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From ashes to old-growth forests: How do long-term changes in forest structure affect understory plant diversity after wildfires in Yellowstone National Park?

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ABSTRACT

The increasing frequency and intensity of wildfires are having a profound and lasting impact on forest structure, succession, and biodiversity. Understanding these processes is essential for predicting successional trajectories and developing management and conservation strategies. We aim to investigate the long-term (> 140 years) dynamics of understory plant diversity following wildfires and assess how post-fire changes in forest structure influence these diversity patterns in Lodgepole pine forests of Yellowstone National Park, USA. We surveyed 25 forest stands representing five post-fire successional stages, including old-growth forests. At each plot, we measured forest structure, canopy features, and plant diversity (richness, composition, and between-community beta diversity) to assess how post-fire succession shapes forest structure-diversity relationships. Additionally, we assessed the association between successional stages and beta-diversity. Species richness and compositional diversity exhibited a U-shaped pattern along post-fire successional stages, with greater diversity observed in the early and late phases of forest succession. Between-community beta diversity did not show any trend with increasing temporal distance. Species turnover was the dominant component of beta diversity variation. Forest structure and canopy features influenced plant diversity. Deadwood amount and heterogeneity-related variables (e.g., variability of Leaf Area Index) had a positive relationship with species richness and compositional diversity. These findings suggest that maintaining or enhancing structural heterogeneity through deadwood retention, canopy structural complexity, and variability in tree size can promote plant diversity in fire-affected forests. Conservation strategies should recognize the ecological value of early and late successional stages and avoid management practices that reduce structural complexity.

1. Introduction

Globally, forests are under increasing threat due to anthropogenic climate change and related shifts in disturbance regimes (Altman et al., 2024; Seidl et al., 2017). Wildfire is a critical disturbance in many forest ecosystems, and its complex ecological impacts are related to the intensity and frequency of the fire events (Kashian et al., 2005; Capitanio and Carcaillet, 2008; Turner et al., 2016; Day et al., 2017), with megafires expected to become more frequent in the future (Riley and Loehman, 2016; Sayedi et al., 2024). As a high-intensity disturbance, wildfires provide initial conditions for secondary succession, exerting a pivotal role in modulating forest structure dynamics, spatial patterns of vegetation, and plant diversity (Burkle et al., 2015; Vedovato et al., 2025). Their ecological effects can extend for centuries across multiple successional stages (Capitanio and Carcaillet, 2008; Adámek et al., 2016), since the recovery of forest structural characteristics is a long-term process and may diverge substantially from pre-disturbance states even after centuries (Seidl and Turner, 2022). Despite the

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wealth of research focusing on forest succession following wildfires (Turner et al., 1997; Schoennagel et al., 2004; Grau-Andrés et al., 2024), incorporating multiple stages of post-fire succession—including old-growth forests—is still critical in ecological studies.

Changes in forest structure and canopy features during post-fire succession strongly influence plant diversity, particularly the understory (Andrade et al., 2021), which often accounts for more than 80 % of the total plant species richness (Landuyt et al., 2019).

Forest structure influences understory plant communities primarily through the regulation of resource availability and their spatial heterogeneity (Helbach et al., 2022; Chelli et al., 2024; Matsuo et al., 2024). Therefore, structural changes in the tree layer during the post-fire succession can affect plant growth and community composition by modifying microclimatic, nutrient, and light conditions (Landuyt et al., 2018; Matsuo et al., 2021). For instance, the increased light availability of open canopies in early successional stages may create favourable conditions for light-demanding, non-forest species which rapidly exploit these resources (Muñoz Mazón et al., 2022). As forest succession progresses and stand age increases after fire, tree biomass accumulates and the canopy cover increases, providing a significant reduction in light penetration (Turner et al., 2004, 2016). The low-light conditions created by a closed canopy are expected to reduce understory plant richness and abundance, with the selection of a few shade-tolerant species (Romme et al., 2016). In later stages (i.e., old-growth forests), structural heterogeneity becomes a dominant factor in shaping plant diversity, primarily driven by gap dynamics (Bartels and Chen, 2010; Hilmers et al., 2018). This is because old-growth forests have an increase in tree mortality, which contributes to the accumulation of deadwood and the formation of canopy gaps (Strittholt et al., 2006). These gaps subsequently create opportunities for the establishment of new trees, resulting in a heterogeneous structure composed of trees of varying ages, sizes, and heights (Hilmers et al., 2018). This structural heterogeneity in old-growth forests is thought to foster the coexistence of understory species with different environmental requirements (e.g., shade-tolerant and light-demanding species), thereby promoting a more complex and rich plant community (Bartels and Chen, 2010; Helbach et al., 2022).

This theoretical U-shaped dynamic of understory plant richness during forest succession has been frequently described (Gosper et al., 2013; Hilmers et al., 2018; Bartha et al., 2020). However, there are contrasting results regarding changes in plant species richness after wildfire, with some studies reporting that the adverse effects of wildfire initially reduce plant species richness, which then tends to recover over time as these effects diminish (e.g., Liu et al., 2017; Grau-Andrés et al., 2024) and others reporting little to no change (e.g., Schoennagel et al., 2004). Since species richness is only one facet of biodiversity and often uncoupled from other diversity metrics, (see Schoennagel et al., 2004; Capitanio and Carcaillet, 2008; Fletcher Jr. et al., 2025), there is a need to adopt more appropriate approaches to comprehensively measure changes in plant diversity during succession (Chelli et al., 2024). Ecologists are therefore increasingly focusing on shifts in the species composition between plant communities (Han et al., 2018). In this context, the classical beta diversity indices can be partitioned into species turnover (i.e., the degree of species replacement) and nestedness (i.e., the degree of species loss) components, which together provide an explanatory framework for understanding processes underlying species compositional changes (Guclu et al., 2024; Heino et al., 2024). Community similarity generally decreases with increasing spatial and temporal distance (Jones et al., 2012; Hatosy et al., 2013), leading to an increase in β-diversity (Baselga, 2010; Torres et al., 2022). Therefore, β-diversity is expected to progressively increase with increasing temporal distance between successional stages, mainly driven by species turnover resulting from marked environmental differences among stages (Han et al., 2018; Guclu et al., 2024).

