. While these data are suitable training data for presence-only modeling of a minimum predicted distribution (Elith et al. 2006; VanDerWal et al. 2009; Baltensperger and Huettmann 2015a, 2015b), they represent a conservative underestimate of the actual distribution of martens on the KENWR.

Ecological niche modeling.—For the purpose of assessing and quantifying changes in the distribution of martens on the Kenai Peninsula over time, we selected 2 subsets of records from the larger data set to be used as training data for 2 decadal models. Records from 1988–2001 and 2002–2010 were used as training data sets for a "1990s" model and a "2000s" model. The 1990s model data set included records from as early as 1988 (the earliest year that trapped martens were recorded by the ADFG) until 2001. The 2000s model included records from 2002 (the 1st year martens were detected on the KENWR in decades) and all subsequent detections of martens on the Kenai Peninsula.

A total of 195 presences between 1988 and 2001, and 228 presences between 2002 and 2010 were used as training data. Using the *Extract Values to Multi-point* tool in ArcGIS 10.2, locations where martens were present were attributed with 33 environmental predictors (Drew et al. 2011; Evans et al. 2011; Table 1). Environmental predictors included a variety of interacting climatic, topographic, anthropogenic, and ecological variables with either documented or hypothesized effects on occurrence of martens including physiological limitations (Marchand 1987; Buskirk et al. 1989; Berg 2005), habitat selection (Bailey 1986; Brainard 1995; Bull et al. 2005; Baltensperger 2009), prey availability (Formozov 1965; Merritt 2001; Boonstra and Krebs 2006; Solonen 2006), and disturbance (Tigner et al. 2015) at both ecosystem and landscape scales. We used decade-specific values for dynamic variables in the 1990s and 2000s models. Climatic variables were downscaled from predictions and records of the International Panel on Climate Change (IPCC) to 771-m resolutions (www.snap.uaf.edu/methods/downscaling). All other continuous variables had 60-m resolutions, which was the finest-scale resolution at which data were available.

Because the 2 data sets were composed of presence-only data points, lacking "true absences," it was necessary to develop "pseudo-absence" data sets for modeling (Elith et al. 2006; VanDerWal et al. 2009). To describe the study area, we used 1,000 points, randomly distributed across the Kenai Peninsula and attributed with the same environmental variables. To select the most appropriate pseudo-absence scenario, we investigated the performance of other pseudo-absence training sets that were constrained by forested habitat types or buffered around presence points (Zaniewski et al. 2002; Engler 2004), but the random pseudo-absence scenario with 1,000 points resulted in the model with the lowest overall balanced error rate (Elith et al. 2006; VanDerWal et al. 2009).

We used RandomForests (Salford Systems Inc., San Diego, California—Breiman 2001) to create optimized rule sets to describe patterns in both the 1990s and 2000s training data sets. We randomly withheld 20% of each data set from the modeling processes as testing data. RandomForests also uses only a random subset of data points and predictor variables (known as "bagging") while growing trees (n = 1,000), which helps to avoid issues such as model over-fitting (Breiman 1996; Cutler et al. 2007) and spatial autocorrelation (Evans et al. 2011; Kirkwood et al. 2016). Nonparametric models (such as RandomForests) do not require independence of samples, and the recursive bagging of data points and predictors breaks spatial associations among autocorrelated points (Evans et al. 2011). Additionally, spatial structure in a training set can be sufficiently explained by using a high number of spatial environmental predictors, such as the 33 included in our models (Kirkwood et al. 2016).

The resulting model was stored as a "grove" file, and then "scored," or projected, to a regular 1-km resolution lattice of points (created using the *Create fishnet* tool and attributed with the 33 environmental predictors in ArcGIS 10.2). The 1-km lattice was rasterized to create continuous maps that predicted the relative indices of occurrence (RIO) of martens for the 2 time periods analyzed. Model performance was evaluated using the area under the receiver operator curve (AUC ROC—Pearce and Ferrier 2000) as well as the percentages of correctly predicted presences (sensitivity) and absences (specificity) using the withheld validation data set. We used TreeNet software (Salford Systems Inc., San Diego, California) to create partial-dependence plots from the classification trees to visualize trends for the top variables (variable importance index > 50) in both models.

