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Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms

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Summary

1. Ecological disturbances are often hypothesized to alter community assembly processes that influence variation in community composition (β -diversity). Disturbance can cause convergence in community composition (low β -diversity) by increasing niche selection of disturbance-tolerant species. Alternatively, disturbance can cause divergence in community composition (high β -diversity) by increasing habitat filtering across environmental gradients. However, because disturbance may also influence β -diversity through random sampling effects owing to changes in the number of individuals in local communities (community size) or abundances in the regional species pool, observed patterns of β -diversity alone cannot be used to unambiguously discern the relative importance of community assembly mechanisms.

2. We compared β -diversity of woody plants and inferred assembly mechanisms among unburned forests and forests managed with prescribed fires in the Missouri Ozarks, USA. Using a null-model approach, we compared how environmental gradients influenced β -diversity after controlling for differences in local community size and regional species abundances between unburned and burned landscapes.

3. Observed β -diversity was higher in burned landscapes. However, this pattern disappeared or reversed after controlling for smaller community size in burned landscapes.

4. β -diversity was higher than expected by chance in both landscapes, indicating an important role for processes that create clumped species distributions. Moreover, fire appeared to decrease clumping of species at broader spatial scales, suggesting homogenization of community composition through niche selection of disturbance-tolerant species. Environmental variables, however, explained similar amounts of variation in β -diversity in both landscapes, suggesting that disturbance did not alter the relative importance of habitat filtering.

5. Our results indicate that contingent responses of communities to fire reflect a combination of fire-induced changes in local community size and scale-dependent effects of fire on species clumping across landscapes.

6. Synthesis. Although niche-based mechanisms of community assembly are often invoked to explain changes in community composition following disturbance, our results suggest that these changes also arise through random sampling effects owing to the influence of disturbance on community size. Comparative studies of these processes across disturbed ecosystems will provide important insights into the ecological conditions that determine when disturbance alters the interplay of deterministic and stochastic processes in natural and human-modified landscapes.

Key-words: community composition, community size, determinants of plant community diversity and structure, ecological drift, environmental filtering, niche-based community assembly, Ozarks, prescribed fire, restoration ecology, temperate oak–hickory forest

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Introduction

Community assembly is hypothesized to reflect the interplay of dispersal from a regional species pool, environmental filtering, local biotic interactions and ecological drift (Hubbell 2001; Vellend 2010; Chase & Myers 2011; HilleRisLambers *et al.* 2012). To test the relative importance of these mechanisms, ecologists often examine how environmental filters such as disturbance alter variation in community composition (β -diversity). However, the mechanisms by which disturbance influences patterns of β -diversity are not yet generalizable. Depending on how disturbance modifies environmental conditions and colonization from the species pool, it could alter β -diversity through either environmental filtering or stochastic colonization and extinction processes that create ecological drift (e.g. Chase 2007; Vellend *et al.* 2007; Jiang & Patel 2008; Belote, Sanders & Jones 2009; Myers & Harms 2011; Tonkin & Death 2013; Vanschoenwinkel, Buschke & Brendonck 2013). A richer understanding of the mechanisms by which disturbance alters β -diversity would not only help advance community assembly theory, but also our knowledge of how to preserve and restore biodiversity in human-modified ecosystems.

Disturbance may alter β -diversity by changing the relative importance of community assembly mechanisms that influence spatial aggregation (clumping) of species across landscapes. One popular way to assess the importance of clumping processes is to partition variation in β -diversity into components explained by environmental and spatial gradients (e.g. Cottenie 2005; Legendre *et al.* 2009). However, most metrics of β -diversity that are used to quantify the relative importance of environmental and spatial processes are also strongly influenced by three other factors: local densities of individuals (community size), the relative abundances of species and the size of the species pool (McGill 2010; Chase & Myers 2011; Kraft *et al.* 2011; Chase & Knight 2013). In particular, because β -diversity is linked to α - and γ -diversity (e.g. $\beta = \gamma/\alpha$; Whittaker 1972), any process that changes α -diversity – such as changes in community size or the species abundance distribution – will alter β -diversity when the species pool (γ -diversity) remains relatively unchanged (Anderson *et al.* 2011; Chase & Myers 2011; Chase *et al.* 2011). Likewise, changes in the species pool (γ -diversity) can potentially alter β -diversity in the absence of disturbance-generated changes in environmental and spatial processes. To disentangle the clumping component of β -diversity from variation in community size and species pools, a null model can be used to simulate the β -diversity that would be expected in the absence of processes that cause clumping of species across the landscape (e.g. Kraft *et al.* 2011). The deviations from the null model (β -deviations) can then be partitioned across environmental and spatial gradients, thereby lending insight into potential mechanisms of community assembly (Myers *et al.* 2013).

Here, we use this framework to test the hypothesis that disturbance alters β -diversity through random sampling effects owing to changes in local community size and regional species

abundances. This hypothesis makes predictions about the effects of disturbance on observed patterns of β -diversity, β -deviations, and correlations between β -deviations, environmental variables and spatial variables. For example, disturbance could increase observed β -diversity if it decreases α -diversity by reducing community size (Orrock & Fletcher 2005; Orrock & Watling 2010) or species evenness (McGill 2010; Chase & Knight 2013) at random with respect to species identity. If disturbance simply changes α -diversity by altering community size or species abundances rather than clumping of species across landscapes, then β -deviations and their relationships with environmental and spatial variables should not differ between disturbed and undisturbed landscapes. In contrast, disturbance may influence clumping of species in two opposing ways. First, disturbance may increase clumping through divergent niche selection of species across environmental gradients, resulting in habitat filtering. Fire, for example, may increase clumping of fire-intolerant species in particular habitats (Pausas & Verdú 2008; Crandall & Platt 2012), resulting in narrow habitat breadths of species across environmental gradients. In this case, disturbance should increase β -deviations and lead to stronger correlations between β -deviations and environmental gradients in disturbed relative to undisturbed landscapes. Similarly, disturbance may increase clumping through dispersal limitation if species become rare in post-disturbance landscapes (Hurt & Pacala 1995). This should lead to stronger correlations between β -deviations and spatial gradients in disturbed relative to undisturbed landscapes. Secondly, disturbance may decrease clumping through convergent niche selection of disturbance-tolerant species, resulting in homogenization of community composition (e.g. Chase 2007; Vellend *et al.* 2007). In this case, disturbance may decrease β -deviations and lead to weaker correlations between β -deviations and environmental gradients in disturbed relative to undisturbed landscapes. To the extent that disturbance changes β -deviations across environmental gradients, this would suggest an important role for ecological mechanisms other than changes in community size or species abundances as drivers of β -diversity.

We compared β -diversity and inferred assembly mechanisms within disturbed and undisturbed landscapes using an unintended experiment in the Ozark ecoregion of Missouri, USA. Historically, fires played an important role in the Ozarks by maintaining oak savannas rich in herbaceous plant diversity (Nelson 2012), but as in many other parts of the world, human suppression of fires has resulted in landscapes dominated by closed-canopy forests. Consequently, prescribed fires have become an important tool used by land managers to restore Ozark ecosystems to more historical conditions. A typical assumption among land managers and naturalists is that tree communities in unburned landscapes are more homogeneous (lower β -diversity) because many species of fire-intolerant trees increase their habitat breadth in the absence of fire (Batek *et al.* 1999; Nelson 2012). In the parlance of community assembly theory, this would imply that the relative importance of habitat filtering increases with fire. However, fire could also increase β -diversity by decreasing community size or species evenness in the regional species pool. To test

this hypothesis, we compared patterns of observed woody plant β -diversity and β -deviations among fire-managed forests and unburned forests with similar edaphic and topographic gradients after controlling for differences in community size and the species abundance distribution between landscapes.

