Quantifying pyrodiversity and its drivers

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Abstract

Pyrodiversity likely begets biodiversity in many ecosystems, yet no consensus surrounds how best to quantify the phenomenon and its drivers remain largely untested. We present a generalizable functional diversity approach for measuring pyrodiversity, which incorporates multiple fire regime traits and can be applied across scales. Further, we tested the socioecological drivers of pyrodiversity among forests of the western United States. Largely mediated by burn activity, pyrodiversity was positively associated with actual evapotranspiration, climate water deficit, wilderness designation, elevation, and topographic roughness but negatively with human population density. These results indicate pyrodiversity is maintained in productive areas with strong annual dry periods and minimal fire suppression. This novel approach along with an improved understanding of pyrodiversity's drivers can facilitate future studies investigating how the pyrodiversity-biodiversity relationship varies among taxa, regions, and fire regimes.

Introduction

Fire is a fundamental ecological process (McLauchlan *et al.* 2020) that plays a central role in biome distribution and biodiversity globally (Bond *et al.* 2005; He *et al.* 2019). Fire patterns and their ecological consequences differ according to a number of important fire regime characteristics including burn frequency, severity, seasonality and spatial pattern (Keeley *et al.* 2011; van Wagtendonk *et al.* 2018). Much effort has gone into quantifying the central tendencies of these fire regime characteristics (e.g. mean fire return interval) and their underlying drivers (Agee 1996; Krawchuk & Moritz 2011; Archibald *et al.* 2013), but until recently what determines the inherent variation of fire regime characteristics, known as pyrodiversity, has received little attention. Martin and Sapsis (1992) first proposed pyrodiversity begets biodiversity by creating heterogeneous landscapes composed of dissimilar habitats and ecological niches. Since the theory was formalized, the potential importance of heterogeneity in fire regimes for ecosystem pattern and function has gained increasing attention both in research and ecosystem management (Parr & Andersen 2006; He *et al.* 2019). However, the expanded scrutiny has come with little consistency in definition or application of the pyrodiversity concept. A generalizable approach for quantifying pyrodiversity and an improved characterization of the phenomena's socioecological drivers is necessary for advancing understanding of its ecological importance.

The presumed link between pyrodiversity and biodiversity has influenced conservation efforts, particularly where prescribed burning or "patch mosaic burning" is used to diversify fire histories across a managed landscape (Parr & Andersen 2006). However, the development of robust ecological linkages to pyrodiversity has been hampered by our limited ability to fully capture relevant fire history components with sufficient spatial resolution, and temporal extent. This limitation may no longer apply as computing capabilities and spatial data availability have advanced considerably in recent years (e.g. Parks *et al.* 2019). For example, the "visible mosaic" represented by the landscape pattern created by the most recent wildfire and subsequent

successional processes can be easily observed (Minnich 1983; Turner & Romme 1994). However, observing the "invisible mosaic" that includes components of fire history such as the timing and severity of previous fire events requires access to remotely sensed fire histories. Ecological legacies attributable to this invisible mosaic nevertheless can influence biodiversity, and assessing its relative importance may be necessary for effective conservation in fire-prone ecosystems (Parr & Andersen 2006; Brown & York 2017).

The complexity associated with distilling relevant fire regime components (subsequently referred to as "traits") into a measure of pyrodiversity has resulted in varied approaches. Often these methods have focused a single fire regime trait such as burn severity (Tingley *et al.* 2016; Steel *et al.* 2019) or frequency (Taylor *et al.* 2012; Brown & York 2017). Such approaches implicitly assume a single trait serves as a surrogate for other fire regime characteristics and captures the most relevant aspects of pyrodiversity (He *et al.* 2019). This is likely a valid assumption in some cases, but without an understanding of how fire regime traits covary this can result in misleading conclusions (Keeley *et al.* 2011). Other studies have incorporated multiple traits and treated unique combinations as distinct "species" when applying biodiversity metrics such as Simpson's diversity index (Ponisio *et al.* 2016). However, traditional diversity metrics do not account for the trait-distance between species and in the case of fire histories, definitions of species are sensitive to how continuous measures are classified into levels (e.g. four or more classes of burn severity). Hempson et al. (2018) proposed perhaps the most generalizable method of assessing multiple dimensions of pyrodiversity by quantifying pyrodiversity as the multivariate range (convex hull) of four fire traits. However, their method is limited to coarse-scale analyses and is not able to capture critical within-fire traits, such as variation in burn severity and spatial pattern (i.e. patch size). Together these assessments and others provide valuable contributions to our understanding of pyrodiversity's ecological role, but a more comprehensive and consistent approach is necessary to test whether pyrodiversity promotes biodiversity absolutely or if the relationship varies among ecosystems and taxa.

Fire regime central tendencies are controlled by climate, topography and human influence (Agee 1996; Archibald *et al.* 2013), and are reciprocally dependent on the structure and flammability of extant vegetation (Bond *et al.* 2005). Through the annual and seasonal availability of solar energy and water balance, climate determines distributions of vegetation types, primary productivity and fuel flammability (Stephenson 1998; Krawchuk & Moritz 2011). Topography also influences water balance, but can further exert direct control on fire behavior (van Wagtendonk *et al.* 2018), which in the aggerate likely influences fire patterns across landscapes (Povak *et al.* 2018; Hessburg *et al.* 2019). Humans have influenced wildland fire for millennia either through direct management, accidental ignitions, or indirectly through alterations of vegetation via land-use change (Marlon *et al.* 2008; Bowman *et al.* 2011; Archibald *et al.* 2013), but many areas have shifted from historic fire use that was locally driven and variable across landscapes to contemporary broad-scale fire management (dominated by suppression) that has homogenized landscapes (Hessburg *et al.* 2005; Marlon *et al.* 2012). These underlying drivers likely influence variation in fire patterns as well, either directly or as mediated by total burn activity.

