Evaluating the role of fire disturbance in structuring small reptile communities in temperate forests

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23

24 **Abstract**

25

26 Fire is an integral disturbance shaping forest community dynamics over large scales. However,
27 understanding the relationship between fire induced habitat disturbance and biodiversity
28 remain equivocal. Ecological theories including the intermediate disturbance hypothesis (IDH)
29 and the habitat accommodation model of succession (HAM) offer predictive frameworks that
30 could explain faunal responses to fire disturbances. We used an 80 year post-fire
31 chronosequence to investigate small reptile community responses to fires in temperate forests
32 across 74 sites. First, we evaluated if changes in species richness, abundance and evenness
33 post-fire followed trends of prior predictions, including the IDH. Second, using competing
34 models of fine scale habitat elements we evaluated the specific ways which fire influenced
35 small reptiles. Third, we evaluated support for the HAM by examining compositional changes of
36 reptile community post-fire. Relative abundance was positively correlated to age post-fire while
37 richness and evenness showed no such associations. The abundance trend was as expected
38 based on the prior prediction of sustained population increase post-disturbance, but the trend
39 for richness contradicted the prediction of highest diversity at intermediate levels of
40 disturbance (according to IDH). Abundance changes were driven mainly by changes in
41 overstorey, ground layer, and shelter, while richness and evenness did not associate with any
42 vegetation parameter. Community composition was not strongly correlated to age since fire,
43 thus support for the HAM was weak. Overall, in this ecosystem, frequent fire disturbances can

44 be detrimental to small reptiles. Future studies utilizing approaches based on species traits
45 could enhance our understanding of biodiversity patterns post-disturbance.

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48 **Key Words**

49 Reptile community, fire, disturbance, vegetation structure, succession, intermediate
50 disturbance hypothesis, habitat accommodation model

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54 **Introduction**

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56 Fire is a common disturbance in many ecosystems around the world (Driscoll et al. 2010; Spies
57 et al. 2012; Westgate et al. 2012), with profound effects on the diversity and composition of
58 communities over large spatial and temporal scales (Friend 1993; Lindenmayer et al. 2008;
59 Driscoll et al. 2010). Fires modify natural succession by changing habitat structure and
60 environmental condition, for example, by altering soil moisture and nutrient levels, reducing
61 the biomass and composition of woody vegetation and the litter layer (Russell et al. 1999;
62 Haslem et al. 2011). Fire is also commonly used as a management tool conducted by
63 government agencies for a variety of purposes such as fuel reduction, and for managing
64 biodiversity (Friend 1993; Russell et al. 1999).

65

66 The succession of animal communities over time is often intricately linked to fire events (e.g.
67 Friend 1993; Valentine et al. 2012). Thus, a better understanding of the community dynamics
68 and the different succession patterns following disturbances would benefit the management of
69 natural assets (Dornelas 2010). This is an especially important issue now as fire management
70 has become a global conservation priority (Russell et al. 1999; Parr and Andersen 2006; Driscoll
71 et al. 2010). Furthermore fire regimes are expected to be significantly altered by climate
72 change (Dale et al. 2001). For example, inappropriate fire regimes, such as fire suppressions or
73 overly frequent burns, are also implicated in the declines of some mammal and bird species
74 (Russell et al. 1999; Anderson et al. 2005). Therefore, research is needed to identify desirable

75 fire management practices to balance human needs and the maintenance of biodiversity (Parr
76 and Andersen 2006).

77
78 Given the importance of fires for ecological management, a number of theories have been
79 developed for predicting biotic responses post-disturbance (Connell 1978; Mackey and Currie
80 2000; Lindenmayer et al. 2008). Prominent disturbance theories include the intermediate
81 disturbance hypothesis (IDH; Connell 1978), which predicted the occurrence of highest species
82 richness at intermediate levels of disturbance (Mackey and Currie 2000; Mackay and Currie
83 2001), and the habitat accommodation model (HAM; Fox 1982), which suggested a predictable
84 sequence of post-disturbance recovery that is linked to the succession of plant communities
85 over time (Fox 1982; Greenberg et al. 1994; Driscoll and Henderson 2008).

86
87 We use small terrestrial reptiles as indicators to monitor biodiversity changes post-fire (see
88 Magaton 2011). While reptile communities show a wide variety of responses to fires, including
89 positive (e.g. Fredericksen and Fredericksen 2002; Legge et al. 2008), negative (e.g.
90 Cunningham et al. 2002), and neutral (e.g. Radke et al. 2008; Ruthven et al. 2008), there is little
91 consensus to whether such responses could be generalized within broader disturbance theories
92 (Lindenmayer et al. 2008), especially in temperate forest ecosystems (Greenberg and Waldrop
93 2008; Ruthven et al. 2008; Cano and Leynaud 2010).

94
95 Therefore, our overall aim was to test the predictive ability of disturbance theories in animal
96 communities in response to fire history in temperate forests of southeastern Australia.

Specifically, we had three aims. First, we aimed to investigate if responses in reptile community metrics (richness and abundance) follow the trends predicted by existing theories. We used the intermediate disturbance hypothesis (IDH) to test for variations in species richness, as it is one of the best tested ecological concepts (Svensson et al. 2012). As predicted by the IDH, peak diversity was expected to occur at the mid-point of forest succession where pioneer and climax species co-exist (Fig. 1a; Connell 1978). However, the IDH is unsuitable for other community metrics (Svensson et al. 2012), and predicting species abundance patterns post-disturbance to date lacks a strong conceptual framework. This is in part because animal abundance shifts post-disturbances are often context-dependent, multi-directional, and unrelated to changes in diversity (Dornelas 2010). However, based on ecological plausibility, species abundance was expected to increase with increasing age since fire (Fig. 1b). This is because mature vegetation is often structurally more complex (Lindenmayer et al. 2009), which increase the availability of microhabitats providing more resources, cover against predators and better opportunities for thermoregulation (Fox 1982; Howard et al. 2003; Garden et al. 2007).

