Processes of deterministic community assembly change as fire severity increases

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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, 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. 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 beta diversity. 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. Disturbance may mediate the relationship of taxonomic and functional diversity. Disturbance is expected to alter species assemblages through processes of environmental filtering and species interactions (Maire et al. 2012); but, importantly, these responses 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) 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. 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 using the slope between species richness and Q across the burn severity gradient for all four years of the study (Baker et al. 2021). To make the slope more interpretable, species richness was standardized between 0 and 1 to place it on the same scale as Q.

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

Effect of fire severity on beta diversity

Fire severity had a significant effect on the trajectories of taxonomic β-deviations (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. Although the β-deviation trajectories for the unburned and low-severity plots were significantly different from each other, they had a similar shape and direction; both increased from year 1 to year 3, peaked in year 3, and began to decline in year 4. The β-deviation trajectory for the high-severity plots had a unique shape and direction, decreasing from year 1 to year 2 and then increasing from year 2 to year 4.

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. As with the taxonomic β-deviations, the unburned and low-severity plots had a similar shape and direction; both increased from year 1 to year 2, peaked in years 2 and 3, and were decreasing by year 4. The functional β-deviations for high-severity plots had a positive trajectory for all four years.

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). In the unburned plots, 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, adj. *p* < 0.001; functional: F[1] = 15.03, R2 = 0.29, adj. *p* < 0.001) and low-severity plots (taxonomic: F[1] = 4.44, R2 = 0.11, adj. *p* < 0.001; functional: F[1] = 6.67, R2 = 0.16, adj. *p* = 0.009), while the unburned and low-severity plots were not different from each other (taxonomic: F[1] = 2.04, R2 = 0.05, adj. *p* = 0.064; functional: F[1] = 1.05, R2 = 0.03, adj. *p* = 0.983).

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

Some sort of mirroring of the results/introduction. Talk about changing fire regimes. Implications for management.

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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** | **Years 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 |