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Research Article

Wombat burrows are hotspots for small vertebrates in a landscape subject to gigafire

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Abstract

Ecosystem engineers modify their environment and influence the availability of resources for other organisms. Burrowing species, a subset of allogenic engineers, are gaining recognition as ecological facilitators. Burrows created by these species provide habitat for a diverse array of other organisms. Following disturbances, burrows could also serve as ecological refuges, thereby enhancing ecological resistance to disturbance events. We explored the ecological role of Common Wombat (*Vombatus ursinus*) burrows using camera traps in forests of southeastern Australia. We compared animal activity at paired sites with and without burrows, from the same fire severity class and habitat. We examined how animal activity at Common Wombat burrows was affected by the 2019–20 Black Summer bushfires in Australia. We predicted that burrows would serve as hotspots for animal activity and as refuges in burned areas. The activity of several species including Bush Rat (*Rattus fuscipes*), Agile Antechinus (*Antechinus agilis*), Lace Monitor (*Varanus varius*), Painted Button-quail (*Turnix varius*), and Grey Shrike-thrush (*Colluricincla harmonica*) increased at sites where Common Wombat burrows were present, while other species avoided burrows. Species that were more active at burrows tended to be smaller mammal and bird species that are vulnerable to predation, whereas species that avoided burrows tended to be larger mammals that might compete with Common Wombat for resources. Species composition differed between sites with and without burrows, and burrow sites had higher native mammal species richness. The association of several species with burrows persisted or strengthened in areas that burned during the 2019–20 Black Summer bushfires, suggesting that Common Wombat burrows may act as ecological refuges for animals following severe wildfire. Our findings have relevance for understanding how animals survive, persist, and recover following extreme wildfire events.

Key words: allogenic engineer, Black Summer bushfires, ecological facilitation, eucalypt forests, fire refuge, fire severity.

Ecosystem engineers modify their environment by influencing resources available to other organisms (Jones et al. 1997; Coggan et al. 2018). Modification by ecosystem engineers occurs via 2 pathways: autogenic engineers, which alter the environment by modifying themselves (e.g., trees and coral; Jones et al. 1994); and allogenic engineers, which alter the environment by mechanically changing the form of biotic and abiotic materials (e.g., dam-building beavers; Jones et al. 1994). Ecosystem engineers are distributed across terrestrial, freshwater, and marine environments (Jones et al. 1994), and include species from an array of taxonomic groups, including invertebrates, reptiles, birds, and mammals.

Species that displace soil through burrowing, digging, and foraging—known as bioturbators—play an important role as ecosystem engineers and often provide resources for co-occurring species (Whitford and Kay 1999; Coggan et al. 2018). Bioturbation modifies soil by changing water run-off and erosion (Halstead et al. 2020) and increasing water infiltration (Fleming et al. 2014; Davies et al. 2019), which alters the chemical properties of soils (Guy and Kirkpatrick 2021) and can enhance seed germination (Eldridge and James 2009; Fleming et al. 2014). For example, in Australia, the bioturbation activity of Quenda (*Isoodon fusciventer*) increases soil nutrients and microbial activity, promoting seedling growth (Valentine et al. 2018). In addition, well-digging by feral equids in North American deserts increases water availability and vertebrate richness (Lundgren et al. 2021). Such engineering activities can provide important resources and enhance local biodiversity.

Burrow engineers are a subset of bioturbators that combine bioturbation with the creation of often large and complex burrow

systems. Burrow creation is a facilitative interaction whereby commensal species exploit resources offered from burrows, including the provision of shelter from predators and extreme conditions, as well as foraging and breeding opportunities. For instance, American Badger (*Taxidea taxus*) burrows are exploited by 31 species, including numerous mammal species that use the burrows for shelter (Andersen et al. 2021). Similarly, Gopher Tortoise (*Gopherus polyphemus*) burrows are used by over 60 vertebrate species (Dziadzio and Smith 2016), and Giant Armadillo (*Priodontes maximus*) burrows are visited by over 50 vertebrate species (Desbiez and Kluyber 2013). In northern Australia, deep nesting warrens created by Sand Goanna (*Varanus gouldii*) provide shelter for at least 28 vertebrate species (Doody et al. 2021). Hence, the habitat created by burrow engineers can result in hotspots of animal activity through ecological facilitation.