Materials and methods

TREE COMMUNITY SAMPLING IN UNBURNED AND BURNED LANDSCAPES

From May to June 2012, we sampled 93 forest plots across two large state parks located in the central Ozark region of Missouri, USA: Ha Ha Tonka State Park (37°58' N, 92°45' W; c. 1500 ha) and Lake of the Ozarks State Park (38°05' N, 92°35' W; c. 7000 ha). In both parks, managers have been using prescribed fires to restore oak–hickory forests to historical conditions for approximately 30 years. For this study, we sampled relatively large burn units (c. 40–260 ha) that have been burned at a frequent interval of 3–5 fires per decade since 1998 (mean = 4 fires per decade). All of the burn units contained a well-developed understorey plant community (dominated by grasses and forbs) and overstorey tree community (dominated by larger diameter size classes) that is typical of frequently burned forests in the region, indicating that our study sites have been restored to a similar degree. Many of the burn units are located adjacent to large, environmentally similar areas that have remained unburned over the same time period. We selected three pairs of sites containing burn units and nearby unburned controls: one in the northern section of Lake of the Ozarks, one in the southern section of Lake of the Ozarks and one in the southern section of Ha Ha Tonka (see Fig. S1 in Supporting Information). The three sites had similar overall species composition and within-site β -diversity (see Fig. S2). In each site, we recorded the abundance of all woody plant species ≥ 2 cm in diameter at breast height (excluding lianas) in 10 × 50 m plots distributed across a wide but similar range of environmental conditions in unburned and burned landscapes. In each landscape, we sampled 10–12 plots in

each of four contrasting habitat types (east-facing slopes, west-facing slopes, ridges and valleys; $N = 46$ total plots in unburned landscapes; $N = 47$ total plots in burned landscapes) that have been shown to strongly influence β -diversity in other unburned forests in the region (Myers *et al.* 2013).

ENVIRONMENTAL AND SPATIAL GRADIENTS

To compare the relative importance of environmental and spatial factors between unburned and burned landscapes, we sampled plots across similar geographic distances (mean = 12.2 and 11.7 km, range = 0.01–25.9 and 0.03–26.4 km for unburned and burned landscapes, respectively) and selected plot locations to minimize correlations between environmental conditions and geographic distances (see Fig. S3). We quantified environmental conditions of each plot using 13 soil variables and four topographic variables (Table 1). Soil variables were measured from a composite sample of five, 10-cm soil cores collected every 5 m on alternating sides of the plot centreline using a 2.5-cm-diameter, open-end soil probe (AMS Inc., American Falls, ID, USA). Samples were analysed for available cations (Ca, K, Mg), cation-exchange capacity, exchangeable acidity, organic material, particle size (clay, sand, silt), nitrogen (ammonium, nitrate), pH and phosphorus at the Soil and Plant Testing Laboratory at the University of Missouri, Columbia, Missouri. Topographic variables included aspect (eastern aspect and northern aspect), mean elevation and slope obtained from field measurements or a geographic information system.

NULL-MODEL AND STATISTICAL ANALYSES

We tested our predictions using a three-tiered approach. First, we measured observed β -diversity as the dissimilarity between each pair of plots within each burn type using both an abundance-based (Bray–Curtis) and an incidence-based (Jaccard) metric. Secondly, we used a null model to simulate the compositional dissimilarity that would be expected in the absence of processes that cause clumping of species within each landscape (expected β -diversity). In the null model, individuals were distributed at random, while holding the number of

Table 1. Significance of environmental and spatial variables used in the distance-based redundancy analyses of observed β -diversity (β -obs) and β -deviations (β -dev) of Bray–Curtis dissimilarities in unburned and burned forests. Environmental variables were modelled using axes derived from principal components (PC). For each PC, the three variables that correlated most strongly are listed in decreasing order of the strength of the correlation. P -values are shown for significant variables retained after forward model selection

Unburned forests			Burned forests		
Variables*	β -obs	β -dev	Variables*	β -obs	β -dev
Environment			Environment		
PC1: Ca, Mg, pH	0.005	0.005	PC1: Ca, Mg, pH	0.005	0.005
PC2: CEC, Clay, N. acidity	0.013	0.015	PC2: Clay, P, NH ₄	0.005	0.005
PC4: Slope, P, NH ₄	0.010	0.005	PC3: P, Slope, Sand	0.005	0.005
PC5: Aspect, K, CEC	0.016	0.015	PC4: Elev, Slope, NH ₄	0.005	0.005
PC6: NH ₄ , Slope, K	0.005	0.010	PC5: Aspect, NH ₄ , Elev	0.010	0.010
PC7: Elev, Aspect, P	0.015	0.005	PC8: K, NO ₃ , Sand	0.025	0.042
PC8: Clay, CEC, Org. Matt.	0.005	0.005	PC11: NO ₃ , Sand, Slope	–	0.043
PC10: NO ₃ , K, Elev	–	0.010	PC12: Mg, Silt, CEC	0.015	0.020
			PC14: Mg, Ca, Clay	0.015	0.015
Space			Space		
Longitude	0.015	0.010	Longitude	0.005	0.005

*Variable descriptions: Aspect = plot aspect (radians), Ca = soil calcium (mg kg⁻¹), CEC = soil cation-exchange capacity (meq per 100 g), Clay = soil clay (%), Elev = plot elevation (m), K = soil potassium (mg kg⁻¹), Mg = soil magnesium (mg kg⁻¹), N. acidity = soil neutralizable acidity (meq per 100 g), NH₄ = soil ammonium (ppm), NO₃ = soil nitrate (ppm), Org. Matt. = soil organic matter (%), P = soil phosphorus (Bray-I phosphorus; mg kg⁻¹), pH = soil pH (1–14), Sand = soil sand (%), Silt = soil silt (%), slope = plot slope (degrees).

individuals in each plot and the total regional abundance of each species constant within the two burn types. We then calculated a standardized effect size (β -deviation) as the difference between the observed and mean expected dissimilarities from 2000 iterations of the null model, divided by the standard deviation of expected values (Kraft *et al.* 2011; Myers *et al.* 2013). We tested for differences in β -diversity using nonparametric analysis of variance based on distance-to-centroid values (Anderson *et al.* 2011). We also tested for differences in mean numbers of individuals per plot (community size) and mean species richness per plot (α -diversity) using linear mixed-effects models with burn type (unburned, burned) as a fixed effect and sites as random effects. Species accumulation curves were similar for both landscapes (see Fig. S4), indicating that the size of the plots did not strongly influence observed differences in local diversity.

