

# Robustness of habitat-based surrogates of animal diversity: a multitaxa comparison over time

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## Summary

1. Many animal taxa respond strongly to spatial and temporal variation in vegetation structure and floristic composition, suggesting that changes in vegetation could be a cheap and readily observable surrogate for changes in animal assemblages. Yet there is considerable uncertainty about how different taxa respond to vegetation over time, potentially limiting the application of habitat-based surrogates to many areas of applied ecology.

2. We examined the strength and temporal consistency of habitat-based surrogates of three different vertebrate taxa in a landscape with multiple vegetation types. We used regression models to quantify the relationships between six vegetation attributes (species richness and percentage cover of overstorey, midstorey and understorey) and three measures of bird, mammal and reptile assemblages (abundance, species richness and composition).

3. We found that overstorey richness and cover had both consistent and strong positive effects on bird assemblages. Vegetation effects were generally weaker and more variable for mammals and reptiles compared with birds. Each taxon displayed different temporal dynamics following fire, with negative effects on birds and mammals, but positive short-term effects on reptiles. Surprisingly, fire increased vegetation effects on birds, but did not consistently alter vegetation effects on mammals or reptiles, indicating a lack of concordant responses among taxa.

4. *Synthesis and applications.* Empirical testing of habitat-based surrogates of multiple animal taxa is needed to identify reliable and consistent management proxies. Our study suggests that habitat-based surrogates could be useful metrics for quantifying changes in bird assemblages through time and after fire, but that the same metrics could not be applied to mammal and reptile assemblages. The absence of both strong and consistent effects of vegetation attributes across the three groups of vertebrates suggests that taxon-specific habitat surrogates may be required to detect changes over time and after disturbance within heterogeneous landscapes.

**Key-words:** biodiversity, birds, conservation, indicator, landscape, mammals, management, reptiles

## Introduction

The enormous complexity of ecosystems presents a great challenge to measuring and understanding changes in biodiversity (Rodrigues & Brooks 2007; Lewandowski, Noss & Parsons 2010; Magurran & McGill 2011). This has resulted in the use of surrogate measures to act as a simpler proxy for changes in biodiversity (Caro 2010; Kessler *et al.* 2011). One such approach is the use of habitat-based surrogates, which are environmental variables that act as an indirect measure of biodiversity (McGeoch 1998;

Gollan *et al.* 2009; Banks-Leite *et al.* 2011; Lindenmayer *et al.* 2014).

There is a substantial body of evidence showing that animal assemblages respond strongly to spatial and temporal variation in vegetation structure and floristic composition (Tews *et al.* 2004; McElhinny *et al.* 2006; Schaffers *et al.* 2008; Qian & Kissling 2010). By extension, these vegetation attributes might be a cheap and readily observable surrogate for the impacts of environmental change on animal populations (Banks-Leite *et al.* 2011). Yet the extent to which vegetation attributes might be used to reliably and consistently reflect changes in animal assemblages from an explicit surrogacy perspective has

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received little attention (Gollan *et al.* 2009; Banks-Leite, Ewers & Metzger 2013).

Reliance on habitat-based surrogates for monitoring changes in animal communities has been limited by a number of problems. First, the surrogate group (i.e. that which is measured, typically vegetation) and the target group (i.e. that which the surrogate is a proxy for, often an animal taxon) may respond differently to particular drivers of change, thus weakening any causal relationship between surrogate and target taxa. Yet, a strong surrogacy relationship is exactly what is required to detect and accurately monitor biotic changes, such as the recovery of biodiversity following a disturbance. Secondly, any given surrogate may be more effective for one target taxon than another, but the taxonomic breadth of surrogacy relationships is rarely tested or elucidated (Gollan *et al.* 2009; Caro 2010; Kessler *et al.* 2011; Larsen *et al.* 2012). Thus, it is unclear to what extent a habitat-based surrogate might accurately reflect change in one taxon but not another. Finally, surrogacy relationships can vary across spatial scales (Banks-Leite, Ewers & Metzger 2013; Westgate *et al.* 2014) and may be weaker when examined at smaller 'within-landscape' scales compared with coarser extrapolated data at regional or continental scales (Rodrigues & Brooks 2007). However, it is at smaller scales where surrogacy relationships have some of their greatest utility as guides to changes in biodiversity and informing management decisions. While some aspects of these problems are well known (Rodrigues & Brooks 2007; Mellin *et al.* 2011; Larsen *et al.* 2012; Banks-Leite, Ewers & Metzger 2013), there have been relatively few empirical evaluations of habitat-based surrogates across distinct vegetation types (Cushman *et al.* 2008), after disturbance (Brennan *et al.* 2006), and over time (Fuller & Rothery 2013; Lindenmayer *et al.* 2014). Additional comprehensive studies are therefore needed to identify robust habitat-based surrogates that perform well for monitoring the effects of environmental change across different taxa.