Refuges are features that facilitate survival or persistence of species during and following disturbance (Keppel et al. 2012; Reside et al. 2019). There is some evidence that burrow engineers can create refuges for other species: for instance, burrows of Southern Hairy-nosed Wombat (*Lasiorhinus latifrons*) and Desert Tortoise (*Gepherus agassizzi*) are used by birds to escape extreme heat (Attwood 1982; Walde et al. 2009). The increased use of burrows by commensal species during disturbance events is consistent with the stress-gradient hypothesis, which predicts that facilitative interactions between species are most important in harsh ecological conditions (Bertness and Callaway 1994; Lowney and Thomson 2021).

Fire is a global driver of environmental change (Pausas and Keeley 2021) and has shaped the evolution of species over millions of years (Pausas and Parr 2018; Nimmo et al. 2021). Retreating to "fire refuges"—features that allow for the survival, persistence, and reestablishment of populations during and following fire (Robinson et al. 2013)—is 1 strategy that animals deploy during and after fire (Nimmo et al. 2019; Jolly et al. 2022). The occurrence of refuges created by ecosystem engineers has rarely been considered within this context (Dawson et al. 2019; Reside et al. 2019), but could theoretically enhance the resistance of wildlife to a range of disturbances, while resources provided by these engineers could hasten recovery. Knapp et al. (2018) provides some support for the importance of burrow engineers in fire-prone landscapes, showing that vertebrate use of Gopher Tortoise (*G. polyphemus*) burrows increased >8-fold at sites that experienced prescribed burns compared to unburned sites. Given that the frequency of large, severe wildfires is predicted to increase as a result of climatic change (Wu et al. 2021), fire refuges created by ecosystem engineers could play a particularly critical role in the future.

The 2019–20 Australian Black Summer bushfires were a series of megafires and gigafires (fires >10,000 and 100,000 ha, respectively; Linley et al. 2022) that were unprecedented in their scale (Nolan et al. 2020) and severity (Collins et al. 2021). These fires burnt >10 million ha of southeastern Australian forests (Wintle et al. 2020), including a record amount (1.8 million ha) burnt at high severity (Collins et al. 2021), impacting nearly 3 billion native vertebrate animals (van Eeden et al. 2020). During these bushfires, viral stories emerged on social media of wombats herding native wildlife into their burrows to protect them from fire. While these stories were ultimately dismissed (Nimmo 2020), an element of truth could still be gleaned from them.

Wombats (family Vombatidae) are the largest burrowing marsupials on earth (Evans et al. 2006). There are 3 extant wombat species, all of which occur in Australia. The Common Wombat (*Vombatus ursinus*; Fig. 1), also known as a Bare-nosed Wombat, has the largest distribution of the 3 species (Taylor 1993; Evans 2008; Baker and Gynther 2023), which coincides with several of the 2019–20

bushfires (Fig. 2). Despite being listed as Least Concern by the IUCN (2008), the species has undergone substantial decline across its range since European colonization (Roger et al. 2007), with climate change predicted to cause further range contractions (Graham et al. 2019). Common Wombat are active in forests after fire (Lunney and O'Connell 1988), thus having an ability to maintain burrows in burnt habitat. Wombats excavate and use multiple burrows (Thornett et al. 2017), which consist of a large network of underground tunnels (Swinbourne et al. 2016b). Common Wombat burrows can be upwards of 15 m long, with multiple entrances—and can be deep, complex, and multichambered (Triggs 2009; Browne et al. 2021). Soil turnover from burrow construction can vary from 2.8 to 9.8 t/ha (Triggs 2009) and the soil in mounds contain increased nitrogen, which supports higher herb cover (Guy and Kirkpatrick 2021).