Conventional β-diversity assesses compositional changes among communities along environmental gradients but overlooks within-community patterns of species assemblages (Tsakalos et al., 2022). To this goal, an additional β-diversity measure based on information theory models, namely compositional diversity (CD, Juhász-Nagy, 1984, 1993; Tsakalos et al., 2022) provides information on the variability of species assemblages within a community, offering insights into species interactions and ecosystem complexity (Chelli et al., 2024).

Species richness and compositional diversity can be either coupled or uncoupled along temperate deciduous forest successions (Bartha et al., 2020). When the two diversity measures are uncoupled in advanced stages of forest succession, species richness remains stable, but CD increases (Chelli et al., 2024). This means that a constant number of species can be arranged differently within a community, revealing more diverse assemblages and a higher level of species interactions.

A more comprehensive understanding of the long-term trajectories of post-fire forest succession and the role of forest structure in shaping patterns of understory vegetation is essential for elucidating the self-recovery mechanisms of forest ecosystems after disturbance (Lindenmayer et al., 2010). Additionally, it will provide a theoretical basis to develop ecological restoration assessment frameworks and adaptive management strategies in fire-affected landscapes. The Yellowstone National Park (YNP) provides an ideal ecological setting for studying post-fire forest succession: it is the world's first national park, is characterised by natural fire disturbance regimes, and features a detailed mapping of areas affected by wildfires (Romme, 1982; Tinker et al., 2003; Van Wagtendonk, 2007; NPS Datastore, 2024).

Our objective is to assess how the forest structure dominated by Lodgepole pine (*Pinus contorta*), characterising different stages of succession after fire, shapes understory plant communities in YNP. Our study complements the current knowledge by (a) considering a long post-fire chronosequence (> 140 years), including old-growth forests unaffected by fire, and (b) using multiple plant diversity metrics.

We propose the following hypotheses (See Fig. 1):

H1. Understory species richness and within-community β-diversity (compositional diversity) display a U-shaped pattern along the stages of post-fire forest succession.

H2. Between-communities β-diversity increases between more temporally distant stages along the post-fire forest succession. Furthermore, we expect that (**H2a**) species turnover is the main component of beta diversity.

H3. Forest structure and canopy features affect understory plant diversity. In particular, variables related to structural and canopy heterogeneity (e.g., variability of tree height, diameter, and canopy cover) and those related to higher amounts of light and nutrient resources (e.g., canopy openness, deadwood) have a positive relationship with understory plant diversity.

2. Methods

2.1. Study area

The study area is located in Yellowstone National Park (Fig. 2), which is part of the Northern Rockies ecoregion (Hostetler et al., 2021). The park extends for 2.2 million acres (about 9000 km^2) on a volcanic plateau. The climate is characterized by mild summers and cold, snowy winters (Kiel et al., 2025). The forested landscape is primarily dominated by Lodgepole pine (*Pinus contorta*), with higher-elevation Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) woodlands in late-successional phases, alongside drought-tolerant Douglas-fir (*Pseudotsuga menziesii*) stands and patchy riparian deciduous forests (Despain, 1997).

2.2. Sampling design and data collection

Combining fire history vector data (1881–2020) obtained from the GIS Office of Yellowstone National Park (NPS Datastore, 2024) and the

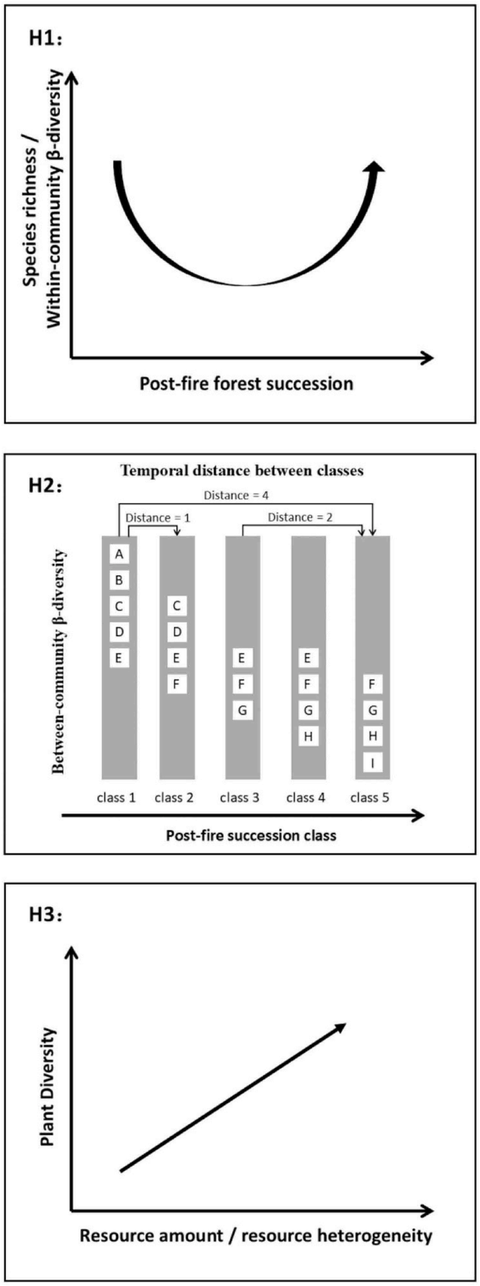

Fig. 1. Conceptual framework and underlying hypotheses of the study. Detailed hypotheses (H) are provided in the main text. In H2, The Letters A–I indicate hypothetical species that appear or disappear in different succession classes. Class 1, fires between 1996–2005; class 2, fires between 1975–1985; class 3, fires between 1924–1933; class 4, fires between 1881–1889; class 5, no fires or fires before 1881.