Our second aim considered that as fires are coarse-scale disturbances which structure reptile populations through fine scale alterations of habitat structure (e.g. Pianka 1973; Jellinek et al. 2004; Brown and Nelson 1993; Brown et al. 2008), it is necessary to determine the specific habitat elements are underlying reptile responses. For example, in temperate ecosystems most terrestrial reptiles depend on structural heterogeneity of the ground and shrub layer (Brown 2001; Taylor and Fox 2001; Jellinek et al. 2004), and the amount of insolation (Urlus 2009). To evaluate the importance of specific habitat elements altered by fire disturbances on reptile

community metrics we considered different vegetation attributes as distinct hypotheses based on ecological plausibility, using an information theoretic approach.

Our third aim was to test the habitat accommodation model of succession (HAM; Fox 1982), and determine whether there was a succession of reptiles in relation to the age of post-fire vegetation, in terms of community composition (turnover of species and their relative abundances), as the habitat suitability changes for each species.

Materials and methods

Study area

Our study area was located in the East Gippsland region of Victoria, Australia, which encompassed a large network of reserves managed for biodiversity conservation. We conducted this study in Cape Conran Coastal Park (37°49'S, 148°44'E), Murrungowar State Forest (37°37'S, 148°44'E), Bemm State Forest (37°41'S, 148°52'E) and Club Terrace State Forest (37°64'S, 148°49'E). We selected these sites because fire had been a common form of disturbance across these landscapes, the history of which is well mapped and documented, dating back to 1939. The fires consisted of both wildfires and prescribed low-intensity burns, which were conducted extensively by government agencies to avoid heavy fuel accumulation, regenerate recently logged areas, and for floral and faunal management (Friend 1993; DSE 2009). Our study area extended from the coast to approximately 21 km inland, covering

approximately 43,000 ha. Annual rainfall in the region averaged 1080 mm (Bureau of Meteorology 2010).

The study area is also impacted by other disturbances including logging and introduced predators (DSE 2009). However, these should not confound the effects of fires, as fox management on this landscape had no impacts on reptiles (Urlus 2009), and timber harvesting had been not conducted for over 30 years on any of our sites prior to sampling, which is deemed sufficiently long for forest recovery for small reptile communities (see e.g. Alexander et al. 2002; Heltzel and Leberg 2006).

Broad vegetation types

Our study area was dominated by two broad vegetation types: 1) banksia woodland consisting mainly of *Banksia serrata* and *Banksia integrifolia*, along with some eucalypt species, particularly *Eucalyptus consideniana*; and 2) eucalypt forest, dominated by *Eucalyptus sieberi* and *Eucalyptus globoidea* (Parks Victoria 2005). However, we did not distinguish between these vegetation types (eucalypt forest vs. banksia woodland) in our site stratification, because fine scale attributes of the ground layer and understorey are arguably more important for small terrestrial reptiles than Ecological Vegetation Classes (EVC), which are based more broadly on vegetation of the overstorey (see Jellinek et al. 2004; Wanger et al. 2009). Previous work on this landscape also suggested that EVC had no influence on the composition of small reptile communities (Urlus 2009).

Study design

We selected 74 sites throughout the study area, chosen to provide a range of time since last fires in years ranging from very recently burnt (0 years since fire) to sites that are unburnt since records were first kept in 1939 (thus over 71 years post-fire), which was assigned an age of 80 years post-burn. This chronosequence technique assumes that spatially separated sites regenerate equally over time, thus allowing comparisons between sites based on their age since burning (Letnic et al. 2004). To meet the stratifications, sites were not spaced equidistantly. However, a minimum distance of 250 m was maintained between sites to ensure independence among sampling, based on the daily movement potentials of small skinks, the most common reptiles in the area (Heatwole and Taylor 1987).

Sampling protocol

We used pitfall trapping to sample for small terrestrial reptiles. A line of pitfall traps was constructed at each site, comprising five 20-L buckets spaced 5 m apart, with the opening flush with the ground surface. A 30 cm high plastic drift fence passed over the centre of each bucket. Trap lines were kept at least of 20 m away from roads in order to avoid edge effects disrupting reptile movements (Heatwole and Taylor 1987). Trapping was conducted from late 2008 to early 2011, for a total of 14,084 trap nights (each pitfall bucket counted as single trap). Sampling was restricted to summer. Sites were used for a maximum of two seasons. The sites that we surveyed in any particular year were always represented by a wide range of fire classes

(i.e. years since fire). Traps were checked daily, with animals identified and released at the point of capture. Incidental observations of reptiles outside the traps were included where appropriate in analyses of species richness. Nomenclature followed that of Wilson and Swan (2008).

Vegetation assessments

To explore the mechanisms underlying community response to fires, we surveyed the vegetation at each site, as correlations between reptile diversity and key structural elements of the habitat (which are often disturbance related) were common (e.g. Brown 2001).

Assessments were undertaken at two spatial scales: two quadrats of 25 m² offset from the terminal buckets by 1.5 m, and a circular sampling area 20 m in radius surrounding the pitfall line. Within the quadrats, we assessed leaf litter depth, canopy cover, horizontal vegetation density and the amount of bare substrate cover. Within each circular sampling area (1,056 m²), we measured the total basal area of trees (DBH > 10 cm) and log volume. Subsequent analyses were made on the response of each vegetation parameter to fire history using generalized additive models (GAM), estimated using maximum likelihood (McCullagh and Nelder 1989). Results showed that habitat elements from the ground layers were significantly correlated to time since fire (Appendix 4).

Data analysis

We used three community metrics to assess responses of reptile communities to fire: species richness, relative abundance, and evenness (measured using Simpson's Index of Diversity). As sampling effort between sites were not exactly equal (see Appendix 2), we used captures per 100 trap nights to measure relative abundance, and randomly discarded data to make the sampling intensity of each site equal to those of the least sampled sites (31 sampling days) before analyzing richness and evenness.

We used generalized additive models (GAM) to relate reptile species richness and abundance to time since fire, estimated using maximum likelihood (McCullagh and Nelder 1989; Kelly et al. 2011). Smoothed terms (time since fire), using smoothing splines, were considered significant when P-values were < 0.05 . This approach is considered more suitable than specific deterministic functions as it provides a flexible framework for building biodiversity response models, as predictors can be fitted as either non-linear or linear terms.

