Processes of deterministic community assembly change as fire severity increases

Ian Winick\*1 and Rachel Mitchell1

1School of Natural Resources and the Environment, University of Arizona, Tucson, USA.

Ian Winick ([iaw1@arizona.edu](mailto:iaw1@arizona.edu)) Corresponding Author

Open research statement will go here

Community ecology, community assembly, fire, disturbance, beta diversity, functional diversity, null model

ABSTRACT

INTRODUCTION

There is a robust literature linking taxonomic biodiversity to ecosystem function via plant functional traits (biodiversity-ecosystem function, BEF; Zavaleta et al. 2010, Isbell et al. 2011, Maestre et al. 2012, Pasari et al. 2013, Gross et al. 2017, Hautier et al. 2018, Grman et al. 2018). Disturbance regimes, which impact taxonomic and functional diversity of communities, are changing globally, occurring at new frequencies and higher intensities than previously experienced (Turner 2010; Seidl et al. 2017; Mueller et al. 2020; Altman et al. 2024). Prior work has demonstrated that disturbance initiates the process of community assembly (Jiang and Patel 2008; Burt and Clary 2016), but the effects of atypical disturbance on taxonomic and functional diversity is less well understood. Classically, the Intermediate Disturbance Hypothesis proposes a unimodal “hump-shaped” response of biodiversity to increasing disturbance severity, however multiple studies have revealed no consistent pattern, and these studies often do not account for novel or high magnitude disturbance events. Similarly, the classic understanding of BEF relationships relies on the assumption that greater taxonomic biodiversity begets greater functional biodiversity, and thus greater stability of ecosystem services. Following a disturbance event, community assembly acts on plant functional traits, filtering species into a community with the traits that enable survival. Whether this process leads to concomitant increases in species and functional diversity over time, and whether this process varies in response to disturbance severity, is poorly understood. Here, we address this critical knowledge gap by quantifying the relationship between taxonomic and functional diversity for four years across a fire severity gradient.

Recent work in ecosystem-level responses to wildfire have strongly indicated that wildfire severity affects community assembly processes with consequences for successional outcomes and ecosystem function. Fire-adapted forests have been widely observed by land managers to convert to alternate community types, such as shrublands and grasslands, when fire severity exceeds historic norms (Guiterman et al. 2022). These alternate community outcomes following high-severity fire provide evidence that mechanisms of ecosystem resistance and resilience have been overcome and alternate mechanisms may be at work (Falk et al. 2022; Coop et al. 2020). Much of the research on forest responses to fire severity has focused on dominant canopy species, where changes to forests along fire severity gradients have been attributed to mechanisms such as distance to seed source, reburning, warming, and drought being exerted on canopy species (Coop et al. 2016; Chambers et al. 2016; Owen et al. 2017; Haffey et al. 2018; Davis et al. 2019). While changes in assembly mechanisms likely extend to the community scale, including the understory (Coop 2023; Taber and Mitchell 2023; 2024), research on forest community-scale responses to high severity fire is lacking compared to research on canopy species alone.

Beyond forest ecosystems, community assembly responses to disturbance have been explored in the context of dispersal limitation, extinction/colonization, niche theory, and environmental homogenization (Vellend et al. 2007; Catano, Dickson, and Myers 2017; Tatsumi et al. 2020; Torres, Parra, and Moreno 2022; Godsoe, Bellingham, and Moltchanova 2022). Typically, these studies have examined one or a few types of disturbance but generally have not explored the effect of differing severities or intensities, especially atypically severe disturbance, on the process of community assembly over time. Exploring taxonomic and functional responses to a disturbance gradient can reveal whether taxonomic and functional diversity recover in tandem, and whether this process is driven by strong or weak environmental trait filtering, high redundancy, or niche differentiation. Comparing the response of taxonomic and functional diversity across a fire-severity gradient and over time may offer valuable mechanistic insights into how atypically severe wildfires are altering community assembly and ecosystem function.

One way to measure community responses to disturbance is by using beta diversity: the spatial variability of diversity. Beta diversity links plot-level diversity (α) to regional diversity (γ) and is shaped by processes at both scales. There are several metrics of beta diversity in use with varying scales of similarity, dissimilarity, and distance (see Anderson et al. 2011), but here we broadly define high beta diversity as high spatial variability (heterogeneous) and low beta diversity as low spatial variability (homogeneous). Deviations in beta diversity from null expectations (i.e., the difference between observed beta diversity and the beta diversity of the community randomized by a null model) can reveal underlying community assembly processes (Kraft et al. 2011; Myers et al. 2015; Catano, Dickson, and Myers 2017). If the difference between the observed beta diversity and the null expectation (β-deviation) is different from zero, meaning the observed beta diversity is not equal to random, then deterministic community assembly processes are at work. The direction of this deviation is informative: β-deviations greater than zero (i.e. beta diversity is higher than random) indicate that the community is relatively heterogeneous given α and γ and species are aggregating, while β-deviations less than zero (i.e. beta diversity is lower than random) indicate that the community is relatively homogeneous given α and γ and species are dispersed. β-deviations that are equal to zero (i.e., beta diversity is equal to random) indicate that deterministic assembly processes are not at work and that the community is assembling randomly. However, there is little agreement whether or how disturbance affects β-deviations. For example, Kim et al. (2018) found that grass harvesting increased the beta diversity of ants in a tallgrass prairie while Chase (2007) found that drought decreased beta diversity of artificial pond communities. Myers et al. (2015) found no effect of fire on the beta diversity of woody species in a temperate forest.

A possible reason that the current body of research may lack consensus is that the temporal dimension of community assembly is often left unexplored. Community assembly is a temporal process, so observed BEF relationships are highly dependent on the stage of assembly if a given ecosystem is not at equilibrium. Armitage (2016) found that the strength of richness and respiration relationships changed over the course of succession in artificial microbial communities, with positive relationships peaking at mid-succession. Mori et al. (2017) found that the causal relationship of richness and soil properties reversed during soil microbial succession and the importance of complementarity effects increased with successional age. Therefore, the measurement of temporal trajectories may capture statistically significant changes in ecosystem processes that would not be resolved if the same ecosystem was observed statically or across a single timestep (Huxley et al. 2023).