Here we develop a comprehensive method for quantifying pyrodiversity using four fire regime traits within a functional diversity framework. We apply this measure of pyrodiversity broadly across all forested areas in the western United States and assess how pyrodiversity varies with climate, topography and human influence. This approach is fully reproducible, can be applied from fine- to broad-scales using associated R code, and can help advance our understanding of the role of pyrodiversity in the maintenance of biodiversity and ecological function.

Material and Methods

Pyrodiversity Calculation

We calculate pyrodiversity using a measure of functional dispersion (FDis) defined by Laliberté and Legendre (2010), and applied via the "FD" R package (Laliberté *et al.* 2014). FDis is similar to Rao's quadratic entropy and is analogous to the univariate weighted mean absolute deviation. It is independent of species richness (Laliberté & Legendre 2010), which is preferable when the boundaries between species are unclear and the

number of species varies among communities. FDis measures the mean multidimensional distance of unique species from the centroid of a community, weighted by abundance (Fig. 1a). In the case of pyrodiversity, unique combinations of fire regime traits (fire histories) are considered individual species, a landscape is considered the community of interest, and the abundance is calculated as the frequency (number of pixels) of each unique history. A functional diversity approach is an improvement on more traditional measures of diversity (e.g. richness and Simpson's diversity) because it incorporates information about distance of individuals in multidimensional trait-space rather than assuming each unique combination of fire histories are equally and fully distinct. For example, when using Simpson's diversity index, two points burned by the same fires but with slightly different severity would be considered unique, as well as equally different from a pixel with no recent fire history despite the two burned pixels supporting relatively similar habitat. Functional richness, as measured by the volume of the minimum convex hull, can also be a useful metric of pyrodiversity (Hempson *et al.* 2018), but is sensitive to outliers and thus not a reliable estimator of dispersion (Laliberté & Legendre 2010). Finally, FDis allows for differential weighting of traits, which allows explicit testing of the relative importance of different components of pyrodiversity.

Generation of trait surfaces

We used four fire regime traits to calculate pyrodiversity: 1) fire return interval (frequency), 2) burn severity, 3) burn season, and 4) patch size (Fig. 1b). These traits are commonly used to define fire regime groups, are important determinants of ecosystem process in fire-adapted systems (Agee 1996; van Wagtendonk *et al.* 2018), and follow the original characteristics of pyrodiversity defined by Martin and Sapsis (1992). We mapped each of the four fire regime traits across the western United States using fire perimeter data from the national Monitoring Trends in Burn Severity database (www.mtbs.gov). This database includes all moderate to large fires in the region between 1984 and 2018 (> 404 ha; Eidenshink *et al.* 2007). Burn intervals were calculated as the difference between burn years of overlapping fire perimeters, as well as the first and final year of the dataset. Burn season was determined by the ignition date and were transformed to cosine of radians to account for the cyclical nature of date (e.g. so that the last and first day of the year are consecutive). Burn severity was calculated for each fire using Landsat imagery (TM and OLI sensors) and Google Earth Engine following Parks et al. (2019). The Parks model uses a Random Forest Algorithm to estimate values of composite burn index (CBI) at a resolution of 30 m. Model validation shows severity estimates are most accurate in forest ecosystems of western North American (Parks *et al.* 2019). We calculated patch size by defining distinct patches in each burn year using the CBI categories of unchanged, low-, moderate- and high-severity as defined by Miller and Thode (2007).

When calculating contemporary fire regime traits, values are often averaged across a period of record or only the most recent fire event is used. For example, fire frequency could be quantified as the mean of inter-fire intervals since reliable records began or the time since the previous fire (Steel *et al.* 2015). Both options are sub-optimal if the phenomenon of interest (e.g., biodiversity) is sensitive to recent events but previous fires (the "invisible mosaic") maintain some influence over landscape pattern and process (Brown & York 2017). We bridge these extremes by implementing a recency-weighted average when calculating pixel-wise trait values. Specifically, trait values from recent fires (or intervals) receive the greatest weight with the weight or importance of earlier events decaying with order. We rely on future applications of this pyro-diversity method to test and parameterize this importance decay rate for the ecosystem and processes of interest. Here we assigned a decay rate of 0.5, for which each prior value receives half the weight of the more recent. We chose to weight by fire order rather than time or interval length to avoid confounding between weighting and the fire frequency trait being measured. Trait rasters using the 0.5 decay rate can be found at https://figshare.com/articles/Pyrodiversity_westCONUS/12478832 and code is available at https://github.com/zacksteel/pyrodiversity for generating custom trait surfaces for future research. These data can be used to calculate pyrodiversity either across broad extents as demonstrated here or locally around biodiversity survey locations.

Pyrodiversity Trait Covariance

While FDis accounts for redundancy among traits (Laliberté & Legendre 2010), understanding how fire traits

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covary is valuable for categorizing fire regime groups, as well as assessing the mechanisms by which variation in fire traits affects ecosystem pattern and process. We calculated correlations among the four pyrodiversity traits at the watershed scale. To test whether correlations varied with the amount of recorded fire history, we systematically filtered out less frequently burned watersheds with increasing higher thresholds of number of fires recorded. Specifically, correlations were made among traits for all study watersheds with minimum number of fires ranging from zero to fifteen.

