Increasing Fire Severity decouples the relationship between taxonomic and functional diversity

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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). Plant traits mechanistically link taxonomic diversity to ecosystem function, as a greater variety of traits is expected to generate higher levels of ecosystem function. Key to this expectation is the assumption that as taxonomic diversity increases, functional diversity must also increase. Disturbance regimes, which act on plant functional traits to influence taxonomic diversity (TD), 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), and the intermediate disturbance hypothesis (IDH) suggests that intermediate levels of disturbance may lead to greater taxonomic (and thus functional) diversity compared to more or less frequent or intense disturbance (Richter et al. 2019; Connell 1978). The IDH 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. Whether taxonomic (TD) and functional (FD) diversity respond concomitantly to disturbance, and whether this relationship differs across a disturbance severity gradient is poorly understood. Here, we address this critical knowledge gap by quantifying the relationship between TD and FD over 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 regeneration of 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). In dry western conifer forests, the understory plant community holds the bulk of biodiversity and contributes significantly to multiple ecosystem functions. Furthermore, the generally shorter life-spans of understory species are likely to more rapidly reveal changes in assembly mechanisms (Coop 2023; Taber and Mitchell 2023; 2024)

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 TD and FD recover in tandem, which would support the idea that biodiversity-supported ecosystem functions will also 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 TD and FD across a fire-severity gradient and over time offers valuable mechanistic insights into how atypically severe wildfires are altering trajectories of community assembly with consequences for ecosystem function.

Atypical disturbance and altered assembly mechanisms can have consequences that extend beyond the relationship between FD and TD; strong environmental filtering during assembly may homogenize communities over space and time. 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, 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. Currently, 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 difficult to explore. 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. For example, 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 (Lavorel and Garnier 2002; Dı́az and Cabido 2001), understanding whether and how TD and FD recover temporally after disturbance is critically important. Theory predicts that TD and FD are coupled (Petchey and Gaston 2002) and thus should respond in tandem to drivers such as disturbance. However, observational studies have found that TD and FD do not necessarily assemble in tandem. For example, Baker et al. (2021) found that changes in FD of benthic macroinvertebrates lagged behind TD 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 TD and FD may be mediated by disturbance. Disturbance is expected to alter species assemblages through processes of habitat filtering and niche differentiation (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 TD and FD in a boreal forest and attributed this result to the differential filtering of competitive, generalist, and disturbance-tolerant species along the disturbance gradient.

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 TD and FD 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) high-severity fire will differentially alter the trajectory of assembly processes, driving a decrease in beta diversity over time compared to no fire and low-severity fire;

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 2025.

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 (Appendix).

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 (n = 33 species). Where trait values could not be found for a given species, values of close congeners were used when available (n = 5 species). 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 the observed plant family (n = 6 species) See Appendix for the detailed trait table.

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 TD and FD, 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). 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; Appendix). 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 increasing FRed, as species similarity increases as species are added within plots. 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 FD. We consider TD and FD 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; Oksanen et al. 2022). 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

Effect of fire severity on beta diversity

Taxonomic β-deviations were non-linear and 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 also non-linear, but were closer to zero than the taxonomic β-deviations and ranged from negative to positive. This indicates that, given α and γ, the FD across plots was closer to random than TD, but we observed both homogeneity and heterogeneity of FD across plots. Our quadratic regressions revealed that fire severity had a significant effect on the trajectories of functional β-deviations, as well (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 TD, 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

The slope of the line between standardized species richness and Q varied with burn severity and year (Fig. 2, Table 2). Coupling of TD and FD was only observed in the unburned plots, where the slopes were positive, relatively steep, relatively stable through time, and significantly correlated. In the low-severity plots, the slopes were positive, but varied in steepness through time, and were not significantly correlated; FRed was the lowest in year 1 and then increased each year as the slopes became less steep. In the high-severity plots, the slopes varied in both steepness and direction and were not significantly correlated; FRed was high in year 1, decreased in years 2 and 3, and increased again in year 4.

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). For the unburned, low-severity, and high-severity plots, mean species richness was 4.10 (SD=1.71), 4.83 (SD=2.75), and 5.11 (SD=1.24), while mean Q was 0.069 (SD=0.072), 0.144 (SD=0.087), 0.283 (SD=0.124), respectively.

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).

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

DISCUSSION

Disturbance regimes are changing globally, with uncertain consequences for the assembly and functioning of ecological communities (Turner 2010; Seidl et al. 2017; Mueller et al. 2020; Altman et al. 2024). Wildfire regimes, in particular, have experienced wide deviations from historic norms from the complete exclusion of wildfire to catastrophic wildfires of high-severity (Parks and Abatzoglou 2020; Falk et al. 2022). Our results suggest that high severity fire alters community assembly processes in forest understories, decoupling functional and taxonomic diversity and leading to functionally and taxonomically distinct communities relative to undisturbed or lightly disturbed areas.

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 partially 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 greater 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. Contrary to our first prediction, however, the trajectory of beta diversity following high-severity fire was not distinctly negative. The taxonomic β-deviations for the high-severity plots were parabolic such that beta diversity decreased from year 1 to year 2 but increased from year 2 to year 4. The functional β-deviations for the high-severity plots were only weakly parabolic and, unexpectedly, showed a nearly monotonic increase in beta diversity from year 1 to year 4.

