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RESEARCH ARTICLE

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# Combined effects of climate and fire-driven vegetation change constrain the distributions of forest vertebrates during the 21st century

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## Abstract

**Aim:** Biodiversity conservation relies in part on enduring habitat in protected areas. In fire-prone ecosystems, shifts in species' ranges will result both from changes in climate and fire-catalysed vegetation change, which could lead to niche contraction and undermine protected-area efficacy. We explored these dynamics for three forest species with varied niches representative of other taxa and different hypothesized responses to fire-regime change (black-backed woodpecker, *Picoides arcticus*; North American marten, *Martes* spp.; and red squirrel, *Tamiasciurus hudsonicus*). We asked: How do the extent and spatial pattern of these species' distributions change during the 21st century based on the independent and joint effects of climate and vegetation?

**Location:** Greater Yellowstone Ecosystem (Wyoming, USA).

**Methods:** For each species, we developed separate distribution models based on climate and forest attributes, projected under four climate-fire scenarios (a 2 × 2 design with moderate and high temperature and precipitation change). A spatially explicit forest landscape model calibrated for Greater Yellowstone was used to project fire and forest dynamics through 2100, and climate suitability was estimated with MaxEnt.

**Results:** Suitable habitat for all three species based on climate or vegetation alone frequently did not overlap on the landscape, and habitat patches became simpler in shape and farther apart. Climatically suitable habitat for the black-backed woodpecker increased in all scenarios, and suitable forest structure expanded by a factor of 30 in dry scenarios with more fire. Climatically suitable habitat for martens declined with warming and drying; the area of suitable vegetation fell >80% with fire-driven losses of mature forest. Red squirrel habitat was maintained in all scenarios, but was sensitive to aridity, and patches were redistributed and compacted.

**Main conclusions:** Projections based on climate alone may misrepresent future species distributions, especially where disturbances accelerate vegetation change. Our results identify important consequences of fire-regime change for wildlife in forests dominated by obligate-seeder or fire-sensitive conifers.

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KEYWORDS
biodiversity, climate change, fire, protected areas, species distribution models

## 1 | INTRODUCTION

Climate change will profoundly influence wildlife by shifting environmental conditions at rates that exceed the capacity of some species to keep pace and by altering biotic processes and disturbance regimes that constrain habitat availability within physiologically suitable areas (Bellard et al., 2012; Parmesan, 2006; Scheffers et al., 2016). In the face of multiple changing drivers, global biodiversity conservation during the Anthropocene relies in part on the persistence of species in protected areas (Brondizio et al., 2019), but climate change is altering the efficacy of static reserves. Global protected areas do not evenly represent climate (Elsen et al., 2020), and they may fail to meet global conservation targets (Dobrowski et al., 2021) or protect the conditions that support biodiversity across much of the world (Araújo et al., 2004; Pecl et al., 2017). In the United States, national parks are geographically biased towards mountainous areas where climate is changing rapidly, and temperature increases of more than 2°C are projected for most of this area (Gonzalez et al., 2018). The direct impacts of climate on biodiversity (e.g. temperature change) act together with indirect impacts, those mediated by biological processes and disturbance regimes. Wildfire has been a primary driver of the structure and function of ecosystems for millennia (Bowman et al., 2009), but increased fire activity is emerging as a globally significant driver of biodiversity loss (Kelly et al., 2020). Exposure to indirect climate change impacts will be particularly high in forested ecosystems dominated by obligate-seeder tree species, where climate-driven increases in fire activity are rapidly altering forest extent, composition and structure (Bowman et al., 2020; McDowell et al., 2020).

Improved representation of indirect climate impacts in species distribution models (SDMs), including vegetation structure and disturbances, remains a top research need in conservation biology (Elith & Leathwick, 2009; Urban et al., 2016). Climate-based modelling is predicated on the ability of species to track suitable environments, often upslope and poleward. However, observed shifts frequently lead or lag those predicted by climate velocity alone because biological interactions (e.g. facilitation and competition) mediate the direct impacts of climate (HilleRisLambers et al., 2013). Models based on climate alone can improve understanding of species' niches, their potential response to climate change, and guide their conservation (Anderson, 2013), but including measures of non-climatic dimensions of species niches promises to improve model realism, accuracy and applicability (Nowrouzi et al., 2019; Thuiller et al., 2018; Tietjen et al., 2017), especially in ecosystems where fire strongly regulates vegetation (Crimmins et al., 2014; De Cáceres et al., 2013; Hradsky et al., 2017; Kelly et al., 2017; Regos et al., 2018; Reside et al., 2012). The existence of alternative ecosystem states under identical climates, for example, forests and savannas that are maintained by differences in fire regime (Pausas, 2015; Ratajczak et al., 2014), indicates that individualistic species responses to climate alone are insufficient to predict ecosystem structure and composition (Pausas & Bond, 2021). Because the processes that govern vegetation dynamics and their interaction with animals are complex, incorporating these processes into SDMs often requires integrating multiple, independent modelling approaches (Franklin, 2010).

Driven by increasing aridity, annual area burned is rising in fire-prone forests around the world, particularly in the western United States, where managing fire and vegetation in contiguous, mostly undeveloped landscapes is difficult (Abatzoglou et al., 2021; Abatzoglou & Williams, 2016; Westerling et al., 2006). Some contemporary fire activity is consistent with historical fire regimes, but fire-driven changes in forest extent, structure and composition are beginning to emerge (Coop et al., 2020; Prichard et al., 2017; Stevens-Rumann et al., 2018). These trends are particularly strong in the northern US Rocky Mountains (Harvey et al., 2016a, 2016b; Parks & Abatzoglou, 2020; Westerling et al., 2011), including the Greater Yellowstone Ecosystem (GYE; Wyoming, USA), which serves as a natural laboratory for understanding fire-prone forests in the Anthropocene (Turner, 2010). If projected changes in fire activity are realized, the distributions of species adapted to forest ecosystems of the past are likely to shift in the coming decades. Although studies are increasingly aimed at projecting future forest conditions (Buotte et al., 2019; Turner et al., 2021), anticipating the consequences of fire-driven forest change for wildlife has received less attention (Kelly et al., 2020).

We explored how climate change and increased fire in the GYE could affect the distribution of forest-dependent vertebrates during the 21st century. We selected three species with contrasting niches and different expected responses to changes in fire and climate to explore consequences of projected scenarios on their distributions. Black-backed woodpecker (*Picoides arcticus*), North American marten (*Martes* spp.) and red squirrel (*Tamiasciurus hudsonicus*) play key roles in forest ecosystems, for example, by (but not limited to) creating habitat for secondary cavity-nesters, mediating trophic dynamics and influencing the expression of fire-adaptive traits, respectively. They represent varied responses to future climate- and fire-regime change that would be difficult to model for all taxa of interest.

We considered the consequences of climate- and fire-regime change for these species under four alternative future climate-fire scenarios. Although there is an emerging consensus that the western United States will become more arid, we represented uncertainty in future projections by selecting global circulation models (GCMs) from the fifth phase of the Coupled Model Intercomparison Project (CMIP5) that project wetter and drier futures in our study region (Abatzoglou & Brown, 2012) and representative concentration pathways (RCPs) that represent moderate and substantial

temperature increases (Taylor et al., 2012). This 2 × 2 design—warm-wet, warm-dry, hot-wet, hot-dry—organizes our analysis of potential future habitat changes and allows for inference into the relative importance of temperature and aridity. Using these representative forest-obligate vertebrates and integrating climate-based SDMs with estimates of habitat suitability in forest simulations, we asked: How do the extent and spatial pattern of these species' distributions change during the 21st century based on the independent and joint effects of climate and vegetation? We expected warming temperatures to constrain habitats for all three species, with larger changes for black-backed woodpecker and marten, whose core ranges are in boreal regions, than for the red squirrel, which spans a broad contemporary climate gradient. We further expected climatically suitable areas to shift upslope and northward. For marten and red squirrel, which avoid recent burns and require mature forest, we expected habitat to be reduced with fire-driven changes in forest structure, but that the black-backed woodpecker—a burned forest specialist—would benefit from increased fire. We hypothesized that rapid fire-driven changes in forest structure would lead to spatial and temporal mismatches in the vegetation and climatic dimensions of species' niches. Finally, we expected that patches of potential habitat with both suitable climate and forest structure would become smaller, simpler and more isolated and that these changes would increase with warming and drying. Using these independent models of the abiotic suitability of environments (climate) and biotic associations (forest vegetation), we parse two key dimensions of species niches, revealing where and when these axes intersect or diverge in space and time, and how the combination of niche dimensions impacts representative vertebrate taxa.

