



Ground-dwelling mammal diversity responds positively to productivity and habitat heterogeneity in a fire-prone region

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Abstract. Environmental heterogeneity has a consistent, positive effect on species diversity globally, principally due to increased niche space in heterogeneous environments. In flammable ecosystems, fire-mediated heterogeneity (pyrodiversity) is expected to increase species diversity, and the application of diverse fire regimes is a common management goal. We used landscape-scale sampling units and linear mixed models to determine the response of ground-dwelling mammal alpha, beta, and gamma diversity to spatial habitat heterogeneity (functional heterogeneity) and three indirect measures of spatial heterogeneity, two pyrodiversity indices based on fire history maps, and another based on mapped vegetation types. In addition, we tested the consistency of species diversity responses across a productivity gradient and examined the extent to which prescribed fire influenced habitat heterogeneity. Beta diversity responded positively to habitat heterogeneity across the productivity gradient, but more strongly at high compared with low productivity. In contrast, alpha and gamma diversity responded positively to productivity, while a weak negative effect of habitat heterogeneity on alpha diversity was also evident. At the scale of our investigation, the productivity gradient across the study area was the most influential driver of species diversity. Spatial heterogeneity within 100-ha landscapes increased community differentiation among sites (beta diversity), had a weak negative effect on alpha diversity, but had no influence on landscape-scale species richness (gamma diversity). The occurrence of recent fire had a strong, positive effect on habitat heterogeneity, while the diversity of vegetation types and postfire age classes had a smaller positive influence. Our findings show that prescribed fire can be used to increase landscape-scale structural heterogeneity, but this will not always result in additional species. Finally, we suggest that using a functional representation of spatial heterogeneity (e.g., the spatial arrangement of habitat structure) as a predictor of species diversity is likely to reveal responses that may otherwise be overlooked. Modern remote-sensing technologies will aid the development of habitat-based heterogeneity metrics across large spatial extents.

Key words: beta diversity; biodiversity; fire management; habitat complexity; landscape; patch mosaic burning; prescribed fire; spatial pattern.

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INTRODUCTION

Both theory and empirical evidence support a positive relationship between species diversity

and environmental heterogeneity; the spatial and temporal variability in conditions (Chesson 2000b, Tews et al. 2004, Levine and HilleRisLambers 2009, Stein et al. 2014a). Across landscapes,

increasing environmental heterogeneity results in a wider array of resources, facilitating niche differentiation and the coexistence of multiple species (Chesson 2000*a, b*). However, continued increases in heterogeneity may eventually reduce the extent of suitable conditions for some species, increasing extinction probability and causing the diversity–heterogeneity relationship to be hump-shaped (Allouche et al. 2012).

In many parts of the world, fire is an agent of landscape change and a key driver of biodiversity (Bowman et al. 2009, Parkins et al. 2018, He et al. 2019). Spatially and temporally variable fire regimes are expected to result in heterogeneous fire mosaics capable of supporting diverse biological communities (Parr and Brockett 1999, Parr and Andersen 2006, Kelly et al. 2017*a*), leading to a predicted positive relationship between fire-mediated heterogeneity and biodiversity, often referred to as the pyrodiversity begets biodiversity hypothesis (Martin and Sapsis 1992). Several potential mechanisms underlie this general hypothesis; for example, changes in composition (the number, type, and relative abundance of fire-derived states), configuration (the spatial arrangement of states), or temporal variation in states due to changes in fire frequency and seasonality may all influence the diversity of animal communities (Kelly et al. 2017*a*).

Tests of the pyrodiversity–biodiversity hypothesis for animals have rendered mixed results; positive relationships have been identified in some cases (Fuhlendorf et al. 2010, Maravilhas and Vasconcelos 2014, Sitters et al. 2014*b*, Ponisio et al. 2016, Tingley et al. 2016, Beale et al. 2018), but not in others (Pastro et al. 2011, Davies et al. 2012, Kelly et al. 2012, Avitabile et al. 2015, Prowse et al. 2017). This is likely due to a number of factors, including the presence of interactions between fire and other processes (Nimmo et al. 2014, Hradsky et al. 2017), and the use of pyrodiversity metrics that may not reflect the mechanisms underlying biodiversity responses to fire. For instance, variables such as fire age class and fire severity are often used to represent change in fire-mediated spatial pattern (Taylor et al. 2012, Sitters et al. 2014*b*, Tingley et al. 2016), but provide an indirect link to the structural and food resources that animals require. In contrast, metrics incorporating direct measures of important resources (e.g., vegetation attributes representing

food and shelter; hereafter referred to as functional heterogeneity metrics) are expected to better reflect the underlying relationships between fire regimes and animal diversity (Fahrig et al. 2011, Kelly et al. 2017*a*).

At landscape scales, species diversity can be partitioned into alpha, beta, and gamma diversity where alpha is local (site-based) species diversity, beta represents spatial turnover between sites within landscapes, and gamma is whole-of-landscape species diversity (Whittaker 1960, 1972, Anderson et al. 2011). Across landscapes, fire-mediated heterogeneity is expected to promote community turnover (beta diversity) in space, thus increasing gamma diversity (Farnsworth et al. 2014). However, gamma diversity can also be influenced by alpha diversity, which may be driven by other properties of fire mosaics, such as the extent of old vegetation, and the response of beta diversity to fire-mediated heterogeneity may depend on both fire severity and spatial scale (Pastro et al. 2011, Farnsworth et al. 2014, Burgess and Maron 2016). More generally, the results of diversity–heterogeneity analyses depend on how species diversity is quantified (Stein et al. 2015); thus, a comprehensive assessment of diversity–heterogeneity relationships requires the use of multiple diversity measures (Farnsworth et al. 2014, Dorph et al. 2020).