In this study, we examine the extent to which potential habitat surrogates are robust predictors of animal biodiversity over time. We selected a range of habitat variables (percentage cover and species richness of overstorey, mid-storey and understorey vegetation strata) as potential surrogates of bird, mammal and reptile assemblages. Our study area consisted of multiple vegetation communities within a single landscape (Lindenmayer *et al.* 2008b; Barton *et al.* 2014) and provides a rare opportunity to test habitat surrogacy relationships across a wide gradient in vegetation structure more commonly studied at much larger spatial scales. We assessed the relationship between each vegetation attribute and the abundance, species richness and assemblage composition of each vertebrate taxon and asked the following questions:

**1.** Which vegetation variables have strong effects on the different animal taxa? At the outset of our investigation, it remained unclear which animal taxon might respond

most strongly to the vegetation variables. However, we reasoned that there is likely to be greater concordance among taxa if they shared similar ecologies. We therefore anticipated that mammals and reptiles would exhibit similar responses to vegetation variables due to their occurrence at ground level and close association with understorey vegetation (Fox, Taylor & Thompson 2003; Lindenmayer *et al.* 2008c; Pereoglou *et al.* 2011), whereas birds were likely to have a different response due to their strong association with vertical vegetation structure (MacArthur & MacArthur 1961; Barton *et al.* 2014).

**2.** Which vegetation variables have consistent effects over time and across taxa? Both structural and floristic attributes of vegetation have been shown to change in response to disturbance (Morrison *et al.* 1995; Onaindia *et al.* 2004), which in some cases appear to be the underlying drivers of animal responses to disturbance (Fox, Taylor & Thompson 2003; Pereoglou *et al.* 2011; Barton *et al.* 2014). Consequently, we anticipated that changes in vegetation structure and floristic composition would be reflected by change in animal assemblages, but that the precise relationship between plant and animal variables would vary after fire and over time.

By examining the strength and consistency of vegetation–animal relationships across taxa and over time, our study provides important new insights into which vegetation attributes might be a consistent candidate for use as a habitat-based surrogate of animal biodiversity. Our work also reveals potential weaknesses, such as relying on one taxon over another, that underpin key assumptions of biodiversity surrogates, but which are rarely tested empirically. This has implications for biodiversity management as it can assist with the identification of the limitations and strengths of different candidate surrogate variables.

## Materials and methods

### STUDY AREA AND DESIGN

We conducted this study in Jervis Bay Territory, approximately 200 km south of Sydney in south-east Australia (150°70' East, 35°15' South). Jervis Bay Territory includes Booderee National Park, which covers 7500 hectares (see Fig. S1, Supporting Information). A distinctive feature of Booderee National Park is its heterogeneous cover of multiple vegetation communities, ranging from tall eucalypt forest to dry heathland (Taws 1997; Pereoglou *et al.* 2013).

In September 2003, 105 permanent study sites were established across the National Park, with the number of sites in each vegetation types generally proportional to the amount of cover of that vegetation. Each site was marked with a 100-m transect line, with permanent markers placed at 0, 20, 40, 60, 80 and 100 m. In December 2003, a wildfire burnt approximately 50% of Booderee National Park and 50% of the study sites, with a bias towards the eastern side of the park (Fig. S1, Supporting information). This provided an opportunity to conduct a 'natural experiment' on the effects of fire on vegetation and fauna in this unique landscape. Of course, it was impossible to randomly allocate fire to

the sites in this study after such an event, and we acknowledge the potential for bias in our results as a consequence.

#### DATA COLLECTION

##### *Vegetation structure and floristics*

In December 2004, 2006, 2007 and 2009, we measured six attributes of the structure and floristics of the vegetation (hereafter called 'vegetation attributes') in two 20 × 20 m plots located at the 20- to 40-m and 60- to 80-m points in each site. The attributes were percentage cover and species richness of each of three strata: overstorey (>10 m), midstorey (2–10 m) and understorey (<2 m). We took the average of the measures from the two plots to give a single measure for each attribute at each site in each year and used these data in our subsequent analysis.

##### *Birds*

We completed bird surveys in September 2004, 2006, 2007 and 2009. September is the breeding season for a majority of species in Booderee National Park, and when most summer migrants have arrived. For each survey year, we performed two repeats of bird surveys at the 20-m and 80-m markers in each site, resulting in four surveys per site per survey year. We recorded all birds seen or heard within a 50-m radius of the survey points during a 5-min period, excluding birds flying overhead. We conducted surveys between dawn and mid-morning. Repeat surveys were performed on a different day and by a different observer to incorporate day and observer effects (Lindenmayer, Wood & MacGregor 2009). We pooled the four surveys from each site to give one set of observations per site per year.

