

Scaling up the diversity–resilience relationship with trait databases and remote sensing data: the recovery of productivity after wildfire

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Abstract

Understanding the mechanisms underlying ecosystem resilience – why some systems have an irreversible response to disturbances while others recover – is critical for conserving biodiversity and ecosystem function in the face of global change. Despite the widespread acceptance of a positive relationship between biodiversity and resilience, empirical evidence for this relationship remains fairly limited in scope and localized in scale. Assessing resilience at the large landscape and regional scales most relevant to land management and conservation practices has been limited by the ability to measure both diversity and resilience over large spatial scales. Here, we combined tools used in large-scale studies of biodiversity (remote sensing and trait databases) with theoretical advances developed from small-scale experiments to ask whether the functional diversity within a range of woodland and forest ecosystems influences the recovery of productivity after wildfires across the four-corner region of the United States. We additionally asked how environmental variation (topography, macroclimate) across this geographic region influences such resilience, either directly or indirectly via changes in functional diversity. Using path analysis, we found that functional diversity in regeneration traits (fire tolerance, fire resistance, resprout ability) was a stronger predictor of the recovery of productivity after wildfire than the functional diversity of seed mass or species richness. Moreover, slope, elevation, and aspect either directly or indirectly influenced the recovery of productivity, likely via their effect on microclimate, while macroclimate had no direct or indirect effects. Our study provides some of the first direct empirical evidence for functional diversity increasing resilience at large spatial scales. Our approach highlights the power of combining theory based on local-scale studies with tools used in studies at large spatial scales and trait databases to understand pressing environmental issues.

Keywords: fire resistance, fire tolerance, functional diversity, Landfire, MODIS, NatureServe, path analysis, resprout ability, seed mass, southwest United States

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Introduction

The anthropogenic alteration of ecosystems – including climate change, increased nutrient availability, land-use change, fragmentation, and altered disturbance regimes – is occurring globally at unprecedented scales and rates (Vitousek *et al.*, 1997; Ellis, 2011; Diffenbaugh & Field, 2013). These rapid ecological changes can often result in full ecosystem collapse or dramatic regime

shifts (Scheffer *et al.*, 2001; Folke *et al.*, 2004). However, some systems exhibit little change or quickly recover (Peterson *et al.*, 1998; Gunderson, 2000). A mechanistic understanding of why some systems have irreversible response to disturbances while others recover relatively quickly – what affects resilience – is of key importance for understanding threats to biodiversity (Sala *et al.*, 2000) and for preserving ecosystem function (Folke *et al.*, 2004).

The resilience of an ecosystem can be defined both as the amount of disturbance a system can absorb while

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remaining in the same state and/or function (i.e., 'ecological resilience'; Holling, 1973, 1996), and as the ability of a system to recover state/function following disturbance (i.e., 'engineering resilience'; Holling, 1996). Many studies have recommended promoting biodiversity as a practical measure for increasing resilience (e.g., Chapin *et al.*, 2000; Fischer *et al.*, 2006; Suding, 2011; Bernazzani *et al.*, 2012). For example, several metrics of biodiversity were promoted as a means of increasing resilience of Habitat Conservation Plans under the Endangered Species Act (e.g., native species diversity in grasslands, diversity in age structure of forests; Bernazzani *et al.*, 2012). Similarly, in sustainability science, biodiversity is presented as a proxy for ecological resilience of 'critical natural capital' (Brand, 2009). Likewise, promoting native species and functional diversity is put forth as a 'guiding principle' for commodity production landscapes (Fischer *et al.*, 2006). In general, biodiversity (particularly functional diversity) is thought to increase resilience because the function of any given species lost to a disturbance can be replaced by other functionally redundant species in high-diversity ecosystem (Holling, 1973; Walker, 1995; Elmqvist *et al.*, 2003; Suding, 2011).

Despite the widespread acceptance of a generally positive relationship between biodiversity and resilience both conceptually and in practice, empirical evidence for this relationship remains fairly limited in scope and localized in scale (Hobbs *et al.*, 2011; Suding, 2011; Mori *et al.*, 2013). To our knowledge, only two studies to date have explicitly tested the resilience of productivity to disturbance, both in small-scale experimental grasslands. In one study, recovery of grass biomass was positively related to biodiversity 2 years after a small-scale (1 m²) disturbance (Pfisterer & Schmid, 2002). In another experimental grassland, recovery of biomass in 1 m² plots was positively related to biodiversity, but the relationship was driven by a single grass species (Van Ruijven & Berendse, 2010). To date, no studies have tested the relationship between biodiversity and resilience at the large landscape and regional scales most relevant to management, conservation, and restoration practices. Identifying how biodiversity relates to resilience across larger spatial scales is critical for projecting the ecological consequences of increasingly widespread large disturbances (Suding, 2011; Li *et al.*, 2014).