Pyrodiversity drivers

We assessed the hypothesized drivers of climate, topography and human influence on pyrodiversity using a 1) pyrodiversity model and a 2) burn activity model. These models represent direct and indirect (burn activity-mediated) effects on pyrodiversity, respectively (Fig. 1c). We model direct effects on pyrodiversity as:

[Eq. 1]

$$
\begin{aligned}
\text{pyrodiversity} y_{i,j} \sim\ & Beta(\overline{P}_{i,j}, \theta) \\
logit(\overline{P}_{i,j}) =\ & \alpha_0 + \alpha_j + \\
& \beta_{\text{AET}} * X_{1,i} + \beta_{\text{CWD}} * X_{2,i} + \beta_{AET*CWD} * X_{1,i} * X_{2,i} + \\
& \beta_{\text{elev}} * X_{3,i} + \beta_{\text{rough}} * X_{4,i} + \beta_{elev*rough} * X_{3,i} * X_{4,i} + \\
& \beta_{\text{pop.den}} * X_{5,i} + \beta_{\text{wild}} * X_{6,i} + \\
& \beta_{\text{prop.burn}} * X_{7,i} + \beta_{\text{prop.burn}^2} * X_{8,i} \\
\alpha_j \sim\ & Normal(0, \sigma_{HUC4})
\end{aligned}
$$

Where actual evapotranspiration (β_{AET}), accumulated climate water deficit (β_{CWD}) and their interaction ($\beta_{AET*CWD}$) are estimates of climatic effects. Elevation (β_{elev}), roughness (β_{rough}), and their interaction ($\beta_{elev*rough}$) are topographic effects. Population density ($\beta_{\text{pop.den}}$) and proportion of watershed i 's land area in wilderness (β_{wild}) are surrogates for human influence. We hypothesize much of the effects of these ultimate drivers are mediated by burn activity, here represented by proportion of flammable area burned between 1985 and 2018 ($\beta_{\text{prop.burn}}$) and its quadratic ($\beta_{\text{prop.burn}^2}$). This metric is cumulative and can exceed 1 in the case of multiple burns in the same area. Our sample unit i are forested watersheds delineated by the 10-digit Hydrologic Unit Code (HUC10; median area = 755 km^2). We account for spatial structuring of these units by including larger watershed j (2-digit HUC2s; median area = 437,000 km^2), within which HUC10s are nested, as varying random intercepts. In total we assessed 1971 watersheds and 3306 fires.

To quantify indirect effects on pyrodiversity, we modeled proportion burned area as a function of the same climate, topographic, and human influence variables as in equation 1, excluding $\beta_{\text{prop.burn}}$ and $\beta_{\text{prop.burn}^2}$ (Eq. S1). This burn activity model is linked with the pyrodiversity model via a Bayesian multivariate and multi-level model using the brms and rstan packages in R (Bürkner 2017; Stan Development Team 2018; R Core Team 2019). The multivariate model allows us to predict direct and indirect effects of the ultimate drivers and quantify their combined effect while properly propagating uncertainty through the model chain. In this way marginal effects are estimated by first fitting the burn activity model to generate a posterior distribution of proportion burned area and subsequently incorporating this full distribution as predictors of $\beta_{\text{prop.burn}}$ and $\beta_{\text{prop.burn}^2}$ in the pyrodiversity model. Model code, data, and additional methodological details can be found in the supplementary material.

Results

Watersheds experienced a wide range of fire activity during the study period, with a median of 2 fires (mean = 3; range: 0-48). These fires resulted in a median of 3.6% (mean = 16%; range = 0-250%) of the flammable area burned. The median watershed had a pyrodiversity value of 0.04 (mean = 0.09; range = 0-0.35). Hotspots of pyrodiversity include watersheds in the North Cascades of Washington state, the Northern Rocky Mountains within and around the Frank Church-River of No Return Wilderness, Yellowstone National

Park, the Mogollon Rim region of Arizona and New Mexico, and the mountainous regions of California especially the Klamath Mountains, and parts the Sierra Nevada (Fig. 2).

When including watersheds with no recent fire history, variation in burn frequency, patch size, and severity are highly correlated. However, when sequentially excluding areas with less active fire histories, theses correlations quickly dissipate. The correlation between frequency and patch size approximates 0.5 when considering watersheds with 14 or more fires since 1985. The frequency-severity correlation drops below 0.5 once watersheds with fewer than 8 fires are excluded. Patch size and severity plateau at approximately 0.65 when considering watersheds with 10 or more fires. Seasonality is largely uncorrelated with the other three fire regime traits, starting between 0.13 and 0.23 when watersheds with at least one fire are included, and dropping below or near zero when restricting correlations to areas with more active fire histories (Fig. 3).

Climate, topography, and human influence metrics show clear effects on proportion of flammable area burned between 1985 and 2018. Proportion wilderness followed by climatic variables showed the strongest relative effects. Proportion burned area increased with proportion wilderness with a scaled effect (β_{wild}) of 0.70 (90% confidence interval [CI] = 0.53, 0.86). Climatic water deficit (CWD) also had a strong positive effect (β_{CWD} = 0.53; CI = 0.47, 0.59), as did actual evapotranspiration (AET; β_{AET} = 0.10; CI = 0.048, 0.16), and the interaction of CWD and AET ($\beta_{AET*CWD}$ = 0.27; CI = 0.23, 0.31). Both topographic roughness (β_{rough} = 0.15; CI = 0.11, 0.19) and elevation (β_{elev} = 0.084; CI = 0.011, 0.16) are positively associated with burn area, but these variables interact negatively ($\beta_{elev*rough}$ = -0.10; CI = -0.14, -0.068). Human population density was negatively associated with proportion burned area with an effect estimate ($\beta_{\mathrm{pop.den}}$) of -0.15 (CI = -0.183, -0.109) (Table S1).