Further, diversity–heterogeneity relationships may vary with productivity. For example, a recent individual-based spatially explicit model invoking trade-offs between competitive ability and stress tolerance in plants (Grime 1973) demonstrated a positive diversity–heterogeneity relationship at both low productivity and high productivity but negative or hump-shaped relationships at intermediate productivity (Yang et al. 2015). However, this model simulated communities of sessile organisms and assumed competitive ability and stress tolerance were important mechanisms driving community composition. It is unclear how productivity may affect diversity–heterogeneity relationships for mobile organisms, and in cases where competition or stress tolerance is not driving community composition. Our focus is on ground-dwelling mammal diversity, and many species known to occur in our study area (Swan et al. 2015, Sukma et al. 2019) are highly mobile and may not compete strongly with each other due to different

diets and habitat preferences. For example, common and sympatric species such as eastern grey kangaroo (*Macropus giganteus*), swamp wallaby (*Wallabia bicolor*), bush rat (*Rattus fuscipes*), and agile antechinus (*Antechinus agilis*) use different resources (Lazenby-Cohen and Cockburn 1991, Moore et al. 2002, Di Stefano et al. 2009, Fordyce et al. 2016) which likely limit competition at both high productivity and low productivity.

In this paper, we have three aims.

1. To determine the response of ground-dwelling mammal alpha, beta, and gamma diversity to spatial heterogeneity. Conceptually, spatial heterogeneity is more closely linked to beta diversity than to alpha or gamma diversity (Farnsworth et al. 2014, Burgess and Maron 2016), so our strongest expectation was of a positive beta-diversity response. Further, to test the effect of direct (functional) and indirect heterogeneity metrics we derived a functional metric from measured habitat attributes and indirect metrics from maps of fire history and vegetation type. We expected beta diversity to respond more strongly to functional heterogeneity than to our indirect measures.
2. To test the consistency of observed diversity–heterogeneity responses across a productivity gradient. Due to our focus on mobile organisms and evidence of limited competition between many species in our study area, we expected similar diversity–heterogeneity relationships across the productivity gradient.
3. To determine the main drivers of functional heterogeneity. Habitat structure is influenced by multiple factors, but in fire-managed landscapes prescribed fire is likely to have a major effect. We expected the application of prescribed fire to increase landscape-scale functional heterogeneity, but for heterogeneity to also vary with other factors such as vegetation type and topography.

We conducted our study in the Otway Ranges, southeastern Australia, which has a well-documented history of fire management and strong productivity gradient arising from a change in soils and rainfall. We quantified ground-dwelling

mammal diversity and environmental heterogeneity using 100-ha landscapes as sampling units. This approach enabled a realistic appraisal of how landscape-scale changes in heterogeneity are affecting the biota (Fahrig 2003, Bennett et al. 2006). Further, inferences can be made at the scale at which management actions (e.g., prescribed fire) are applied, making them highly relevant for conservation management.

MATERIALS AND METHODS

Study area

This study was conducted in a 59,000-ha section of the Otway Ranges in southern Victoria, Australia (Fig. 1). The climate of this region is temperate with cool wet winters and warm dry summers. There is an elevation, rainfall, and productivity gradient across the study area from low lying, drier areas in the northeast (150 m above sea level, 625 mm mean annual rainfall, and 3.6 Mg C/ha), to wetter areas in the southwest at higher elevations (650 m above sea level, 1167 mm mean annual rainfall, and 8.2 Mg C/ha; weather data from Aireys Inlet [northeast] and Mt Cowley [southwest], Bureau of Meteorology 2018; productivity data downloaded from <http://www.bccvl.org.au>). These conditions are reflected by changing vegetation communities, from heathland in the northeast to tall wet forest in the southwest. The six main vegetation types in the study area are described in Appendix S1: Table S1. The topography is undulating at lower elevations and becomes increasingly complex at higher elevations. The study area has been subject to fires of varying spatial extent and severity. Wildfires in 1939 and 1983 burnt large sections of the Otway Ranges, and prescribed burning (generally fires of 100–1000 ha) has been undertaken extensively for wildfire mitigation since 2000.

Study design

We used 100-ha circular landscape sampling units enabling us to capture variation in landscape composition. Further, 100 ha represents the upper-limit home range size of ground-dwelling mammals present in the study area (Van Dyck and Strahan 2008) and is commensurate to the size of most prescribed burns. Landscapes were located by establishing 500 random points along the road network, and then

