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Pyrodiversity promotes avian diversity over the decade following forest fire

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An emerging hypothesis in fire ecology is that pyrodiversity increases species diversity. We test whether pyrodiversity—defined as the standard deviation of fire severity—increases avian biodiversity at two spatial scales, and whether and how this relationship may change in the decade following fire. We use a dynamic Bayesian community model applied to a multi-year dataset of bird surveys at 1106 points sampled across 97 fires in montane California. Our results provide strong support for a positive relationship between pyrodiversity and bird diversity. This relationship interacts with time since fire, with pyrodiversity having a greater effect on biodiversity at 10 years post-fire than at 1 year post-fire. Immediately after fires, patches of differing burn severities hold similar bird communities, but over the ensuing decade, bird assemblages within patches of contrasting severities differentiate. When evaluated at the scale of individual fires, fires with a greater heterogeneity of burn severities hold substantially more species. High spatial heterogeneity in severity, sometimes called 'mixed-severity fire', is a natural part of wildfire regimes in western North America, but may be jeopardized by climate change and a legacy of fire suppression. Forest management that encourages mixed-severity fire may be critical for sustaining biodiversity across fire-prone landscapes.

1. Introduction

A dominant theory in biogeography is that environmental diversity begets biodiversity [1,2], whether by promoting resource partitioning [3] or catalysing cross-trophic interactions [4]. Relatedly, the intermediate disturbance hypothesis asserts that disturbance can be a driver of diversity through sustaining species with widely different disturbance sensitivities and inhibiting dominance [5]. The term 'pyrodiversity', first coined in the ecological literature by Martin & Sapsis [6], encapsulates the idea that landscapes with greater heterogeneity in age, size and severity of post-fire patches would support a greater diversity of species. The different components of a fire regime (i.e. frequency, size, seasonality, spatial configuration and severity) that contribute to pyrodiversity [7,8] each may play independent or interactive roles in governing biodiversity.

The hypothesis that pyrodiversity begets biodiversity, although developed as a thought experiment independent of biodiversity theory [6], has become increasingly influential in guiding land management and biodiversity conservation [9–11]. Evaluations of the pyrodiversity–biodiversity hypothesis, however, have been equivocal, with different studies showing weak responses of species to pyrodiversity [11–13], strong responses to pyrodiversity [14,15] or no response [16,17]. Pyrodiversity–biodiversity tests have almost universally been conducted as tests of fire age structure, in which pyrodiversity is defined in terms of the diversity of differently aged post-fire patches across a landscape [11,13] or as spatial variation in the frequency or seasonal timing of fire [14]. There is little justification

for why the temporal aspect of fire regimes has been studied so much more intensely than other aspects of pyrodiversity, except that the time since last fire is perhaps the most readily quantifiable aspect of pyrodiversity [18,19].

By contrast, burn severity is a key aspect of fire regimes that has often been neglected in discussions and empirical tests of the pyrodiversity–biodiversity hypothesis. Burn severity is a measure of vegetative change that arises as a consequence of the interaction between fire intensity (i.e. how much heat is produced) and the pyro-sensitivity of vegetation (a complex species- and biome-specific trait). Intensity is not constant within a fire, but varies in response to topography, substrate, fuel loads and weather [7]. A single fire, although frequently classified by its average severity, creates a patchwork of different burn severities, ranging from high-severity zones with complete vegetative loss to unburned habitat refugia within the fire perimeter. Patches of high-severity fire can be expected to lead directly to increased gamma biodiversity by resetting successional processes and creating habitat for early seral reliant species [20]. Indeed, high-severity fire has been shown to be critical for many species [21], and there is some evidence that in certain systems, biodiversity may increase as a result of high-severity fire [22,23]. Implicit in the pyrodiversity–biodiversity hypothesis, however, is that biodiversity does not derive simply from high-severity fire, but as a consequence of a mosaic of burn severities that in sum support a more diverse biological community than simply the union of an unburned and a completely burned community. The extent to which different suites of species occupy habitat patches burned at different severities and how these discrete communities influence local and regional biodiversity is a critical but largely unexplored topic.

Ecological succession adds additional complexity to the pyrodiversity–biodiversity question. Fire is generally thought to reset successional processes, although because of retention or alteration of legacy habitat structures (e.g. patches of unburned vegetation, snags, downed wood), burned habitats cannot be considered entirely equivalent to early seral states. Much attention has been focused on how communities of organisms change from before to immediately after fires [24,25], or whether communities show resilience to fire over multi-decadal time frames (e.g. 20–100 years) [10,26,27], with little focus on how communities change during the potentially transformative early years following fire. In addition, it remains unclear how time since fire impacts species biodiversity within fires [24], or how changes in biodiversity over time may be mediated by other aspects of pyrodiversity. Given the spatio-temporal complexities of forest succession, burn severity and community response [28], biodiversity following fire could plausibly be greatest immediately after fire (e.g. 1–2 years) or after succession has progressed (e.g. 8–10 years). Because of the lack of studies investigating biodiversity change over sub-decadal scales, even the expected direction of how pyrodiversity may interact with time since fire is unknown.