Thirdly, we compared the degree to which patterns of observed β -diversity and β -deviations were explained by environmental and spatial variables using distance-based redundancy analysis (dbRDA). To account for collinearity among environmental variables, we performed a principal component analysis (PCA) on the 17 environmental variables measured in both unburned and burned landscapes and used PCA axes as explanatory variables. Our initial set of spatial variables included plot geographic coordinates (latitude and longitude) and spatial eigenfunctions with positive eigenvalues (positive spatial autocorrelation) obtained from principal coordinates of neighbour matrices (Borcard *et al.* 2004; Legendre *et al.* 2009). For unburned plots, there was one spatial eigenvector with a positive eigenvalue and it was highly correlated with geographic coordinates (Pearson's $r = 0.93$ – 0.99). For burned plots, there were two spatial eigenvectors with positive eigenvalues, one of which was highly correlated with geographic coordinates (Pearson's $r = 0.91$ – 0.98). In addition, latitude and longitude were highly correlated for both unburned and burned plots (Pearson's $r = 0.96$). To avoid redundant spatial variables, we therefore only included two spatial variables in the dbRDA for burned plots (longitude and one spatial eigenvector) and one spatial variable in the dbRDA for unburned plots (longitude). Secondly, because the response variable in dbRDA represents a distance and cannot be negative, we added the value of the smallest β -deviation to all β -deviations to make them non-negative. Thirdly, to avoid overestimation of the explained variance, we performed forward model selection to obtain significant explanatory variables (Blanchet, Legendre & Borcard 2008). Forward model selection resulted in eight and nine significant environmental PCA axes for unburned and burned forests, respectively (Table 1). These variables were then used to partition variation in observed β -diversity and β -deviations into individual fractions explained by environmental, spatial and spatially structured environmental variables. We tested for differences between burned and unburned landscapes in the fractions explained by environmental and spatial variables using bootstrap tests based on 999 iterations (Peres-Neto *et al.* 2006). For all models, we report results based on adjusted R^2 values. We obtained similar results for both metrics of β -diversity and therefore present results for the Jaccard metric in the Supporting Information (see Figs S5 and S6).

Finally, we compared relationships between β -diversity (observed β -diversity and β -deviations) and geographic distance among pairs of plots within unburned and burned landscapes using multiple regression on distance matrices (Lichstein 2007). These regressions included Bray–Curtis dissimilarity as a dependent variable, and geographic distance, burn type (unburned or burned) and the interaction between geographic distance and burn type as independent variables. We evaluated the significance of the regression coefficients using 2000 permutations of the response variable (Lichstein 2007). All analyses were performed using R (R Development Core Team 2013).

Results

COMMUNITY SIZE, SPECIES RICHNESS AND ABUNDANCE

Overall, our results supported the hypothesis that prescribed fires influence community structure mainly through effects on local community size (numbers of individuals). Fires influenced community structure at both local and regional spatial scales. Burned landscapes contained approximately half the number of individuals as unburned landscapes at local scales (mean = 28 and 52 stems per plot, respectively; ANOVA: d.f. = 89, $F = 73.4$, $P < 0.0001$; Fig. 1a,d) and regional scales (1335 and 2423 total stems, respectively). Burned landscapes also had significantly lower α -diversity than unburned landscapes (mean = 6.2 and 9.5 species per plot, respectively; d.f. = 89, $F = 26.9$, $P < 0.0001$; Fig. 1b,e). In contrast, the overall shape of the species abundance distribution did not differ significantly between landscapes (Fig. 1c,f; Kolmogorov–Smirnov test: $P = 0.6094$). However, burned landscapes contained more rare species (e.g. 14 vs. 10 species with ≤ 8 total stems, respectively) and fewer common species (e.g. 1 vs. 5 species with ≥ 130 total stems, respectively) (Fig. 1c,f; see Table S1). For example, 28 species (73%) had higher total numbers of individuals, seven species had twice as many individuals, and seven species (e.g. *Acer rubrum*, *Amelanchier arborea*, *Lindera benzoin*) were only present in unburned relative to burned landscapes (see Table S1 and Fig. S7). In contrast, four species (e.g. *Carya glabra*, *Cercis canadensis*, *Quercus muehlenbergia*) had approximately twice as many individuals, and five species (e.g. *Aesculus pavia*, *Carya ovata*, *Quercus imbricaria*) were only present in burned landscapes (see Table S1 and Fig. S7).

PATTERNS OF β -DIVERSITY

Observed β -diversity was higher in burned landscapes (Fig. 2a; homogeneity of multivariate dispersion on average distance to centroids: d.f. = 91, $F = 4.5$, $P = 0.03$). This pattern, however, was explained by higher null-expected β -diversity in burned landscapes (Fig. 2b; d.f. = 91, $F = 41.8$, $P = 0.0001$). As a result, β -deviations were similar in burned and unburned landscapes (Fig. 2c; d.f. = 91, $F = 0.2$, $P = 0.62$). β -deviations were positive in both landscapes, indicating an important role for processes that create clumping of species across landscapes.

ENVIRONMENTAL AND SPATIAL INFLUENCES ON β -DIVERSITY

Environmental and spatial variables explained similar proportions of β -diversity in unburned and burned landscapes (Fig. 3). The full models, including all variables, explained 23–26% and 22–31% of the variation in β -diversity in unburned and burned landscapes, respectively. After forward model selection, environmental, spatial and spatially structured environmental variables combined to explain *c.* 26–29% of the variation in