When proportion of flammable area burned is included as a predictor of pyrodiversity it has by far the greatest effect, with much of the ultimate effects of climate, topography and human influence being mediated by this variable. The proportion burned area is strongly positively associated with pyrodiversity ($\beta_{\mathrm{prop.burn}}$ = 2.5; CI = 2.4, 2.5), with a negative quadratic term ($\beta_{\mathrm{prop.burn}^2}$ = -0.78; CI = -0.80, -0.77). These parameter estimates indicate a pyrodiversity peak when an average of 63% (CI = 61%, 65%) of a watershed has burned between 1985 and 2018 (Table S1; Fig. 4a). This apparent maximum equates to a 53-year fire rotation (CI = 51, 54 years), a measure of the time required to burn an area equivalent to the size of a landscape (Heinselman 1973). In some cases, the combined direct and indirect effects on pyrodiversity are reinforcing (e.g. topography) while others dampen their ultimate influence (e.g. climate). For a given level of fire activity, pyrodiversity is negatively associated with CWD (β_{CWD} = -0.048; -0.068, -0.029) and AET (β_{AET} = -0.019; CI = -0.035, -0.003) with a positive interaction ($\beta_{AET*CWD}$ = 0.014; CI = 0.001, 0.027) between the two climate variables. The combined marginal indirect and direct effects show CWD and AET interact to produce low pyrodiversity when watersheds lack an annual dry period but high pyrodiversity in productive areas coupled with dry periods (Fig. 4b). Similar to the burn activity model, elevation (β_{elev} = 0.035; CI = 0.013, 0.057) and topographic roughness (β_{rough} = 0.016; CI = 0.004, 0.028) are positively associated with pyrodiversity, with a likely slight negative interaction between the two ($\beta_{elev*rough}$ = -0.013; CI = -0.026, 0.00). Consequently, pyrodiversity is maximized either at higher elevations or relatively low elevations with variable topography (Fig. 4c). When accounting for the level of burn activity, the direct effect of human population density on pyrodiversity is positive ($\beta_{\mathrm{pop.den}}$ = 0.029; CI = 0.017, 0.04) and proportion wilderness shows no clear direct effect (β_{wild} = 0.022; CI = -0.022, 0.066). Combined with a clearly positive indirect effect of proportion wilderness, and negative indirect effect of population density, watersheds in designated wilderness have higher pyrodiversity on average, while more populated areas have marginally lower pyrodiversity (Fig. 4d & e).

Discussion

The concept of pyrodiversity has received considerable attention in recent years as the inevitability of wildfire and its fundamental role in many ecosystems is increasingly recognized. While pyrodiversity clearly has appeal and applicability to many ecological disciplines, to date the concept remains nebulous with varied and often narrow definitions. Here we present a generalizable functional diversity approach to quantifying pyrodiversity and tested its drivers across forested watersheds of the western United States. At the HUC10 watershed scale,

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pyrodiversity was strongly but non-linearly related to fire activity with an observed pyrodiversity peak when approximately 63% of the flammable land area burned over the 33-year study period (equivalent to a 53-year fire rotation). Of the ultimate drivers tested, climate and proportion wilderness showed the strongest controls on pyrodiversity with productive but seasonally dry watersheds in wilderness areas most often characterized by variable fire histories. Areas with high topographic roughness or high elevation as well as areas with low human population density also tended to be more pyrodiverse. Correlations among individual pyrodiversity traits declined with the number of fires observed in a given watershed, suggesting the use of a single fire regime trait (e.g. severity) may be appropriate for describing pyrodiversity following isolated fire events but is insufficient for characterizing landscapes with active fire regimes. A multi-dimensional approach supported by moderate- to high-resolution spatial data is likely necessary to capture the inherent complexity of fire across landscapes and bioregions.

Drivers of pyrodiversity

Climate exerts strong controls on biome distribution and fire regimes globally, while topography is often omitted from or considered less important in assessments at the fire regime level (Whittaker 1975; Stephenson 1990; Archibald *et al.* 2013). Here we establish that climatic control extends to variation in current fire patterns both directly and indirectly as mediated by burn activity (Fig. 4b). Relative to climate, we found elevation and topographic roughness to have small but meaningful effects on proportion area burned and pyrodiversity (Fig. 4c; Table S1). Hempson et al. (2018) found a negative relationship between pyrodiversity and precipitation with a pyrodiversity peak in dry areas of Africa, but no discernible effect of topographic roughness. This observed relationship with precipitation is consistent with our finding that pyrodiversity increases with climatic water deficit but is somewhat at odds with our finding of a positive relationship with actual evapotranspiration, which is related to precipitation. Together these assessments indicate pyrodiversity is dependent both on the production of vegetative biomass and its seasonal availability to burn as fuel. Topographic roughness may be important in supporting intra-fire variability if rapid changes in terrain disrupt fire behavior and break up patches of fire severity (Estes *et al.* 2017; Povak *et al.* 2018). However, topography may exert little control on variability of fire-level metrics such as fire size and maximum burn intensity (Hempson *et al.* 2018).