In order to easily quantify change in distribution over time, continuous models were reclassified into binary rasters showing predicted presences and predicted absences. Thresholds for each model were selected by maximizing the sum of specificity and sensitivity (Manel et al. 2001; Jimenez-Valverde and Lobo 2007). The 1990s binary model was then subtracted from the 2000s binary model using the *Raster Calculator* in ArcGIS 10.2 to depict regions of loss, persistence, and gain in distribution of martens (e.g., Baltensperger and Huettmann 2015b). Continuous rasters were also subtracted from one another to quantify changes in RIO over time.

Table 1.—List of predictor variables used in models, type of data (categorical or continuous), temporal consistency (static or dynamic; decade-specific data were used for dynamic variables), their online sources, and variable importance values (0–100) for the 1990s and 2000s spatial models of the distribution of martens (*Martes americana*) in the Kenai Peninsula, Alaska. The score of the top variable is always 100. Continuous layers have a 60-m resolution. KENWR = Kenai National Wildlife Refuge.

Variable name	Data type	Temporal consistency	Data source	Variable importance	
				1990s	2000s
Aspect	Continuous	Static	http://nhd.usgs.gov	0.1	0.6
Distance to Anadromous Streams	Continuous	Static	www.asgdc.state.ak.us	0.3	1.0
Distance to Cabins	Continuous	Static	KENWR	12.2	36.5
Distance to Coastline	Continuous	Static	www.asgdc.state.ak.us	0.9	3.5
Distance to Glaciers	Continuous	Static	www.asgdc.state.ak.us	13.0	18.7
Distance to Lakes	Continuous	Static	http://nhd.usgs.gov	0.3	1.0
Distance to Recreation Points	Continuous	Static	KENWR	47.9	70.2
Distance to Residences	Continuous	Static	KENWR	1.1	6.0
Distance to Roads	Continuous	Static	www.asgdc.state.ak.us	16.1	36.7
Distance to Seismic Lines	Continuous	Static	www.asgdc.state.ak.us	20.8	17.8
Distance to Streams	Continuous	Static	http://nhd.usgs.gov	0.6	2.3
Distance to Trails	Continuous	Static	www.asgdc.state.ak.us	50.5	59.1
Distance to Villages	Continuous	Static	www.asgdc.state.ak.us	20.3	9.7
Elevation	Continuous	Static	http://nhd.usgs.gov	2.8	15.0
Fire Year	Continuous	Dynamic	http://agdc.usgsgov/data/projects/fhm	0.2	0.5
Insect Damage	Binary	Dynamic	http://agdc.usgsgov/data/projects/fhm	0.1	0.4
Landcover	Categorical	Static	KENWR	100.0	100.0
Mean 1st Day of Freeze	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	0.9	8.7
Mean 1st Day of Thaw	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	2.3	22.2
Mean Number of Grow Days	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	1.1	18.7
Mean Spring Precipitation	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	1.0	5.2
Mean Spring Snow-Day Fraction	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	3.4	26.8
Mean Summer Precipitation	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	0.4	4.1
Mean Summer Temperature	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	2.8	25.5
Mean Fall Precipitation	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	1.4	8.2
Mean Fall Snow-Day Fraction	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	0.7	12.4
Mean Fall Temperature	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	0.8	9.2
Mean Winter Precipitation	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	4.8	9.1
Mean Winter Snow-Day Fraction	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	0.5	4.7
Mean Winter Temperature	Continuous	Dynamic	www.snap.uaf.edu/tools/data-downloads	14.5	6.7
Slope	Continuous	Static	http://ned.usgs.gov	0.4	1.1
Soil Ecotype	Categorical	Static	www.asgdc.state.ak.us	80.4	70.4
Surficial Geology	Categorical	Static	www.asgdc.state.ak.us	27.5	29.7

Results

Records of occurrence.—Between 1906 and 1987, we found just 27 records of martens occurring on the western Kenai Peninsula (Supplementary Data SD1; Bailey 1986; Magoun and Vernam 1987; Schumacher et al. 1989; Arctos 2016). State of Alaska trapping records documented that following cessation of a strychnine poisoning program in 1915 and because of perceived low population levels (Palmer 1938), marten-trapping seasons were closed on the western Kenai Peninsula between 1916 and 1960 (Morton and Jozwiak 2008). This period of absence also corresponded with the collapse of the Kenai fur market (Loshbaugh 2014). As such, we found no records of martens occurring west of the Kenai Mountains from 1910 until 1955, when marten tracks were identified near Botenintin Lake, 30 km west of the mountains (KENWR 1995).