Because community assembly acts on functional traits, and functional traits link species abundance and ecosystem functions mechanistically, understanding whether and how taxonomic and functional diversity recover temporally after disturbance is critically important. Theory predicts that taxonomic and functional diversity are coupled (Petchey and Gaston 2002) and thus should respond in tandem to drivers such as disturbance. However, observational studies have found that taxonomic and functional diversity do not necessarily assemble in tandem. For example, Baker et al. (2021) found that changes in functional diversity of benthic macroinvertebrates lagged behind taxonomic diversity and Villéger et al. (2012) found that high taxonomic beta diversity did not translate to high functional beta diversity in tropical fish communities. The relationship between taxonomic and functional diversity may be mediated by disturbance. Disturbance is expected to alter species assemblages through processes of environmental filtering and species interactions (Maire et al. 2012). Importantly, the responses of species assemblages are driven by functional identity rather than taxonomic identity (McGill et al. 2006). Indeed, Biswas and Mallik (2011) found that disturbance severity altered the coupling of taxonomic and functional diversity in a boreal forest and attributed this result to the differential filtering of competitive, generalist, and disturbance-tolerant species along the disturbance gradient. example…just preserving the comment

We use a null model approach to study local-scale changes in community assembly across a burn severity gradient in the understory community of a fire-adapted ponderosa forest ecosystem. Using repeated measures of both taxonomic and functional beta diversity, we measure the effect of burn severity on post-fire community assembly trajectories. We also measure the coupling of taxonomic and functional diversity across the burn severity gradient through time. Finally, we compare the compositional outcomes of community assembly across the burn severity gradient four years following fire. We predict that:

1) the trajectory of community assembly processes will change as fire severity increases;

2) high severity fire will decouple taxonomic and functional diversity; and

3) altered assembly processes and taxonomic-functional decoupling will be associated with altered taxonomic and functional outcomes.

METHODS

Study Site

This study was conducted within and immediately adjacent to the perimeter of the 2019 Museum Fire, located approximately 1.6 km north of Flagstaff, Arizona, USA (35.252169, -111.634913 WGS84). This fire burned in late July of 2019, with a total of 793.6 hectares burned. The Museum Fire was a mixed-severity fire and was characterized by patches of varying severity, including very low-, low-, moderate-, and high-severity patches present (USDA Forest Service, 2019) and did not receive any seeding treatments post-fire. The canopy is dominated by *Pinus ponderosa* and *Quercus gambelii* with *Juniperus deppeana*, *Pinus strobiformis*, and *Pseudotsuga menziesii* interspersed. Elevations within the burn scar range from approximately 2240 m to approximately 2760 m above sea level. Our research plots were monumented at lower elevations within this range, between 2251 and 2328 m above sea level. All plots were located on slopes with a southeasterly aspect, with slopes between 20 and 30 degrees. Soils are based on mixed igneous parent material, with both Alfisol and Mollisol soil orders.

The precipitation averages 52.17 cm (National Weather Service 2025), with a bimodal precipitation regime. An average of 28% of annual precipitation falls in winter, while 34% occurs in summer due to the southwestern monsoon (Hereford 2007). The thirty-year (1993-2023) average maximum, minimum, and average temperatures are 33.33°C, -20.56°C, and 8.28°C, respectively (National Weather Service 2025). See Appendix for annual weather data.

Plot Establishment

Plots were established in May of 2020, 10 months following the fire. We established 60 4 m × 4 m research plots across the burn severity gradient, with 20 plots located within unburned (U), low-severity (L), and high-severity (H) burn areas. Unburned plots were located immediately outside of the burn perimeter and no further than 470 m from the edge of the fire perimeter. Burn severity classifications for these research plots were initially derived from the USDA Burned Area Emergency Response (BAER) map, which is based on Burned Area Reflectance Classification remote-sensing data that have been verified by field crews (Parsons et al. 2010; Noll and Malis-Clark 2020). BAER classifications are based on relative change in soil organic matter and soil structure due to fire (Keeley 2009). We confirmed burn severity classifications for each plot by visually assessing first-order fire severity effects in May 2020 including vegetation cover within plots, the presence of bare mineral soil within plots, and overstory mortality within an approximately 25-m radius of the center of each research plot. Indicators of low severity fire included extant understory vegetation, low bole scorch height, and less than 50% overstory mortality. Indicators of high-severity fire included more than 50% bare mineral soil and more than 90% overstory mortality. Each research plot was subdivided into four 1-m2 subplots located 1 m apart. For this study, one 1-m2 subplot was used per plot. See Taber and Mitchell (2023, 2024) for more information on experimental design and concurrent research projects.

Data collection

Community composition

Community composition and abundance data were collected in the 1-m2 subplots in the second week of September for four consecutive years, beginning in 2020 (approximately 13 months post fire). Individuals were identified to the species level and absolute species cover was recorded to the nearest 0.25% using a modified Daubenmire method. Species accounting for less than 0.25% of cover on a given plot were recorded with a value of 0.2% cover. All nomenclature follows the USDA NRCS Plants Database (https://plants.usda.gov/) accessed in 2023.

Plant traits

We analyzed three plant traits: SLA (mm2 g−1), LDMC (g g−1), and height (m). Our species pool contains 60 species (Appendix). For 21 species (19 of which accounted for 85% of species cover), traits were measured from individuals on-site. All measurements followed standardized collection protocols (Garnier et al. 2001; Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Measurements on individuals were collected regardless of sun exposure, slope, or aspect, but only mature, healthy leaves were measured. Height was measured for 20–25 individuals per species. For species with <20 individuals, height was recorded for all individuals present. The height of *Quercus gambelii* was measured as the median height of 20 understory (<2m) individuals. The median was used instead of the mean because *Q. gambelii* is a canopy species at maturity and therefore the height of individuals in the understory is skewed rather than normally distributed. To measure SLA and LDMC, one leaf sample was taken from individuals of each species. For species with <20 individuals, we collected between 3 and 10 leaves from an individual, aiming for a total of 20 leaves per species. Leaf area for all samples was determined using a CID-203 leaf area meter (CID Bio-Science; Camas, Washington USA). All fresh samples were rehydrated by placing petioles in distilled water for at least 6 h before being scanned and weighed following Garnier et al. (2001). After leaf area and fresh mass were measured, leaf samples were dried at 70 °C for 72 h, then reweighed. SLA and LDMC were then calculated from the area and mass data for each sample.