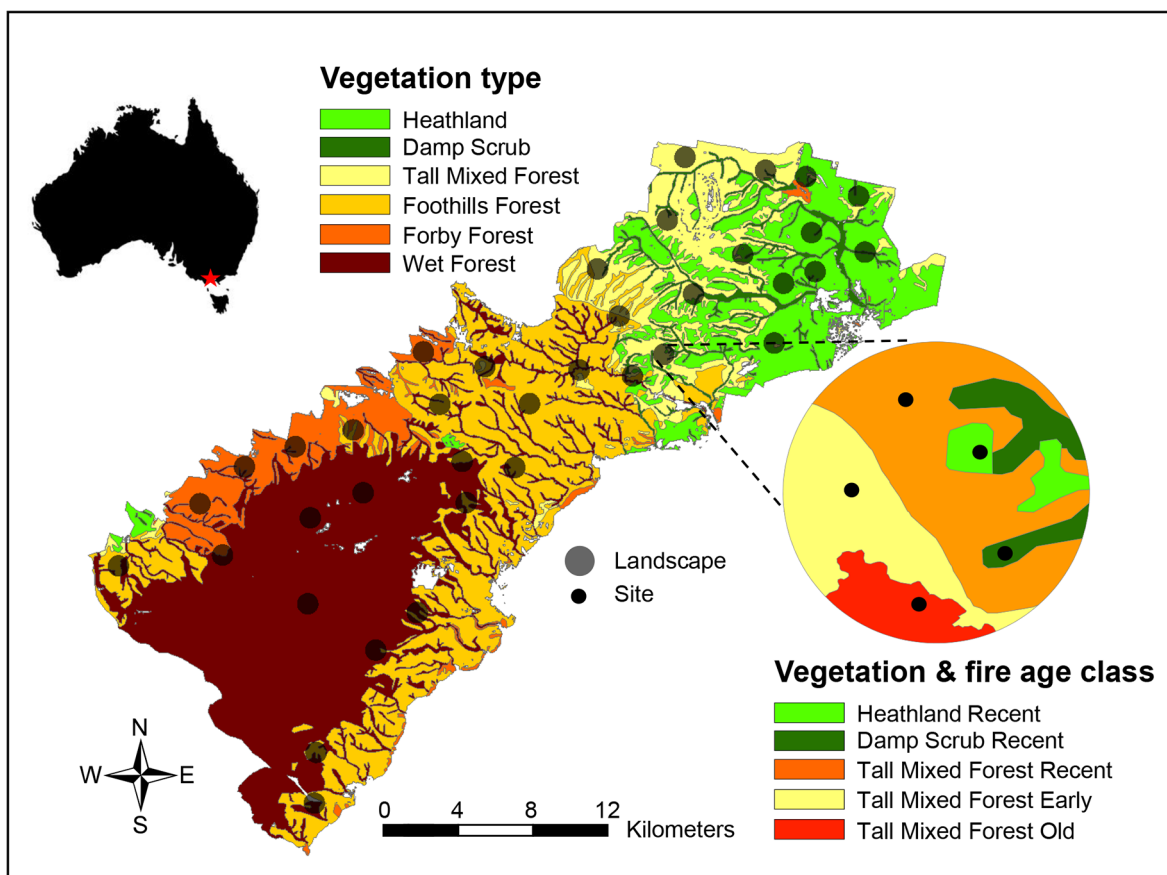


Fig. 1. Location of the study area in the Otway Ranges, southeastern Australia, showing the location of each 100-ha landscape. The blowout shows a single landscape containing three vegetation types and three age classes; different colors represent combinations of vegetation type and age class.

choosing locations from this pool at random such that (1) a similar number of landscapes (5–7) were in each main vegetation type, (2) landscapes were ≥ 3 km apart, and (3) landscapes contained a range in both the number of vegetation types and four postfire age classes, reflecting major stages of postfire growth and development (Cheal 2010). Thirty-two landscapes were established in year 1 (2010) and four more were established in year 2 (2011), resulting in a total of 36 landscapes. Within landscapes, the number of vegetation types and postfire age classes ranged from one to four, and the number of vegetation type and age class combinations ranged from one to six.

Within each landscape, we positioned five sites (in two cases six) using a restricted random

protocol ($n = 182$). Sites were positioned randomly such that they sampled all vegetation type and age class combinations that were present. At each site, we established a 100-m transect along a random bearing, ensuring that transects were at least 50 m from tracks and 100 m from each other.

Data collection

We surveyed ground-dwelling mammals twice, first between October and February (spring/summer) 2010/2011 and then again between October and February 2011/2012 using live trapping and camera trapping (Swan et al. 2015). Live trapping was conducted on three consecutive nights per season using 12 Elliott traps (type A: $9 \times 10 \times 33$ cm) spaced evenly along

the 100-m transect at each site. Traps were baited with a mixture rolled oats, peanut butter, golden syrup, and pistachio essence, and unbleached cotton wadding was added to the back of the trap as insulation.

A ScoutGuard 550v camera (HCO Outdoor Products, Norcross, Georgia, USA) and a Reconyx HC500 camera (Reconyx, Holmen, Wisconsin, USA) were deployed at the 20 m and 80 m mark of each transect, respectively. Each camera was mounted on a tree 50 cm above the ground and pointed at a bait station placed 2.5 m away. The bait station consisted of five tea infusers containing bait suspended 30 cm above the ground on a wooden stake. Vegetation between the camera and bait station was removed to improve the clarity of animals in the photographs. Cameras were left in place for 19 d on their highest sensitivity setting, and three pictures were taken each time they were triggered. Species identification from photographs was completed by four researchers with similar levels of experience using a reference guide (Menkhorst and Knight 2004) and accumulated photographs of clearly identifiable species.

