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RESEARCH ARTICLE

# Spatiotemporal patterns of diversity and diversity-stability relationships as a function of compounding disturbances and forest management

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**Abstract**

*Context* Consistent with the diversity-stability hypothesis, high wildlife diversity has been associated with increased resilience and stability of ecosystem services and functions. Nevertheless, ecological non-stationarity associated with climate change challenges the concept of stability. Furthermore, ambiguity surrounding appropriate diversity metrics to use has hindered the ability of natural resource managers to leverage the potential benefits of biodiversity conservation.

*Objectives and methods* We aimed to infer how diversity and compositional stability might be affected by multiple climate and disturbance stressors, including management activity.

*Methods* We used a spatially explicit landscape succession model to predict spatiotemporal patterns of beta diversity for terrestrial vertebrates representing three trophic groups (herbivores, insectivores, and predators) over an 80-year time span.

*Results* Trends in diversity were driven by species gains at higher elevations and species losses at lower elevations, however, species reorganization was modified by both mean species turnover (i.e. replacement of species across space) as well as management intensity. Higher species turnover was associated with greater among-site compositional stability and decreased local compositional change attributed to species losses for all trophic groups. Increasing management intensity further increased beta diversity across all elevations whereas decreasing management intensity led to spatial homogenization of herbivores and insectivores at low elevations. High management intensity also weakened naturally occurring diversity-stability relationships at larger spatial scales.

*Conclusions* Increasing management intensity may be beneficial at lower elevations where projections anticipate species losses and homogenization. Additionally, conserving areas of high diversity will likely

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be important for promoting future compositional stability for trophic groups that support key ecological processes.

**Keywords** Diversity-stability hypothesis · Beta diversity · Climate change · Biodiversity · Management

## Introduction

Biodiversity can have profound impacts on ecosystem stability through time and space. According to the diversity-stability hypothesis, ecological communities with higher species diversity are associated with greater persistence of important ecosystem functions and services, including carbon sequestration, productivity, and nutrient cycling (Tilman et al. 1996; Altieri 1999; Ruifrok et al. 2015; Yang et al. 2019). As such, biodiversity conservation has recently become a priority for sustainable management practices (Kuuluvainen et al. 2021; Oettel & Lapin 2021). Nevertheless, synergistic effects of climate change with other human-driven and natural disturbances are increasingly altering species composition on local- to landscape-level scales (Oliver & Morecroft 2014; Kelly et al. 2020). Species losses or wildlife community reorganization can lead to irreversible changes to ecosystem patterns and processes that may either improve or detract from resilience to future environmental perturbations and impact the services that these systems provide (Cardinale et al. 2012). Whether the diversity-stability hypothesis still holds true given increased intensity and frequency of compounding disturbance events, including management activity, remains largely untested.

Biodiversity is known to influence stability in ecological communities in several ways, including, 1) through complementarity where niche differentiation facilitates the persistence of multiple species whose collective participation support a specific ecosystem function (Loreau & Hector 2001), 2) through redundancy in which species are interchangeable in their contribution to a specific ecosystem function (McCann 2000; Biggs et al. 2020), and 3) through species asynchrony in which species differ in their responses to acute or prolonged environmental changes thereby decreasing the likelihood of community collapse and subsequent loss of ecosystem functioning (Tilman 1996; de Mazancourt et al. 2013; Sasaki et al. 2019). When all these factors are present, overall ecosystem function can likely withstand modest local species losses associated with sudden or gradual environmental change (Yachi & Loreau 1999). In contrast, landscapes characterized by low diversity are more likely to experience negative impacts to services with species losses and are therefore suspected to be less robust to environmental change (Oliver et al. 2015; Sasaki et al. 2019).

These interpretations assume that ecological communities exist within an equilibrium where resilient communities can return to and maintain a stable ecosystem state following disturbance, also known as ecological stationarity (Tilman 1996). Climate change threatens the idea of ecological stationarity because disturbances work synergistically with changing climatic conditions to push ecological communities outside their historical range of variation (Milly et al. 2008). Species additions or replacements in transforming ecosystems can drastically alter existing interactions and patterns, leading to new ecosystem states and potentially altering overall ecosystem function (Pecl et al. 2017). Whether diversity can promote stability in communities experiencing increased frequency and intensity of disturbance associated with climate change and human activity moves beyond the traditional evaluation of the diversity-stability hypothesis and requires further investigation (Tilman 1996; Sankaran & McNaughton 1999; García-Palacios et al. 2018).

Ecological stability has been characterized in many ways (Grimm & Wissel 1997). Stability or, inversely, variability in communities may be attributed to spatial and temporal patterns of aggregate properties, such as biomass, productivity, and abundance, or compositional similarities or dissimilarities among species assemblages (Cottingham et al. 2001; Lamy et al. 2021). Recent studies have focused on assessing compositional stability because of its ability to explain underlying mechanisms driving changes in ecosystem properties, such as biomass and species abundance (Mellin et al. 2014; Hillebrand et al. 2017a; Wisnoski et al. 2023). As such, understanding how species assemblages may reorganize in response to environmental change is an essential step in understanding how ecosystem function may be altered in transforming systems. Alpha, beta, and gamma diversity metrics have been used to quantify

compositional variability, however, the contribution and interpretation of each metric for stability is dependent on the spatial scale at which these metrics are assessed (Mellin et al. 2014; Cardinale et al. 2018). While alpha diversity may be a good predictor of local-level ecological stability, it may not perform as well as other metrics (e.g. beta diversity) in predicting stability in ecological functions over larger spatial scales (Hillebrand et al. 2017a, b; Catano et al. 2020). For example, in landscapes altered by climate change, environmental filtering may lead to biotic homogenization that is not detectable on a local-scale. Beta diversity links local-scale species richness with landscape-level patterns of diversity to provide more detailed information on biodiversity change and subsequent impacts to ecosystem function and stability (Cazalis 2022). Furthermore, the two components of beta diversity–turnover and nestedness – can be used to measure trends in species composition across larger spatial scales, including homogenization, and attribute those trends to underlying processes (Socolar et al. 2016). Nestedness accounts for dissimilarity in species composition associated with species gains and losses among sites, such that individual units may be subsets of other more species rich units (Baselga 2010). In contrast, species turnover measured the replacement of some species by others between sites, independent of differences in species richness. Species turnover, in particular, can elucidate how communities may be reorganizing along topographical gradients or in response to acute or prolonged disturbance (Jankowski et al. 2009).

In forested systems in North America, individual natural disturbances such as wildfire, beetle damage, and human-caused disruptions such as fragmentation and climate change may result in sudden or delayed changes in species composition and ecosystem structure (Malhi et al. 2020). To confront these changes and improve ecosystem resilience to future disturbance, management activities such as forest thinning and fuel reduction are often used to alter forest structure to reduce the spread and severity of disturbance events. Nevertheless, compounding environmental stressors can alter ecological communities in ways that are difficult for managers to predict, prepare for, and respond to (Chmura et al. 2011; Stephens et al. 2014; Moriarty et al. 2016; Northrup et al. 2019). Furthermore, natural resource management has not traditionally targeted biodiversity conservation as an intervention goal, thus there is limited empirical evidence of how varying levels of management intensity may affect spatiotemporal patterns in species assemblages in a climate change-driven system. Using beta diversity metrics to monitor compositional variability can help elucidate how ecosystem function and resilience may be changing in response to multiple stressors, including management activity (Dell et al. 2019; Jones et al. 2021). Concurrently, uncovering how management activities may or may not buffer ecological communities from species gains, losses, and compositional homogenization can help managers better decide when, where, and how much—if any—management is needed to support stability in transforming landscapes.