While the taxonomic β-deviations of all fire severities were strongly negative, indicating non-random homogeneity of species across plots and within fire severities, 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 with, at times, strong temporal fluctuations. We attribute this to the relatively low species diversity of this ecosystem, such that small changes in species turnover that drive low taxonomic beta diversity result in comparatively large changes in functional turnover that drive high functional beta diversity. This difference between taxonomic and functional β-deviations indicates that different assembly mechanisms are each acting on TD and FD. Indeed, Marcacci et al. (2021) and Wu et al. (2022) both found that that species turnover drives taxonomic beta diversity while nestedness drives functional beta diversity in farmland birds along an urbanization gradient and in riverine diatoms, respectively, consistent with our observation that TD and FD are assembling by separate mechanisms. However, while we found that functional beta diversity was greater than taxonomic beta diversity, this result is not consistent with beta diversity patterns in other systems. Villéger et al. (2012; 2013), Wang et al. (2021), and Wu et al. (2022) all found that taxonomic beta diversity was higher than functional beta diversity in estuarine fish communities, riverine macroinvertebrate metacommunities, and riverine diatom communities, respectively.

Functional beta diversity was much more stable than taxonomic beta diversity through time. Taxonomic β-deviations displayed large changes between years, with a maximum change of 23 standard deviations in the low-severity plots from year 1 to year 2 (Fig. 1a), while the change in functional β-deviations for the same plots across the same time step was 4.65 standard deviations (Fig. 1b). Although the direction of change in beta diversity from year to year is similar between TD and FD, they do not necessarily change together. Kramer (2025) found a similar pattern in tropical tree communities, where temporal changes in taxonomic beta diversity were more pronounced than functional beta diversity. Dig deeper. Why?

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. Therefore, we can see that a single state of a community may be less important than the trajectory by which it arrived there.

Coupling of taxonomic and functional diversity

We predicted that high-severity fire would decouple TD and FD due to the strength of environmental filtering in high-severity burn areas selecting against sensitive trait syndromes. While TD and FD were strongly coupled in our unburned plots, TD and FD were decoupled by both low-severity and high-severity fire (Fig. 2, Table 2), in partial agreement with our prediction. Where TD and FD were coupled in the unburned plots, FRed was low, meaning accumulating species were functionally distinct. We observed increasing FRed through time in the low-severity plots and an unstable pattern of FRed in the high-severity plots.

Our measurements of FRed, combined with our measurements of FD and β-deviations, suggest that fire severity affected the importance of habitat filtering (Keddy 1992) and niche differentiation (MacArthur and Levins 1967). In the unburned plots, low maximum FD compared to the other severity classes indicates that habitat filtering limited the total number functional syndromes that were able to colonize the unburned plots. The low FRed in the unburned plots indicates that, among the functional groups that were able to colonize the unburned plots, these functional groups were distinct, suggesting that niche differentiation is limiting the similarity of species (Fig. 2a; Mouillot, Dumay, and Tomasini 2007). However, the near-random β-deviations in the unburned plots indicate that this habitat filtering acted more strongly at the community-level than at the plot-level (Fig 1b); habitat filtering was working at the community level, but niche differentiation was working at the plot level.

In the high-severity plots, we see a shift in the strength of these mechanisms. High FRed indicates that within-plot habitat filtering was dominant, rather than niche differentiation, because species within plots are functionally similar. Increasing spatial heterogeneity of FD through time (Fig. 1b) suggests that the habitat filtering that was driving high FRed is variable from plot to plot. In other words, habitat filtering was weak at the community-level in the high-severity plots, allowing for a greater range of FD than the unburned plots, but was strong and variable at the plot-level, driving the variable convergence of traits within plots. In the low-severity plots, we see intermediate levels of habitat filtering and niche differentiation.

Community outcomes

Four years after fire, the high-severity plots had distinct taxonomic and functional composition, while the unburned and low-severity plots were not significantly different, which is consistent with our third prediction. Other studies have also observed that disturbance can alter the composition of ecological communities. Dixon et al. (2024) found that repeated soil disturbance altered the composition of a pine savanna community more than a single disturbance. Carnell and Keough (2020) found that high disturbance severity in a kelp forest resulted in a compositional shift toward a sea urchin barren. Whether these shifts will lead to long-term changes in composition and structure, leading to ecosystem type conversion (Singleton et al. 2021; Coop et al. 2020; Falk et al. 2022), is unclear.

CONCLUSIONS

As disturbance regimes deviate from historical norms, the mechanisms and outcomes of ecosystem recovery are at risk of being altered. We have demonstrated that the trajectory of community assembly and the coupling of TD and FD were altered following an unusually intense disturbance, which has important implications for the maintenance of biodiversity and the stability of ecosystem function over time. It has been assumed that the recovery of TD implies the recovery of ecosystem function via FD (Isbell et al. 2011; Zavaleta et al. 2010). However, our findings suggest that the recovery of TD does not guarantee the recovery of FD and reliant ecosystem functions. This is particularly important for resource management. Resource managers may be faced with deciding whether the current state of ecological resources are a feasible management objective in the face of severe disturbance (Schuurman et al. 2020).

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Table 1. Results of multiple quadratic regression analyses on taxonomic and functional β-deviations.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **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. Results of linear regression analyses of Rao’s quadratic entropy (Q) and species richness normalized between 0 and 1.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **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 |

Figure 1. Trajectories of (a) taxonomic β-deviations and (b) functional β-deviations by burn severity for the first four years after fire, measured using multiple quadratic regressions. Taxonomic β-deviations are calculated using Bray-Curtis dissimilarity and functional β-deviations are calculated using an additive partition of Rao’s quadratic entropy. Error bars represent standard deviation.

Figure 2. Regression analysis of Rao’s quadratic entropy (Q) in response to normalized species richness for four years after fire across a burn severity gradient: (a) unburned, (b) low-severity, and (c) high-severity.

Figure 3. Non-metric multidimensional scaling (NMDS) ordination plots across the burn severity gradient. Community composition is measured using (a) taxonomic diversity and (b) functional diversity. Ellipses represent 95% confidence intervals. Open circles represent plots. Closed symbols represent group centroids. Only the high-severity group is significantly different according to PERMANOVA.