Determining the role of different aspects of pyrodiversity in driving species diversity patterns is critical given that patterns in fire occurrence are shifting in response to climate change across much of the world [29,30]. In western North America—the focus of our study—the average annual area burned in wildfires [31,32] as well as the area affected by high-severity fire [33] has increased greatly. More specifically, the average annual area of montane conifer forest burned in wildfires has increased more than sixfold over the past four decades [31,32] with the area burned in large wildfires increasing by an average of 355 km^2 annually from 1984 to 2011 [34]. The area affected by high-severity fire, in which most of the canopy vegetation is killed, is also increasing [35,36] and contrasts starkly with fire regimes prior to European-American settlement [37] (but see [38]). With the increasing prominence of larger, higher severity fires on the landscape, it is important to understand how shifting fire regimes affect the floral and faunal diversity of these fire-prone systems.

Here, we evaluate whether pyrodiversity begets biodiversity with an extensive dataset (over 38 000 detection records) from avian surveys across approximately 465 000 ha of burned conifer forest in the Sierra Nevada and Southern Cascade mountains of California, USA. We limit our definition of pyrodiversity to heterogeneity in burn severity, and calculate it as the standard deviation of per cent change in canopy cover following fire within a focal area (e.g. a fire perimeter or survey radius). Using bird diversity measurements at two scales (survey points and entire fires) over 10 years following fire, we test the following statistical hypotheses: bird diversity will increase with (i) average burn severity [22] and (ii) pyrodiversity [11,15]; (iii) the effect of pyrodiversity on bird diversity will change with time since fire [24,28], and (iv) these effects will act both on local (i.e. 100 m) and regional (i.e. entire-fire) spatial scales [39]. If pyrodiversity represented by heterogeneity in burn severity positively interacts with time to increase biodiversity, this would suggest that the temporal processes of community change following fire are heterogeneous across severities, and indicate skewed rather than parallel processes of community change. The dynamic nature by which biodiversity changes during the decade after fire may help illuminate more general processes that govern responses of communities to disturbance.

2. Material and methods

(a) Study area and data collection

This study was conducted during 2009–2014 as part of a bioregional monitoring programme in burned conifer forests. In these forests, fires typically burn with variable intensity leaving differing severities of vegetative change on the landscape. Within a single fire there are patches of high, medium and low severity, as well as unburned patches (no change or increase in canopy cover). Ground cover typically burns in all cases, but the degree to which the canopy is reduced depends on intensity relative to tree species. Each year we used GIS layers from the United States Department of Agriculture (USDA) Forest Service to extract data for all fires that had occurred during the previous 10 years across 10 National Forest units in California and that burned at least 50 ha of conifer forest at medium or high severity. From this available pool, approximately 50 fires were selected at random for surveys in any given year, independent of sampling in previous years (figure 1).

The first time each fire was surveyed, between 3 and 12 survey points (median = 9) were established at least 250 m apart along a linear transect with a randomly selected starting point within the fire perimeter. When fires were revisited in subsequent years, attempts were made to re-sample at the same locations. Where post-fire salvage logging occurred at points prior to surveys ($n = 247$, 9.7% of points; as defined by the Forest Activity Tracking System database: http://www.fs.fed.us/r5/rsl/clearinghouse/gis-download.shtml), affected survey points were subsequently excluded from analysis.

Surveys began within 10 min of official local sunrise, were completed by 3.5 h after sunrise and were conducted between