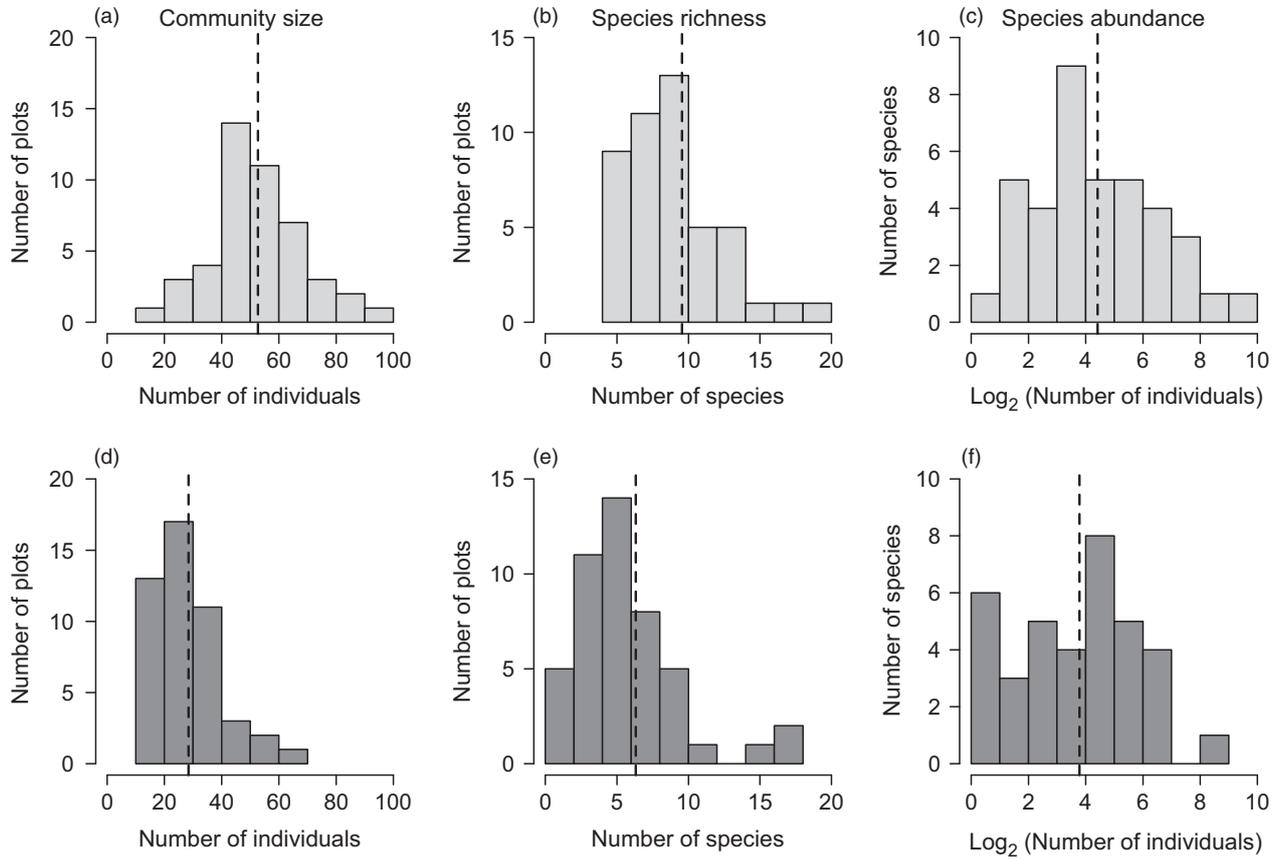


Fig. 1. Histograms of (a, d) local community size (number of individuals per plot), (b, e) local species richness (α -diversity) and (c, f) regional species abundance of woody plants in unburned (top panels, light grey bars, $N = 46$ plots) and burned (bottom panels, dark grey bars, $N = 47$ plots) landscapes. The vertical dashed lines show the means of the distributions.

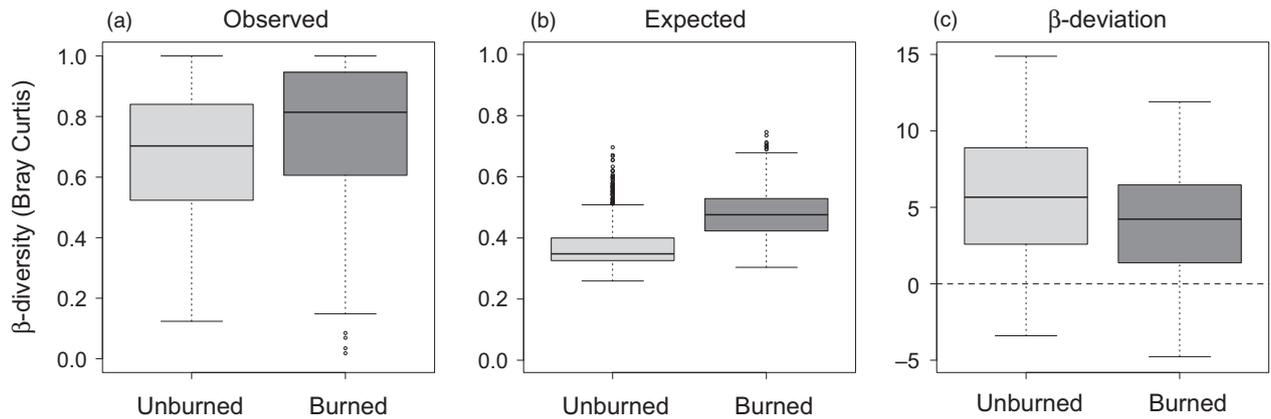


Fig. 2. β -diversity (Bray–Curtis dissimilarity) in unburned and burned landscapes. (a) Observed β -diversity. (b) Expected β -diversity from a null model that includes the total number of individuals in each plot and the species abundance distribution in each landscape, but excludes processes that cause spatial aggregation (clumping) of species within each landscape. (c) Standardized effect size of β -diversity (β -deviations). Boxes represent the median and 25th/75th percentile for all pairwise comparisons between plots, and whiskers extend to 1.5 times the interquartile range. Note that most β -deviations are positive in both landscapes, indicating clumping of species that leads to higher β -diversity than expected by chance (dashed line).

observed β -diversity and *c.* 22–21% of the variation in β -deviations in unburned and burned landscapes, respectively (Fig. 3). Moreover, environmental variables accounted for most of the explained variation in observed β -diversity (22–26%) and

β -deviations (19.0–19.1%). In contrast, spatial and spatially structured environmental variables combined explained only a small fraction of observed β -diversity (4–3%) and β -deviations (3–2%). Importantly, the proportion of β -deviations explained

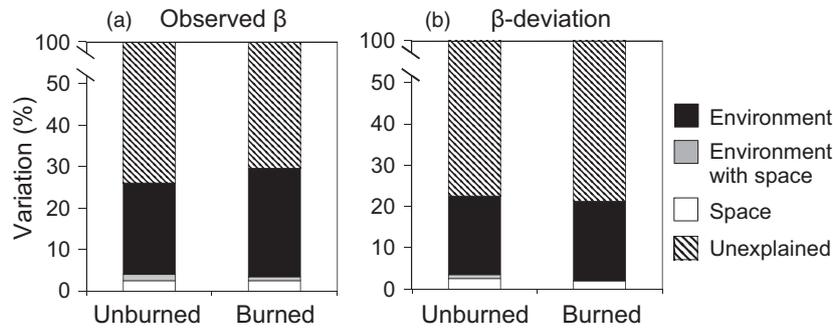


Fig. 3. β -diversity (Bray–Curtis dissimilarity) explained by environmental and spatial variables in unburned and burned landscapes. Variation in (a) observed β -diversity and (b) β -deviations explained by environmental and spatial variables (Table 1). The partitions show the adjusted R^2 values for environmental variables, spatially structured environmental variables, spatial variables and the unexplained variation after forward model selection. Note the break in the y-axes. Spatially structured environmental variables explained a negligible fraction of observed β -diversity and β -deviations (0.2–1.5%).

by environmental or spatial variables did not differ between unburned and burned landscapes (bootstrap tests: environmental fractions, $P = 0.52$; spatial fractions, $P = 0.40$). There were also no clear changes in the relative importance of different environmental variables between the two landscapes (e.g. soil vs. topographic variables; Table 1). The proportion of unexplained variation in observed β -diversity was high in both landscapes (73–70%), and this proportion increased for β -deviations (78–77%) (Fig. 3).

Pairwise differences in β -diversity between plots increased with geographic distance (Fig. 4). The difference in mean observed β -diversity between unburned and burned landscapes remained consistent across geographic distances (permutation test for differences in intercepts: $P = 0.0025$; permutation test for differences in slopes: $P = 0.185$; Fig. 4a). In contrast, the difference in mean β -deviations between unburned and burned landscapes increased with geographic distance, resulting in significantly higher β -deviations in unburned landscapes at larger geographic distances compared

to smaller geographic distances (permutation test for differences in intercepts: $P < 0.0005$; permutation test for differences in slopes: $P < 0.0005$; Fig. 4b).