## 2 | METHODS

### 2.1 | Study area

Our study was focused on the Greater Yellowstone Ecosystem (GYE), a 10.8-million ha ecosystem that includes large federally protected national parks, national forest, tribal lands and private property. The area is prone to large, infrequent, high-severity fires in subalpine forests (Higuera et al., 2011) and frequent low-severity fires in the lower montane; many native species possess fire-adaptive traits that enable their coexistence with fire (Baker, 2009). Fires in this region are allowed to burn to meet management objectives when they do not threaten human safety or infrastructure, and these ecosystems support the intact plant and animal communities that historically characterized the northern US Rocky Mountains.

The climate of the GYE is continental, with warm-dry summers and cold snowy winters. Most precipitation falls as snow, which peaks in December. Mean temperature peaks in July and reaches its minimum in December (1981–2010 climate normals at Old Faithful, Wyoming; Western Regional Climate Center, 2021). Vegetation communities are shaped by elevational and topographic gradients in temperature and moisture (Despain, 1990; Dirks & Martner, 1982; Knight et al., 2014). Low-elevation grassland and shrub-steppe valleys transition upslope to montane woodlands of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and aspen (*Populus tremuloides*). Mid- to high elevations are heavily forested by lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), with the abundance of whitebark pine (*Pinus albicaulis*) increasing towards upper treeline.

We conducted our analysis in five >50,000 ha forested landscapes of the GYE, amounting to a total study area of 279,488 ha that spans the range of environmental and ecological conditions found in regional forests (Figure 1). The southern end of our study area is characterized by topographically complex lower montane forests with a high proportion of Douglas-fir and aspen (Davy, 2007). The central landscapes cover the gently rolling rhyolitic Yellowstone Plateau and are dominated by lodgepole pine, but Engelmann spruce and subalpine fir dominate at cool-mesic sites (Despain, 1990). The northern landscape spans a steep elevation-driven gradient from lower to upper treeline and includes all of the regional forest types (Brown, 2016).

### 2.2 | Study species

The black-backed woodpecker (*Picoides arcticus*) is native to boreal and cold temperate forests and favours forests burned at high severity within the previous decade. Burned areas, almost exclusively, provide nesting locations and population sources (Dudley et al., 2012; Hutto, 1995; Nappi & Drapeau, 2009; Saab & Powell, 2005). *P. arcticus* inhabits burned forests because of the abundance of saproxylic beetles that feed on the tissue of recently killed conifers and opportunities to bore and nest in snag cavities. Nest densities are greater in recently burned mature forests than young forests (Dudley et al., 2012; Vierling et al., 2008). Because they are the primary excavators of high-quality nesting cavities, *P. arcticus* are ecosystem engineers that create habitat for secondary cavity-nesting birds, small mammals, and arthropods (Tarbill et al., 2015). These secondary cavity-nesters then disperse seeds and spores that accelerate vegetative recovery. In this way, woodpeckers facilitate the regeneration of forest vegetation and wildlife in fire-prone forests (Dixon & Saab, 2000).

The North American marten (*Martes americana* and *caurina*) is native to boreal and cold temperate forests of North America. Martens regulate small mammal populations and are themselves influenced by non-consumptive effects of larger predators (Prugh & Sivy, 2020). Martens were a commercial fur species and are sensitive to habitat loss from logging and development, which together reduced population sizes and ranges over the last century (Buskirk & Ruggiero, 1994; Thompson et al., 2012). Martens occupy mesic subalpine conifer forests with complex vertical and horizontal structures, which provide habitat for prey and protected sites for breeding, denning and rearing (Buskirk & Ruggiero, 1994; Thompson et al., 2012). We here use *Martes* to refer to both species of the genus in North America (*M. caurina and M. americana*), which were studied

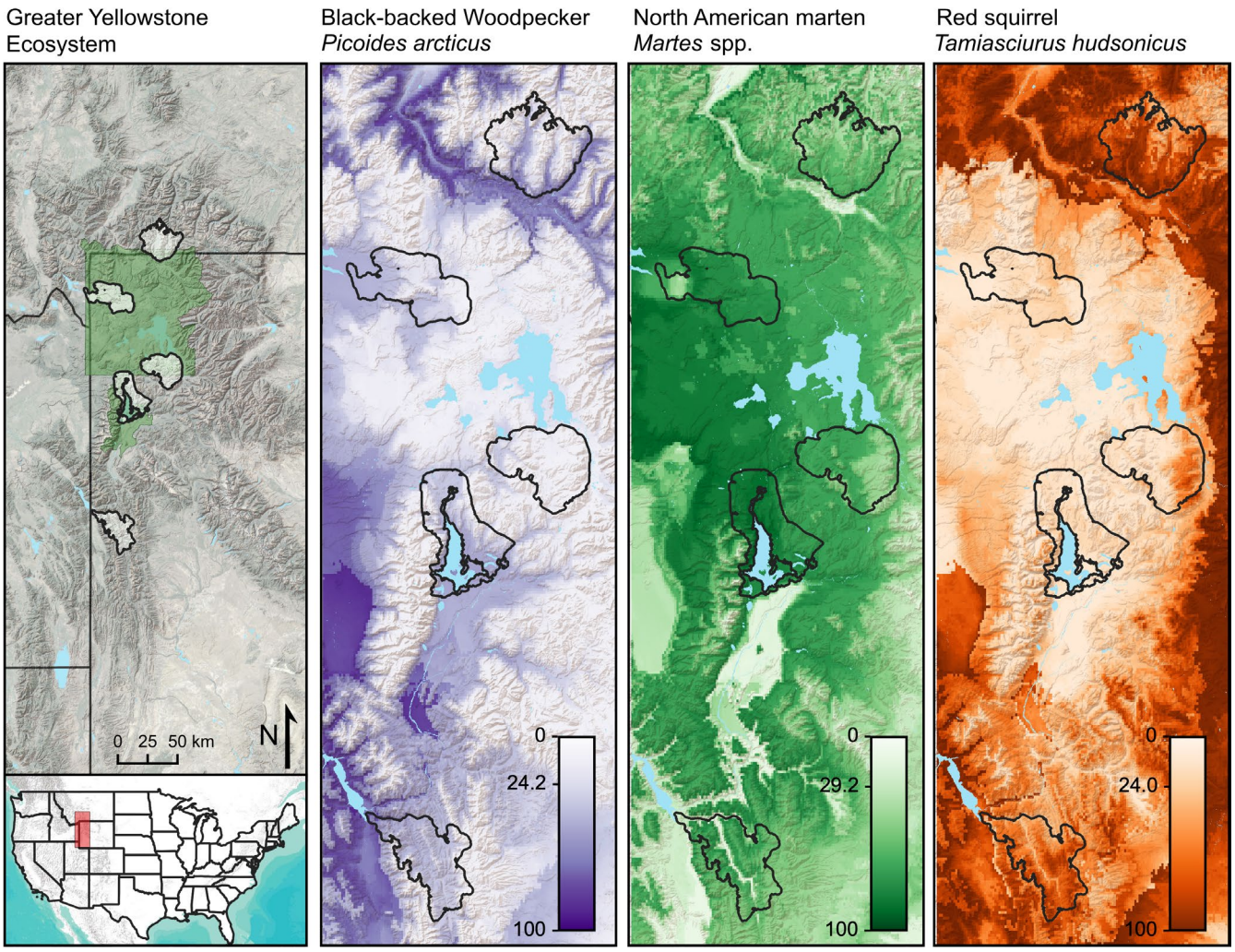



**FIGURE 1** Map of study area and historical species distribution models for *Picoides arcticus*, *Martes americana* and *caurina*, and *Tamiasciurus hudsonicus*. Left panel: Green polygon indicates the boundaries of Yellowstone and Grand Teton National Parks; study landscapes are outlined in black and shaded white and state boundaries are shown by thin black lines. Other panels: Coloured shading indicates the relative occupancy rate (ROR) estimated by MaxEnt models based on bioclimatic predictors. Marked values on colour scales indicate the ROR threshold value that optimizes predictive accuracy of the model

and managed as one species, *M. americana*, before recent genomic studies distinguished them (Dawson et al., 2017; Lucid et al., 2020).

