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CORRESPONDING AUTHOR EMAIL: david.lindenmayer@anu.edu.au

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Do temporal changes in vegetation structure predict changes in bird occurrence additional to time since fire?

David B. Lindenmayer [1, 2, 3, 4]
Steven G. Candy[1, 5]
Sam C. Banks[1]
Martin Westgate[1]
Karen Ikin[1,2,3]
Jennifer Pierson[1]
Ayesha Tulloch[1,2,3]
Philip Barton[1]

[1]Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia
[2]ARC Centre of Excellence for Environmental Decisions, The Australian National University, Canberra, ACT 2601, Australia
[3]National Environmental Science Program, The Australian National University, Canberra, ACT 2601, Australia
[4]Long-term Ecological Research Network, Terrestrial Ecosystem Research Network, The Australian National University, Canberra, ACT 2601, Australia
[5]SCandy Statistical Consulting Pty Ltd, 70 Burwood Drive, Blackmans Bay, Tasmania 7052, Australia

ABSTRACT

Fire is a major ecological process in ecosystems globally. Its impacts on fauna can be both direct (e.g. mortality) and indirect (e.g. altered habitat), resulting in population recovery being driven by several possible mechanisms. Separating direct from indirect impacts of fire on faunal population recovery can be valuable in guiding management of biodiversity in fire-prone environments. However, resolving the influence of direct and indirect processes remains a key challenge because many processes affecting fauna can change concomitantly with time since fire.

We explore the mechanisms influencing bird response to fire by posing the question: *Can temporal changes in vegetation structure predict changes in bird occurrence on sites, and can these be separated from other temporal changes using the surrogate of time since fire?* We conducted a 12-year study of bird and vegetation responses to fire at 124 sites across six vegetation classes in Booderee National Park, Australia. Approximately half of these sites, established in 2002, were burnt by a large (> 3000 ha) wildfire in 2003. To disentangle collinear effects of temporal changes in vegetation and direct demographic effects on population recovery that are subsumed by time since fire, we incorporated both longitudinal and cross-sectional vegetation effects in addition to time since fire within logistic structural equation models.

We identified temporal changes in vegetation structure and richness of plant and bird species that characterized burnt and unburnt sites in all vegetation classes. For nine bird species, a significant component of the year trend was driven by temporal trends in one of three vegetation variables (number of understory or midstory plant species, or midstory cover). By contrast, we could not separate temporal effects between time since fire and vegetation attributes for bird species richness, reporting rate, and the occurrence of 11 other bird species.

Our findings help identify species for which indirect effects of vegetation dominate recovery and thus may benefit from vegetation management where conservation actions are required and, conversely, those species for which direct effects of time since fire drive recovery, where simply leaving a system to recover following the last disturbance will be sufficient.

Key words: biodiversity conservation, disaggregation, multiple regression, occurrence, vegetation, wildfire, MODMED

INTRODUCTION

Fire is a key ecological process that can have substantial impacts on biodiversity (Bowman et al. 2009, Moritz et al. 2014, DellaSala and Hanson 2015). Many studies document temporal trends in animal populations following fire, particularly in response to one variable – time since the last fire (Smucker et al. 2005, Kelly et al. 2015). Indeed, time since fire is often considered the key descriptor of disturbance history in succession-based perspectives on disturbance ecology (Nimmo et al. 2012) (reviewed by Pulsford et al. 2016).

Although the effects of time since fire are frequently examined in studies of fauna, the ecological mechanisms underlying faunal responses are rarely explicitly examined. Fire can have direct impacts on individuals through mortality either at the time of the event or immediately following (Bell et al. 2001, Thonicke et al. 2001), with subsequent temporal patterns of population recovery ('time since fire' effects) limited by the rate of recolonization of burnt sites or growth of populations that survived the fire (Banks et al. 2011) or colonization of burnt sites by early successional species (Swanson et al. 2011). An alternative mechanism is that habitat suitability is altered by fire with subsequent effects on food availability (Whelan 1995), the availability of shelter sites (Lindenmayer et al. 2013) or altered susceptibility to predation (Woinarski et al. 2015). Under this indirect fire-effect mechanism, temporal patterns of faunal population dynamics associated with time since fire are mediated by post-fire temporal changes in vegetation structure, cover and plant species composition (Monamy and Fox 2000, Morrison et al. 2006, Swan et al. 2015, Pulsford et al. 2016).

Separating indirect habitat effects from direct demographic effects of time since fire is critical to understanding the broader role of fire in shaping biodiversity patterns and for guiding management, but such work is challenging because potential drivers of temporal responses in biodiversity can be co-occurring and strongly collinear (Dormann et al. 2013, Swan et al. 2015). For instance, vegetation typically changes in structure and diversity concomitantly with time since fire (Noble and Slatyer 1980, Haslem et al. 2011, Swanson et al. 2011). Furthermore, a faunal response trajectory, such as species occurrence on sites, may change simply due to demographic limitation on recovery rate or change in response to both vegetation and time since fire demographic processes (see the conceptual model in Figure 1). This is a problem because conventional multiple regression techniques may have difficulty in separating the direct demographic (time since fire) versus indirect habitat (change in vegetation) effects on species occurrence.

In this study, we aimed to quantify the contribution made by temporal changes in vegetation structure to time since fire effects on birds. Quantifying the contribution of vegetation change to time since fire effects has important implications for vegetation management and wildlife conservation. This is because it helps determine whether managing disturbance to maintain vegetation structure and plant species composition in fire-prone ecosystems also will cater for fauna. For example, it can help identify whether active vegetation manipulation (such as slashing) or alternative strategies like prescribed burning might be the best strategy for conserving biodiversity in fire-prone environments (Baker 2000, DellaSala and Hanson 2015).

Specifically, we asked the questions: Can temporal changes in vegetation structure post-fire predict changes in bird occurrence on sites, and can these be separated from other temporal demographic changes using the surrogate of time since fire? That is, can indirect effects of vegetation change be separated from other temporal demographic changes that may be subsumed by the simple direct predictor of time since fire? Using a long-term study of birds and vegetation cover, we tested a series of inter-related hypotheses (Figure 1, Table 1, Appendix S1) that linked temporal changes in various measures of bird biodiversity with temporal changes in vegetation cover and the time elapsed since the last major fire. The first 'direct effect' hypothesis was that the main driver of species differences over years was only time since fire (which might show simply as year trends). Essentially, turnover is limited by demographic rates and not the impacts of fire on habitat suitability. The second 'indirect effect' hypothesis was that the temporal component of a trend in species occurrence was driven only by temporal changes in plant species richness or various measures of vegetation cover. Essentially, demographic rates do not limit occurrence in suitable habitat. The last 'combined effects' hypothesis was that trends over time were due to the combination of direct and indirect fire impacts with the latter mediated by vegetation responses.