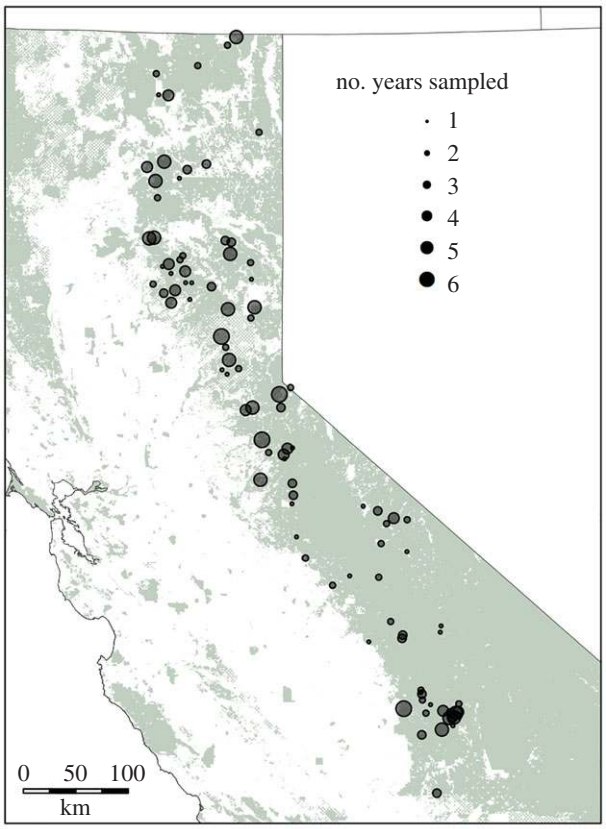

Figure 1. Map of study areas in California where avian surveys were conducted at multiple points in burned forest. Each dot represents a single surveyed fire with the size of the dot corresponding to the number of years each fire was surveyed. Green background shows all public lands in California. (Online version in colour.)

9 May and 18 July each year. At each survey point, we conducted an unlimited radius point count during which we recorded all terrestrial birds seen or heard. Points were visited once per year, and surveys lasted between 5 and 7 min in duration depending on the year. Surveys were subdivided into intervals of varying numbers of minutes to provide intra-survey temporal replication conducive to modelling detection probabilities [40]. Surveys began with a 3 min survey interval followed by either a single 2 min survey interval in 2009 or two 2 min intervals thereafter.

The final dataset for analysis was organized into a four-dimensional array, $y_{i,j,k,t}$, where $i = 1, \ldots, 124$ avian species, $j = 1, \ldots, 1106$ survey points, $k = 1, \ldots, 3$ survey intervals and $t = 1, \ldots, 6$ years. Of the 1106 survey points, 484 were visited in 1 year, 282 in 2 years, 160 in 3 years, 105 in 4 years, 64 in 5 years and 11 in all 6 years.

(b) Environmental covariates

Inference was based on the predicted occurrence of species at sites while accounting for environmental relationships of individual species by using a suite of environmental factors to better parametrize our model of community occurrence correcting for imperfect detection. Variable selection was conducted *a priori* based on prior experience modelling species occurrence over a wide variety of post-fire forest conditions in the Sierra Nevada [41] as well as focused studies of habitat usage by birds in other western post-fire ecosystems (e.g. [42]). Specific variables chosen included: (i) elevation, derived from a 30 m California digital elevation model [43]; (ii) number of years since fire (range 1–10 years); (iii) pre-fire per cent tree canopy cover, calculated by averaging midpoints of mean per cent tree cover within 100 m buffers around survey points (derived from 100 m resolution California Multi-source Land Cover Data: http://frap.cdf.ca.gov/data/frapgisdata-sw-fveg_download.php), and (iv) burn severity, as measured by change in per cent canopy cover based on the satellite-derived, relativized difference normalized burn ratio score [44] provided by the USDA Forest Service (J. D. Miller 2015, personal communication). For summary of community trends, burn severity at points was made categorical based on the canopy change score: unburned (less than 5%), low (5 to 19%), medium (20 to less than 69%) and high (greater than or equal to 70%). Points classified as unburned were nonetheless located within fire perimeters and were often proximal to burned areas, so while they showed no canopy cover change post-fire, they should not be misconstrued as controls (i.e. unburned points outside the fire perimeter).

(c) Modelling framework

We used a multi-species hierarchical occupancy model [45–47] to explore the interaction of pyrodiversity and time since fire on dynamic bird assemblages in recently burned forest stands. The strength of these models is that they estimate the probability of occupancy of every species without *a priori* assumptions of how species should co-occur, allowing estimation of community descriptors (e.g. species richness) that can only be estimated when data for all species are available [48].

We developed a temporally dependent Bayesian hierarchical model, where $y_{i,j,k,t}$ is a binomial random variable that indicates if species i was detected ($y_{i,j,k,t} = 1$) or not detected ($y_{i,j,k,t} = 0$) at sampling point j during survey interval k in year t. We used a mixture model specification to describe the data generating process in terms of probability distributions, such that $y_{i,j,k,t} \sim \text{Bernoulli}(p_{i,j,k,t} \cdot z_{i,j,t})$, where $z_{i,j,t}$ is a latent variable used to indicate true occurrence of species i at point j in year t, modelled as $z_{i,j,t} \sim \text{Bernoulli}(\psi_{i,j,t})$. The probability of detecting species i at point j during sampling visit k in year t is defined as $p_{i,j,k,t}$. We assume that a detection ($y_{i,j,k,t} = 1$) represents a true occurrence ($z_{i,j,t} = 1$) but that a non-detection ($y_{i,j,k,t} = 0$) could be the outcome of either a true absence ($z_{i,j,t} = 0$ with probability $1 - \psi_{i,j,t}$) or a true presence ($z_{i,j,t} = 1$ with probability $1 - p_{i,j,k,t}$).

