Wildfire in rainforest margins is associated with variation in mammal diversity and habitat use

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ABSTRACT

Context. Rainforests typically evolved without the influence of fire or with only low-intensity fires, making them vulnerable to contemporary increases in fire frequency and intensity. Rainforest-associated species are predicted to be less adaptable than generalist species, but little is known about how fire in rainforest margins affects their habitat use and behaviour. **Aims.** We investigated how mammal community composition, diversity, probability of habitat use and probability of movement were affected by wildfires that occurred in rainforest margins in South East Queensland, Australia, in 2019–20. **Methods.** We deployed camera traps at 23 sites spanning the following three fire-habitat categories: unburnt rainforest (UR), burnt rainforest (BR) and surrounding burnt sclerophyll forest (BS), and used passive detection to analyse habitat use and behaviour. **Key results.** Fire-habitat category had little influence on community composition. Species diversity was highest in unburnt rainforest compared with burnt rainforest and surrounding burnt sclerophyll forest. The probability of habitat use was highest in unburnt rainforest for both the long-nosed bandicoot (*Perameles nasuta*, estimated mean probability (95% CI): UR = 57.1% (22.98, 85.6), BR = 0%, BS = 0%) and the fawn-footed melomys (*Melomys cervinipes*: UR = 100%, BR = 87.5% (46.3, 98.3), BS = 50% (20.0, 80.0)). Probability of movement for the bush rat (*Rattus fuscipes*) increased with increasing elevation in burnt sclerophyll and was unaffected by elevation in unburnt and burnt rainforest. **Conclusions.** Rainforest margins that experienced wildfire had reduced species diversity, most likely owing to a reduction in habitat use by rainforest-associated species. Movement patterns of mammal species were complex and not consistently related to recent fire history. **Implications.** Rainforest margins and associated species are likely to be negatively affected by increasing wildfire intensity and frequency. In addition to urgent climate-change mitigation, land management that prevents wildfire incursion is likely to benefit rainforest communities in future.

Keywords: behavioural ecology, bushfire recovery, community ecology, ecological modelling, fire ecology, habitat use, mammal diversity, mammal ecology, wildfire.

Introduction

Many ecosystems around the world evolved in landscapes regularly shaped by fire (Keeley and Pausas 2022). In fire-prone regions, periodic fire events foster ecosystem resilience by reducing fuel loads and promoting landscape complexity, biodiversity and ecosystem services (Spies *et al.* 2014). However, climate change and other interacting stressors are altering fire regimes globally (Flannigan *et al.* 2013; Kelly *et al.* 2020). The occurrence of high-severity wildfires at larger spatial scales is set to continue in the future (Flannigan *et al.* 2013; Stephens *et al.* 2014; Bowman *et al.* 2020). Understanding how wildfire events affect ecosystems, and how they subsequently recover, is essential to develop management strategies to mitigate negative consequences of wildfire.

Gullies and pole-facing slopes are exposed to less solar radiation and, thus, have higher moisture content, which naturally supports rainforest vegetation (Wood *et al.* 2011; Robinson *et al.* 2013). Rainforests receive a high annual rainfall and have high humidity (Leigh 1975; Yates *et al.* 1988), which buffers rainforest vegetation from fire (Wood *et al.* 2011;

Robinson *et al.* 2013). This means that rainforests have historically avoided being affected by repeated fire events (Russell-Smith and Stanton 2002; Cochrane 2003), and that resident plant communities have low proportions of species with fire-adaptive traits (e.g. especially post-fire seeding; Clarke *et al.* 2015; Lawes *et al.* 2022), compared with fire-prone ecosystems. When fires do occur in rainforests, they are typically infrequent, of low intensity, and most often occur in drier rainforest or only in rainforest margins (Sanford *et al.* 1985; Cochrane and Laurance 2002; Steffensen 2020). With drought severity and length increasing in many regions as a result of climate change (Vicente-Serrano *et al.* 2020; Laidlaw *et al.* 2022), rainforest margins are becoming more frequently affected by wildfires (Vicente-Serrano *et al.* 2020; Laidlaw *et al.* 2022). Rainforest fire can cause tree mortality, which creates gaps and subsequent changes in microclimate (Brando *et al.* 2014; De Frenne *et al.* 2021). Fire in rainforests can cause a positive feedback, whereby more flammable species invade rainforest margins, which may drive further increases in fire frequency (Cochrane and Laurance 2008; Fletcher *et al.* 2020; Hines *et al.* 2020). While there is evidence of resprouting in rainforest tree species after fire (Baker *et al.* 2022), little is known about the trajectory of ecosystem recovery in rainforest margins. Will they recover to their pre-disturbance state? Or will fire cause a shift into an alternative ecosystem state?

Animal population recovery after fire is shaped by a complex suite of factors including species' biology, niche width, geographic context, resource availability, vegetation recovery, landscape fire regime, weather and local climate (Kelly *et al.* 2012; Nimmo *et al.* 2014; van Mantgem *et al.* 2015; Banks *et al.* 2017; Smith 2018). Generalist species might recolonise burnt areas more quickly than specialists do, especially in habitats with a long recovery time (Zwolak and Foresman 2007; Smith *et al.* 2013; Ondei *et al.* 2021). By contrast, specialist animal species associated with one or a few habitat plant species or functional types are likely to be more sensitive to changes in fire regimes (Charles *et al.* 2024). Increased dominance of generalist species can reduce species diversity in recently burnt areas (Ondei *et al.* 2021). Understanding the mechanisms behind fire-related changes in animal communities is critical to design appropriate management strategies. For example, post-fire recolonisation might be impossible if dispersal is limited, which has led to translocation of species that have become locally extinct following fire (Mitchell *et al.* 2022). However, translocation will fail if animals are moved to areas without habitat or food resources. Research that quantifies dispersal, behaviour and movement post-fire could therefore contribute to understanding whether active management is warranted (Smith *et al.* 2016; Nimmo *et al.* 2019).