The tools available to link patterns of biodiversity and resilience at larger scales have been rapidly developed in recent years. Remote sensing has proved a powerful tool for biodiversity monitoring and conservation planning (Stoms & Estes, 1993; Gould, 2000; Duro *et al.*, 2007; Wiens *et al.*, 2009; Li *et al.*, 2014). For example, wildfires are a large-scale periodic

disturbance, which often have limited *in situ* access due to their frequent occurrence in rugged, remote terrain and their inherent danger to humans (Kennedy *et al.*, 2012). Remote sensing has been highly effective at monitoring fire potential, severity, frequency, and the recovery of biodiversity (Robinson, 1991; Eva & Lambin, 2000; Lentile *et al.*, 2006; Wiens *et al.*, 2009) providing data that may not be otherwise available. Similarly, trait databases (e.g., TRY, USDA plants, Kew SID) now provide data to more realistically and empirically ground models that have previously been limited to using taxonomic data that do not consider the functional traits of species (Kattge *et al.*, 2011). It is important to note however, these tools are subject to several sources of uncertainty which are not present in small-scale studies. For example, vegetation data derived from the USGS Landfire Existing Vegetation Type classification system (USGS, 2012) do not include rare and subordinate species. While there is general evidence that species contribute to ecosystem function based on their abundance within a given ecosystem (Grime, 1998; Garnier *et al.*, 2004), supporting the use of these data, there are some cases where subordinate species may contribute more strongly to ecosystem functioning (Mariotte, 2014). Similarly, trait databases often do not include locally measured trait data or intraspecific trait variation, both of which may be important for trait-based studies (Albert *et al.*, 2011; Violle *et al.*, 2012; Cordlandwehr *et al.*, 2013). Despite their inherent limitations, remote sensing and trait databases allow us to address fundamental questions in ecology at spatial scales that would not be feasible through field studies and have the potential to provide new insights into the factors influencing ecosystem resilience.

Functional diversity is thought to increase resilience because communities with a diverse set of response traits (high functional diversity) are buffered against environmental change – the function of any given species lost to a disturbance can be replaced by other species within high-diversity ecosystems (Holling, 1973; Walker, 1995; Elmqvist *et al.*, 2003; Suding, 2011; Standish *et al.*, 2014). However, recent advances in functional ecology suggest that the functional diversity of a community is comprised of multiple dimensions (Mason *et al.*, 2005) and two key dimensions that have proved useful in trait-based studies are functional richness and functional dispersion (Mouchet *et al.*, 2010; Schleuter *et al.*, 2010). Functional richness (FRic) describes the volume of trait space occupied by species in a community regardless of the shape of the distribution and can be conceptualized as the multivariate equivalent of the range of traits within a community (Cornwell *et al.*, 2006). Functional dispersion (FDis) is the mean distance in multidimensional trait space of

individual species to the centroid of all species and can be conceptualized as the degree of trait dissimilarity among species within a community (Mason *et al.*, 2005; Laliberte & Legendre, 2010). Importantly, the relative importance of these two components of functional diversity for ecosystem resilience remains untested. Identifying which component of functional diversity (FRic: having a wide range of trait strategies, or FDis: having species with dissimilar strategies) contributes most to resilience has important implications for land managers looking for practical recommendations of how to maximize resilience of a given ecosystem.

In this study, we 'scale up' the biodiversity–resilience relationship to examine whether the functional diversity within woodland and forest ecosystems influences resilience across a large geographic region. Specifically, we examine the recovery of productivity after wildfire across the four-corner region of the southwest United States of America (Fig. 1). We focus on the resilience of productivity because it provides a response that is easy to compare across multiple woody ecosystems and it is generally correlated with ecosystem health (e.g., Rapport *et al.*, 1998). This area encompasses a wide range of ecosystems from cold desert woodlands to forested mountains, which vary in functional diversity both among systems and across climatic and topographic gradients (Butterfield, 2015). This area is also characterized by frequent wildfires (Westerling *et al.*, 2006; O'Connor *et al.*, 2014), providing an easily identifiable baseline disturbance. Using a novel combination of

remote sensing (to identify fire extent, vegetation types, and productivity response), trait databases (to determine functional diversity for each vegetation type), and path analysis we ask the following: (1) does greater functional diversity at the regional scale confer ecosystem resilience in productivity to disturbance by fire, (2) how does variation in environmental conditions (e.g., topography, macroclimate) across the region influence ecosystem resilience, either directly or indirectly via changes in functional diversity, and (3) which dimension of functional diversity – functional richness or dispersion – contributes most to the biodiversity–resilience relationship. We additionally compare our results to a model that includes species richness instead of functional diversity to aid in the interpretation of our results.

Materials and methods

Study region

The study area extent, from eastern Arizona to eastern Colorado and New Mexico, was chosen to span a range of ecoregions in the four-corner region of the southwest United States of America (Fig. 1). This area encompasses ecosystems with a variety of species and functional diversity across climatic and topographic gradients with increasingly frequent wildfires (Westerling *et al.*, 2006; Littell *et al.*, 2009; O'Connor *et al.*, 2014). We focused on woodlands and forests which were the most commonly burned ecosystems in the study region. Vegetation types range from low-elevation basin woodlands

