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Managing for biodiversity: The effects of climate, management and natural disturbance on wildlife species richness

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Abstract

Aim: Managers are increasingly facing an uncertain future given changing climates and ecological trajectories. The interacting effects of climate, natural disturbance, and management actions complicate future projections, and there is a need for approaches that integrate these factors—especially for predicting future vegetation and species richness.

Location: Central Sierra Nevada Mountains, USA.

Methods: We used outputs from a spatially explicit landscape disturbance succession model that incorporated forest management actions, disturbance, and climate to estimate habitat and potential species richness for 202 vertebrate species and five functional groups from 2020 to 2100. We examined species richness outcomes of three forest management scenarios under three climate trajectories. We modelled broadscale drivers of landscape-level species richness, and proximate effects of management and disturbance at each pixel.

Results: Climate and forest management scenario had significant effects on potential species richness across the landscape, particularly at lower elevations; however, only management had significant effects at higher elevations. We found no effect of the interaction between climate and management scenario. The historical climate and the minimal management scenario generally resulted in higher species richness compared with other scenarios. Positive proximate effects generally included mechanical thinning and prescribed fire, as well as low and medium severity fire and beetle outbreaks. High severity fire had a consistently negative effect on species richness. We also quantified the contribution of protected areas and found that protected areas had higher species richness compared with ecologically similar unprotected lands, especially in climate futures that deviated from the historical climate.

Main Conclusions: Our findings highlight that managing for biodiversity is complex, and effects of climate, disturbance, and management differ among species, functional groups, topography and scales. However, landscape disturbance succession models provide a science-based tool for untangling broadscale drivers and proximate effects of biodiversity and managing for ecological integrity in a changing climate.

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KEYWORDS

biodiversity, climate change, Forest management, spatially explicit landscape disturbance succession model, species richness, wildlife habitat

1 | INTRODUCTION

Managers face multiple uncertainties in predicting trends in wildlife species and biodiversity, and in understanding the future outcomes of management actions on habitats given a changing climate and associated disturbances. Wildlife response to climate change can vary widely and these responses can be compounded by other threats such as human development, pollution, and invasive species (Brodie et al., 2013). Furthermore, there are many uncertainties in climate models and in predicting the rate and magnitude of vegetation and habitat change (Martens et al., 2021; Prentice et al., 2007). However, ecological prediction and management of ecosystems are important for the conservation of native wildlife and biodiversity—key components of landscape ecological integrity (Wurtzebach & Schultz, 2016). Therefore, approaches are needed that provide managers with data on future predictions of wildlife and biodiversity, as well data on how these predictions might change given various management actions.

Because of uncertainties in predicting future vegetation and wildlife habitat, many approaches that do not require vegetation variables have been developed to inform management for conserving biodiversity into the future. These approaches use abiotic features such as topographic and climatic variables to predict wildlife habitat (e.g. Beier & Brost, 2010; Lawler et al., 2015) and rely on the assumption that these landscape components influence the bottom up processes that give rise to vegetation and wildlife. The limitations of these approaches for local scale applications include their inability to account for (1) forest management decisions, (2) natural disturbances, (3) stochastic events, and (4) vegetation and vegetation dynamics. All of these factors, in addition to the abiotic factors mentioned above, will interact to affect the extent and spatial arrangement of wildlife habitat (McRae et al., 2008).

A promising option for estimating future vegetation and habitat that integrates biotic and abiotic factors is landscape disturbance succession models (LDSMs; Gustafson et al., 2011; Keane et al., 2015). LDSMs can incorporate forest management scenarios along with natural disturbances, which allows for a more realistic modelling of vegetation disturbance and succession dynamics. Previous wildlife studies that have taken advantage of LDSMs have evaluated the effects of different management scenarios on wildlife habitat (e.g. Larson et al., 2004; Scheller et al., 2011; Shifley et al., 2008; White et al., 2022). LDSMs have now advanced to predict future vegetation under a changing climate while accounting for stochasticity and uncertainty (Scheller et al., 2018), making them highly effective for understanding the potential outcomes of (1) climate scenarios, (2) management scenarios, and (3) the interaction of climate and management

on wildlife habitat and biodiversity (e.g. McDowell et al., 2021; Nitschke et al., 2020). Model outputs can be used to produce spatially explicit maps of vegetation types and conditions, seral stage, biomass, carbon, and disturbance frequency and intensity. In turn, these outputs can be used to make inferences about a wide array of values, including wildlife habitat, biodiversity, cultural and social benefits and impacts, economic costs, ecosystem services, and the socio-ecological resilience across forested landscapes as a whole (Manley et al., *in review*; Povak et al., *in review*). Outputs can be used by managers to determine how disturbances are affecting wildlife habitat and biodiversity across a landscape over time, and how management can enhance wildlife habitat and biodiversity conservation.

Forest management strategies are commonly designed to reduce forest fuels with the expectation of lowered fire intensity in the short term and improved ecological integrity in the long term (Evans et al., 2022; North et al., 2021). We were interested in determining the broadscale drivers and proximate effects of forest management, disturbance, climate, and their interactions on wildlife species richness and ecosystem function. We used a LDSM to predict future habitat conditions for over 200 vertebrate species across a large landscape in the central Sierra Nevada Mountains of California, USA. We simulated three forest management scenarios and three climate trajectories to estimate and predict reproductive habitat change for vertebrate species for 80 years into the future (2020–2100). We evaluated management scenarios that represented a range of size and frequency of management actions across the study area, with the following predicted outcomes:

- We predicted that climate change would negatively affect species richness, given that the current suite of species reflects current habitat and climate conditions (Thomas et al., 2004). Because climate affects the entire landscape, we also predicted that the effect of climate on species richness would exceed that of management.
- We predicted that the interaction of climate and management would have the greatest effect on potential species richness driven by changes in habitat, natural disturbance, and management type (McRae et al., 2008).
- We predicted that proximate effects of management treatments on species richness may not mirror broadscale patterns given that stand-scale responses may create a diversity of habitat values, and thus support higher species richness in aggregate (Schall et al., 2018; Stephens et al., 2012).
- Lastly, we predicted that protected areas may support high levels of biodiversity over the next century given that they experience a more active disturbance regime (Jones & Tingley, 2022; Thom & Seidl, 2016).

2 | METHODS

2.1 | Study area

The study area was the Tahoe Central Sierra Initiative (TCSI) landscape, stewarded by a collaborative partnership to improve forest health and resilience through strategic, science-based management. The 1 million hectare TCSI landscape, extends from Downieville, California in the north, to the Lake Tahoe basin in the east, to Placerville and Grass Valley, California to the west (Figure 1). It includes a range of landownerships comprised of federal, state, nonprofit, and private entities. The TCSI landscape spans a substantial elevational gradient, from western foothills at ~900 m to the crest of the Sierra Nevada Mountains at over 3300 m and is comprised of many ecological zones. Foothill shrublands and woodlands dominate the lower elevations of study area. These transition to lower montane forests, then to upper montane forests as elevation increases. Subalpine forest and alpine meadows and shrublands are present at higher elevations in the study area. Climate in the study area is primarily Mediterranean, with hot dry summers and cool wet winters, and precipitation falling as snow in higher elevation areas.

Fire is a regular and naturally occurring disturbance in the study area due to the amount of fuel on the landscape during dry summers. Therefore, many of the vegetation types are fire-adapted. The historic fire return interval varies across the different ecological zones from 11 to 151 years with a mean across the study area of 55 years (van de Water & Safford, 2011). Currently, the fire return interval is longer than the historical return interval and when fires do occur, there is a higher proportion of high severity fire relative to the historical period (Safford & Stevens, 2017). Bark beetles are also disturbance agents in the study area that can cause sometimes widespread tree mortality (Fettig et al., 2019).

2.2 | LANDIS II modelling

The research presented here is one piece of a larger effort to quantify landscape resilience under different management scenarios with climate change. As part of this research, the LANDIS-II LDSM (hereafter, LANDIS; Scheller et al., 2007) was used to simulate spatial distribution and dynamics of forests at 10-year time steps from 2020 to the year 2100. The LANDIS model, as described in Maxwell et al. (2022), incorporated forest management scenarios, natural disturbances such as fire and insect outbreaks, and climate change across the TCSI using 180 m pixels. This model used the net ecosystem carbon and nitrogen extension (Scheller et al., 2011), which tracks biomass of age/species cohorts and includes several carbon and nitrogen pools. Vegetation dynamics are responsive to climate, as well as a range of in situ disturbances such as insect outbreaks and fire. Therefore, vegetation death, establishment, growth and succession respond to changes in climate

and disturbance concurrently. Native vegetation data outputs from LANDIS consisted of biomass by age class by tree species and shrub functional types (e.g. N-fixing obligate seeders, non-N-fixing post-fire resprouters). We matched these biomass outputs to relevant stand metrics, such as quadratic mean diameter (QMD) and canopy cover, in order to estimate habitat suitability for vertebrate species (see below).