Fire can affect animal movement and behaviour in the short term (during and immediately after fires) and in the long term through indirect influences on movement during post-fire habitat succession (Hulton VanTassel and Anderson 2018; Nimmo *et al.* 2019). Immediately after fire, resources are depleted, which can increase competition and predation risk and thus alter behaviour (Sutherland and Dickman 1999; Nimmo *et al.* 2019; Doherty *et al.* 2022). Animals in safe environments tend to display behaviours such as foraging, eating, grooming and reproductive behaviours (Middleton *et al.* 2013; Hegab *et al.* 2015). In unsafe environments, animals are more likely to have faster and more directional movement to avoid and escape predation (Middleton *et al.* 2013; Hutchen and Hodges 2019). Thus, if the post-fire environment represents an unsafe environment, this should be reflected in high-intensity directional movement. Studies of animal movement could therefore indicate the extent of post-fire recovery in animal populations and assist post-fire conservation management.

In this study, we quantified the recovery of a mammal community in rainforest margins ~15 months after an Australian wildfire. Specifically, we aimed to investigate the effect of fire and habitat type on mammal community composition and diversity. We also investigated the probability of habitat use and movement for individual species. On the basis of theoretical and empirical research on fire and habitat specialisation (Smith *et al.* 2013; Charles *et al.* 2024), we hypothesised that wildfire would more negatively affect rainforest-associated species than habitat generalists. This knowledge will enhance our understanding of how animals recover from wildfires in rainforests, improving the capacity for conservation managers to appropriately manage ecosystems post-fire in rainforest margins.

Materials and methods

Study location and fire characteristics

This study was conducted in Main Range National Park (27°48′57″S, 152°15′56″E) within the Gondwana World Heritage Area (WHA), South East Queensland, Australia. The Gondwana WHA covers 366,507 ha across New South Wales (308,942 ha) and Queensland (59,121 ha) and contains vast tracts of subtropical rainforest across 40 protected areas (Department of Climate Change, Energy, the Environment and Water 2020). The climate is subtropical, and the annual average rainfall of the area is 1043 mm (Fick and Hijmans 2017). The annual mean temperature is 15.9°C, with mean maximum and minimum temperatures of 27.2 and 3.2°C (Fick and Hijmans 2017). In Queensland, ~51% of the Gondwana WHA is rainforest vegetation (Broad Vegetation Groups, BVG, 1–7) whereas 47% is sclerophyllous eucalypt vegetation (BVG 8–17) (Neldner *et al.* 2019).

Our study sites were at Cunningham's Gap (Fig. 1), ~120 km south-west of Queensland's capital city Brisbane, ranging in elevation from 543 to 917 m above sea level. This area experienced unprecedented wildfires between September 2019 and January 2020 (Nolan *et al.* 2020),

following severe drought and record-high fire weather (Hines *et al.* 2020). Approximately 46% of the Queensland section of the Gondwana WHA was affected by fire during this event. In Main Range National Park, these wildfires affected 60% of sclerophyll and 17% of rainforest vegetation (Hines *et al.* 2021), with much of the fire-affected area at rainforest margins (Fig. 1).

Study design and data collection

Fire-severity data were obtained for our study sites from the Queensland Government Open Data Portal accessed in February of 2021 (Queensland Government 2021). Sites were chosen on the basis of satellite-mapped fire severity (Hines *et al.* 2021), which was verified visually during placing of camera traps by using evidence of burned trees in burned areas. Most burnt rainforest sites were burned at low to moderate severity, whereas most of the burned sclerophyll sites were burned at high to extreme severity (Fig. 1). The sclerophyll eucalypt forests in the region are managed by government agencies, often with low to moderate planned burns, which attempt to mitigate impact of severe unplanned fires (Queensland Herbarium 2024).

Given our interest in rainforest margins, we selected study sites spanning the rainforest margins and compared them with sites in the rainforest interior and in the surrounding eucalypt (open sclerophyll) vegetation. Margins, by their nature, only span a few hundred metres, a spatial scale

exceeding the daily movement distances of many small to medium-sized mammals (Miles *et al.* 1981). Mammals using these margins are therefore also likely to use the surrounding habitat in addition to margins. Our study thus quantifies mammal activity and habitat use in burnt rainforest margins, rather than residency. This helped us understand the extent to which burnt margins represent either 'intact' rainforest for mammals to use or disturbed surrounding vegetation. Fire penetration varied from 0 to 300 m into the rainforest and burn severity was not uniform across this area. We did not sample unburnt eucalypt vegetation because almost all the eucalypt vegetation in the study area was burnt at moderate to high severity (Fig. 1).