Between 1988 and 2001, ADFG sealing records showed that just 4 martens were trapped on the Kenai Lowlands versus 957 in the Kenai Mountains (Fig. 2). In 2002, a single juvenile male marten was accidentally captured by KENWR staff targeting Canada lynx (*Lynx canadensis*) near the Discovery Well hemlock stand in the Kenai Lowlands. At the time, this was the 1st documented record of a marten in the region in 47 years. This discovery led to a carcass purchase program that resulted in the documentation of 90 locations of martens across the Kenai Peninsula since 2002, 53 of which occurred west of the Kenai Mountains (Fig. 3a). Between 2002 and 2010, a total of 888 martens were reportedly harvested on the eastern Kenai Peninsula as well as 115 marten on the western peninsula, including from several UCUs where martens had not been previously detected (Figs. 2 and 3b). The ADV survey in 2006 detected 34 occurrences of marten tracks on the KENWR in regions previously thought to be devoid of martens.

1990s distribution model.—Model predictions for the 1990s distribution (1988–2001) of martens on the Kenai Peninsula showed high relative indices of occurrence (RIO > 0.7) in the valley bottoms of the Kenai Mountains below tree-line (Fig. 3a). Intermediate RIO values (0.3–0.7) were predicted as far west as Skilak Lake. Low to intermediate RIO values (0.0–0.3) occurred across the majority of the Kenai Lowlands and at high elevations above tree-line and on ice fields. The AUC ROC was 0.98, and using an optimized threshold of 0.57,

specificity was 96.6% and sensitivity was 96.8%, all of which indicate excellent model performance.

Variable importance rankings and partial-dependence plots provided insight into the nonlinear patterns among top model predictors. The 1990s model prediction was largely driven by patterns in landcover, highlighting the importance of white spruce, Lutz spruce, Sitka spruce, mixed conifer, paper birch (*Betula papyrifera*), mixed deciduous, and mixed forest in contrast to black spruce and other nonforested landcover types that were negatively correlated with martens (Table 1; Supplementary Data SD3a). Soil ecotype was the 2nd most influential predictor in the model (Table 1), and the partial-dependence plot highlighted positive correlations among maritime uplands and lowlands with marten RIO (Supplementary Data SD3b). Most boreal soil ecotypes were negatively correlated with RIO, with the exception of boreal valleys and coastal plains in lowland and upland areas (Supplementary Data SD3b). In addition, RIO values were higher in proximity to anthropogenic variables such as distance to trails (< 6 km; Supplementary Data SD3c), recreation sites (< 9 km), villages (< 22 km), cabins (< 0.43), and roads (< 15 km; Table 1). In contrast, marten RIO was negatively related to seismic lines at distances < 18 km.

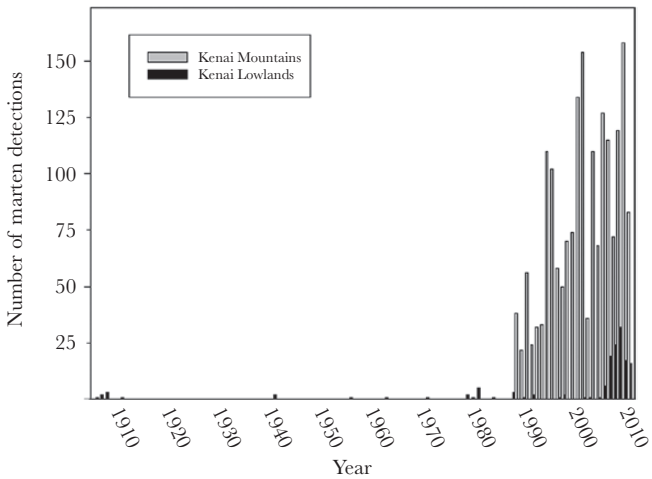

Fig. 2.—Number of detections of American martens (*Martes americana*) on the Kenai Lowlands and in the Kenai Mountains, Alaska, from 1906 to 2010. Detections were compiled from museum records, Alaska Department of Fish and Game (ADFG) sealing records, trapper surveys, live-captures, and incidental observations. Marten carcasses were sealed by ADFG beginning in 1988.