Second, we tested the relationships between the three community metrics and fine scale vegetation features using an information theoretic approach (Burnham and Anderson 2002). Seven predictor variables were identified *a priori* (Appendix 2), and incorporated into four groups (structure of ground layer, shrub layer, overstorey, and shelter availability) each comprising one to several explanatory variables (Appendix 2 and 3). We generated 12 candidate models using generalized additive modeling (GAM; Appendix 3), including a null model (no variables entered) and global model (incorporating all variables). Using a null model reduced the likelihood of selecting a model derived from random effects, while the global

model explored potential interactions from all elements. Model selection and inference was based on the Akaike information Criterion (AIC), which we calculated for each model, as well as the difference between the AIC of the target model and that of the model with best fit (ΔAIC), with models having $\Delta\text{AIC} \leq 2$ considered to be substantially supported, as long as the null model was not similarly supported ($\Delta\text{AIC} \leq 2$; Table 1; Burnham and Anderson 2002).

Deducing spatial patterns in ecology is potentially confounded by spatial autocorrelation (Dormann et al. 2007). Generalized additive mixed models (GAMM) are able to incorporate differential spatial correlation structure to potentially improve model fit (Dormann et al. 2007; Zuur, 2009). Here we used site-specific latitude and longitude to capture the spatial relationship among sites considering both coarse-scale measures (abundance and richness post-disturbance) and fine scale vegetation measures. For these variables, a model selection approach was used to ascertain the presence and type (exponential, spherical, ratio, linear and Gaussian) of the spatial autocorrelation structure. A total of five candidate models were generated, each representing a different type of correlation structure. These were compared to a non-spatially correlated model (Appendix 7). For vegetation associations, we only tested for spatial autocorrelations in the global model which included all vegetation characteristics. To be conservative, we regarded spatial autocorrelation to be significant if the highest ranked spatially autocorrelated model was within 2 AIC units of the non-spatially considerate model (Appendix 7), and we used that model as our final result. For fine scale vegetation analyses, in case spatial autocorrelation was detected, we reran the model selection using GAMM to incorporate the spatial elements into every model tested (Appendix 3), otherwise the original

GAM results were retained. Spatial autocorrelation was detected for responses of relative abundance and species evenness to age since fire, as well as the vegetation associations of species richness and evenness. Thus results of spatially considered GAMM models were presented for those analyses (Table 1; Appendix 7 and 8).

Third, reptile community composition in relation to age post-fire was assessed with Permutational Multivariate Analysis of Variance (PerMANOVA), using Bray-Curtis dissimilarity index as the distance measure. We conducted PerMANOVA on $\log(x+1)$ transformed data. Data were grouped into five categories based on their fire history (0 to 3 years post-fire, 4 to 14 years, 15 to 24 years, 25 to 40 years, and over 40 years). Post-hoc analyses were conducted using the Tukey's HSD test (Oksanen et al. 2011).

Statistical analyses were undertaken in the R statistical package 2.13.0 (R Development Core Team 2010). GAMs were run in the extension package mgcv version 1.7-5 (Wood 2006). Model selections were run using the package MuMIn version 1.0 (Logan 2010). PerMANOVA, along with its graphical representations and post-hoc tests were conducted in package vegan (Oksanen et al. 2011).

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271 **Results**

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273 Survey results

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275 We captured a total of 2691 reptiles, representing 14 species (10 lizard and 4 snake species).

276 The most common species were the yellow-bellied water skink *Eulamprus heatwolei* (40.6% of

277 captures), garden skink *Lampropholis guichenoti* (34.0% of captures), weasel skink *Saproscincus*

278 *mustelinus* (11.4% of captures), and the delicate skink *Lampropholis delicata* (7.6% of captures),

279 with each occurring in over 75% of all sites, and as a whole comprising 93.5% of total captures.

280 Other species were captured infrequently, with none occurring in more than half of all sites

281 (Appendix 1). Species richness ranged from 3 to 9 per site.

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283 Reptile community responses post-fire to predicted patterns

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285 Strong correlations with time since fire were observed for reptile abundance (N-Par $F = 10.71$,

286 $edf = 1$, $P = 0.002$), which increased over time post-fire (Fig. 2a). Species richness also appeared

287 to increase with age since fire, though the trend was not significant (Chi. sq = 2.014, $edf = 1$, $P =$

288 0.244). There were no relations between age since fire and species evenness (N-Par $F = 0.013$,

289 $edf = 1$, $P = 0.909$). For relative abundance, this pattern was similar to the trend predicted (Fig.

290 1b), but the trend for both richness and evenness were different to prior predictions (Fig. 1a;

291 Fig. 2).

Fine-scale vegetation attributes explaining reptile responses

For reptile abundance, there were three closely ranked models with substantial support ($\Delta AIC \leq 2$), the overstorey vegetation, the interactive effect of overstorey and vegetation density, and the interactive effect of overstorey and ground layer (Table 1). For species richness, the null model received substantial support and was ranked more than 2 AIC units above the next best model. For species evenness, there were three models with $\Delta AIC \leq 2$, though the null model was similarly supported. Thus, the responses for species richness and evenness were likely random (Table 1).

Community composition responses

PerMANOVA results showed that the relationship between reptile community composition and post-fire age was significant ($df = 4$, adjusted $R^2 = 0.108$, $P = 0.004$), indicating that sites of different fire ages contained a different assemblage of species (or different abundances of the same assemblage). However, post-hoc tests showed that there were few distinct separations in community composition between sites recently burned areas with that of longer unburnt areas (Fig. 3; Appendix 6).

Discussion

In temperate forest ecosystems, fire is often both an important natural disturbance (Parr and Andersen 2006) and a widely used management tool (Friend 1993; Lindenmayer et al. 2008; DSE 2009). Understanding post-fire responses of animals improves our understanding of the impact of disturbances, provides insights for species conservation and habitat restoration, and allows investigations of assembly rules in fire-prone environments (Santos and Poquet 2010). Developing models of biodiversity metrics over long time scales helps understanding changes at a scale over which major successional processes take place (Kelly et al. 2011).