*Tamiasciurus hudsonicus*, the red (or pine) squirrel, is a small rodent native to forests throughout the northern and western United States and across Canada that feeds primarily on conifer seeds, but also on fruits, leaves and fungi (Maser & Maser, 1988). By extracting and caching conifer seeds and dispersing fungal spores, red squirrels are nodes in trophic webs, mediators of mycorrhizal symbiosis and agents of selection. Grizzly bears (*Ursus arctos horribilis*) raid caches of nutrient-dense whitebark pine (*Pinus albicalus*) seeds that squirrels bury, yielding a significant food source for the endangered grizzly (Podruzny et al., 1999). A large portion of squirrel diets in some ecosystems is composed of mushrooms, the fruiting organs of extensive mycorrhizal networks that facilitate nutrient acquisition by trees (Maser & Maser, 1988). Finally, high predation of lodgepole pine (*Pinus contorta* var. *latifolia*) seeds by red squirrels selects against serotiny, opposing the selective pressure of fire that favours serotiny and producing spatially complex patterns in the expression of this consequential trait (Benkman & Siepielski, 2004; Talluto & Benkman, 2014).

## 2.3 | Distribution modelling overview

We built distribution models for each species based on climate alone and vegetation alone, then applied these models separately and together to project future potential habitat (Figure 2). We estimated the distribution of each species within the five landscapes historically and projected them under four climate scenarios. We used CanESM2 (Chylek et al., 2011), a regionally wet scenario, and HadGEM2-ES (Collins et al., 2011), a regionally dry scenario, for contrasting aridity. To contrast future temperature increases, we used two RCPs from the fifth IPCC assessment, RCP 4.5 (warm) and RCP 8.5 (hot). We simulated future fire and forest dynamics under each

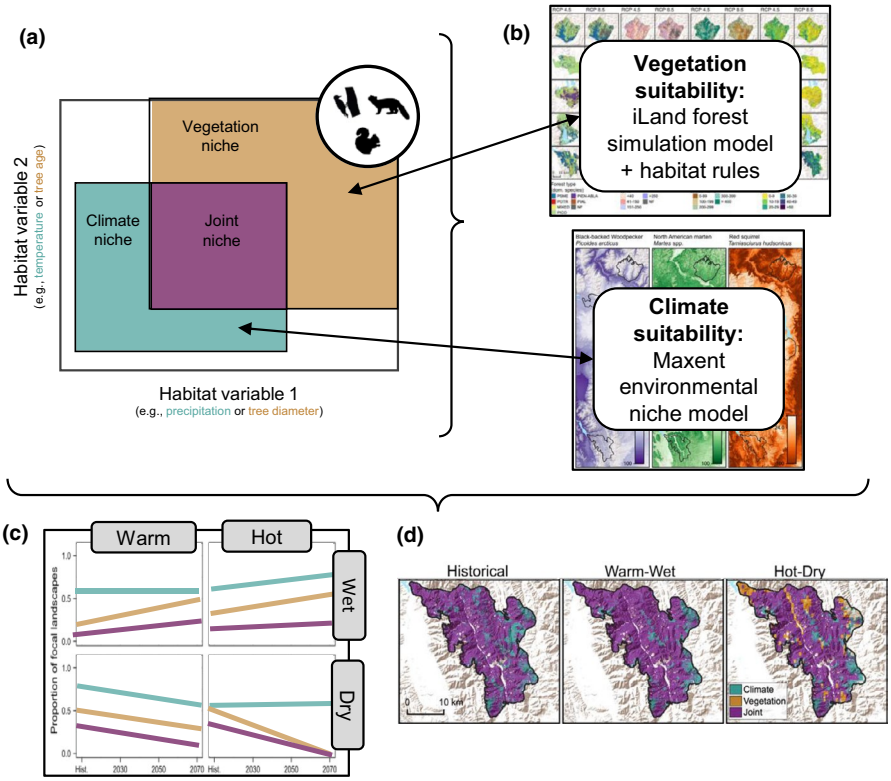



**FIGURE 2** Conceptual figure illustrating modelling approach. Species niche based on vegetation alone, climate alone and both dimensions jointly for three species (a) was estimated using a forest simulation model, habitat rules and MaxEnt (b). The proportion of the study area that was suitable in terms of each dimension and both together were estimated for the early 21st-century and three future periods under four climate-fire scenarios (c). The geographic pattern of species' realized niche in each dimension and jointly was mapped, and landscape metrics were calculated for suitable patches (d)

climate scenario, assessed potentially suitable area in each dimension separately and together, and mapped these areas in the past and future. Finally, we quantified spatial patterns of jointly suitable habitat using landscape metrics.

## 2.4 | Species distribution models based on climate

We developed species distribution models based on climate by using presence-only occurrence data obtained from VertNet, an aggregator of museum specimen collections (Constable et al., 2010). We downloaded all available records by searching for the genus and epithet of each species, selected a subset of records where geospatial uncertainty was <5 km, and thinned records such that none were within 1 km. A complete list of institutions and collections that provided data is in Table S1. Historical climate predictors were obtained from the WorldClim v2.1 dataset (Fick and Hijmans 2017), which includes 19 biologically meaningful variables derived from monthly temperature and precipitation data summarized for 1970–2000 at ~1-km resolution. Downscaled future projections of these bioclimatic predictors under our four climate scenarios were obtained for three 30-year periods: 2020–2049, 2040–2069 and 2060–2089 (Navarro-Racines et al., 2020).

Climate-based distributions were modelled using the MaxEnt algorithm (Phillips et al., 2006), which estimates the relative likelihood of occurrence by comparing the statistical distribution of predictor values at observed and background locations and is optimized for presence-only datasets (Elith et al., 2011). We included all available bioclimatic predictors because the MaxEnt algorithm is robust to collinear predictors (Feng et al., 2019). We excluded product features, increased the beta multiplier coefficient to 2 and left other parameters at default values (see Table S2 for complete list of MaxEnt parameters) to minimize model over-fitting and produce biologically interpretable response curves (Merow et al., 2013; Figures S2, S3, S4). We randomly selected 5000 background points for each predictor variable from within the bounding box of the occurrence data. Then, we used internal cross-validation to repeatedly ($n$ = 10) partition occurrence data and associated predictor values into subsets for training (70%) and testing (30%) and built SDMs on the training partitions using MaxEnt. Prediction accuracy was assessed on the testing partition using area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS). Finally, we built a final SDM from the mean response of all 10 models (all models had an AUC score ≥0.89 so none were excluded). We quantified variable importance in the mean model by comparing predictions from models based on actual and shuffled variable values, replicated 10 times (Thuiller et al., 2009).

The mean model for each species was used to predict the relative occupancy rate (ROR) at each 1-ha cell of the landscapes during the early 21st-century ("historical") and three future climate periods. We transformed continuous ROR values into a presence/absence index by identifying a threshold in ROR that minimized the difference between specificity and sensitivity (Liu et al., 2005). We estimated 95% confidence intervals around the mean model threshold based on the 2.5th and 97.5th percentile of optimal thresholds in the 10-model set. Finally, we summed the total suitable area across all five landscapes in each period (historical, 2030s, 2050s, 2070s) based on the mean, lower and upper thresholds to determine the central

tendency and confidence intervals for each period. Modelling was implemented in R v4.0.1 (R Core Team, 2018) using the "biomod2" package (Thuiller et al., 2009).