Climate-related variables were substantially less influential in model development, but there were direct relationships between RIO and mean winter (December–February) temperatures above −6.5°C as well as mean winter precipitation greater than 200 mm, respectively (Table 1). Snow-day fraction was positively correlated with occurrence of martens when snow fell on > 45% of days in the fall (October–November), < 65% and > 76% of days in winter, and < 58% of days in spring (March–April; Table 1). Fire and insect damage were notably among the 3 least important predictors in the model.

2000s distribution model.—The model depicting the 2002–2010 distribution of martens showed similar patterns of occurrence as the 1990s model throughout the mountainous portions of the Kenai Peninsula (Fig. 3). In contrast, the 2000s model predicted high RIO values in the northwestern portion of the Kenai Lowlands, and low values in the southwestern Kenai Peninsula (Fig. 3b). Additionally, the area of intermediate RIO in the 2000s model extended farther west from Skilak Lake toward Lake Tustumena and the coast, as well as at the head of Kachemak Bay, in part a reflection of additional detections of martens in these areas (Fig. 3b). The 2000s model received an AUC ROC score of 0.96, and using a threshold of 0.43, specificity and sensitivity equaled 91.4% and 91.7%, respectively, indicating very good model performance.

Important predictors and their relationships for the 2000s model were similar to the 1990s model (Table 1). Landcover

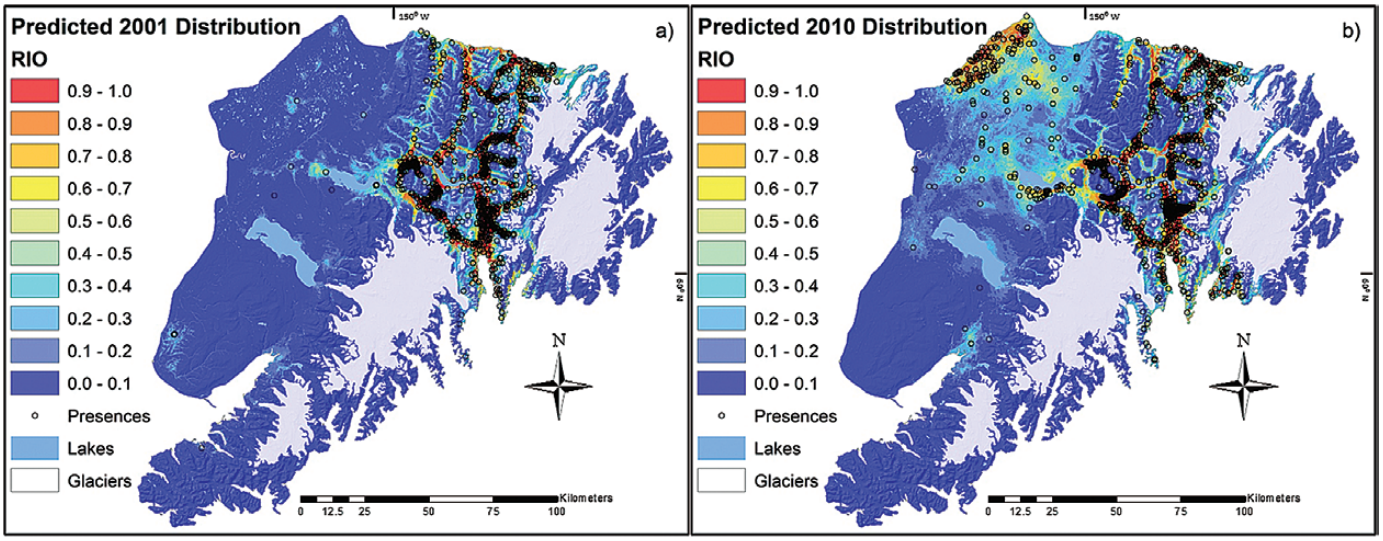

Fig. 3.—Documented detections and predicted distributions of American martens (*Martes americana)* for a) 1988–2001, and b) 2002–2010 on the Kenai Peninsula, Alaska. Model periods are separated by the rediscovery of martens on the Kenai National Wildlife Refuge in 2002. RIO = relative index of occurrence.