When species were too rare outside of sample plots for trait collection, data were collected from the TRY database and from primary literature sources. Where trait values could not be found for a given species, values of close congeners were used when available. For all remaining trait values, we used the average trait values of the observed genus (e.g. trait values for *Linum neomexicana* were calculated as the average trait values for all *Linum* species in Laughlin et al. (2010)) or the average trait value for all observed species. See trait table in Appendix for details.

Statistical analysis

All analyses were conducted using R version 4.1.1 (2021-08-10). For all analyses, absolute species cover data were relativized using Wisconsin double standardization using the *wisconsin* function in the R package vegan, version 2.6-4 (Oksanen et al. 2022).

Calculating Beta Diversity

We calculated taxonomic beta diversity of each severity-year as the mean Bray-Curtis dissimilarity using the function *vegdist* in the vegan package. We calculated functional beta diversity using Rao’s quadratic entropy (Q), standardized between 0 and 1, in the following additive partition:

(1)

where Q*αij*is the plot-level Q for year *i* and severity *j*, and Q*γij* is the Q of the species pool for year *i* and severity *j* (de Bello et al. 2010). Q*γij* was calculated using the relative abundance of each species averaged across all plots in a given severity class (de Bello et al. 2021). Q was calculated using the *dbFD* function in the FD package (Laliberté et al. 2014).

Resampling

To estimate the standard error of the beta diversity measurements, we resampled the Bray-Curtis distance matrices and Q*αij* for all plots 999 times with replacement, with the size of each resample equal to the size of the distance matrices and Q*αij*, respectively.

Null Model

We constructed a null model to estimate the expected random beta diversity. Our null model fixed plot-level species richness, but randomly selected species for each plot from our observed species pool. The observed species pool includes all species observed across any severity over all four years (n = 60 species). The entire observed species pool was represented in each simulation, such that every species occurred in at least one of the simulated plots (n = 60 plots), but not necessarily in a given severity class (n = 20 plots). Species cover values were randomly selected from a uniform distribution between 0.2-100% cover and then relativized in the same way as the observed cover data using Wisconsin double standardization. We calculated the deviation of each resampled beta diversity value from the expected random beta diversity value (β-deviation) as the standard effect size (SES) based on 999 iterations of the null model:

(2)

See Appendix to access R code.

Trajectory of β-deviation

To evaluate the effect of burn severity on the temporal trajectories of taxonomic and functional β -deviations, we used multiple regression with taxonomic and functional β-deviation as response variables and the interaction of burn severity, and year since fire as the effect variables. To accommodate potential non-linearity in the data, we added a quadratic term for year since fire and compared the quadratic model with a linear model using Akaike ’s information criterion (AIC; Akaike 1987). Where there was a difference in AIC scores of >4, we selected the model with the lower AIC score.

Coupling of taxonomic and functional diversity

To evaluate the coupling of taxonomic and functional diversity, we examined the level of functional redundancy (FRed) using the slope between species richness and Q across the burn severity gradient for all four years of the study (Baker et al. 2021). A steep positive slope indicates low FRed, as additional species are functionally distinct and increase Q. A slope of zero indicates high FRed, as additional species are not functionally distinct and do not change Q. A negative slope indicates functional convergence, as species similarity increases as species are added. To make the slope more interpretable, species richness was standardized between 0 and 1 to place it on the same scale as Q. Following this approach, a slope of 1 represents maximum species richness being associated with maximum functional diversity. We consider taxonomic and functional diversity to be coupled when the regression analysis reveals a significant relationship at α=0.05.

Comparing Community Composition

To analyze changes in taxonomic and functional composition, we tested the difference in community composition by burn severity class four years after fire (the final year of species cover data) using PERMANOVA with the *adonis2* function in the vegan package (Anderson 2001; 2017). Since the adonis2 functional does not provide pairwise comparisons of groups (i.e. severity), we performed a post-hoc pairwise PERMANOVA using the *pairwise.adonis* function in the pairwiseAdonis package (Martinez Arbizu 2020). We analyzed taxonomic community composition using Bray-Curtis dissimilarity and community matrices with relativized species cover. We analyzed functional community composition using Euclidian distance and community matrices with community weighted means (CWM) for each of our three traits (SLA, LDMC, height). For this ordination analysis, the traits were log-transformed. Significant PERMANOVA results can not indicate whether groups differ in centroids or dispersion around centroids, so we also applied a test for beta dispersion, a multivariate analog to the Levene’s test (Anderson, Ellingsen, and McArdle 2006).

RESULTS

Three plots were lost during the 4 years of data collection: 2 in low-severity, 1 in high-severity. These 3 plots were removed from our data for the years they were missing, bringing the total number of plots to n = 57. Plots that had no vegetation cover in year 1 after fire were also omitted from analysis for that year (low-severity: n = 1; high-severity: n = 8), but they were included in analyses in years when they had vegetation cover.

Effect of fire severity on beta diversity

The taxonomic β-deviations were significantly below zero in all severities over all four years. This indicates that, given α and γ, the species across plots were more homogeneous than if the community was assembling from the species pool randomly. However, the trajectories of taxonomic β-deviations varied significantly by severity, as revealed by our quadratic regression (F[11/11,976] = 16,617.06, *p* < 0.001, R2 = 0.94/0.94; Fig. 1a). Both the low-severity plots (Estimate = 3.93, SE = 0.08, t = 51.34, *p* < 0.001) and the high-severity plots (Estimate = -9.12, SE = 0.08, t = -119.03, *p* < 0.001) had significantly different trajectories than the unburned plots. For the low-severity plots, the β-deviations were similar to the unburned plots in year 1 after fire and then remained higher for years 2 through 4. For the high-severity plots, the β-deviations followed a more variable trajectory compared to the unburned plots. The high-severity β-deviations were higher than the unburned plots in year 1 after fire, lower in year 2, similar in year 3 and then higher again in year 4. Although the trajectories of the unburned and low-severity β-deviations were significantly different from each other, they had a similar shape and direction, while the trajectory of the high-severity β-deviations had a unique shape and direction.