##### *Mammals and reptiles*

Surveys of ground-dwelling mammals and reptiles were completed in 2004, 2006, 2007 and 2009 using a standardized combination of traps along the length of the 100-m transect of each site: (i) a 380-mm-deep × 300-mm-diameter pitfall trap was established at the 0-m, 20-m, 40-m, 60-m, 80-m and 100-m points along each transect; (ii) a black plastic drift fence connected the 0-m and 20-m, 40- to 60-m and 80- to 100-m pitfall buckets; (iii) a single 1-m-deep × 80-cm-diameter large pitfall trap (a large garbage bin) was established at the 50-m midpoint along each transect; and (iv) Elliott traps (Elliott Scientific Equipment, Upwey, Vic., Australia) were placed 0, 10, 20, 30, 40, 50, 60, 70, 80 and 90 m along the transect. Each trap was baited with a mixture of peanut butter and rolled oats; (v) small wire cage traps (20 × 20 × 50 cm) were placed 20, 40, 60 and 80 m along the transect; and (vi) a large wire cage trap (30 × 30 × 60 cm) was placed at the 0-m and 100-m points along the transect. Surveys at each site involved opening all traps on four consecutive days and nights, except on a very small number of occasions when it rained heavily, and traps were closed after 3 days to reduce the potential for animal mortality from trapping. Sets of scales on each captured reptile, or an ear on each captured mammal, were marked with a semi-permanent white pen so that it would be recognized as a recapture if it were trapped again during the 4-day capture period. Surveys of our sites were completed during the warmer months of the year between November and March

(Lindenmayer *et al.* 2008a,c). Trapping data were pooled across trap type and the 4 days of trapping (excluding re-captures) to give a single measure of abundance and richness of mammals or reptiles from each site in each year.

In sum, our data collection produced species counts for three taxa of animals (birds, reptiles and mammals) from 105 sites across a wide range of vegetation types (see Fig. S1, Supporting information). Observations were made on the sites in 4 years: 2004, 2006, 2007 and 2009. Of these sites, 46 were burnt by a wildfire in December 2003.

#### DATA ANALYSIS

##### *Response variables*

Abundance, species richness and composition are fundamentally different properties of a biotic assemblage (Magurran & McGill 2011). We calculated abundance and species richness as the sum of individuals or species of each animal taxon recorded within a single site in a particular year. For species composition, we used the Bray–Curtis dissimilarity index applied to  $\log_e(1 + x)$ -transformed species count data to calculate a dissimilarity matrix for each animal taxon. We excluded species that occurred in two or fewer sites (for each year). We then carried out a principal coordinate analysis (PCoA) based on this matrix, deriving an assemblage composition score for each site, using the R function 'biplot.pcoa' from the package 'APE' (Paradis, Claude & Strimmer 2004). We analysed PCoA site scores from the first axis only, as this accounted for the greatest amount of variation in species composition among sites (19, 37 and 37% for birds, mammals and reptiles, respectively).

##### *Explanatory variables*

We investigated the effects of untransformed and transformed versions of the six vegetation attributes described above, using  $\log_e(x + 1)$  for both counts and proportions. Proportions were bounded at 100% as well as at 0%, but examination of plots of the relationships indicated little change in the effect of increasing vegetation near to 100%, so there was no need for a transformation like the logit, which respects that boundary. We also investigated differences between years and between sites of different burnt status.

##### *Regression models*

We fitted regression models to quantify the relationship between each of the response variables and the full set of explanatory variables described above, including interactions, using the generalized linear mixed model facilities of GENSTAT (VSNI 2013). This resulted in nine different regression models (one for each assemblage measure of each taxon).

For models of animal abundance and richness, we used negative binomial regression or Poisson regression if there was no detectable aggregation in the counts. Aggregation, also called dispersion, is a measure of heterogeneity in the negative binomial model, with infinite aggregation corresponding to the Poisson model (Hilbe 2011). For assemblage composition data, we used linear models. We fitted 'site' as a random effect in all our models to incorporate repeated measures of sites in different years.

**Table 1.** Estimated aggregation parameters for abundance and species richness count data of birds, mammals and reptiles

Taxon	Response	Aggregation	SE
Birds	Richness	$\infty$ (Poisson)	–
	Abundance	6.2	0.5
Mammals	Richness	$\infty$ (Poisson)	–
	Abundance	32.9	11.5
Reptiles	Richness	$\infty$ (Poisson)	–
	Abundance	5.0	1.0

We checked the assumption of linearity of effects (on the log scale of species richness and abundance) with additive models (cubic smoothing splines).