Habitat structure surveys were conducted at all sites between February 2011 and September 2012. Sites that were burned less than three years before or immediately after the first season's mammal surveys were reassessed during the second season to capture rapid structural change present in early successional heath and forests. We measured a suite of habitat structure variables that were both potentially influenced by fire and important for a range of ground-dwelling mammal species (Catling et al. 2000, McElhinny et al. 2006) and selected five previously shown to drive ground-dwelling mammal occurrence in the study area (Swan et al. 2015); vegetation cover at three vertical strata (0–0.2 m, 0.2–0.5 m, and 1–2 m), litter depth, and the cover of coarse woody debris (CWD). Vegetation cover was recorded at 33 evenly spaced points along each 100-m transect using the point intercept technique. In the 0–0.2 m strata, cover was estimated as the mean number of touches per point, while in the higher strata it was estimated as the frequency of presences. Litter depth was recorded at each of the 33 points using a vertically held ruler, and these values were averaged to generate a site-level estimate of litter depth.

Coarse woody debris cover was recorded by measuring the cross section of each log larger than 5 cm in diameter and 50 cm in length intersecting the transect. Cover was then estimated as the sum of intersecting lengths divided by the total length of the transect.

Data analysis

All analyses were conducted in R v. 3.5.2 (R Development Core Team 2018).

Drivers of ground-dwelling mammal diversity.— We pooled data from traps and cameras to derive a site-by-species presence–absence matrix which was used to calculate alpha, beta, and gamma diversity within each landscape, using data from sites ($n = 5$ [in two cases 6] per landscape) as subsamples. We repeated this process separately for the two survey seasons (2010/2011 and 2011/2012) and included both data sets in the analysis (see Statistical modeling below). It was necessary to keep data from the two seasons separated because of the four new landscapes added in season two and because fire occurred in 10 landscapes between the first and second surveys, changing their characteristics. Alpha diversity was calculated as the mean number of species per site, and gamma diversity as the total number of species in each landscape. We calculated beta diversity as the multisite formulation of the Simpson dissimilarity index (Baselga et al. 2007) using the package betapart (Baselga and Orme 2012). The Simpson index is considered a robust turnover measure because it represents species replacement rather than dissimilarity from nested compositions and differences in numbers of species (Baselga et al. 2007). Values of this index are scaled from 0 to 1, with values of 0 and 1 representing complete compositional similarity and dissimilarity among sites, respectively.

We investigated the response of alpha, beta, and gamma diversity to five predictor variables, three indirect heterogeneity metrics (fire age class diversity, vegetation type diversity, and the presence or absence of recent fire), one functional heterogeneity metric (a habitat heterogeneity index), and a measure of the productivity gradient across the study area (net primary productivity; Table 1). Age class and vegetation type diversity were quantified using Shannon's

diversity index and calculated using the ArcGIS extension Patch Analyst Version 5 (Rempel et al. 2012). Recent fire was defined as the presence of at least one fire event ≤ 5 yr prior to sampling. Habitat heterogeneity was calculated as the mean habitat dissimilarity from all pairwise combinations of sites within each landscape. We used the Bray–Curtis dissimilarity metric and applied it to the five habitat structure variables described above using the R package *vegan* (Oksanen et al. 2015). Landscape-scale net primary productivity was calculated as the mean of site-level values extracted from a raster surface (250-m resolution) representing mean annual net primary productivity between 1971 and 2000 (downloaded from <http://www.bccvl.org.au>). Net primary productivity is equal to plant photosynthesis less plant respiration and represented as Mg C/ha (Stein et al. 2014b). Response and predictor variables were centered and standardized (subtraction of mean and division by standard deviation) to improve the interpretation of main effects in the presence of interactions and to allow for the comparisons of coefficients (Schielzeth 2010). Correlations between the four predictor variables were $\leq |0.58|$ making them suitable for inclusion in the same regression model.

Drivers of habitat heterogeneity.—We investigated the response of the habitat heterogeneity index to fire age class and vegetation type diversity, the presence or absence of recent fire, net primary productivity, and topographic roughness, another variable representing potentially important landscape-scale patterns that may influence habitat heterogeneity. Topographic

roughness reflected landscape complexity resulting from variation in topographic position (Table 1).

Statistical modeling.—We modeled the response of alpha, beta, and gamma diversity to age class and vegetation type diversity, the presence or absence of recent fire, the habitat heterogeneity index, and net primary productivity using a linear mixed model (LMM) run in the *nlme* package (Pinheiro et al. 2018). For each response variable, we generated 25 models including each predictor on its own (five models), all pairs of predictors in additive combinations (10 models), and all pairs of predictors in interactive combinations (10 models). Landscape ID was specified as a random factor to account for repeated surveys (Zuur et al. 2009). We did not include season (2010/2011 and 2011/2012) as a predictor as we aimed to avoid overfitting by keeping models simple, and preliminary analysis showed that effects were similar in each season. Further, predictor variables were modeled as linear fixed effects as preliminary data exploration did not identify any clear nonlinear relationships.

The purpose of constructing the set of 25 models was to identify a parsimonious model for primary inference. To achieve this, the models in each set were ranked using Akaike's information criterion (corrected for small sample size AIC_c) and coefficients, predictions, and R^2 values were derived from the top-ranked model. We used a version of R^2 designed for mixed-effects models, calculating both marginal R^2 , the variance explained by fixed effects, and conditional R^2 , the variance explained by both

Table 1. Predictor variables used in the analyses of ground-dwelling mammal diversity and habitat heterogeneity within 100-ha landscapes in the Otway Ranges, southeastern Australia.