### 2.5 | Species distribution models based on forest structure

We next developed criteria (Van Horne & Wiens, 1991) that described species-specific habitat suitability based on stand-level forest attributes including stand-level (1 ha) average tree density, diameter and age; tree species richness; and recent fire activity. Criteria were based on an extensive literature review and consultation with species experts (Table 1). It was not possible to relate species occurrence and vegetation data in correlative models (as was done for climate) because future vegetation data are simulated, and analogous historical vegetation data (i.e. continuous 1-ha resolution forest composition and structure data extending across specific landscapes) are not available. Inferring potential wildlife occupancy based on site characteristics and life history is appropriate when demographic and resource data are not available or compatible (Brooks, 1997; Hansen et al., 1993; Irwin, 1994; Lindenmayer et al., 2008).

Future forest structure was simulated for each climate scenario using the process-based forest landscape and disturbance model, iLand (Seidl et al., 2012, 2014), which was previously calibrated for the GYE (Braziunas et al., 2018; Hansen et al., 2018; Hansen & Turner, 2019; Turner et al., 2019). iLand simulates individual tree establishment, growth and mortality as a function of parameters controlling species' responses to light, temperature, nutrient and water availability, competition and disturbance. Individual tree outputs were aggregated to 1-ha annual resolution by species. The timing, location and potential maximum size of fires were estimated using a statistical fire-climate model (methods extended from Westerling et al., 2011). Fire spread occurred dynamically within iLand as a function of fuel availability, weather and topography, and fire severity results from the interaction among these variables and species traits. Forest structure and composition in turn emerge dynamically from these processes of growth and disturbance. For each climate scenario and landscape, 20 simulations were generated in which annual burned area (and thus vegetation responses) varied stochastically. The present analysis is a companion to Turner et al. (2021), where the magnitude, direction and timing of climate- and fire-driven changes in forest ecosystems of the GYE are assessed using the same forest simulations. We briefly summarize those findings here but refer readers to Turner et al. (2021) for a detailed treatment.

We applied vegetation suitability indices to simulated forest structure in each landscape at the beginning of each decade of the 21st century. For each species, a cell was determined to be suitable in terms of vegetation if the forest attributes and recent fire activity in the cell met all criteria (Table 1). We summarized vegetation suitability into one historical period (corresponding to simulated vegetation in 2010) and three future periods (2020–2049, 2040–2069 and 2060–2089) by calculating the mean suitability for each cell during the period (i.e. suitability in 2 of 3 decades was summarized as suitable). We summed the total suitable area across all five landscapes in each period (historical, 2030s, 2050s, 2070s), during each of 20 simulations, and from this pool identified the central tendency and 95% confidence intervals.

### 2.6 | Joint effects of climate and vegetation suitability

After assessing potential climate and vegetation suitability separately, we overlaid these models to estimate the joint habitat suitability for each grid cell during the early 21st-century and three future periods. We incorporated uncertainty in both dimensions of the joint niche by intersecting climate models based on the mean, upper and lower MaxEnt thresholds with vegetation models from each forest simulation, resulting in 60 versions of the joint estimates (3 climate model thresholds × 20 forest simulations) for each period, from which we identified the central tendency and 95% confidence intervals. Then, the joint niche was derived from the spatial intersection of the binary climate and vegetation grids. To produce maps of the joint models and calculate landscape metrics, we aggregated the vegetation model simulations by marking the cell suitable if it was suitable in more than 50% of the 20 simulations and intersecting it only with cells that were climatically suitable based on the mean MaxEnt threshold.

### 2.7 | Analyses

We compared species distributions among climate scenarios by summing the total suitable area across all five landscapes during each time period and dividing by the total area (279,488 ha). We compared the amount of habitat available as a function of vegetation and climate separately to understand which dimension was more limiting through time. We also mapped the distributions in each dimension alone and jointly for each period. We quantified spatial patterns in the joint distribution during each period using area-weighted mean patch metrics that describe the size (patch size; the size of each distinct patch in ha), connectedness (nearest-neighbour distance; large values, in metres, indicate long distances between distinct patches) and shape (shape index, a patch's unitless perimeter:area ratio relative to a square) of suitable patches (Cushman et al., 2008; McGarigal et al., 2002). Spatial analyses were conducted using the "raster" (Hijmans et al., 2015) and "landscapemetrics" (Hesselbarth et al., 2019) R packages.

## 3 | RESULTS

### 3.1 | 21st-century climate, fire and forest dynamics

Fire activity did not increase under warm or hot future temperatures in the wet scenarios (CanESM-2), and forest extent, composition and structure remained similar to historical conditions

**TABLE 1** Parameters used to define vegetation suitability

| | Qualitative associations | Forest attribute thresholds |
|---|---|---|
| Black-backed Woodpecker (*Picoides arcticus*) | • Severely burned, large-diameter snags hosting beetles (Cerambycidae and Buprestidae)<br>• Large enough to bore cavity | 1. Burned, >50% tree mortality<br>2. Prefire tree density ≥200/ha<br>3. Prefire mean conifer diameter ≥20 cm |
| References | Hutto, (1995, 2008), Saab et al., (2007); Saab et al., (2009), Dudley et al., (2012), Latif et al., (2013); Latif et al., (2019), Tremblay et al., (2015), Stillman et al., (2019) | |
| North American marten (*Martes* spp.) | • Mature stands of large-diameter trees<br>• Complex horizontal and vertical structure<br>• Topped trees, hollows, downed wood | 1. Tree density ≥50/ha<br>2. Tree basal area ≥18 $m^2$<br>3. Mean conifer diameter ≥20 cm<br>4. Stand age ≥75 years |
| References | Buskirk & Ruggiero, (1994), Coffin et al., (1997), Payer & Harrison, (2003), Proulx et al., (2006), Thompson et al., (2012) | |
| Red squirrel (*Tamiasciurus hudsonicus*) | • Mature forested stands of cone-producing conifers<br>• Redundant cone supply | 1. Tree density ≥50/ha<br>2. Cone production:<br>3. ABLA mean dbh ≥30 cm or,<br>4. PIEN mean dbh ≥38 cm or,<br>5. PSME mean dbh ≥20 cm or,<br>6. PICS mean dbh ≥20 cm or,<br>7. PIAL present<br>8. >1 species of conifer |
| References | Ferner, (1974), Smith, (1981), Podruzny et al., (1999), McKinney & Fiedler, (2010) | |

*Note:* PIEN: Engelmann spruce (*Picea engelmannii*), ABLA: subalpine fir (*Abies lasiocarpa*), PICS: lodgepole pine (*Pinus contorta*), PIAL (*Pinus albicaulis*), dbh: diameter at 1.4 m.

(Turner et al., 2021). However, in the dry scenarios (HadGEM2-ES), fire activity increased substantially, with greater increases in annual area burned in the hot vs. warm scenario. The extent of forest cover (stands with >50 trees $ha^{-1}$) was reduced in both dry scenarios, and the remaining forests were sparser, younger and smaller (Figure S1). Forest composition also shifted, with increased coverage of Douglas-fir and aspen and decreased coverage of Engelmann spruce, subalpine fir and lodgepole pine (Turner et al., 2021).

Climate-based SDM's characterized ecologically plausible relationships between species relative likelihood of occurrence and bioclimatic variables (Figures S2, S3, S4) and the relative importance of predictors (Figure S5) reflected the species' ecology. Models yielded reasonable estimates of contemporary species distributions across our study region (Figure 1), and evaluations indicated high predictive accuracy (cross-validated models had mean AUC scores ≥0.89 and TSS scores ≥0.65; Table S3).

Climatically suitable habitat for the black-backed woodpecker increased under all scenarios (Table 2, Figure 3), and high-elevation areas that were not suitable historically became so by 2030 (Figures S6, S7, S8). In contrast, the area where vegetation was suitable was much lower and varied among scenarios (Table 2, Figure 3). Availability of recently burned forests with appropriate prefire structure was low in both wet scenarios but increased with fire activity in the hot-dry scenario around mid-century (Table 2, Figure 3). When considering both dimensions jointly, potential habitat was driven by availability of suitable forest structure rather than climate. Relative changes were large because the extent of this ephemeral habitat was low during the historical period (Table 2, Figure 3). Given the small suitable area at any given time, the area-weighted mean patch size for the joint niche was zero until 2070 (Figure 6). Small patches of suitable habitat available around 2070 in the hot-dry simulation were far apart and simple in shape (Figure 6).