## Results

### BIRD, REPTILE AND MAMMAL ASSEMBLAGES

Our surveys across the 105 sites and four different years detected 102 bird species (15 439 records), 14 reptile species (1248 records) and 10 mammal species (3344 records). Bird assemblage structure (Fig. S2a, Supporting information) varied from sites characterized by the presence of heathland species such as eastern bristlebird *Dasyornis brachypterus* Latham to sites with forest species such as the brown thornbill *Acanthiza pusilla* Shaw and yellow-faced honeyeater *Lichenostomus chrysops* Cabanis. Mammal assemblage structure (Fig. S2b, Supporting information) varied from sites characterized by the presence of the habitat generalist long-nosed bandicoot *Perameles nasuta* Geoffroy to sites with forest-dwelling brown antechinus *Antechinus stuartii* Macleay. Reptile assemblage structure (Fig. S2c, Supporting information) varied from sites characterized by the presence of multiple reptile species to sites dominated by the woodland-dwelling delicate skink *Lampropholis delicata* de Vis.

### FIT OF MODELS

We show the estimated aggregation parameters for the models of species richness and abundance in Table 1. For all three animal assemblage variables (abundance, richness and composition),  $\log_e$ -transformed vegetation measures were better than the untransformed measures for representing the pattern of the data in the type of model we fitted, and in reducing the deviance of the data (deviance is the extension of the residual sum of squares, appropriate for assessing generalized linear models like negative binomial and Poisson regression). In some cases, there was evidence of nonlinearity in the relationship between response and explanatory variables, but this was usually at the extreme ends of the range of an explanatory variable.

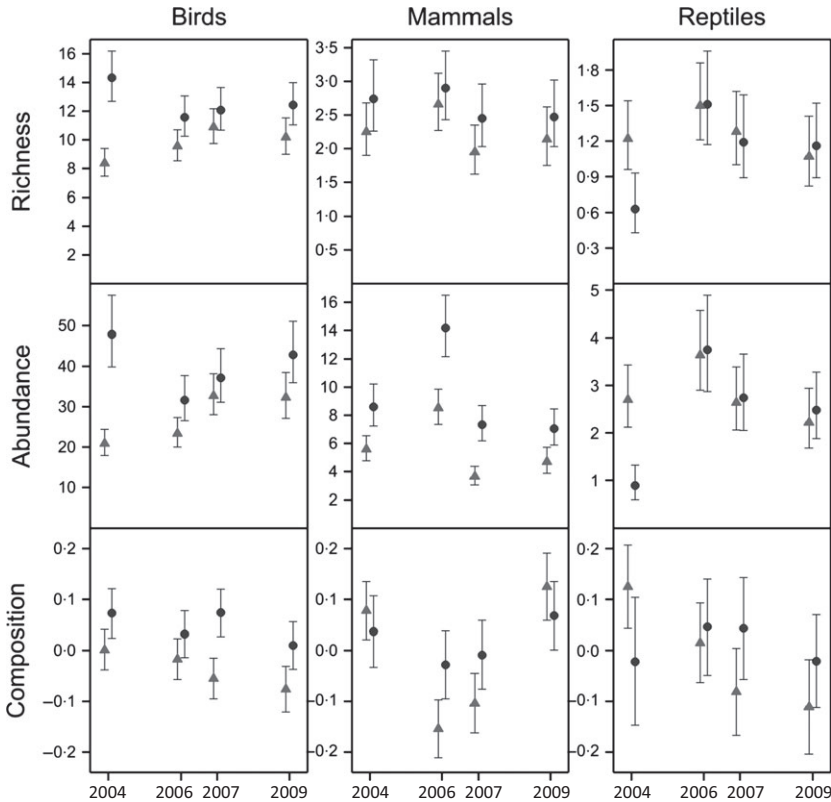
In all nine regression models (three response variables by three animal taxa), we found seven instances of a

three-factor interaction between year, burnt status and any of the vegetation attributes (Table S1, Supporting information). This is slightly higher than that expected by chance for 54 tests, but the size of the effects was small in each case compared with the size of the main effects. There were also seven instances of an interaction between year and vegetation attributes (Table S1, Supporting information). Due to the lack of these particular interactions, we focus on summarizing our analyses in terms of (i) interactions between year and burnt status (adjusting for the effects of all vegetation attributes and their interaction with burnt status), and (ii) interactions between burnt status and the vegetation attributes (adjusting for the effect of year, burnt status and the interaction between them).

Importantly, the six vegetation attributes were partially confounded with each other, particularly within the pairs of measurements (species richness and percentage cover) made in each stratum. We therefore present the effect of each vegetation attribute on its own, ignoring the other five attributes but adjusting for the effects of year and burnt status. This gives estimates of the effect of changes in each vegetation attribute, but also includes unspecified effects of other variables. For example, the effect of a change in overstorey cover from 0 to 10% actually represents the effect of that change plus the average changes in the other vegetation measures because of the partial confounding. This approach seemed more useful than estimates of effects for each measure keeping the other measures constant. This is because each of the specified effects corresponds to what an observer might observe and measure in a similar site.