To understand how synergistic effects of diversity, compounding disturbances, and forest management may influence emerging patterns of diversity and stability in ecological communities, we used a spatially explicit landscape succession model to quantify spatiotemporal changes in terrestrial wildlife species composition of three prominent trophic groups (herbivores, insectivores, and predators) over 80 years. We first analyzed the influence of spatial complexity on patterns of diversity alone, then incorporated regional patterns of beta diversity and forest management scenarios to assess the following questions: 1) How do patterns of beta diversity change over space and time under climate change?, 2) Does high spatial beta diversity reduce temporal compositional variability in a system affected by climate change?, and 3) Can forest management alter spatiotemporal patterns of beta diversity and beta diversity-stability relationships in a changing climate? Information gathered from our analyses were used to inform science-based decision-making efforts in the central Sierra Nevada Mountains of California, USA.

## Methods

### Study area

Our study area encompassed a 970,000-ha forested landscape in the central Sierra Nevada mountains of California and Nevada, USA (Fig. 1). This landscape was defined as part of the Tahoe Central Sierra Initiative Planning project with a goal to implement planning and research efforts that promote ecosystem

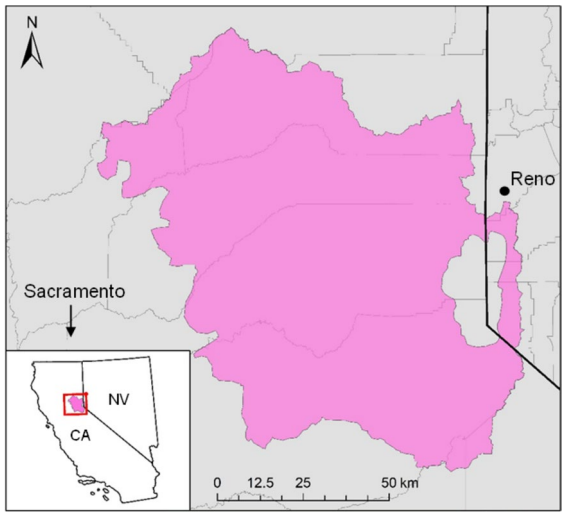


**Fig. 1** Map depicting the Tahoe Central Sierra Initiative study area in central California and Nevada, United States

resilience (Manley et al. 2023). Elevation of the study area ranges from 900 to 3300 m and includes forested terrestrial vegetation communities from oak woodlands on low-elevation, west-facing slopes to mixed conifer and alpine at mid- to high elevations. At lower elevations, vegetation communities are rain-driven, while at high elevations communities are snow-driven. The study area encompasses private and public lands, including wilderness areas, state-managed land, other federally managed land, rural communities, and small cities.

### *Dynamic* modeling*: LANDIS-II, climate change, and forest management*

We used the LANDIS-II forest vegetation framework to simulate effects of climate change, forest management, beetle damage, and wildfire on vegetation (Scheller et al. 2007). LANDIS-II is a spatially explicit landscape simulation model that has been used to model forest growth and succession dynamics in forested ecosystems across the globe. Within LANDIS-II, we implemented the Net Ecosystem Carbon and Nitrogen extension (Scheller et al. 2011), which models forest establishment and growth and provides a total ecosystem accounting of carbon and nitrogen. Vegetation dynamics are responsive to climate, as well as a range of in situ disturbances such as insect outbreaks and fire. We modeled vegetation and disturbance dynamics for 80 years at 180-m resolution, and derived forest structure and compositional characteristics from biomass within age class and tree or shrub species cohorts. We chose to forecast forest composition and structural change using a less conservative climate modeling approach, which we felt best represented current trends in emissions. The MIROC-ESM (Model for Interdisciplinary Research on Climate-Earth System Model; Watanabe et al. 2011) predicts a warmer, drier future for central California coupled with representative concentration pathway 8.5 (RCP 8.5), which best represents a "business as usual" emissions future.

We assigned habitat suitability for faunal species for each raster cell at each time step to a habitat type based on the California Wildlife Habitat Relationship (CWHR) system (California Department of Fish and Wildlife 2014). We estimated habitat types by cross walking cell-level biomass outputs to relevant stand metrics that described forest type, canopy cover, quadratic mean diameter (QMD), and seral stage (below). Each 180-m cell was classified into one of 14 vegetation types depending on the dominant species present at that timestep (Zeller et al. 2023). We developed regression models from Forest Inventory and Analysis data (FIA; https://www.fia.fs.fed.us) 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 cm, 1–6 cm, 6–11 cm, 11–24 cm, > 24 cm). We also developed regression equations to estimate percent canopy cover from vegetation type, seral stage, and plot biomass. Canopy cover was estimated for each raster cell and then assigned to one of five cover 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 terrestrial vertebrate species following the methods outlined by White et al. (2022).

We selected three LANDIS-II management scenarios from six total scenarios used in a larger modeling effort within the study area (Maxwell et al. 2022). The three management scenarios were selected to represent a range of treatment intensities that varied by the type of management applied, its frequency, and spatial footprint. In a low intensity management scenario, mechanical forest

thinning occurred only within the wildland-urban interface (402 m buffer from human development and private timberlands); in a moderate intensity management scenario, landscape-wide mechanical forest thinning and prescribed fire management mimicked a 30–50 year return interval; and in a high intensity management scenario, landscape-wide mechanical forest thinning and prescribed fire management mimicked the historical natural fire cycle (20–40 year return interval). The low intensity scenario treated 23,000 ac $\cdot$ yr$^{-1}$, moderate treated 81,000 ac $\cdot$ yr$^{-1}$, and the high scenario treated 127,000 ac $\cdot$ yr$^{-1}$. Both the moderate and high intensity scenarios included treatments within and beyond the wildland-urban interface, including roadless and wilderness management areas.

## Wildlife habitat modeling

The CWHR system uses scientific records and expert input to estimate wildlife species habitat use based on discretely defined vegetation communities. We selected native, non-migratory terrestrial wildlife species for which breeding habitat occurred within the bounds of the TCSI. We classified habitat as either non-habitat, cover, feeding habitat, or breeding habitat, respectively on a scale from 0 to 0.33. We chose to focus on breeding habitat as the best approximation of species occurrence and therefore filtered the CWHR output to reflect this decision. To do this, we converted the CWHR scale to binary by converting any value less than 0.3 (least likely breeding habitat) to zero and anything greater than or equal to 0.3 (most likely breeding habitat) to one. We used these new binary values to approximate potential presence and absence for 203 species (Appendix A). For all further purposes of this paper, this approximation is used to describe patterns of diversity and diversity-stability relationships.