Climatically suitable habitat for marten declined slightly in the warm-wet scenario and substantially in the hot-dry scenario (Table 2, Figure 3). By 2070, climatically suitable areas in the hot scenarios were found only at high elevations (Figure 4.) Suitable area based on vegetation alone was much less extensive (Table 2, Figure 3) and declined in the warm-wet and hot-dry scenarios. In dry scenarios, both dimensions decreased proportionally (Table 2, Figure 3), but the change was larger for climate under the hot scenario and for vegetation in the warm scenario. Suitable area based on vegetation alone was most abundant in the southernmost study landscape (Figure 4), but climatically suitable area shifted upslope into increasingly small patches; thus, little area of intersection between suitable vegetation and climate remained by 2070 (Figure 4). In all other landscapes, vegetation was the greater constraint as large areas that were climatically suitable lacked mature forest. When climate and forest structure were considered jointly, habitat for the pine marten declined in all scenarios, substantially in both hot scenarios. Marten habitat patches became smaller, further apart, and simpler in shape (Figure 6). The mean area-weighted patch size for marten was >8500 ha at the beginning of the century but by 2070 was 3115 ha in the warm-wet scenario and only 25 ha in the hot-dry scenario. The average distance between marten habitat patches increased, exceeding 500 m by 2070 (Figure 6).

Climatically suitable habitat for red squirrel increased in the wet scenarios (Table 2, Figure 3). Historically, the area suitable based on vegetation alone was similar to that of climate alone.

TABLE 2 Numerical summary of modelled changes in suitable habitat for three species

| | | Scenario | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Warm-wet | | | | | | Hot-wet | | | | | |
| Species | Dimension | Hist | 2030 | 2050 | 2070 | Net | Proportion | Hist | 2030 | 2050 | 2070 | Net | Proportion |
| Black-backed | Climate | 54 | 93 | 99 | 100 | +46 | +85 | 54 | 97 | 100 | 99 | +45 | +84 |
| woodpecker | Vegetation | 0 | 1 | 0 | 0 | +0 | +47 | 0 | 1 | 1 | 0 | +0 | +30 |
| | Joint | 0 | 1 | 0 | 0 | +0 | +55 | 0 | 1 | 1 | 0 | +0 | +36 |
| American | Climate | 98 | 90 | 82 | 91 | −7 | −7 | 98 | 60 | 50 | 34 | −65 | −66 |
| marten | Vegetation | 39 | 35 | 32 | 32 | −7 | −19 | 40 | 35 | 33 | 29 | −11 | −27 |
| | Joint | 37 | 32 | 27 | 27 | −10 | −27 | 38 | 24 | 18 | 7 | −31 | −82 |
| Red squirrel | Climate | 53 | 79 | 72 | 80 | +27 | +52 | 53 | 82 | 77 | 84 | +31 | +59 |
| | Vegetation | 50 | 52 | 54 | 56 | +6 | +12 | 51 | 52 | 53 | 56 | +5 | +10 |
| | Joint | 30 | 41 | 39 | 45 | +15 | +51 | 30 | 42 | 41 | 47 | +17 | +56 |
| | | Warm-dry | | | | | | Hot-dry | | | | | |
| | | Hist | 2030 | 2050 | 2070 | Net | Proportion | Hist | 2030 | 2050 | 2070 | Net | Proportion |
| Black-backed | Climate | 54 | 99 | 100 | 100 | +46 | +85 | 54 | 96 | 100 | 96 | +42 | +77 |
| woodpecker | Vegetation | 0 | 3 | 3 | 5 | +4 | +1278 | 0 | 2 | 3 | 10 | +9 | +2796 |
| | Joint | 0 | 3 | 3 | 5 | +4 | +1356 | 0 | 2 | 3 | 10 | +9 | +2947 |
| American | Climate | 98 | 56 | 76 | 67 | −32 | −32 | 98 | 74 | 48 | 22 | −76 | −78 |
| marten | Vegetation | 38 | 34 | 26 | 22 | −16 | −43 | 39 | 37 | 27 | 16 | −22 | −58 |
| | Joint | 36 | 16 | 20 | 13 | −23 | −63 | 37 | 26 | 11 | 1 | −36 | −97 |
| Red squirrel | Climate | 53 | 56 | 49 | 41 | −13 | −24 | 53 | 35 | 42 | 45 | −8 | −14 |
| | Vegetation | 50 | 50 | 44 | 44 | −6 | −11 | 50 | 53 | 47 | 37 | −13 | −27 |
| | Joint | 29 | 30 | 23 | 15 | −14 | −48 | 30 | 18 | 22 | 22 | −8 | −27 |

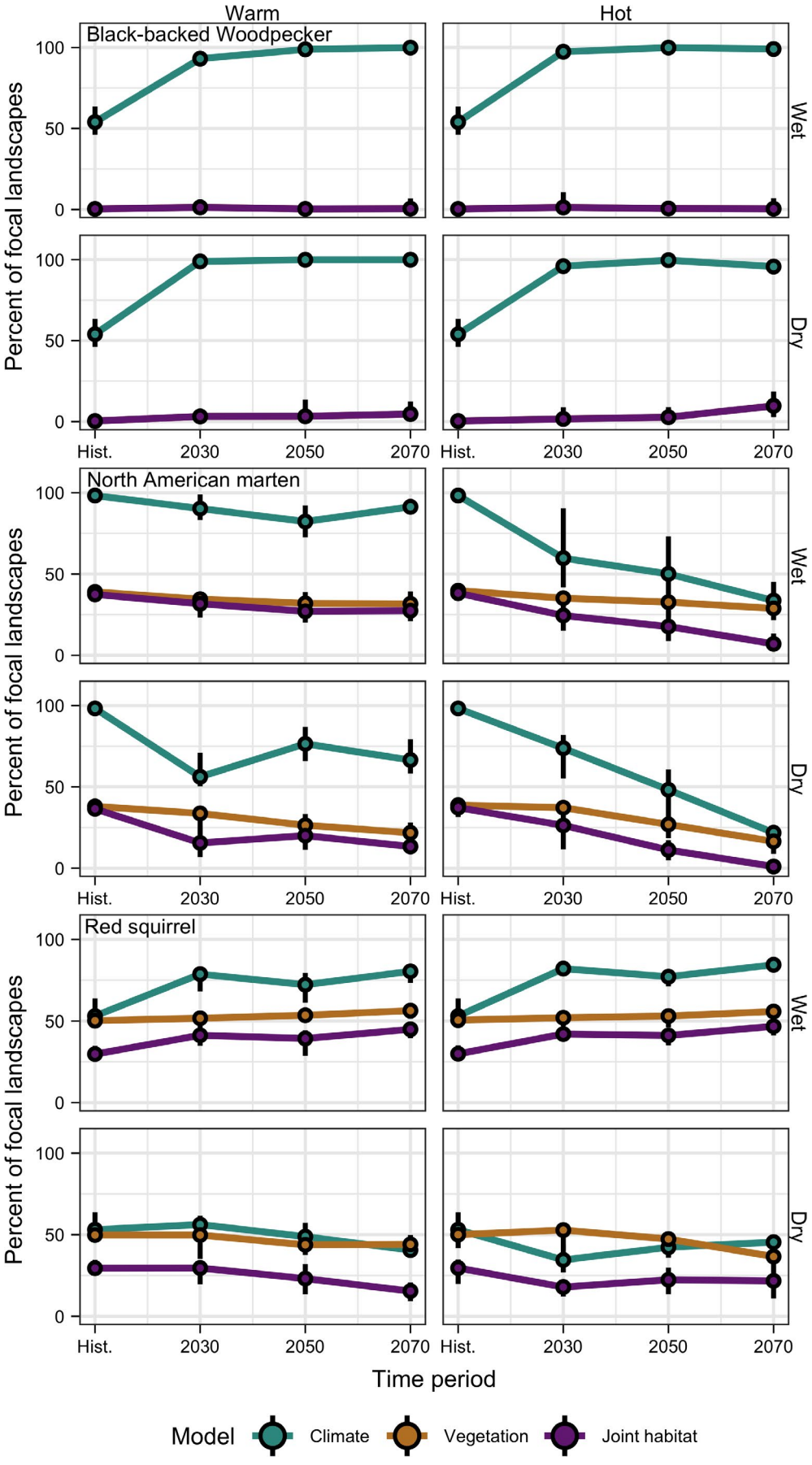
*Note:* Tables show percentage of total study area estimated to be suitable habitat in terms of climate only ("Climate"), vegetation only ("Vegetation") and both dimensions jointly ("Joint") during the early 21st century ("Hist") and during three future periods ("2030," "2050" and "2070") under four climate scenarios ("Warm-Wet," "Hot-Wet," "Warm-Dry" and "Hot-Dry"); change in absolute percentage between 2070 and the historical period ("Net"); and proportional change in percentage expressed as a percent between 2070 and the early 21st century ("Proportion").