Predictor variable	Description	Range
Age class diversity [†]	Diversity of fire age classes present within landscapes calculated using Shannon's diversity index	0–1.20
Vegetation type diversity [†]	Diversity of vegetation types present within landscapes calculated using Shannon's diversity index	0–1.54
Habitat heterogeneity index [†]	Mean dissimilarity in habitat structure between sites within landscapes measured using the Bray–Curtis dissimilarity index	0.14–0.38
Net primary productivity [†]	Mean net primary productivity per landscape (Mg C/ha)	3.80–7.94
Recent fire [†]	Recent fire present if at least one site was burnt ≤ 5 yr prior to sampling, otherwise absent	Present/absent
Topographic roughness [‡]	Standard deviation of elevation within each landscape	8.2–52.9

[†] Predictor variables used to model ground-dwelling mammal diversity.

[‡] Additional predictor variable used to model the habitat heterogeneity index.

fixed and random effects (Nakagawa and Schielzeth 2013). For each of the three response variables, coefficients from models within 2 AIC_c units of the best are presented in Appendix S1: Table S2. We used the MuMIn package (Barton 2018) to conduct model selection and to calculate R^2 , and the ggplot2 package (Wickham 2016) to draw graphs.

We modeled the response of the habitat heterogeneity index to age class diversity, vegetation type diversity, the presence or absence of recent fire, net primary productivity, and topographic roughness using the LMM described above. Our objective was to quantify the response of the habitat heterogeneity index to each predictor separately, and to determine the predictor with the strongest effect, so we built five separate models and ranked them using AIC_c .

Assumptions of normality and homogeneity of variance were checked using residual plots, and no violations were detected. Imperfect detection was not accounted for in the modeling process. In our study area, detectability is correlated with abundance for many species (Swan et al. 2015) and as such occupancy estimates of individual species may be unreliable (Welsh et al. 2013). Further, the sampling effort at each site using both camera trapping and Elliot trapping resulted in a high level of confidence (>80% for most species) that species were detected when present (Appendix S1: Table S3).

RESULTS

In total, 11 native ground-dwelling mammal species were recorded during the two survey years within the 36 landscapes (Appendix S1: Table S3). Alpha diversity ranged from 1.4 to 5.2 (mean 3.0), beta diversity ranged from 0 to 0.78 (mean 0.36), and gamma diversity ranged from 2 to 9 (mean 5.9).

There was no clear best model for predicting alpha, beta, or gamma diversity (Appendix S1: Table S2). Coefficients from the highest ranked models show that alpha and gamma diversity responded positively to net primary productivity (Table 2). Alpha diversity increased by 64% and gamma diversity increased by 24% along the productivity gradient (Fig. 2). Further, alpha-diversity responded negatively to the

habitat heterogeneity index. However, the confidence limits overlapped zero by a small amount and the strength of the effect was moderate compared with net primary productivity (Table 2).

Beta diversity responded positively to the habitat heterogeneity index across the productivity gradient, but the strength of the response was moderately greater at high compared with low productivity (Table 2). For example, at the 75th percentile of the productivity range (7.4 Mg C/ha) beta diversity increased by 136% along the range of the habitat heterogeneity index, while at the 25th percentile (5.1 Mg C/ha) the increase was 75% (Fig. 3).

The habitat heterogeneity index responded more strongly to the presence or absence of recent fire than to other potential drivers (Table 3). The presence of recent fire increased the mean (lower 95% CL, upper 95% CL) value of the index by 27% (14%, 40%). Vegetation type diversity and age class diversity also had a positive influence on the habitat heterogeneity index (Table 3).

DISCUSSION

We used landscape-scale sampling units to determine the response of ground-dwelling mammal alpha, beta, and gamma diversity to fire-mediated landscape heterogeneity. Additionally, we tested the consistency of diversity responses across a productivity gradient and evaluated the influence of fire on the habitat heterogeneity index. Beta diversity responded positively to habitat heterogeneity across the productivity gradient, but the strength of the response was moderately greater at high compared with low productivity. In contrast, alpha diversity and gamma diversity were positively influenced by productivity, but did not respond to any measure of fire-mediated heterogeneity. The presence of recent fire and both age class and vegetation type diversity had a positive effect on habitat heterogeneity, indicating that heterogeneity in vegetation structure can be manipulated at the landscape scale by the application or suppression of fire, but also that it is driven by natural spatial variation in vegetation type. We discuss the insights arising from this work and consider the implications

Table 2. Standardized estimates, 95% confidence intervals (95% low, upp), and R^2 values associated with the best AIC_c model predicting alpha, beta, and gamma diversity of ground-dwelling mammal diversity within 100-ha landscapes in the Otway Ranges, southeastern Australia.

Model	Parameter	Estimate	95% low	95% upp	$R^2(m)$	$R^2(c)$	P value
Alpha diversity							
HHI + NPP							
	HHI	-0.17	-0.38	0.05	0.33	0.40	0.13
	NPP	0.51	0.29	0.73			<0.001
Beta diversity							
HHI \times NPP							
	HHI	0.44	0.19	0.69	0.21	0.37	<0.01
	NPP	0.00	-0.25	0.26			0.99
	HHI:NPP	0.26	0.03	0.50			0.03
Gamma diversity							
NPP							
	NPP	0.28	0.04	0.52	0.08	0.08	0.02

Notes: Marginal R^2 ($R^2 m$) refers to variance explained by fixed effects only, and conditional R^2 ($R^2 c$) refers to the variance explained by fixed and random effects combined. HHI is habitat heterogeneity index; NPP is net primary productivity.

for biodiversity management in flammable landscapes.