Using previous work in this system as a baseline [41], we modelled detectability as a function of three covariates:

$$\text{logit}(p_{i,j,k,t}) = \alpha 0_i + \alpha 1_i \text{day}_{j,t} + \alpha 2_i \text{day}_{j,t}^2 + \alpha 3_i \text{time}_{j,t} + \alpha 4_i \text{effort}_k,$$

where $\text{day}_{j,t}$ is the Julian day of the year, $\text{time}_{j,t}$ is the time of day at which the survey started and effort_k is a dummy variable separating the first 3 min survey interval ($\text{effort}_{k=1} = 1$) from the subsequent 2 min survey intervals ($\text{effort}_{k>1} = 0$), as detectability is expected to differ between initial and subsequent survey intervals.

We modelled the occurrence probability during the first year of surveys at each point, $\psi_{i,j,1}$, as a logit-linear function of relevant covariates:

$$\text{logit}(\psi_{i,j,1}) = \beta 0_i + \beta 1_i \text{severity}_j + \beta 2_i \text{elev}_j + \beta 3_i \text{elev}_j^2 + \beta 4_i \text{pre.canopy}_j + \beta 5_i \text{fire.years}_{j,1} + \beta 6_i \text{fire.years}_{j,1}^2,$$

where $\beta 0_i$ is a species-specific intercept, and $\beta 1_i$–$\beta 6_i$ are the effects of environmental covariates on species i, representing the effects of burn severity, elevation (linear and quadratic terms), pre-fire canopy cover and years since fire (linear and quadratic terms), respectively.

For subsequent survey years, $t = 2, \ldots, 6$, we modified the occupancy model such that occupancy for species i at point j was dependent on whether or not the species was present the previous year:

$$\text{logit}(\psi_{i,j,t>1}) = \beta 0_i + \beta 1_i \text{severity}_j + \beta 2_i \text{elev}_j + \beta 3_i \text{elev}_j^2 + \beta 4_i \text{pre.canopy}_j + \beta 5_i \text{fire.years}_{j,t} + \beta 6_i \text{fire.years}_{j,t}^2 + \phi_i z_{i,j,t-1},$$

where ϕ_i is a species-specific temporal auto-logistic parameter [49]. We chose not to parametrize a fully dynamic model

Table 1. Posterior means of parameter estimates of generalized linear model tests of bird species richness as a function of pyrodiversity (defined here as heterogeneity in burn severity), time since fire, and mean burn severity at two different spatial scales. (All parameters excluding time since fire showed 95% Bayesian credible intervals (95 CI) that did not include zero. Prior to model fitting, covariate values were standardized with a mean of 0 and a standard deviation of 1.)

	point-level		fire-level	
parameter	mean	95 CI	mean	95 CI
intercept	1.493	1.473 to 1.512	2.174	2.064 to 2.283
burn severity	−0.053	−0.073 to −0.032	−0.045	−0.079 to −0.012
pyrodiversity	0.022	0.002 to 0.042	0.088	0.055 to 0.122
time since fire	0.017	−0.002 to 0.037	0.024	−0.002 to 0.051
pyrodiversity × time since fire	0.024	0.004 to 0.043	0.032	0.002 to 0.062
number of points	—	—	0.094	0.081 to 0.107

(i.e. with explicit colonization and extinction) as inference was focused on estimated occurrence derived from ψ.

Species-specific covariate parameters ($\beta 0_i$–$\beta 6_i$ and $\alpha 0_i$–$\alpha 4_i$) and ϕ_i come from parameter-specific community-level hyper-distributions following the form:

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta),$$

where μ_β and σ_β are hyper-parameters representing the community-level mean and standard deviation for each of i species-level parameters for a β. All first-order continuous occupancy and detectability covariates were standardized to a mean of 0 and a standard deviation of 1.

We fitted the model to the data with JAGS [50] using the R statistical programming language v. 3.2.1 [51]. In all cases, we used vague priors (i.e. normal with $\mu = 0$, $\tau = 0.01$; gamma with $r = 0.1$, $\lambda = 0.1$), as we did not have prior information on covariate relationships for such a large community. We ran three chains of 25 000 iterations with a burn-in of 5000 followed by a posterior draw of 1000 thinned by 100, yielding a posterior sample of 300 across all chains. Convergence was assumed when the Gelman–Rubin statistic of all monitored parameters calculated across both chains was less than 1.1 [52].