In this study, three forest management scenarios with increasing intensity and extent of management were examined: the minimal management scenario (MMS)=minimal management consisting of forest treatments in proximity to infrastructure and private industrial timberlands; the broadscale management scenario (BMS)=broadscale management treatments across the entire landscape on a 30–50 years return interval; and the reference condition management scenario (RCMS)=reference condition management reflecting more frequent and extensive management treatments matching the historical frequency of disturbance (20–40 years return interval) including more prescribed fire as a management treatment. The MMS treated 9307 ha annually by mechanical thinning on private land and in the wildland-urban interface defence zone (within 400 m of infrastructure). The BMS treated 32,800 ha annually (nearly 4 times the area treated in MMS) that additionally included the wildland-urban interface threat zone (>400–2000 m from infrastructure), general forest areas, roadless areas, and wilderness. Mechanical thinning and prescribed fire were both applied in BMS. The RCMS treated 51,395 ha annually (nearly 6 times the area treated in MMS) across the entire landscape, and matched the historical fire return interval for forests in this region. In the RCMS, prescribed fire comprised 30% of the treatments in the general forest and roadless areas. Management prescriptions are further described in Maxwell et al. (2022).

Three climate change trajectories were used in modelling outcomes for each of the management scenarios. The 'Historical' climate scenario randomly sampled years from 1980 to 2020, using data from gridMET (Abatzoglou, 2013). Future climate change models all indicate warmer and drier conditions but vary in the projected degree of change in temperature and precipitation. The 'CNRM' climate trajectory represented a relatively cooler and wetter future (CNRM-CM5), while the 'MIROC' trajectory represented a more extreme warmer and drier future (MIROC5). Both the CNRM and MIROC projections were from the Coupled Model Intercomparison Project Phase 5 and used 8.5 as the relative concentration pathway, which represents the expected future emission levels (Schwalm et al., 2020). Climate data were aggregated into 10 elevational bands using daily historical or projected down-scaled data from gridMET or MACAv2-METDATA (Abatzoglou & Brown, 2012).

The LANDIS outputs for each management scenario, climate trajectory, and 10-year time step were used as inputs to estimate vertebrate species habitat. Because LANDIS is a stochastic simulator, five separate runs were conducted to account for random stochasticity in the modelling output.

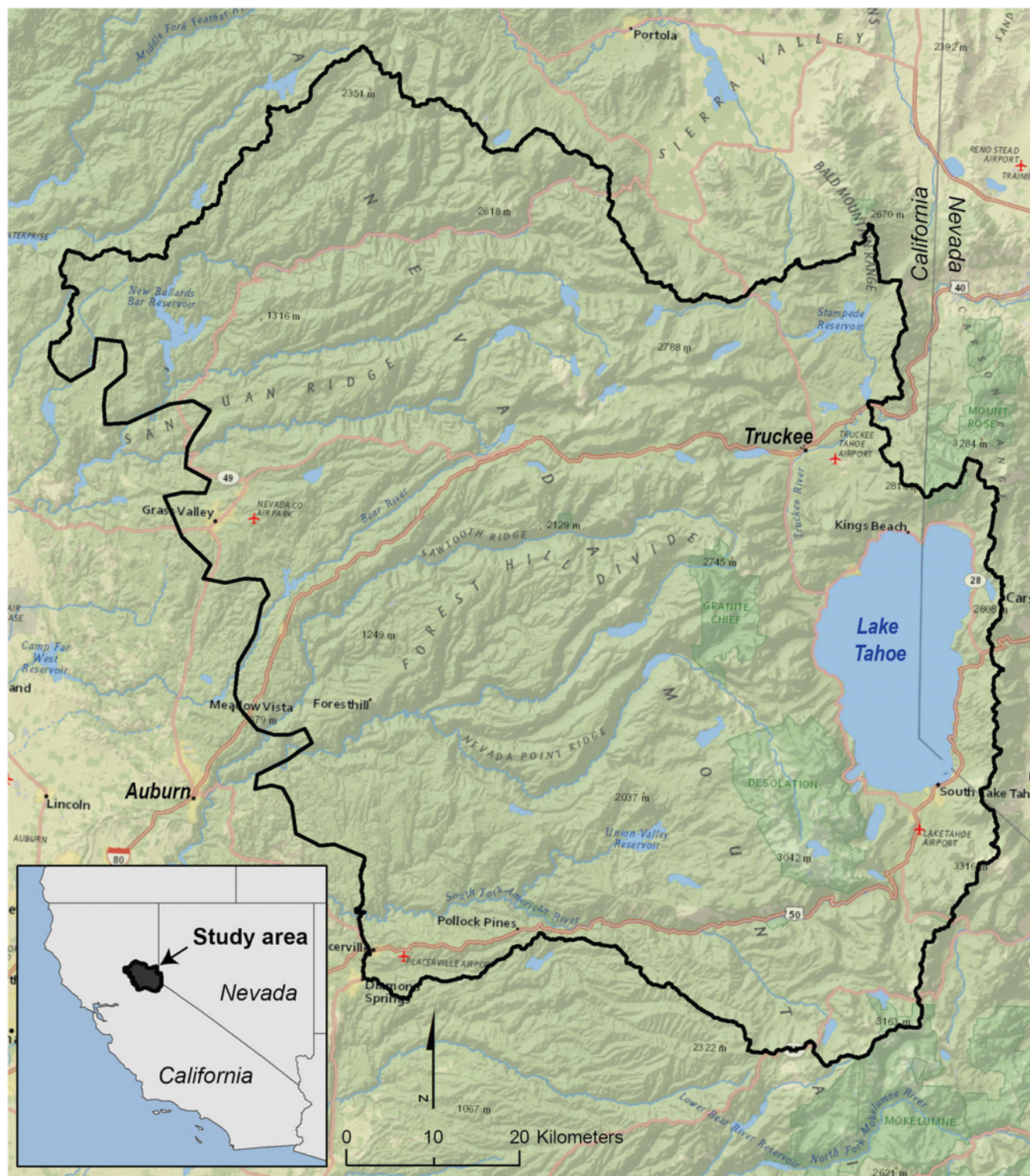


FIGURE 1 Tahoe Central Sierra Initiative study area in the Sierra Nevada Mountains, USA.

2.3 | Estimating trends in potential species richness

Following White et al. (2022), the California Wildlife Habitat Relationships System (CWHR; California Department of Fish and Wildlife, 2014) was used to identify vertebrate wildlife species associated with current and future predicted vegetation conditions. We queried

CWHR software (v 9.0) to select species that (1) were native to the TCSI landscape, (2) overlapped with Alpine, Amador, Butte, El Dorado, Nevada, Placer, Plumas, Sierra or Yuba counties, and (3) had year-long presence in those counties. We subsequently filtered out species that did not have reproductive habitat in any of the cover types simulated by the LANDIS model or were primarily associated

with aquatic environments. This resulted in identifying 202 species for the habitat modelling: 95 birds, 81 mammals and 26 reptiles (Appendix A).

The LANDIS raster outputs were matched to vegetation type, percent canopy cover, and average diameter (used to represent seral stage), which constitute the three elements of habitat type in the CWHR data base. Because the LANDIS succession Net Ecosystem Carbon and Nitrogen extension used for this study does not track individual trees, we followed a similar protocol as White et al. (2022) to estimate seral stage and canopy cover. Each 180-m cell was classified into one of 14 vegetation categories depending on the dominant species present at that timestep (Appendix B). We developed regression models from Forest Inventory and Analysis (FIA) data to estimate diameter from cohort ages, which we then used to calculate the weighted mean diameter (weighted by cohort biomass) for each plot. The weighted mean diameter was then binned into seral stages (<1, 1–6, 6–11, 11–24 and >24 cm). We also developed regression equations to estimate percent canopy cover from vegetation type, seral stage, and plot biomass. Canopy cover was estimated from LANDIS cells and then binned into five classes (<10%, 10%–25%, 25%–40%, 40%–60%, >60%). From the categorical maps of vegetation type, seral stage, and canopy cover class, we used the CWHR database to estimate habitat suitability for the 202 vertebrate species.

The CWHR data base applies suitability values of 0, 0.11, 0.22 or 0.33 (ranging from no suitability to high suitability) to vegetation type (e.g. Douglas fir), seral stage (e.g. sapling tree, medium/large tree) and canopy cover (e.g. sparse, dense) for reproductive habitat, with summed values across these three categories ranging from 0 to 1.0. For estimating habitat suitability across the study area, we were only interested in high quality reproductive habitat. We assumed that reproductive habitat was the best proxy for population status, and to be conservative, we only included species that had a combined reproductive habitat value of ≥ 0.33 for any given pixel and time step. We produced binary maps from the reproductive habitat outputs by classifying anything <0.33 as zero and anything ≥ 0.33 as 1. To calculate overall species habitat richness (hereafter 'potential species richness'), we summed these binary maps for each time step across all species.