We classified sites into the following three 'fire-habitat' categories, a factorial variable incorporating both habitat and burn status: unburnt rainforest (Fig. 1*b*), burnt rainforest (Fig. 1*c*) and burnt sclerophyll (Fig. 1*d*). Although burn status and habitat type were confounded by the nature of fire in this system (typically burning large areas of sclerophyll forest and only rainforest margins), our analysis accounted for variation in distance to the rainforest boundary at each site (described below). We thus focused on the combined influence of burn status and habitat in our investigation. After selecting sites broadly on the basis of fire-habitat category, most sites were selected in the proximity to walking tracks because regenerating rainforest vegetation is functionally impenetrable owing to regrowth of native and non-native early successional plant
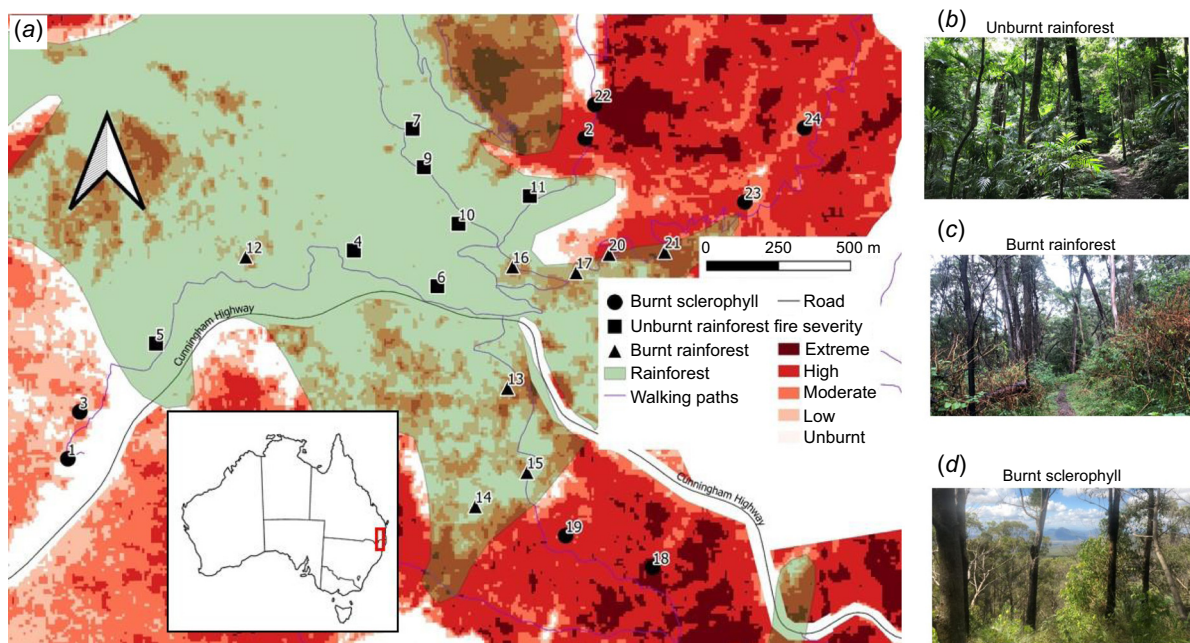

Fig. 1. (*a*) Location of 23 study sites within the Gondwana World Heritage Area, South East Queensland, Australia. The area, encompassing rainforest within surrounding eucalypt (sclerophyll) vegetation, was heavily affected by fire in 2019, with fire burning into the rainforest margins. Our study sites represented the following three fire-habitat categories: (*b*) unburnt rainforest, (*c*) burnt rainforest and (*d*) burnt sclerophyll. Rainforest vegetation was classified as Broad Vegetation Groups 1–7 (Neldner *et al.* 2019).

species. Sites were at least 100 m from each other, with an average distance between sites being 265 m (range = 124–439 m). A total of 23 sites was included in the final study design, including 8 in burnt sclerophyll, 8 in burnt rainforest and 7 in unburnt rainforest (Fig. 1). Although this study was limited in the number of sites, we interpreted our results in the context of this design and also conducted rarefaction and extrapolation to assess the effects of incomplete sampling.

At each site, we installed two camera traps between 0.5 and 3 m of one another, one vertically facing down, ~55 cm from the ground, and one horizontally, pointing parallel to the ground, ~100 cm from the ground. The only exception to this was Site 15, which had only a horizontal camera because of a field logistical error (which we accounted for in our analysis, described below). Camera-trap brands differ in their performance in detecting animals (Driessen *et al.* 2017). However, because of equipment constraints, we used a combination of Swift Enduro ($n = 29$) and Reconyx HC600 HyperFire ($n = 16$) (Churchill *et al.* 2023; Frost *et al.* 2023; Watchorn *et al.* 2024). To reduce the risk of influencing results from different camera brands, we assigned all horizontal cameras as Swift Enduros, whereas vertical cameras (which we predicted to have a lower capture rate) were a mix of Swift and Reconyx cameras (randomly assigned). The settings were identical on both camera brands. The balanced setting was used for night mode to minimise blur and maximise range. Camera sensitivity was set at moderate, and five photos were taken per trigger to maximise the chance of species identification and allow behaviour to be recorded. After the fifth photo was taken, there was a 30-s delay before cameras could be triggered again. All cameras were activated simultaneously for a total of 30 days (26 April–25 May 2021), ~15 months post-fire. Vegetation directly in front of the field of view that was likely to create false triggers was carefully moved aside, but we did not clear vegetation to the extent that it was likely to affect animal behaviour.

Data on vegetation structure were recorded at each site for the understorey (0–1 m), mid-storey (1–5 m) and canopy (>5 m). Each stratum was assessed on a four-point scale, as open (1), sparse (2), moderate (3) or dense (4). This protocol was based on appendix B in a standardised Vegetation Assessment Guide (open = 0–25%, sparse = 25–50%, moderate = 50–75%, dense = 75–100%) (Department of Environment 2013). Estimates were made visually by the same person (RRB) in the area above and surrounding the cameras. This coarse method of habitat assessment was designed to supplement the remotely sensed fire-severity data. Data on environmental co-variates were included in our analysis to assess the influence of other key environmental variables and survey bias, in addition to fire and habitat type. These data were obtained using standard functions in QGIS, namely, distance to highway (range = 72.58–1183.36 m; average = 382 m), distance to nearest walking path (range = 7.8–186.51 m; average = 39.67 m) and distance to rainforest boundary (range = 4.09–459.72 m; average = 178.24 m). Elevation (range = 543–906.89 m; average = 751.01 m) data were obtained from an online

tool using study site positions and sea level as an altimetric reference, with a margin of error of ~10 m (dCode, see https://www.dcode.fr/earth-elevation, accessed 23 June 2021).