(d) Derived estimates of community structure

We used posterior samples of the true occurrence state matrix, $z_{i,j,t}$, to derive diversity estimates corrected for imperfect detection. The z-matrix is the posterior prediction of the true occurrence status of every species at each surveyed point through time. We extracted the z-matrix at each Markov chain Monte Carlo iteration to derive species richness (alpha diversity), aggregate across space or time (gamma diversity), and compare the composition of species assemblages (beta diversity). As all diversity metrics come from the z-matrix, all derived diversity metrics account for imperfect detection and include propagated uncertainty.

We used the detection-corrected posterior z-matrix to calculate multiple spatial and temporal indices of diversity in burned forests. Point-level richness was calculated as the sum of the true occurrence matrix for a given point and number of years after fire. Similarly, we estimated fire-level richness for each sampled year as the number of species estimated to occur at least once across all points surveyed within a fire.

We calculated gamma diversity as the number of bird species found at least once within each burn-severity class (low, medium, high severity and unburned) and number of years post-fire (1–10), pooling data across all 97 surveyed fires. As different numbers of survey points of each severity class were surveyed in each year, comparisons of gamma diversity across severity and age classes required rarefaction to a common number of samples [53]. We rarefied gamma diversity across all severity-year classes by randomly selecting 35 points (without replacement) from the z-matrix for each severity-year class and calculating the number of species found at one or more of those points in any year. We repeated this rarefaction 20 times for each posterior draw. These rarefied gamma diversity measures also formed the basis of dissimilarity calculations for severity-year communities. For each pair of rarefied severity-year samples from the posterior of the z-matrix, we calculated dissimilarity (i.e. turnover or beta diversity) as 1 minus the Sørensen similarity index [54]. As with other derived community metrics, this yielded a posterior distribution of community dissimilarity for each rarefied pair of samples.

(e) Effects of pyrodiversity on avian diversity

While recent work has used the Shannon or Simpson index of integer-based post-fire age classes to represent pyrodiversity across fires [13,15], we used the standard deviation of burn-severity scores to measure pyrodiversity within fires. As burn-severity scores are continuous and range from 0 (unburned canopy) to 100 (complete canopy loss), the standard deviation of burn severity provides an index from approximately 0 to 70, with values over 40 representing highly pyrodiverse fires consisting of equal parts high- and low-severity stands. Pyrodiversity for individual survey points was calculated as the standard deviation of all burn-severity values within 100 m of the survey point. Pyrodiversity per fire was quantified as the standard deviation of severity values within 100 m of all survey points at a fire, combined. Both points and fires showed a wide range of pyrodiversity scores (point mean = 15.9, point range = 0–46.2, fire mean = 33.6, fire range = 4.0–40.5), and in both cases, there was no linear relationship to mean severity (as both lower- and higher severity fires generally have lower pyrodiversity).

To test the relationship between pyrodiversity and bird species diversity, we used posterior estimates of both point- and fire-level species richness as the response variable in a generalized linear model (GLM). For each draw of the posterior distribution, we ran a Poisson GLM testing species richness as a function of: (i) the number of years since fire, (ii) the mean burn severity (per point, or per fire), (iii) the standard deviation of burn severity (per point, or per fire), and (iv) an interaction between time since fire and the standard deviation of severity. For GLMs of richness at the scale of the fire, we additionally included (v) the number of points surveyed per fire.

3. Results

(a) Pyrodiversity

Avian species richness increased, on average, over the range of measured pyrodiversity but decreased over the range of