Here we investigated the responses of reptile communities to fires in mesic forests across a post-fire chrono-sequence of over 71 years, a time frame sufficiently long for forest recovery to post-succession state (see Taylor and Fox 2001), and showed that reptile responses to fires could potentially persist for over half a century, which is beyond the maximum fire age used in many studies (e.g. Letnic et al. 2004).

Abundance patterns post-fire

Reptile abundance responded strongly to fire history, and appeared to increase with years since burning, which concurred with our predictions that species abundance should increase asymptotically with time post-disturbance (Fig. 1b). This increase did not appear to begin until

30 years post-fire, which may reflect the extensive time that is potentially needed for animal populations to fully recover from disturbances (Fig. 2). This finding is consistent with previous studies which reported higher reptile abundances in more mature vegetation (e.g. Masters 1996; Brown 2001; Legge et al. 2008). Our finding of reduced relative abundances of reptiles in recently disturbed areas concurred with previous studies in that it could be due to direct mortalities (Russell et al. 1999), as well as a result of rapid habitat changes following disturbances, and that these decreased population sizes (e.g. through emigration and starvation) do not recover until the habitat is restored (Mushinsky 1985; Heatwole and Taylor 1987). Reptiles are known to associate with certain habitat types based on fine scale features (Greenberg et al. 1994; Garden et al. 2007; Mott et al. 2010). Fires modify the habitat, such as by removing the understorey and enhancing the presence of herbaceous vegetation (Russell et al. 1999). Hence, the availability of key resources necessary to accommodate a greater population, such as food and shelter (e.g. arthropods in the leaf litter, which many skink species feed upon), could be drastically altered with increasing levels of fire disturbance (Heatwole and Taylor 1987; Pardon et al. 2003). However, it should be noted that sites that were unburnt for the longest time period do not contain the highest abundances. This could be a result of insufficient site replication towards the end of the chronosequence, or that our chronosequence was not long enough to reflect reptile succession in full as the presence of reptiles were known to respond to time since fire at a scale of over 100 years (Nimmo et al. 2012).

Species richness, evenness and IDH

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357 Neither reptile species richness nor richness was strongly related to age since fire, although
358 richness appeared to increase with time. Post-fire changes in species richness did not follow the
359 bell-shaped curve as proposed by the IDH (Connell 1978; Fig. 1a; Fig. 2b). This is not unexpected
360 given that support for IDH was not always consistent in terrestrial ecosystems (e.g.
361 Lindenmayer et al. 2008). The reptile communities at our study sites were relatively
362 depauperate (site of highest richness containing only seven species), and highly homogenous
363 (most sites were dominated by four highly abundant species). That both species richness and
364 evenness were uncorrelated to age since fire may suggest that fires do not differentially affect
365 various species significantly, and that the rarer species, which may be more specialized in their
366 habitat requirements than the four common generalist skink species, do not contribute
367 significantly to community responses to ecological disturbances (Ford et al. 1999; Letnic et al.
368 2004).

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370 Vegetation associations underlying community responses

371

372 Our models utilizing fine scale habitat elements showed that reptile abundance responded
373 strongly to vegetation of the overstorey, which appeared to be the primary habitat variable
374 influencing community structure in this landscape, both by itself and through interactive effects
375 with ground layer structure and shelter availability (Table 1). This could be because structurally
376 complex canopy layer provide increased cover against predators, especially birds (Lunney et al.
377 1991; Wanger et al. 2009). Data from vegetation analyses also showed that ground layer

characteristics including deep leaf litter layers and high percentage of ground cover were also associated with long-unburnt vegetation (Appendix 4). This was confirmed by models examining fine scaled habitat elements, in which reptile abundances were associated with those ground characteristics (Table 1). In contrast, it is interesting that species richness was not related to any fine scale habitat elements, which was in contrary to previous studies which reported associations with ground layer characteristics, such as litter depth and ground cover (e.g. Brown and Nelson 1993; Wanger et al. 2009).

Community composition and HAM

The habitat accommodation model (HAM; Fox 1982) suggests a predictable sequence of animal succession linked to the post-fire age of vegetation (e.g. variables such as litter depth), with different species fluctuating in abundance according to the suitability of the physical condition for them (Driscoll and Henderson 2008; Wanger et al. 2009). In this temperate forest ecosystem, post-fire age appeared to significantly influence the composition of reptile communities, and thus there was some support for the HAM. However, the relatively low R^2 value and post-hoc tests showed that this change may have been gradual and quite weak, with the significant result being an artifact of sampling rather than biological significance. In any case, there was not a sharp change in community composition between relatively recent burned sites and that of long unburnt sites (Appendix 5 and 6). It is also uncertain how much the change in compositional change is related to vegetation changes, as not all of the species we studied responded to the vegetation parameters we measured (Hu et al. unpublished data).

This could be due to the rapidity with which certain vegetation parameters recover after fires, including litter depth. Also, many of our study species could not be clearly classified as early, mid or late successional species (Pianka 1973; Friend 1993; Lindenmayer et al. 2008; Wilson and Swan 2008). It is possible that apart from fires and their ensuing vegetation changes, reptile succession patterns in these landscapes were also influenced by environmental processes such as spatial variations in resource availability and interspecific competition (Letnic et al. 2004).

Implications

Temperate forests cover a large part of southeastern Australia, in which fire is a frequent disturbance. In order to maintain biodiversity values, current fire management should aim to provide optimal benefit to the fauna which they impact through appropriate adjustments of fire frequencies. Here we found that significant increases in abundance are sustained through time since fire over a 80 year chronosequence. This suggests that the ways which fires are managed in this ecosystem can have implications for decades to come, and that frequent burning may be detrimental to small reptiles. Retaining long unburnt mature vegetation could be helpful from a demographic stand point, as larger population sizes are usually considered desirable ecologically (Lindenmayer et al. 2009). While none of the species we captured were listed as threatened, short fire return intervals could negatively affect the viability of populations at local scales (Westgate et al. 2012). These fluctuations in population sizes could also impact ecological processes, as many small reptiles contribute to ecological functions, such as decomposition, via their controls on arthropod populations (Pianka 1973; Heatwole and Taylor 1987; Hooper et al.