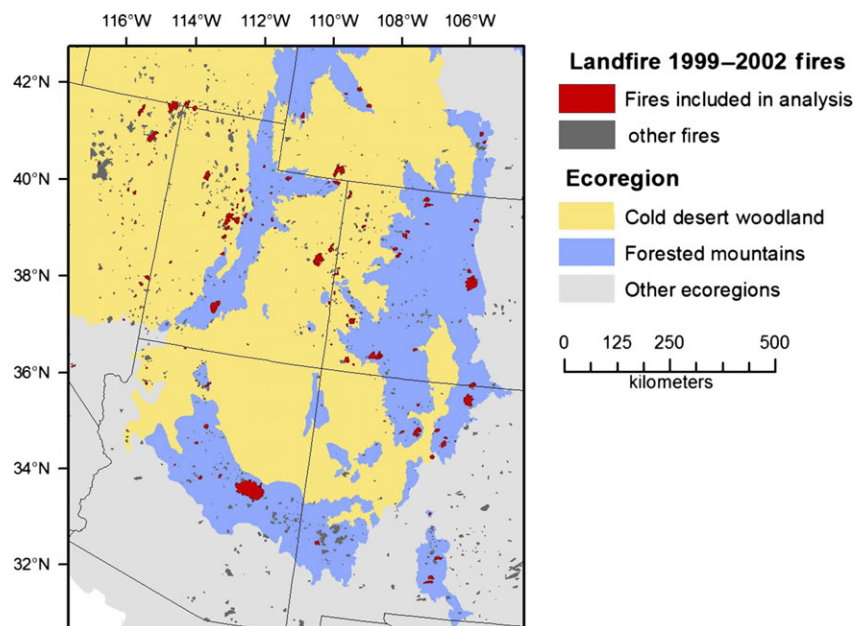


Fig. 1 Study area in the four-corner region of the southwest United States of America highlighting the fire perimeters (red) that included one or more pixels of high-severity fire burning a single vegetation type used in this analysis. Our study focused on two dominant ecoregions: cold desert, woodlands, and forested mountains.

to high-elevation forests, including 16 total types as defined by the USGS Landfire Existing Vegetation Type (EVT) classification system (USGS, 2012; Table S1). Existing vegetation types are mesoscale classifications representing vegetation types that recur consistently across similar physical habitats that can be reliably mapped at 30 m resolution through remotely sensed and topographic data (Corner *et al.*, 2003).

Fire extent and severity

We used the Landfire disturbance product (USGS, 2012) to identify all 'wildland fires' that burned between 1999–2002 in the study region (1999 is the first year available in the Landfire dataset). Fires identified by the Landfire disturbance product are derived from 30 m resolution Landsat imagery via the Monitoring Trends in Burn Severity (MTBS) and Burned Area Reflectance Classification (BARC) products. These datasets use changes in reflectance of the land surface following fire events to identify both extent and severity (low, medium, high) of the burn. High-severity fires lead to near 100% loss of green vegetation, although high severity does not necessarily indicate a stand killing fire (USGS, 2012). Individuals or species may survive fires even if all green leaves are destroyed. However, by focusing on high-severity fires, we increase the likelihood that the response measured postfire is predominantly due to recovery (new growth, reseeding, resprouting) and not strongly influenced by vegetation remnants that did not burn.

We combined the fire disturbance and existing vegetation type (EVT) layers to identify areas of a single vegetation type that burned with a high-severity fire. The pixel resolution for this analysis was 250 m, consistent with the MODIS normalized difference vegetation index (NDVI) products used to measure recovery (see *Resilience metrics* below). To be included in the analysis, at least 95% of the 250 m pixel must have burned between 1999 and 2002 with more than 50% of the burned area within the pixel classified as a high-severity fire. Additionally, at least 90% of the 250 m pixel had to be the same land cover class based on the existing vegetation layer. Finally, the pixel could not have any subsequent disturbance in the Landfire disturbance product during the remaining time series (2003–2010).

In addition to identifying disturbed pixels, we also identified undisturbed control pixels to normalize our measure of resilience (see *Resilience metrics*, below) among vegetation types. By normalizing with undisturbed control pixels, we aimed to control for interannual variability in our resilience measurement as well as for the large difference in NDVI between forests and woodlands. Candidate control pixels had no disturbance from 1999 to 2010 according to the Landfire disturbance product, were within 2 km of a fire perimeter, and contained at least 90% of a single existing vegetation type that matched the disturbed pixel.

Environmental predictors

For every disturbed pixel, we extracted topographic and macroclimatic covariates. Elevation (in meters), aspect, and slope (in degrees) were derived from the shuttle radar topog-

raphy mission (SRTM) gridded data at 90 m resolution. As aspect is a circular variable, we transformed this variable where $\cos(\text{aspect})$ represents the north and south component of aspect, while $\sin(\text{aspect})$ represents the east–west component of aspect. Here, we only focus on $\cos(\text{aspect})$ (the north–south component) as microclimate is most strongly influenced by the differences in incoming solar radiation among north- and south-facing aspects (Dobrowski *et al.*, 2009). Average values were calculated at a 250 m resolution aligned with MODIS pixels used to calculate recovery (see below). Macroclimatic covariates were mean annual temperature (MAT) and mean annual precipitation (MAP), both extracted from PRISM (Daly *et al.*, 2002) interpolated climate data. Here, we use both macroclimatic and topographic variables as predictors because the topographic variables can provide an indication of the importance of microclimatic variation which may not be evident within the coarse (800 m) scale of our macroclimatic data (Dobrowski, 2011).

Species and functional diversity

The species present within existing vegetation type (Table S1) were extracted through NatureServe (www.natureserve.org). We used the vegetation associations (e.g., *Juniperus monosperma*/*Agave lechuguilla* woodland and *Pinus edulis*/*Achnatherum scribneri* woodland are associated with 'Colorado Plateau Pinyon-Juniper Shrubland') within each vegetation type to create a list of all species within each vegetation type. Species richness ranged between 21 and 59 species per vegetation type. As an estimate of community composition within each vegetation type, we then used the number of times a species occurred in a different vegetation association (e.g., *Juniperus monosperma* occurred in 22 separate vegetation associations within the Colorado Plateau Pinyon-Juniper Shrubland vegetation type) divided by the total number of occurrences of all species across all association types within each vegetation type. While this approach does not include rare and subordinate species, it captures the species that likely contribute most to ecosystem function (Garnier *et al.*, 2004) by capturing the species that are widespread across the vegetation type.