### TEMPORAL CHANGES IN ANIMAL ASSEMBLAGES AFTER FIRE

We found a significant and large interactive effect of year and burnt status on all three animal taxa ( $P < 0.05$ , except where noted below), even after adjusting for combined vegetation effects (Fig. 1). Table S2 (Supporting information) presents summaries of the effects in the models we fitted. These are expressed as changes in each response variable corresponding to a change from 0 to 1 vegetation species or from 0 to 10% vegetation cover (% change 1), or from 1 to 2 or 10 to 20% (% change 2), in each of three vegetation strata. Values of % change 2 are smaller than % change 1 because of the nature of the  $\log_e(1 + x)$  transformation. The abundance and species richness of bird assemblages from burnt sites was nearly half that of unburnt sites in 2004, but then returned to similar levels in 2006 and 2007 before returning to a large difference again in 2009. Bird assemblages changed to include more heath-associated species in burnt areas in 2007 and 2009. For mammals, richness and abundance was always lower in burnt sites across all 4 years of surveys, even though these measures varied considerably from year to year (the interaction of year by burnt status



**Fig. 1.** Mean (with 95% confidence limits) species richness, abundance and composition measures for three taxa over time, by burnt status of sites (red triangles = burnt; blue circles = unburnt). Means are adjusted for effects of all six vegetation measures and of burnt status and for the interaction between the vegetation measures and burnt status.

was not significant, richness  $P = 0.86$ , abundance  $P = 0.37$ ). Mammal composition shifted to include more generalist bandicoots and fewer forest-associated antechinus in 2006 and 2007, but then switched to have more antechinus in 2009. By contrast, reptiles were both more abundant and species rich in burnt sites compared with unburnt sites in 2004, but there was no difference between burnt and unburnt sites in subsequent years. Reptile assemblages shifted to have more woodland-associated delicate skinks in burnt sites in 2004, but much fewer in 2007.

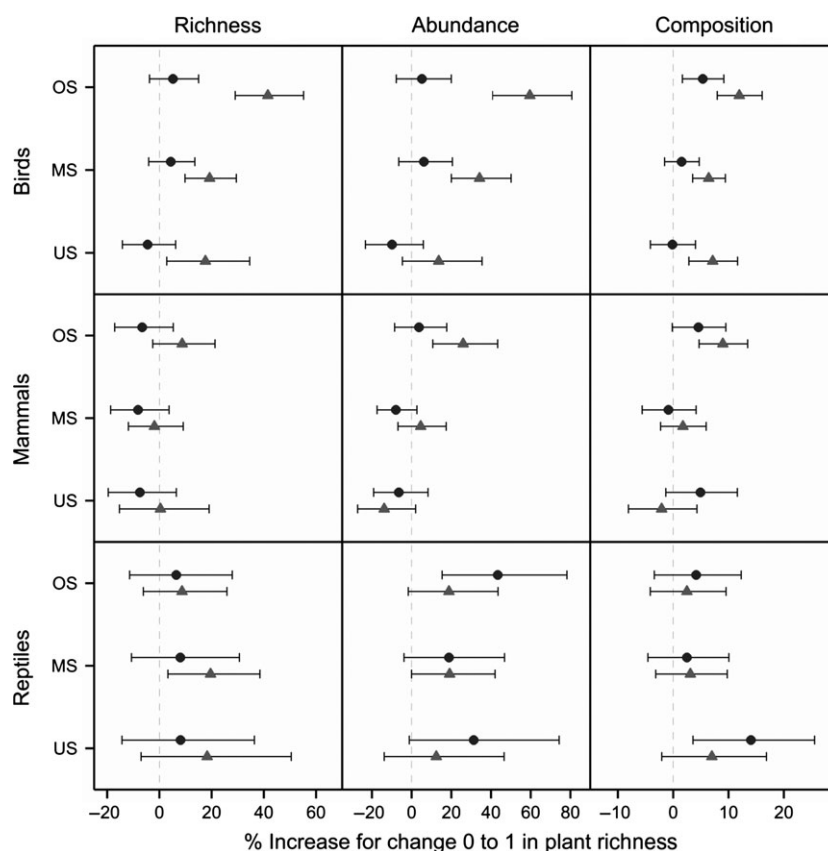
#### EFFECTS OF PLANT SPECIES RICHNESS

We found several significant effects of plant species richness on animal assemblages, after adjusting for the effects of year and the interaction between year and burnt status. Effects varied in strength and direction depending on stratum and animal taxon. We show these effects in Fig. 2 (values given in Table S3, Supporting information), which gives the estimated mean percentage change in the animal assemblage measures corresponding to a change from 0 to 1 plant species in each vegetation stratum (Table S3, Supporting information also gives the estimated percentage change corresponding to a change from 1 to 2 species, for comparison). For birds, we found that the plant species richness of all strata in burnt sites had strong and positive effects on bird assemblages, whereas effects were weaker on unburnt sites and negative (though non-significant) for the understorey stratum. For example, an increase in

overstorey plant richness from 0 to 1 species in burnt sites was associated with a 42% increase in bird species richness and 60% increase in abundance. There were much smaller effects for mammals, although the overstorey effect on abundance was still significant at burnt sites. A positive overstorey effect on composition at burnt and unburnt sites was complicated by an interaction with year: the vegetation effect was significant only in 2006 and was much smaller in other years. There was noticeably more variability in the responses of reptiles, but all three vegetation strata had positive effects on reptile abundance at burnt and unburnt sites (though not all were significant). Both overstorey and understorey vegetation had positive effects on reptile composition.