To better understand how ecosystem function may be affected by changes in patterns of diversity over time, we grouped species into three key trophic groups: herbivores, insectivores, and predators. In total, we included 97 herbivore species, 103 insectivores, and 58 predators. Species were sorted into groups based on their dominant feeding habits. If species were strong omnivores (n = 50), they were placed in multiple groups (ex: black bears, birds, raccoons).

## Spatial and temporal beta diversity indices

We used the Sørensen family of compositional dissimilarity indices to calculate both spatial and temporal beta diversity to track changes in terrestrial wildlife species composition (Table 1). All calculations were completed in Program R (R Core Team 2022). We incorporated functions from the R package betapart to calculate spatial dissimilarity within a 1-km$^2$ moving window (Baselga & Orme 2012). The 1-km$^2$ moving window allowed us to detect compositional change for species with relatively small home ranges as well as species with intermediate to large ranges (Melo et al. 2009). We calculated dissimilarity as the mean of pairwise differences between a focal cell and all its neighbors within each 1-km$^2$ neighborhood. We further partitioned our spatial dissimilarity results using the Baselga framework (Baselga 2010), which allowed us to isolate the turnover component of beta diversity (i.e. species replacement across space: $\beta_{sim}$). $\beta_{sim}$ is independent of richness differences and therefore represents true species replacement across space (Baselga & Leprieur 2015). $\beta_{sim}$ was scaled from 0 to 1, with 0 indicating identical species composition among 180-m$^2$ cells within the 1-km$^2$ neighborhoods and 1 indicating complete dissimilarity in composition among constituent raster cells. We qualitatively assessed trends in $\beta_{sim}$ among trophic groups through time and quantitatively assessed the contribution of mean current $\beta_{sim}$ (i.e., initial spatial species turnover from 2020) to emerging trends in other diversity metrics and for subsequent diversity-stability relationships as described below.

We calculated local temporal variability in species composition (i.e. temporal beta-diversity index: TBI; Legendre 2019) between current and future time steps for each 180-m$^2$ raster cell. We used the current time step, 2020, as a reference to measure dissimilarity to each subsequent time step (e.g.: 2020 to 2030, 2020 to 2040, etc.). Because species composition change is directional in temporal comparisons, we partitioned TBI into percent of dissimilarity attributed to either species gains or losses for each pairwise time step (Legendre 2019). We interpreted species losses as species leaving a locality to track suitable climatic and vegetation conditions elsewhere through time and we interpreted species gains as species arriving in new localities where emerging climatic and vegetation conditions became suitable within the cell.

**Table 1** Description of beta diversity indices used in a spatiotemporal analysis of terrestrial wildlife diversity in the central Sierra Nevada Mountains, USA, from 2020 to 2100

| Metric | Description | Interpretation | Shorthand | Statistical Test |
|---|---|---|---|---|
| Regional species turnover | Among-site spatial measure of species dissimilarity, partitioned from the spatial beta diversity calculation (moving window calculation across study area) | Increasing values indicate increasing spatial diversity in species composition | $\beta_{sim}$ | Predictor, GLM and LM with BoxCox transformation |
| Temporal compositional variability | Local-level measure of temporal beta diversity among cells through time | Higher values indicate greater dissimilarity in local communities through time | TBI | Response, GLM |
| Temporal species loss | Measure of species losses partitioned from the temporal beta diversity calculation (single cell comparison across time) | Higher values indicate greater percent of total temporal beta diversity attributed to species losses at the local-scale | $TBI_{loss}$ | Response, GLM |
| Percent change in regional species turnover | Mean percent change in species turnover partitioned from the spatial beta diversity calculation (moving window calculation) from 2020–2100 | Higher values indicate increasing spatial diversity in species composition. Negative values indicate increasing homogenization | $\%\Delta\ \beta_{sim}$ | Response, Cohen's D |
| Among-site compositional stability | Inverse coefficient of variation for spatial species turnover from 2020–2100 partitioned from the spatial beta diversity calculation (moving window calculation) | Higher values indicate greater stability in species composition over time | $\beta_{simICV}$ | Response, LM with BoxCox transformation |

We interpreted trends in species losses in space and time as an indicator of changing species composition. We scaled the index of temporal species loss ($TBI_{loss}$) between 0 and 1, with 0 indicating no detectable temporal change in species composition attributable to species losses between T1 and T2 and 1 indicating that 100% of temporal change in species composition was attributable to species losses.

To reduce computational burden and achieve meaningful statistical results, we took a random sample of points across the TCSI study area. To determine an adequate number of sample points, we progressively increased the number of potential random points by increments of 500 until the sample proportionally represented the distribution of underlying topographic and diversity metrics within the study area. Because landscape conditions changed between simulated years, the extent of usable wildlife breeding habitat within our study area also changed slightly between years. To address this, we additionally eliminated random points that fell in cells that contained no data for any year. We extracted all diversity metrics to these points for further analysis for each of the three following research topics. Our methods resulted in a total of 4,900 samples.

Q1: Diversity over space and time in the context of climate change

To address our first question, how patterns of diversity change across space and through time in a changing climate, we used random forest and regression trees to assess relationships between our spatial and temporal beta diversity metrics and topographic features such as elevation, slope, terrain ruggedness, and aspect. Initial visual observation of patterns and trends in beta diversity metrics suggested a strong influence of elevation. We modeled all topographic features at a 30-m resolution and extracted values to our 4900 random sample points. We evaluated random forest models using a tenfold cross validation technique trained on 80% of the original dataset. We used a grid search method to identify optimal hyperparameters that minimized model root mean squared error (RMSE), and the final model was validated using the testing set. We assessed predictor variable importance based on their percent contribution to mean square error. Of the topographic variables assessed, elevation was consistently associated with the highest mean percent increase in mean square error in our random forest models (62.76%IncMSE ± 51.95 SD). We further examined how our data may be partitioned along splits of elevation by examining single regression trees for each model. We used the root splits for elevation to inform further analyses.

Q2: Compositional variability as a function of species turnover and climate change

To examine our second question–does high spatial diversity reduce temporal compositional variability in a system affected by climate change–we measured compositional variability using three statistical approaches and evaluations were made at two spatial scales. At the local scale (180-$m^2$ cells), we assessed compositional variability as mean temporal variability in species composition (TBI) and mean percent of temporal change attributed to local species losses ($TBI_{loss}$). We interpreted high values of mean TBI (at or approaching 1) as being highly variable through time, whereas low values (at or approaching 0) were interpreted as having low variability through time. We interpreted high values of $TBI_{loss}$ as high likelihood that compositional change was associated with species losses and low values as low likelihood that compositional change was associated with species losses. At the neighborhood scale (1-$km^2$) of our spatial beta diversity metrics, we assessed spatial compositional variability by measuring stability in spatial species turnover (herein, among-site stability or $\beta_{simICV}$) over time. We calculated $\beta_{simICV}$ as the inverse temporal coefficient of variation of $\beta_{sim}$ for future years 2030 to 2100 (Wagg et al. 2022). High values of $\beta_{simICV}$ indicated high stability in among-site species composition over time whereas low values indicated low stability.