Functional diversity was calculated for each of the 16 vegetation types based on (1) categorical traits associated with fire tolerance and resistance and (2) seed mass. We analyzed these traits separately as they represent different potential strategies for increasing resilience to fire. Categorical traits associated with fire tolerance/resistance were extracted from the USDA Plants database (<http://plants.usda.gov>) and included growth habit (graminoid, herb, subshrub, shrub, tree), fire tolerance (yes, no), fire resistance (low, medium, high), and resprout ability (yes, no). Growth form is associated with ecophysiological adaptations to maximize photosynthetic production and shelter from severe climatic conditions (Perez-Harguindeguy *et al.*, 2013). Fire tolerance indicates the ability of a species to regrow, or reestablish from seed postfire. Fire resistance indicates a set of traits that allow plant species to resist burning (e.g., height taller than flames, thick bark; Lavorel & Garnier, 2002). Resprout ability indicates a postdisturbance recovery strategy where species do not have to recruit from seed, but

can resprout after the destruction of most of their above-ground biomass, and is important for persistence in systems where disturbances are common (Perez-Harguindeguy *et al.*, 2013). Growth habit data were available for all 239 species found across the 16 vegetation types, and data on the remaining three traits were available for 119 species. While other traits (bark thickness, nonstructural carbohydrates) may be better indicators of species responses to fire, we chose these traits because they are freely available for a large number of species from existing plant trait databases.

Seed mass (the oven-dry mass of an average seed of a species) is generally related to dispersal ability, a reproductive strategy where species that produce few large seeds are thought to be better competitors and those that produce many small seeds are thought to be better dispersers (Cadotte, 2007); however, some large seeds do have modifications that allow for long-distance dispersal. Seed mass data were available for 144 of the 239 species in our dataset from the Kew Royal Botanical Gardens Seed Information Database (<http://data.kew.org/sid/>). We classified species into five categories of seed mass – extra small: <0.1 g/1000 seeds, small: <1 g/1000 seeds, medium: <10 g/1000 seeds, large: <100 g/1000 seeds, and extra-large: <1000 g/1000 seeds. Species without seed mass data were assigned a category based on the other members of the genus, as seed mass is generally phylogenetically conserved (Moles *et al.*, 2005). If individuals of a given genus fell into multiple categories, we assigned species without seed mass data to the most common category in that genus.

For our two sets of traits (fire resistance/tolerance traits and seed mass), we calculated functional richness and functional dispersion using the FD package (Laliberté & Legendre, 2010) in R 2.15 (R Core Team, 2014). Functional richness (FRic) measures the ranges of trait values in a community and is calculated as the minimum convex hull volume that includes all the species considered (Cornwell *et al.*, 2006). When calculated for a single trait, such as seed mass, functional richness is the difference between the maximum and minimum functional values present in the community (Mason *et al.*, 2005). Functional dispersion (FDis), which indicates the degree of trait dissimilarity (the inverse of functional redundancy) among species, is calculated as the mean distance of each species in multidimensional trait space to the centroid of all species and is statistically independent of species richness (Laliberté & Legendre, 2010).

Resilience metric: productivity response

To measure recovery of vegetation productivity after a fire, we obtained remote sensing-based phenology metrics from 2001 to 2010 for the study area from the USGS EROS Center (<http://phenology.cr.usgs.gov/>). The phenology metrics were derived from a time series of weekly maximum NDVI in the USGS eMODIS collection (<https://lta.cr.usgs.gov/emodis>) at 250 m spatial resolution. We used the time-integrated NDVI (TIN), a daily integration of NDVI above the minimum during the growing season, as a proxy of annual primary productivity (Pettorelli *et al.*, 2005). To account for

the effects of confounding factors during any given year (e.g., interannual variability of climate) and normalize the productivity response among vegetation types, we calculated the ratio of TIN in a burned pixel to the median TIN value of corresponding control pixels, which have the same vegetation type as the burned pixel, for every year from 2001 to 2010, and then fitted a regression line of the ratios on year after fire (or vegetation age): $\frac{\text{TIN}_{\text{burned}}}{\text{median TIN}_{\text{control}}} = a + b \times \text{age}$. We then used the slope of the regression line (b) as an indicator of recovery of vegetation productivity.

Statistical analysis

To screen data (i.e., test for nonlinear relationships among our variables) and to aid in the interpretation of our results, we first explored univariate relationships among each diversity metric (species richness, FRic, FDis) and our macroclimatic [mean annual temperature (MAT) and mean annual precipitation (MAP)] and topographic (slope, aspect, elevation) variables for each fire. We tested for both linear and nonlinear (quadratic) relationships for each response measure and selected the best fit using Akaike information criteria (Burnham & Anderson, 2004). We then used path analysis to investigate links among macroclimate, topography, diversity, and the recovery of productivity after fire (resilience). We built an initial model (Fig. 2) that included the direct effects of climate and topography on the productivity response as well as their direct effect on diversity, and subsequently, diversity's direct effect on the productivity response.