successional stages outlined by Romme and Despain (1989), we determined four fire age classes: class 1, including recently burned stands with large logs, dominated by dense and young Lodgepole pines (fires between 1996–2005; i.e., 19–28 years since the last fire); class 2, stands similar to class 1 but less dense due to a self-thinning process (fires between 1975–1985, but including the megafire of 1988; i.e., 36–49 years since the last fire); class 3, including still structurally homogeneous stands of mature Lodgepole pine, with sparse logs (fires between 1924–1933; i.e., 91–100 years since the last fire); class 4, including more structurally heterogeneous stands with Lodgepole pine of all ages and young fir and spruce (fires between 1881–1889; i.e., 135–143 years since the last fire). Subsequently, we selected a fifth age class (before 1881) corresponding to the successional stage of climax Lodgepole pine-dominated forests unaffected by fire, based on available knowledge. QGIS 3.22.4 Białowieża (QGIS Development Team, https://qgis.org/), was employed to select polygons characterized by a single fire event. Additionally, a vegetation cover map sourced from the Yellowstone National Park GIS Office was used to verify the overlap between the spatial distribution of Lodgepole pine forests and the fire age classes polygons.

To ensure representative sampling and minimize spatial autocorrelation, we randomly selected sampling plots with a minimum distance of approximately 200 m from each other (Legendre, 1993; Dormann et al., 2007) in each age class. Subsequently, we prioritized plots located within a buffer zone between 1000 m and 2000 m from the roads to minimize anthropogenic influence while ensuring site accessibility. Overall, our sample included 25 plots, 5 plots allocated to each age class (Fig. 2). During field operations, the forest successional stage description was verified, and the fire age class was confirmed. If field access to a designated plot was hindered, the nearest neighbour within the same fire age class has been selected as an alternative.

Each plot was surveyed in July 2024. First, we established a 400 m^2 (20 m × 20 m) plot as a sampling area. In this area, we compiled a list and assessed the abundance (in terms of cover) of vascular plant species. Second, within the same area, we established a 100 m circular transect composed of 1000 contiguous 10 cm × 10 cm sample units (microplots, Chelli et al., 2024). Within the microplots, we recorded the presence of understory vascular plant species, encompassing both herbaceous and woody species, with a height less than 1.3 m (i.e., breast height; see also Bricca et al., 2021). Species nomenclature follows the USDA PLANTS Database (https://plants.usda.gov). Third, we collected data on forest structure and canopy cover in each plot. The forest structure was sampled in four 5 m × 5 m areas located at the corners of each plot. We counted the overall number of trees (diameter $>$ 2 cm at breast height). We measured their height (using Vertex III and Transponder T3; resolution: 0.1 m) and diameter at breast height (resolution: 0.01 m) to calculate mean values and variability (coefficient of variation) of tree diameter and height, as well as plot-level stem density. The lying deadwood was visually estimated (Ligot et al., 2012) as a percentage of cover in the 400 m^2 plot. Canopy features were measured with digital cover photography (DCP) by taking at 1.3 m nine upward-facing pictures after dividing the plot into a 3 m × 3 m grid. RAW canopy images were converted to JPEG images using the 'bRaw' R package (Chianucci, 2022) and then processed using the coveR package (Chianucci et al., 2022) to calculate mean Leaf Area Index (LAI) and its variability within the plot as the coefficient of variation.

2.3. Plant diversity measures

To evaluate biodiversity, we considered three indices: species richness, between-community beta diversity, and within-community beta diversity (i.e., compositional diversity, CD). All analyses were based on presence/absence data. Species richness and between-community β-diversity were based on the total list of species recorded on 400 m^2 at each plot. Between-community β-diversity was quantified using the Sørensen dissimilarity index, which was further partitioned into its two additive components: species turnover and nestedness, using the 'beta.pair' function from the 'betapart' package (Baselga and Orme, 2012). To calculate compositional diversity (i.e., within-community β-diversity, Chelli et al., 2024), we used data from the circular transect. This metric is part of the information-theory models proposed by Juhász-Nagy (1984), (1993), and it was computed using the 'comspat' function implemented in the 'comspat' package (Tsakalos et al., 2022). Since CD can be calculated as a function of the spatial scale (i.e., length of sampling units), we used the maximum CD value in each transect, indeed, the use of maximum CD is suggested to simplify the presentation of community patterns and dynamics (Bartha et al., 1998).