We employed two techniques that enhance inferences from multiple regression analysis through separating the co-linear effects of time since fire and vegetation change. Our first approach was to split each structural vegetation variable (such as percent understory cover) into its longitudinal (i.e. over time) and cross-sectional (i.e. across sites) components (Diggle et al. 2002). This method enabled us to discriminate between the spatial and temporal effects of each explanatory variable on bird populations and assemblages. Our second approach was to use moderated-mediation analysis (MODMED) to separate the effect of time since fire into direct and indirect effects. MODMED is a form of structural equation modelling that allows manipulation of regression equations from linear models (Baron and Kenny 1986, Preacher et al. 2007), linear mixed models (Bauer et al. 2006), and logistic regression (MacKinnon et al. 2007). The application of structural equation modelling, and in particular MODMED, has been common in psychometric analysis and more recently in ecology (see Grace et al. 2009 for a review). For example, Grace and Keeley (2006) examined the mediation of fire intensity on the effect of age of California shrubland on the degree of post-fire recovery in plant diversity. However, MODMED has not yet been applied in combination with the disaggregation of a mediating variable into its longitudinal and cross-sectional components. Between them, these two methods allowed us to address the issues of confounding and collinearity of regressors that have traditionally limited ecologists' attempts to understand the effects of fire on faunal assemblages.

METHODS

Study area and survey design

We conducted this study in Booderee National Park, a ~6500 ha reserve located 200 km south of Sydney, south-eastern Australia. The area has a temperate maritime climate. In 2002, we established 124 permanent long-term sites across the six major vegetation types recognised throughout Booderee National Park (Lindenmayer et al. 2014b): temperate rainforest, eucalypt forest, eucalypt woodland, heathland, shrubland and sedgeland (Figure 2; Appendices S2 and S3). We distributed survey sites widely across the entire study area to limit geographic bias, and replicated sites within each vegetation type with the number of samples proportional to the total area occupied by each class. Each site was a permanent 100 metre long transect.

Fire in Booderee National Park

Booderee National Park has a well-documented history of fire. There have been 198 fires since 1968 with two major large-scale conflagrations in that time (in 1973 and 2003). The majority of fires have been small scale, low-intensity prescribed burns but small uncontrolled wildfires also have been common. The median size of fires is 4.95 ha. The last major fire in Booderee National Park was in 2003 and it burnt approximately half of the reserve. Fires in Booderee National Park are spatially heterogeneous and there are typically patches of unburnt vegetation left within the boundaries of any given fire event (Lindenmayer et al. 2009a).

The primary fire variable of interest was time since the last fire, in part because it has been found to be important in studies conducted elsewhere in different ecosystems (e.g. Saab et al. 2007, Kelly et al. 2015). For this investigation, the variable **time since fire** corresponded to the date of the survey at a site and the time elapsed since the 2003 fire. A total of 56 of our 124 long-term sites were burnt in the 2003 fire. Notably, none of the sites burnt in 2003 have been reburnt since that time. Our 68 unburnt sites encompassed representatives of all of the six major vegetation types. To account for this, we included the variable **2003 burn status** to distinguish burnt and unburnt sites.

We also explored the effects of fire severity in our study as it also can have important impacts on biodiversity (e.g. Kotliar et al. 2007, Fontaine and Kennedy 2012, Lindenmayer et al. 2014a). The continuous variable **severity of the 2003 fire** was based on a fire severity category using on-the-ground field observations of the direct effects of the 2003 fire on vegetation cover: **(a)** no fire, **(b)** low severity fire in which none of the vegetation layers were killed, **(c)** moderate severity fire in which the understory and midstory were burnt but not killed and the overstory remained unburnt, and, **(d)** high severity fire in which the midstory was killed and the overstory was burnt (see Appendix S3). For sites where there was a mix of fire severities, we chose the one that was dominant.

The final primary fire regime variable we explored was the number of past fires at a site, a reflection of the fire history. The variable **number of fires** corresponded to the number of fires at a site over the past 35 years (prior to the 2003 fire). Data on the number of fires at a site were derived from extensive on-the-ground mapping of the location and size of each of the 198 fires known to have occurred in Booderee National Park since 1968. Some of our 124 sites have experienced up to five different fires since fire records began in 1968 whereas other have remained unburnt during that time (Lindenmayer et al. 2014b).

We also constructed the variables **date of the last fire** (as at 2013) and **years since the last fire** which corresponded to the number of years from the date of a given survey back to the date of the last fire. Associated with the variable years since the last fire, we also included a variable which corresponded to the **type of fire** (unplanned wildfire versus prescribed burn) that occurred on a site.

Vegetation surveys

We established vegetation plots measuring 20 m x 20 m at the 20-40 m and 60-80 m points along each of our 124 sites to gather vegetation covariates for use in modelling of the response of birds to fire and vegetation cover. We completed five repeated vegetation surveys (in 2004, 2006, 2007, 2009, and 2012). The same observer (CM) conducted all surveys. The measured vegetation variables used in our analyses were visual estimates of the number of canopy layers (taking values 1, 2, or 3), percent cover of the understory midstory, and overstory, and counts of the number of plant species in the understory, midstory, and overstory.

Surveys of birds

Our survey design involved conducting five minute point interval counts (sensu Pyke and Recher 1983) in late September each year at the 20 m and 80 m points along each transect. Each site was surveyed twice on a different day by a different observer (four surveys per site per year) to reduce day effects on detection and overcome potential observer heterogeneity problems (Cunningham et al. 1999). We recorded all birds seen or heard and assigned observations to different distance classes from a point – 0-25 m, 25-50 m, 50-100 m, and > 100 m. Our survey protocol was specifically designed to quantify site occurrence, and for our statistical analyses (see below) we did not assume that individual counts at the two points on the same site were independent. We worked hard to account for known sources of variation in our surveys in the most appropriate and feasible manner by: **(i)** using a large number of sites and surveying multiple points per site (local spatial heterogeneity), **(ii)** surveying on multiple days (temporal heterogeneity) and **(iii)** using multiple observers (observer heterogeneity) (Cunningham et al. 1999, Lindenmayer et al. 2009b).

STATISTICAL ANALYSIS

Temporal changes in plant species richness and vegetation structure

We investigated how vegetation variables responded to time since the 2003 fire by fitting Poisson Generalized Linear Mixed Models GLMMs (using glmmadmb) (Skaug et al. 2013) to the number of plant species in each of the understory and midstory. We fitted percent cover for each canopy class (i.e. understory, midstory and overstory) using a pseudo-binomial response GLMM. We fitted this model using the gamm function in the mgcv R-library (Wood 2006) because it allows a dispersion parameter to be fitted to account for the fact that percent cover can be considered a pseudo-binomial response variable in the quasi-likelihood setting (Wedderburn 1974). To obtain a site by year value, we rounded up the average value for a given vegetation attribute across the two 20 m x 20 m survey plots (ranging from 1 to 100) to give a pseudo-binomial response variable.