The functional β-deviations were closer to zero than the taxonomic β-deviations and ranged from negative to positive. This indicates that, given α and γ, the functional diversity across plots was closer to random than taxonomic diversity, but we observed both homogeneity and heterogeneity of functional traits across plots. Our quadratic regressions revealed that fire severity had a significant effect on the trajectories of functional β-deviations (F[11/11,976] = 2248.78, *p* < 0.001, R2 = 0.67/0.67; Fig. 1b). Both the low-severity plots (Estimate = 1.29, SE = 0.04, t = 29.36, *p* < 0.001) and the high-severity plots (Estimate = -0.49, SE = 0.04, t = -11.25, *p* < 0.001) had significantly different trajectories than the unburned plots. For the low-severity plots, the β-deviations were similar to the unburned plots in year 1 after fire, and then remained higher for years 2 through 4. The low-severity β-deviations were negative in year 1 after fire, positive in years 2 and 3, indicating functional heterogeneity across plots, and then were indistinguishable from zero in year 4, indicating functional randomness across plots. For the high-severity plots, the β-deviations were higher than the unburned for all four years. The high-severity β-deviations were positive in year 1, indistinguishable from zero in year 2, and positive in years 3 and 4. As with the taxonomic diversity, the trajectories of the unburned and low-severity β-deviations were significantly different from each other, but they had a similar shape and direction, while the trajectory of the high-severity β-deviations had a unique shape and direction

By year 4, the unburned plots had the lowest β-deviations both taxonomically and functionally, while the low-severity plots had the highest taxonomic β-deviations and the high-severity had the highest functional β-deviations.

Coupling of taxonomic and functional diversity

Plots with only one species have a Q = 0 and were omitted from this analysis (year 1: n = 9; year 2: n = 4; year 3: n = 3; year 4: n = 3; total n = 19 out of 224 measurements of Q). The slope of the line between standardized species richness and Q varied with burn severity and year (Fig. 2, Table 2). Coupling of taxonomic and functional diversity was only observed in the unburned plots, where the slopes were positive, relatively steep, relatively stable through time, and significant. In the low-severity plots, the slopes were positive, but varied in steepness through time, and were not significant. In the high-severity plots, the slopes varied in both steepness and direction and were not significant.

Community composition

Our PERMANOVA revealed that severity had a significant effect on both taxonomic composition (F[2] = 4.83, *p* < 0.001) and functional composition (F[2] = 7.85, *p* < 0.001) four years after fire (Fig. 3).

Our post-hoc pairwise PERMANOVA revealed that, both taxonomically and functionally, the high-severity plots were significantly different from the unburned plots (taxonomic: F[1] = 8.20, R2 = 0.18, *p* < 0.001; functional: F[1] = 15.03, R2 = 0.29, *p* < 0.001) and low-severity plots (taxonomic: F[1] = 4.44, R2 = 0.11, *p* < 0.001; functional: F[1] = 6.67, R2 = 0.16, *p* = 0.009), while the unburned and low-severity plots were not different from each other (taxonomic: F[1] = 2.04, R2 = 0.05, *p* = 0.064; functional: F[1] = 1.05, R2 = 0.03, *p* = 0.983). All Pvalues for PERMANOVA results are adjusted.

Our test of beta dispersion revealed that there were significant differences in dispersion in taxonomic diversity (F[2] = 3.27, *p* = 0.046) across the severity gradient, but not functional diversity (F[2] = 2.40, *p* = 0.100). A post-hoc Tukey’s honestly significant difference test revealed that, for taxonomic diversity, only the low-severity and high-severity plots significantly differed in dispersion (*p* = 0.054).

DISCUSSION

Disturbance regimes are changing globally with uncertain consequences for the assembly and functioning of ecological communities. Wildfire regimes, in particular, have experienced wide deviations from historic norms from the complete exclusion of wildfire to catastrophic wildfires of high-severity. Here, we provide evidence that high-severity fire altered the trajectories and mechanisms of community assembly in an ecosystem adapted to low-severity fire.

Trajectories of community assembly

High-severity fire altered the trajectory of community assembly mechanisms, as measured using β-deviations, for the first four years following fire, which was consistent with our first prediction. The trajectories of the low-severity and unburned plots were also significantly different from each other, which was due to the β-deviations of the low-severity plots being less negative than the unburned plots, however they followed a similar pattern of assembly through time. The high-severity plots, on the other hand, followed a distinct pattern through time.

An important aspect of our results lies in our approach of measuring trajectories rather than β-deviations alone because community assembly is a temporal process. If we had only measured beta diversity for one year, then the pattern we observed and the conclusions we might draw would depend heavily on the year that we chose. For example, in year 2, the low-severity plots had a positive functional β-deviation, while the functional β-deviation of the high-severity plots could not be distinguished from zero (Fig 1b). If we had only measured the community in year 2, we might conclude that low-severity fire was initiating deterministic assembly processes that drive community aggregation, while high-severity fire initiated random assembly. However, if we measured the community only in year 4, we may have drawn the exact opposite conclusion because the functional β-deviations of the low-severity plots became indistinguishable from zero, while the β-deviations of the high-severity plots became positive. Therefore, we can see that a single state of a community may be less important than the trajectory by which it arrived there.

That said, we can still speculate on the meaning of the individual β-deviation measurements in each year. Our null model was naïve to burn severity and successional age. Therefore, our null communities were randomized such that any species from the observed species pool could colonize any plot during any year. Given this lack of constraint, the strongly negative taxonomic β-deviations are not surprising because the fully randomized communities are not subjected to the processes that drive species rarity and commonness. Therefore, we expect that the fully randomized communities will have higher taxonomic beta diversity than the observed communities. Interestingly, while the taxonomic β-deviations of all fire severities were strongly negative, indicating non-random homogeneity of species across plots, functional β-deviations were close to zero and frequently positive in the low-severity and high-severity plots. In other words, our plots were taxonomically homogeneous while, at the same time, functionally heterogeneous. We attribute this to the low diversity of this ecosystem, such that small changes in taxonomic turnover that drive low taxonomic beta diversity result in comparatively large changes in functional turnover that drive high functional beta diversity. This is interesting because… Expand!