For each model, we removed variables to find the model with the lowest Akaike information criterion (AIC), assessed model fit with chi-square (χ^2) tests, root mean square error of approximation (RMSEA), and goodness-of-fit index (GFI). χ^2

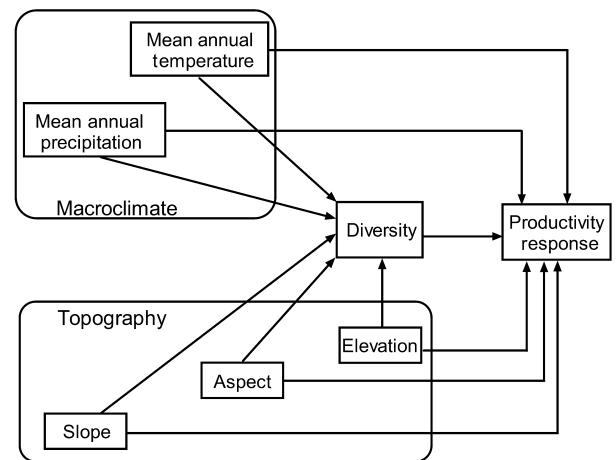


Fig. 2 General form of the path analysis evaluated for productivity response (resilience) including the role of diversity (represented as species richness or functional richness (FRic) and functional dispersion (FDis) in our analysis). Path coefficients are standardized prediction coefficients (Grace & Bollen, 2005).

values associated with a P -value >0.05 (suggesting that observed and expected covariance matrices are not different) and a RMSEA < 0.05 and GFI > 0.95 indicate a good model fit (Kline, 2010). Path analysis was conducted using the Lavaan package (Rosseel, 2012) implemented in R (R Core Team, 2014). In our results (Fig. 3a–c), nonsignificant pathways (arrows) have been removed (as compared to the initial model) and marginally significant pathways ($0.05 < P < 0.10$) are indicated by gray-dashed lines.

Results

Vegetation recovery dataset

The disturbance dataset identified a total of 7 715 250 m pixels meeting the selection criteria of high-severity burns of a single vegetation type, representing 189

unique fire events and including 44 unique land cover classes. The undisturbed control dataset included a total of 74 138 pixels, but control pixels with the same vegetation type as the burned pixels were not always available. After subsetting this dataset to focus only on woodland or forest vegetation types with appropriate control pixels, our final dataset contained 6603 total pixels from 133 unique fire events (Table S2) and encompassed 16 unique land cover classes (Table S1).

Univariate relationships

Species richness and each metric of functional diversity for both fire traits and seed mass showed varied direct linear relationships with topography and climate (Table 1).