Because functional groups contribute different roles in maintaining ecological processes and ecological integrity, we were interested in estimating not only overall habitat for species, but also habitat for functional groups. We selected the following functional groups since they represent primary ecological drivers in these forested landscapes and had adequate sample sizes from our species list, with some species (true omnivores) belonging to more than one group: cavity excavators/nesters (hereafter 'cavity excavators'; $n=21$), herbivores ($n=97$), insectivores ($n=103$), predators ($n=58$) and seed/spore dispersers (hereafter 'seed dispersers'; $n=18$; Appendix A). We then summed the binary habitat maps for each functional group. Based on previous analyses, we expected differences in current and future biodiversity along the west to east elevational gradient, so we also summarized results for two elevation zones

(lower elevation areas in the western half of the study area and higher elevation areas in the eastern half of the study area) parsed by the median elevation of the landscape (1706 m).

2.4 | Broadscale drivers of potential species richness

To evaluate the broadscale drivers of disturbance in the form of climate trajectories and forest management scenarios, and their interaction on potential species richness, we conducted 2-way ANOVAs in R software (R Core Team, 2021) with the sum of the potential species richness across the study area at each time step and iteration as the response variable and with management scenario and climate regime as independent variables. We also tested for an interaction of management scenario and climate on potential species richness. We conducted these ANOVAs for all species and for each of the five functional groups. We then repeated the ANOVAs for lower and higher elevation zones separately.

2.5 | Proximate disturbance effects on potential species richness

To examine proximate effects of different types of disturbance on potential species richness, we used the following LANDIS outputs for each raster pixel on the landscape: mechanical thinning, prescribed burning, fire severity, and beetle outbreaks. LANDIS generates annual raster outputs for beetle infestations, fire severity and management (Maxwell et al., 2022). Mechanical thinning data were provided as the amount of biomass removed, and the prescription (removal of smaller diameter trees) was consistent across all treatments. We classified any thinning in a pixel as a 1 and then summed annual occurrences of thinning over each of the 10-year time steps for each iteration. For prescribed fire (modelled as low severity), we summed prescribed burning activity for each pixel over each 10-year time step for each iteration. For beetle activity (typically resulting in large tree mortality), we classified any beetle activity in a pixel for a year as a 1 and then summed beetle activity over each 10-year time step for each iteration. For wildfire, we examined the effect of fire severity by classifying the LANDIS output fire rasters into low, medium or high categories based on percent mortality. We then summed fire activity for each intensity class over each 10-year time step for each iteration. Because our species richness data were over-dispersed, we used a negative binomial regression in the R software environment to investigate relationships between potential species richness and mechanical thinning, prescribed fire, low/medium/high severity fire, and beetle activity. Specifically, we used the *negbinirr* function from the 'mfx' R package (Fernihough, 2019) to obtain incidence rate ratios and estimate percent change in species richness given an occurrence of each disturbance. We did not include individual climate variables since these were not available at the per-pixel scale.

2.6 | Potential species richness in protected areas

In addition to management and disturbance dynamics, we examined the contribution of protected areas to support potential species richness and ecological integrity. We used the Protected Areas Database for the United States (v3.0; USGS, 2022) to categorize protected areas into (1) Wilderness Areas and Wild and Scenic Rivers (456 km², 4.6% of the study area), (2) Inventoried Roadless Areas (1017 km², 10.4% of the study area, and (3) all other protected areas (99 km², 1% of the study area), which included Areas of Critical Environmental Concern, Recreation Management Areas, Research or Educational Areas, National Scenic Areas, and Botanical Areas. Because the protected areas were mostly at higher elevations, we sampled points within and outside of protected areas in areas that had similar ecological characteristics as follows. We first divided the study area into seven ecological strata based on elevation, slope and aspect with the 'rassta' package in R (Fuentes et al., 2021). We then randomly sampled 1000 points in each strata and only used points from strata that had at least 80 points fall within protected areas to ensure adequate representation. We then used the *svyglm* function in the 'survey' R package (Lumley, 2004, 2020) to incorporate the strata identified above in a generalized linear model to estimate change in potential species richness over the 80-year period (richness in 2100 minus richness in 2020) as a function of whether an area was protected or not and the protected area status.

3 | RESULTS

3.1 | Trends in potential species richness

In general, across all management scenarios and climate trajectories, we observed differences in trends of overall potential species richness between lower and higher elevation zones (Figure 2). In the year 2020, we observed lower species richness at higher elevations, and higher species richness interspersed with moderate richness at lower elevations (Figure 2). This pattern shifted noticeably through time with species richness decreasing at lower elevations and increasing at higher elevations by 2100 (Figure 2). The lower elevation zone trended toward more homogeneous and moderate numbers of species and this effect was especially pronounced in the MMS (Figure 2). The same trends observed for overall potential species richness were also observed for all the functional groups; however, the changes were not as homogeneous as for all species combined (Figure 3; Appendix C).

We then examined the data at the two elevation zones (lower and higher) separately. We found that potential species richness consistently declined over time in lower elevation forests (Figure 4; Appendix D), but increased in higher elevation forests. Overall, species gains at higher elevations were larger than low elevation losses (Figure 4; Appendix D). Lower management intensity tended to favour higher species richness; the MMS generally

had more species habitat gains in higher elevation areas and fewer losses in lower elevation areas than the BMS and RCMS. At lower elevations, the BMS tended to have more species losses than the RCMS.

3.2 | Broadscale drivers of potential species richness

For all species across all elevations, potential species richness was generally reduced with greater management and more intensive climate change (Table 1). Statistically, richness was slightly higher for MMS compared to the other two management scenarios and, similarly, richness was higher for historical climate compared to the other two climate trajectories (Figure 5). ANOVA results indicated that management had a greater effect than climate across all elevations, and that there was no interaction between the two drivers (Table 1). However, biodiversity responded to different drivers in each elevation zone. At lower elevations, climate was the primary driver of potential species richness, which declined with increasing magnitude of climate change. However, both management and climate were significant at lower elevations (Table 1). At higher elevations, management was the primary driver of potential species richness, which declined with increasingly intensive management (Figure 5).

For functional groups at all elevations, the effects of management and climate were both significant (Table 1), and no significant interactions were found. Management scenario had a stronger effect for all functional groups except for insectivores, where climate was more influential (Table 1). All functional groups except for cavity excavators had higher potential richness with the MMS and the historical climate regime (Appendix E). Cavity excavators had higher potential richness with the most intensive management scenario and climate trajectories (RCMS and MIROC, respectively; Appendix E). At lower elevations, again, management and climate were both significant, but climate had the greater effect on richness for all functional groups except for herbivores, where management had the greater effect (Table 1). The historical climate regime was consistently associated with higher potential richness for all functional groups (Appendix E). At higher elevations, management scenario and climate were both significant only for cavity nesters, with management scenario having more of an effect than climate (Table 1). For insectivores and predators, only management scenario was significant, while neither driver was significant for herbivores or seed dispersers (Table 1). For functional groups with significant effects, the MMS was associated with higher potential richness (Appendix E).

3.3 | Proximate disturbance effects on potential species richness

We then evaluated the effects of each of the six proximate effects of potential species richness across all elevations. We found that