We interpret the negative relationship between human population density and pyrodiversity to reflect highly successful fire exclusion and suppression efforts across much of North America (Marlon *et al.*2012). Changes in vegetative structure and fire patterns attributable to fire suppression have already been documented in fire-adapted ecosystems (Hessburg *et al.* 2005; Steel *et al.* 2015; Lydersen & Collins 2018), and these findings indicate pyrodiversity is almost certainly lower in such systems than historic levels. The strong positive effect of proportion wilderness likely reflects the fire policy of many US wilderness areas, which strive to restore pre-suppression era fire regimes (Stephens *et al.* 2016). Wilderness areas that explicitly allow lightning-caused wildfires to be used for resource objectives (van Wagtendonk 2007) appear to contain greater levels of pyrodiversity. However, the benefit of wilderness is likely highly context dependent. Some of the most pyrodiverse areas in the western United States fall within wilderness areas such as Yosemite National Park (Collins *et al.* 2007), Frank Church-River of No Return Wilderness, Bob Marshall Wilderness and the Gila Wilderness (Parks*et al.* 2014), but not in the wildness areas of Olympic National Park characterized by a very wet climate. Interestingly, Sequoia-Kings Canyon National Park in the southern Sierra Nevada of California was an early pioneer in the use of both prescribed and managed natural fire (van Wagtendonk 2007; Stevens *et al.* 2020) but does not appear particularly pyrodiverse, while an area just to its south (Kern Plateau, Sequoia National Forest) does (Fig. 2).

The full nature of human influence on pyrodiversity is likely more complex than can be captured by the necessarily coarse measures of population density and wilderness designation. At sub-watershed scales, the use of prescribed and cultural burning are likely important contributors to pyrodiversity in some areas (Lewis 1973; Bird *et al.* 2018). Tribal burning in California serves an array of cultural purposes and creates diverse habitat mosaics that sustained meadows, woodlands, wetlands, coastal prairies, and grasslands (Lewis 1973; Anderson 2013). Many Tribes used a system of patch burning that manipulated vegetation at fine spatial

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scale to meet their management objectives. How these cultural fire regimes impact pyrodiversity deserves continued evaluation where fire histories exist at finer scales than the national MTBS dataset.

Updating pyrodiversity-biodiversity theory

Fire dramatically shapes vegetation community composition and pattern, creating heterogeneity in habitat types and successional stages across space and time (Turner 2010). Landscape heterogeneity and associated diversity of ecological niches are often tightly tied to greater levels of biodiversity (Turner & Gardner 2015). These well-established associations are the basis for the proposal that pyrodiversity begets biodiversity (Martin & Sapsis 1992). In the three decades since Martin and Sapsis (1992) first articulated the hypothesis, an increasing number of studies have provided evidence to support their theory (Ponisio *et al.* 2016; Tingley *et al.* 2016; Brown & York 2017; Beale *et al.* 2018; Steel *et al.* 2019), while others have found the relationship to be weak or non-existent (Parr *et al.* 2004; Davies *et al.* 2012; Kelly *et al.* 2012). These occasionally conflicting findings as well as our results showing high variation in pyrodiversity across ecosystems indicate the functional relationship between pyrodiversity and biodiversity may not be absolute but rather is limited or context dependent. For example, we observed a maximum pyrodiversity among watersheds with an approximate 53-year fire rotation. This rate of fire activity and pyrodiversity is unlikely to optimize biodiversity across all ecosystems with highly varied historical relationships with wildfire.

We propose constraints to the pyrodiversity-biodiversity relationship are related to an ecosystem's historic fire regime and that on average biodiversity may be maximized at levels of pyrodiversity characteristic of the conditions under which ecological communities assembled. This updated hypothesis leads to expected and testable functional forms under different conditions. In fire regimes characterized by relatively frequent fire and variable high-severity patch sizes, such as those found in the semi-dry forests of North America, the peak in biodiversity may occur at moderate to high levels of pyrodiversity (Fig. 5a). In less active fire regimes such as wet temperate forests, the biodiversity peak may occur at lower levels of pyrodiversity either because fire-adapted species have been filtered from the regional species pool and/or fire-adaptive traits have not evolved in situ (Miller & Safford In Press). Ecosystems with little variation in burn severity such as savannas may see an analogous mid-pyrodiversity peak (Davies *et al.* 2018), above which more severe fires threaten to convert the system to grassland (Fig. 5b). The threat of tipping points or type-conversions may be especially acute in ecosystems like tropical rainforest which have little to no history of lightning wildfire and to which native species are poorly adapted (Silveira *et al.* 2016). Where fire activity and pyrodiversity increase in these ecosystems the biodiversity response may be predominantly negative (Fig. 5c). The theoretical dependence of the pyrodiversity-biodiversity relationship on historic fire regimes is supported by Miller and Safford (In Press) who provide evidence that plant biodiversity is maximized where burn severities match the predominant historical disturbance regime of an ecosystem. Alternatively, He et al. (2019) proposed the association is constrained by species:area relationships and that at very high levels of pyrodiversity declining patch sizes limit the number of species present. This hypothesis predicts a biodiversity peak at moderate to high levels of pyrodiversity similar to Fig. 5c.