#### EFFECTS OF VEGETATION PERCENTAGE COVER

There were also several significant effects of vegetation cover on each animal assemblage. We present these effects in Fig. 3 (values given in Table S3, Supporting information) and give the estimated mean percentage change in each animal assemblage corresponding to a change in vegetation cover from 0 to 10% in each stratum (Table S3, Supporting information also gives the estimated percentage change corresponding to a change from 10% to 0% cover, for comparison). For birds, there was a larger positive effect of overstorey cover in burnt sites than unburnt sites, but larger negative effects of understorey cover. For mammals, the largest effect was from understorey vegetation cover, which was positive in unburnt sites, but



**Fig. 2.** Mean percentage increase (with 95% confidence limits) of species richness, abundance and composition measures for three taxa, corresponding to a change from 0 to 1 in plant species in each of the three storeys, by burnt status of sites (red triangles = burnt; blue circles = unburnt). Means are adjusted for effects of year and burnt status, and their interaction, but are not adjusted for effects of other vegetation measures. OS, overstorey; MS, midstorey; US, understorey.

negative in burnt sites: this was most apparent for mammal composition. A small but significant positive effect of overstorey cover on mammal composition was again complicated by an interaction with year, with 2006 again having a larger effect than the other years. For reptiles, there was a positive effect of overstorey and midstorey vegetation cover on richness and abundance, but there were no large differences between burnt and unburnt sites. Understorey cover had a negative effect on these responses at burnt sites.

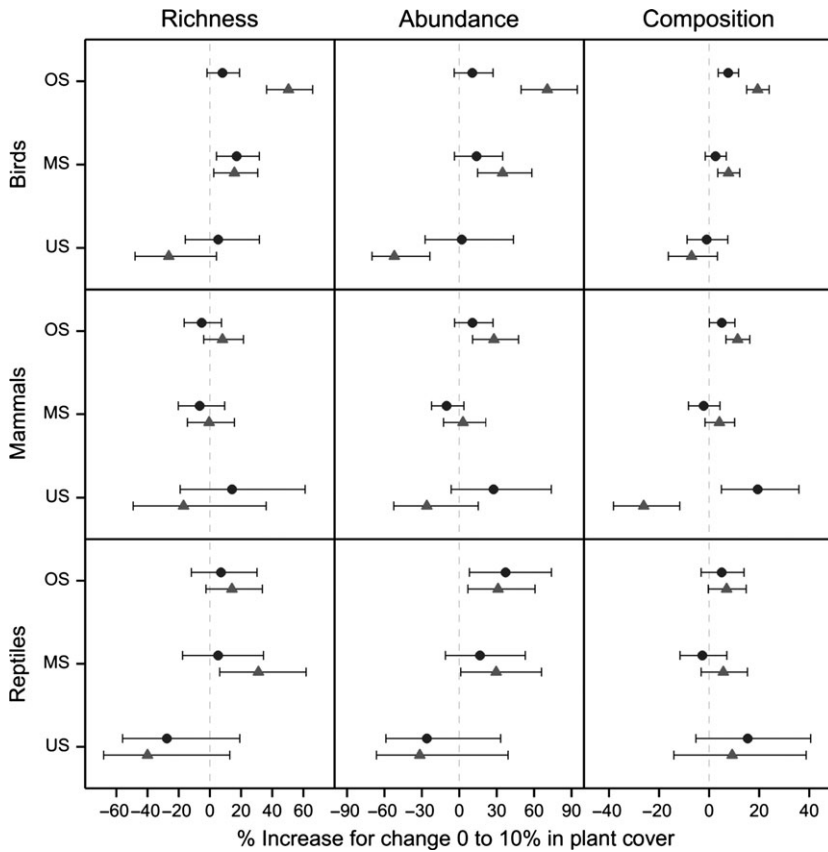
## Discussion

There are major gaps in our knowledge of whether surrogacy relationships are robust over time, after disturbance, across different taxa, and at scales appropriate to biodiversity management. In this paper, we have tested and compared the responses of multiple animal taxa to identical vegetation attributes within the same landscape, an approach rarely undertaken before. By addressing each of these gaps, our study has revealed that fundamental vegetation attributes have limited utility as strong or consistent surrogates of animal diversity. Further, we found that wildfire altered the relationship between some vegetation attributes and measures of bird and mammal assemblages, while reptile assemblages showed weaker responses to vegetation irrespective of fire. This mix of results highlights the lack of congruent responses of different

vertebrate groups to a single vegetation attribute, as well as the highly variable (and sometimes opposite) effects of fire on the relationship between plant and animal covariates. Below, we discuss the importance of making the distinction between strong and consistent effects of habitat-based surrogates, and the importance of fire in changing the underlying relationship between vegetation measures and animal assemblages.