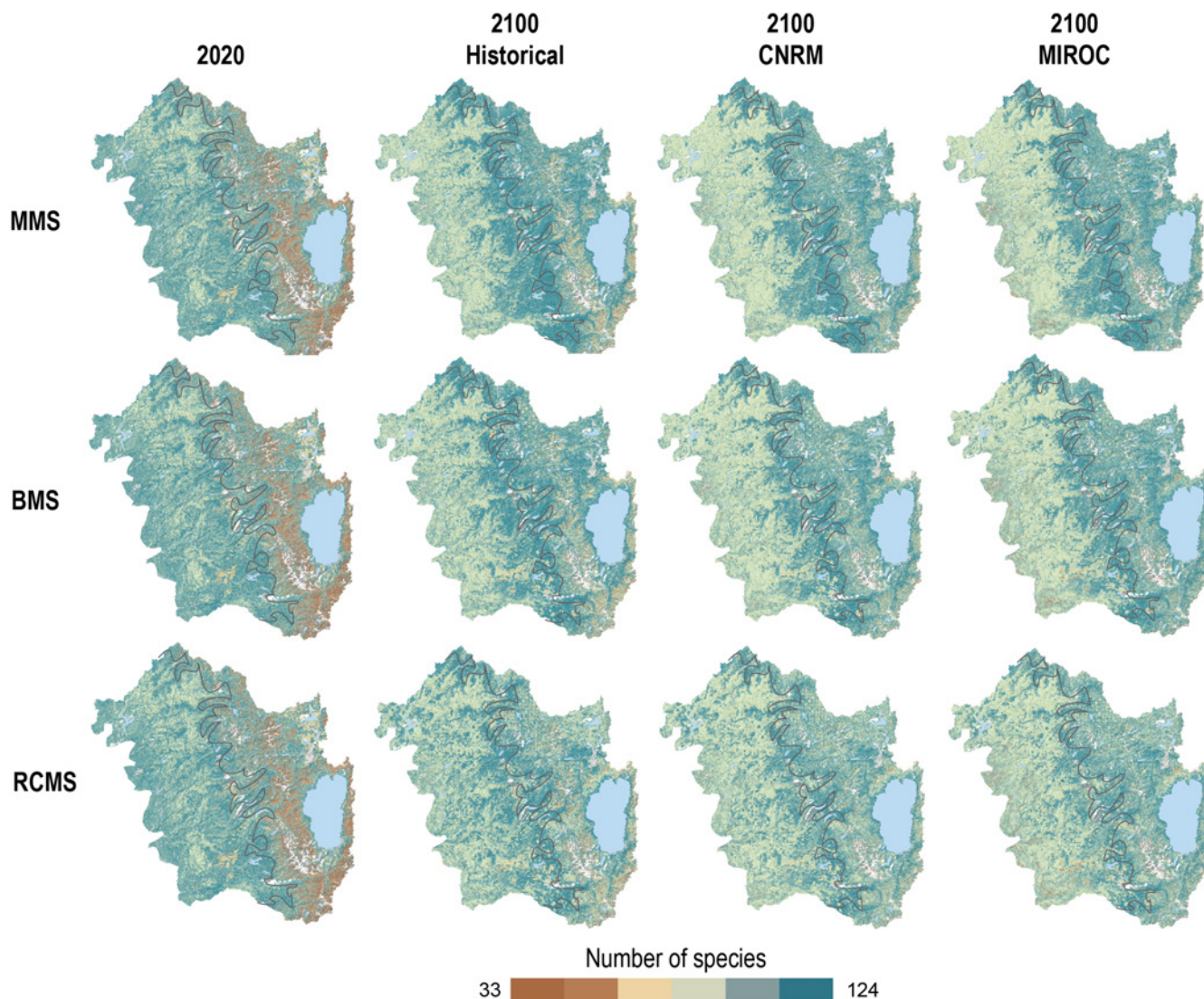


FIGURE 2 Potential species richness based on reproductive habitat for 202 wildlife species in the central Sierra Nevada, California. Potential richness (averaged across the five simulation runs) for the initial time step (2020) and final time step (2100) are shown for three forest management and three climate scenarios. For reference, the grey line in all the maps represents the median elevation (1706 m) of the study area. BMS, Broadscale Management Scenario; MMS, Minimal Management Scenario; RCMS, Reference Condition Management Scenario.

the occurrence of a mechanical thinning action, prescribed fire, low or medium severity wildfire, or beetle outbreak increased potential species richness across all species. High severity wildfire decreased potential species richness (Figure 6). The individual functional groups also had a net positive effect of all disturbance types other than high severity fire, with a few notable exceptions. Seed dispersers showed a decrease in potential richness with prescribed fire and medium severity fire, and for mechanical thinning (CNRM and MIROC only), and for low severity fire for the more extreme MIROC climate (Figure 6). Predators also experienced a decrease in potential richness with beetle outbreaks for the historical and CNRM climates. Interestingly, the positive effects of prescribed fire were higher for CNRM and MIROC climates compared to the historical climate.

In the lower elevation areas, only the effect of mechanical thinning was positive for all species and all climate scenarios

(Appendix Fa). Medium and high severity fire had negative effects on potential species richness for all species (Appendix Fa). The effect of prescribed burning was positive for the CNRM and MIROC climates, but equivocal for the historical climate (Appendix Fa). The effect of low severity fire was positive for the historical and CNRM climates but equivocal for the MIROC climate (Appendix Fa). The effect of beetle outbreak was positive for the MIROC climate but negative for the historical and CNRM climates (Appendix Fa). In higher elevation areas, the direction of effect for all management and disturbance occurrences were generally the same as for the entire landscape but varied in degree of effect (Appendix Fb). Functional groups were relatively consistent across both elevations, but notable exceptions were cavity nesters, where mechanical thinning had a negative effect at high elevations, and predators where low and medium severity fire had a negative effect at low elevations (Appendix Fb).

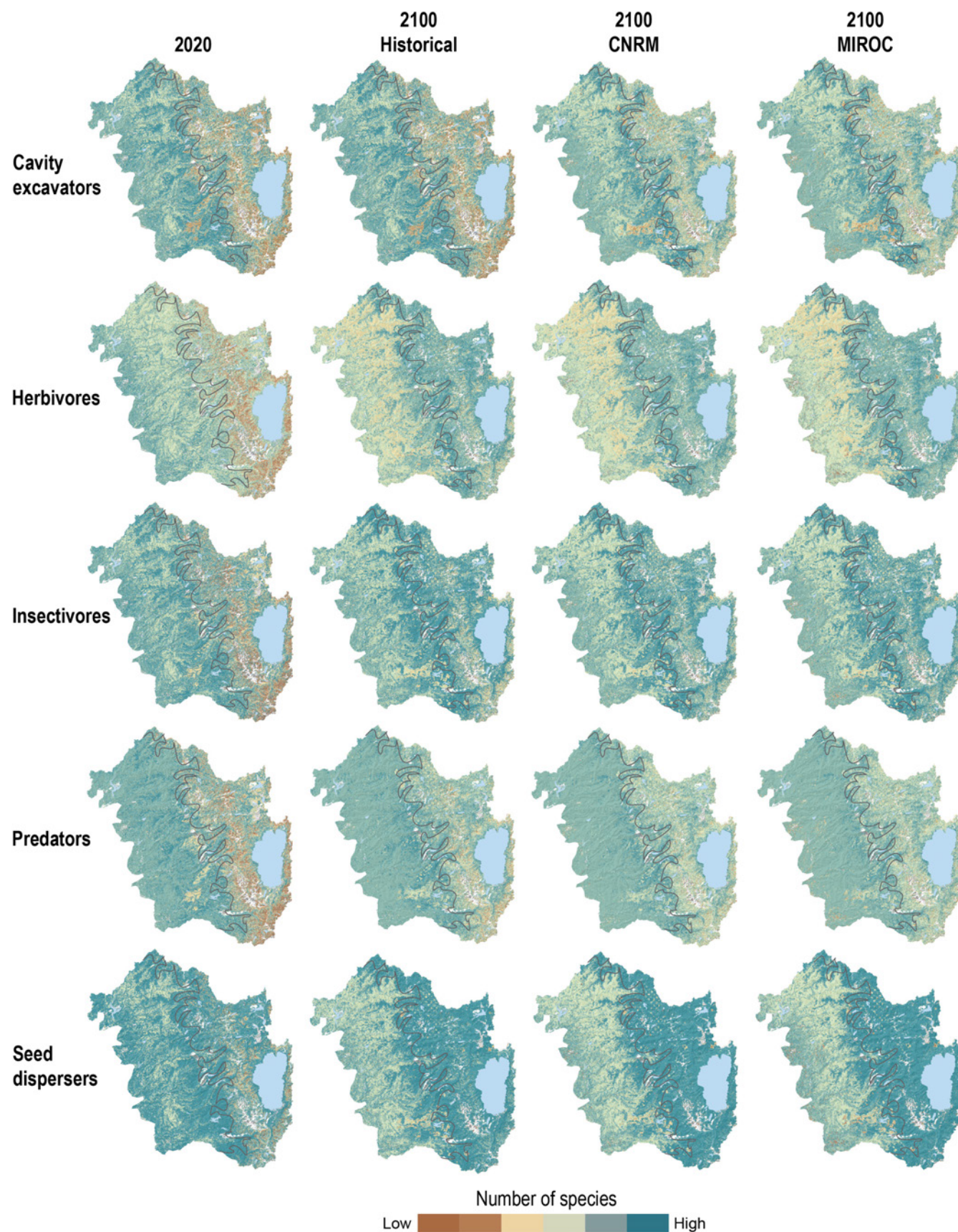


FIGURE 3 Potential species richness of breeding habitat for five functional groups of vertebrate species in the central Sierra Nevada, California. Potential richness at the initial time step (2020) and final time step (2100) are shown for the BROADSCALE Management Scenario and for all three climate projections, historical, CNRM and MIROC. Results for the other two management scenarios, minimal and reference condition, are provided in Appendix C.