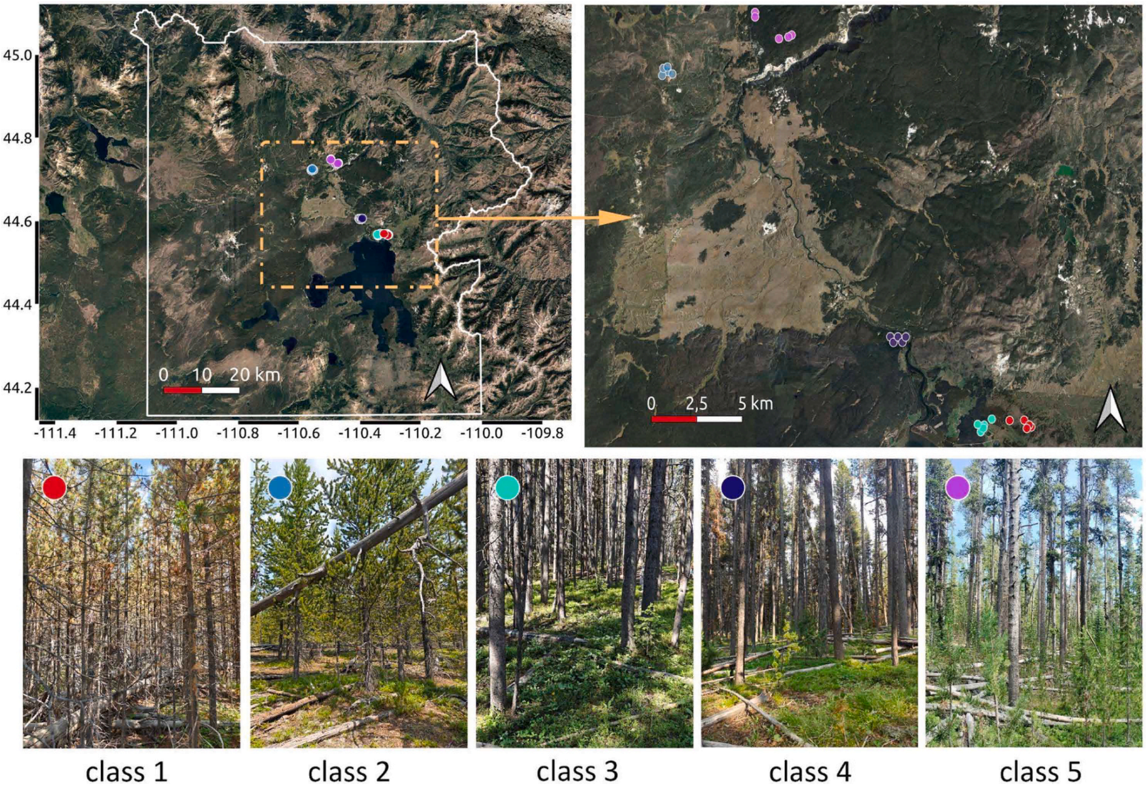

Fig. 2. Locations of study plots within Yellowstone National Park, USA. The white border in the upper-left inset indicates the boundary of Yellowstone National Park. Colors indicate different forest successional stages (classes 1–5), with insets displaying representative photographs of each forest class. Class 1, fires between 1996–2005; class 2, fires between 1975–1985; class 3, fires between 1924–1933; class 4, fires between 1881–1889; class 5, no fires or fires before 1881.

2.4. *Data analyses*

To investigate how forests vary along the successional gradient, we first standardized all numerical variables related to diversity and forest structure by rescaling their values to a 0–1 range (Storch et al., 2018). To model changes in forest structure and canopy features along the successional gradient, we employed generalized additive models (GAMs) with cubic regression splines. To assess patterns of understory diversity, GAMs were directly fitted with post-fire succession stage treated as an ordered numeric predictor, modelling changes in compositional diversity (CD) and species richness over time. To test for differences between classes while considering them as ordered categories, we employed the function ‘ordAOV’ from the package ‘ordPens’ (Gertheiss et al., 2023).

Between-community β-diversity was analyzed based on all pairwise comparisons between plot classes at temporal (i.e., successional) distances of 1–4, with the mean β-diversity for each plot calculated as the average dissimilarity between that plot and all plots from other classes at each temporal distance. Given the hypothesis of increasing dissimilarity between more distant stages along the post-fire forest succession, monotonic trends were tested using the Jonckheere–Terpstra test with 10,000 permutations implemented via the ‘jonckheere.test’ function in the ‘clinfun’ R package. To identify plant species significantly associated with specific successional stages, we used Indicator Species Analysis (ISA). We used the ‘indval’ function from the ‘labdsv’ R package (Roberts, 2023). Significant indicator species were selected based on IndVal $\geq 50\ \%$ and $p \leq 0.05$ (Tejeda-Cruz et al., 2008). To assess the effects of forest structure on biodiversity, linear regression models were applied to variables with normally distributed residuals. In contrast, generalized linear models (GLMs) with the Poisson family were used for variables that did not meet the normality assumption. We performed all analyses using R version 4.4.2 (R Core Team, 2024).

3. Results

Both compositional diversity and species richness of the understory exhibited a significant U-shaped pattern along the post-fire successional gradient (CD: $F = 5.63$, $p = 0.009$; richness: $F = 9.49$, $p = 0.001$; Fig. 3). Higher diversity values were observed in both the early successional stage and in old-growth forests, suggesting that both young and mature stands support greater understory species richness and compositional diversity.

The Jonckheere–Terpstra test detected no significant monotonic trends in total between-community β-diversity (Sørensen index, $p = 0.169$), turnover ($p = 0.305$), or nestedness ($p = 0.586$) with increasing distance between forest successional classes (Fig. 4). Further analysis using non-metric multidimensional scaling (NMDS) confirmed a high degree of similarity in species composition among successional classes (see Figure S1). Total β-diversity was primarily driven by species turnover; in contrast, the nestedness component contributed minimally and remained consistently low across all distance classes (Fig. 4).

Significant indicator species were only identified in class 1, including the shrub *Ribes montigenum* and herbaceous species *Aquilegia flavescens, Astragalus miser, Carex raynoldsii, Cirsium foliosum,* and *Potentilla recta*. Among them, *Ribes montigenum* had the highest indicator value (83.3 %; Table 1).