Prior to modelling, correlation analysis was conducted on all environmental co-variates and fire-habitat category (Supplementary Fig. S1), with Pearson correlation coefficient of $\geq|0.7|$ being considered highly correlated (Dormann *et al.* 2007). Canopy cover was highly correlated with fire-habitat category (Pearson correlation coefficient = -0.75, Fig. S1) and was removed from the final set of environmental co-variates.

Image processing

Images were sorted manually to remove 'false triggers' (i.e. images with no animals present) and non-mammal species. Mammals (native and introduced) were identified to the lowest taxonomic level possible following Van Dyck *et al.* (2013). Animals were considered independent using a combination of time elapsed since last trigger (10 min) and the spatial position of individuals within each image.

Each image containing an animal was initially assigned to one of seven behavioural categories (using the sequence of images to assist categorising behaviour). There were too few data within these categories for analysis, so they were further classified into movement behaviour (walking or running, hopping or jumping, and climbing) and stationary behaviour (grooming, foraging or eating, alert and sitting still). Following initial image processing, data were sent to two ecologists with local mammal experience to check identifications and data were amended following their advice.

Response variable definition

We analysed mammal community composition (dissimilarity), diversity and, for individual species, the probability of habitat use and probability of movement. All variables were analysed at the site level (23 observations), except for movement, which was analysed at the level of independent capture events.

Community composition was quantified using a principal component analysis (PCA), which reduces correlated variables (represented by a site × species matrix of abundances) into a series of uncorrelated components (Abdi and Williams 2010). PCA was performed using the 'prcomp' function, in base *R* (ver. 4.2.0, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/).

Probability of habitat use was analysed using presence or absence data from independent capture events from camera traps. To ensure adequate data for probability of habitat-use analysis, any species that had absences at more than 85% of sites was excluded from analysis (*Phascolarctos cinereus* and *Sus scrofa* excluded).

We analysed probability of movement for species with more behavioural observations than double the number of

study sites (>46 observations), because species with less data were found to lead to model-fitting problems. This excluded the following five of the nine recorded species with sparse data: *Phascolarctos cinereus*, *Sus scrofa*, *Antechinus stuartii*, *Perameles nasuta* and *Trichosurus caninus*. For each independent capture event, we classified behaviour (defined in the Image Processing section) as movement (1) or stationary (0), such that we could model the probability of movement for each species separately. For each independent event, we used the most common behaviour from all images in sequence, as being representative of their behaviour state. Of the 925 animal observations, 15 (1.6%) displayed an equal amount of both behaviours and were excluded from the analysis.

Analysis

We conducted preliminary analysis to determine whether including Site 15, which had only a horizontal and no vertical camera, would bias our results. Across all sites, horizontal cameras captured a greater number of individuals (mean = 32.7, range = 0–200) than did vertical cameras (mean = 7.4, range = 0–74). Fitting models with and without Site 15 showed that model rankings were not affected by including this site (data not shown); thus, we retained Site 15 in our final data set.

We modelled community composition by using the first two components of the PCA, which explained the majority of the variation in the mammal community composition (95.78%). We plotted these two principal components to visualise community composition and the species contributing most to community-level variation. The first two principal components were then modelled using linear regression in base *R* (R Foundation for Statistical Computing).

To determine whether estimates of species diversity would be affected by incomplete sampling and variability across fire-habitat categories, we used rarefaction and extrapolation of Hill numbers (effective number of species) (Chao *et al.* 2014). Hill numbers are directly comparable to each other because they are mathematically unified, with the parameter q representing variability in the effect of evenness on species diversity (Chao *et al.* 2014). The orders of q are as follows: species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$) (Chao *et al.* 2014). Rarefaction and extrapolation of Hill numbers allowed us to compare species diversity assemblages in the three fire-habitat categories and make statistical inferences despite incomplete sampling (Chao *et al.* 2014). We used the *R* package *iNEXT* (ver. 3.0.0, T. C. Hsieh, K. H. Ma and A. Chao, see https://cran.r-project.org/package=iNEXT) to produce rarefaction and extrapolation curves for all fire-habitat categories by using both sample size-based and coverage-based estimates for the three orders of q following Chao *et al.* (2014). We inferred differences among fire-habitat categories when confidence intervals (from 200 bootstrapped replications) did not overlap.

Probability of habitat use of individual species was analysed at the site level by using binomial generalised linear models with a logit-link function in base *R* (R Foundation for Statistical Computing). Probability of movement was analysed at the level of an individual capture event by using generalised linear mixed models in the *R* package *lme4* (ver. 1.1-36, see https://github.com/lme4/lme4/; Bates *et al.* 2015). For the movement models, we included a random effect for site to account for spatial clustering of movement observations within sites.