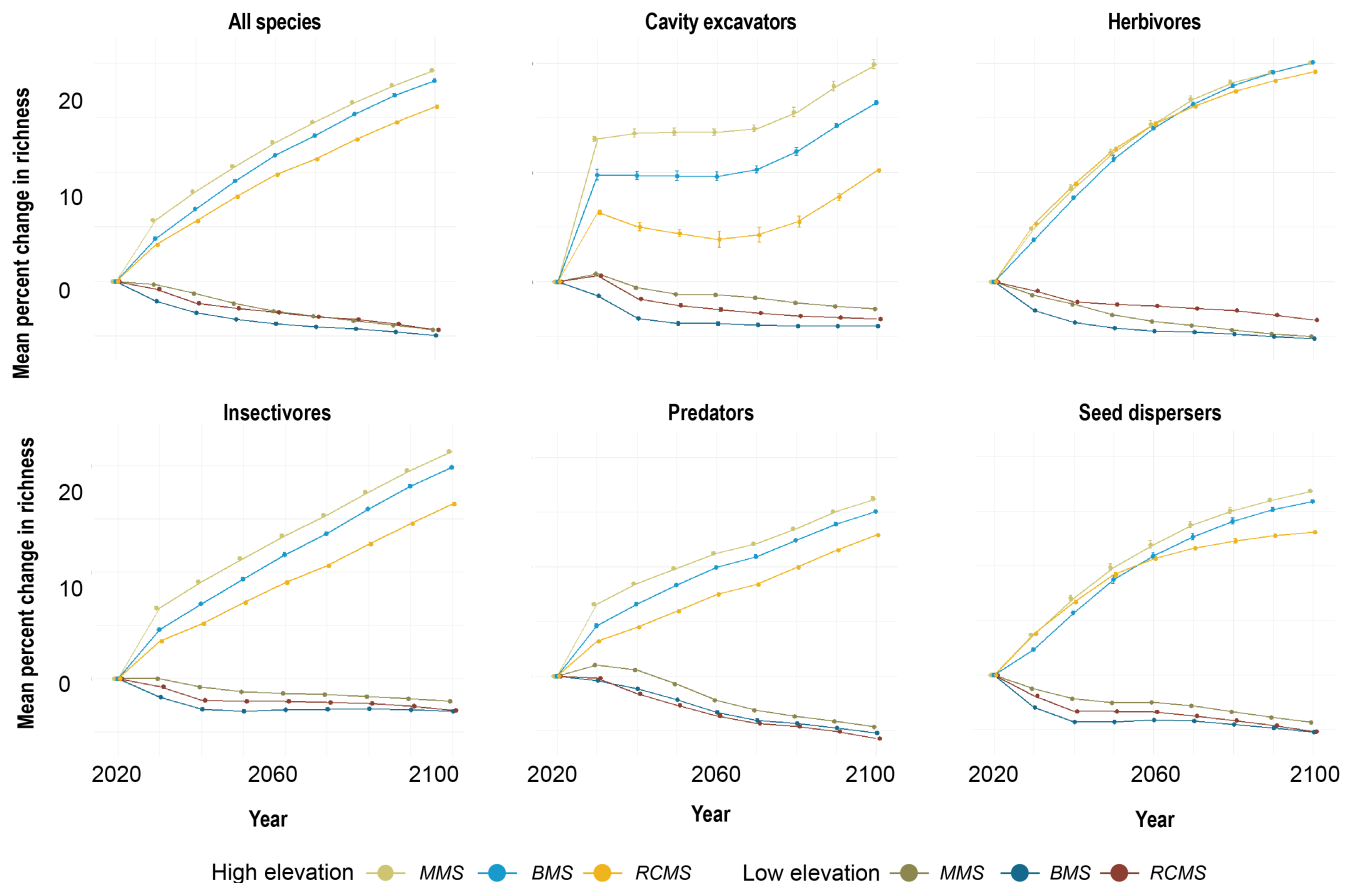


FIGURE 4 Percent change in species habitat richness across high (>1706 m) and low (≤ 1706 m) elevation zones for all species and each of the five functional groups. We calculated the mean of the sums to obtain the mean cumulative richness across all five iterations per scenario. Then we calculated the percent change from the year 2020. Standard error bars are also included. Results from the MIROC climate projection are shown. BMS, Broadscale Management Scenario; MMS, Minimal Management Scenario; RCMS, Reference Condition Management Scenario. The Historical and CNRM results are provided in Appendix D.

3.4 | Contribution of protected areas to potential species richness

We found that protected areas supported higher potential species richness than unprotected areas, with protected areas providing habitat for approximately 11–18 more species than unprotected areas with similar elevations, slopes and aspects (Figure 7). This increased capacity was much greater and statistically significant for the two future climate trajectories than for the historical climate. Potential species richness in protected areas under the BMS and RCMS were slightly higher than with MMS. We did not find notable differences in potential species richness among the different types of protected areas (Appendix G).

4 | DISCUSSION

Our LDSM modelling framework yielded new insights into the individual and combined effects of climate, management and disturbance across a mountainous landscape in the Sierra Nevada. Our results showed broad effects of both climate and forest management on potential species richness and no interaction between

climate and management, suggesting these factors may act independently on species richness at large scales. Our results indicate that climate change will have an overall negative effect on species richness in the central Sierra Nevada compared with the historical climate, especially in lower elevation areas. At more local scales, we found many positive effects on potential species richness from mechanical thinning, prescribed burning, low and medium severity fire, and beetle outbreaks, although the magnitude of this effect varied with functional group. High severity fire had consistently negative effects on potential species richness.

Our first prediction, that climate change would negatively affect biodiversity, was supported. The historical climate was associated with higher potential species richness across the study area and potential species richness declined with more extreme climate change predictions. This is likely due to species in our study area having evolved to utilize habitat associated with historical climate. Therefore, changes in climate and downstream changes in vegetation may result in more losses of species habitat for the two climate change scenarios, CNRM and MIROC. Generally, the higher potential species richness observed with the historical climate was followed by the relatively wetter cooler CNRM projection, then the warmer,

TABLE 1 Results from 2-way ANOVAs with the sum of species richness across all elevations, lower elevations and higher elevations as a function of forest management scenario and climate.

	Management scenario			Climate		
	F-statistic	Degrees of freedom	p-value	F-statistic	Degrees of freedom	p-value
All elevations						
All species	12.35	2	<.001	8.98	2	<.001
Cavity excavators	185.56	2	<.001	7.01	2	<.001
Herbivores	7.895	2	<.001	6.155	2	.002
Insectivores	83.95	2	<.001	118.26	2	<.001
Predators	89.56	2	<.001	39.74	2	<.001
Seed dispersers	21.74	2	<.001	8.51	2	<.001
Lower elevations						
All species	27.95	2	<.001	73.95	2	<.001
Cavity excavators	113.80	2	<.001	199.90	2	<.001
Herbivores	87.33	2	<.001	16.11	2	<.001
Insectivores	102.70	2	<.001	176.40	2	<.001
Predators	21.78	2	<.001	45.69	2	<.001
Seed dispersers	38.83	2	<.001	92.14	2	<.001
Higher elevations						
All species	7.33	2	<.001	0.003	2	.997
Cavity excavators	75.67	2	<.001	43.20	2	<.001
Herbivores	0.29	2	.751	0.78	2	.457
Insectivores	14.14	2	<.001	0.30	2	.740
Predators	22.66	2	<.001	1.13	2	.323
Seed dispersers	1.10	2	.335	0.14	2	.872

Note: p-values less than .05 are in bold font. Interactions between management scenario and climate were also tested, but none were significant and, therefore, they are not presented here.

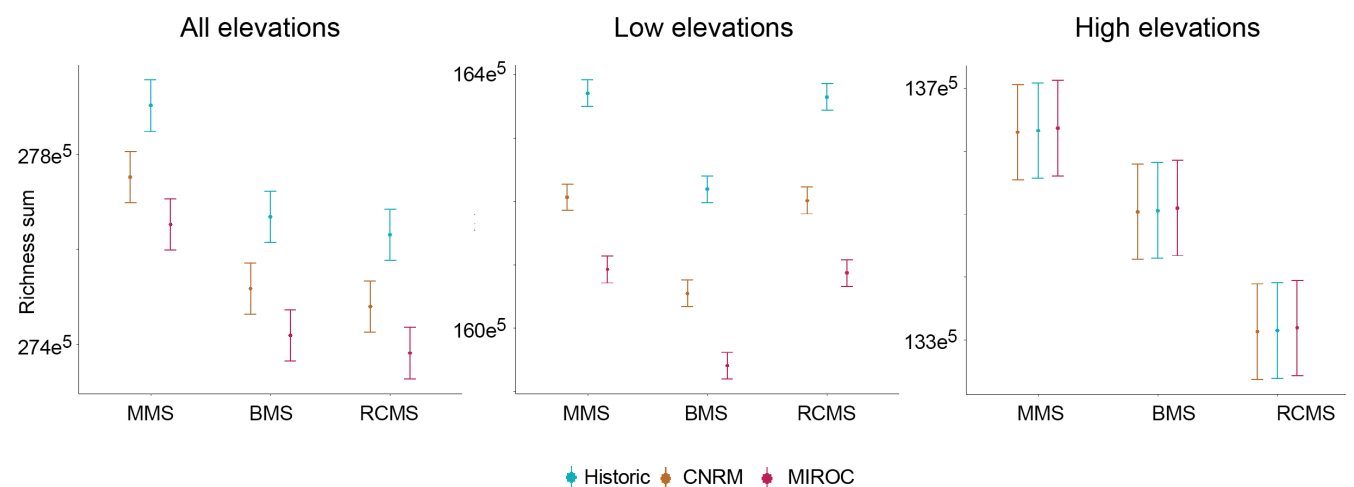


FIGURE 5 Predicted mean and 95% confidence intervals of potential species richness sums (across the five model iterations and for all time steps) across all elevations, at lower elevations (≤ 1706 m) and at higher elevations (> 1706 m) for each combination of three management scenarios (MMS, BMS and RCMS) and three climate trajectories (Historical, CNRM and MIROC), listed in increasing order of intensity. BMS, Broadscale Management Scenario; MMS, Minimal Management Scenario; RCMS, Reference Condition Management Scenario. Plots for the functional groups are provided in Appendix E.

drier MIROC projection. However, some functional groups benefited more from a changing climate. For example, cavity excavators tended to have higher potential richness with the MIROC climate projection.