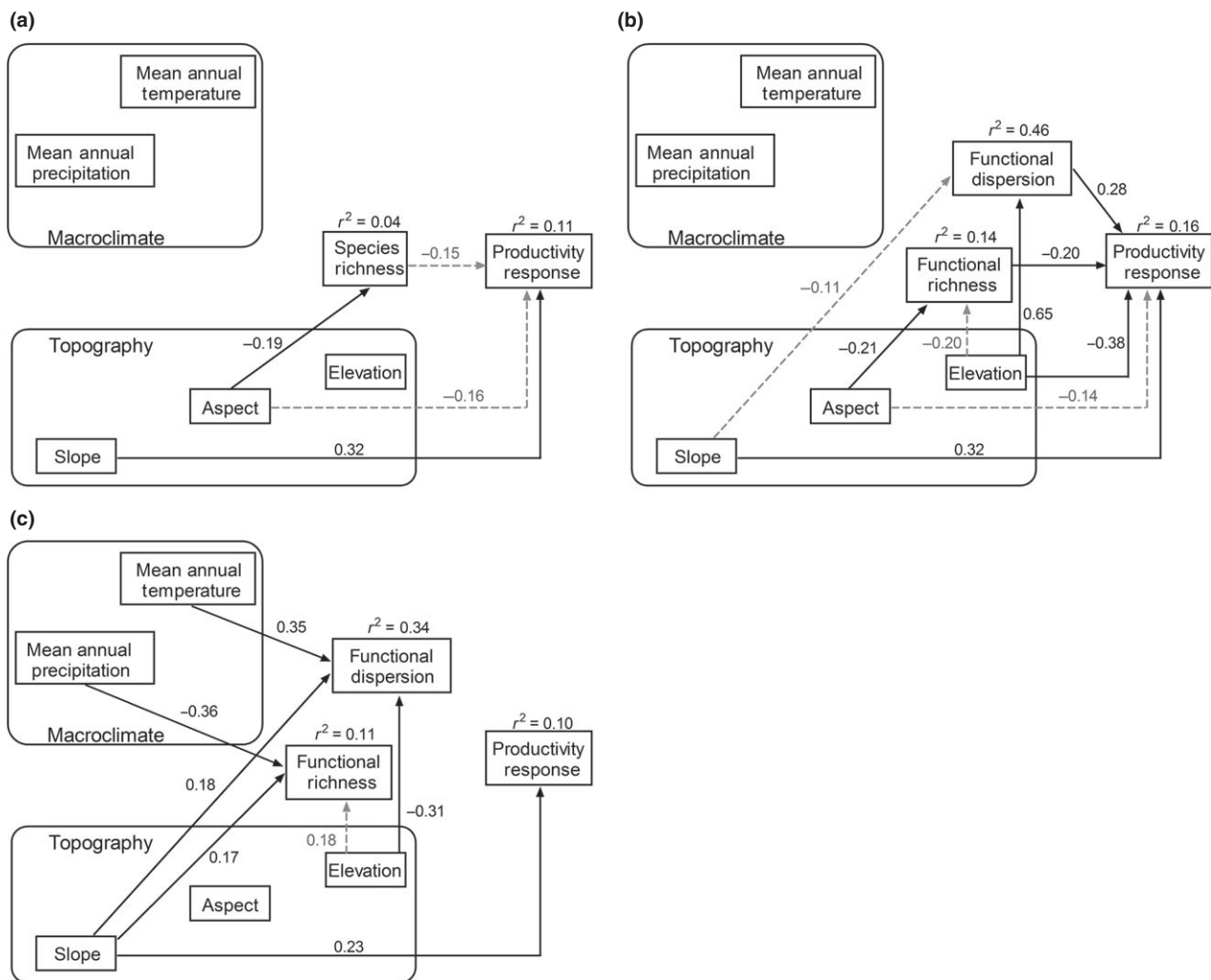


Fig. 3 Path analyses testing the hypothesis that diversity increases the resilience of productivity to fire for (a) species richness, (b) functional diversity based on fire tolerance/regeneration traits, and (c) functional diversity based on seed mass. Path coefficients are standardized prediction coefficients (Grace & Bollen, 2005). Pathways not found to be influential (nonsignificant $P > 0.1$) are removed, and marginally significant pathways ($P < 0.1$ and $P > 0.05$) are represented by gray-dashed lines.

Table 1 The relationships between the three metrics of biodiversity (SR: species richness, and FRic: functional richness and FDis: functional dispersion for both fire traits and seed mass) and the predictor variables in our model. Direction of relationship indicated by + (positive relationship) or – (negative relationship), NS indicates a nonsignificant relationship. ‘N–S aspect’ is $\cos(\text{aspect})$ describing the north–south component of aspect, a circular variable.

Biodiversity measure	Response metric	Predictor variable	Direction of relationship	r^2	F-statistic
Species richness	Species richness	Mean annual temperature	NS	NS	NS
		Mean annual precipitation	NS	NS	NS
		Slope	NS	NS	NS
		N–S aspect	–	0.04	6.65*
		Elevation	NS	NS	NS
Fire resistance/tolerance	FRic	Mean annual temperature	+	0.06	9.31*
		Mean annual precipitation	–	0.06	9.61*
		Slope	NS	NS	NS
		N–S aspect	–	0.05	6.96*
		Elevation	–	0.07	10.52*
	FDis	Mean annual temperature	–	0.16	27.34***
		Mean annual precipitation	+	0.20	36.31***
		Slope	NS	NS	NS
		N–S aspect	NS	NS	NS
		Elevation	+	0.43	109.80***
Seed mass	FRic	Mean annual temperature	NS	NS	NS
		Mean annual precipitation	NS	NS	NS
		Slope	+	0.08	12.76***
		N–S aspect	NS	NS	NS
		Elevation	NS	NS	NS
	FDis	Mean annual temperature	+	0.22	40.57***
		Mean annual precipitation	–	0.11	17.74***
		Slope	NS	NS	NS
		N–S aspect	NS	NS	NS
		Elevation	–	0.20	35.12***

FRic, functional richness; FDis, functional dispersion; N–S aspect, north–south aspect; NS, nonsignificant relationships. Bold text, significant relationships: * $P < 0.05$, ** $P < 0.001$, *** $P < 0.001$.

Path analysis

The model including species richness was found to have a close fit to the data ($\chi^2 = 0.01$, $df = 1$, $P = 0.94$; RMSEA = 0.00; GFI = 0.999), but only explained a relatively small amount of the variance in productivity response ($R^2 = 0.11$, Fig. 3a). Importantly, species richness only marginally positively influenced the recovery of productivity ($P = 0.07$). In the final model, only slope had direct effects on productivity response to fire, where productivity recovered more quickly in communities on steeper slopes (Table 2). Aspect had a marginal influence on recovery of productivity ($P = 0.06$). Species richness was influenced by aspect, with higher richness on south-facing aspects, but as the species richness only marginally influenced productivity response the indirect effect of aspect on productivity is also only marginal. In summary, we did not find that species richness significantly predicted the resilience of productivity to wildfire.

The model including functional diversity based on fire response/tolerance traits was found to have a close fit to the data ($\chi^2 = 0.52$, $df = 3$, $P = 0.91$; RMSEA = 0.00; GFI = 0.999) and explained more of the variance in productivity response ($R^2 = 0.16$, Fig. 3b) than the model with species richness. In the final model slope, elevation, functional richness, and functional dispersion all had direct effects on productivity response to fire, where productivity recovered more quickly in communities on steeper slopes, at lower elevations (Table 2), with less functional richness, and with greater functional dispersion. Aspect also influenced postfire recovery, but only via its indirect effect through functional richness (Fig. 3b). Elevation also influenced postfire recovery via its indirect effect through functional dispersion (Fig. 3b). In summary, we found that communities with greater functional dispersion in fire response/tolerance traits were more resilient in productivity to wildfire.

The model including functional diversity based on seed mass was found to have a close fit to the data

Table 2 Direct, indirect, and total standardized effects on resilience (productivity response) based on path analyses. Significant effects in bold, NS = nonsignificant relationships. Italicized values indicate marginally significant values ($P < 0.1$).