Discussion

Disturbance often has variable effects on β -diversity (Chase 2007; Vellend *et al.* 2007; Jiang & Patel 2008; Belote, Sanders & Jones 2009; Myers & Harms 2011; Tonkin & Death 2013; Vanschoenwinkel, Buschke & Brendonck 2013). Although it is tempting to invoke different community assembly processes to explain variation in β -diversity within and among studies, we suggest that the results from most studies of β -diversity cannot be used to unambiguously identify changes in assembly mechanisms that influence clumping of species in disturbed and undisturbed landscapes. Here, we find that observed β -diversity was higher in burned relative to unburned landscapes (Figs 2a and 4a). At the local scale, burned communities also had approximately half the number

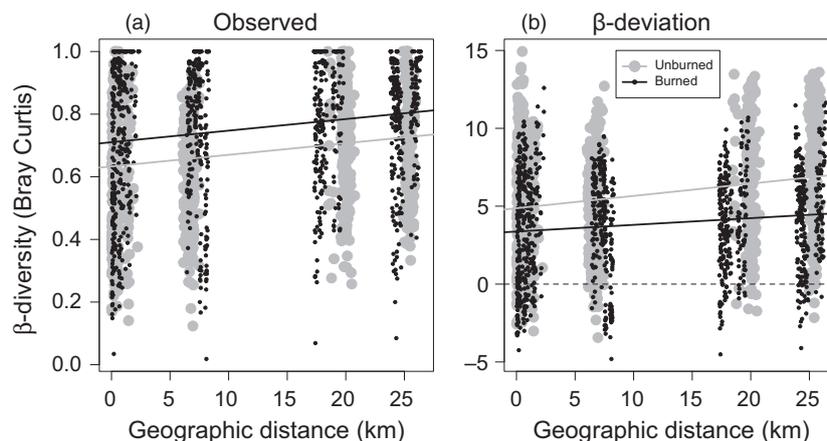


Fig. 4. Relationships between β -diversity (Bray–Curtis dissimilarity) and geographic distance between pairs of plots in unburned (light grey and larger circles) and burned landscapes (black and smaller circles). (a) Observed β -diversity. (b) β -deviations. Best-fit lines from multiple regression on distance matrices are shown in each panel: (a) intercept = 0.63 (unburned) and 0.70 (burned); slope = 3.69×10^{-6} (unburned and burned); (b) intercept = 4.84 (unburned) and 3.38 (burned); slope = 7.91×10^{-5} (unburned) and 4.24×10^{-5} (burned). The dashed line in (b) represents the β -diversity expected from a null model that excludes processes that cause spatial aggregation (clumping) of species within each landscape.

of individuals as unburned communities (smaller community size) and lower species richness (α -diversity). At the regional scale, burned landscapes also had more rare species and fewer common species, but the overall shape of the species abundance distribution did not differ significantly between landscapes (Fig. 1). These changes lead to the expectation that β -diversity should increase, even when there is no change in clumping of species and underlying mechanisms of community assembly (Chase & Myers 2011; Chase & Knight 2013). Consistent with this prediction, we found that the overall dissimilarity between burned and unburned landscapes disappeared after using a null model to control for differences in community size and the species abundance distribution, resulting in similar β -deviations in the two landscapes (Fig. 2c). Moreover, prescribed fires did not influence the effect of environmental and spatial factors on β -deviations (Fig. 3). These results support the hypothesis that the observed change in β -diversity in burned landscapes primarily reflected random sampling effects owing to changes in local community size.

The positive β -deviations observed in both burned and unburned landscapes indicate that species were more clumped in their distributions than expected by chance. This pattern can emerge through habitat filtering, dispersal limitation or a combination of assembly mechanisms. Thus, similarities in β -deviations in burned and unburned landscapes could reflect either a similar influence of one or more of these processes in both landscapes, or a shift in the relative importance of different processes that create similar emergent patterns (Myers *et al.* 2013). Although overall patterns of β -deviations were similar in unburned and burned landscapes (Fig. 2c), β -deviations were significantly lower in burned relative to unburned landscapes (Fig. 4b). In addition, the difference in β -deviations between landscapes increased with spatial scale, suggesting that fire decreases clumping at broader scales through niche selection of fire-tolerant species. This could occur if larger geographic areas contain more of the habitat types in which fire-tolerant species are common, if fire reduces dispersal or establishment limitation of fire-tolerant species (Keeley & Zedler 1978), or if fire decreases habitat filtering across environmental gradients. However, spatial variables explained a relatively small amount of the variation in β -deviations in both landscapes (<5%), suggesting a relatively weak influence of dispersal limitation on clumping. Moreover, environmental variables explained a higher and similar amount of variation in β -deviations in burned and unburned landscapes, suggesting that fire did not influence the relative importance of habitat filtering. Although our observational analyses cannot explicitly discern why β -deviations were similarly influenced by environmental gradients in burned and unburned landscapes, we discuss some possibilities below.

Based on field observations and commonly held views on the historical influences of fire in the Ozarks (Batek *et al.* 1999; Nelson 2012), we expected that prescribed fires would increase β -deviations by restricting fire-intolerant species to certain types of habitats, thereby reducing their habitat breadth and increasing clumping. For example, eastern red

cedars (*Juniperus virginiana*) and maples (*Acer* spp.) are often restricted to marginal habitats in forests with periodic fires, but expand their habitat breadth in unburned forests. Indeed, our results suggest that the abundance and occupancy of many species was negatively influenced by prescribed fire (see Table S1 and Fig. S7), a pattern that may be explained by traits associated with fire intolerance such as thin bark (e.g. *A. rubrum*, *A. arborea*, *L. benzoin*) or reduced carbohydrate storage (e.g. *A. rubrum*; Huddle & Pallardy 1996). Other species with more fire-tolerant traits, such as some species of oaks and hickories (e.g. *C. glabra*, *Q. muehlenbergia*, *Quercus stellata*), had higher abundances in burned landscapes. Counter to our expectations, these population-level effects did not lead to stronger non-random patterns at the community level (β -deviations) in burned landscapes. Nevertheless, it is possible that fire-tolerant species have broader habitat breadths than fire-intolerant species and are thus less subject to habitat filtering that would lead to β -deviations. This mechanism, however, is unlikely to explain our results because β -deviations were similarly influenced by environmental gradients in both burned and unburned landscapes (Fig. 3).

Fire may also influence β -deviations by altering the interplay between ecological drift and niche selection. The majority (>75%) of the variation in β -deviations in both landscapes was unexplained by either spatial or environmental variables (Fig. 3). Some of this unexplained variation is certainly due to unmeasured factors such as local microclimate, biotic processes such as competition and interactions with natural enemies that may influence clumping (Condit *et al.* 2000) and weak apparent habitat filtering of different species with similar functional traits (Pausas & Verdú 2008; Swenson 2011). Moreover, ecological drift could reduce the strength of niche selection across environmental gradients (Vellend *et al.* 2014), resulting in decreased clumping within habitats. This process can become exacerbated when community size is small (Orrock & Fletcher 2005; Orrock & Watling 2010), as observed in burned landscapes (Fig. 1). In addition, sites with similar environments could have dissimilar species composition as a result of priority effects that lead to multiple stable equilibria (e.g. Molofsky & Bever 2002). Disturbances, such as fire, can reduce the likelihood of multiple stable equilibria (e.g. Fukami & Lee 2006; Chase 2007; Jiang & Patel 2008). These opposing effects of disturbance could contribute to a high degree of unexplained variation in disturbed landscapes.

Our results have implications for restoration of fire-managed ecosystems. Although the effects of prescribed fires have been well documented for selected plant species in the Ozarks (e.g. Huddle & Pallardy 1996), the way in which these effects scale-up to influence spatial patterns of biodiversity is often unclear. Our results show that while fires appear to increase β -diversity, suggesting a possible shift in mechanisms of community assembly, this pattern appears to result primarily from fire-induced changes in local densities of individuals. Once changes in local densities are controlled, fires have the opposite influence on β -diversity (Figs 4b and S5c). Moreover, fire appeared to decrease clumping of species more

strongly at broader spatial scales (Fig. 4b), suggesting scale-dependent effects of fire on homogenization of community composition. These results suggest that ecologists should exercise caution in using observed patterns of β -diversity alone as benchmarks for restoration of biodiversity and ecosystem function in landscapes managed with fire. Instead, our study illustrates how ecological disturbances such as fires may alter β -diversity through stochastic processes that are not necessarily related to changes in clumping of species across environmental gradients. Comparative studies of these processes across disturbed ecosystems will provide important insights into the ecological conditions that determine when disturbance alters the interplay of deterministic and stochastic processes in natural and human-modified landscapes.