Finally, we used linear and generalized linear modeling approaches to evaluate the potential role of elevation and mean species turnover ($\beta_{sim}$) for all future timesteps (2030–2100) on explaining observed patterns and trends in the 1) local temporal variability of species turnover (TBI), 2) local compositional change attributed to species losses ($TBI_{loss}$) over time and, 2) among-site stability ($\beta_{simICV}$) for each trophic group. We used a generalized linear model with binomial error distribution and logit link function to assess relationships between mean $\beta_{sim}$ and mean TBI and $TBI_{loss}$ (Ferrier et al. 2007). To assess relationships

between mean current $\beta_{sim}$ (2020) and mean future trends in $\beta_{simICV}$, we used linear regression modeling and applied the Box-Cox transformation technique to normalize our dependent data (Box & Cox 1964). Elevation was scaled using the z-score prior to all analyses.

Q3: Management impacts to spatiotemporal patterns of diversity and diversity-stability relationships

To address our third question–can management intervention alter spatiotemporal patterns of diversity and compositional diversity-stability relationships in a changing climate–we used the modeling approaches described above and included management intensity as a predictor of trends in TBI, $TBI_{loss}$, and $\beta_{simICV}$. Additionally, we assessed the influence of management intensity on percent change in spatial species turnover (%Δ $\beta_{sim}$) from 2020 to 2100. We interpreted negative values for %Δ $\beta_{sim}$ as trending toward homogenization whereas positive values indicated increasing dissimilarity overtime. We chose to use mean spatial species turnover ($\beta_{sim}$) to represent homogenization because it is a true measure of species replacement, whereas total spatial beta diversity is not independent of richness differences.

For all analyses, we treated management scenario as a factor with three levels (low, moderate, and high). We used Cohen's D effect size calculations to detect potential differences among management scenarios for %Δ $\beta_{sim}$. We assessed how management intervention may be impacting diversity-stability relationships by including management intensity as an interacting explanatory variable with $\beta_{sim}$ in our models predicting TBI, $TBI_{loss}$, and $\beta_{simICV}$.

## Results

Q1: Diversity over space and time in the context of climate change

Elevation was depicted as the root node in each regression tree analysis with splits along an elevational range of 1271 m to 2107 m. The average root node split for elevation was 1738.89 m ± 295.95 SD. 1700 m is near the current persistent snowline in the central Sierra Nevada Mountains (Shulgina et al. 2023) and, therefore, this value was used to split our dataset into two categories for further analyses where elevation wasn't specifically targeted as a predictor: low elevation (< 1700 m) and high elevation (≥ 1700 m). This two-way split in elevation was particularly evident for static patterns of $\beta_{sim}$ as well as trends in temporal dissimilarity (TBI) among trophic groups.

The three trophic groups displayed slightly different patterns in mean spatial species turnover ($\beta_{sim}$) in 2020 and 2100 (Fig. 2). At lower elevations, insectivores maintained the highest overall mean $\beta_{sim}$ for future time steps 2030–2100 (0.094 ± 0.049 SD), whereas predators had the lowest mean $\beta_{sim}$ (0.046 ± 0.028 SD). At higher elevations, herbivores replaced insectivores as having

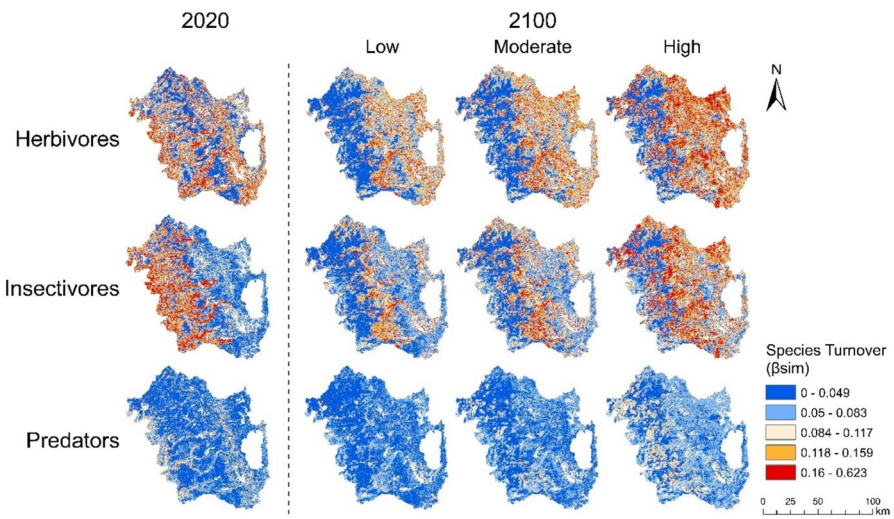


**Fig. 2** Among-site spatial species turnover ($\beta_{sim}$) for three trophic groups (herbivores, insectivores, predators) between two timesteps (2020 and 2100) and for three forest management intensity scenarios (low, moderate, high). Study area encompasses 1-M ha of the central Sierra Nevada Mountains, USA

the highest overall mean future $\beta_{sim}$ ($0.116 \pm 0.040$ SD) and predators again had the lowest mean $\beta_{sim}$ ($0.052 \pm 0.021$ SD). There was no notable difference in mean $\beta_{sim}$ for herbivores in 2020 between high and low elevations ($<1700$ m: $0.106 \pm 0.059$ SD; $\geq 1700$ m: $0.104 \pm 0.063$ SD), however, by 2100 mean $\beta_{sim}$ had decreased at lower elevations and increased at higher elevations ($<1700$ m: $0.067 \pm 0.058$ SD; $\geq 1700$ m: $0.106 \pm 0.043$ SD). For insectivores, mean $\beta_{sim}$ was higher at low elevations in 2020 ($<1700$ m: $0.125 \pm 0.065$ SD; $\geq 1700$ m: $0.064 \pm 0.046$ SD), but by 2100 this difference became less apparent as mean $\beta_{sim}$ decreased at lower elevations and increased slightly at higher elevations ($<1700$ m: $0.077 \pm 0.056$ SD; $\geq 1700$ m: $0.078 \pm 0.039$ SD). Similar to herbivores, there was little difference in mean $\beta_{sim}$ between higher and lower elevations for predators in 2020. Unlike herbivores and insectivores, mean $\beta_{sim}$ for predators remained similar between 2020 and 2100 at higher elevations ($2020 \geq 1700$ m: $0.050 \pm 0.040$ SD; $2100 \geq 1700$ m: $0.050 \pm 0.024$ SD), however, mean $\beta_{sim}$ decreased slightly at lower elevations ($2020 < 1700$ m: $0.054 \pm 0.039$ SD; $2100 < 1700$ m: $0.046 \pm 0.031$ SD).