In addition to uncertainties surrounding the mechanisms of the pyrodiversity-biodiversity relationship, perceiving the full pyrodiversity-biodiversity functional form is dependent on the range of pyrodiversity observed. Partially observed relationships could be attributed to limited sampling effort or modern shifts in fire regimes away from historic conditions. For example, where fire activity has been artificially reduced, pyrodiversity may be lower than the biodiversity optimum across a study region and biodiversity would appear to increase with pyrodiversity absolutely (Steel *et al.* 2019; Fig. 5i). Indeed, Martin and Sapsis (1992) developed their original theory in the context of extensive fire-suppression in the mixed-conifer forests of California, where the detrimental effects of an uncharacteristic lack of pyrodiversity was perhaps most apparent.

Changing fire regimes

Humans have altered fire regimes directly through management and indirectly by altering the earth's climate, and such shifts are almost certainly also changing pyrodiversity. Perhaps the most clear effects of altered fire regimes on pyrodiversity are seen where fire exclusion and suppression policies have dramatically reduced

burned area and shifted fire severity patterns in fire-adapted forests (Mallek *et al.*2013). Conversely, climate change is increasing fire activity by lengthening fire seasons and increasing water deficits (Flannigan*et al.* 2009; Abatzoglou & Williams 2016; Westerling 2016; Hessburg *et al.* 2019). Given the strong link between climatic water deficit, fire activity and pyrodiversity, these changes may increase pyrodiversity in the short term where deficits of fire activity currently exist but could result in lower levels of pyrodiversity for areas with high levels of contemporary burn activity (Fig. 4a). Additionally, in many areas larger fires are increasingly accompanied by ever larger and simpler shaped patches of high-severity effects (Stevens*et al.* 2017; Steel *et al.* 2018), which could result in lower pyrodiversity at fine scales. Where the frequency of high-severity fire exceeds the natural range of variation of an ecosystem, higher rates of type-conversion (e.g. from forests to shrubland) may occur (Coppoletta *et al.* 2016; Welch *et al.* 2016). This may be particularly problematic in dry areas where a further increase in water deficit can lead to a consistent loss in productivity (Hessburg *et al.* 2019) or when wildfires interact with other climate-exacerbated disturbances such as periodic drought and beetle infestations (Coop*et al.* In Press). Ultimately, climate-related shifts in pyrodiversity are likely to be uneven across the western United States and globally. How these changes impact biodiversity and ecosystem process may depend on whether emerging pyrodiversity patterns result in a dramatic departure from historic fire regimes (Fig. 5).

Conclusions

We developed a generalizable trait-based approach and provide reproducible code for quantifying pyrodiversity at regional to local scales. This method has several advantages over previous efforts to quantify pyrodiversity: 1) It uses a functional diversity framework that captures multi-dimensional dispersion of pyrodiversity traits. 2) It leverages Landsat imagery and Google Earth engine to measure intra-fire variation anywhere validated severity models exist. While we demonstrate its utility at the regional scale, the 30m resolution of the underlying data also allow calculation of pyrodiversity at scales relevant to point or plot-based biodiversity survey methods. 3) This method allows flexible weighting of individual fire traits and the relative importance of the visible/invisible mosaic. This novel approach, along with an improved understanding of the ultimate drivers of pyrodiversity provides opportunities to more consistently and comprehensively test the influence of pyrodiversity on biodiversity and other ecosystem processes. Doing so across regions, management approaches, and ecological communities will increase our ability to manage fire and conserve biodiversity as fire regimes continue to shift with accelerating global change.

Acknowledgements

References

Abatzoglou, J.T. & Williams, A.P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* , 113, 11770–11775.

Agee, J.K. (1996). *Fire Ecology of Pacific Northwest Forests* . Island Press.

Anderson, M.K. (2013). *Tending the Wild: Native American Knowledge and the Management of California's Natural Resources* . Univ of California Press.

Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L. & Bradstock, R.A. (2013). Defining pyromes and global syndromes of fire regimes.*PNAS* , 110, 6442–6447.

Beale, C.M., Mustaphi, C.J.C., Morrison, T.A., Archibald, S., Anderson, T.M., Dobson, A.P., *et al.* (2018). Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas.*ECOLOGY LETTERS* , 21, 557–567.

Bird, R.B., Bird, D.W., Fernandez, L.E., Taylor, N., Taylor, W. & Nimmo, D. (2018). Aboriginal burning

promotes fine-scale pyrodiversity and native predators in Australia's Western Desert. *BIOLOGICAL CON-SERVATION* , 219, 110–118.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist* , 165, 525–538.

Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., *et al.* (2011). The human dimension of fire regimes on Earth. *Journal of Biogeography* , 38, 2223–2236.

Brown, J. & York, A. (2017). Fly and wasp diversity responds to elements of both the visible and invisible fire mosaic.*INTERNATIONAL JOURNAL OF WILDLAND FIRE* , 26, 434–443.

Bürkner, P.-C. (2017). brms: An R Package for Bayesian multilevel models using Stan. *Journal of Statistical Software* , 80, 1–28.

Collins, B.M., Kelly, M., van Wagtendonk, J.W. & Stephens, S.L. (2007). Spatial patterns of large natural fires in Sierra Nevada wilderness areas. *Landscape Ecology* , 22, 545–557.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S., Higuera, P.E., Hurteau, M.D., *et al.* (In Press). Wildfire-driven forest conversion in western North American landscapes. *Bioscience* .

Coppoletta, M., Merriam, K.E. & Collins, B.M. (2016). Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* , 26, 686–699.

Davies, A.B., Eggleton, P., van Rensburg, B.J. & Parr, C.L. (2012). The pyrodiversity-biodiversity hypothesis: a test with savanna termite assemblages. *JOURNAL OF APPLIED ECOLOGY* , 49, 422–430.