Coupling of taxonomic and functional diversity

We predicted that high-severity fire would decouple taxonomic and functional diversity, but taxonomic and functional diversity were decoupled by both low-severity and high-severity fire (Fig. 2, Table 2). We observed coupling only in the unburned plots, where we saw relatively low FRed, meaning accumulating species were functional distinct. In the low-severity plots, FRed was the lowest observed in year 1 and then increased each year as the slopes became less steep. The high-severity plots had an unstable pattern of FRed through time; we observed weak functional convergence in year 1, relatively high FRed in years 2 and 3, and functional convergence again in year 4.

Given the FRed results, the relative magnitude of niche differentiation and habitat filtering changed along the severity gradient. In the unburned plots, the combination of low FRed and relatively low measures of functional diversity (Fig. 2a) indicates that both habitat filtering and niche differentiation were at work. In the low-severity plots, low FRed in year 1 indicates that niche differentiation dominated early after disturbance but gave way to habitat filtering as FRed increased in time. In the high-severity plots, high FRed and functional convergence indicate that within-plot habitat filtering was most dominant. Considering these results together with the functional β-deviations, we begin to understand the spatial scales at which these mechanisms are working. Where functional β-deviations are positive for the low- and high-severity plots, habitat filtering effects vary between plots. Where functional β-deviations are random or near-random,

Community outcomes

REFERENCES

Akaike, Hirotugu. 1987. “Factor Analysis and AIC.” *Psychometrika* 52 (3): 317–32. https://doi.org/10.1007/BF02294359.

Altman, Jan, Pavel Fibich, Volodymyr Trotsiuk, and Nela Altmanova. 2024. “Global Pattern of Forest Disturbances and Its Shift under Climate Change.” *Science of The Total Environment* 915 (March):170117. https://doi.org/10.1016/j.scitotenv.2024.170117.

Anderson, Marti J. 2001. “A New Method for Non-Parametric Multivariate Analysis of Variance.” *Austral Ecology* 26 (1): 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

———. 2017. “Permutational Multivariate Analysis of Variance (PERMANOVA).” In *Wiley StatsRef: Statistics Reference Online*, 1–15. John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118445112.stat07841.

Anderson, Marti J., Thomas O. Crist, Jonathan M. Chase, Mark Vellend, Brian D. Inouye, Amy L. Freestone, Nathan J. Sanders, et al. 2011. “Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist.” *Ecology Letters* 14 (1): 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Anderson, Marti J., Kari E. Ellingsen, and Brian H. McArdle. 2006. “Multivariate Dispersion as a Measure of Beta Diversity.” *Ecology Letters* 9 (6): 683–93. https://doi.org/10.1111/j.1461-0248.2006.00926.x.

Armitage, David W. 2016. “Time-Variant Species Pools Shape Competitive Dynamics and Biodiversity–Ecosystem Function Relationships.” *Proceedings of the Royal Society B: Biological Sciences* 283 (1838): 20161437. https://doi.org/10.1098/rspb.2016.1437.

Baker, Nathan Jay, Francesca Pilotto, Phillip Joschka Haubrock, Burkhard Beudert, and Peter Haase. 2021. “Multidecadal Changes in Functional Diversity Lag behind the Recovery of Taxonomic Diversity.” *Ecology and Evolution* 11 (23): 17471–84. https://doi.org/10.1002/ece3.8381.

Bello, Francesco de, Carlos P. Carmona, André T. C. Dias, Lars Götzenberger, Marco Moretti, and Matty P. Berg. 2021. *Handbook of Trait-Based Ecology: From Theory to R Tools*. Cambridge: Cambridge University Press. https://doi.org/10.1017/9781108628426.

Biswas, Shekhar R., and Azim U. Mallik. 2011. “Species Diversity and Functional Diversity Relationship Varies with Disturbance Intensity.” *Ecosphere* 2 (4): art52. https://doi.org/10.1890/ES10-00206.1.

Burt, Jennifer W., and Jeffrey J. Clary. 2016. “Initial Disturbance Intensity Affects Recovery Rates and Successional Divergence on Abandoned Ski Slopes.” *Journal of Applied Ecology* 53 (2): 607–15. https://doi.org/10.1111/1365-2664.12584.

Catano, Christopher P., Timothy L. Dickson, and Jonathan A. Myers. 2017. “Dispersal and Neutral Sampling Mediate Contingent Effects of Disturbance on Plant Beta-Diversity: A Meta-Analysis.” *Ecology Letters* 20 (3): 347–56. https://doi.org/10.1111/ele.12733.

Chambers, Marin E., Paula J. Fornwalt, Sparkle L. Malone, and Mike A. Battaglia. 2016. “Patterns of Conifer Regeneration Following High Severity Wildfire in Ponderosa Pine – Dominated Forests of the Colorado Front Range.” *Forest Ecology and Management* 378 (October):57–67. https://doi.org/10.1016/j.foreco.2016.07.001.

Chase, Jonathan M. 2007. “Drought Mediates the Importance of Stochastic Community Assembly.” *Proceedings of the National Academy of Sciences* 104 (44): 17430–34. https://doi.org/10.1073/pnas.0704350104.

Coop, Jonathan D. 2023. “Postfire Futures in Southwestern Forests: Climate and Landscape Influences on Trajectories of Recovery and Conversion.” *Ecological Applications* 33 (1): e2725. https://doi.org/10.1002/eap.2725.

Coop, Jonathan D., Sean A. Parks, Sarah R. McClernan, and Lisa M. Holsinger. 2016. “Influences of Prior Wildfires on Vegetation Response to Subsequent Fire in a Reburned Southwestern Landscape.” *Ecological Applications* 26 (2): 346–54. https://doi.org/10.1890/15-0775.