Drivers of and trends in mean local temporal compositional variability (TBI) were consistent among all trophic groups. At elevations below 1700 m, TBI was driven by species losses whereas species gains drove TBI above 1700 m (Fig. 3). Additionally, the trend in TBI increased logarithmically over time for all trophic groups and management scenarios. Insectivores had the highest mean TBI over 80 years from 2020 to 2100 for both high and low elevations ($<1700$ m: $0.154 \pm 0.114$ SD; $\geq 1700$ m: $0.223 \pm 0.152$ SD). Predators displayed the lowest mean TBI from 2020 to 2100 at lower elevations ($<1700$ m: $0.097 \pm 0.066$ SD), whereas herbivores displayed the lowest mean TBI at higher elevations ($\geq 1700$ m: $0.203 \pm 0.113$ SD). TBI was higher overall at higher elevations as

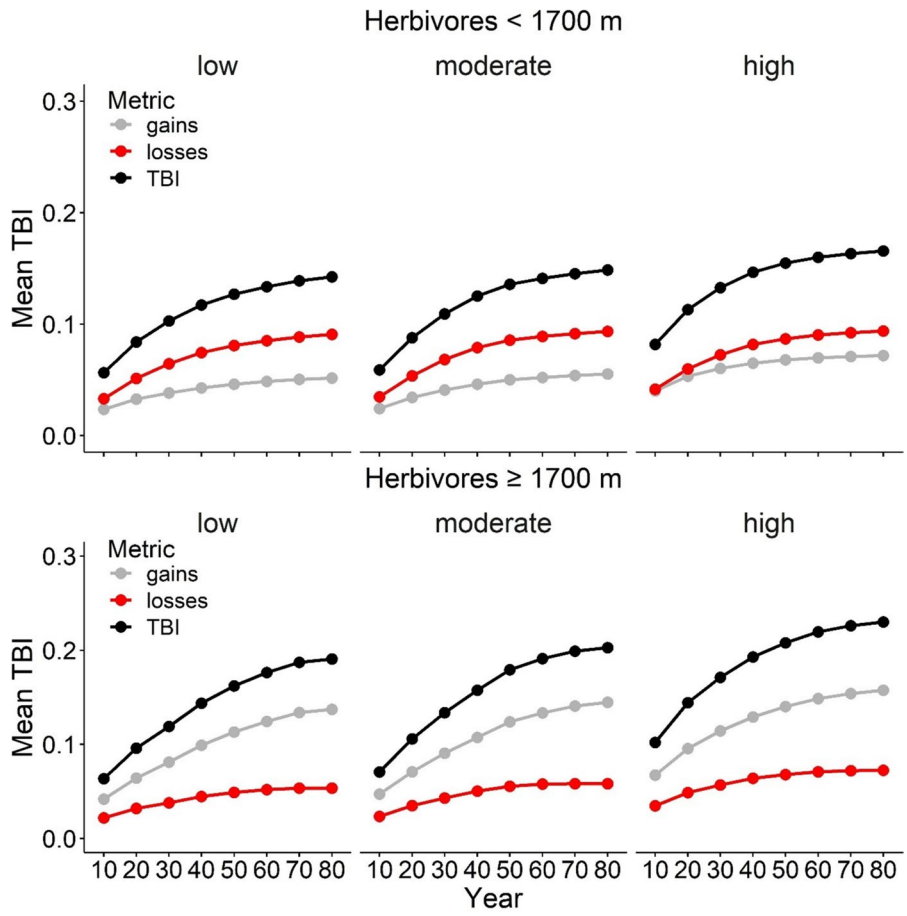


**Fig. 3** Trend in mean local temporal compositional variability of herbivores expressed by total temporal beta diversity (TBI) and its components of species gains (gray) and losses (red). Dissimilarity was assessed among sequential lag years between 2020 and 2100 and at low ($<1700$ m) and high ($\geq 1700$ m) elevation areas in the central Sierra Nevada Mountains, USA

compared to lower elevations across an 80-year time span for all trophic groups.

Q2: Compositional variability as a function of species turnover and climate change

Although local variability in temporal species composition (TBI) trended higher with increasing elevation, among-site compositional stability ($\beta_{simICV}$) displayed varied trends dependent on trophic group, indicating that individual cell-based changes in species losses were not always driving change in regional patterns of diversity over time (Fig. 4). TBI was positively associated with mean current (2020) among-site spatial turnover ($\beta_{sim}$) for all trophic groups (herbivores coefficient: 4.75, SE: 0.66, $p < 0.001$; insectivores coefficient 4.78, SE: 0.68, $p < 0.001$; predators coefficient: 6.90; SE: 1.10, p-value $< 0.001$). For insectivores and predators, the strength of the relationship between $\beta_{sim}$ and TBI decreased with every unit increase in elevation (insectivores coefficient: -2.89, SE: 0.71, $p < 0.001$; predators coefficient: -3.23, SE: 1.12, $p = 0.004$). All trophic groups displayed increasing $\beta_{simICV}$ with increasing current $\beta_{sim}$ independent of elevation. However, for herbivores, with each unit increase in elevation, the effect of $\beta_{sim}$ on $\beta_{simICV}$ decreased, indicating that the influence of $\beta_{sim}$ on $\beta_{simICV}$ decreased at high elevations (coefficient: -1.35, SE: 0.12, $p < 0.001$). There was also a positive relationship between $\beta_{sim}$ and $\beta_{simICV}$ for predators, however, unlike herbivores and insectivores, the relationship between elevation and $\beta_{simICV}$ was negative, indicating lower stability at high elevations (coefficient: -0.10, SE: 0.01, $p < 0.001$). Additionally,

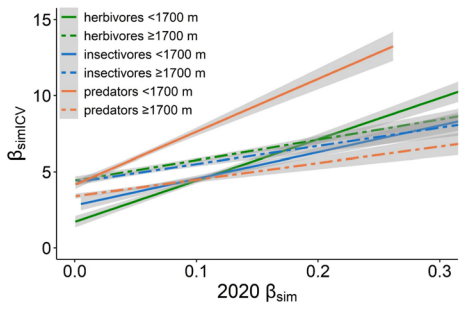


**Fig. 4** Stability of species composition ($\beta_{simICV}$) by mean current spatial species turnover for 2020 ($\beta_{sim}$) grouped by trophic group (herbivores, insectivores, and predators) and elevation category in the central Sierra Nevada Mountains, USA

there was no significant interaction between $\beta_{sim}$ and elevation for predicting $\beta_{simICV}$ for insectivores or predators.

Elevation was negatively associated with mean $TBI_{loss}$ for all trophic groups, indicating that species losses were more apparent at lower versus higher elevations. For all trophic groups, mean current $\beta_{sim}$ (2020) was negatively associated with mean $TBI_{loss}$ (herbivores coefficient: -3.29, SE: 0.51, $p < 0.001$; insectivores coefficient: -2.33, SE: 0.55, $p < 0.001$; predators coefficient: –15.31, SE: 0.91, $p < 0.001$). Unlike the relationship with $\beta_{simICV}$, the effect of $\beta_{sim}$ on $TBI_{loss}$ increased with every unit increase in elevation for herbivores, indicating that the influence of $\beta_{sim}$ on $TBI_{loss}$ was greater at high elevations (herbivores coefficient: 4.05, SE: 0.60, $p < 0.001$). There was no significant interaction with elevation for either insectivores or predators, indicating consistency in the relationship between $\beta_{sim}$ and $TBI_{loss}$ independent of elevation.