Our other expectation, that the effect of climate would exceed that of management, was only supported in lower elevations of our study area. This is a surprising finding because higher elevation areas have been experiencing and are predicted to experience more rapid

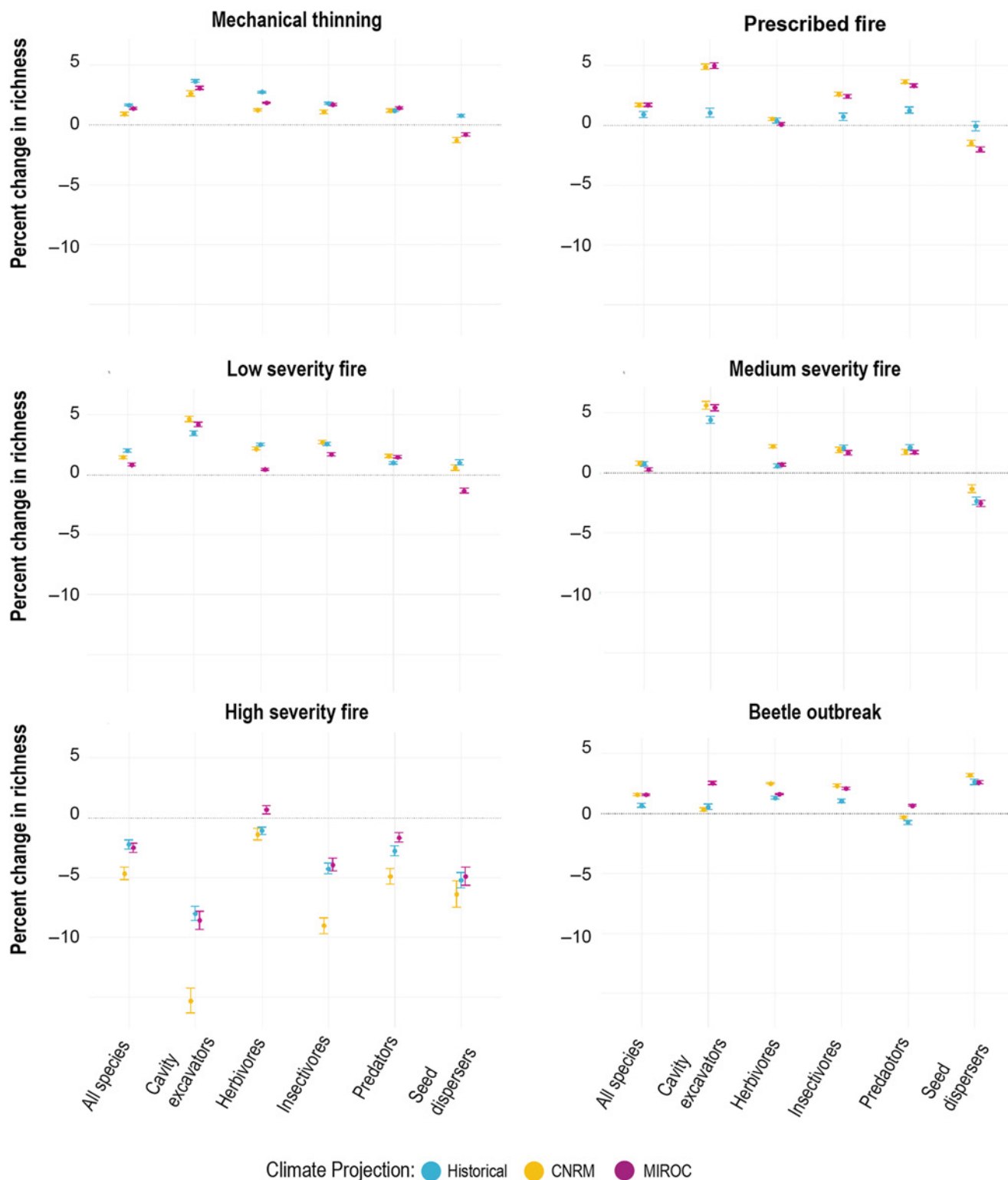


FIGURE 6 Proximate management and disturbance effects on potential species richness. Plots show expected rate of change in potential species richness (as percent change with confidence intervals) as a function of management and disturbance effects. For example, for the CNRM climate, a single high severity fire within a 10-year time step equates to an almost 5% decrease in potential species richness.

climatic changes with a warming climate than lower elevation areas (Palomo, 2017; Pepin et al., 2015), and we expected those climatic changes to have a negative downstream effect on potential species richness. Instead, we observed an increase in richness at higher

elevations through time, and at the final time step, the potential species richness values at higher elevations more closely resembled those at the beginning time step at lower elevations. This suggests that the lower elevation forests may be acting as leading-edge

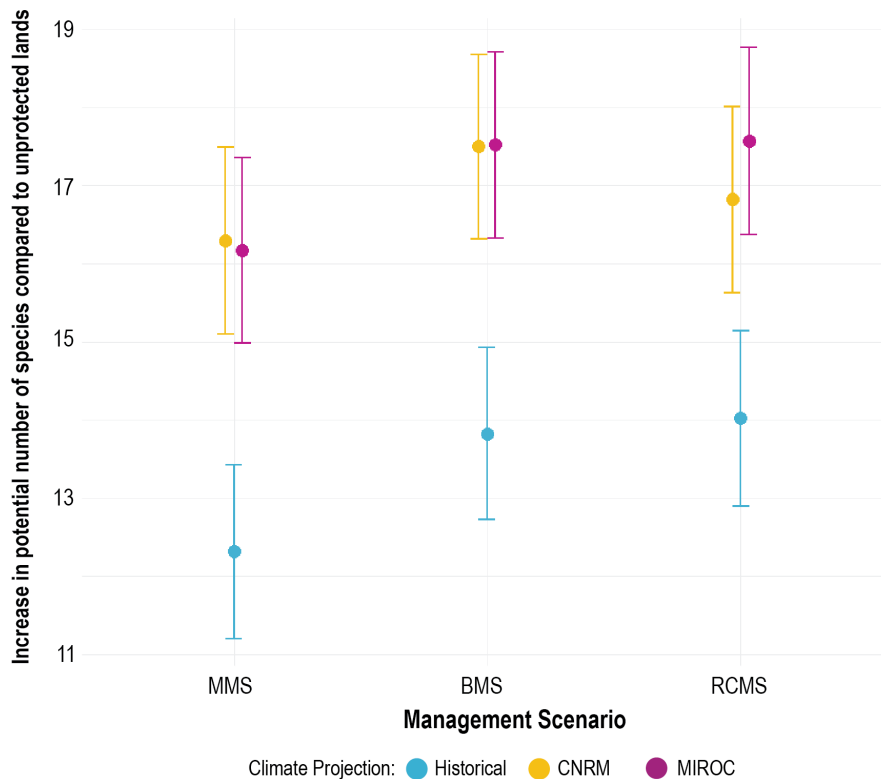


FIGURE 7 Potential species richness increases in protected areas compared with unprotected areas, controlling for elevation, slope and aspect, across three different management scenarios (MMM, BMS, RCMS) and three climate trajectories (historical CNRM, MIROC), presented in order of increasing intensity. BMS, Broadscale Management Scenario; MMS, Minimal Management Scenario; RCMS, Reference Condition Management Scenario.

forests which will shift uphill with climate and, as a consequence, increase potential species richness at higher elevations. This uphill shift in vegetation has been observed in many mountain systems (Lenoir et al., 2008; Marshall et al., 2020; Vitasse et al., 2021) and indicates that higher elevation areas may compensate for species losses at lower elevations.

We did not find support for our prediction that the interaction of climate and management would have the greatest effects on potential species richness. Across the entire landscape, and at higher elevations in particular, management had a greater effect than climate on potential species richness. This highlights a few important factors; (1) management can be effective for maintaining ecological integrity in higher elevation areas despite a changing climate and changing ecological trajectories, and (2) complex interactions and stressors other than climate and management may be operating in this system that were not captured in our study.