Wombat burrows are exploited by a range of species: a study showed that Common Wombat burrows were visited by 11 other species including possums, rodents, and birds (Old et al. 2018). Similarly, Thornett et al. (2017) recorded 11 vertebrate species that used burrows of Southern Hairy-nosed Wombat. The internal temperatures of wombat burrows are typically cooler and more stable than aboveground temperatures (Finlayson et al. 2003; Evans 2008; Swinbourne et al. 2016b), which can allow them to act as thermal refuges during heatwaves (Attwood 1982). Fossorial South-eastern Slider (*Lerista bougainvillii*) have also been observed exploiting the soil mounds around burrows, suggesting that burrows might offer increased thermoregulatory opportunities (Hodgson and Ritchie 2023). This prompts the question: could Common Wombat burrows also provide refuge to animals from the impacts of fire?

In this study, we monitored the activity (i.e., the number of detection events separated by >30 min) of a range of native vertebrates around Common Wombat burrows in habitats that burned at varying severity during the 2019–20 bushfires, and at nearby unburned sites. We hypothesized that: (i) if Common Wombat are ecological facilitators via their bioturbation, then animal activity will be higher around burrows compared to nearby sites without burrows—the affinity of species with burrows will differ depending on their shelter and resource requirements, and hence community composition will differ between burrows and ecologically similar areas lacking burrows; and (ii) if Common Wombat burrows are acting as fire refuges, then the negative impacts of fire on animal activity—which we expect to be widespread given the severity of the 2019–20 bushfires—will be reduced at burrows located in burned habitat, and

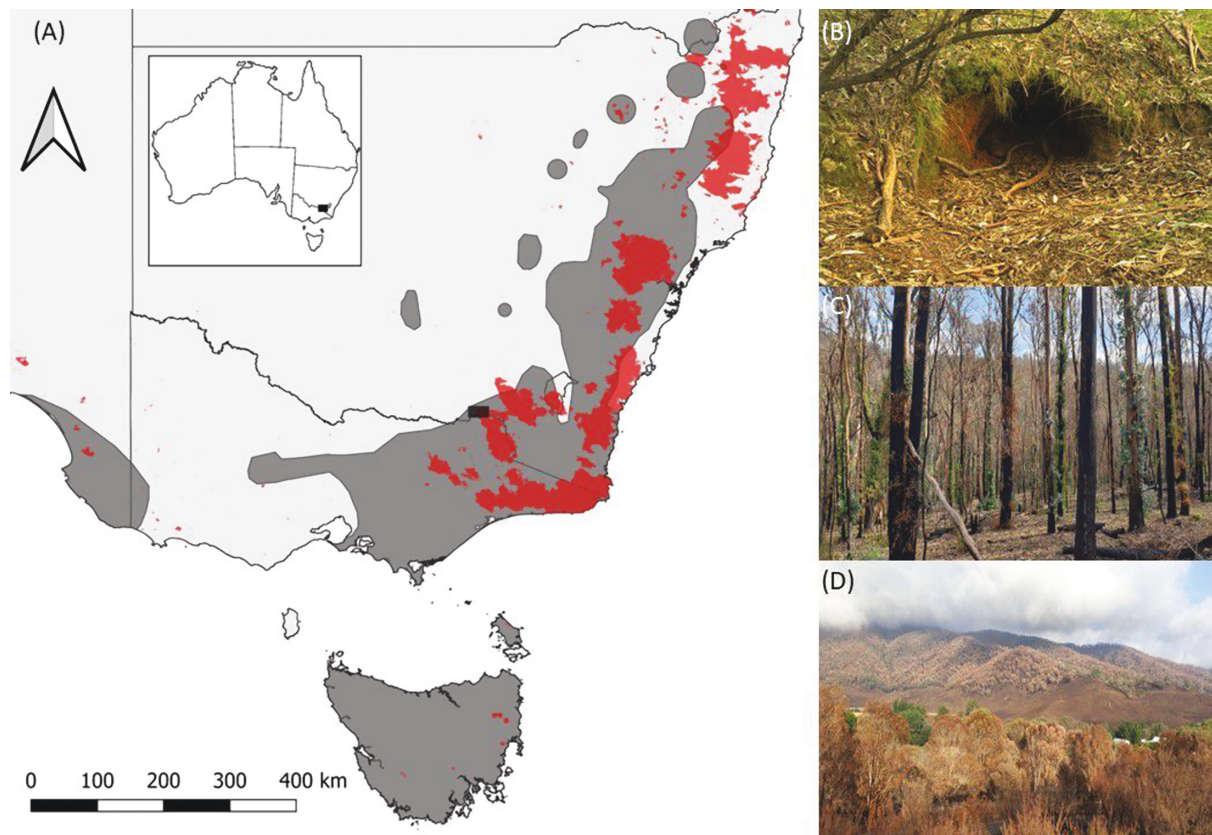**Fig. 1.** An adult and juvenile Common Wombat (*Vombatus ursinus*).