Q3: Management impacts to spatiotemporal patterns of diversity and diversity-stability relationships

For herbivores and insectivores, mean percent change in species turnover from 2020 to 2100 ($\%\Delta\beta_{sim}$) was negative at low elevations under low and moderate management intensity, indicating increasing homogenization. At higher elevations, however, herbivores and insectivores displayed increasing among-site species turnover across all management scenarios. In contrast, mean $\%\Delta\beta_{sim}$ was positive for all management scenarios and both elevation categories for predators. Additionally, for predators, pairwise effect size calculations indicated negligible effects among management scenarios within each elevation category. The largest negative mean $\%\Delta\beta_{sim}$ for all trophic groups occurred in the low intensity management scenario below 1700 m (insectivores: $-5.02 \pm 13.26$ SD; herbivores: $-4.47 \pm 26.02$ SD; predators: $6.71 \pm 25.18$ SD; Fig. 5), indicating a high degree of homogenization. The most positive mean $\%\Delta\beta_{sim}$ occurred in the high intensity management scenario at or above 1700 m for all trophic groups (insectivores: $15.65 \pm 20.64$ SD; herbivores: $15.96 \pm 116.42$ SD; predators: $41.92 \pm 142.14$ SD). Overall, there was greater variability in $\%\Delta\beta_{sim}$ at higher elevations as compared to lower elevations and predators displayed the greatest variability among trophic groups.

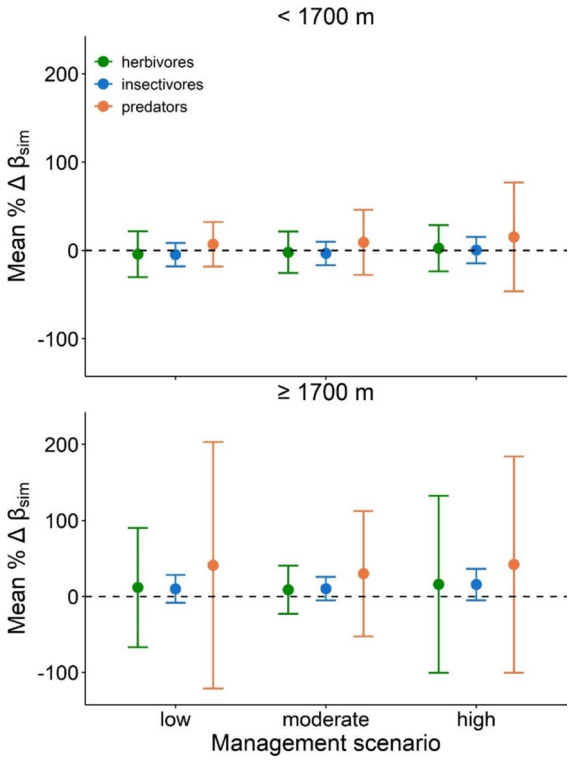


**Fig. 5** Mean percent change in spatial species turnover (%Δ $\beta_{sim}$) ± standard deviation as a function of management intensity for three trophic groups and two elevation categories (< 1700 and ≥ 1700 m) in the central Sierra Nevada Mountains, USA

For herbivores and insectivores, pairwise effect size calculations indicated that low intensity management resulted in increased homogenization as compared to high intensity management below 1700 m (herbivores Cohen's D: − 0.26, 95% CI: − 0.31—-0.20; insectivores Cohen's D: − 0.37, 95% CI: − 0.42–0.31). %Δ$\beta_{sim}$ was not notably different for the moderate intensity scenario as compared to the low intensity scenario for any trophic group or elevation category. Additionally, insectivores were the only trophic group that displayed higher %Δ$\beta_{sim}$ values for high intensity management as compared to the low intensity management ≥ 1700 m (Cohen's D: − 0.29, 95% CI: − 0.35- − 0.23).

Overall, mean among-site compositional stability ($\beta_{simICV}$) increased with increasing management intensity across all elevations for both herbivores and predators. For herbivores, the high intensity management scenario had a mean $\beta_{simICV}$ of 6.68 ± 5.96 SD at low elevations and 6.76 ± 3.86 SD at high elevations. Unlike herbivores, however, $\beta_{simICV}$ was lower for predators at or above 1700 m as compared below 1700 m under the highest management intensity (< 1700 m: 7.73 ± 5.55 SD, ≥ 1700 m: 4.76 ± 2.89 SD). Similar to herbivores and predators, mean $\beta_{simICV}$ for insectivores below 1700 m was highest for high intensity management (7.09 ± 5.99 SD) and lowest for low intensity management (4.97 ± 5.03 SD). However, for insectivores at higher elevations, $\beta_{simICV}$ was highest for moderate intensity management (5.24 ± 2.78 SD) and lowest for high intensity management (5.01 ± 2.79 SD).

Management intensity did not significantly affect positive relationships between mean current (2020) among-site species turnover ($\beta_{sim}$) and local temporal compositional variability (TBI) for any trophic group or elevation class. Similarly, increasing management intensity did not change the direction of relationships between mean current (2020) $\beta_{sim}$ and $\beta_{simICV}$ for any trophic group, however, the strength of the relationship between $\beta_{sim}$ and $\beta_{simICV}$ decreased with increasing management intensity in some scenarios (Fig. 6). Specifically, high intensity management was significantly associated with a decline in the effect of mean $\beta_{sim}$ on $\beta_{simICV}$ as compared to low intensity management for herbivores and insectivores at low elevations (herbivores coefficient: -1.05, SE: 0.25, $p < 0.001$; insectivores coefficient: -0.74, SE: 0.20). There was no significant effect of management on the relationship between mean $\beta_{sim}$ and $\beta_{simICV}$ for predators below 1700 m. At elevations at or above 1700 m, increasing management intensity did not change the direction or strength of the relationship between mean $\beta_{sim}$ and $\beta_{simICV}$ for either herbivores or insectivores. In contrast, for predators, high management intensity was associated with a decreased effect of mean $\beta_{sim}$ on $\beta_{simICV}$ at high elevations (coefficient: − 0.48, SE: 0.22, $p = 0.026$). These relationships were only found for high intensity management. Moderate intensity management had no effect on relationships between mean $\beta_{sim}$ on $\beta_{simICV}$ for any trophic group at either elevation category.