For community composition and probability of movement, we used a two-stage model-selection procedure (Burnham and Anderson 2002). Because of data limitations (23 observations), we did not fit more than one co-variate with the fire-habitat category design variable in any analysis. First, we fitted fire-habitat category with one environmental co-variate in an additive and interactive formulation and selected the best-fitting formulation to use in the second stage. We then fitted each co-variate with fire-habitat category, using its best-fitting formulation (additive or interactive) to determine which set of variables best explained the data. Each set of models was fitted with a fire-habitat category only model (no co-variates) and a null model (no predictor variation), as a baseline against which to compare the more parameterised models. Models were ranked by second-order Akaike information criterion (AICc) using *AICcmodavg* (ver. 2.3-1, M. J. Mazerolle, see https://cran.r-project.org/package=AICcmodavg). The model with the lowest AICc was assumed to have the greatest fit and models within ΔAICc < 2 were assumed to be equivalent. For probability of habitat use, the above model structures were too complex to obtain meaningful results. We thus analysed the probability of habitat use for each species with only two univariate models, namely, the fire-habitat category model and the null model. The ΔAICc between these two models was used to determine the strength of the fire-category effect, by using the same process as for the other response variables.

To estimate the effect of each variable in the top model for community composition, we used the 'predict' function in *R* (R Foundation for Statistical Computing) and calculated confidence intervals as estimate ±1.96 × standard error. For probability of habitat use and probability of movement (i.e. models with a logit-link function), parameter estimates and confidence intervals were derived on the link scale then back-transformed using the 'invlogit' function in the *arm* package (ver. 1.13-1, A. Gelman and Y. Su, see https://CRAN.R-project.org/package=arm) to ensure they were bound between 0 and 1.

Results

A total of 38,390 images was collected during this study, 15,361 (40%) of which contained at least one animal (thus 23,029 images (60%) were false triggers). The following

nine mammal species were identified to species level (Supplementary Table S1): *Melomys cervinipes* (fawn-footed melomys), *Rattus fuscipes* (bush rat), *Thylogale stigmatica* (red-legged pademelon), *Thylogale thetis* (red-necked pademelon), *T. richosurus caninus* (short-eared brushtail possum), *Perameles nasuta* (long-nosed bandicoot), *Antechinus stuartii* (brown antechinus), *Phascolarctos cinereus* (koala) and *Sus scrofa* (pig).

The first two principal components explained the majority (95.78%) of variation in mammal species composition (PC1 = 58.17% and PC2 = 37.60% variance explained, Fig. S2*a*). Visually, principal component analysis showed some overlap between burnt rainforest and burnt sclerophyll sites, whereas unburnt rainforest sites tended to cluster separately (Fig. S2*b*). Clusters were driven mainly by *T. stigmatica* on PC1 and *R. fuscipes* and *M. cervinipes* on PC2 (Fig. S3). However, statistical models indicated no effect of fire-habitat category or any environmental co-variates on either of the first two principal components (the null model was ranked highest, Table S2). The second-ranked model for PC2 was within ΔAIC < 2 of the null model and included an interaction between fire-habitat category and mid-storey (Table S2, Fig. S4).

For sample size-based estimates of species diversity, rarefaction and extrapolation indicated that the effective number of species was highest in unburnt rainforest for species richness ($q = 0$) and Shannon's diversity ($q = 1$)

(Fig. 2*a, b*). However, for $q = 0$, this difference was evident only for small sample sizes (<200 individuals) and not large sample sizes (<200 individuals, Fig. 2*a*). For $q = 2$, the sample size-based estimates were lowest in the burnt sclerophyll forest and similarly high in unburnt and burnt rainforests (Fig. 2*c*). Coverage-based estimates of diversity showed a similar pattern, being highest in unburnt rainforest for $q = 0$ and $q = 1$, whereas burnt sclerophyll and burnt rainforest were more similar in species diversity (Fig. 2*d, e*). For $q = 2$, burnt sclerophyll had the lowest estimated species diversity (Fig. 2*f*), whereas the burnt and unburnt rainforest sites did not differ. Taken together, the results showed an increase in species diversity from burnt sclerophyll to burnt rainforest and unburnt rainforest. They also suggest that dominance and rarity (i.e. species evenness) influence the ability to detect fire and habitat effects on species diversity. Differences among fire-habitat categories were more evident for estimates incorporating evenness ($q > 0$), than for $q = 0$, which does not incorporate evenness.

Probability of habitat use was associated with fire-habitat category weakly in *M. cervinipes* (ΔAICc = −1.89) and more strongly in *P. nasuta* (ΔAICc = −6.62) (Fig. 3, Table 1). *Melomys cervinipes* was found at 100% of unburnt rainforest sites, 87.5% of burnt rainforest sites and 50% of burnt sclerophyll sites (Fig. 3*a*). *Perameles nasuta* was found at 57.1% of unburnt rainforest sites and was completely absent from other fire-habitat categories (Fig. 3*b*). There was no
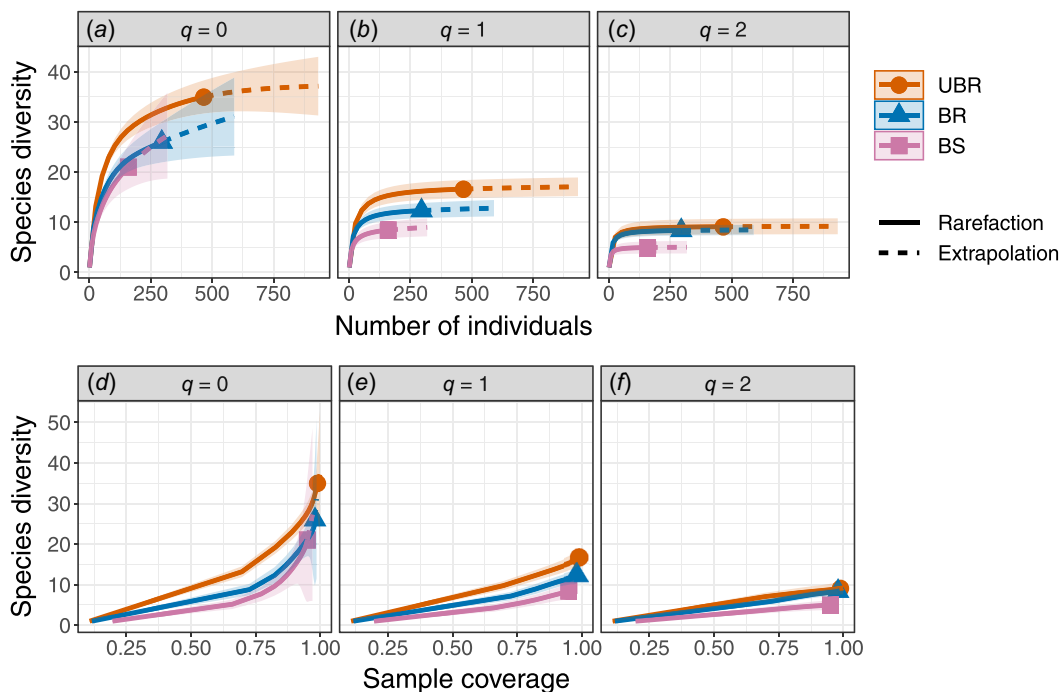