### CONSISTENT VS. STRONG EFFECTS OF VEGETATION WITHIN AND ACROSS TAXA

Overstorey vegetation richness and cover nearly always had a positive effect on the abundance, richness and composition of each animal taxon, indicating that canopy vegetation had a consistent effect across multiple taxa (Table 2). However, some of these effects were only moderate or weak (and non-significant) for mammals and reptiles, and the strongest effects were for birds. This confirms our initial expectation that birds would respond to overstorey vegetation (MacArthur & MacArthur 1961; Barton *et al.* 2014). The finding that overstorey had both consistent and strong effects on bird assemblages suggests that broad habitat classifications that distinguish between canopy cover and extent, which has been attempted at landscape scales (Oliver *et al.* 2004; Cushman *et al.* 2008), are effective surrogates of bird assemblage diversity even at relatively small scales.



**Fig. 3.** Mean percentage increase (with 95% confidence limits) of species richness, abundance and composition measures for three taxa, corresponding to a change from 0 to 10% vegetation cover in each of three storeys, by burnt status of sites (red triangles = burnt; blue circles = unburnt). Means are adjusted for effects of year and burnt status, and their interaction, but are not adjusted for effects of other vegetation measures. OS, overstorey; MS, midstorey; US, understorey.

Mammals and reptiles often showed strong responses to understorey vegetation cover, which again agreed with our initial expectation of their stronger association with ground-layer variables. There was also a surprising change in the direction of the effect of understorey cover on mammal assemblage composition after fire, with an increase in the prevalence of bandicoots among

assemblages from burnt sites. This has been reported in previous work (Lindenmayer *et al.* 2008a), but our study suggests this may be driven by an increase in understorey cover. Notably, the effect of understorey cover was consistently negative across all three animal taxa, but this was only in sites burnt by fire, and effects were mostly weak. Nevertheless, understorey cover could be a useful

**Table 2.** Summary of strong vs. consistent effects of vegetation on the three animal taxa

	Strength of effect	Consistency of effect	Recommendation
Overstorey	Strong effects on bird richness, abundance and composition, especially in burnt sites. Strong effect on reptile abundance only, especially in unburnt sites. Weak effects on mammals.	Effects were consistently positive for all three animal taxa.	Effects of OS cover and richness were consistently positive across taxa, but only strong for birds. OS vegetation cover is an effective surrogate for bird diversity.
Midstorey	Moderate effects on bird abundance, especially in burnt sites. Generally weak effects on mammals and reptiles.	Some differences between taxa.	Effects were both inconsistent across taxa, and only moderate or weak. MS vegetation cover is not an effective surrogate.
Understorey	Strong effects on mammal assemblage composition, but direction of effect depends on disturbance. Moderate effects on reptile richness.	US cover consistently had negative effects on the abundance and richness of all taxa, but only in burnt sites.	Effects of US cover were consistently negative across taxa, but moderate in strength, and only in burnt sites. Could be an effective surrogate for loss of diversity after disturbance.

surrogate for the loss of diversity of multiple vertebrate taxa after fire (Table 2).

Reasons for why most of the six vegetation measures did not have consistent or strong effects on mammal and reptile assemblages might be related to the influential role of other key habitat variables such as food or nesting resources. Further, the relatively high spatial heterogeneity of vegetation types within our study landscape, and the close proximity of many of our sites, may be a critical factor driving the absence of concordant responses among taxa. Further, the use of different sampling methods of mammals and reptiles (compared with birds) is also a potential explanation for the different responses observed, with trapping being a very different survey technique than real-time point counts of birds.

Importantly, the effects of the number of plant species and percentage cover of vegetation on the animal assemblages were confounded and difficult to disentangle. For example, the addition of a single tall tree species to a heath or open woodland site will necessarily increase both the amount of cover and the richness of the overstorey stratum. Such confounding among variables has been reported previously (Cade, Noon & Flather 2005; Banks-Leite, Ewers & Metzger 2013) and shows that causal mechanisms linking habitat variables to changes in animal assemblages may be difficult to identify.

#### THE EFFECT OF FIRE ON HABITAT-BASED SURROGATES

After adjusting for combined vegetation effects, we found that fire had large negative effects on bird and mammal richness and abundance, but positive effects on reptile richness and abundance. This highlights the overwhelming effect that fire has on animal assemblages beyond the effect of vegetation. However, fire also dramatically altered the effects of the vegetation attributes on animal assemblages. This was most evident with the significantly stronger effects of vegetation in all strata on bird assemblages in burnt sites. The enhanced vegetation effects on bird assemblages in burnt sites may have been due to the loss of vegetation structure. In the absence of normal levels of cover, what cover remained appears to have had a disproportionate effect on determining the spatial occurrence of birds across our sites and suggests that animals respond more strongly to vegetation in a recently burnt environment. Few studies have examined habitat–animal associations specifically from an applied surrogacy perspective after intense disturbances such as fire (Brennan *et al.* 2006). This makes our result important because it demonstrates that particular vegetation attributes are not only robust to disturbance, but could improve their surrogacy potential, at least for birds.