In contrast to significant effects of management found for relationships between mean $\beta_{sim}$ and $\beta_{simICV}$, there were no significant differences among management scenarios for predicting $TBI_{loss}$ from mean $\beta_{sim}$ for any trophic group below or above 1700 m. This result indicates that areas of high current (2020)

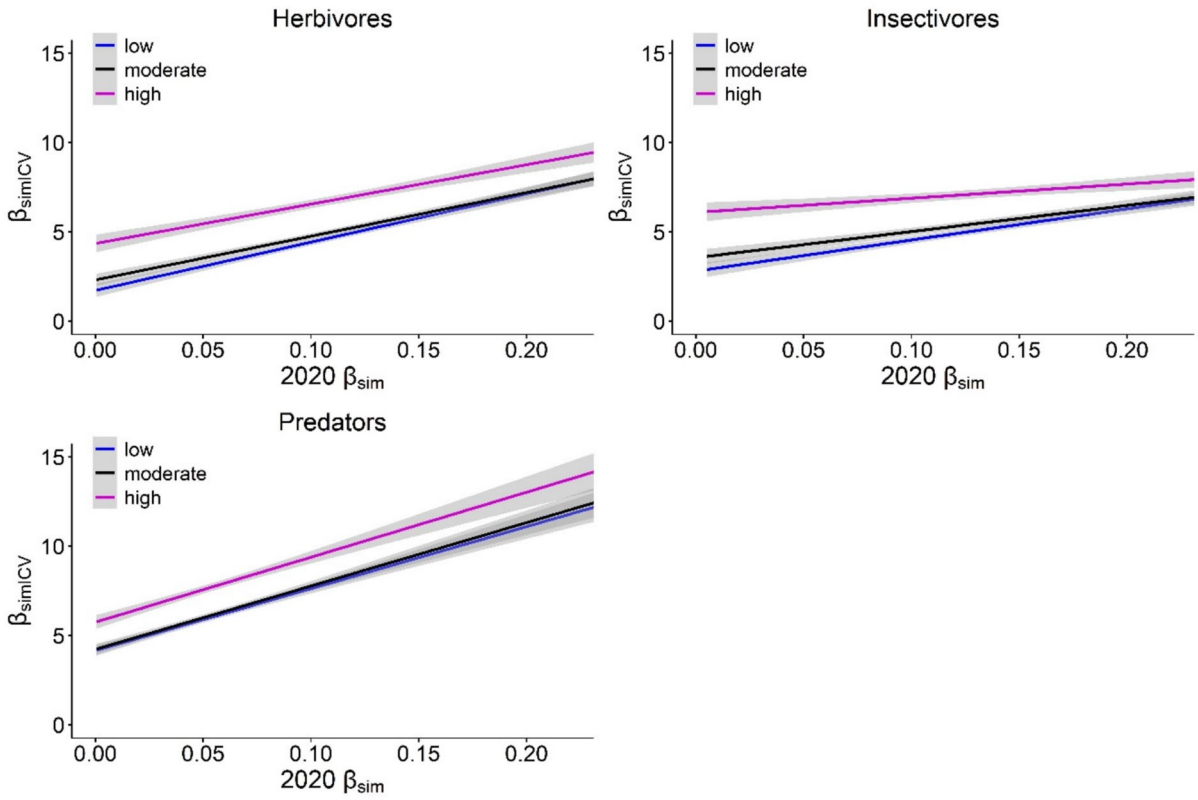


**Fig. 6** Stability in among-site species composition ($\beta_{simICV}$) from 2030 to 2100 by mean current (2020) species turnover ($\beta_{sim}$) grouped by management scenario for three trophic groups (herbivores, insectivores, and predators) at elevations below 1700 m in the central Sierra Nevada Mountains, USA

spatial species turnover continued to be associated with reduced temporal compositional variability associated with species losses independent of altered management intensity.

## Discussion

Using a multi-metric approach, we demonstrated distinct differences along a topographic gradient and among management scenarios and trophic groups for patterns of beta diversity across space and through time and for key diversity-stability relationships in an era of climate change. In general, regions that had higher current among-site species turnover also displayedhigher among-site compositional stability through time and reduced temporal compositional variability attributed to species losses; however, management intensity and elevational gradients influenced the strength of these relationships. These observed differences may have important implications for ecosystem function.

In montane systems, species reorganization in response to climate change is particularly evident due to topographic complexity, including steep elevational gradients (Elsen & Tingley 2015). On mountain ranges in western North America, species are expected to shift upslope in response to warming temperatures or shift to areas where micro- and macroclimate conditions are likely to remain stable for longer periods of time, such as north-facing slopes or within disturbance refugia (Morelli et al. 2020). Range shifts have been evidenced for multiple species and trophic groups in temperate montane systems (Moritz et al. 2008; Tingley et al. 2012). Consistent with previous studies, we observed changes in patterns of diversity through time along a substantial elevational gradient. This gradient represented large changes in dominant

forest types in snow- versus rain- dominated precipitation regimes. For all trophic groups, local-scale changes in patterns of diversity were driven by species losses at low elevations and species gains at high elevations. Additionally, regional species composition for herbivores and insectivores trended toward homogenization at lower elevations, although some of these patterns were modified by management intensity (see below). Such patterns in shifting species distributions are indicative of changing climatic conditions and may reduce the diversity of functions and services provided by ecosystems (Savage & Vellend 2014; Daru et al. 2021). At lower elevations, in rain-driven vegetation communities, management intensity had the greatest impact on mitigating climate-driven trends in and relationships pertaining to wildlife species diversity. In contrast, in high elevation snow-driven systems, climate-driven changes leading to emerging patterns of homogenization or compositional species loss were not evidenced in our study and therefore the mitigating influence of increasing management intensity was less apparent.

These patterns and trends differed among trophic groups, however. Trends in herbivore and insectivore diversity were sensitive to changes in elevation and management. In particular, percent change in among-site species turnover over time switched from negative to positive on average with increased elevation and management intensity. Due to their reliance on vegetation composition and structure for a variety of life history traits and activities, herbivores and insectivores may be particularly sensitive to habitat changes, such as shifting cover types, forage, and phenology (Thackeray et al. 2017). In contrast, for predators, average percent change in among-site species turnover remained positive despite fluctuating elevation or management intensity. Predators also displayed different patterns in among-site compositional stability, with decreased stability at higher elevations as compared to herbivores and insectivores which displayed increased stability at higher elevations. Our predator group included top predators (mountain lion) as well as mesocarnivores (e.g., fox and fisher), birds, and reptiles. These species use a variety of habitats and therefore patterns of diversity may be less affected by changing landscape patterns, particularly at lower elevations (Brechtel et al. 2019).

Diversity can stabilize ecosystems in many ways, including by promoting the persistence of important ecosystem services (García-Palacios et al. 2018). Nevertheless, accelerated intensity and frequency of disturbance and the threat of ecological transformation projected under climate change remains an understudied potential challenge to important diversity-stability relationships across spatial scales (De Boeck et al. 2018). In a high emissions future, our results indicated that local species assemblages increasingly became more dissimilar with time, indicating that the types and abundance of species are shifting in response to changing environmental conditions. Nevertheless, in areas where spatial species turnover was initially high, among-site compositional stability remained high through time. This result was consistent across trophic groups, elevation classes, and management intensities. Relevant to transforming ecological systems, areas that sustain high spatial beta diversity may facilitate asynchronous species responses to disturbances which can promote stability of aggregate properties, such as biomass, and ecosystem function through time (Wilcox et al. 2017; Lamy et al. 2021; Wisnoski et al. 2023). Although important aggregate properties might be maintained across larger spatial scales, functions and services provided at local scales may still fluctuate as species assemblages adjust to changing environmental conditions. In contrast to among-site compositional stability, our study revealed that local temporal compositional variability increased with increasing spatial species turnover. Disturbance can alter species composition at local levels by increasing habitat heterogeneity, allowing colonization by new species (Belote et al. 2012). Our findings support the notion that high among-site diversity can help compensate for species losses through colonization and species sorting (Loreau et al. 2003). Consistently, we found that higher spatial species turnover was associated with lower temporal compositional variability associated with species losses for all trophic groups and management scenarios.