Biodiversity measure	Predictor	Pathway to productivity	Effect
Species richness	Species richness (SR)	Direct	<i>−0.15</i>
		Indirect through SR	NS
		Total effect	NS
	Mean annual temperature	Direct	NS
		Indirect through SR	NS
		Total effect	NS
	Mean annual precipitation	Direct	NS
		Indirect through SR	NS
		Total effect	NS
	Slope	Direct	0.32
		Indirect through SR	NS
		Total effect	0.32
	Aspect	Direct	<i>−0.16</i>
		Indirect through SR	<i>0.02</i>
		Total effect	<i>−0.14</i>
	Elevation	Direct	NS
		Indirect through SR	NS
		Total effect	NS
Fire resistance/tolerance	Functional dispersion (FDis)	Direct	0.28
		Indirect through FDis	NS
		Total effect	NS
	Functional richness (FRic)	Direct	<i>−0.20</i>
		Indirect through FDis	NS
		Total effect	NS
	Mean annual temperature	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Mean annual precipitation	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Slope	Direct	0.32
		Indirect through FDis	<i>0.09</i>
		Total effect	NS
	Aspect	Direct	<i>−0.14</i>
		Indirect through FDis	0.04
		Total effect	0.04

Table 2 (continued)

Biodiversity measure	Predictor	Pathway to productivity	Effect
Seed mass	Elevation	Direct	−0.38
		Indirect through FDis	0.18
		Total effect	−0.04
	Functional dispersion (FDis)	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Functional richness (FRic)	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Mean annual temperature	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Mean annual precipitation	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Slope	Direct	0.32
		Indirect through FDis	NS
		Total effect	0.32
	Aspect	Direct	NS
		Indirect through FDis	NS
		Total effect	NS
	Elevation	Direct	NS
		Indirect through FDis	NS
		Total effect	NS

($\chi^2 = 1.53$, $df = 4$, $P = 0.82$; RMSEA = 0.00; GFI = 0.997) but explained the least amount of the variance in productivity response to fire ($R^2 = 0.10$, Fig. 3c). In the final model, only slope had a direct effect on postfire recovery with there being a faster recovery of productivity in communities on steeper slopes (Table 2). Unlike the model with fire traits, we did not find that functional diversity (neither FRic nor FDis) of seed mass influenced postfire recovery.

Discussion

Ecosystem resilience is increasingly being promoted as a key concept in the conservation of ecosystem function in the face of global change (Mori *et al.*, 2013; Lavorel *et al.*, 2015; Reyer *et al.*, 2015). Moreover, it has been suggested that functional diversity may help promote resilience within a given ecosystem because the function of any given species lost to a disturbance can be replaced by other species in functionally diverse ecosystems (Holling, 1973; Sundstrom *et al.*, 2012). Although small-scale studies support the importance of functional diversity for resilience (e.g., Chillo *et al.*, 2011; Pillar *et al.*, 2013), our study is the first to scale up this relationship to the large spatial scales most relevant to land managers and conservation practitioners. Overall, we found that functional diversity in traits associated with fire tolerance/resistance was a better predictor of how quickly vegetation productivity recovered following wildfire than species richness or the functional diversity of seed mass. Our results provide novel support that high functional dispersion in traits associated with fire tolerance/resistance may contribute to the recovery of productivity after wildfire across a wide range of ecosystems from cold desert woodlands to forested mountains (Table S1).

Species richness was a poor predictor of the resilience of communities, and our model explained little of the variation in recovery of productivity with richness only having a marginal effect ($P = 0.07$). As the diversity–resilience relationship is predicted to be strongest in ecosystem with many functional strategies for coping with a disturbance (Holling, 1973; Walker, 1995; Elmqvist *et al.*, 2003; Suding, 2011), our results suggest that species richness is a poor proxy for the diversity of functional strategies among species within the ecosystems studied here. This result supports trait-based analyses suggesting that functional diversity is a better metric than species diversity for predicting ecosystem response to environmental change (Lavorel & Garnier, 2002; Diaz *et al.*, 2004; McGill *et al.*, 2006). Importantly, for the diversity–resilience relationship, our results reinforce existing concerns about species richness. By itself, species richness may be a poor indicator of an ecosystem's ability to maintain biodiversity and ecosystem function over long time periods (Fleishman *et al.*, 2006).

We found that communities with high functional dispersion and low functional richness in traits associated with fire tolerance/resistance recovered more quickly from wildfire (Fig. 3b). Plant species have many adaptations to fire (Keeley *et al.*, 2011), and our results suggest that to recover productivity after a wildfire the

breadth of the overall trait space (high functional richness) is less important than having species with diverse, but not necessarily broadly different, strategies (high functional dispersion). For example, our results suggest that managers could build ecosystems more resilient to fire by restoring species with a diversity of just a few strategies (e.g., just resprout ability and fire tolerance) rather than focusing on including all possible strategies (e.g., fire tolerance, fire resistance, and resprout ability). While our results suggest a slightly more nuanced version of the functional diversity–resilience relationship, the basic principle remains the same – that some degree of increased functional diversity (functional dispersion in our case) promotes ecosystem resilience. As this is one of the first studies to assess multiple metrics of functional diversity in the resilience of productivity, we do not know whether this is a general trend and additional research investigating these patterns across other ecosystems and disturbances is needed.