Fig. 2. (*a–c*) Sample size-based and (*d–f*) coverage-based estimates of species diversity (±95% confidence intervals) by using rarefaction (solid lines) and extrapolation (dashed lines) on the basis of Hill numbers ($q = 0$, 1, 2) for mammal communities in three fire-habitat categories. Solid symbols and line represent the reference sample (total number of observed individuals). UBR, unburnt rainforest; BR, burnt rainforest; BS, burnt sclerophyll.
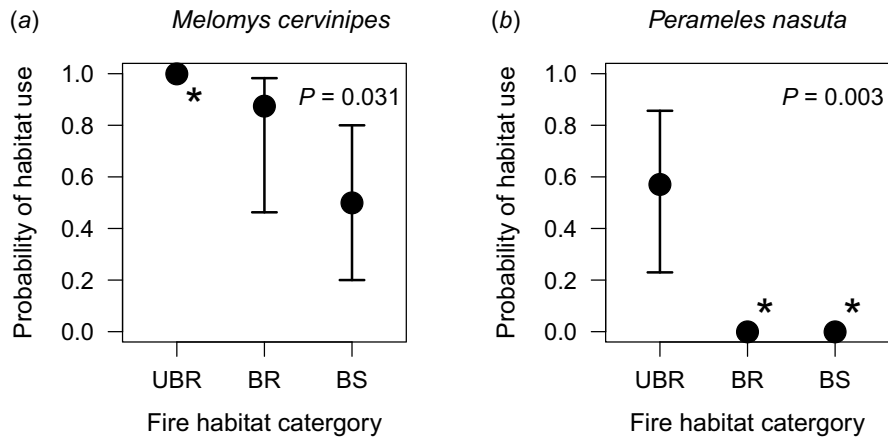
Fig. 3. Estimated probability of habitat use (±95% confidence interval) for (*a*) *Melmomys cervinipes* and (*b*) *Perameles nasuta* in fire-affected rainforest margins of South East Queensland, Australia. Asterisks (*) indicate the inability to calculate confidence intervals as presence or absence was absolute for that species in these fire-habitat categories. UBR, unburnt rainforest; BR, burnt rainforest; BS, burnt sclerophyll.

effect of fire-habitat category on the probability of habitat use for other mammal species (Table 1, Fig. S5).

Probability of movement was affected by fire-habitat category and environmental co-variates for *R. fuscipes* (Table 2). The top-ranked model for probability of movement in *R. fuscipes* included an interaction between fire-habitat category and elevation (Fig. 4). Elevation had little effect on probability of movement for *R. fuscipes* in burnt and unburnt rainforest (Fig. 4*a, b*) and a positive effect on probability of movement in burnt sclerophyll forest (Fig. 4*c*). For *M. cervinipes*, the second-ranked model (fire-habitat category × elevation) was within ΔAICc < 2 relative to the first-ranked null model (Table S3, Fig. S6). There were no notable effects on probability of movement for any other species (Table S3).

Discussion

We examined the impact of an Australian wildfire on a mammal community in rainforest margins and found that community composition was not strongly affected by a variable describing the fire status and habitat type ('fire-habitat category'). Rarefaction and extrapolation showed a trend for unburnt rainforests to have higher species diversity than in burnt rainforest and burnt sclerophyll forest. The ability to detect differences in mammal species diversity among fire-habitat categories was therefore influenced by community evenness (rarity and dominance), with differences becoming more evident when evenness was incorporated in the diversity estimates. Fire-habitat category affected the probability of habitat use of two rainforest-associated mammal species; *P. nasuta* used only unburnt rainforest habitat, and *M. cervinipes* used both burnt and unburnt rainforest habitats, with lower habitat use in surrounding burnt sclerophyll forest.

Movement of *R. fuscipes* increased with an increasing elevation in sclerophyll forest, but was unaffected by elevation in burnt and unburnt rainforest. This study has highlighted that fire in rainforest affects species diversity and the probability of habitat use in rainforest-associated species. Fire also created variation in movement for one generalist species, indicating that animals alter their behaviour when fire interacts with environmental features.