Biodiversity conservation has not traditionally been a target of natural resource management in western North America, however, and this lack of focus on biodiversity could have unintended detrimental impacts on overall forest health and function (Lindenmayer et al. 2000; Thorn et al. 2017). For example, snags and coarse woody debris, often removed in wildfire-targeted forest treatments, are important resources for several wildlife species in forested

systems (Riffell et al. 2011; Sullivan et al. 2021). Furthermore, forest management strategies that help facilitate the development of old growth forest across large extents may have a negative impact on the prevalence of early successional habitat and early-seral dependent species assemblages, reducing regional diversity (Swanson et al. 2010). In contrast, forest management can have positive impacts on biodiversity and ecosystem function. Silviculture treatments to reduce wildfire spread and severity can increase landscape heterogeneity and structural forest diversity, thereby increasing local- to regional-scale patterns of diversity (Carey 2003; Verschuyl et al. 2011; Oettel & Lapin 2021). In our study, increasing the footprint and frequency of management led to positive percent change in spatial species turnover over time, whereas minimal intervention led to increased homogenization at low elevations where compositional change associated with species losses was high. These results suggest that forest management has the potential to conserve important ecosystem services through biodiversity conservation, particularly if biodiversity conservation becomes a target to guide management actions (Carey et al. 1999; Hagan & Whitman 2006; Sitters & Di Stefano 2019; Zeller et al. 2023).

Although increasing management intensity was associated with increased among-site compositional stability and reduced likelihood of species homogenization associated with species losses at lower elevations, it also contributed to large positive gains in diversity at high elevations. Species gains at high elevations with climate change may have both unintended positive and negative consequences to ecosystem services. Novel species interactions resulting from species gains and diversifying systems may lead to local or regional extirpation of some species through competition or can facilitate the coexistence of species through environmental modifications and mutualisms (Young et al. 2001). Our modeling was unable to assess the impacts of novel interactions and, overall, there remains a need to better understand how community-level reorganization may impact future patterns of diversity (Alexander et al. 2015). Additionally, we found that increasing management intensity weakened positive relationships between mean spatial species turnover and among-site compositional stability for herbivores and insectivores at low elevations and for predators at high elevations. Decreased contribution of diversity to among-site compositional stability under high intensity management may either indicate a decoupling of this important process or a relaxing of this process as management becomes a more prominent driver of landscape conditions and emerging patterns of diversity at larger spatial scales (Kuuluvainen et al. 2021). In contrast, management intensity did not significantly alter positive relationships between spatial species turnover and local variability in patterns of diversity through time. This lack of an effect of management may indicate that compositional change in local communities is more strongly driven by disturbance and environmental fluctuations associated with climate change. Recognizing both the importance of beta diversity and management for promoting regional compositional stability may help managers strike a balance to conserve existing healthy, diverse communities and to restore diversity where it may be lacking.

Our results should be interpreted through a lens of species presence potential given habitat conditions, rather than true species presence, as we were not able to model individual species dispersal or adaptive capacity in response to changing environmental conditions. This lack of empirical data for validating the modeled habitat-species relationships, in addition to our inability to model immigration into the study area and restriction of analyses to breeding habitat, could have led to over- or underestimation of species presence. Nevertheless, evidence from empirical studies of climate- and disturbance-driven range shifts of wildlife and their habitat support our findings for shifting spatial patterns of diversity (Forister et al. 2010; Rowe et al. 2015; Mamantov et al. 2021), and we believe the trends we found are robust to these potential shortcomings. However, both drivers and proximate and ultimate consequences of large-scale range shifts are highly complex and require further study. Furthermore, LANDIS-II is intended to generate simulations over large landscapes and time scales, necessitating model simplification that, while informed by the best current knowledge of system dynamics, limits our ability to capture all ecological interactions and processes that could influence resulting patterns of diversity. By assessing wildlife diversity in its complexity, we were able to detect meaningful trends that could aid in making management decisions. Climate change is altering the spatial scale at which management plans and goals are developed

to achieve long-term effectiveness (Gaines et al. 2022). After completing independent analyses of shifting trends in species richness (alpha diversity) for the Tahoe Central Sierra planning area, our team felt we may be missing key information that could explain shifting patterns of diversity as impacted by climate change, disturbance, and management (Zeller et al. 2023). The beta diversity indices we used for this research helped illustrate how underlying environmental processes drive regional patterns and trends in wildlife composition through space and time. Unlike alpha diversity, beta diversity can provide insight into how patterns of species composition at local scales influences changes in larger metapopulations and communities (Ruhí et al. 2017; Fontana et al. 2020). Conservation and management decisions made at a local scale remain important, however, losing sight of how those activities influence greater communities hinders the ability of managers to detect shifts in overall ecosystem health and function and may eventually lead to loss in biodiversity over time (Messier et al. 2019; Jaeger et al. 2022). Beta diversity indices used in this study, such as temporal species loss and compositional stability, can provide important insight into where and how fast communities may reorganize in response to acute (e.g., wildfire and management) and prolonged (e.g., climate change) disturbances (Mori et al. 2018). This information can be used to help managers better determine when, where, and what management actions are needed to support healthy functioning landscapes.

Natural disturbances are important drivers of biodiversity, however, direct human impacts and climate change are altering ecosystem conditions and their responses to natural disturbances, affecting overall ecosystem function (Kelly et al. 2020). Widespread, high severity disturbances are becoming more common and have been linked to increasing regional to landscape-level homogenization of ecological communities (Weeks et al. 2023). Restoring or maintaining low to moderate severity disturbance to ecological systems can promote maintenance of biodiversity and reduce the likelihood and frequency of high severity events (Viljur et al. 2022). Furthermore, if these actions specifically target biodiversity as a management goal, they may also foster the ability of ecological communities to remain resilient in the face of climate change and associated ecological transformation (Oliver et al. 2015; Hisano et al. 2018). To our knowledge, this is the first study to investigate how compounding effects of climate change, natural-, and human-caused disturbance impact relationships between species compositional structure and compositional stability. Our results indicate that compositional diversity will continue to play an important role in supporting community structure through changing climatic conditions. Additionally, management can create mosaic environments that promote diversity for multiple trophic groups when biodiversity is represented in its complexity and carefully considered in designing management approaches.

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**Author contributions** PM initiated the study, coordinated funding support, and guided study design. NP and SF ran the LANDIS-II modeling and provided the crosswalks to CWHR. KH performed beta diversity and stability analyses and drafted the initial manuscript. All authors contributed substantially to manuscript drafts and approved of the final version.

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**Data availability** The datasets and programming code generated or analyzed during the study are available in a public repository on GitHub (https://github.com/klhefty/TCSI-Beta-Diversity-Analysis) and as supplementary information accompanying this manuscript.

**Declarations**

**Competing interests** The authors declare no competing interests.

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