Temporal changes in the bird community

We analysed three aspects of the bird community at each site: species richness; total reporting rate; and species-specific reporting rate for the 20 most prevalent bird species. Species richness was defined as the sum of species observed in that site and year combination. Reporting rate was defined as the number of occurrences of a given species out of the number of possible detection “opportunities” (Npo), i.e. the four surveys. Total reporting rate was the sum of the reporting rates across all species.

We elected not to complete detectability/occupancy analyses in our study of individual species for a range of key reasons. Most importantly, past detailed statistical analyses on the topic of detection/occupancy (e.g. Welsh et al. 2013) suggests that the current statistical methods for detection/occupancy may not improve model fit and in some cases can make the outcomes worse. Moreover, it is currently not possible to determine when detection occupancy improves model fit and when it does not (Welsh et al. 2015).

We modelled each response variable at the site by year level with GLMMs (Bolker et al. 2009), using either the glmer (Bates et al. 2014) or glmmadmb (Skaug et al. 2013) functions (R Development Team 2006). These functions evaluate the marginal likelihood by approximation of the integral of the conditional likelihood across the assumed Gaussian distribution for the site random effects (Skaug and Fournier 2006). However, GLMMs failed to fit for most of the species that we modelled; in these cases we dropped the site random effect term, simplifying model fitting to a standard binomial/logistic generalized linear model (GLMs) (McCullagh and Nelder 1989).

Species richness and total reporting rate were count data without zero values and were treated as truncated Poisson response variables with an "offset" of log(Npo) to model Poisson rates. Welsh et al. (1996) used the truncated negative binomial regression in modelling count data for which there is a logical absence of zero counts, whereas we fitted using glmmadmb the truncated Poisson; a special case of the above model. We fitted the species-specific reporting rate models using a binomial sample size of Npo.

Model 1: Direct Effects of Time Since Fire

Model 1 tested the hypothesis that direct effects of time since fire predicted bird response to fire (Figure 1). Model 1 was fitted to all the above response variables in turn, and incorporated time-invariant predictors of 'vegetation type' and '2003 burn status' as additive and interactive effects, and 'fire frequency' and 'fire severity' as additive effects. The time-varying predictor was the interaction of '2003 burn status' with 'years since the 2003 fire' (with values of 1, 3, 4, 6, and 9 years), which we coded as a continuous variable. We tested for both linear and quadratic effects of 'years since 2003' (Appendix S1, Figures S1 and S2). For simplicity, we hereafter refer to these interactions as 'time since fire' and report year trends.

To investigate whether this simplified modelling framework adequately captured the qualitative and quantitative features of the relevant temporal dynamics, we compared Model 1 and a related model that investigated alternative aspects of the fire regime (Appendix S6). Further, we investigated a model that extended Model 1 by incorporating the interaction of 'time since 2003' (as both linear and quadratic terms) and 'broad vegetation class' as well as the 3-way interaction between these terms and 'burnt versus unburnt in 2003'. However, both these alternative model did not improve fit relative to our initial model (Model 1; see Appendices S6 and S7), and so we do not discuss these models further in the main body of this manuscript.

Model 2: Direct Longitudinal and Cross-sectional Effects of Structural Vegetation Variables

Model 2 tested the hypothesis that temporal change in structural vegetation attributes drive bird occurrence (Figure 1). We ran this model using as covariates each of the three most important vegetation attributes identified during preliminary analyses (see Appendix S2): number of plant species in the understory, number of plant species in the midstory and percent cover of the midstory, as well their log-transformed counterparts to explore quadratic relationships. This model fitted the same time-invariant predictors as Model 1, but replaced the time-varying predictors with the interactions of '2003 burn status' with two new linear vegetation terms. These represented the disaggregation of the vegetation structural attributes into temporal (i.e. longitudinally or within site across time) and spatial components (i.e. cross-sectional or between sites).

We derived the cross-sectional component by taking the value of the selected variable in that site and year, and duplicating it across all years for that site. The longitudinal value was simply the initial value for that variable, minus the cross-sectional value. (This approach was derived from equation 2.2.4 of Diggle et al. (2002); see Appendix S4 for a full description, and Figures S1 and S2 for schematic representations). This disaggregation for the vegetation variables was possible because these covariates vary both across sites and within sites over time, whereas the 'years since 2003' covariate varied only within sites across time (Cunningham et al. 2014). We examined the level of support for each vegetation variable using the sign and statistical significance of the coefficient of its longitudinal component.

Model 3: Direct and Indirect Effects of Time Since Fire Mediated by Structural Vegetation Variables

Model 3 tested the hypothesis that the combined direct and indirect effects of time since fire and temporal vegetation change drive faunal response after a fire (Figure 1). For each response variable, we calculated Model 3 a number of times, to give separate models for each combination of survey years (n=5) and vegetation structural variables (n=6), i.e. total n_{models}=30 per response. Each run of this model included the time-invariant predictors in Model 1 and 2, the interaction of '2003 burn status' with 'years since the 2003 fire', and the interaction of '2003 burn status' with the temporal and spatial vegetation components, thereby combining terms from Models 1 and 2. We then adjusted the coefficients from each iteration of Model 3 using the MODMED approach (Preacher et al. 2007) (Figure 1, Appendix S1). To do this, we incorporated a conditional indirect effect term resulting from a corresponding 'mediation' model. This model uses the temporal covariate (or its log transformation, Appendix S8) for a particular vegetation variable as the dependent variable in a separate linear regression to estimate the effects of time since fire (both linear and quadratic terms for 'years since 2003') on temporal change in that vegetation attribute. Model 3 thus disaggregates the direct effects of time since fire and vegetation change and the conditional indirect effects of time since fire on vegetation. The standard error of the estimate of the conditional indirect effects was obtained exactly using a second order Taylor series given by Equation (3) of Preacher et al. (2007) (see Appendix S5) and the significance level was approximated by comparing the estimate divided by its standard error to nominal critical values of -2 and +2 (see Appendix S5).

Model Comparison

We began our model comparison stage by deriving a single set of coefficient estimates for each combination of predictor and response variables. This was necessary because our method involved constructing a separate model for each survey year (n=5). We calculated 'final' versions of Models 1, 2 and 3 by averaging coefficients and standard errors across the five versions of each model (see Appendix S5). From this 'averaged' set of coefficients and their standard errors, we were also able to calculate P-values to give a measure of the statistical significance of each variable across all survey years. Each of our models tested different postulates (Table 1; see Figures S1 and S2); but in terms of model comparison, our interest was in whether there are significant direct and conditional indirect effects of time since fire (as mediated in this last case by vegetation variables). Consequently, if the terms involved for both of these effects were significant, then Model 3 was by definition the best fitting of these models (due to nesting of each of Models 1 and 2 within Model 3). This was consistent with our analytical emphasis on structural equation modelling which focused on addressing questions about causal processes (as opposed to being focused on selecting a parsimonious set of predictors) (see also Grace et al. 2009).