This area did not change significantly in either wet scenario but decreased in the hot-dry scenario. When climate and forest structure were considered jointly, habitat for the red squirrel increased under both wet scenarios, but habitat declined under the warm-dry and hot-dry scenarios. The relative change in habitat was smallest for red squirrel among our study species under the dry scenarios (Table 2, Figure 3), and this was the only species to show opposite directions of change. Although total habitat area across all landscapes did not change substantially in any scenario, in the hot-dry scenario the habitat that remained was less evenly distributed across the GYE and instead was focused in the topographically complex southern and northern landscapes (Figure 5). Habitat area expanded and was more evenly distributed than during the historical period under the warm-wet scenario. Habitat patches were large (>10,000 ha) in all scenarios by the end of the century and distances between patches did not meaningfully change, but patches became slightly simpler in shape.

## 4 | DISCUSSION

Our findings indicate that the amount and spatial pattern of potential habitat for forest-dependent vertebrate species could change substantially during the 21st century in response to the combined effects of increasing temperatures, changes in precipitation and fire-induced changes in forest structure and composition. Importantly, our findings highlight the strong potential for fire to catalyse forest changes that lead to geographic mismatches between two key dimensions of species' niches—the physiological suitability of environments (climate) and the resources that create habitat (vegetation). Furthermore,

FIGURE 3 Estimated habitat area based on climate-only, vegetation-only and joint suitability models under four CMIP5 future climate projections ("wet" = CanESM2, "dry" = HadGEM2-ES, "warm" = RCP 4.5 and "hot" = RCP 8.5). Habitat area is shown as the percentage of the 279,488-ha study area. Error bars indicate 95% confidence intervals based on variability among a 10-model training set (climate-only), 20 vegetation simulations (vegetation-only) or both (joint model)


Warm
Hot
Black-backed Woodpecker
North American marten
Red squirrel
Wet
Dry
Percent of focal landscapes
0
50
100
Hist.
2030
2050
2070
Time period
Model
Climate
Vegetation
Joint habitat

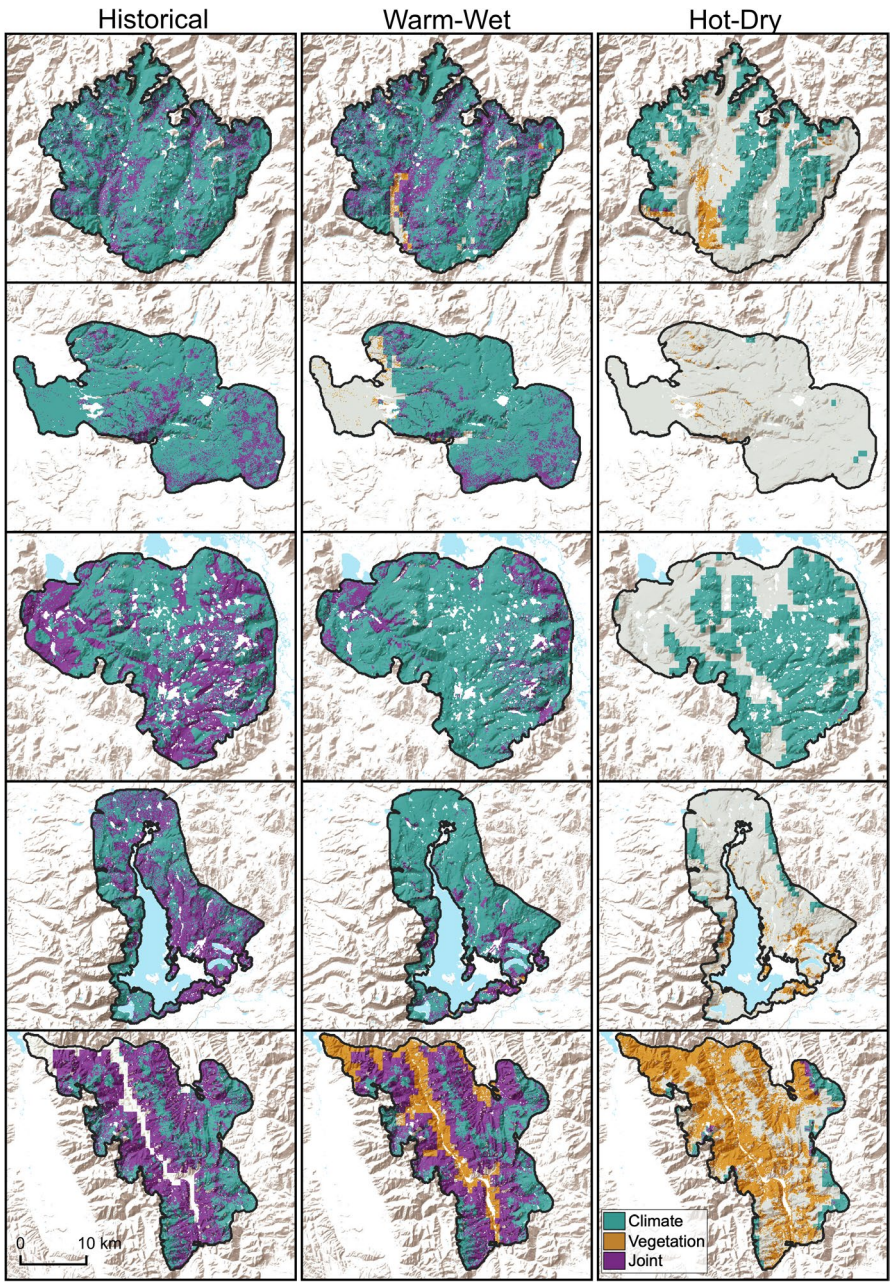



**FIGURE 4** Estimated historical and future (2070) distribution of the North American marten (*Martes* spp.) based on climate-only, vegetation-only and joint suitability models during the 21st century under alternative future climate-fire scenarios, warm-wet (CanESM2; RCP 4.5) and hot-dry (HadGEM2-ES; RCP 8.5)

relative change in total habitat across the region provides an incomplete picture because it can mask geographic divergence in niche dimensions and the redistribution of habitat into simpler and more isolated patches. Our study also explicitly incorporated uncertainties in the magnitude and nature of future climate change. Differences among climate scenarios in the magnitude of temperature increases between RCP's and in future precipitation between regionally wet and dry GCMs resulted in variable habitat trajectories. Our study provides evidence that efforts to conserve biodiversity within static protected areas will be threatened both by a changing climate and by disturbance-driven changes in vegetation, particularly in fire-prone forests. Protected areas that represent a wide gradient in contemporary climate and vegetation will be best positioned to safeguard the multiple dimensions of species niches.