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Data accessibility

Data deposited in the Dryad repository: <http://datadryad.org/resource/doi:10.5061/dryad.j2qv8> (Myers 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Occupancy and abundance of 43 woody plant species in unburned and burned landscapes.

Figure S1. Geographic locations of study sites in the Missouri Ozarks.

Figure S2. Species composition of the study sites.

Figure S3. Relationship between environmental dissimilarity and geographic distance between plots in unburned and burned landscapes.

Figure S4. Species-accumulation curves in unburned and burned landscapes.

Figure S5. β -diversity (Jaccard dissimilarity) in unburned and burned landscapes.

Figure S6. β -diversity (Jaccard dissimilarity) explained by environmental and spatial variables in unburned and burned landscapes.

Figure S7. Proportional change in species abundances between unburned and burned landscapes.

SUPPORTING INFORMATION

Table S1. Regional occupancy and abundance of 43 woody plant species (≥ 2 cm in diameter at breast height) in unburned and burned forest plots (10 x 50 m) in the Missouri Ozarks (N = 46 unburned plots, N = 47 burned plots).

Species	Code	Occupancy (No. plots)		Total abundance	
		Unburned	Burned	Unburned	Burned
<i>Acer negundo</i>	ACENEG	0	2	0	2
<i>Acer rubrum</i>	ACERUB	7	0	16	0
<i>Acer saccharum</i>	ACESAC	2	1	21	4
<i>Aesculus pavia</i>	AESPAV	0	2	0	34
<i>Amelanchier arborea</i>	AMEARB	11	0	14	0
<i>Carya cordiformis</i>	CARCOR	16	8	108	27
<i>Carya glabra</i>	CARGLA	6	13	13	32
<i>Carya ovata</i>	CAROVA	0	10	0	25
<i>Carya texana</i>	CARTEX	25	12	210	35
<i>Carya tomentosa</i>	CARTOM	27	16	84	45
<i>Celtis occidentalis</i>	CELOCC	8	4	14	8
<i>Celtis tenuifolia</i>	CELOCC	2	2	4	2
<i>Cercis canadensis</i>	CERCAN	6	10	12	26
<i>Cornus drummondii</i>	CORDRU	1	1	1	1
<i>Cornus florida</i>	CORFLO	38	16	592	109
<i>Diospyros virginiana</i>	DIOVIR	13	5	39	10
<i>Euonymus atropurpureus</i>	EUOATR	4	0	5	0
<i>Frangula caroliniana</i>	FRACAR	11	4	28	13
<i>Fraxinus americana</i>	FRAAME	13	14	59	27
<i>Gleditsia triacanthos</i>	GLETRI	2	4	3	6
<i>Juglans nigra</i>	JUGNIG	8	9	16	24
<i>Juniperus virginiana</i>	JUNVIR	14	6	61	19
<i>Lindera benzoin</i>	LINBEN	4	0	10	0
<i>Morus rubra</i>	MORRUB	11	3	17	8
<i>Ostrya virginiana</i>	OSTVIR	3	2	5	2
<i>Platanus occidentalis</i>	PLAOCC	3	1	3	1
<i>Prunus americana</i>	PRUAME	3	0	6	0
<i>Prunus serotina</i>	PRUSER	11	5	24	12
<i>Quercus alba</i>	QUEALB	43	23	282	82
<i>Quercus bicolor</i>	QUEBIC	3	1	19	3
<i>Quercus imbricaria</i>	QUEIMB	0	3	0	13
<i>Quercus macrocarpa</i>	QUEMAC	0	1	0	1
<i>Quercus marilandica</i>	QUEMAR	9	7	52	58
<i>Quercus muehlenbergii</i>	QUEMUE	6	11	10	31

<i>Quercus rubra</i>	QUERUB	15	15	62	38
<i>Quercus stellata</i>	QUESTE	21	35	233	443
<i>Quercus velutina</i>	QUEVEL	40	20	226	83
<i>Rhus copallinum</i>	RHUCOP	1	0	3	0
<i>Sassafras albidum</i>	SASALB	19	6	85	8
<i>Sideroxylon lanuginosum</i>	SIDLAN	8	6	10	8
<i>Tilia americana</i>	TILAME	3	2	3	3
<i>Ulmus americana</i>	ULMAME	3	0	5	0
<i>Ulmus rubra</i>	ULMRUB	19	17	73	92
<hr/>					
Total number of individuals:				2423	1335
Total number of species:				38	36
<hr/>					

Figure S1. Map of plot locations in unburned (black triangles) and burned (red circles) forests in the Missouri Ozarks, USA (N = 46 unburned plots, N = 47 burned plots). The two pairs of unburned and burned sites in the top right are located in the northern and southern sections of Lake of the Ozarks State Park (Camden and Miller Counties, MO), respectively, whereas the pair of sites in the bottom left is located in Ha Ha Tonka State Park (Camden County, MO).

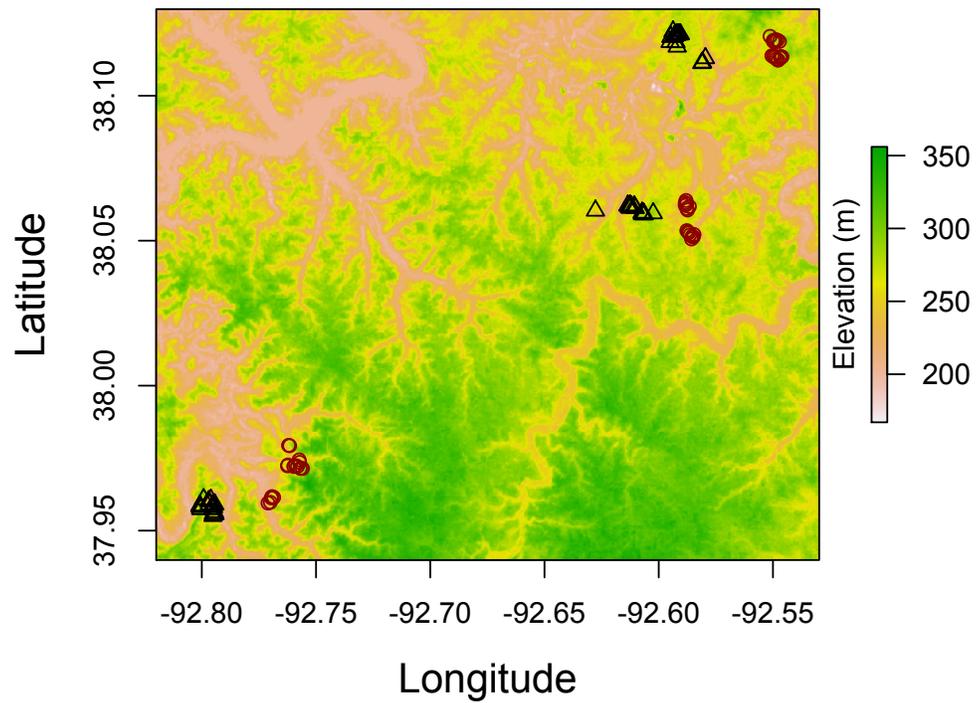


Figure S2. Species composition in the three sample sites: HHT = Ha Ha Tonka State Park; LOZ 1 = northern section of Lake of the Ozarks State Park; LOZ 2 = southern section of Lake of the Ozarks State Park (Fig. S1). (a) Ordination of woody plant species composition (Bray-Curtis dissimilarity) derived from nonmetric multi-dimensional scaling (NMDS; stress = 0.18). Points close together in ordination space indicate plots with similar species composition; lines represent the total variation in species composition within each site. (b) Boxplots of distance-to-centroid values (Bray-Curtis dissimilarity) for plots within sites. Note the overall similarity in species composition across sites in (a) and the similarity in average distance-to-centroids in (b) (homogeneity of multivariate dispersion: $df = 90$, $F = 1.75$, $P = 0.17$).