Coop, Jonathan D, Sean A Parks, Camille S Stevens-Rumann, Shelley D Crausbay, Philip E Higuera, Matthew D Hurteau, Alan Tepley, et al. 2020. “Wildfire-Driven Forest Conversion in Western North American Landscapes.” *BioScience* 70 (8): 659–73. https://doi.org/10.1093/biosci/biaa061.

Cornelissen, J. H.C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. “A Handbook of Protocols for Standardised and Easy Measurement of Plant Functional Traits Worldwide.” *Australian Journal of Botany* 51 (4): 335–80. https://doi.org/10.1071/BT02124.

Davis, Kimberley T., Solomon Z. Dobrowski, Philip E. Higuera, Zachary A. Holden, Thomas T. Veblen, Monica T. Rother, Sean A. Parks, Anna Sala, and Marco P. Maneta. 2019. “Wildfires and Climate Change Push Low-Elevation Forests across a Critical Climate Threshold for Tree Regeneration.” *Proceedings of the National Academy of Sciences* 116 (13): 6193–98. https://doi.org/10.1073/pnas.1815107116.

De Bello, Francesco, Sébastien Lavergne, Christine N. Meynard, Jan Lepš, and Wilfried Thuiller. 2010. “The Partitioning of Diversity: Showing Theseus a Way out of the Labyrinth.” *Journal of Vegetation Science* 21 (5): 992–1000. https://doi.org/10.1111/j.1654-1103.2010.01195.x.

Etienne Laliberté, Pierre Legendre, Bill Shipley. 2014. “FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R Package Version 1.0-12.1.” https://doi.org/10.32614/CRAN.package.FD.

Falk, Donald A, Philip J van Mantgem, Jon E Keeley, Rachel M Gregg, Christopher H Guiterman, Alan J Tepley, Derek JN Young, and Laura A Marshall. 2022. “Mechanisms of Forest Resilience.” *Forest Ecology and Management* 512 (May):120129. https://doi.org/10.1016/j.foreco.2022.120129.

Garnier, E., B. Shipley, C. Roumet, and G. Laurent. 2001. “A Standardized Protocol for the Determination of Specific Leaf Area and Leaf Dry Matter Content.” *Functional Ecology* 15 (5): 688–95. https://doi.org/10.1046/j.0269-8463.2001.00563.x.

Godsoe, William, Peter J. Bellingham, and Elena Moltchanova. 2022. “Disentangling Niche Theory and Beta Diversity Change.” *The American Naturalist* 199 (4): 510–22. https://doi.org/10.1086/718592.

Grman, Emily, Chad R. Zirbel, Tyler Bassett, and Lars A. Brudvig. 2018. “Ecosystem Multifunctionality Increases with Beta Diversity in Restored Prairies.” *Oecologia* 188 (3): 837–48. https://doi.org/10.1007/s00442-018-4248-6.

Gross, Nicolas, Yoann Le Bagousse-Pinguet, Pierre Liancourt, Miguel Berdugo, Nicholas J. Gotelli, and Fernando T. Maestre. 2017. “Functional Trait Diversity Maximizes Ecosystem Multifunctionality.” *Nature Ecology & Evolution* 1 (5): 0132. https://doi.org/10.1038/s41559-017-0132.

Guiterman, Christopher H., Rachel M. Gregg, Laura A. E. Marshall, Jill J. Beckmann, Phillip J. van Mantgem, Donald A. Falk, Jon E. Keeley, et al. 2022. “Vegetation Type Conversion in the US Southwest: Frontline Observations and Management Responses.” *Fire Ecology* 18 (1): 6, s42408-022-00131-w. https://doi.org/10.1186/s42408-022-00131-w.

Haffey, Collin, Thomas D. Sisk, Craig D. Allen, Andrea E. Thode, and Ellis Q. Margolis. 2018. “Limits to Ponderosa Pine Regeneration Following Large High-Severity Forest Fires in the United States Southwest.” *Fire Ecology* 14 (1): 143–63. https://doi.org/10.4996/fireecology.140114316.

Hautier, Yann, Forest Isbell, Elizabeth T. Borer, Eric W. Seabloom, W. Stanley Harpole, Eric M. Lind, Andrew S. MacDougall, et al. 2018. “Local Loss and Spatial Homogenization of Plant Diversity Reduce Ecosystem Multifunctionality.” *Nature Ecology & Evolution* 2 (1): 50–56. https://doi.org/10.1038/s41559-017-0395-0.

Hereford, Richard. 2007. “Climate Variation at Flagstaff, Arizona -- 1950 to 2007: U.S. Geological Survey Open-File Report 2007-1410.” 2007. https://pubs.usgs.gov/of/2007/1410/.

Huxley, Jared D., Caitlin T. White, Hope C. Humphries, Soren E. Weber, and Marko J. Spasojevic. 2023. “Plant Functional Traits Are Dynamic Predictors of Ecosystem Functioning in Variable Environments.” *Journal of Ecology* 111 (12): 2597–2613. https://doi.org/10.1111/1365-2745.14197.

Isbell, Forest, Vincent Calcagno, Andy Hector, John Connolly, W. Stanley Harpole, Peter B. Reich, Michael Scherer-Lorenzen, et al. 2011. “High Plant Diversity Is Needed to Maintain Ecosystem Services.” *Nature* 477 (7363): 199–202. https://doi.org/10.1038/nature10282.

Jiang, Lin, and Shivani N. Patel. 2008. “Community Assembly in the Presence of Disturbance: A Microcosm Experiment.” *Ecology* 89 (7): 1931–40. https://doi.org/10.1890/07-1263.1.

Keeley, J. E. 2009. “Fire Intensity, Fire Severity and Burn Severity: A Brief Review and Suggested Usage.” *International Journal of Wildland Fire* 18 (1): 116–26. https://doi.org/10.1071/WF07049.