The relationship between functional richness in traits associated with fire tolerance/resistance and resilience was influenced indirectly by aspect, where communities on north-facing aspects had higher functional richness. This negative relationship between functional richness and aspect may result from cooler/more benign microclimates on north-facing aspects supporting a wider range of functional strategies (Kleidon & Mooney, 2000; Currie *et al.*, 2004; Spasojevic *et al.*, 2014) resulting in higher diversity of fire tolerance/regeneration traits and, in turn, lower resilience on north-facing aspects; these results contrast with work by Ireland & Petropoulos (2015) who found greater recovery on north-facing aspects in a fire in Western Canada. Moreover, the relationship between functional dispersion in traits associated with fire tolerance/resistance and resilience was influenced indirectly by elevation, where communities on at higher elevations had higher functional dispersion. This positive relationship between functional diversity and elevation may result from environmental filtering in low-elevation woodlands reducing the diversity of functional traits among co-occurring species (Weiher & Keddy, 1995; Spasojevic & Suding, 2012). Furthermore, we found that slope and elevation directly influenced resilience – greater recovery of productivity was observed on steeper slopes and at lower elevations. Lower elevations in this system have longer growing seasons (Weiss *et al.*, 2004; Crimmins *et al.*, 2008, 2011; Inouye, 2008) which may allow productivity to recover more quickly than higher-elevation systems where recovery may be hindered by the shorter growing season. The greater recovery of productivity on steeper slopes may not be an effect of slope *per se*, but could suggest that systems within

topographically complex landscapes may be more resilient to fire. Specifically, mesic sites (often found on flat/shallow slopes) often support greater densities of fire-intolerant species (Lydersen & North, 2012; Kane *et al.*, 2015) which may reduce the recovery of productivity postfire.

Functional diversity of seed mass did not influence recovery from wildfire (Fig. 3b). Seed mass is often related to a trade-off between dispersal ability and competitive ability where species often produce few large seeds that are thought to be better competitors or many small seeds that are thought to be better dispersers (Grime, 1977; Cadotte, 2007). In xeric forests with stand-destroying fires, this competition-colonization mechanism has been proposed to be one method in maintaining diversity (Clark & Ji, 1995), but our results do not support this hypothesis. However, it is important to note that while seed mass is generally, phylogenetically conserved (Moles *et al.*, 2005), the coarse nature of our seed mass data may have masked potential responses. Examinations with species-specific seed mass data may resolve the relationship between functional diversity of seed mass and the resilience of productivity to fire. Moreover, understanding the potential role of competition-colonization trade-offs for the recovery of productivity after a wildfire may have benefited from data on other dispersal traits (dispersal syndrome, seed release height) or traits associated with competition (specific leaf area, wood density), which together better describe these different plant strategies. However, these data are not currently available in existing trait databases for our focal species.

Understanding the properties underlying the resilience of an ecosystem can help to identify ecological disturbance thresholds past which ecosystem recovery may no longer be possible (Hobbs *et al.*, 2011; Suding, 2011). We found that topography may directly influence ecosystem resilience (slope directly influenced the recovery of productivity after wildfire) and macroclimate may influence underlying functional diversity within an ecosystem (Figs 3b,c). This result suggests that changes to these underlying ecosystem properties may fundamentally alter the resilience of an ecosystem in ways that may only be discernable by examining the multivariate links between ecosystem properties, functional diversity, and resilience. Combining path analysis, remote sensing, and trait databases with predictive models of vegetation change may prove a powerful approach to understand changes to ecosystem resilience and, more importantly, the potential for ecological thresholds to be crossed and subsequent regime shifts or ecosystem collapse (Scheffer *et al.*, 2001; Folke *et al.*, 2004).

Despite growing interest in the causes and consequences of ecosystem resilience and in understanding how local-scale processes 'scale up' to larger spatial scales, most studies to date have yet to integrate these concepts explicitly when testing the diversity-resilience relationship. It is important to note that issues still remain in scaling up local-scale processes to larger spatial scales. Our models explained a relatively small amount of the variation in the productivity response. Some of this unexplained variation likely reflects the coarse nature of the variables we used. For example, variation within a pixel in productivity, fire, or vegetation may contribute to our relatively low explanatory power. Similarly, research has shown that larger-scale climate data, such as the PRISM data we used here, are sensitive to topographic complexity (Luoto & Heikkinen, 2008), which may explain the lack of a role of macroclimatic variables in our study. Future research incorporating heterogeneity in factors such as stand age (e.g., Stephens *et al.*, 2013; Taylor *et al.*, 2014), finer resolution recovery measures (e.g., metrics derived from 30 m Landsat time series), or higher-resolution climate data (e.g., downscaled climate variables) may help increase the predictive power of our approach and lead to a greater understanding of the biodiversity-resilience relationship. However, our goal here was to assess the biodiversity-resilience relationship with existing tools that are readily available to land managers. While more detailed data could be collected using field surveys or by conducting trait measurements, the logistic support to conduct these studies is often lacking. Nonetheless, our study provides some of the first direct empirical evidence for functional diversity increasing resilience at the scale relevant to large-scale management.

Conclusions

Numerous studies have argued that resilience may be threatened by the observed and projected loss of species (Sala *et al.*, 2000) or functional diversity (Laliberté *et al.*, 2010) due to global change (Chapin *et al.*, 2000; Standish *et al.*, 2014). By merging the tools used in large-scale studies of biodiversity (i.e., remote sensing) with trait databases and multivariate analyses, our results highlight the power of combining theory based on local-scale studies with data from large spatial scales to understand pressing environmental issues. This approach has great potential to allow us to better predict how global change may alter ecosystem resilience and recognize when critical thresholds may be crossed.

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Supporting Information

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

Table S1. General information about the dataset broken down by the 16 targeted vegetation types.

Table S2. General information about the dataset broken down by the 133 unique fire events.