was again the highest-ranking predictor; however, in this model black spruce (in addition to other forest types) was positively correlated with occurrence of martens (Supplementary Data SD4a). Soil ecotypes were also important in this model, sharing many of the same associations with RIO as in the 1990s model (Supplementary Data SD4b). The exceptions were the maritime (eastern Kenai) subalpine and alpine mountains category, and the boreal (western Kenai) upland peatlands and lowland flood plains and terraces categories, which were positively associated with RIO in the 2000s model. Conversely, the boreal alpine and boreal upland glaciated plains and hills categories became somewhat negatively associated with RIO in the later model. Anthropogenic variables were ranked with higher importance in the 2000s model versus the 1990s model (Table 1). The most important among these were distance to recreation sites and distance to trails, which were positively correlated with marten RIO at distances < 5 km and < 6 km, respectively (Supplementary Data SD4c and SD4d). Distance to roads (< 11 km) and cabins (< 0.49 km) were also positively correlated with the RIO, whereas martens were negatively associated with seismic lines at distances < 19 km.

Climate predictors were more important in the 2000s model than in the 1990s model, but remained as relatively unimportant contributors to the model (Table 1). Occurrence of martens was positively related to mean snow-day fraction when snow fell on < 45% of days in spring and < 52% of days in fall. Dates of thaw (before March 1) and growing season length (> 206 days) were also associated with occurrence of martens, more so than in the 1990s model (Table 1). A positive relationship between summer (June–August) temperatures above 13.4°C and occurrence of martens also contributed modestly to the model (Table 1). Fire and insect damage predictors contributed the least to the model.

Change-detection analysis.—A change-detection analysis was used to contrast the 2 distribution models. It highlighted areas where martens appear to have expanded their distribution across the Kenai Lowlands, around Skilak Lake, and at higher elevations in the Kenai Mountains (Figs. 4a and 4b). Regions of distributional contraction were most evident in the northern Kenai Mountains near the Turnagain Arm and the village of Hope (Figs. 4a and 4b). Gains in distribution between the 2 time periods totaled 1,377 km^2, whereas losses amounted to just 40.6 km^2. This resulted in a net gain of 1,336 km^2 on the Kenai Peninsula where martens were predicted to occur in 2010 but where they were absent prior to 2002.

Discussion

We were able to develop the 1st spatial predictions for martens in Alaska under contemporary conditions using a multi-sourced, long-term data set. Based on patterns in occurrence records and model predictions, our results show that martens have expanded their distribution westward from the Kenai Mountains gradually over the past 60 years, but principally during the past 15 years (Figs. 2–4). Models demonstrated the importance of landcover and soil ecotype classifiers for both time periods, and the increasing importance of anthropogenic and climactic factors in predicting distribution patterns over time (Supplementary Data SD3 and SD4). While dynamic climate variables were less important than static landscape variables in developing models, the increasing importance of the former points to the emerging effects of climate change on the distribution of martens across the Kenai Peninsula. The ADV survey was a useful technique for documenting the presence of martens across the KENWR in areas that had traditionally been difficult to survey, and where martens were previously not known to occur, though densely canopied forest can make analyses difficult.

Historical trends.—Martens may once have been distributed across the Kenai Peninsula, although they may never have occurred in great abundance on the KENWR (Figs. 2 and 3). A wildlife poisoning effort (Palmer 1938), over-trapping (MacDonald and Cook 2009), and the destruction of large areas of potential habitat by 2 wildfires (1947 and 1969—Morton et al. 2006) may partially explain the long period of absence