Drivers of ground-dwelling mammal diversity

Empirical evidence points to a close relationship between the composition of vertebrate communities and vegetation structure (Tews et al. 2004), with spatial habitat heterogeneity often promoting community differentiation (Williams et al. 2002, López-González et al. 2015, Zellweger et al. 2017). If increased landscape-scale heterogeneity results in niche differentiation and the addition of species, a positive relationship between heterogeneity metrics and both beta diversity and gamma diversity is expected. We found a strong positive relationship between habitat heterogeneity and beta diversity, but this was not reflected in increased gamma diversity, indicating that observed community differentiation within structurally heterogeneous landscapes was not caused by the addition of new species. Inspection of the raw data showed that species tended to be detected at fewer sites in landscapes with high values of the heterogeneity index compared to landscapes with low values, implying that high values of beta diversity in heterogeneous landscapes were due to the increased patchiness of species distributions. Our findings reflect a neutral outcome for conservation management, as increased landscape heterogeneity resulted in compositional

differences among sites without a net increase in the number of species at the landscape scale (gamma diversity).

Species may have been more patchily distributed in heterogeneous landscapes because the increased diversity of habitat conditions altered patterns of animal movement. Heterogeneity in our study landscapes was driven by the occurrence of recent fire, and a greater diversity of growth stages and vegetation types, likely resulting in the presence of small, high-quality resource patches for some species and a reduction in resource quality for others. For instance, recent fire attracts eastern grey kangaroos, *Macropus giganteus* (Meers and Adams 2003), but causes other species dependent on resources consumed by fire to be restricted to or retreat into nearby unburnt vegetation (Robinson et al. 2013, Fordyce et al. 2016, Swan et al. 2016). Similarly, many of the most heterogeneous landscapes contained riparian vegetation, which is known to represent high-quality habitat and support more species than surrounding vegetation types in our study area and elsewhere (Swan et al. 2014, Hamilton et al. 2015). We suggest that in some cases, animal movement in heterogeneous landscapes may have been reduced due to fire-based resource depletion leading to real or perceived movement barriers at recently burnt sites. In other cases, the presence of small high-quality patches (e.g., riparian vegetation or a preferred

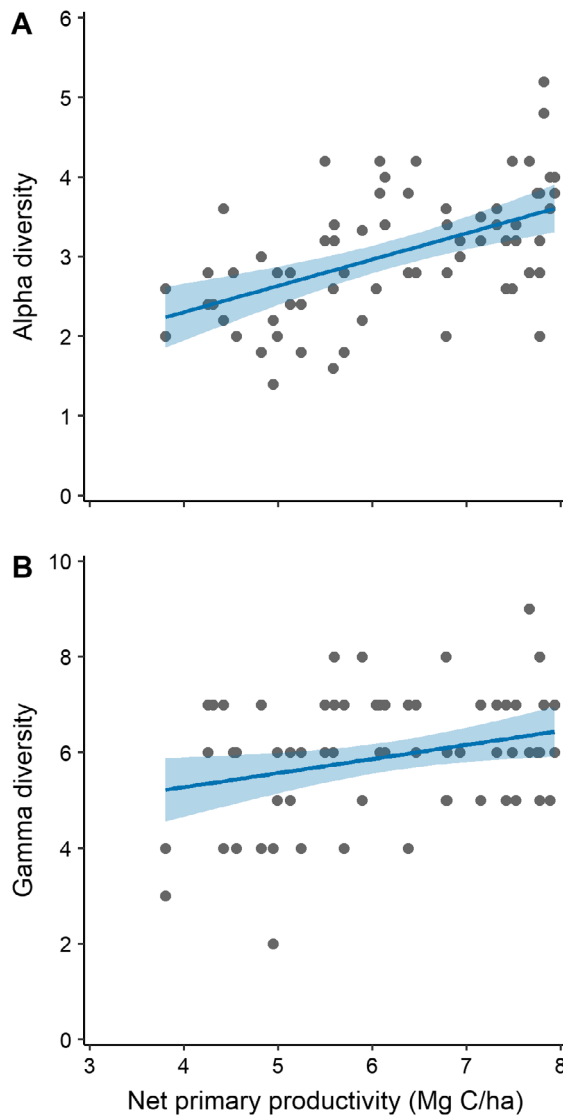


Fig. 2. Response of ground-dwelling mammal alpha (A) and gamma (B) diversity to net primary productivity within 100-ha landscapes in the Otway Ranges, southeastern Australia. The predictions (solid lines) and 95% confidence limits (shading) were generated from general linear mixed models. The raw data are represented by the gray dots.

growth stage) may have reduced home range size, as in this situation individuals do not need to move far to access resources (Saïd et al. 2009, Di Stefano et al. 2011a). The avoidance of or attraction to particular sites in heterogeneous landscapes is consistent with our finding that