As predicted, we found that proximate effects of management treatments did not mirror the outcome of broadscale drivers, but for reasons counter to what we expected. For example, due to homogenization of forests from historical fire suppression and exclusion policies (Collins et al., 2017; Haugo et al., 2019), we predicted that the two more intensive forest management scenarios, BMS and RCMS, would increase forest heterogeneity and thus biodiversity, while management actions at the pixel level might reduce species richness in the short term. However, our results found the opposite effect. At the scale of the pixel, potential species richness responded positively to mechanical thinning across all climate and forest management scenarios and prescribed fire except

for when the historical climate was used. This aligns with findings from other studies that have found stable or increasing habitat for species with forest thinning (Demarais et al., 2017; Verschuyll et al., 2011) and prescribed burning (Fontaine & Kennedy, 2012; McDowell et al., 2021; Sitters et al., 2015). But we observed lower potential species richness at the landscape level for the management scenarios that incorporated more thinning and prescribed burning (BMS and RCMS) compared with the MMS. The pixel-level gains in species richness may have been tempered by increasing extreme disturbances, like high severity fire, which had a negative effect on species richness and a larger footprint on the landscape for the BMS and RCMS scenarios, potentially increasing landscape homogeneity (Appendix H).

Given that we observed higher potential species richness in higher elevation areas, where most of the protected lands are in this system, it is not surprising our last prediction, that protected areas were associated with higher potential species richness, was supported. However, an important finding was that under a changing climate, protected areas were associated with higher potential richness compared with the historical climate, indicating the increased importance of these areas for biodiversity in the future. We did not find an effect of protected area status, indicating all categories of protection are important for maintaining biodiversity in this landscape.

We did not find many differences in potential species richness responses to broadscale drivers or proximate effects between all species and each functional group, or among functional groups. We expected differences since these groups have different

functional traits, which can result in different responses to forestry practices and environmental changes (de Groot et al., 2016; Elmqvist et al., 2003), but many species in our landscape spanned functional groups and thus few were true herbivores, or insectivores, for example, which might have resulted in a blurring between the functional groups and a more homogenized response to climate, management, and disturbance. However, we did observe some notable differences. For example, cavity nesters had a larger positive response to prescribed, low, and medium severity fire, and a larger negative response to high severity fire than other functional groups. These responses have been documented in other studies that show fire severity affects snag retention, density, and habitat variation and thus presence of cavity nesters (Keele et al., 2019; Saab et al., 2004). Conversely, herbivores did not have as strong of a negative response to high severity fire. In fact, herbivore richness increased with high severity fire for the MIROC climate projection. This may be due to fire causing reduced vegetation height, which can reduce predation opportunities and increase the amount of secure habitat, especially for smaller herbivores (Eby et al., 2014).

Our study included certain limitations. For example, though we estimated habitat for over 200 species, we did not have empirical data on species presence and could not develop fine-scaled models based on actual occurrence. Nor did our species habitat models include factors other than vegetation, like topography or human development. Therefore, our species models may be overestimating habitat for some species, though in aggregate, this was not likely to bias general trends in potential species richness. We were also unable to model species that are currently absent in our study area, but may shift their ranges into our study area given future changes in vegetation and climate. These shifts would change our species richness metric and may result in fewer losses at low to mid elevation areas in our system. However, we do not believe overall patterns of responses would change given the number and diversity of species we included in our analysis. One final caveat to our results is that we only examined one measure of biodiversity, species richness. Other measures such as beta diversity and associated species composition and turnover metrics may offer more insights into the effects of management, disturbance, and climate on biodiversity (Cazalis, 2022; Hefty et al., *in review*; Jones et al., 2022).

In sum, LDSMs are a powerful tool to help understand the complex relationships between changing ecological trajectories, climate, increased risk of extreme disturbance and management. The ability of LDSMs to simulate different management approaches and provide outputs that allow for the investigation of the consequences of those approaches on ecological integrity and other goals can help managers reduce the uncertainty of downstream effects of management actions in a changing climate. In the TCSI, we found that climate will have a negative effect on species richness, but at small scales, management actions can have positive effects on species richness. Though we predicted that

species richness may increase at higher elevations, we also found that targeted actions at lower elevations are likely to be necessary for maintaining the ecological integrity of this landscape over the long term.

AUTHOR CONTRIBUTIONS

PM initiated the study and all authors conceptualized the approach and analyses. NP and SF ran the LANDIS-II modeling and provided the crosswalks to CWHR. KZ performed the remaining analyses, and drafted the initial manuscript. All authors contributed substantially to manuscript drafts and approved of the final version.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.22658698>.

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REFERENCES

- Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, 33, 121–131. <https://doi.org/10.1002/joc.3413>
- Abatzoglou, J. T., & Brown, T. J. (2012). A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology*, 32, 772–780. <https://doi.org/10.1002/joc.2312>

- Beier, P., & Brost, B. (2010). Use of Land Facets to Plan for Climate Change: Conserving the Arenas. *Not the Actors. Conservation Biology*, 24(3), 701–710. <https://doi.org/10.1111/j.1523-1739.2009.01422.x>
- Brodie, J. F., Post, E. S., & Doak, D. F. (2013). *Wildlife conservation in a changing climate*. University of Chicago Press.
- California Department of Fish and Wildlife. (2014). California Interagency Wildlife Task Group. CWHR version 9.0.
- Cazalis, V. (2022). Species richness response to human pressure hides important assemblage transformations. *Proceedings of the National Academy of Sciences*, 119(19). <https://doi.org/10.1073/pnas.2107361119>
- Collins, B. M., Fry, D. L., Lydersen, J. M., Everett, R., & Stephens, S. L. (2017). Impacts of different land management histories on forest change. *Ecological Applications*, 27, 2475–2486. <https://doi.org/10.1002/eap.1622>
- de Groot, M., Eler, K., Flajšman, K., Grebenc, T., Marinšek, A., & Kutnar, L. (2016). Differential short-term response of functional groups to a change in forest management in a temperate forest. *Forest Ecology and Management*, 376, 256–264. <https://doi.org/10.1016/j.foreco.2016.06.025>
- Demarais, S., Verschuyt, J. P., Roloff, G. J., Miller, D. A., & Wigley, T. B. (2017). Tamm review: Terrestrial vertebrate biodiversity and intensive forest management in the U.S. *Forest Ecology and Management*, 385, 308–330. <https://doi.org/10.1016/j.foreco.2016.10.006>
- Eby, S. L., Anderson, T. M., Mayemba, E. P., & Ritchie, M. E. (2014). The effect of fire on habitat selection of mammalian herbivores: The role of body size and vegetation characteristics. *The Journal of Animal Ecology*, 83, 1196–1205. <https://doi.org/10.1111/1365-2656.12221>
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1, 488–494. [https://doi.org/10.1890/1540-9295\(2003\)001\[0488:RDECA\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0488:RDECA]2.0.CO;2)
- Evans, S., Holland, T., Long, J., Maxwell, C., Scheller, R., Patrick, E., & Potts, M. (2022). Modeling the risk reduction benefit of forest management using a case study in the Lake Tahoe Basin. *Ecology and Society*, 27. <https://doi.org/10.5751/ES-13169-270218>
- Fernihough, A. (2019). `lmfx`: Marginal effects, odds ratios and incidence rate ratios for GLMs.
- Fettig, C. J., Mortenson, L. A., Bulaon, B. M., & Foulk, P. B. (2019). Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *Forest Ecology and Management*, 432, 164–178. <https://doi.org/10.1016/j.foreco.2018.09.006>
- Fontaine, J. B., & Kennedy, P. L. (2012). Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecological Applications*, 22, 1547–1561. <https://doi.org/10.1890/12-0009.1>
- Fuentes, B. A., Dorantes, M. J., & Tipton, J. R. (2021). `rassta`: Raster-based Spatial Stratification Algorithms.
- Gustafson, E. J., Sturtevant, B. R., Shvidenko, A. Z., & Scheller, R. M. (2011). Using landscape disturbance and succession models to support forest management. In C. Li, R. LaFortezza, & J. Chen (Eds.), *Landscape ecology in forest management and conservation: Challenges and solutions for global change* (pp. 99–118). Springer. https://doi.org/10.1007/978-3-642-12754-0_5
- Haugo, R. D., Kellogg, B. S., Cansler, C. A., Kolden, C. A., Kemp, K. B., Robertson, J. C., Metlen, K. L., Vaillant, N. M., & Restaino, C. M. (2019). The missing fire: Quantifying human exclusion of wildfire in Pacific Northwest forests, USA. *Ecosphere*, 10, e02702. <https://doi.org/10.1002/ecs2.2702>
- Hefty, K. L., Povak, N. A., Manley, P. N., Flake, S., & Zeller, K. A. (in review). Altered spatiotemporal patterns of diversity and diversity–stability relationships as a function of compounding disturbances and forest management.
- Jones, G. M., Brosi, B., Evans, J. M., Gottlieb, I. G. W., Loy, X., Núñez-Reguero, M. M., Ober, H. K., Pienaar, E., Pillay, R., Pisarello, K., Smith, L. L., & Fletcher, R. J., Jr. (2022). Conserving alpha and beta diversity in wood-production landscapes. *Conservation Biology*, 36, e13872. <https://doi.org/10.1111/cobi.13872>
- Jones, G. M., & Tingley, M. W. (2022). Pyrodiversity and biodiversity: A history, synthesis, and outlook. *Diversity and Distributions*, 28, 386–403. <https://doi.org/10.1111/ddi.13280>
- Keane, R. E., McKenzie, D., Falk, D. A., Smithwick, E. A. H., Miller, C., & Kellogg, L.-K. B. (2015). Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling*, 309–310, 33–47. <https://doi.org/10.1016/j.ecolmodel.2015.04.009>
- Keele, E. C., Donovan, V. M., Roberts, C. P., Nodskov, S. M., Wonkka, C. L., Allen, C. R., Powell, L. A., Wedin, D. A., Angeler, D. G., & Twidwell, D. (2019). Relationships between wildfire burn severity, cavity-nesting bird assemblages, and habitat in an eastern ponderosa pine forest. *The American Midland Naturalist*, 181, 1–17. <https://doi.org/10.1674/0003-0031-181.1.1>
- Larson, M. A., Thompson, F. R., Millspaugh, J. J., Dijk, W. D., & Shifley, S. R. (2004). Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling*, 180, 103–118. <https://doi.org/10.1016/j.ecolmodel.2003.12.054>
- Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., Heller, N. E., Pressey, R. L., Sanderson, E. W., & Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology*, 29(3), 618–629. <https://doi.org/10.1111/cobi.12505>
- Lenoir, J., Gegout, J. C., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.
- Lumley, T. (2004). Analysis of complex survey samples. *Journal of Statistical Software*, 9, 1–19.
- Lumley, T. (2020). `survey`: Analysis of complex survey samples.
- Manley, P. N., Povak, N. A., & Wilson, K. N. (in review). A framework for socio-ecological resilience to inform climate change management strategies across forested landscapes. *Frontiers in Forests and Global Change*.
- Marshall, L., Perdijk, F., Dendoncker, N., Kunin, W., Roberts, S., & Biesmeijer, J. C. (2020). Bumblebees moving up: Shifts in elevation ranges in the Pyrenees over 115 years. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20202201.
- Martens, C., Hickler, T., Davis-Reddy, C., Engelbrecht, F., Higgins, S. I., von Maltitz, G. P., Midgley, G. F., Pfeiffer, M., & Scheiter, S. (2021). Large uncertainties in future biome changes in Africa call for flexible climate adaptation strategies. *Global Change Biology*, 27, 340–358. <https://doi.org/10.1111/gcb.15390>
- Maxwell, C., Scheller, R. M., Long, J. W., & Manley, P. (2022). Forest management under uncertainty: The influence of management versus climate change and wildfire in the Lake Tahoe Basin, USA. *Ecology and Society*, 27, 1–11. <https://doi.org/10.5751/ES-13278-270215>
- McDowell, N. G., Tan, Z., Hurteau, M. D., & Prasad, R. (2021). Trade-offs of forest management scenarios on forest carbon exchange and threatened and endangered species habitat. *Ecosphere*, 12, e03779. <https://doi.org/10.1002/ecs2.3779>
- McRae, B. H., Schumaker, N. H., McKane, R. B., Busing, R. T., Solomon, A. M., & Burdick, C. A. (2008). A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling*, 219, 77–91. <https://doi.org/10.1016/j.ecolmodel.2008.08.001>
- Nitschke, C. R., Trouvé, R., Lumsden, L. F., Bennett, L. T., Fedrigo, M., Robinson, A. P., & Baker, P. J. (2020). Spatial and temporal dynamics