Davies, H.F., McCarthy, M.A., Rioli, W., Puruntatameri, J., Roberts, W., Kerinaiua, C., *et al.* (2018). An experimental test of whether pyrodiversity promotes mammal diversity in a northern Australian savanna. *JOURNAL OF APPLIED ECOLOGY* , 55, 2124–2134.

Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B. & Howard, S. (2007). A Project for Monitoring Trends in Burn Severity.*fire ecol* , 3, 3–21.

Estes, B.L., Knapp, E.E., Skinner, C.N., Miller, J.D. & Preisler, H.K. (2017). Factors influencing fire severity under moderate burning conditions in the Klamath Mountains, northern California, USA.*Ecosphere* , 8, e01794.

Flannigan, M.D., Krawchuk, M.A., Groot, W.J. de, Wotton, B.M. & Gowman, L.M. (2009). Implications of changing climate for global wildland fire.*Int. J. Wildland Fire* , 18, 483–507.

He, T., Lamont, B.B. & Pausas, J.G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews* , 94, 1983–2010.

Heinselman, M.L. (1973). Fire in the Virgin Forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* , 3, 329–382.

Hempson, G.P., Parr, C.L., Archibald, S., Anderson, T.M., Mustaphi, C.J.C., Dobson, A.P., *et al.* (2018). Continent-level drivers of African pyrodiversity. *ECOGRAPHY* , 41, 889–899.

Hessburg, P.F., Agee, J.K. & Franklin, J.F. (2005). Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* , Relative Risk Assessments for Decision –Making Related To Uncharacteristic Wildfire, 211, 117–139.

Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., *et al.* (2019). Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests.*Front. Ecol. Evol.* , 7.

Keeley, J., Bond, W., Bradstock, R., Pausas, J. & Rundal, P. (2011).*Fire in Mediterranean Ecosystems: Ecology, Evolution and Management* . Cambridge University Press, Cambridge.

Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J., Clarke, M.F., *et al.* (2012). Managing fire mosaics for small mammal conservation: a landscape perspective. *Journal of Applied Ecology* , 49, 412–421.

Krawchuk, M.A. & Moritz, M.A. (2011). Constraints on global fire activity vary across a resource gradient. *Ecology* , 92, 121–132.

Laliberte, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology* , 91, 299–305.

Laliberte, E., Legendre, P. & Shipley, B. (2014). *FD: measuring functional diversity from multiple traits, and other tools for functional ecology* . R. .

Lewis, H. (1973). *Patterns of Indian burning in California: ecology and ethnohistory* . Anthropology Paper. Ballena Press, Romona, New Mexico.

Lydersen, J.M. & Collins, B.M. (2018). Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems* , 21, 1348–1363.

Mallek, C., Safford, H., Viers, J. & Miller, J. (2013). Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* , 4, art153.

Marlon, J.R., Bartlein, P.J., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., *et al.* (2008). Climate and human influences on global biomass burning over the past two millennia. *Nature Geosci* , 1, 697–702.

Marlon, J.R., Bartlein, P.J., Gavin, D.G., Long, C.J., Anderson, R.S., Briles, C.E., *et al.* (2012). Long-term perspective on wildfires in the western USA. *PNAS* , 109, E535–E543.

Martin, R. & Sapsis, D.B. (1992). Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In: *Proceedings of the Conference on Biodiversity of Northwest California Ecosystems* . Cooperative Extensions, University of California, Berkeley, CA.

McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., *et al.* (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* , 0, 1–23.

Miller, J.D. & Thode, A.E. (2007). Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment* , 109, 66–80.

Miller, J.E. & Safford, H. (In Press). Are plant community responses to wildfire contingent upon historical disturbance regimes? *Global Ecology and Biogeography* .

Minnich, R.A. (1983). Fire Mosaics in Southern California and Northern Baja California. *Science* , 219, 1287–1294.

Parks, S.A., Holsinger, L.M., Koontz, M.J., Collins, L., Whitman, E., Parisien, M.-A., *et al.* (2019). Giving Ecological Meaning to Satellite-Derived Fire Severity Metrics across North American Forests.*Remote Sensing* , 11, 1735.

Parks, S.A., Miller, C., Nelson, C.R. & Holden, Z.A. (2014). Previous Fires Moderate Burn Severity of Subsequent Wildland Fires in Two Large Western US Wilderness Areas. *Ecosystems* , 17, 29–42.

Parr, C.L. & Andersen, A.N. (2006). Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm.*CONSERVATION BIOLOGY* , 20, 1610–1619.

Parr, C.L., Robertson, H.G., Biggs, H.C. & Chown, S.L. (2004). Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* , 41, 630–642.

Ponisio, L.C., Wilkin, K., M'Gonigle, L.K., Kulhanek, K., Cook, L., Thorp, R., *et al.* (2016). Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology* , 22, 1794–1808.

Povak, N.A., Hessburg, P.F. & Salter, R.B. (2018). Evidence for scale-dependent topographic controls on wildfire spread. *Ecosphere* , 9, e02443.

R Core Team. (2019). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Silveira, J.M., Louzada, J., Barlow, J., Andrade, R., Mestre, L., Solar, R., *et al.* (2016). A Multi-Taxa Assessment of Biodiversity Change After Single and Recurrent Wildfires in a Brazilian Amazon Forest. *Biotropica* , 48, 170–180.

Stan Development Team. (2018). *RStan: the R interface to Stan* .