Community composition was not strongly affected by fire-habitat category in our study, but there was a visual trend for community dissimilarity between unburnt areas and burnt areas. By contrast, other studies have found strong effects of fire (including burnt area vs unburnt area, time since fire and fire mosaic) on community composition (Briani *et al.* 2004; Francl and Small 2013; Cazetta and Vieira 2021; Zylinski *et al.* 2022). One particular study, in a neotropical savanna, found that the lack of arboreal mammals in burnt areas led to significant difference in assemblages (Cazetta and Vieira 2021). Although not strong, the slight variation in community composition between the unburnt rainforest and burnt areas was likely to be driven by the low probability of habitat use of *P. nasuta* and *M. cervinipes* in burnt areas. Bandicoots, including *P. nasuta*, are ecosystem engineers (Valentine *et al.* 2017, 2018; Halstead *et al.* 2020) because they dig to obtain food (invertebrates, fungi and tubers), leading to higher soil moisture content, reduced fuel load, and changes in soil properties, including increased organic carbon, microbial activity and fungi (Valentine *et al.* 2017, 2018; Halstead *et al.* 2020; Ryan *et al.* 2020; Hopkins *et al.* 2021). Thus, changes in even one species following wildfires could potentially have a disproportionate influence on ecosystem function. Loss of these kinds of species could affect ecosystem recovery (Byers *et al.* 2006). More research on the time it takes for fire-sensitive ecosystem engineers to recover

Table 1. Model estimates (on the logit scale) of the probability of habitat use of individual species as a function of fire-habitat category across rainforest margins in South East Queensland, Australia.

Species	Term	Estimate	Standard error	P-value	ΔAICc
Antechinus stuartii	Intercept (unburnt rainforest)	0.288	0.764	0.159	1.39
	Burnt rainforest	−1.386	1.118		
	Burnt sclerophyll	−2.234	1.313		
Melomys cervinipes	Intercept (unburnt rainforest)	19.566	Intercept at boundary	0.031	−1.89
	Burnt rainforest	−17.62	–		
	Burnt sclerophyll	−19.566	–		
Perameles nasuta	Intercept (unburnt rainforest)	0.288	0.764	0.003	−6.62
	Burnt rainforest	−20.854	Boundary		
	Burnt sclerophyll	−20.854	Boundary		
Rattus fuscipes	Intercept (unburnt rainforest)	19.566	Intercept at boundary	0.465	3.54
	Burnt rainforest	−17.62	–		
	Burnt sclerophyll	−17.62	–		
Thylogale stigmatica	Intercept (unburnt rainforest)	0.916	0.837	0.378	3.13
	Burnt rainforest	−0.405	1.111		
	Burnt sclerophyll	−1.427	1.111		
Thylogale thetis	Intercept (unburnt rainforest)	−0.288	0.764	0.565	3.93
	Burnt rainforest	−0.811	1.118		
	Burnt sclerophyll	0.288	1.041		
Trichosurus caninus	Intercept (unburnt rainforest)	0.288	0.764	0.159	1.39
	Burnt rainforest	−1.386	1.118		
	Burnt sclerophyll	−2.234	1.314		

P-values were calculated for the fire-habitat category term rather than individual levels within that term. For each species, the change in AICc (ΔAICc) between the null model and the fire-habitat category model is shown.

Table 2. Probability of movement for *Rattus fuscipes* across rainforest margins in South East Queensland, Australia, ranked by AICc.

Models	K	AICc	ΔAICc	AICc Wt	Cum. Wt	log L
FHC × Elevation	7	470.19	0.00	0.93	0.93	−227.93
FHC + Distance to highway	5	476.48	6.29	0.04	0.97	−233.15
Null	2	479.19	9.00	0.01	0.98	−237.58
FHC + Distance to path	7	479.70	9.51	0.01	0.99	−232.68
FHC	4	480.50	10.30	0.01	0.99	−236.19
FHC + Mid-storey	7	481.26	12.07	0.00	1.00	−233.96
FHC + Distance to rainforest boundary	5	482.31	12.11	0.00	1.00	−236.06
FHC + Understorey	6	484.44	14.25	0.00	1.00	−236.10

Movement was modelled as a function of fire-habitat category (FHC) and environmental co-variates. For all other species, the null model was ranked highest (Table S3). K, number of parameters; AICc, second order Akaike Information Criterion; ΔAICc, change in AICc; AICc Wt, AICc weight; Cum. Wt, cumulative AICc weight; log L, logarithmic likelihood of model given the data.

in burnt areas is necessary to understand their contribution to ecosystem recovery.

Rarefaction and extrapolation allowed us to examine species diversity while accounting for incomplete sampling of the mammal community and potentially low detectability. Species diversity tended to be highest in unburnt rainforest, lower in burnt rainforest and lowest overall in burnt sclerophyll forest, depending on the extent to which community evenness was incorporated (i.e. variation in *q*). Coupled with our results of habitat use, this is likely because there are more rainforest-associated mammals using unburnt rainforest. Mammal diversity in other studies has shown variable responses to fire events, including increases, decreases and no change (Kelly *et al.* 2012; Sharp Bowman *et al.* 2017; He *et al.* 2019; Santosa and Kwatrina 2020; Ondei *et al.* 2021). Our results are important because there is limited research on mammal diversity in burnt rainforest, given that rainforests have not typically experienced frequent or intense wildfire. The results suggest that unburnt rainforests are important for mammal biodiversity. However, larger sample sizes than we were able to use here are needed to more confidently generalise patterns in rainforest species diversity.