Fig. 2. (A) The Australian distribution of the Common Wombat (*Vombatus ursinus*; dark gray; IUCN 2008) in relation to the areas burned in the 2019–20 Black Summer bushfires (red; Department of Agriculture 2020), and the study location (black); (B) a Common Wombat burrow; (C) the early stages of postfire regrowth; and (D) landscape impacts of the 2019–20 Black Summer bushfires at Woomargama National Park, New South Wales, Australia (images in C and D courtesy of Kylie Durant).

these buffering effects should be most apparent at sites that burned at high severity, consistent with the stress-gradient hypothesis.

Materials and methods.

Study area.

We conducted this study at Woomargama National Park (24,185 ha) and Woomargama State Forest (7,120 ha), New South Wales, Australia. Geology consists predominantly of steeply sloping Silurian Koetong granite, with soils consisting of yellow to red podsolics (NSW National Parks and Wildlife Service 2009). The average annual rainfall is 886 mm, with the majority of rainfall occurring in winter and spring (Bureau of Meteorology 2023). The area consists of continuous eucalypt forest and woodland communities. Dominant canopy species consists of a mix of *Eucalyptus* spp., primarily Broad-leaved Peppermint (*E. dives*), Narrow-leaved Peppermint (*E. radiata*), and Brittle Gum (*E. mannifera*; NSW National Parks and Wildlife Service 2009). Both mid and ground stories consist of a mix of shrubs and grasses (NSW National Parks and Wildlife Service 2009). The area has undergone historical land use changes including mining, forestry, and agricultural activities (NSW National Parks and Wildlife Service 2009). During the 2019–20 bushfires, the Green Valley/Tunnel Road fire complex was part of a larger gigafire (Linley et al. 2022) in which 6 fires merged and burned 632,315 ha. The fire burned ~18,119 ha of Woomargama National Park and Woomargama State Forest at mixed severities, occurred predominantly on the eastern side of the park, started by lightning strike on 29 December 2019, and was extinguished by 18 February 2020. Fires in these environments can have long-lasting impacts on ecosystems (Bradstock 2008; Williams et al. 2008).

Site selection.

We used a paired design to assess the use of Common Wombat burrows in differing fire severity treatments, in comparison to nearby areas with the same fire severity but without a burrow. Common Wombat burrows were selected from ground searching the study area in conjunction with fire severity maps. Ground-truthing revealed the extreme impact of the fires on vegetation throughout the study area, with many large trees killed and under-story regrowth and canopy resprouting occurring postfire (Fig. 2). Using the Australian Google Earth Engine Burnt Area Map of the 2019–20 bushfires (Aus GEEBAM; Department of Agriculture 2020) fire severity maps were used to classify the change in vegetation. Aus GEEBAM fire classes were derived from changes in a vegetation index following fire, in comparison to nearby ecologically similar areas that escaped the fire (Department of Agriculture 2020). Aus GEEBAM fire classes are: unburnt, where little or no change in the vegetation index was observed; low and moderate severity, where moderate change to reference unburnt area was detected; high severity, where the vegetation was mostly scorched; and very high severity, where vegetation was consumed (Department of Agriculture 2020).