RESULTS

Temporal changes in plant species richness and vegetation structure

We identified strong and consistent changes in measures of plant response over the 10 year duration of our study. For example, the number of understory plant species increased on unburnt and burnt sites between 2003 and 2013 (Figure 3a). We re-analysed our datasets to account for broad vegetation class effects and explore whether summarizing results for all vegetation masked between-vegetation type responses to fire. The relative improvement in residual deviance for the broad vegetation class-specific year trend version of Model 1 was 1.7%, indicating that temporal changes in the number of understory plant species between 2003 and 2013 characterised both sites burnt in 2003 and those unburnt at that time and for all six of the broad vegetation types. We recorded similar findings for the number of midstory plant species and the percent cover of the midstory (Figure 3b & c).

Bird species richness and reporting rate

We found strong evidence for a significant ($P < 0.05$) temporal increase in bird species richness, both for burnt and unburnt sites (2003 fire) (Figure 4; see Appendix S13 for a species list and scientific names). The pattern of this increase differed between burnt and unburnt sites: whilst richness was higher on unburnt sites, the rate of increase was higher on burnt sites. For this response variable, we found no significant conditional indirect effect of vegetation variables (Table 2). We found similar trends in total reporting rate, with significant temporal increases in burnt and unburnt sites, but no significant conditional indirect effect of vegetation (Table 2).

Temporal responses of individual species of birds

We discovered a wide range of time since fire responses (as judged by the significance of the regression coefficients in Table 3) among the 20 bird species that we modelled (Table 2). These included: **(1)** positive across all sites (e.g. Eastern Spinebill [Figure 5a] and Red Wattlebird), **(2)** negative across all sites (e.g. Spotted Pardalote [Figure 5b] and Crimson Rosella), **(3)** positive on burnt sites but unchanged on unburnt sites (e.g. Little Wattlebird [Figure 5c] and Variegated Fairy-wren), **(4)** positive on unburnt sites but unchanged on burnt sites (e.g. Eastern Bristlebird and Grey Shrike-thrush), **(5)** negative on burnt sites but unchanged on unburnt sites (e.g. Eastern Yellow Robin, White-throated Treecreeper), and **(6)** unchanged over time both on burnt and unburnt sites (Grey Fantail and White-browed Scrubwren) (see Table 2).

Change in vegetation variables was linearly associated with increasing time (as per the patterns quantified in Figure 3). Most bird species also showed significant changes in prevalence over time. For 11 of the 20 species we modelled, it was not possible to resolve whether time since fire or one of the vegetation variables was the primary driver of the temporal changes in bird species. For the remaining nine species, MODMED analyses revealed that the conditional indirect effect of years since the 2003 fire was mediated by one of the structural vegetation variables (i.e. number of understory plant species, number of midstory species, and percent cover of midstory species), with three species responding to each of these variables (Table 2; Appendix S7). Of these nine species, six exhibited significant ($P<0.05$) indirect responses only on the burnt sites. In addition, for the Yellow-faced Honeyeater, we identified significant positive trends with time since fire quantified by both direct and conditional indirect coefficients for both linear and quadratic components. That is, indirect effects mediated by vegetation structure effects do not explain all of the trend patterns over time, suggesting that other (unmeasured) factors are important. Graphs that display standardised coefficients for each of Models 1 and 3 for each of the 20 bird species are given in Appendices S9 to S12.

DISCUSSION

Documenting temporal responses of biodiversity to natural and human disturbances has long been a major topic of study in ecology (Bradstock et al. 2012, DellaSala and Hanson 2015, Pulsford et al. 2016). Disturbances such as fire can have large impacts on vegetation structure and plant species composition (Franklin et al. 2002, Haslem et al. 2011), which are major predictors of habitat suitability for a wide range of animals (MacArthur and MacArthur 1961, Morrison et al. 2006). Yet, identifying the specific ecological processes underlying temporal patterns of recovery of animal populations after fire remains a key concern (Engstrom et al. 1984, Barton et al. 2014).

We used structural equation modelling and enhanced regression analyses to examine longitudinal and cross-sectional effects of disturbance. This approach aimed to address the underlying causal processes influencing bird response (rather than selecting a “best model” comprising a parsimonious set of predictors; (Grace et al. 2009)) and enabled us to distinguish between: **(a)** those species for which there was a direct effect of time since fire, and **(b)** taxa for which there was an indirect effect of time since fire mediated through temporal changes in vegetation (see Table 3). For those species with direct effects, a potential mechanism underlying occurrence may be the time required to colonize a site or for residual populations remaining onsite to recover following fire. In contrast with indirect mechanisms, direct mechanisms may operate irrespective of the structure and composition of the vegetation at that site.

Our long-term study yielded five key findings. First, we documented major temporal changes in plant species richness and vegetation, both on burnt and unburnt sites in all vegetation classes (Figure 3). Second, we documented major temporal changes in bird species richness and the occurrence of many bird species, although the trend were highly varied (see Table 2). Third, there was a significant positive temporal trend with vegetation (ignoring years since fire) for 10 of the 20 bird species and the two aggregate measures of species richness and reporting rate (Model 2, Table 3). Fourth, testing of competing postulates/models (Table 1) revealed that the answer to our key overarching question – Can temporal changes in vegetation structure post-fire predict changes in bird occurrence on sites, and can these be separated from other temporal changes using the surrogate of time since fire? – was complex and multi-faceted. This was because it varied markedly depending on whether a composite (aggregate measure) (i.e. species richness and reporting rate) or the occurrence of individual species was the response variable (Table 3). The driver of year trends could be separated between time since fire effects and vegetation attribute effects for nine bird species. That is, a component of the year trend was driven by temporal trends in one of the three vegetation variables (number of understory plant species, number of midstory plant species, or percent cover of the midstory) (see Table 2 and Table 3). For these nine species, the indirect effects of vegetation variables were always positive and statistically significant, a result broadly consistent with the findings of analyses on mammals and fire responses (e.g. by Swan et al. 2015). However, the direct effect of years since 2003 fire on these species differed, with a strong increasing trend for the Yellow-faced Honeyeater, no detectable trend for the Grey Shrike-thrush, White-browed Scrubwren, Little Wattlebird and Lewin's Honeyeater, and a strong declining trend for the Grey Fantail, White-throated Treecreeper, and Spotted Pardalote (Tables 2 and 3). Fifth and finally, it was not possible to detect a significant conditional indirect effect of vegetation attributes using any of the three variables measured for bird species richness, reporting rate, and the occurrence of the majority (N= 11) of individual species (see Table 2). This result underscored the inherent difficulty in attributing direct versus indirect effects for either or both change in vegetation structure or time since fire on bird occurrence.