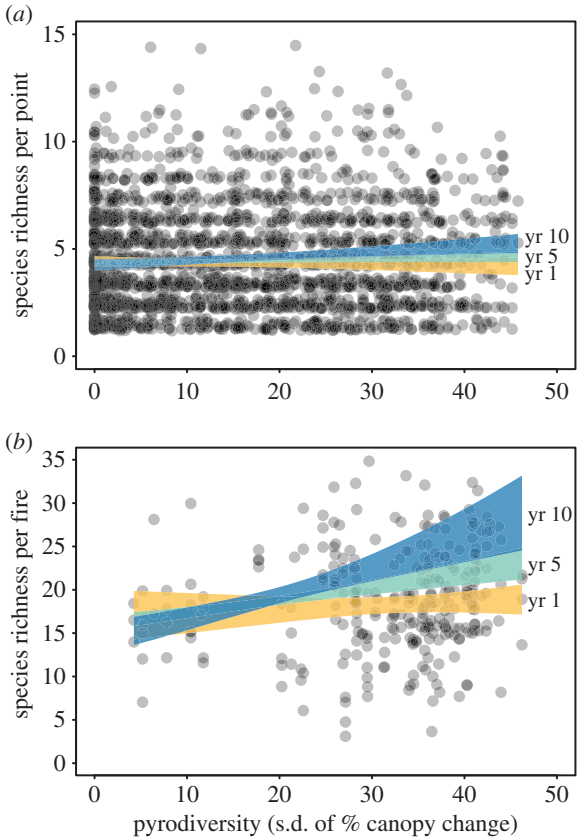

Figure 2. Tests of the pyrodiversity–biodiversity hypothesis at the scale of individual survey points (*a*) and entire fires (*b*). Models of posterior estimates of species richness showed strong relationships of pyrodiversity with avian species richness and a positive interaction with time since fire. Coloured lines show 95 CI for pyrodiversity–biodiversity relationships for three different time periods: 1, 5 and 10 years following fire. (Online version in colour.)

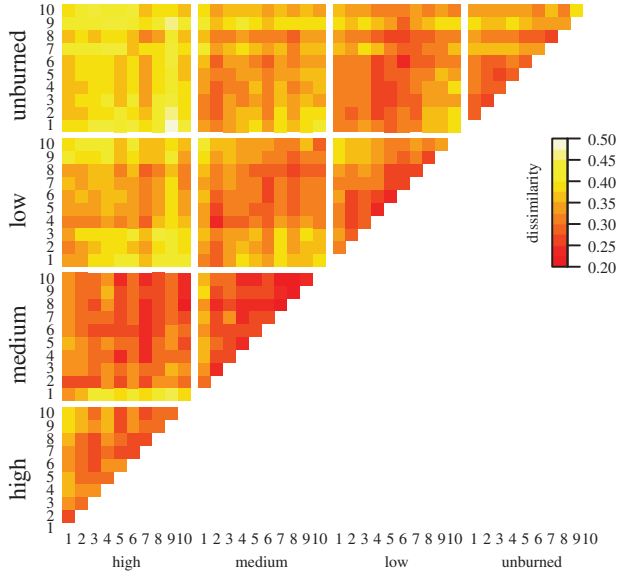

Figure 3. Dissimilarity of avian communities across all severity and post-fire year combinations. Beta diversity was estimated using the Sørensen index, and represents the dissimilarity of one community to another, with red indicating low dissimilarity and white indicating high dissimilarity (a value of 1 indicates no shared species). Bird communities farther apart along the severity gradient are generally more dissimilar to one another (i.e. high-severity communities are more similar to medium-severity communities than to low or unburned), and within burn-severity classes, communities closer in age (years since fire) are more similar to each other. In all cases, colours refer to posterior mean dissimilarity using rarified communities within each severity-year class. (Online version in colour.)

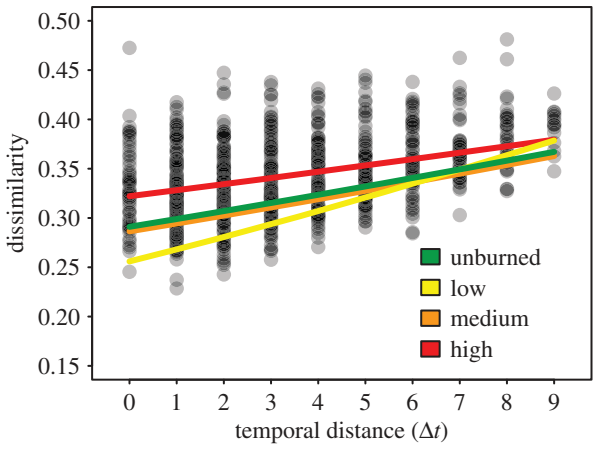

Figure 4. Bird communities showed greater dissimilarity with increasing numbers of intervening years. Each dot represents an estimate of dissimilarity across two rarefied severity-year bird communities, and temporal distance (Δt) measures the absolute difference in years across severity-year comparisons. Strongly increasing dissimilarity with temporal distance within severity classes indicates that communities diverge over time. Lines represent mean posterior linear estimates of the trend for each of four burn-severity classes: unburned (green), low (yellow), medium (orange) and high (red) severity. (Online version in colour.)

mean burn severity. Findings were similar for both point- and fire-level species richness (table 1), although the effect size for pyrodiversity was four times larger for fire-level richness. Additionally, pyrodiversity positively interacted with time since fire. The effect size of this interaction was great enough that for avian richness at individual survey points, time since fire explained a switch from a decreasing or flat pyrodiversity–biodiversity slope at 1 year post-fire to an increasing pyrodiversity–biodiversity slope at 10 years post-fire (figure 2*a*). For entire fires, the pyrodiversity–diversity slope was much steeper at 10 years post-fire than immediately following fires (figure 2*b*). Independent of this interaction, there was no clear effect of time since fire on bird diversity (table 1).