Kim, Tania N., Savannah Bartel, Bill D. Wills, Douglas A. Landis, and Claudio Gratton. 2018. “Disturbance Differentially Affects Alpha and Beta Diversity of Ants in Tallgrass Prairies.” *Ecosphere* 9 (10): e02399. https://doi.org/10.1002/ecs2.2399.

Kraft, Nathan J. B., Liza S. Comita, Jonathan M. Chase, Nathan J. Sanders, Nathan G. Swenson, Thomas O. Crist, James C. Stegen, et al. 2011. “Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients.” *Science* 333 (6050): 1755–58. https://doi.org/10.1126/science.1208584.

Laughlin, Daniel C., Jessica J. Leppert, Margaret M. Moore, and Carolyn Hull Sieg. 2010. “A Multi-Trait Test of the Leaf-Height-Seed Plant Strategy Scheme with 133 Species from a Pine Forest Flora: *The LHS Plant Strategy Scheme*.” *Functional Ecology* 24 (3): 493–501. https://doi.org/10.1111/j.1365-2435.2009.01672.x.

Maestre, Fernando T., José L. Quero, Nicholas J. Gotelli, Adriá Escudero, Victoria Ochoa, Manuel Delgado-Baquerizo, Miguel García-Gómez, et al. 2012. “Plant Species Richness and Ecosystem Multifunctionality in Global Drylands.” *Science (New York, N.Y.)* 335 (6065): 214–18. https://doi.org/10.1126/science.1215442.

Maire, Vincent, Nicolas Gross, Luca Börger, Raphaël Proulx, Christian Wirth, Laíse da Silveira Pontes, Jean-François Soussana, and Frédérique Louault. 2012. “Habitat Filtering and Niche Differentiation Jointly Explain Species Relative Abundance within Grassland Communities along Fertility and Disturbance Gradients.” *New Phytologist* 196 (2): 497–509. https://doi.org/10.1111/j.1469-8137.2012.04287.x.

Martinez Arbizu, Pedro. 2020. “pairwiseAdonis: Pairwise Multilevel Comparison Using Adonis. R Package Version 0.4.1.”

McGill, Brian J., Brian J. Enquist, Evan Weiher, and Mark Westoby. 2006. “Rebuilding Community Ecology from Functional Traits.” *Trends in Ecology & Evolution* 21 (4): 178–85. https://doi.org/10.1016/j.tree.2006.02.002.

Mori, Akira S., Saori Fujii, Ryo Kitagawa, and Dai Koide. 2015. “Null Model Approaches to Evaluating the Relative Role of Different Assembly Processes in Shaping Ecological Communities.” *Oecologia* 178 (1): 261–73. https://doi.org/10.1007/s00442-014-3170-9.

Mori, Akira S., Takashi Osono, J. Hans C. Cornelissen, Joseph Craine, and Masaki Uchida. 2017. “Biodiversity–Ecosystem Function Relationships Change through Primary Succession.” *Oikos* 126 (11): 1637–49. https://doi.org/10.1111/oik.04345.

Mueller, Stephanie E., Andrea E. Thode, Ellis Q. Margolis, Larissa L. Yocom, Jesse D. Young, and Jose M. Iniguez. 2020. “Climate Relationships with Increasing Wildfire in the Southwestern US from 1984 to 2015.” *Forest Ecology and Management* 460 (March):117861. https://doi.org/10.1016/j.foreco.2019.117861.

Myers, Jonathan A., Jonathan M. Chase, Raelene M. Crandall, and Iván Jiménez. 2015. “Disturbance Alters Beta-Diversity but Not the Relative Importance of Community Assembly Mechanisms.” *Journal of Ecology* 103 (5): 1291–99. https://doi.org/10.1111/1365-2745.12436.

National Weather Service. 2025. “NOWdata - NOAA Online Weather Data.” NOAA’s National Weather Service. 2025. https://www.weather.gov/wrh/Climate?wfo=fgz.

Noll, John, and Karen Malis-Clark. 2020. “Ask a Ranger: The Museum Fire, One Year Later, Part Two.” Arizona Daily Sun. August 20, 2020. https://azdailysun.com/news/local/enviro/ask-a-ranger-the-museum-fire-one-year-later-part-two/article\_01b01126-8aa9-5240-b942-f39effe0fecf.html.

Oksanen, Jari, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R.B. O’Hara, et al. 2022. “Vegan: Community Ecology Package. R Package Version 2.6-4.” https://doi.org/10.32614/CRAN.package.vegan.

Owen, Suzanne M., Carolyn H. Sieg, Andrew J. Sánchez Meador, Peter Z. Fulé, José M. Iniguez, L. Scott Baggett, Paula J. Fornwalt, and Michael A. Battaglia. 2017. “Spatial Patterns of Ponderosa Pine Regeneration in High-Severity Burn Patches.” *Forest Ecology and Management* 405 (December):134–49. https://doi.org/10.1016/j.foreco.2017.09.005.

Parsons, Annette, Peter R. Robichaud, Sarah A. Lewis, Carolyn Napper, and Jess T. Clark. 2010. “Field Guide for Mapping Post-Fire Soil Burn Severity.” *Gen. Tech. Rep. RMRS-GTR-243. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 49 p.* 243. https://doi.org/10.2737/RMRS-GTR-243.

Pasari, Jae R., Taal Levi, Erika S. Zavaleta, and David Tilman. 2013. “Several Scales of Biodiversity Affect Ecosystem Multifunctionality.” *Proceedings of the National Academy of Sciences* 110 (25): 10219–22. https://doi.org/10.1073/pnas.1220333110.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. “New Handbook for Standardised Measurement of Plant Functional Traits Worldwide.” https://doi.org/10.1071/BT12225.

Petchey, Owen L., and Kevin J. Gaston. 2002. “Functional Diversity (FD), Species Richness and Community Composition.” *Ecology Letters* 5 (3): 402–11. https://doi.org/10.1046/j.1461-0248.2002.00339.x.

Seidl, Rupert, Dominik Thom, Markus Kautz, Dario Martin-Benito, Mikko Peltoniemi, Giorgio Vacchiano, Jan Wild, et al. 2017. “Forest Disturbances under Climate Change.” *Nature Climate Change* 7 (6): 395–402. https://doi.org/10.1038/nclimate3303.