There may be many underlying causes for the varying responses to time since fire and vegetation structure and plant species richness in this study. For example, nectarivores such as the Yellow-faced Honeyeater could respond to nectar availability as the indirect effect of years since 2003 mediated by either number of species or midstory vegetation cover (where most nectar resources occur). For all nine species, the conditional indirect coefficients were often as strong (or stronger) than the direct coefficients related to the trend in time since fire, and were also all positive, indicating the positive effect of recovery of vegetation after fire on occurrence. A positive trend in indirect effects could be due to increased availability of food such as increased invertebrates for small insectivorous bird species (Whelan 1995) like the White-throated Treecreeper and Spotted Pardalote.

Finally, we acknowledge that a potential limitation of the analyses underpinning our study was that was assumed detectability was equal between burnt and unburnt sites. However, detectability may differ. For example, in burnt habitats bird detection may be higher than in unburnt as sound travels further and birds may need to come to the ground more to feed.

Life history attributes and bird responses

There do not appear to be any general life history attributes common to species that displayed similar responses to fire or vegetation (e.g. consistency with Models 1, 2 and 3). For example, two of the species that declined with time since fire, the Crimson Rosella and Spotted Pardalote, share very few life history attributes. Three of the species exhibiting strong temporal increases over the 10-year duration of our investigation (Eastern Spinebill, Red Wattlebird, and New Holland Honeyeater) were honeyeaters. However, other species in this large group either did not exhibit a temporal response (Lewin's Honeyeater) or increased over time only on burnt sites (Little Wattlebird; Figure 5, Table 2). One factor that appears to play a role in direct effects is site fidelity, with the exception that one declining species was sedentary rather than being migratory or nomadic (Table 2).

Our analyses also identified species for which there was no evidence of temporal trends associated with either vegetation or time since fire on sites burnt in 2003. An example was the Eastern Whipbird (Table 2). We suggest that these kinds of patterns might arise if, for example, these species maintain high levels of site affinity and persist at sites irrespective of disturbance and vegetation cover (Lindenmayer et al. 2014a). These varying results further suggest there are likely to be an array of different factors influencing the temporal changes among the various species that we modelled and their temporal responses appear not to be readily predicted on the basis of life history attributes.

Temporal changes in vegetation

The positive trends in plant species richness and vegetation cover across both unburnt and burnt sites and among all six broad vegetation classes suggest that within-site ecological changes driven by fire were weaker than the changes across the whole landscape *per se*. The reasons for these intriguing park-wide, and cross vegetation-type changes in vegetation cover remain unclear. They are not associated with observer differences as the same experienced botanist (CM) completed all five repeated vegetation surveys that underpinned this investigation. Notably, there have been no increases in invasive plant species over the duration of this study. It is possible they are linked with broader climate effects that have not been examined here.

Implications for management

The results of this study have important implications for management as they can inform approaches to managing disturbance to maintain vegetation structure and plant species composition that will also cater for the requirements of fauna (Clarke 2008). We were able to identify a range of species for which increasing vegetation cover and plant species richness of the understory and midstory layers made an important contribution to their temporal trajectory (Tables 2 and 3). Such results showing bird responses to multiple vegetation attributes, fire attributes and survey year effects underscore the critical importance of long-term studies of biodiversity and fire (Pons and Clavero 2009, Recher et al. 2009). Indeed, we argue that the complex array of temporal and other responses observed in this investigation would not have been identified with traditional cross-sectional (space-for-time) analyses that are generally the norm in ecological studies of fire and biodiversity.

Second, our analyses can help identify those species which appear to be responding to key drivers in addition to time since fire and vegetation. Such species may need management actions beyond those linked with vegetation manipulation and/or fire control to ensure their conservation. For example, we found strong evidence that the Spotted Pardalote was declining across the entire study area – both in burnt and unburnt sites, and in all vegetation types. Reserve-wide changes in predation regimes might be a possible cause of the temporal dynamics of this species. We hypothesize that because the Spotted Pardalote nests in burrows in the ground it may be particularly susceptible to ecosystem-wide changes in predation pressure exerted by animals such as snakes. If further studies were to result in this hypothesis being upheld, then species such as the Spotted Pardalote may need management actions beyond those linked with vegetation manipulation and/or fire control to ensure their conservation.

Third, our analyses included data for the Eastern Bristlebird, and Booderee National Park is a stronghold for this endangered species (Lindenmayer et al. 2009a). We identified a significant positive temporal trend for this species in sites that escaped fire in 2003 (Table 2). Notably, none of the vegetation variables we analysed proved to be important predictors for the occurrence of this species. This finding suggests that long unburnt areas (i.e. places not burnt for ~ 10 years or more) will be important for the persistence of the Eastern Bristlebird and efforts to exclude frequent fire will be an important part of the strategic plan of management for the reserve. In addition, where wildfire leaves patches if unburnt vegetation it will be important for the conservation of the Eastern Bristlebird that such green areas are not subsequently damaged in so-called “black-out” burning operations (Lindenmayer et al. 2008).

CONCLUSIONS

We have used a large long-term dataset to separate the effects of time since fire from vegetation recovery after fire on faunal responses. This is a challenging problem to address because key drivers of temporal responses in biodiversity can be co-occurring and strongly collinear (Monamy and Fox 2000). We found that we could not separate temporal effects between time since fire and vegetation attributes for bird species richness, reporting rate, and the occurrence of the majority of individual species. However, we separated time since fire effects and vegetation effects for nine species, and it **was** possible to tease apart the relative importance of different potential explanatory variables. For a number of bird species, we found that a significant component of the year trend was driven by temporal trends in one of three vegetation variables. Determining which (if any) species are influenced by indirect versus direct drivers is critical for guiding management (Baker 2000, Clarke 2008). This is because it can help identify for which species vegetation manipulation or prescribed burning might be the best strategy for maintaining or restoring populations in disturbed environments.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Appendix S1: Conceptual models of potential inter-relationships between fire, time and vegetation characteristics as drivers of bird occurrence on sites

Appendix S2: Brief description of vegetation types at Booderee National Park and used to stratify surveys of long-term field survey sites

Appendix S3: Summary of experimental design

Appendix S4: Cross-sectional versus Longitudinal Regression Coefficients for a Structural Vegetation Variable

Appendix S5: Direct versus Conditional Indirect Years since Fire effects with Mediation by a Structural Vegetation Variable

Appendix S6: Temporal changes in plant species richness and vegetation structure

Appendix S7: Tests of competing variants of Model 1 for individual species of birds

Appendix S8: Bird responses and using log transform data for vegetation covariates

Appendix S9: Fire and Years since fire standardised regression coefficients for Model 1

Appendix S10: Conditional indirect effects of time since fire quantified as linear and quadratic terms mediated by the longitudinal component of vegetation structural variable NUS

Appendix S11: Conditional indirect effects of time since fire quantified as linear and quadratic terms mediated by the longitudinal component of vegetation structural variable NMS

Appendix S12: Conditional indirect effects of time since fire quantified as linear and quadratic terms mediated by the longitudinal component of vegetation structural variable logCMS

Appendix S13: List of birds recorded in repeat surveys in Booderee National Park

Table 1. Postulates[a] associated with the trend for bird species occurrence and years since 2003 ("*Y*"), the trend with increasing vegetation structural diversity or cover (i.e. nominal vegetation variable denoted "V"), or indirect component of a positive trend in years since 2003 as mediated by increasing vegetation structural diversity or cover at Booderee National Park. The final column in Table 1 corresponds to the model test results that are summarized in Table 2.