2005; Wilson and Swan 2008), as well as being prey to tertiary consumers themselves, and thus transfer energy and nutrient through ecosystems. However, extrapolating these findings to make recommendations for current fire management is not advised as their effects on other forest taxa are not fully known, and also because spatial variations in responses to time since fires could exist even for the same species (Nimmo et al. 2012).

A similar study investigated the effects of timber harvesting, another prevalent disturbance, on small reptile communities in the same study area (Magaton 2011). Comparison of results showed that fire and logging had different influences on reptile communities, as while a significant response was also registered for abundance patterns post-logging, the trend was different to that observed post-fire (Fig. 2), being peaked at an intermediate level of disturbance, and was lower in both recently disturbed and long undisturbed habitats (Magaton 2011). This could be because that the ecological impacts of timber harvesting are generally greater than that of fire (e.g. Greenberg et al. 1994) and thus facilitating different recovery processes for multiple forest elements including vegetation structure which many reptiles depend on (Heatwole and Taylor 1987; Urlus 2009).

Conclusion

The productivity and capacity of ecosystems is shown to be reflected not only by species richness, a commonly used community metric in ecological studies (Dornelas 2010), but also the relative abundance of species, which responded strongly to a common disturbance process

(McGill et al. 2007; Gaston and Fuller 2008). However, given the complex nature of these forest ecosystems, and it is likely that various landscape factors, such as biogeography and disturbance regimes, all interact to drive community dynamics. We concur with previous studies (e.g. Penn et al. 2003) in advocating for more comprehensive studies over larger scales in order to better understand and establish predictable patterns of forest fauna to fires, as such studies are rare and much needed (but see Kelly et al. 2011). Future studies could also undertake an experimental approach to fire management (Nimmo et al. 2012) and explore mechanisms underpinning these biodiversity responses by incorporating functional traits of individual species (Lindenmayer et al. 2008; Westgate et al. 2012).

460

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466

467 **REFERENCES**

468

469 Alexander JSA, Scott DJ, Loyn RH (2002) Impacts of timber harvesting on mammals, reptiles and

470 nocturnal birds in native hard-wood forests of East Gippsland, Victoria: a retrospective

471 approach. *Austral For* 65:182-210.

472 Brown GW (2001) The influence of habitat disturbance on reptiles in a box-ironbark eucalypt

473 forest of south-eastern Australia. *Biodivers Conserv* 10:161-176.

474 Brown GW, Nelson JL (1993) Influence of successional stage of *Eucalyptus regnans* (mountain

475 ash) on habitat use by reptiles in the Central Highlands, Victoria. *Aust J Ecol* 18:405-417.

476 Brown GW, Bennett AF, Potts JM (2008) Regional faunal decline – reptile occurrence in

477 fragmented rural landscapes of south-eastern Australia. *Wildlife Res* 35:8-18.

478 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical

479 information-theoretic approach, 2nd edn. Springer-Verlag, New York, USA.

480 Cano PD, Leynaud GC (2010) Effects of fire and cattle grazing on amphibians and lizards in

481 northeastern Argentina (Humid Chaco). *Eur J Wildlife Res* 56:411-420.

482 Connell JH (1978) Diversity in tropical forests and coral reefs. *Science* 199:1302-1310.

483 Cunningham SC, Babb RD, Jones TR, Taubert BD, Vega R (2002) Reaction of lizard populations to

484 a catastrophic wildfire in a central Arizona mountain range. *Biol Conserv* 107:193-201.

485 Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo

486 AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change

487 and forest disturbances. *BioScience* 51:723-734.

488 Denslow JS (1980) Patterns of plant species diversity during succession under different
489 disturbance regimes. *Oecologia* 46:18-21.

490 Dornelas M (2010) Disturbance and change in biodiversity. *Philos T Roy Soc B* 365:3719-3727.

491 Dormann CF, McPherson JM, Araujo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W,
492 Kissling WD, Kuhn I, Ohlemuller M, Peres-Neto PR, Reineking B, Schroder B, Schurr FM,
493 Wilson R, (2007) Models to account for spatial autocorrelation in the analysis of species
494 distributional data: a review. *Ecography* 30:609-628.

495 Driscoll DA, Henderson MK (2008) How many common reptile species are fire specialists? A
496 replicated natural experiment highlights the predictive weakness of a fire succession
497 model. *Biol Conserv* 141:460-471.

498 Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N,
499 Fensham R, Friend G, Gill M, James S, Kay G, Keith DA, MacGregor C, Russell-Smith J, Salt
500 D, Watson JEM, Williams RJ, York A (2010) Fire management for biodiversity
501 conservation: key research questions and our capacity to answer them. *Biol Conserv*
502 143:1928–1939.

503 DSE (2009) Management procedures for timber harvesting, roading and regeneration in
504 Victoria's State forests. Department of Sustainability and Environment, Victoria.

505 Ford WM, Menzel MA, McGill DW, Laerm J, McCay TS (1999) Effects of a community restoration
506 fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecol*
507 *Manag* 114:233-243.

508 Fox BJ (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*
509 63:1332-1341.

510 Fredericksen TS, Ross BD, Hoffman W, Ross E, Morrison ML, Beyea J, Lester MB, Johnson BN
511 (2000) The impact of logging on wildlife: a study in northeastern Pennsylvania. *J Forest*
512 98:4-10.

513 Friend GR (1993) Impact of fire on small vertebrates in Mallee woodlands and heathlands of
514 temperate Australia: a review. *Biol Conserv* 65:99-114.

515 Garden JG, McAlpine CA, Possingham HP, Jones DN (2007) Habitat structure is more important
516 than vegetation composition for local-level management of native terrestrial reptile and
517 small mammal species living in urban remnants: A case study from Brisbane, Australia.
518 *Austral Ecol* 32:669-685.

519 Gardner TA, Barlow J, Peres CA (2007) Paradox, presumption and pitfalls in conservation
520 biology: the importance of habitat change for amphibians and reptiles. *Biol Conserv*
521 138:166-179.

522 Gaston KJ, Fuller RA (2008) Commonness, population depletion and conservation biology.
523 *Trends Ecol Evol* 23:14-19.

524 Greenberg CH, Neary DG, Harris LD (1994) Effect of high-intensity wildfire and silvicultural
525 treatments on reptile communities in sand-pine scrub. *Conserv Biol* 8:1047-1057.