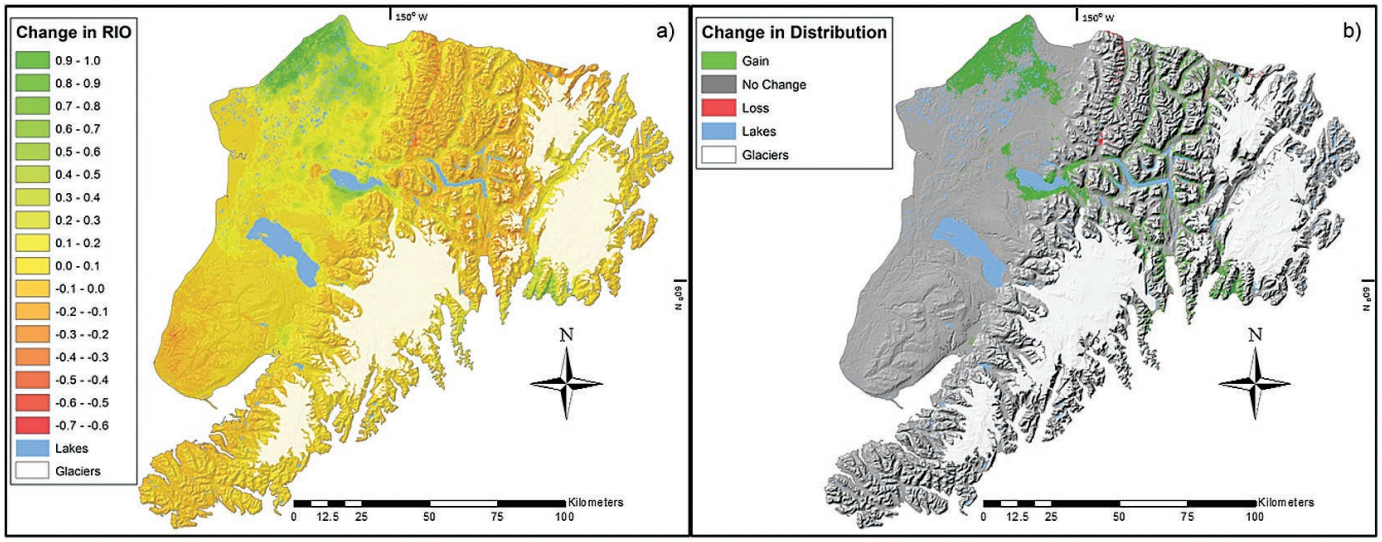

Fig. 4.—Change-detection analysis depicting a) change in relative index of occurrence (RIO), and b) change in presence-absence of martens (*Martes americana*) on the Kenai Peninsula, Alaska, from 1988–2001 to 2002–2010.

of martens on the KENWR during at least the 1st half of the 20th century (Fig. 2; MacDonald and Cook 2009). Beginning with the observation at Botenintin Lake in 1955, sparse reports of martens on the western Kenai Peninsula gradually became more common, culminating with regular reports of martens by the mid-2000s (Fig. 2). Conclusions based on historical records and anecdotal observations should, of course, be met with caution given the potential for sampling and other biases (e.g., ADFG does not record trapping effort and perceptions of higher marten densities in the mountains likely led to higher trapping effort there—McKelvey et al. 2008). However, because of the consistent, documented absence of martens during the mid-20th century, followed by their subsequent identification using sealed records in the Kenai Lowlands, we believe these data are strong evidence of a slow recolonization of martens on the western peninsula following extirpation around the turn of the 20th century.

Modeled change in distribution.—Analyses of changes in distribution illustrated the historic record as they predicted the expansion of likely distributions of martens westward across the Kenai Lowlands over the past decades. We suspect that the Kenai Lowlands historically represented an area of suboptimal marten habitat, given its shallow snow cover, cold winter temperature inversions, active fire history, and stands of smaller-diameter trees, especially in comparison to mountainous areas that contain higher marten densities (Magoun and Vernam 1987; Klein et al. 2005). These suboptimal conditions may explain the very slow colonization of the Kenai Lowlands by martens following extirpation.

While the exact reasons for the expanded distribution are unclear, important predictors in our models hint at possible drivers. Forest changes resulting from successional and climate shifts (Magoun and Vernam 1987; Klein et al. 2005; Morton et al. 2006; Dial et al. 2016) may have increased the suitability of the Kenai Lowlands for martens and at least partially explain the observed distribution shifts of martens. Unfortunately, the lack of data on spatial landcover and anthropogenic changes has so far precluded us from including these factors as dynamic variables in our analyses, but the increasing importance of dynamic climate variables between the 2 decadal models indicates their growing influence.

Martens tend to favor closed-canopy forests with high abundance of CWD as is common in white–Sitka–Lutz spruce and western hemlock forests (Snyder and Bissonette 1987; Spencer 1987; Schumacher et al. 1989; Corn and Raphael 1992). The open canopies and lower stem densities of black spruce forests, however, generally provide less-suitable habitat for martens (Magoun and Vernam 1987; Chapin et al. 1998; Bull et al. 2005; Baltensperger 2009). Partial-dependence plots of the top variable, landcover, indicated that white spruce and mixed forests were most closely associated with occurrence of martens in the 1990s model. Because locations of martens in the Kenai Mountains were randomly assigned to forested areas of UCUs and because martens are generally associated with mature, closed-canopy forests (e.g., Buskirk 1984; Magoun and Vernam 1987; Chapin et al. 1998; Bull et al. 2005), we assumed that martens were not utilizing other habitats there. As a result, landcover affinities may be biased somewhat toward white–Sitka–Lutz spruce and mountain hemlock forests, and model predictions may slightly underestimate true distributions of martens in the mountains. However, this should have little effect on the relationship with black spruce, which occurs only rarely in the eastern Kenai.