	Site burnt in 2003 (*B*)	**Site unburnt in 2003 (U)**	**Model in analyses***
Positive year trend (+)	$P_{Y+,B}$	$P_{Y+,U}$	Model 1
Negative year trend (-)	$P_{Y-,B}$	$P_{Y-,U}$	Model 1
Positive longitudinal vegetation trend ignoring any year trend	$P_{V,B}$	$P_{V,U}$	Model 2
Positive indirect year trend as mediated by a significant temporal trend in vegetation (MODMED)	$P_{(V\|Y),B}$	$P_{(V\|Y),U}$	Model 3

[a] Or alternative hypothesis to the corresponding null hypothesis of no trend.

Table 2. Qualitative description of year trends and support for propositions for bird species diversity, total reporting rate, individual species reporting rate and structural attributes of vegetation over the period 2004 to 2013 using fitted Models (1), (2), and (3) (see text). Model (1) with terms of broad vegetation category (BVC), burnt vs unburnt in 2003 (B), their interaction (B:BVC), wildfire frequency, burn severity in 2003, Years since 2003 fire (YS03), and interaction B:YS03. Model (2) replaces YS03 and B:YS03 terms with longitudinal and cross-sectional covariate components for one of the vegetation structure variables of number of understory plant species (NUS), number of midstory plant species (NMS), percentage cover of midstory (CMS), and the interaction with B denoted in general as v_L , B: v_L , v_C and B: v_C, respectively. Fire-related covariates in each model are outlined in the text. Model (3) augments Model (1) with terms v_L, B: v_L, v_C, and B: v_C. Blank cells in the table correspond to an absence of significant effects. All effects shown in the cells for respective models are significant at $P<0.05$.

Response Variable[1]	**Prev**[2]	**Year Trend**[3]	**Structural vegetation variable(s)**[4] **for which the proposal is accepted**[5] **and null hypothesis rejected**

		Model (1)			Model (2)		Model (3)	
		$P_{Y+,B,}$ $P_{Y-,B}$ **Burnt**	$P_{Y+,U,}$ $P_{Y-,U}$ **Unburnt**	PDev[6]	$P_{V,B}$ **Burnt**	$P_{V,U}$ **Unburnt**	$P_{(V\|Y),B}$ **Burnt**	$P_{(V\|Y),U}$ **Unburnt**
Number of Species		+	+	0.37	NUS, NMS, logCMS	NUS, logCMS		
Total reporting rate		+	+	0.31	NUS, NMS, logCMS	NUS, NMS, logCMS		
Grey Fantail	0.478			0.11	NUS		NUS	
Eastern Spinebill	0.429	+	+	0.22	NUS, NMS, logCMS		NUS	
Eastern Whipbird	0.394		-	0.07				
Brown Thornbill	0.385	-	+	0.21				
Yellow-faced Honeyeater	0.361	+	+	0.32	NUS, NMS, logCMS	NUS, NMS, logCMS	logCMS	
White-browed Scrubwren	0.327			0.12		NMS		NMS
Little Wattlebird	0.327	+		0.16	NUS, NMS, logCMS	NMS		NMS
White-throated Treecreeper	0.313	-		0.43			logCMS	
Red Wattlebird	0.303	+	+	0.30	NUS, NMS	NUS		
Spotted Pardalote	0.302	-	-	0.36			logCMS	logCMS
Crimson	0.251	-	-	0.21				

Rosella								
Silvereye	0.246	-	-	0.24				
New Holland Honeyeater	0.246	+	+	0.31	NUS, NMS, logCMS	NUS, NMS		
Fan-tailed Cuckoo	0.241	+		0.13	NUS			
Grey Shrike-thrush	0.224		+	0.10	NUS		NUS	
Eastern Bristlebird	0.218		+	0.49				
Rainbow Lorikeet	0.217		+	0.26				
Variegated Fairy-wren	0.197	+		0.09				
Lewin's Honeyeater	0.189			0.40	NMS	NUS, NMS	NMS	
Eastern Yellow Robin	0.183	-		0.14				

[1] Species ordered from top to bottom in decreasing order of prevalence (i.e. proportion of site by year surveys where present).

[2] Prevalence. Proportion occupied out of the sum of plots within sites by year combinations.

[3] Significantly ($P<0.05$) $P_{Y+,B,}$, $P_{Y+,U,}$ increasing trend: (+), $P_{Y-,B,}$, $P_{Y-,U,}$ decreasing trend: (-) . No detectable trend (i.e. accept null hypothesis associated with $P_{Y+,B,}$ $P_{Y-,B}$ and $P_{Y+,U,}$ $P_{Y-,U}$) (blank). Determined from the sign and size of the standardised coefficient for linear and quadratic terms (see Appendices).

[4] Number of understory species, number of midstory species, and percent cover of midstory species.

[5] Determined (as above) from the sign and size of the standardised coefficient for linear and quadratic terms (see Appendices).

[6] Proportion of deviance (PDev) explained which is the same as the coefficient of determination in the case of Gaussian errors.

Table 3. Direct and conditional indirect unstandardized linear and quadratic coefficient estimates as mediated by vegetation variables Number of understory species, number of midstory species, and percent cover of midstory species for species that have a significant conditional indirect effect (sites burnt in Dec 2003, and regression coefficient estimate corresponding to v_L. All coefficient estimates obtained from the fit of a linear model version of Model (1) to v_L as a response variable (α ’s) and Model (3) fitted to species-specific occurrence data (β ’s) (see Appendices S4 and S5).