Forest stand structural and heterogeneity metrics displayed different patterns across successional classes (see Figure S2A, S2B). In particular, mean LAI remained unchanged during the succession while its variability peaked at early and late successional stages. Understory plant diversity patterns were significantly associated with multiple forest structure and canopy features. Species richness exhibited negative relationships with both mean tree diameter ($p = 0.0482$) and mean tree height ($p = 0.0193$), indicating reduced richness in stands dominated by larger trees (Fig. 5a,b). In contrast, richness increased with structural and canopy heterogeneity, as shown by positive associations with the

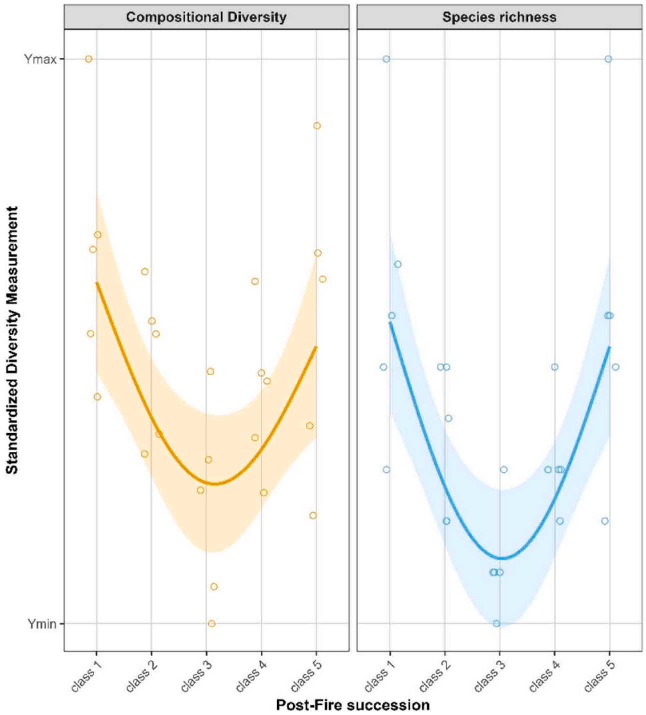

Fig. 3. The standardized (using the 'scale' R function) values of compositional diversity (CD; in orange) and species richness (in blue) from 25 forest stands positioned across five post-fire forest successional classes. Class 1, fires between 1996–2005; class 2, fires between 1975–1985; class 3, fires between 1924–1933; class 4, fires between 1881–1889; class 5, no fires or fires before 1881.

coefficient of variation (CV) of diameter ($p = 0.0459$) and LAI ($p = 0.0149$), as well as with deadwood amount ($p = 0.0295$; Fig. 5c,d, e). Compositional diversity (CD) showed similar patterns. It declined with increasing mean diameter ($p = 0.0229$) and mean height ($p = 0.0045$; Fig. 6a,b) but increased with CV of LAI ($p = 0.0088$) and deadwood amount ($p = 0.02$; Fig. 6c,d). Model summaries are provided in Table S1. Tree density, mean LAI and coefficient of variation of tree height were not significantly associated with changes in both species richness and compositional diversity.

4. Discussion

4.1. *Plant diversity along the post-fire successional gradient*

Our findings reveal a U-shaped pattern of both compositional diversity and species richness during forest succession following wildfire, confirming our H1. This result is consistent with the classical theoretical model of biodiversity change in forest successional ecosystems (Annighöfer et al., 2017; Hilmers et al., 2018; Kuiper et al., 2018). Understory plant diversity is relatively high during the early stage of forest succession following fire disturbance, a pattern consistent with similar studies (Swanson et al., 2011). This can be explained by fire, both facilitating species colonization from other patches and triggering a temporary surge in available resources (e.g., decomposing deadwood), thereby promoting species coexistence in the understory. Moreover, the decline in interspecific competition shortly after fire disturbance facilitates greater diversification of species assemblages (Burkle et al., 2015), leading to elevated CD. With further forest maturation, understory plant diversity declines noticeably. Because the mean LAI remains relatively unchanged and shows no significant association with understory diversity, light availability does not appear to account for the patterns observed in our study. A possible explanation for this decline is the reduced heterogeneity in tree canopy–and therefore LAI–generating homogeneous light conditions at the understory level. In later stages of post-fire forest succession, plant diversity increases. This can be attributed to the resurgence of structural heterogeneity in the forest structure, which facilitates an increase in species richness. At this stage, gaps left by the death of some trees are rapidly colonized by dense cohorts of regenerating trees, and the presence of fallen trunks further creates spatial heterogeneity. Together, these processes contribute to the rise in forest structural heterogeneity, which not only facilitates an increase in species richness but also promotes diversification of species assemblages (Bartha et al., 2020).

CD and species richness were coupled and showed a consistent response across successional stages. This result differs from Chelli et al. (2024), in which a significant decoupling between the two diversity metrics was observed after 300 years of succession in beech (*Fagus sylvatica*) forests. This discrepancy is probably related to the different leaf habit of lodgepole pine (conifer evergreen) and beech (broadleaf deciduous), as well as the density of the canopy; the old-growth beech forest stands considered in Chelli et al. (2024) were very dense; conversely, in Yellowstone National Park, late-successional lodgepole pine stands (class 5) are characterised by an open canopy structure, allowing increased light penetration to the understory. Anyway, the effect of trees on understory extends beyond light penetration including belowground aspects such as mycorrhizal network, root exudates, microbiota, and chemical cues (see Balandier et al., 2022). Additionally, we recognize that the most well-preserved forest stands in the National Park can reach 400–450 years (Romme and Despain, 1989), while the precise age of the stands included in class 5 remains undetermined at present.

4.2. *No temporal distance decay of between-community beta diversity during post-fire succession*

We found no significant monotonic trend in between-community β-diversity with increasing successional distance, indicating that greater age between successional stages does not necessarily lead to increased community dissimilarity, thereby rejecting H2. This contrasts with the common assumption that communities separated by greater successional distances exhibit higher dissimilarity (Torres et al., 2022). The lack of differences in β-diversity across varying temporal distances of classes may be attributed to the absence of a directional trajectory in community composition during succession. The NMDS analysis (Figure S1) further supports this interpretation, showing a considerable overlap among different classes. Constraints imposed by the regional species pool or the broad ecological adaptability of species may lead to a high degree of species sharing among different successional stages, thereby limiting the accumulation of community dissimilarity (Li et al., 2016; Ainsworth and Drake, 2020). We therefore speculate that the pool of species is well adapted to changing conditions along the post-fire forest succession. In this context, the high degree of wildness and minimal anthropogenic alterations to the wildfire regime throughout all areas of the National Park (Romme, 1982) support robust coevolutionary adaptation of species to their ecological environment and its various successional stages. This is confirmed by indicator species analysis, which suggests that only the first class (i.e., immediately after fire) has some indicator species. The youngest stands are characterized by species that persist from the more open habitat conditions present soon after fire. The most prominent among these is *Ribes montigenum*, a disturbance-tolerant pioneer often among the first shrubs to reestablish following fire, where it also provides an important food source for wildlife in early successional stands (USDA, 2018). These habitats can still support species adapted to open conditions, such as *Aquilegia flavescens*, *Cirsium foliosum*, *Carex raynoldsii*, and *Astragalus miser*. However, they also provide opportunities for colonization by invasive species such as *Potentilla recta*, which occurs in disturbed grassy areas impacted by bison activity in Yellowstone. Nitrogen-fixing species, including *A. miser*, are particularly characteristic of the newer post-fire stands in