526 Greenberg CH, Waldrop TA (2008) Short-term response of reptiles and amphibians to
527 prescribed fire and mechanical fuel reduction in a southern Appalachian upland
528 hardwood forest. *Forest Ecol Manag* 255:2883-2893.

529 Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister KE,
530 Spence-Bailey LM, Clarke MF, Bennett AF (2011) *J Appl Ecol* 48:247-256.

531 Heatwole HF, Taylor J (1987) *Ecology of reptiles*. Surrey Beatty & Sons Pty, Chipping Norton,

532 NSW.

533 Heltzel JM, Leberg PL (2006) Effects of selective logging on breeding bird communities in
534 bottomland hardwood forests in Louisiana. J Wildlife Manage 70:1416-1424.

535 Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for
536 conservation. Conserv Biol 6:324-337.

537 Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau
538 M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of
539 biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr
540 75:3-35.

541 Howard R, Williamson I, Mather P (2003) Structural aspects of microhabitat selection by the
542 skink *Lampropholis delicata*. J Herpetol 37:613-617.

543 Hughes AR, Byrne JE, Kimbro DL, Stachowicz JJ (2007) Reciprocal relationships and potential
544 feedbacks between biodiversity and disturbance. Ecol Lett 10:849-864.

545 Huston M, Smith T (1987) Plant succession: life history and competition. Am Nat 130:168-198.

546 Kelly LT, Nimmo DG, Spence-Bailey LM, Haslem A, Watson SJ, Clarke MF, Bennett AF (2011)
547 Influence of fire history on small mammal distributions: insights from a 100-year post-
548 fire chronosequence. Divers Distrib 17:462-473.

549 Legge S, Murphy S, Heathcote J, Flaxman E, Augusteyn J, Crossman M (2008) The short-term
550 effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of
551 the central Kimberley, northern Australia. Wildlife Res 35:33-43.

552 Letnic M, Dickman CR, Tischler MK, Tamayo B, Beh, C-L (2004) The responses of small mammals
553 and lizards to post-fire succession and rainfall in arid Australia. J Arid Environ 59:85-114.

554 Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. P Natl Acad
555 Sci 71:2744-2747.

556 Lindenmayer DB, Wood JT, MacGregor C, Michael DR, Cunningham RB, Crane M, Montague-
557 Drake R, Brown D, Muntz R, Driscoll DA (2008) How predictable are reptile responses to
558 wildfire? Oikos 117:1086-1097.

559 Lindenmayer DB (2009) Forest wildlife management and conservation. Ann NY Acad Sci
560 1162:284-310.

561 Logan M (2010) Biostatistical design and analysis using R: A practical guide. Wiley-Blackwell.

562 Lunney D, Eby P, O'Connell M (1991) Effects of logging, fire and drought on three species of
563 lizards in Mumbulla State Forest on the south coast of New South Wales. Aust J Ecol
564 16:33-46.

565 Mackey RL, Currie DJ (2000) A re-examination of the expected effects of disturbance on
566 diversity. Oikos 88:483-493.

567 Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and
568 peaked? Ecology 82:3479-3492.

569 Magaton, S (2011) Applying disturbance theory to reptile communities in logged forests.
570 Masters Thesis, University of Melbourne.

571 Masters P (1996) The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru
572 National Park, Northern Territory. Wildlife Res 23:39-48.

573 McCullagh P, Nelder JA (1989) Generalized Linear Models, 2nd edition. Chapman & Hall,
574 London.

575 McGill BJ, Etienne RS, Gray JS, Alonso D, Anderson MJ, Benecha HK, Dornelas M, Enquist BJ,
 576 Green JL, He F, Hurlbert AH, Magurran AE, Marquet PA, Maurer BA, Ostling A, Soykan
 577 CU, Ugland KI, White EP (2007) Species abundance distributions: moving beyond single
 578 prediction theories to integration within an ecological framework. *Ecol Lett* 10:995-
 579 1015.

580 Mott B, Alford RA, Schwarzkopf L (2010) Tropical reptiles in pine forests: Assemblage responses
 581 to plantations and plantation management by burning. *Forest Ecol Manag* 259:916-925.

582 Mushinsky HR (1985) Fire and the Florida sandhill herpetofaunal community: with special
 583 attention to responses of *Cnemidophorus sexlineatus*. *Herpetologica* 41:333-342.

584 Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara R, Simpson GL, Solymos P, Stevens MHH,
 585 Wagner H (2011) vegan: community ecology package. R package version 1.17-10.

586 Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol*
 587 *Monogr* 51:145-178.

588 Parks Victoria (2005) Cape Conran Coastal Park Management Plan. Parks Victoria, Bairnsdale.

589 Parr CL, Andersen AN (2006) Patch mosaic burning for biodiversity conservation: a critique of
 590 the pyrodiversity paradigm. *Conserv Biol* 20:1610-1619.

591 Penn AM, Sherwin WB, Lunney D, Banks PB (2003) The effects of a low-intensity fire on small
 592 mammals and lizards in a logged, burnt forest. *Wildlife Res* 30:477-486.

593 Pianka ER (1973) The structure of lizard communities. *Annu Rev Ecol Syst* 4:53-74.

594 Pickett STA, White PS (eds) (1985) The ecology of natural disturbances and patch dynamics.
 595 Academic Press, New York.

596 R Development Core Team (2010) R: a language and environment for statistical computing. R
597 Foundation for Statistical Computing, Vienna.

598 Radke NJ, Wester DB, Perry G, Rideout-Hanzak S (2008) Short-term effects of prescribed fire on
599 lizards in mesquite-Ashe juniper vegetation in central Texas. *Appl Herpetol* 5:281-292.

600 Russell KR, van Lear DH, Guynn Jr DC (1999) Prescribed fire effects on herpetofauna: review and
601 management implications. *Wildlife Soc B* 27:374-384.

602 Ruthven III DC, Kazmaier RT, Jamis MW (2008) Short-term response of herpetofauna to various
603 burning regimes in the South Texas plains. *Southwest Nat* 53:480-487.

604 Santos X, Poquet JM (2010) Ecological succession and habitat attributes affect the postfire
605 response of a Mediterranean reptile community. *Eur J Wildlife Res* 56:895-905.