Taber, Ethan M., and Rachel M. Mitchell. 2023. “Rapid Changes in Functional Trait Expression and Decomposition Following High Severity Fire and Experimental Warming.” *Forest Ecology and Management* 541 (August):121019. https://doi.org/10.1016/j.foreco.2023.121019.

———. 2024. “Experimental Warming Has Limited Impacts on Post-Fire Succession across a Burn Severity Gradient.” *Journal of Vegetation Science* 35 (2): e13248. https://doi.org/10.1111/jvs.13248.

Tatsumi, Shinichi, Joachim Strengbom, Mihails Čugunovs, and Jari Kouki. 2020. “Partitioning the Colonization and Extinction Components of Beta Diversity across Disturbance Gradients.” *Ecology* 101 (12): e03183. https://doi.org/10.1002/ecy.3183.

Torres, Iván, Antonio Parra, and José M. Moreno. 2022. “Effects of Spatial Distance and Woody Plant Cover on Beta Diversity Point to Dispersal Limitation as a Driver of Community Assembly during Postfire Succession in a Mediterranean Shrubland.” *Ecology and Evolution* 12 (7): e9130. https://doi.org/10.1002/ece3.9130.

Turner, Monica G. 2010. “Disturbance and Landscape Dynamics in a Changing World.” *Ecology* 91 (10): 2833–49. https://doi.org/10.1890/10-0097.1.

Vellend, Mark, Kris Verheyen, Kathryn M. Flinn, Hans Jacquemyn, Annette Kolb, Hans Van Calster, George Peterken, et al. 2007. “Homogenization of Forest Plant Communities and Weakening of Species–Environment Relationships via Agricultural Land Use.” *Journal of Ecology* 95 (3): 565–73. https://doi.org/10.1111/j.1365-2745.2007.01233.x.

Villéger, Sébastien, Julia Ramos Miranda, Domingo Flores Hernandez, and David Mouillot. 2012. “Low Functional β-Diversity Despite High Taxonomic β-Diversity among Tropical Estuarine Fish Communities.” *PLOS ONE* 7 (7): e40679. https://doi.org/10.1371/journal.pone.0040679.

Zavaleta, Erika S., Jae R. Pasari, Kristin B. Hulvey, and G. David Tilman. 2010. “Sustaining Multiple Ecosystem Functions in Grassland Communities Requires Higher Biodiversity.” *Proceedings of the National Academy of Sciences* 107 (4): 1443–46. https://doi.org/10.1073/pnas.0906829107.

Table 1.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Response** | **Effect** | **Estimate** | **SE** | **t** | ***p*** | **R2** | **Adj. R2** |
| Taxonomic β-deviation | (Intercept) | -49.115 | 0.604 | -81.324 | **<0.0001** | 0.939 | 0.939 |
| year | 24.657 | 0.924 | 26.695 | **<0.0001** |  |  |
| severityL | -54.862 | 0.854 | -64.233 | **<0.0001** |  |  |
| severityH | 147.243 | 0.854 | 172.393 | **<0.0001** |  |  |
| year2 | -6.599 | 0.408 | -16.171 | **<0.0001** |  |  |
| year:severityL | 84.582 | 1.306 | 64.752 | **<0.0001** |  |  |
| year:severityH | -198.732 | 1.306 | -152.139 | **<0.0001** |  |  |
| year:year2 | 0.532 | 0.054 | 9.814 | **<0.0001** |  |  |
| severityL:year2 | -32.594 | 0.577 | -56.480 | **<0.0001** |  |  |
| severityH:year2 | 77.227 | 0.577 | 133.820 | **<0.0001** |  |  |
| year:severityL:year2 | 3.935 | 0.077 | 51.343 | **<0.0001** |  |  |
| year:severityH:year2 | -9.122 | 0.077 | -119.029 | **<0.0001** |  |  |
| Functional β-deviation | (Intercept) | 2.497 | 0.346 | 7.206 | **<0.0001** | 0.674 | 0.674 |
| year | -5.699 | 0.530 | -10.754 | **<0.0001** |  |  |
| severityL | -18.966 | 0.490 | -38.706 | **<0.0001** |  |  |
| severityH | 8.440 | 0.490 | 17.226 | **<0.0001** |  |  |
| year2 | 2.969 | 0.234 | 12.682 | **<0.0001** |  |  |
| year:severityL | 28.408 | 0.749 | 37.909 | **<0.0001** |  |  |
| year:severityH | -10.652 | 0.749 | -14.215 | **<0.0001** |  |  |
| year:year2 | -0.458 | 0.031 | -14.723 | **<0.0001** |  |  |
| severityL:year2 | -10.933 | 0.331 | -33.022 | **<0.0001** |  |  |
| severityH:year2 | 4.477 | 0.331 | 13.524 | **<0.0001** |  |  |
| year:severityL:year2 | 1.291 | 0.044 | 29.364 | **<0.0001** |  |  |
| year:severityH:year2 | -0.495 | 0.044 | -11.250 | **<0.0001** |  |  |

Table 2.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Severity** | **Year since fire** | **Slope** | **R2** | **Adj. R2** | ***p*** |
| Unburned | 1 | 0.599 | 0.619 | 0.592 | **0.0003** |
| 2 | 0.466 | 0.680 | 0.659 | **<0.0001** |
| 3 | 0.389 | 0.435 | 0.399 | **0.0029** |
| 4 | 0.431 | 0.519 | 0.491 | **0.0005** |
| Low | 1 | 0.829 | 0.193 | 0.135 | 0.0887 |
| 2 | 0.291 | 0.120 | 0.071 | 0.1354 |
| 3 | 0.157 | 0.041 | -0.018 | 0.4178 |
| 4 | 0.082 | 0.049 | -0.019 | 0.4103 |
| High | 1 | -0.017 | 0.001 | -0.124 | 0.9328 |
| 2 | 0.142 | 0.021 | -0.041 | 0.5697 |
| 3 | 0.203 | 0.054 | -0.005 | 0.3516 |
| 4 | -0.257 | 0.040 | -0.017 | 0.4126 |