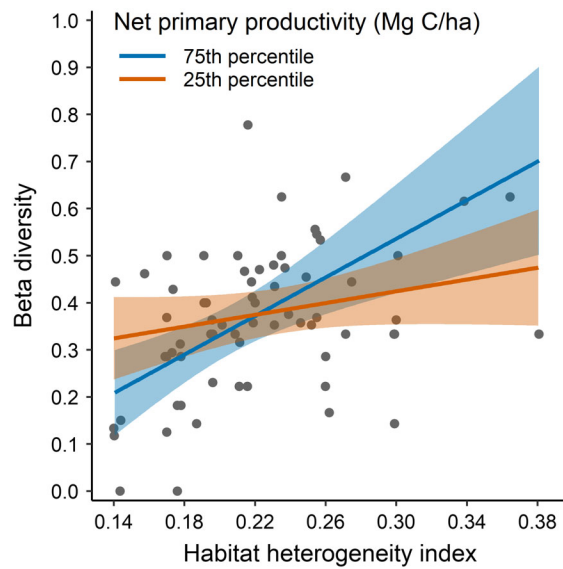


Fig. 3. Response of ground-dwelling mammal beta diversity to the habitat heterogeneity index within 100-ha landscapes in the Otway Ranges, southeastern Australia. Responses are presented at high (75th percentile; blue line) and low (25th percentile; orange line) values of net primary productivity. The predictions (lines) and 95% confidence limits (shading) were generated from a general linear mixed model. The raw data are represented by the gray dots.

beta diversity but not gamma diversity increased with habitat heterogeneity. It is also consistent with the moderate negative response of alpha diversity to habitat heterogeneity.

The response of beta diversity to habitat heterogeneity was positive across the productivity gradient, but the rate of increase was moderately stronger in higher productivity, wetter vegetation compared with lower productivity, dryer vegetation. This may be because productivity limits diversity more at low compared with high levels (Kerr and Packer 1997, Šimová and Storch 2017), facilitating stronger effects of other factors, such as heterogeneity, in high productivity zones. We can find no other studies that test whether the response of mammal beta diversity to disturbance-mediated spatial heterogeneity depends on productivity. Generally, similar studies (Verschuyl et al. 2008, McWethy et al. 2010, Sitters et al. 2016, Beale et al. 2018, Sukma et al. 2019) differ with respect to taxonomic group, response variable, measure of heterogeneity, and

Table 3. The effect of five predictor variables on the habitat heterogeneity index within 100-ha landscapes in the Otway Ranges, southeastern Australia.

Predictor variable	ΔAIC_c	Akaike weight	Estimate (LCL, UCL)	$R^2(m)$	$R^2(c)$
P/A RECENT FIRE	0	0.79	1.03 (0.44, 1.58)	0.20	0.75
VDIV	3.1	0.17	0.40 (0.14, 0.67)	0.15	0.51
ADIV	6.5	0.03	0.46 (0.06, 0.88)	0.15	0.75
NPP	8.7	0.01	-0.26 (-0.54, 0.02)	0.06	0.47
TOPO	11.8	0.00	-0.05 (-0.35, 0.25)	0.00	0.48

Notes: Models were ranked using Akaike's information criterion adjusted for small sample size (AIC_c). The Akaike weight (the probability that the associated model is best in the set), standardized regression estimates with lower (LCL) and upper (UCL) 95% confidence limits, and percent variance explained (R^2) are shown; $R^2(m)$ refers to variance explained by fixed effects only and $R^2(c)$ refers to variance explained by fixed and random effects combined. P/A RECENT FIRE is presence or absence of recent fire; VDIV is vegetation type diversity; ADIV is age class diversity; NPP is net primary productivity; and TOPO is topographic roughness. See Table 1 for detailed variable definitions.

spatial scale, making cross-study comparisons difficult. In African savannahs, pyrodiversity increased bird and mammal species richness more at high compared with low rainfall (Beale et al. 2018), and logging disturbance had a similar effect on bird species richness in high and low productivity landscapes in northwestern United States (McWethy et al. 2010). An explanation for these findings is that the effect of disturbance on species diversity is primarily indirect via changes to vegetation structure and that disturbance-mediated structural change is likely to be greater at high compared with low productivity (Beale et al. 2018). However, this was not the case in our study, as the effect of fire variables on the habitat heterogeneity index did not depend on productivity (analysis not shown). Further, using data from the same landscapes as ours, Sitters et al. (2016) found the response of bird functional diversity to habitat heterogeneity was generally positive in lower productivity dry forest and negative in higher productivity wet forest, while mammal functional diversity measured at sites within the same landscapes responded positively to vegetation structural complexity but was not influenced by productivity (Sukma et al. 2019). Due to the small number of relevant studies and the variability of their design and analyses, determining the conditions under which disturbance-mediated spatial heterogeneity and productivity interact to affect animal diversity requires further research.

Alpha and gamma diversity responded positively to net primary productivity, suggesting that productivity has a major influence on mammal diversity in our study area. Higher rainfall

and increased primary production promote growth rates, larger population sizes, lower extinction rates, and a greater number of co-occurring species (Hawkins et al. 2003, Luo et al. 2012), so increased site and landscape-scale species richness are a general expectation in high compared with low productivity areas. Nevertheless, the response of species richness to productivity may depend on taxonomic group. For instance, in a similarly designed study to ours conducted in the Murray Mallee region of Australia, small mammal gamma diversity responded positively to rainfall, probably due to increased food resources at high rainfall locations (Kelly et al. 2012). In contrast, reptile alpha and gamma diversity increased in hotter, drier parts of the same study area, likely due to a positive response of reptiles to increased temperature (Farnsworth et al. 2014).