Species	**Veg/Burnt (B) or Unburnt (U)**	**Unstandardized Coefficient (SE)**				
		Direct YS03		**Conditional Indirect YS03**		v_L $\hat{\beta}_L$
		Linear $\hat{\beta}_1$	Quadratic $\hat{\beta}_2$	Linear $\hat{\alpha}_1\hat{\beta}_L$	Quadratic $\hat{\alpha}_2\hat{\beta}_L$	
Grey Fantail	NUS-B	-0.258^{ns} (0.264)	-0.503^{**} (0.148)	0.548^{***} (0.238)	0.131^{ns} (0.078)	0.033^{***} (0.013)
Eastern Spinebill	NUS-B	1.117^{***} (0.276)	-0.6444^{***} (0.157)	0.642^{***} (0.246)	0.159^{ns} (0.082)	0.038^{***} (0.014)
Grey Shrike-thrush	NUS-B	-0.326^{ns} (0.306)	-0.1310^{ns} (0.169)	0.815^{***} (0.271)	0.209^{**} (0.092)	0.047^{***} (0.015)
White-browed Scrubwren	NMS-U	-0.231^{ns} (0.159)	-0.0371^{ns} (0.155)	0.288^{***} (0.115)	0.179^{*} (0.088)	0.110^{***} (0.039)
Little Wattlebird	NMS-U	-0.079^{ns} (0.158)	0.2816^{ns} (0.155)	0.276^{***} (0.116)	0.156^{ns} (0.089)	0.108^{***} (0.039)
Lewin’s Honeyeater	NMS-B	0.340^{ns} (0.2473)	-0.332^{ns} (0.227)	0.366^{**} (0.153)	0.119^{ns} (0.089)	0.153^{***} (0.056)
Yellow-faced Honeyeater	logCMS-B	1.095^{***} (0.156)	0.483^{**} (0.146)	0.367^{***} (0.107)	0.204^{***} (0.076)	0.255^{***} (0.073)
White-throated Treecreeper	logCMS-B	0.013^{ns} (0.190)	-0.950^{***} (0.183)	0.343^{***} (0.116)	0.203^{**} (0.083)	0.311^{***} (0.088)
Spotted Pardalote	logCMS-U	-0.542^{**} (0.169)	-0.186^{ns} (0.171)	0.241^{**} (0.104)	0.264^{**} (0.099)	0.208^{**} (0.088)

*** P<0.001, ** P<0.01, * P<0.05, ^{ns} P>0.05

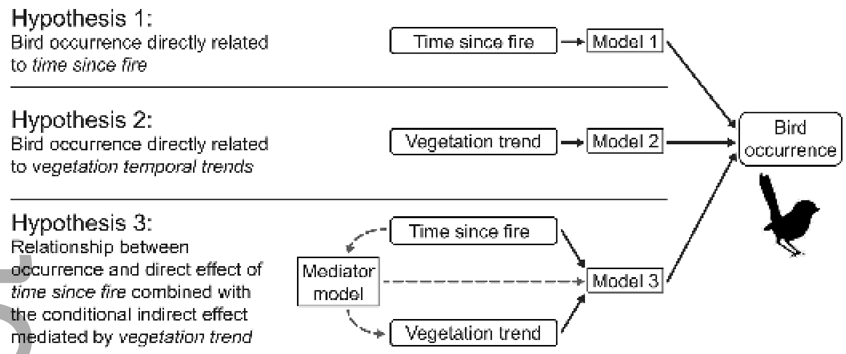
Figure 1. Conceptual diagram of potential inter-relationships between fire, time and vegetation characteristics as drivers of site occurrence by a bird species. Solid arrows indicate direct effects, dashed arrows indicate indirect effects. Mathematical notation and R code for the models are provided in Appendix A.

Figure 2. The location of long-term field survey sites at Booderee National Park.

Figure 3. Temporal trends in a) the number of understory plant species, b) number of midstory plant species, and c) percent cover of midstory species. All variables are shown on the linear predictor (LP) showing SE bars (fine lines) at survey years and twice SE of difference bars (slightly offset for clarity).

Figure 4. Temporal trends in bird species richness on the linear predictor (LP) scale for Model 1 showing SE bars (fine lines) at survey years and twice SE of difference bars (slightly offset for clarity). The total number of species recorded over the duration of the study was 130 (see Appendix S13). The linear predictor scale was used because it relates to the linear and quadratic terms in the covariate years since the 2003 fire and allows the standard error of difference to be presented without transformation.

Figure 5. Temporal trends in the reporting rate of the: A Eastern Spinebill. B. Spotted Pardalote. C. Little Wattlebird on the linear predictor (LP) scale for Model 1 showing SE bars (fine lines) at survey years and twice SE of difference bars (slightly offset for clarity).



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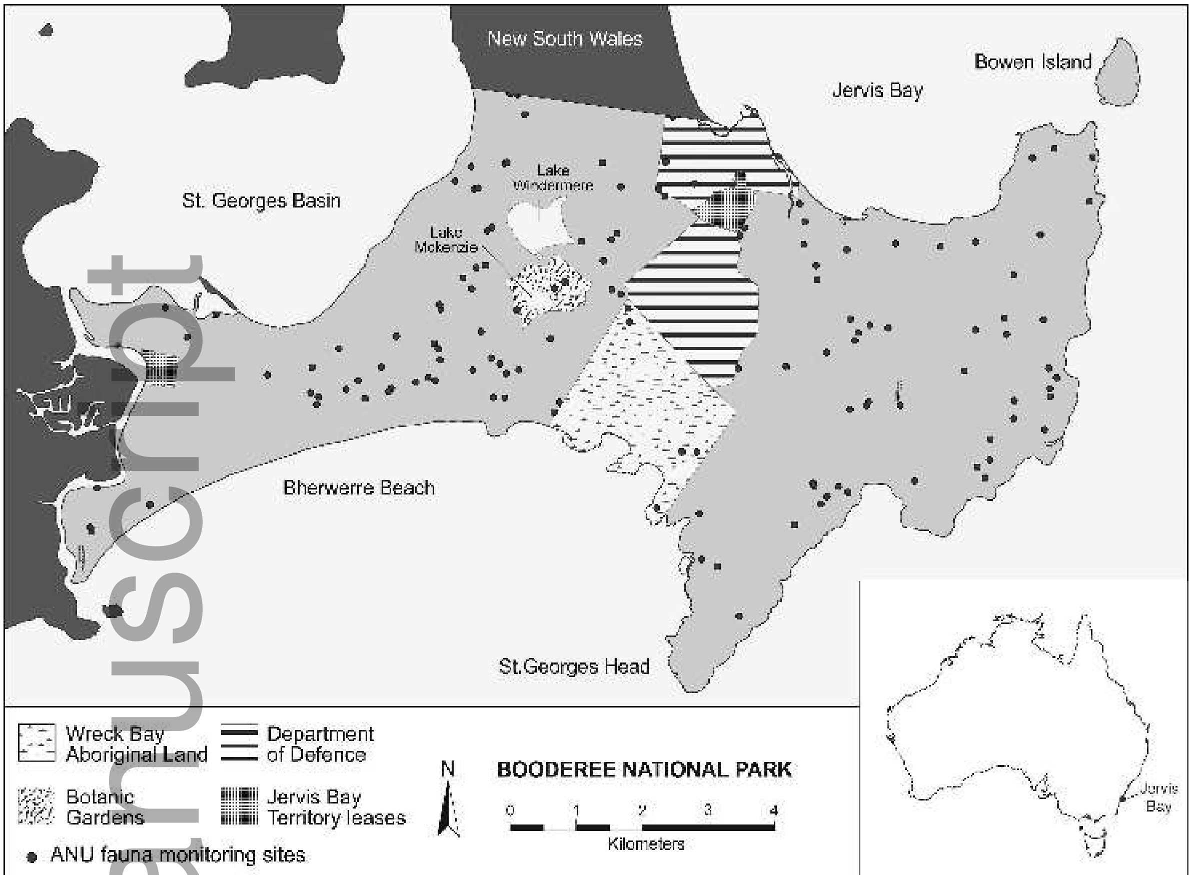