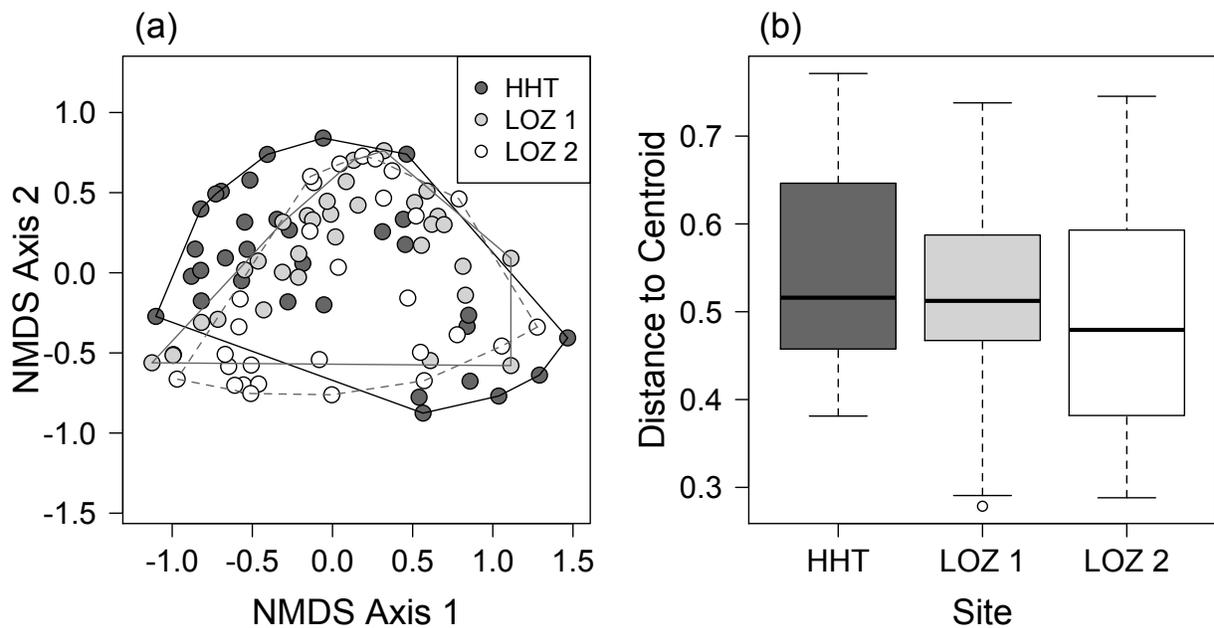


Figure S3. Relationship between environmental dissimilarity and geographic distance between pairs of plots in (a) unburned and (b) burned landscapes. Environmental dissimilarity was calculated using axes derived from principal component analysis (PCA) of soil and topographic variables (Table 1). Regression lines from Mantel tests are shown in each panel. Note that environmental conditions and geographic distances are weakly correlated among pairs of plots in both unburned ($P = 0.81$, $r = 0.03$) and burned ($P = 0.006$, $r = 0.16$) landscapes.

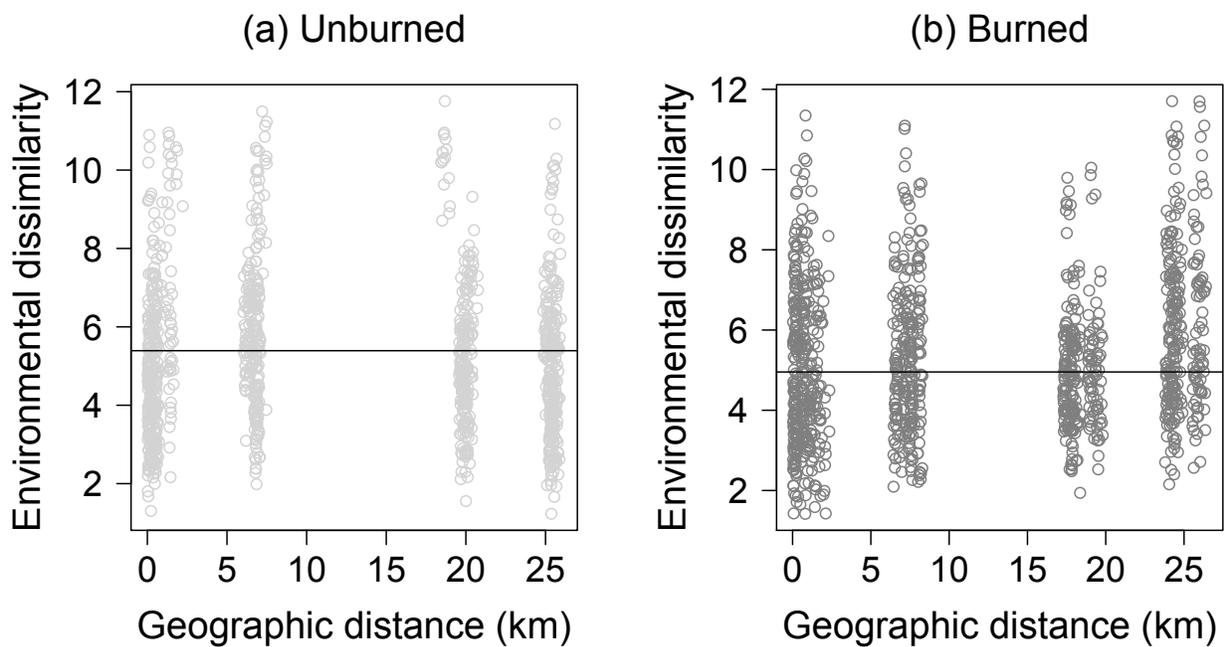


Figure S4. Species-accumulation curves in unburned and burned landscapes. (a) Individual-based curve. (b) Sample-based curve. Solid lines show the average number of species expected for a given number of individuals or sample plots and the shaded areas show the 95% confidence intervals.