We showed that landcover associations changed somewhat in the 2000s model, which still showed a positive relationship between martens and white spruce-mixed forests, but also had a slight positive correlation with black spruce. The change in association with black spruce reflects new documented occurrences of martens on the Kenai Lowlands, where this forest type is more common. Black spruce, however, offers little in the way of CWD and resting sites for martens, especially lowland areas with minimal snow cover (Baltensperger 2009).

Important changes in associations between soil ecotypes and marten RIO reflect shifts in the locations of records of martens over time. Martens have increasingly been detected in the boreal upland peatlands and lowland terraces of the western Kenai as well as in subalpine regions of the eastern Kenai Mountains. These findings, along with the fact that martens were detected in several new UCUs, are consistent with an increased use of lowland black spruce forests and subalpine habitats and suggest that martens have recently been exploiting new habitats. Unfortunately, because of the lack of time series data for several of the top predictors, it remains unclear whether habitats are becoming more suitable for martens, or if martens have recently begun to exploit previously unused but unchanged habitats. However, the results correspond with well-documented climate induced trends in lowland forest drying and rising tree- and shrub-lines that are changing forest conditions and may be aiding the expansion of martens (Klein et al. 2005; Dial et al. 2007, 2016; Ives et al. 2013).

Proximity to anthropogenic features, especially trails, recreation sites, and cabins, may have emerged among the top predictors for 1 of 2 reasons. First, people on the Kenai Peninsula generally use roads and trails to access forested areas and often do not stray far from these features when trapping or observing wildlife. This is demonstrated in the partial-dependence plots (Supplementary Data SD3 and SD4), which showed that a positive association between RIO and these variables exists at < 22 km. In the Kenai Mountains, where much of the available forest cover is restricted to narrow valley bottoms (< 500 m elevation), most observations of martens coincidentally occurred in close proximity to roads, cabins, and recreation points that also are more common in the valleys. As such, many observations may contain an inherent infrastructure-related spatial bias despite the relatively small number of locations detected using aerial videography away from human infrastructure.

Alternatively, the positive association between martens and anthropogenic features could be a real, causative phenomenon. Martens may be positioning themselves near anthropogenic disturbances to improve access to prey, resting sites, or for protection from predators, though the reasons for this association would require investigations of finer-scale habitat use than our models allow. In contrast, martens were negatively associated with seismic lines on the western Kenai, which is consistent with research that also documented a general inverse

relationship between seismic line density and the probability of occurrence of martens in Canada (Tigner et al. 2015).

Among the climate variables analyzed, mean winter temperature was the most important predictor for the 1990s model, showing a positive correlation with the presence of martens. Cold winter temperatures typical of the lowlands also may have precluded martens from inhabiting this area in the 1990s. Prior calculations of thermal exposure showed that between 2000 and 2008, martens at lower elevations experienced more nights when snow cover was insufficient to insulate subnivean resting sites compared to martens at higher elevations (2 nights/1,000 m elevation change—Baltensperger 2009). But despite these constraints, martens have nevertheless expanded their distribution into the Kenai Lowlands during this time. We believe that increasing temperatures (particularly during winter nights) on the Kenai over the past 25 years (Stafford et al. 2000; Berg 2005) may represent an ecological release that has allowed martens to recolonize the Kenai Lowlands.

Additionally, spring snow-day fraction (which was inversely related to occurrence of martens) replaced winter temperature as the most important climatic predictor in the 2000s model (Table 1). The occurrence of martens was positively correlated with areas that received more than one-half of their fall precipitation as snow instead of rain in the 1990s model, although this relationship was inverted in the 2000s model. This directional switch between the 2 time periods suggests that as temperatures have warmed, insulating snow cover in the fall may have become less important. The greater importance of longer growing seasons and earlier spring thaws in the 2000s model indicate that martens are likely benefiting from warming climate conditions, despite any decreases in snow cover.