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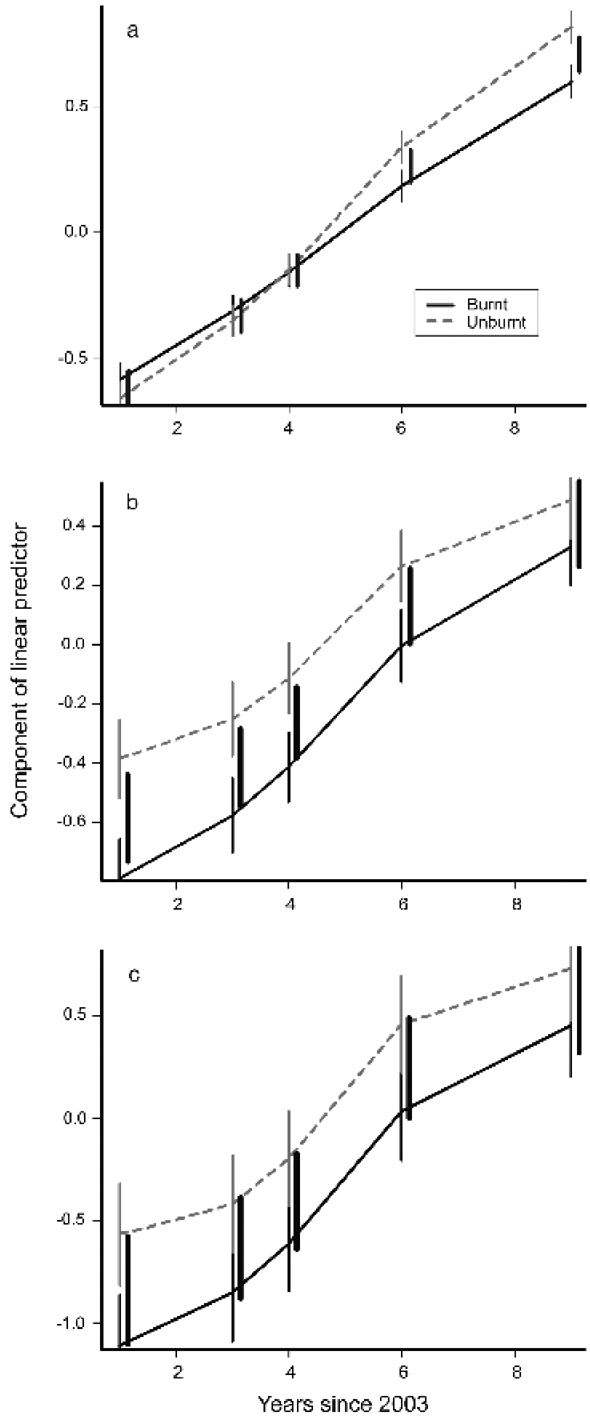

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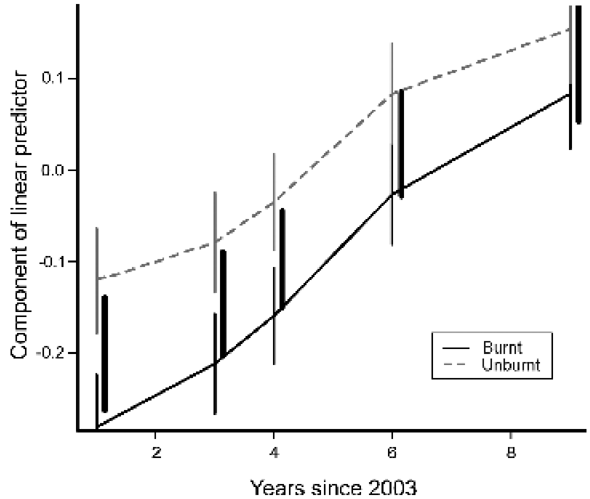

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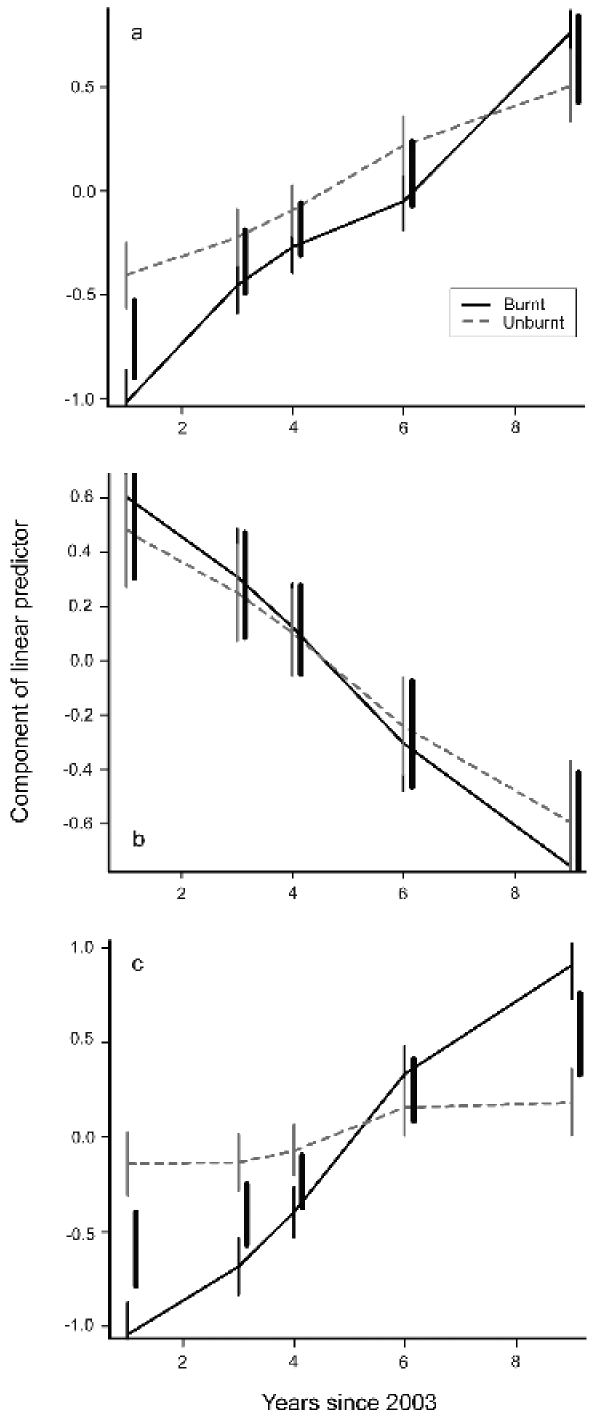

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