606 Spies TA, Lindenmayer DB, Gill AM, Stephens SL, Agee JK (2012) Challenges and a checklist for
607 biodiversity conservation in fire-prone forests: perspectives from the Pacific Northwest
608 of USA and southeastern Australia. *Biol Conserv* 145:5-14.

609 Svensson JR, Lindegarth M, Jonsson PR, Pavia H (2012) Disturbance-diversity models: what do
610 they really predict and how are they tested? *P Roy Soc B* 279:2163-2170.

611 Taylor JE, Fox BJ (2001) Disturbance effects from fire and mining produce different lizard
612 communities in eastern Australian forests. *Austral Ecol* 26:193-204.

613 Temperton VM (2004) *Assembly rules and restoration ecology: bridging the gap between*
614 *theory and practice*. Island Press, Washington, USA.

615 Urlus J (2009) *The influence of vegetation structure and land management on east Gippsland*
616 *reptile communities*. Honours Thesis, Deakin University, Melbourne.

617 Wanger TC, Saro A, Iskandar DT, Brook BW, Sodhi NS, Clough Y, Tscharntke T (2009)
618 Conservation value of cacao agroforestry for amphibians and reptiles in South-east Asia:
619 combining correlative models with follow-up field experiments. J Appl Ecol 46:823-832.
620 Westgate MJ, Driscoll DA, Lindenmayer DB (2012) Can the intermediate disturbance hypothesis
621 and information on species traits predict anuran responses to fire? Oikos (in press).
622 Wilson S, Swan G (2008) A complete guide to reptiles of Australia. New Holland Publishers,
623 Chatswood, NSW.
624 Wood, SN (2006) Generalized additive models: an introduction with R. Chapman and Hall.
625 Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions
626 in ecology with R. Springer.
627

TABLES

Table 1. Top ranked generalized additive models explaining reptile species richness, relative abundance and evenness (represented by Simpson's Index). Number of parameters in each model (K), Akaike Information Criterion (AIC), difference in AIC between top ranked model (lowest AIC value) and model in question (ΔAIC) are shown for each model. Models presented include those with $\Delta AIC < 2$ from top ranked model, as well as null and global models. Refer to Appendices 3 and 4 for detailed model explanations.

Response variable	Model (variable groups)	K	AIC	ΔAIC
Relative abundance	Overstorey	2	552.18	0.00
	Overstorey and Shelter	3	553.93	1.76
	Overstorey and Ground	4	554.11	1.94
	Global	6	556.05	3.87
	None	0	558.84	6.67
Richness	Null	0	229.42	0.00
	Global	6	247.07	17.65
Evenness	Shelter	1	-70.27	0.00
	Shrub	1	-69.83	0.44
	None	0	-69.64	0.63
	Ground	2	-68.80	1.47
	Global	6	-54.80	15.47

FIGURE LEGENDS

Figure 1. Theoretical trends predicted for a) species richness, and b) abundance and evenness of animal communities in response to the level of disturbance. Graphs were modified from those of Svensson *et al.*, (2012). The curvilinear relationship for richness was based on predictions of the intermediate disturbance hypothesis (IDH), where intermediate levels of disturbance enhance the co-existence between early colonizing pioneer species and late-successional species, and thus greatest diversity. The trend for abundance and evenness was based on ecological plausibility, because long undisturbed habitats may contain greater structural complexity, leading to increased availability of resources and shelter, which should accommodate a larger population and greater evenness.

Figure 2. Reptile community responses to fire age across a chrono-sequence of over 71 years: relative abundance, b) species richness and c) species evenness (Simpson's Index). Solid lines represent predictions of generalized additive models, and dashed lines represent ± 2 SE.

Figure 3. Separation in reptile community composition between sites of different fire categories as represented by a) PerMANOVA ordination plot, and b) boxplot displaying centroids of each site. Letters represent statistical differences between different sites. Refer to Methods for definition of fire classes.

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b)

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666 **ELECTRONIC SUPPLEMENTARY MATERIAL**

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668 **Appendix 1.** Reptile species captured across 74 sites in forests of East Gippsland, Victoria.

Species	Family	Number of sites detected (% total)	Total captures
Yellow-bellied water skink <i>Eulamprus heatwolei</i>	Scincidae	71 (96)	1093
Garden skink <i>Lampropholis guichenoti</i>	Scincidae	69 (93)	914
Weasel skink <i>Saproscincus mustelinus</i>	Scincidae	69 (93)	307
Delicate skink <i>Lampropholis delicata</i>	Scincidae	58 (78)	205
Black rock skink <i>Egernia saxatilis intermedia</i>	Scincidae	30 (41)	54
Spencer's skink <i>Pseudemoia spenceri</i>	Scincidae	20 (27)	36
McCoy's skink <i>Anepischtos maccoyi</i>	Scincidae	16 (22)	36
White-lipped snake <i>Drysdalia coronoides</i>	Elapidae	24 (32)	28
Glossy grass skink <i>Pseudemoia rawlinsoni</i>	Scincidae	8 (11)	9
Tiger snake <i>Notechis scutatus</i>	Elapidae	3 (4)	3
Eastern three-lined skink <i>Acritoscincus duperreyi</i>	Scincidae	2 (3)	2
Highland copperhead <i>Austrelaps ramsayi</i>	Elapidae	2 (3)	2
Red-bellied black snake <i>Pseudechis porphyriacus</i>	Elapidae	1 (1)	1
White's skink <i>Egernia whitii</i>	Scincidae	1(1)	1

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672 **Appendix 2.** Fire history and sampling effort of the study sites (n = 74) in forests of east