Our analyses suggested that the lack of an effect of fire on the majority of vegetation effects on mammals and reptiles may be due to these taxa having less strong associations with these variables in the first place. However,

we did detect strong effects of fire *per se*, which might be due to direct mortality, changed food availability or elevated predation rates in the immediate post-fire environment (Erwin & Stasiak 1979; Rochester *et al.* 2010). The increase in captures of reptiles immediately after fire, however, might be due to a combination of increased mobility as they search for more scarce resources, or release from predation by birds or small mammals that decreased in these areas (Lindenmayer *et al.* 2008c).

Many studies have demonstrated the effect of fire on vegetation structure (e.g. Taylor 2010; Russell-Smith, Edwards & Price 2012), and subsequent effects on associated fauna (Fuhlendorf *et al.* 2006; Lindenmayer *et al.* 2008b; Barton *et al.* 2014). Thus, we anticipated that a habitat attribute used as a surrogate of animal diversity might be vulnerable to disturbance effects, and an altered or weaker relationship with associated fauna. Overall, however, we found that bird assemblages were more strongly affected by vegetation, whereas mammals and reptiles exhibited only limited changes in responses to vegetation after fire. Mixed responses to fire among different taxa are not unusual (Pastro, Dickman & Letnic 2011), but we show that these mixed results are also reflected in their responses to habitat-based surrogates.

#### APPLICATIONS TO BIODIVERSITY MANAGEMENT

Rigorous empirical testing is needed to evaluate and identify robust surrogacy relationships. Although many studies have identified vegetation attributes associated with the diversity and composition of vertebrate assemblages (Tews *et al.* 2004; McElhinny *et al.* 2006; Schaffers *et al.* 2008; Qian & Kissling 2010), very few studies have made an explicit comparison among multiple taxa in response to identical vegetation measures within the same landscape. Our study provides new evidence of the variable effectiveness of habitat-based surrogates of three important vertebrate taxa.

From a management perspective, our results support the use of overstorey vegetation as a surrogate for bird assemblages. Both plant species richness and percentage cover of overstorey vegetation had strong effects on the abundance and richness of bird assemblages, and these effects were enhanced at sites burnt by fire. In contrast, our data do not support the nomination of any vegetation attributes as consistent surrogates of mammal or reptile assemblages. This suggests that taxon-specific habitat-based surrogates may be required. However, this would require additional surveys of vegetation and raises the issue of cost in terms of both time and effort. In this case, the direct assessment of each taxon through dedicated surveys could provide greater accuracy of measured changes in richness and abundance than the use of indirect vegetation measures (Lindenmayer & Likens 2011). Such direct measurement of animal populations is also likely to have greater robustness to temporal variability and disturbance.



We build on previous research that has suggested habitat-based surrogates may be a superior class of surrogate relative to other classes of surrogates. This is, in part, due to their potential efficiency and practical value to resource managers and policymakers (Lindenmayer, Margules & Botkin 2000; McElhinny *et al.* 2005). Our detailed assessment of several potential habitat surrogates has highlighted the contrasting responses of different taxa and revealed that birds were the only taxon with both consistent and strong responses. Management decisions based only on bird data, however, may be inappropriate as a guide to management aimed at biodiversity more broadly. Although habitat-based surrogates may be appealing from a practical or cost perspective (Banks-Leite *et al.* 2011), the different ecologies of multiple taxa are difficult to account for with a single, easily measured vegetation attribute. Targeted research to identify a single habitat attribute associated with multiple taxa may prove to be difficult, but might focus on a limiting resource that is shared across taxa. This is because a focus on a shared resource will help to identify links between different taxa and their habitat through a common functional dependence in a key habitat attribute. If this attribute is limiting, then changes in this resources are more likely to be reflected by dependent animal assemblages.

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## Data accessibility

Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.s7d2d> (Barton *et al.* 2014a).

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## Supporting Information

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

**Fig. S1.** Location map of study area.

**Fig. S2.** Ordination plots of bird, mammal and reptile PCoA scores.

**Table S1.** Summary of regression models for three measures of bird, mammal and reptile assemblages (species richness, abundance, composition), and six attributes of vegetation.

**Table S2.** Mean (with 95% confidence limits) species richness, abundance and composition for each animal taxon by year and burnt status.

**Table S3.** Effects of each vegetation attribute (with 95% confidence limits) on species richness, abundance and composition of each animal taxon.