The strong response of alpha and gamma diversity to productivity may be driven by the large productivity gradient we sampled—net primary productivity in our 36 study landscapes ranged between 3.8 and 7.9 Mg C/ha, reflecting the diversity of vegetation communities within our study area. At regional scales, variation in biophysical factors such as precipitation, temperature, and soil fertility may swamp the effects of other potential drivers of species diversity that may be evident at smaller scales. For example, previous research using data from the Otway Ranges showed that fire disturbance had a stronger effect on both animals and plants at smaller compared with larger spatial scales (Cohn et al. 2015, Kelly et al. 2017b). More generally, the response of biodiversity to both biophysical

gradients and spatial heterogeneity depends on scale (Chase and Leibold 2002, Gonzalez-Megias et al. 2007, Veech and Crist 2007). At the scale of our investigation, the productivity gradient across our study area was the most influential driver of species diversity. Spatial heterogeneity within 100-ha landscapes increased community differentiation among sites (beta diversity) but had no clearly detectible influence on site or landscape-scale species richness.

Drivers of habitat heterogeneity

Although fire is a major driver of heterogeneity in flammable ecosystems (He et al. 2019), important landscape-scale patterns also result from other factors such as spatial change in vegetation type and topography (Stein et al. 2015). Further, fire can interact with other disturbances such as grazing to influence both spatial heterogeneity and biodiversity (McGranahan et al. 2012, Davis et al. 2016). Understanding the extent to which fire influences heterogeneity in the presence of other drivers will help land managers achieve their conservation goals.

The presence or absence of recent prescribed fire in our study landscapes was the strongest predictor of habitat heterogeneity, with its presence increasing the heterogeneity index by 27%. In addition, the diversity of fire age classes had a detectible positive influence on the heterogeneity index. Although other factors (e.g., rainfall, topography) are clearly important (Haslem et al. 2016), prescribed fire can influence individual structural attributes (Moreira et al. 2003, Hall et al. 2006, Haslem et al. 2011, Sitters et al. 2014a), composite indices of habitat structure (Coops and Catling 2000, Haslem et al. 2016), and spatial heterogeneity in habitat structure (Holland et al. 2017). Based on this evidence, we suggest that prescribed fire can be used to manipulate landscape-scale structural heterogeneity in predictable ways. Nevertheless, the response of species to fire-mediated structural change is difficult to predict (Nimmo et al. 2014), and determining how fire regimes can be manipulated to alter habitat in ways that benefit biodiversity is an important research goal (Dorph et al. 2020).

Functional metrics of spatial heterogeneity

Beta diversity responded more strongly to functional heterogeneity (the habitat

heterogeneity index) than to our indirect heterogeneity measures derived from fire history and vegetation maps. Several recent studies of vertebrate responses to pyrodiversity have also found simple map-based pyrodiversity metric to be poor predictors of animal diversity (Kelly et al. 2012, Taylor et al. 2012, Farnsworth et al. 2014, Radford et al. 2015, Burgess and Maron 2016) although this is not always the case (Sitters et al. 2014b, Tingley et al. 2016). Simple heterogeneity metrics may not capture the mechanisms underlying species responses to spatial heterogeneity as they are not directly linked to important resources such as food, shelter, and nest sites (Kelly et al. 2017a). In contrast, functional metrics such as our habitat heterogeneity index represent spatial patterns in important resources. For example, ground-dwelling mammals in our study area are known to respond to all five of the structural measures we used to derive our index (Swan et al. 2015), and measures of habitat structure are often shown to be better predictors of vertebrate occurrence and abundance than fire history variables (Di Stefano et al. 2011b, Nimmo et al. 2014, Swan et al. 2015). Using a functional representation of spatial heterogeneity is likely to reveal species responses that may otherwise be overlooked.

We have argued that functional heterogeneity metrics that incorporate vegetation structure will improve the quality of inference in diversity-heterogeneity studies. However, field-based vegetation measurements are time-consuming and are unlikely to be applied across large spatial extents, potentially limiting the utility of this approach. A solution could be to use new remote-sensing technologies that have the capacity to generate high-resolution measures of vegetation structure (Marselis et al. 2016, Coops et al. 2018, Liang et al. 2019). For example, it is possible to derive vertical vegetation components from highly portable (<1 kg) ground-based LiDAR scanners (Marselis et al. 2016). Alternatively, it may be possible to derive more complex map-based heterogeneity measures that better represent functional aspects of spatial pattern. In the context of pyrodiversity, for example, Hempson et al. (2018) calculated pyrodiversity as the minimum multivariate space defined by fire size, season, return interval, and intensity, a metric that was successfully used to predict bird and

mammal species richness across African savannahs (Beale et al. 2018).

CONCLUSION

Alpha and gamma diversity responded positively to net primary productivity, while beta diversity responded positively to the habitat heterogeneity index, a functional measure of spatial heterogeneity in habitat structure. Our findings indicate that the productivity gradient across our study area was the most influential driver of species diversity. Spatial heterogeneity within 100-ha landscapes increased community differentiation among sites (beta diversity) but had no influence on the number of species occurring in the landscape. This represents a neutral outcome for conservation management.

The presence of prescribed fire was the strongest driver of landscape-scale habitat heterogeneity, indicating that the application or suppression of fire can be used to manipulate spatial habitat heterogeneity in predictable ways. Habitat change is a key process underlying the response of animals to fire, so determining how fire can be used to alter habitat in ways that benefit biodiversity is an important research goal. Finally, we suggest that functional indices of spatial heterogeneity incorporating direct measures of important habitat resources may be better predictors of species diversity compared with simple indices derived from patch-based maps. Using modern remote-sensing technologies to directly measure habitat will aid the development of habitat-based heterogeneity metrics across large spatial extents.

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