673 Gippsland, Victoria.

#	Site name	Age since fire	Days sampled	#	Site name	Age since fire	Days sampled
1	PU11	31	39	38	PY73	0	37

2	PU13	31	39	39	PY74	0	37
3	PU15	4	39	40	PY75	29	37
4	PU23	31	39	41	PY77	1	37
5	PU24	4	39	42	PY78	1	37
6	PU25	4	39	43	PY79	1	37
7	PU29	80	39	44	PY80	0	37
8	PU31	2	39	45	PY81	22	37
9	PU32	20	39	46	PY90	29	37
10	PU6	4	39	47	PY91	29	37
11	PU7	4	39	48	PYF50	32	37
12	PU8	28	39	49	PY51	29	37
13	PU9	28	39	50	S1	11	31
14	PY10	29	37	51	S111	21	31
15	PY12	29	37	52	S116a	1	31
16	PY14	32	37	53	S12	7	31
17	PY16	1	37	54	S128	21	31
18	PY162	29	37	55	S13	3	31
19	PY163	29	37	56	S132	6	31
20	PY164	29	37	57	S133	6	31
21	PY17	32	37	58	S14	9	31
22	PY18	1	37	59	S174	5	31
23	PY19	32	37	60	S176	21	31
24	PY20	32	37	61	S178	21	31
25	PY21	5	37	62	S180	21	31
26	PY22	32	37	63	S436	19	31
27	PY26	51	37	64	S5	29	31
28	PY27	51	37	65	S51a	29	31
29	PY28	80	37	66	S52	28	31
30	PY30	1	37	67	S56	42	31
31	PY49	37	37	68	S57	51	31
32	PY49A	37	37	69	S6	20	31
33	PY50	37	37	70	S74	80	31
34	PY52	14	37	71	S76	51	31
35	PY70	1	37	72	S80	71	31
36	PY71	1	37	73	S96	80	31
37	PY72	29	37	74	S99	80	31

Appendix 3. Description of predictor variables used in generalized additive models (GAM) of
reptile communities.

Predictor variable

Variable type

Average leaf litter depth (cm) (litd)

Continuous

Percentage of ground covered by bare substrate (sub)

Continuous

Horizontal vegetation density at 0.5 m above ground (hc05)

Continuous

Percent canopy cover (cancov)

Continuous

Total log volume (m³) per 1056 m² (logvol)

Continuous

Total basal area of trees (m²) per 1056 m² (batree)

Continuous

682

683 **Appendix 4.** Predictor variables included generalized additive models of the relations between
684 reptile community metrics and fine scale vegetation parameters. Models listed were tested
685 against the null model. See Appendix 3 for predictor variable descriptions.

686

#	Model name	Predictor variables included
1	Ground layer	litd + sub
2	Shrub layer	hc05
3	Overstorey	cancov + batree
4	Shelter	Logvol
5	Ground and Shrub	litd + sub + hc05
6	Ground and Overstorey	litd + sub + cancov + batree
7	Ground and Shelter	litd + sub + logvol
8	Shrub and Overstorey	hc05 + cancov + batree
9	Shrub and Shelter	hc05 + logvol
8	Overstorey and Shelter	logvol + cancov + batree
9	Global model (include all variables)	litd + sub + hc05 + cancov + batree + logvol

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692 **Appendix 5.** Vegetation characteristics. GAM modeling showed that litter depth and bare
693 substrate cover were significantly influenced by time since fire (both $p < 0.001$).

694

Vegetation characteristic	edf	F	P
Canopy cover	2.761	2.076	0.104
Total tree basal area	1	0.244	0.623
Vegetation density at 0.5 m	4.452	1.029	0.411
Percent ground cover	7.578	9.258	<0.001 ***
Litter depth	5.398	6.849	<0.001 ***
Log volume	2.242	1.331	0.272

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696 *** $P < 0.001$

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701 **Appendix 6.** Tukey's HSD test showing differences in reptile community composition between
702 sites of different fire categories. Fire categories of 1 to 5 represent a gradient of disturbance,
703 from recently burned sites to long unburnt sites (see Methods for more details).

Group comparison	Difference	P
2 vs 1	0.011	0.968
3 vs 1	-0.003	0.999
4 vs 1	-0.020	0.707
5 vs 1	-0.051	0.061
3 vs 2	-0.014	0.954
4 vs 2	-0.031	0.290
5 vs 2	-0.062	0.014 *
4 vs 3	-0.017	0.882
5 vs 3	-0.048	0.155
5 vs 4	-0.031	0.331

704

705 * P<0.05

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Appendix 7. Determining the presence of spatial autocorrelations and the nature of their correlation structures in models examining community metrics to age since fire. Five different correlation classes were compared to a spatially non-correlated model.

Response	Model rank	Spatial Correlation structure	AIC	Δ AIC
Relative abundance to age since fire	1	Exponential	545.89	0.00
	2	Ratio	547.84	1.95
	3	Spherical	548.13	2.24
	4	Linear	551.70	5.81
	5	Gaussian	552.30	6.41
	6	None	557.89	12.00
Richness to age since fire	1	None	227.81	0.00
	2	Gaussian	229.81	2.00
	2	Exponential	229.81	2.00
	2	Spherical	229.81	2.00
	2	Linear	229.81	2.00
	2	Ratio	229.81	2.00
Evenness (Simpson's Index) to age since fire	1	Ratio	-70.23	0.00
	2	Gaussian	-69.83	0.40
	3	Exponential	-69.35	1.88
	4	None	-65.70	4.53
	5	Linear	-63.70	6.53
	5	Spherical	-63.70	6.53

Appendix 8. Determining the presence of spatial autocorrelations and the nature of their correlation structures in models examining fine scale vegetation associations of the three community metrics. Five different correlation classes were compared to a spatially non-correlated model.

Response	Model rank	Spatial Correlation structure	AIC	ΔAIC
Abundance and vegetation associations (global model)	1	None	561.32	0.00
	2	Exponential	563.41	2.09
	3	Ratio	565.32	4.00
	4	Gaussian	568.05	6.73
	5	Linear	568.11	6.79
	6	Spherical	Model did not converge	
Richness and vegetation associations (global model)	1	Spherical	246.90	0.00
	2	Ratio	246.91	0.01
	3	Gaussian	246.99	0.09
	4	Exponential	247.07	0.17
	5	None	272.86	25.96
	6	Linear	Model did not converge	
Simpson's Index and vegetation associations (global model)	1	Ratio	-55.17	0.00
	2	Gaussian	-54.80	0.37
	3	Exponential	-54.72	0.45
	4	Spherical	-49.64	5.53
	4	Linear	-49.64	5.53
	6	None	3.22	58.39

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