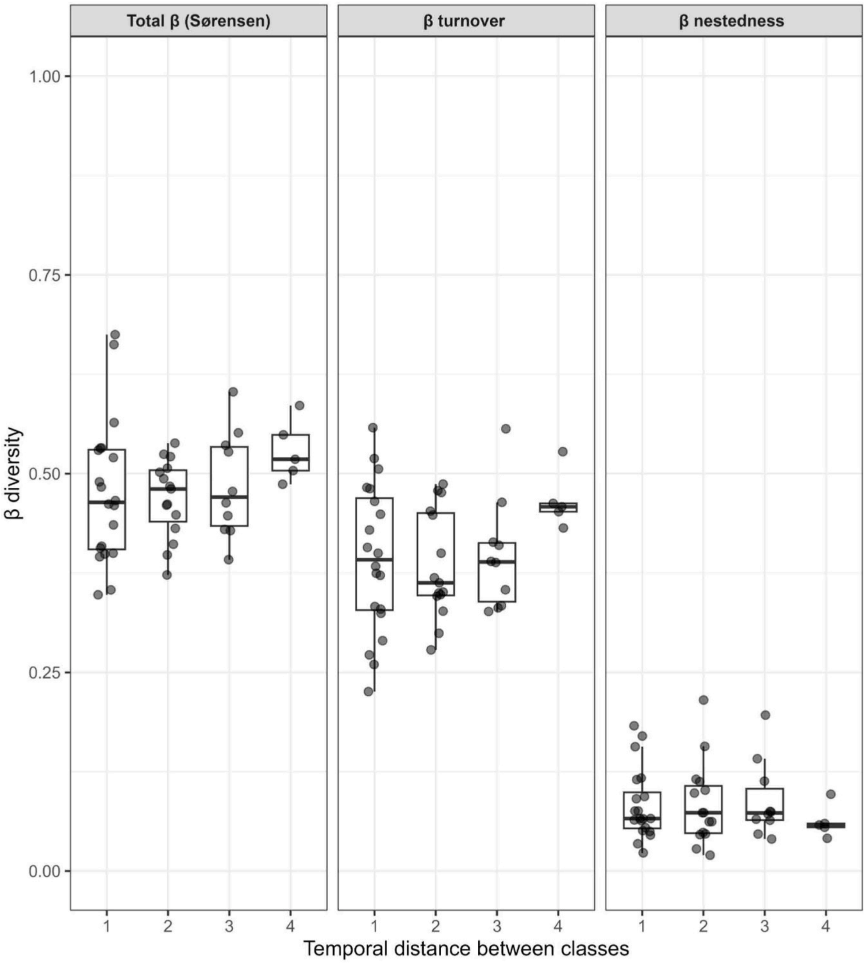

Fig. 4. Boxplots showing total between-community β-diversity (Sørensen index), species turnover, and nestedness components across increasing temporal (i.e., successional) distances between forest successional classes. The x-axis represents class temporal distance, indicating differences in successional stages between pairs of sampling sites.

Table 1
Indicator species analysis for understory plant species, based on comparisons among forest successional classes. Class 1 is the only one having indicator species. Only species with indicator values both significant ($p \leq 0.05$) and ≥ 50 % are shown.

Post-fire stage	Family	Species	Indicator value
class 1	Grossulariaceae	*Ribes montigenum*	83.3 %
	Asteraceae	*Cirsium foliosum*	64.0 %
	Rosaceae	*Potentilla recta*	62.5 %
	Ranunculaceae	*Aquilegia flavescens*	53.3 %
	Cyperaceae	*Carex raynoldsii*	53.3 %
	Fabaceae	*Astragalus miser*	50.0 %

Yellowstone forests. Biological nitrogen fixation is recognized as a key mechanism for reestablishing nitrogen pools depleted by fire. Symbiotic fixers—often shrubs in early successional communities—can contribute substantially more nitrogen compared to asymbiotic sources, and thereby influence early stand development and nutrient availability (Yelenik et al., 2013).

Consistent with H2a, our results demonstrate that differences in community composition across successional stages were predominantly driven by species turnover. In contrast, the contribution of nestedness to overall β-diversity was comparatively limited. This finding is consistent with the results reported by Guclu et al. (2024), who demonstrated that species turnover predominates in Sorensen β-diversity along a forest succession gradient. This indicates that post-fire succession mainly involves species replacement rather than progressive species loss, reflecting environmental filtering and habitat differentiation through time (Socolar et al., 2016).

4.3. *Higher amount of deadwood and heterogeneity of tree diameters and canopy cover foster plant diversity*

Species richness and compositional diversity are similarly affected by forest structural and canopy features. Higher amounts of deadwood are associated with higher values of both metrics of plant diversity. Through its impact on soil characteristics and the creation of diverse microhabitats, deadwood modulates resource quantity and distribution, contributing to increased environmental heterogeneity (Klos and Link, 2018), which in turn affects species composition and diversity. The variability of tree diameter and LAI within the plot is also related to higher plant diversity. Both parameters are indicative of a heterogeneous forest structure and canopy, likely generating a patchiness in light resources for understory species (Tanioka et al., 2020; Helbach et al., 2022).