### 4.1 | Fire-driven spatial mismatch in realized niche dimensions

For all three species we modelled, suitable areas based on climate and vegetation alone often did not overlap (Figures 3, 4, 5 and Figures S6–S12), highlighting the potential for fire-driven niche contraction. In general, areas that were climatically suitable shifted upslope and northward, while patterns of vegetation suitability varied among species and were less coherent spatially, reflecting refugial forest stands that were unburned and/or retained their historical condition. Because forests are dominated by long-lived organisms that can survive in disequilibrium with climate, fire can abruptly catalyse changes in ecosystem structure that might otherwise take decades or centuries to unfold (Bell et al., 2014; Coop et al., 2020;

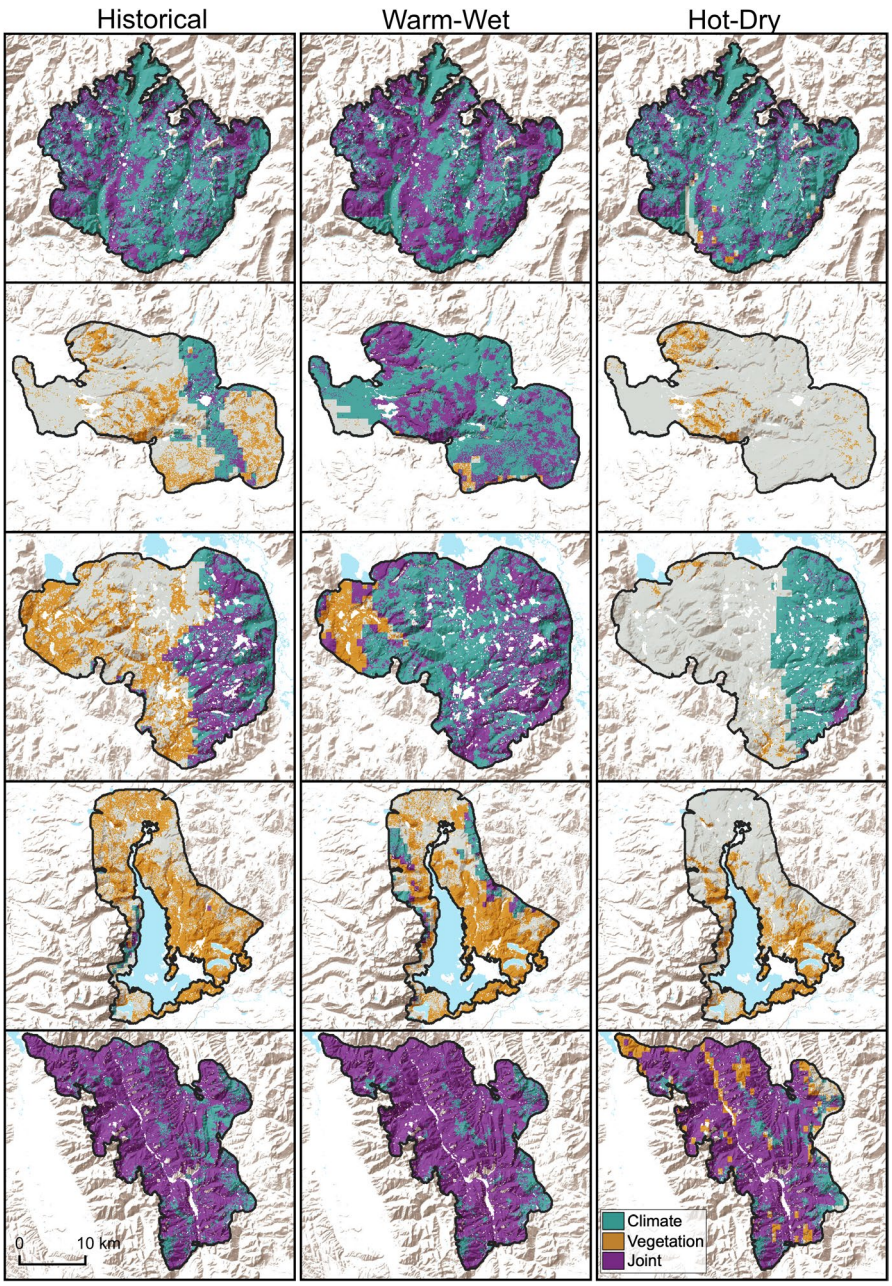



**FIGURE 5** Estimated historical and future (2070) distribution of the red squirrel (*Tamiasciurus hudsonicus*) based on climate-only, vegetation-only and joint suitability models during the 21st century under alternative future climate projections, warm-wet (CanESM2; RCP 4.5) and hot-dry (HadGEM2-ES; RCP 8.5)

Johnstone et al., 2016). For ecosystems where fire regimes are changing, the impact of climate change on vertebrates may manifest through disturbance regimes well before the system becomes climatically unsuitable or vegetation shifts in direct response to climate (e.g. drought mortality).

Altered fire regimes are already initiating habitat loss in ecosystems around the world (Kelly et al., 2020), suggesting the future patterns of change we project for the GYE are plausible. For example, increases in the extent of high-severity fire in the California Sierra Nevada are threatening habitat for the spotted owl (*Strix occidentalis*). Owls were driven out of previously occupied sites affected by high-severity fire, and projections of increasing fire extent and severity are raising concern for the future of the species (Jones et al., 2016). In the US Great Basin, novel fire regimes enabled by the invasion of a non-native annual, cheatgrass (*Bromus tectorum*), have reduced habitat extent, increased rates of nest failure and created ecological traps for the greater sage grouse (*Centrocercus urophasianus*; Bradley et al., 2018, O'Neil et al., 2020). In Australia, extensive fires in 2019 and 2020 led to an abrupt loss of habitat for dozens of species that were already threatened by a prolonged drought (Wintle et al., 2020). These examples, and numerous more from around world (Kelly et al., 2020), illustrate that rates of fire-driven changes can exceed rates of species' adaptive capacity and accelerate the direct impact of climate on species range shifts. Accounting for fire is clearly important when modelling the occurrence of species with known sensitivities to fire effects (O'Neil et al., 2020; Stillman et al., 2019; Walsh et al., 2019). Here, however, we

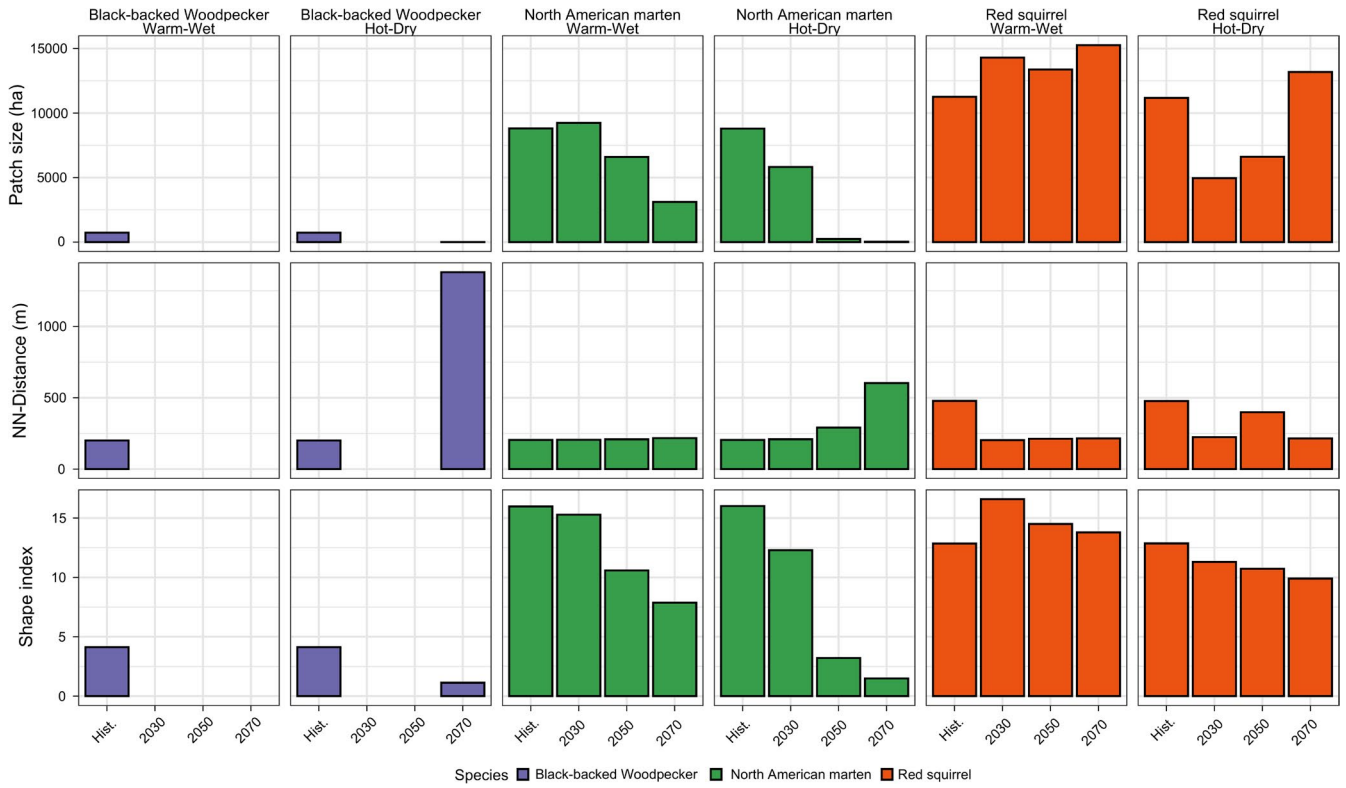



**FIGURE 6** Landscape metrics describing spatial patterns of jointly suitable (climate and vegetation combined) habitat patches historically and during the 21st century under Warm-Wet (CanESM2 RCP 4.5) and Hot-Dry (HadGEM2-ES RCP 8.5) future climate scenarios. All metrics area area-weighted means