In our study, habitat use was affected by fire-habitat category for two rainforest-associated species (*M. cervinipes* and *P. nasuta* had the greatest habitat use in unburnt
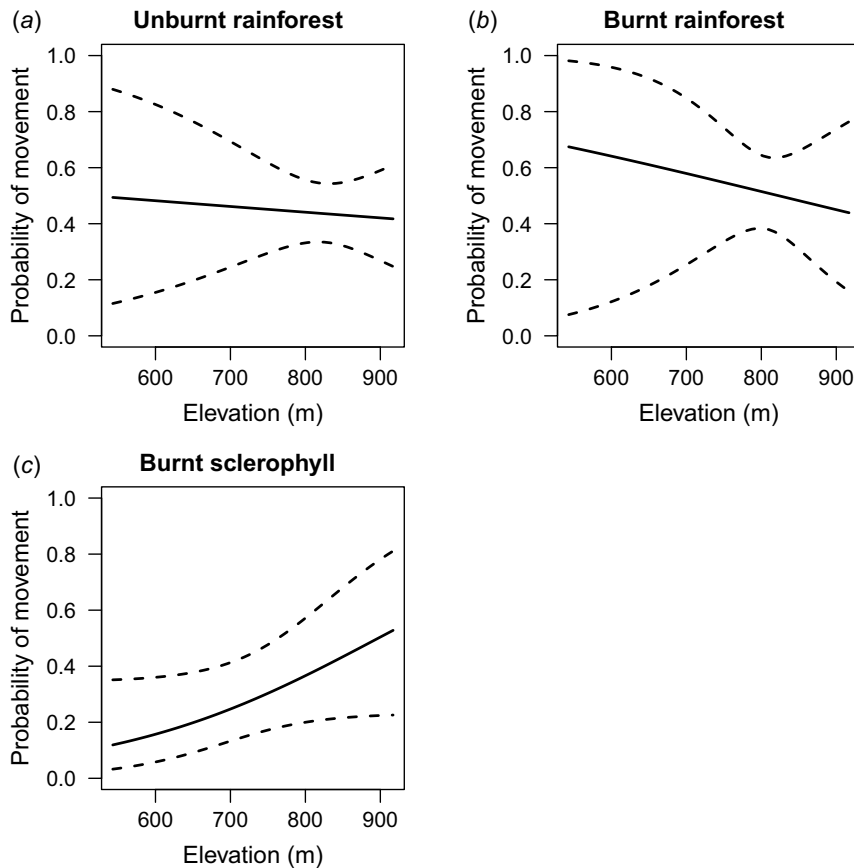
Fig. 4. Estimated probability of movement (±95% confidence interval) of *Rattus fuscipes* in fire-affected rainforest margins of South East Queensland, Australia. The top-ranked model included an interactive effect of elevation and fire-habitat category: (*a*) unburnt rainforest (*b*) burnt rainforest (*c*) burnt sclerophyll.

rainforest) but not for habitat generalists. Despite being a rainforest-associated species, *M. cervinipes* was able to persist in burnt rainforest, a response found in other melomys species (Liedloff *et al.* 2018). By contrast, *P. nasuta* was found only in unburnt rainforest, suggesting that this species is fire sensitive and requires unburnt habitat for nesting and foraging (Pardon *et al.* 2003; MacGregor *et al.* 2015; Fisher *et al.* 2021). Conversely, *P. nasuta* in other areas shows increased habitat use following fire, suggesting its response to fire is species- and context-specific (Hope 2012). The propensity for philopatry in this species (with movements generally of <500 m; Dexter *et al.* 2011) might slow its rate of recovery. Monitoring rainforest margins will help determine whether fire causes ongoing impacts on bandicoot habitat use.

Traditionally, fire ecology research focused on species distributions and abundance but changes in movement and behaviour in the context of fire regimes are increasingly being documented (Hutchen and Hodges 2019; Nimmo *et al.* 2019; Sitters and Di Stefano 2020; Blakey *et al.* 2022; Doherty *et al.* 2022; Santos *et al.* 2022). A study of arboreal mammals, for example, found that rates of the movement from an unburnt rainforest gully into surrounding areas decreased sharply following fire (Banks *et al.* 2015). Fire changes habitat structure and animals appear to modify their behaviour to avoid predators and optimise foraging opportunities (Hutchen and Hodges 2019; Doherty *et al.* 2022). Animals

often perform more directional and rapid movements in unsafe environments, and less directional behaviour in safe environments where fear levels are reduced (Middleton *et al.* 2013; Hegab *et al.* 2015; Hutchen and Hodges 2019); however, we found little evidence for that here.

In our study, movement of the generalist *R. fuscipes* was influenced by an interaction between fire and elevation. In burnt sclerophyll forest, movement probability in *R. fuscipes* was greatest at higher elevations, but was unaffected by elevation in burnt and unburnt rainforest. This may indicate a shift in normal behaviour patterns owing to fire-related vegetation change, or a differing relationship with elevation depending on latitude (Claridge *et al.* 2008). In contrast to our study, post-fire movement in *R. fuscipes* was found to be more tortuous owing to turning at edges of unburnt patches so as to remain in their preferred microhabitat (Fordyce *et al.* 2016). Fire therefore affects mammal movement behaviour in complex ways depending on the environmental context. Future research is needed to draw generalisations about complex post-fire movement patterns.

Recent increases in wildfires globally have intensified public and scientific interest in fire management for protecting human life and property and sustaining biodiversity (Steffensen 2020; Ward *et al.* 2020; Wintle *et al.* 2020; Eliott *et al.* 2021). These events have sparked a new appreciation that fire management must become more active, with

interventions such as post-fire weed and pest management, revegetation or assisted recolonisation now recognised as being critical for biodiversity conservation (Legge *et al.* 2022; Ward *et al.* 2022). Our study was small in spatial scale; however, because of limited research on mammal communities in burnt rainforest, we consider these findings a valuable baseline for future research in this area.

Supplementary material

Supplementary material is available online.

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