Steel, Z.L., Campos, B., Frick, W.F., Burnett, R. & Safford, H.D. (2019). The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. *Sci Rep* , 9, 1–11.

Steel, Z.L., Koontz, M.J. & Safford, H.D. (2018). The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecology* , 33, 1159–1176.

Steel, Z.L., Safford, H.D. & Viers, J.H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* , 6, art8.

Stephens, S.L., Collins, B.M., Biber, E. & Fule, P.Z. (2016). U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* , 7, e01584.

Stephenson, N. (1998). Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* , 25, 855–870.

Stephenson, N.L. (1990). Climatic Control of Vegetation Distribution: The Role of the Water Balance. *The American Naturalist* , 135, 649–670.

Stevens, J.T., Boisrame, G.F.S., Rakhmatulina, E., Thompson, S.E., Collins, B.M. & Stephens, S.L. (2020). Forest Vegetation Change and Its Impacts on Soil Water Following 47 Years of Managed Wildfire. *Ecosystems* .

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P. & Stephens, S.L. (2017). Changing spatial patterns of stand-replacing fire in California conifer forests. *Forest Ecology and Management* , 406, 28–36.

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012). Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *DIVERSITY AND DISTRIBUTIONS* , 18, 519–529.

Tingley, M.W., Ruiz-Gutierrez, V., Wilkerson, R.L., Howell, C.A. & Siegel, R.B. (2016). Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B: Biological Sciences* , 283, 20161703.

Turner, M.G. (2010). Disturbance and landscape dynamics in a changing world [1]. *Ecology* , 91, 2833–2849.

Turner, M.G. & Gardner, R.H. (2015). *Landscape ecology in theory and practice: pattern and process* . Second edition. Springer, New York.

Turner, M.G. & Romme, W.H. (1994). Landscape dynamics in crown fire ecosystems. *Landscape Ecol* , 9, 59–77.

van Wagtendonk, J.W. (2007). The History and Evolution of Wildland Fire Use. *fire ecol* , 3, 3–17.

van Wagtendonk, J.W., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E. & Fites-Kaufman, J.A. (2018). *Fire in California's Ecosystems* . Univ of California Press.

Welch, K.R., Safford, H.D. & Young, T.P. (2016). Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* , 7, e01609.

Westerling, A.L. (2016). Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 371, 20150178.

Whittaker, R.H. (1975). *Communities and Ecosystems* . Macmillan USA, New York.

Figures

Figure 1. A) A simplified example of how pyrodiversity is calculated using the functional dispersion metric (FDis), adapted from Laliberte & Lengendre (2010). x represents the location of j unique fire histories ("species") in multidimensional traits-space, c is the multi-dimensional trait-space centroid of a landscape ("community"), z_j is the trait distance of history j from c, and a_j is the frequency ("abundance") of history j within the landscape. FDis is calculated as the weighted mean distance from c. B) Fire trait surfaces used to calculate pyrodiversity for an example watershed. C) Conceptual model of the causes and effects of pyrodiversity. Solid lines represent direct effects and dashed lines represent mediated relationships.

Figure 2. Pyrodiversity of forested watersheds (HUC10s) in the western United States. Watersheds with less than 50% forest cover were not evaluated and are shown in white. The broader-scale HUC2 watersheds (clipped to the region of interest) are shown as black outlines.

Figure 3 . Correlations among watershed-level (HUC10) fire regime trait dispersion. Comparisons were made across a range of minimum fire numbers by sequentially removing watersheds with fewer recorded burns between 1985 and 2018.

Figure 4 . Drivers of watershed-scale pyrodiversity. A) cumulative percent of flammable area burned from 1985-2018, B) interacting climate effects of water deficit and actual evapotranspiration, C) interacting topographic effects of roughness and elevation, D) effect of wilderness designation, E) effect of human population density. B-E reflect both direct and burn activity-mediated effects. The effect of wilderness is modeled as a proportion of land area, but binary marginal effects are presented here for simplicity. Pyrodiversity is defined as the multivariate dispersion of fire frequency, severity, seasonality, and patch size.

Figure 5. Theoretical functional relationships between pyrodiversity and biodiversity. A positive and absolute relationship is shown as an orange dashed line and solid lines represent example ecosystems where the relationship is limited by the historic fire regime. a) Biodiversity may be greatest at high levels of pyrodiversity in mixed-severity fire regimes before habitat fragmentation or type conversion results in declines. b) In ecosystems with a history of infrequent fire or homogenous burn severities, biodiversity may benefit from some pyrodiversity, but high levels may result in unfilled ecological niches or type-conversion. c) Ecosystems with little natural wildfire may experience declines in biodiversity when any burning occurs due to a lack of fire-adapted traits in the regional species pool. Our ability to perceive the full functional form is limited by the environmental space sampled: i) when observing only low levels of pyrodiversity the instantaneous relationship would appear absolute and positive for all but the non-fire adapted fire regimes. ii) When observing only moderate levels of pyrodiversity, the functional relationship would appear flat or non-existent for b, but still linear for a. iii) When observing only high levels of pyrodiversity the relationship would appear weak or unrelated in many ecosystems but the magnitude of biodiversity would nevertheless depend on an ecosystem's distance from its optimum level of pyrodiversity.

Supplementary Material. Ancillary methods and results in support of the manuscript.

The figure plots Biodiversity (y-axis) against Pyrodiversity (x-axis), with curves labeled a, b, c, vertical shaded bands labeled i, ii, iii, and a dashed line.