demonstrate how effects of disturbance on forest structure act together with climate to shape the distribution of suitable habitats, even for species such as martens and red squirrels (Jones & Tingley, 2021). Although not explicitly modelled for vertebrates here, our results further indicate that fire-driven changes in vegetation could have subsequent, interactive effects with climate (Enright et al., 2015).

Our study also responds to calls for better representation of the processes that lead to contraction of species' realized niches in climate change vulnerability assessments (Scheele et al., 2017). Viewing our analysis through Sheele et al.'s "niche reduction hypothesis," the threat of climate change is not evenly distributed across environmental space but rather is amplified in areas vulnerable to fire-driven vegetation transition. The direct physiological effects of climate change are amplified where plant traits or geography make forests vulnerable to fire-driven loss. In this way, changes in vegetation interact with direct impacts of climate change on vertebrates and constrain species' realized niches to areas that are resilient to increased fire activity.

By mapping changes in suitable habitat in each landscape, our study demonstrated that change in total habitat area across all landscapes can mask meaningful changes in the location and spatial arrangement of habitat. The relative importance of habitat area versus habitat patch configuration as drivers of species richness remains contentious (Fahrig, 2013, 2017; Haddad et al., 2017). In our study, as is often the case on real landscapes, reductions in area *per se* were accompanied by changes in configuration (e.g. the case of the marten), but changes in configuration also occurred without concurrent changes in total habitat area (e.g. the case of the red squirrel). For example, total red squirrel habitat increased or was only slightly reduced during the 21st century in all scenarios, but whereas all five landscapes supported habitat in the historical period, squirrel habitat was completely absent from two landscapes and nearly eliminated from a third by 2070 in the hot-dry scenario (Figure 5). Further, remaining patches were larger, but simpler in shape and concentrated in the southern landscape (Figure 6). Redistribution and reconfiguration of habitat is likely to constrain the ability of species to track climate change and sustain metapopulations within refugial habitats (Fletcher et al., 2018; Pfeifer et al., 2017).

## 4.2 | Accounting for uncertainty in future climate

Accounting for uncertainty in future climate allowed us to investigate a range of potential futures (Figure 3). Increases in aridity and related vegetation mortality are projected for much of the western United States (Williams et al., 2013), and the frequency of extreme droughts is expected to increase (Cook et al., 2020). Our results suggest that dry futures will have cascading negative consequences for forest-dependent wildlife. Changes in the timing and form of precipitation will also have impacts that are not reflected in total precipitation. Variable importance rankings (Figure S5) indicated

that seasonality of precipitation is more important for our study species than total annual precipitation, which is important because the proportion of precipitation that falls as snow, average snowpack depth, length of snow coverage, and ultimately, the amount of water supplied by snowmelt are projected to decline across the western United States (Klos et al., 2014; Lute et al., 2015).

Differences in temperature increases among scenarios were consequential for the woodpecker and marten. Hot scenarios enabled large increases in burned area, which created habitat for the woodpecker and eliminated habitat for the marten. We present both warm (RCP 4.5) and hot (RCP 8.5) forcing pathways because uncertainties regarding emissions from land-use change (e.g. deforestation) and optimism about renewable energy have led to debate on which pathway is more informative (Hausfather & Peters, 2020; Schwalm et al., 2020). We found that meaningful changes in wildlife habitat can occur under both pathways, and these changes were more sensitive to differences in moisture (i.e. differences among GCMs) than temperature (i.e. differences among RCPs).

## 4.3 | Limitations

Our climate-based SDMs were based on presence-only data, assume niche equilibrium and did not account for adaptative potential. Although the MaxEnt algorithm has been widely tested and produces acceptable estimates of relative habitat suitability when true absences are unavailable (Grimmett et al., 2020), presence-only models have less power to discriminate suitable from unsuitable environments than presence–absence models. Classification rates in presence-only models can be inflated and may not reflect functional accuracy (Grimmett et al., 2020; Warren et al., 2020). By selecting species with continental distributions and building SDMs using occurrence and environmental data from across this broad gradient, we expect that our models capture a range of potential relationships and consider our estimates interpolation rather than extrapolation. Adaptations in key traits of our study species could emerge, but the magnitude of change in simulated forest structure we project is likely unprecedented during the Holocene (Higuera et al., 2011; Whitlock, 1993), suggesting that adaptation would need to be substantial and rapid.

Our study areas are representative of environmental gradients within the GYE but do not encompass the full extent of potential habitat nor do they quantify variation in habitat quality within suitable areas. We also did not attempt to model suitable habitat based on life stage. For example, juveniles may use suboptimal habitats or respond differently to forest structure than adults. Juvenile black-backed woodpeckers occupy unburned and low-severity forest patches where predation risk is lower (Stillman et al., 2019, 2021). These nuances do not contradict our results, but rather underscore the value of diversity in forest structure and disturbance history (i.e. pyrodiversity) required by organisms adapted to fire-prone ecosystems (Bowman et al., 2016).

Finally, we integrated two independent modelling procedures, and therefore, errors could compound. Our findings should not be interpreted as management recommendations or forecasts, but rather as scenarios that characterize processes likely to constrain future habitat. By modelling climatic and vegetation suitability separately, we aimed to compare the relative importance of each dimension and to simulate future vegetation change with more process richness (i.e. in response to fire) than correlative approaches would allow.

## 4.4 | Conclusions

Our analysis quantified the relative influence of climate and vegetation on species niches, revealing geographic mismatch between these dimensions. Projected species distributions were almost always more constrained by vegetation than by climate, and shifts were greatest under hot, dry future climate scenarios. We overcame some limitations of existing approaches by integrating climate-based models with forest landscape simulations that incorporate changing fire regimes (Pausas & Bond, 2021; Walsh et al., 2019). Much work remains to better integrate biological mechanisms into estimates of future species distributions (Urban et al., 2016), but accounting for disturbance-driven changes in vegetation is a crucial step (Driscoll et al., 2010). Our findings also highlight the importance of considering diverse taxa during conservation planning. Focusing primarily on megafauna and endangered species could lead to missed opportunities compared with strategies that emphasize common threats, optimization or whole-ecosystem conservation (Ford et al., 2017). Large-scale conservation planning should focus on representing a wide range of climatic conditions and vegetation states in protected areas.

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### CONFLICT OF INTEREST

The authors declare no known conflict of interest.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13470.

## DATA AVAILABILITY STATEMENT

All data presented in this manuscript are archived by the Environmental Data Initiative: https://doi.org/10.6073/pasta/631de982dde024b390c8a28c05e721a6. Code for this analysis is archived on GitHub: https://github.com/tylerhoecker/wildlife.

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## BIOSKETCH

**Tyler J. Hoecker's** work is united by the idea that disturbances act as local catalysts for global environmental change, with a focus on fire in forest ecosystems. He uses field experiments, observational studies, statistical analyses and process-based simulation modelling to anticipate the fate of western forests in a future with a changing climate and more fire. His work uses mechanistic insight at the landscape scale to inform forest management. Tyler is a post-doctoral researcher with the USGS Northwest Climate Adaptation Science Center and is located in Missoula, MT.

Author contributions: TJH and MGT designed the study, interpreted results and wrote themanuscript. TJH conducted analyses.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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