(b) Community dissimilarity by severity and year

Based off the dissimilarity of rarefied gamma diversity for every severity-year combination (figure 3), high-severity and unburned forest showed the greatest dissimilarity in bird communities (mean dissimilarity = 0.392), followed by high- and low-severity forest (mean dissimilarity = 0.362). Conversely, low-severity and unburned forest showed the least dissimilarity (mean dissimilarity = 0.318), followed by medium- and low-severity forest (mean dissimilarity = 0.325). Bird communities differed not only across burn severities but also within burn severities over time. Within each severity class, bird communities showed generally increasing dissimilarity across greater numbers of intervening years (figure 4). This positive linear trend in dissimilarity with temporal distance was found for unburned (95% Bayesian credible interval (95 CI) slope = 0.001–0.073), low- (95 CI slope = 0.031–0.099) and medium-severity forests (95 CI slope = 0.008–0.071), but the credible interval for the positive effect on high-severity forests slightly overlapped zero (95 CI slope = −0.001–0.058).

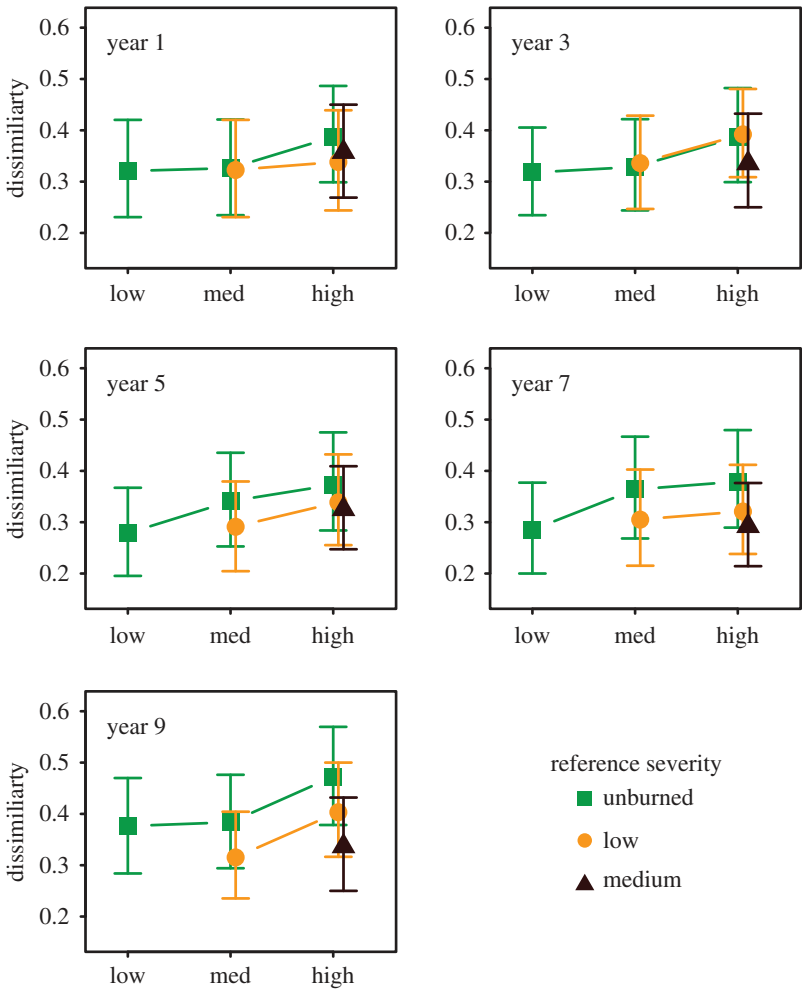

Figure 5. Post-fire landscapes demonstrated diverging bird communities over time across burn-severity classes. At 1 year since fire, bird communities were equally dissimilar, yet by 9 years since fire, different burn severities demonstrated a gradient of community divergence from unburned, to low, medium and high severity, with areas more similar in burn severity also showing more similar bird communities. Each point represents the mean and 95 CI pairwise dissimilarity between two severity classes rarefied across each severity-year combination. (Online version in colour.)

If the temporal processes of community change differ by burn severity, then communities should show divergence over time. Indeed, 1 year after fire, bird communities of all four severity classes (including unburned forest) were equally dissimilar (figure 5), so that communities of unburned forest were just as similar to low-severity forest as they were to high-severity forest. With each additional year following fire, communities showed increasing differentiation, so that by 9 years after fire, unburned forests were more dissimilar from high-severity patches than medium-severity patches were from high-severity patches (figure 5). This differentiation of communities happened gradually over the 10 years following fire and was also gradated by severity, with low- and medium-severity forests intermediate in their dissimilarity to high-severity forests relative to unburned forests.