Our results only partially confirm H3. Mean values of LAI do not significantly affect patterns of plant diversity. LAI is associated with canopy openness and, therefore, to light resource availability for understory species (Majasalmi and Rautiainen, 2020; Quevedo-Rojas et al., 2024). This finding suggests that it is not the quantity of light reaching the forest floor, but rather its heterogeneity that plays a critical role in shaping the diversity of understory plant communities. Such heterogeneity, often driven by sunflecks, can create microsites that favor species

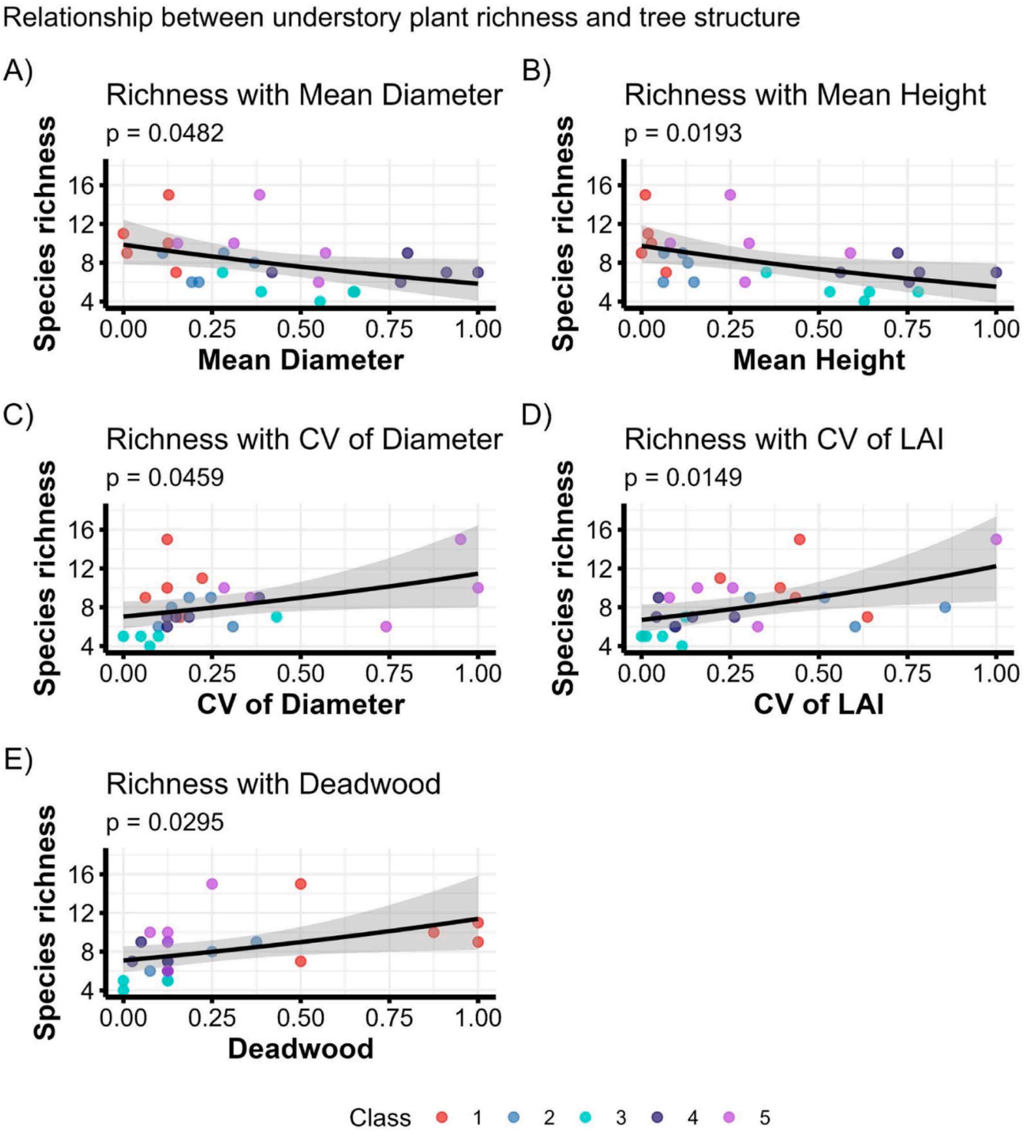

Fig. 5. Relationships between understory plant species richness and forest structural and canopy features, as determined by generalized linear models. Scatter plots illustrate significant linear relationships ($p \leq 0.05$). Points are color-coded to represent different forest successional Classes. Solid black lines represent the fitted linear regression models, with shaded areas indicating 95 % confidence intervals. Class 1, fires between 1996–2005; class 2, fires between 1975–1985; class 3, fires between 1924–1933; class 4, fires between 1881–1889; class 5, no fires or fires before 1881.

coexistence (Chazdon, 1988). More broadly, the overstory can influence understory diversity through multiple, interrelated pathways—including not only light availability, but also competition for belowground resources, litter input, and microclimatic buffering (Balandier et al., 2022). This supports a central hypothesis in explaining patterns of plant diversity—the heterogeneity-diversity relationship—highlighting environmental heterogeneity as a key driver shaping diversity gradients (Stein et al., 2014).

Finally, we find that mean diameter and tree height are negatively associated with plant diversity. We speculate that this is not a causal relationship. Still, it is related to the fact that bigger trees occur between class 3 and 4 of the post-fire succession (i.e., 91—143 years after fire). These stages are characterized by the lowest values of heterogeneity in terms of forest structure and canopy (see Figure S2B). Such structural homogenization may reduce light variability and the availability of microsites suitable for different understory species, thereby leading to lower diversity (Helbach et al., 2022; Sercu et al., 2017).