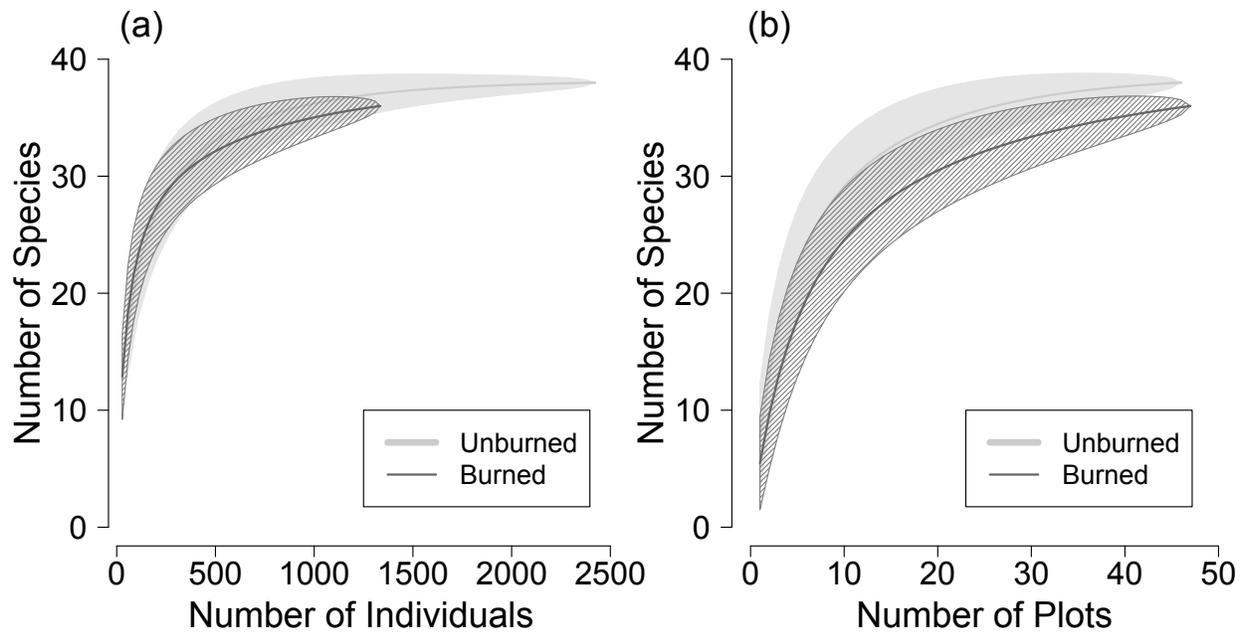


Figure S5. β -diversity (Jaccard dissimilarity) in unburned and burned forests. (a) Observed β -diversity. (b) Expected β -diversity from a null model that includes the total number of individuals in each plot and the species-abundance distribution in each landscape, but excludes processes that cause spatial aggregation (clumping) of species within each landscape. (c) Standardized effect size of β -diversity (β -deviations). Boxes represent the median and 25th/75th percentile, and whiskers extend to 1.5 times the interquartile range. Note that most β -deviations are positive in both landscapes, indicating clumping of species that leads to higher β -diversity than expected by chance (dashed line).

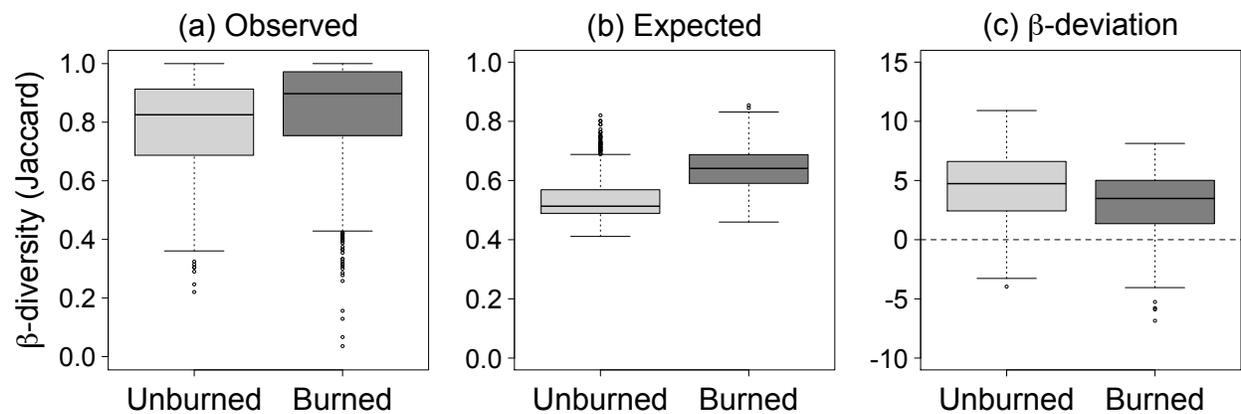


Figure S6. β -diversity (Jaccard dissimilarity) explained by environmental and spatial variables in unburned and burned forests. Variation in (a) observed β -diversity and (b) β -deviations explained by environmental and spatial variables (Table 1). The partitions show the adjusted R^2 values for environmental variables, spatially-structured environmental variables, spatial variables, and the unexplained variation after forward model selection. Note the break in the y-axes. Spatially-structured environmental variables explained a negligible fraction of observed β -diversity and β -deviations (0.5–1.8%). The full models, including all variables, explained 26–27% of the observed β -diversity and 19–20% of the β -deviations in unburned and burned forests, respectively.

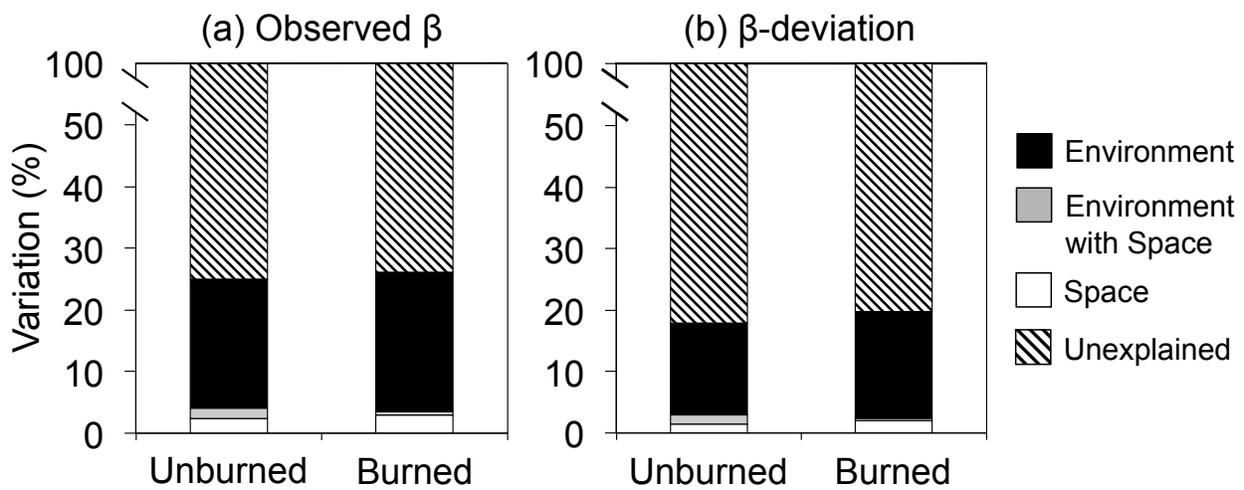


Figure S7. Proportional change in regional species abundances between unburned and burned landscapes, calculated as: $[(\text{total number of individuals in burned plots} - \text{total number of individuals in unburned plots}) / \text{total number of individuals in unburned plots}] \times 100$. Species above zero had higher proportional abundances in burned landscapes, whereas species below zero had higher abundances in unburned landscapes. Bars equal to the dashed line below zero indicate species with no individuals in burned plots, whereas bars larger than the dashed line above zero indicate species with twice as many individuals in burned relative to unburned plots. Results are shown for the 38 species that were present in unburned plots (Table S1). Species codes are listed in Table S1.