4. Discussion

The role of fire in maintaining biodiversity is increasingly appreciated, particularly in semi-arid, fire-prone ecosystems. While it is recognized that the overall degree of burn severity within fires is important in shaping post-fire communities [24,55], little is known about how communities are affected by heterogeneity in severity within fires. Our study follows the changing avian community in the 10 years following fire and evaluates the role of spatial heterogeneity in fire severity and time since fire in structuring diversity using a spatially and temporally extensive dataset from the montane forests of inland California.

Our analysis of the effects of burn severity on bird diversity across two spatial scales indicates strong support of the claim that pyrodiversity increases biodiversity. We found that bird communities differ appreciably across burn severities, with communities showing dissimilarity patterns on a continuum from unburned, to low, medium and high severity (figure 3). The result of this beta diversity is that fires which are more structurally diverse in their burn severity hold more bird species (table 1 and figure 2). Independent of time since fire, fire-level pyrodiversity has a positive effect on bird diversity.

Nevertheless, the clear finding that pyrodiversity, indeed, begets biodiversity incompletely describes the non-parallel processes by which avian communities differentiate during the decade following fire. Rather than communities inhabiting different burn severities showing the greatest dissimilarity immediately following fire, communities showed divergence over time (figure 4) that resulted in the greatest dissimilarity after a decade of succession (figure 5). Differing burn severities and their bird communities have classically been considered different stages along the continuum of succession [21,56].

If this were true for birds, then community change following fire would progress in parallel, with bird assemblages in high-severity forests 'maturing' into assemblages associated with medium-severity forests, assemblages in medium-severity forests maturing into assemblages associated with low-severity forests and so on. While this may yet be true over many decades, our single-decade results provide evidence that—at least for birds in montane conifer forest of North America—burn severity is not analogous to successional stages from the perspective of community change. Instead, within the decade following fire, different burn severities represent unique habitats whose bird communities show differentiation over time, rather than convergence.

In our system, this nonlinearity in community change can be at least partly explained by the complex nature of tree death, snag creation and chaparral growth in semi-arid conifer forests. In the low-severity burned forests we surveyed, most of the canopy persisted after fire. In forests burned at medium and high severity, many trees died during or shortly after fire, eliminating canopy cover and encouraging the growth of dense chaparral and other ground cover throughout the next decade. Montane chaparral creates a distinct habitat that is often quickly colonized by numerous shrub-nesting bird species that are rarer in unburned forests [57,58]. Snags are also critical resources for many bird species after fire. Increasing densities of many bird species after fire—primarily wood excavators, aerial insectivores, and secondary cavity nesters—can be directly tied to snag densities [59,60]. Bird species that forage on insects in dead wood or excavate their own nest cavities are likely to respond to increased resources within the first year or two after fire. Bird species that nest in tree cavities but are not able to excavate their own holes may not find enhanced nesting opportunities during the first year or two after fire, but as additional years pass, increasing numbers of woodpecker-excavated holes probably become available.

Our findings are in contrast with fire-prone shrub systems, such as Australia's mallee. In the mallee, multiple studies have looked at how spatial heterogeneity owing to temporal pyrodiversity affects biodiversity, with results for both birds and reptiles showing limited to no effect [10,11,13]. In contrast with shrubland systems, our finding that biodiversity responds positively to an interaction of pyrodiversity and time since fire possibly results from the complex diversity of habitats created and maintained by fire in conifer landscapes. Indeed, related work on the pyrodiversity–biodiversity hypothesis has found similarly positive results with other taxa in western North America [15], and previous studies have highlighted that different bird species are sensitive to different combinations of fire severity and years since fire [24,28]. Thus, at the scale of individual fires in forested ecosystems, a mosaic of stands of different burn severities—not just the overall degree of burn severity—is likely to produce the greatest diversity of species. The importance of such 'mixed-severity' fire is an emerging principle in fire ecology [21], but mixed-severity fire, which is already at risk owing to the legacy of fire suppression and even-aged stand management [61,62], may become less frequent owing to the increasing prevalence of large and homogeneous high-severity fires resulting from climate change [31,36].

Data accessibility. Data and JAGS code available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.871pc [63].

Authors' contributions. M.W.T., R.B.S., R.L.W. and C.A.H. designed the research. R.B.S. and R.L.W. collected field data. M.W.T. and V.R.-G. conducted the analysis. M.W.T. and R.B.S. drafted the manuscript. All authors provided comments and gave final approval for publication.

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