- of habitat availability and stability for a critically endangered arboreal marsupial: Implications for conservation planning in a fire-prone landscape. *Landscape Ecology*, 35, 1553–1570. <https://doi.org/10.1007/s10980-020-01036-2>
- North, M. P., York, R. A., Collins, B. M., Hurteau, M. D., Jones, G. M., Knapp, E. E., Kobziar, L., McCann, H., Meyer, M. D., Stephens, S. L., Tompkins, R. E., & Tubbesing, C. L. (2021). Pyrosilviculture needed for landscape resilience of dry western United States forests. *Journal of Forestry*, 119, 520–544. <https://doi.org/10.1093/jofore/fvab026>
- Palomo, I. (2017). Climate change impacts on ecosystem services in high mountain areas: A literature review. *Mountain Research and Development*, 37, 179–187. <https://doi.org/10.1659/MRD-JOURNAL-D-16-00110.1>
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., ... Mountain Research Initiative EDW Working Group. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430. <https://doi.org/10.1038/nclimate2563>
- Povak, N. A., Manley, P., & Wilson, K. (in review). Integrating climate adaptation strategies in spatial decision support systems. *Frontiers in Forests and Global Change*.
- Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., & Sykes, M. T. (2007). Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial ecosystems in a changing world, global change—The IGBP series* (pp. 175–192). Springer. https://doi.org/10.1007/978-3-540-32730-1_15
- R Core Team. (2021). R: A language and environment for statistical computing. Version 3.6.2. Accessed June 12, 2019. <https://cran.r-project.org/>
- Saab, V. A., Dudley, J., & Thompson, W. L. (2004). Factors influencing occupancy of nest cavities in recently burned forests. *The Condor*, 106, 20–36. <https://doi.org/10.1093/condor/106.1.20>
- Safford, H. D., & Stevens, J. T. (2017). *Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA* (General Technical Report PSW-GTR-256). Albany CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station 229 P 256. <https://doi.org/10.2737/PSW-GTR-256>
- Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., ... Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Scheller, R. M., Domingo, J. B., Sturtevant, B. R., Williams, J. S., Rudy, A., Gustafson, E. J., & Mladenoff, D. J. (2007). Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, 201(3–4), 409–419. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>
- Scheller, R. M., Hua, D., Bolstad, P. V., Birdsey, R. A., & Mladenoff, D. J. (2011). The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecological Modelling*, 222, 144–153. <https://doi.org/10.1016/j.ecolmodel.2010.09.009>
- Scheller, R. M., Kretchun, A. M., Loudermilk, E. L., Hurteau, M. D., Weisberg, P. J., & Skinner, C. (2018). Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe Basin. *Ecosystems*, 21, 643–656. <https://doi.org/10.1007/s10021-017-0175-3>
- Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020). RCP8.5 tracks cumulative CO₂ emissions. *PNAS*, 117, 19656–19657. <https://doi.org/10.1073/pnas.2007117117>
- Shifley, S. R., Thompson, F. R., Dijak, W. D., & Fan, Z. (2008). Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: A case study of issues, limitations, and opportunities. *Forest Ecology and Management*, 254, 474–483. <https://doi.org/10.1016/j.foreco.2007.08.030>
- Sitters, H., Stefano, J. D., Christie, F. J., Sunnucks, P., York, A., Sitters, H., Stefano, J. D., Christie, F. J., Sunnucks, P., & York, A. (2015). Bird diversity increases after patchy prescribed fire: Implications from a before–after control–impact study. *International Journal of Wildland Fire*, 24, 690–701. <https://doi.org/10.1071/WF14123>
- Stephens, S. L., McIver, J. D., Boerner, R. E. J., Fettig, C. J., Fontaine, J. B., Hartsough, B. R., Kennedy, P. L., & Schwill, D. W. (2012). The effects of forest fuel-reduction treatments in the United States. *Bioscience*, 62, 549–560. <https://doi.org/10.1525/bio.2012.62.6.6>
- Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, 91, 760–781. <https://doi.org/10.1111/brev.12193>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- U.S. Geological Survey (USGS) Gap Analysis Project (GAP). (2022). Protected Areas Database of the United States (PAD-US) 3.0 (ver. 2.0, March 2023) [Data set]. U.S. Geological Survey. <https://doi.org/10.5066/P9Q9LQ4B>
- van de Water, K. M., & Safford, H. D. (2011). A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecology*, 7, 26–58. <https://doi.org/10.4996/fireecology.0703026>
- Verschuyl, J., Riffell, S., Miller, D., & Wigley, T. B. (2011). Biodiversity response to intensive biomass production from forest thinning in North American forests—A meta-analysis. *Forest Ecology and Management*, 261, 221–232. <https://doi.org/10.1016/j.foreco.2010.10.010>
- Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat, C., Rebetez, M., Rixen, C., Strebel, N., Schmidt, B. R., Wipf, S., Wohlgemuth, T., Yoccoz, N. G., & Lenoir, J. (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews*, 96, 1816–1835. <https://doi.org/10.1111/brev.12727>
- White, A., Holland, T., Abelson, E., Kretchun, A., Maxwell, C., & Scheller, R. (2022). Simulating wildlife habitat dynamics over the next century to help inform best management strategies for biodiversity in the Lake Tahoe Basin, California. *Ecology and Society*, 27. <https://doi.org/10.5751/ES-13301-270231>
- Wurtzebach, Z., & Schultz, C. (2016). Measuring ecological integrity: History, practical applications, and research opportunities. *Bioscience*, 66, 446–457. <https://doi.org/10.1093/biosci/biw037>

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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