5. Conclusion

By using a chronosequence spanning from recent burns to old-growth lodgepole pine forests in Yellowstone National Park, we found U-shaped patterns of species diversity, modulated by specific forest structure and canopy features. The study of this unique ecosystem characterised by a millennial natural fire regime provides a basis to develop ecological restoration frameworks and management strategies in fire-affected landscapes. Indeed, while conventional fire management often focuses on removing dead material, our findings show that retaining deadwood and promoting structural heterogeneity significantly benefit understory plant communities. In particular, effective management should promote spatial variability in canopy cover and forest structure, creating microhabitats that support high plant diversity. These strategies must explicitly acknowledge the ecological importance of both early- and late-successional stages, as well as the need to maintain forest structural heterogeneity. Preserving such heterogeneity supports biodiversity at broader spatial scales by fostering compositional differences among stands. Management practices that reduce

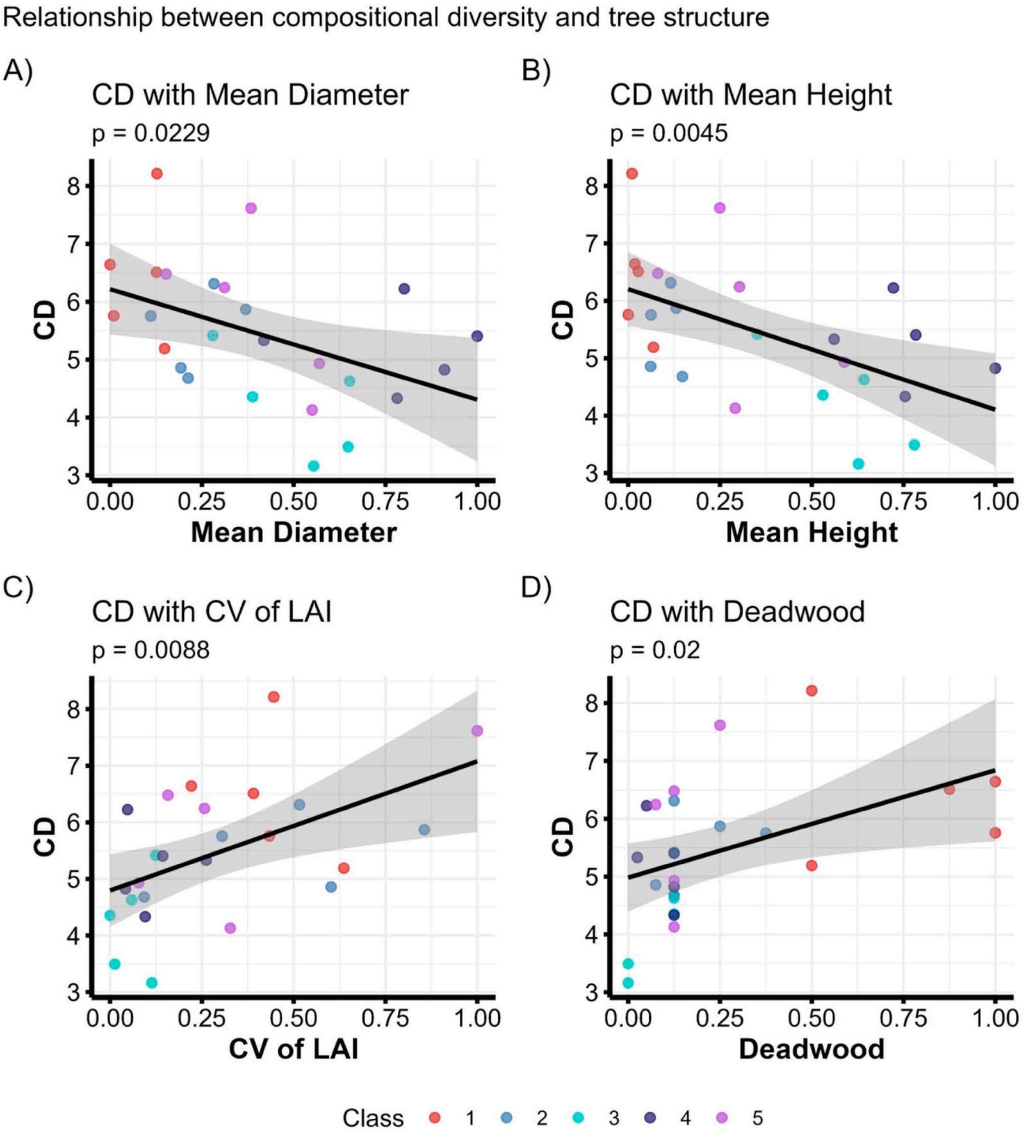

Fig. 6. Relationships between compositional diversity (CD) and forest structural and canopy features as determined by generalized linear models. Scatter plots illustrate significant linear relationships ($p \leq 0.05$). Points are colour-coded to represent different forest successional classes. Solid black lines represent the fitted linear regression models, with shaded areas indicating 95 % confidence intervals. Class 1, fires between 1996–2005; class 2, fires between 1975–1985; class 3, fires between 1924–1933; class 4, fires between 1881–1889; class 5, no fires or fires before 1881.

structural complexity should therefore be avoided.

CRediT authorship contribution statement

Luciano Ludovico Maria De Benedictis: Writing – review & editing, Validation, Software, Methodology. **Roberto Canullo:** Supervision, Investigation. **Marco Cervellini:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Stefano Chelli:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Alysia Cox:** Writing – review & editing, Investigation. **Bartha Sándor:** Writing – review & editing, Methodology. **Ariana Rivera Añazco:** Visualization, Investigation. **Pal Robert:** Writing – review & editing, Investigation. **Zhengxue Zhu:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation. **Giandiego Campetella:** Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

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Relationships There are no additional relationships to disclose.

Patents and Intellectual Property There are no patents to disclose.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123419.

Data availability

Data will be made available on request.

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