While temperatures in the Kenai Lowlands are warmer and snow cover is shallower, martens there appear to have responded by resting in alternative structures such as squirrel (*T. hudsonicus*) middens that provide them with warm, dry resting sites comparable in insulation to subnivean sites (Buskirk 1984; Sherburne and Bissonette 1993; Baltensperger 2009). We observed that squirrel middens ≥ 30 cm deep were sufficient to insulate martens from low temperatures even in the absence of snow cover (Baltensperger 2009). Their ability to adapt behaviorally to cope with potentially stressful thermodynamic conditions, as well as temperature and growing season shifts away from harsh winter conditions, have allowed martens to overcome prior thermal constraints and to colonize the Kenai Lowlands over the past decades.

Implications of climate change.—Although the geographic distribution of martens on the Kenai Peninsula has been expanding over the past decades, it remains to be seen whether this may continue given the warming and drying trends predicted for the future. The long-term trajectory of the distribution of marten populations on the Kenai and throughout their range will be related to their capacity to keep pace with the changing environment and evolving landscapes (O'Brien and Leichenko 2003; Somero 2010; Fulton 2011; Ruhl 2012). Because the impacts of climate change on species persistence will not be smooth, linear, nor uniform (Lovejoy and Hannah 2005; Fulton 2011; Ruhl 2012; Wasserman et al. 2013), distributional responses may not follow the current trajectory. For now, however, it appears that martens in Alaska (near the northern extent of their range) may be benefiting from several climate-related changes and expanding their range. The situation in Alaska stands in contrast to research that has predicted the fragmentation and isolation of marten populations near their southern range limits in the Rocky (Wasserman et al. 2013) and Appalachian Mountains (Carroll 2007) where climate shifts are moving beyond the ecological niche limits of martens.

Martens may also benefit from secondary effects of climate change resulting from longer growing seasons (i.e., reduced periods of thermodynamic stress) and the corresponding increase in primary productivity. Prior research documented an average increase in skull lengths of 400 Alaskan martens by 0.03% over the previous 50 years (Yom-Tov et al. 2008; Supplementary Data SD2). This increase in body size is attributed to shorter, warmer winters that have allowed for accelerated plant growth and a resultant increase in the size and availability of voles and shrews. This may lead to higher caloric intake by martens that could assist in overcoming other physiological constraints (Yom-Tov et al. 2008).

The ability of martens to inhabit areas lacking insulating snow cover, like the Kenai Lowlands, indicates an important adjustment, beneficial for maximizing energy conservation and survival beyond core areas in the Kenai Mountains (Buskirk et al. 1989; Schumacher et al. 1989). Their behavioral plasticity and ability to capitalize on climate change benefits (e.g., increased temperature) may act to diminish the importance of other habitat requirements (e.g., CWD, canopy closure, snow cover) and allow martens to persist in an expanded distributional capacity in previously untenable regions.

In an effort to improve the spatial monitoring of wildlife species, we recommend that regional wildlife management entities make an effort to keep more consistent, spatially explicit records (i.e., require precise GPS coordinates) of trapped furbearers and unsuccessful trapping efforts. More consistent spatial records of furbearers would allow for more robust predictions of the distribution of boreal furbearers at regular time intervals in the future. Comparisons among time intervals would provide valuable opportunities to quantify and monitor the spatial changes of wildlife distributions over time throughout the circumboreal North.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Collated records of martens from 1906 to 2008 on the Kenai Peninsula, Alaska, United States. Records listed here do not include those sealed by the Alaska Department of Fish and Game and records denoted with an * were not included in predictive models. ADV tracks were detected by an aerial digital videography survey flown over the Kenai National Wildlife Refuge.

Supplementary Data SD2.—Morphometrics and necropsy results for marten carcasses collected from trappers on the Kenai Peninsula, Alaska between 2006 and 2008.

Supplementary Data SD3.—Partial-dependence plots depicting the relative contribution and direction of influence for the top variables (variable importance value > 50.0) in the 1990s model: a) landcover, b) soil ecotype, and c) distance to trails.

Supplementary Data SD4.—Partial-dependence plots depicting the relative contribution and direction of influence for the top variables (variable importance value > 50.0) in the 2000s model: a) landcover, b) soil ecotype, c) distance to recreation sites, and d) distance to trails.

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