In total, 28 site pairs (i.e., 56 sites in total) were selected. Site pairs consisted of a Common Wombat burrow (Fig. 2) and a paired site approximately 50 m away in the same fire severity class and in similar habitat (i.e., vegetation type, topography), to act as an

experimental control (Coggan et al. 2018). Fire severity classes were ground-truthed to ensure the classification from maps matched the burn severities on the ground and canopy layers. We reclassified the Aus GEEBAM fire severity classes listed above to include: unburnt areas outside of the fire scar; unburnt areas within the fire scar; low and moderate severities; and high severities that encompasses both high and very high burned areas, as differences between these 2 classes were not obvious on the ground. Seven sites were established within each of the fire severity classes. Preliminary analysis suggested few differences in animal activity in unburned areas outside of and within the fire scar, and so all unburned sites were classified simply as unburned. All sites were located within Eucalypt woodlands with shrubby or grassy understory. Vegetation at sites within the fire scar exhibited significant regrowth, manifesting at various stages depending on the fire severity at each location.

Animal activity.

We surveyed the activity of terrestrial mammals at each site using wildlife cameras (Reconyx HC600 Hyperfire, Reconyx Inc., Holmen, Wisconsin). Each of the 28 site pairs consisted of 2 cameras (56 sites), 1 placed at a Common Wombat burrow and the other at the paired control site. To capture smaller mammals, cameras were fastened to a stake at a 20° downward angle. At burrows, cameras were placed approximately 2 m from the burrow entrance, facing the entrance. Camera orientation was consistent between burrows and control sites, with the only difference being that control sites were oriented toward bare ground. Cameras operated day and night, recording 5 images per burst, with no time delay between bursts, and sensitivity set to high. Cameras were deployed 16 months after the 2019–20 bushfires and operated continuously between June 2021 and April 2022, totaling 16,645 trap-days. Our study followed guidelines (Sikes et al. 2016) and all applicable international, national, and/or institutional guidelines for the use of animals. Research was conducted in accordance with the Charles Sturt University Animal Ethics Committee (permit number A21049) and permissions from relevant management authorities.

Image tagging and data extraction.

Images from 56 cameras were tagged and processed using Wildlife Insights (Ahumada et al. 2020). When present, animals were identified to species level, if species-level identification was not feasible, identification was made to the highest possible taxonomic resolution (typically genus level). This was achieved using Wildlife Insights' artificial intelligence, which automatically detects and identifies species in images (Ahumada et al. 2020), although every image and species identification was independently reviewed by wildlife experts. Behaviors evident in images were manually recorded where possible, including number of individuals and the occurrence of specific behaviors around burrows including: bathing, referring to an animal using water in the burrow to clean themselves; drinking, referring to an animal consuming water from the burrow; entering or emerging, referring to an animal entering or exiting the burrow entirely; inspecting, referring to an animal investigating the burrow entrance but not entering the burrow completely; foraging, referring to animals feeding in or directly around the lip of the burrow; and geophagy, referring to animals consuming soil from the burrow. Classifying behaviors was not always possible due to the small size of some species—e.g., House Mouse (*Mus musculus*) and Agile Antechinus (*Antechinus agilis*), making it difficult to assign a specific behavior to some images. We also recorded dates when burrows were filled with water to assess how often Common Wombat burrows provide a water source to other wildlife. We extracted the tagged image metadata, including site information, date, and time using *camtrapRdelux* package (https://github.com/carlopacioni/camtrapRdeluxe, an extension of *camtrapR* (Niedballa et al. 2016) and the *exiftool* add on (Harvey 2020). We treated all detections as independent events when more than 30 min separated detections of the same species (Cunningham et al. 2018).

Data analysis.

To test our hypothesis that animal activity will be higher around burrows, we fit Bayesian mixed-effects models using the package *brms* (Bürkner 2017), which fits Bayesian models in *stan* which compiles models to sample from posterior distributions (Stan Development Team 2022). We included site pairs as random effects and used 2,000 iterations and 4 chains, with a 2,000-iteration warm-up. We used default priors, which are weakly informative, to improve convergence and sampling efficiency, with minimal impact on estimations. Model parameters are regarded as showing evidence of an effect when the 89% credible interval did not overlap zero (McElreath 2020). We used 89% credible intervals as they are commonly used in Bayesian statistics (Samaš et al. 2021), and due to their relative stability compared to 95% credible intervals (Kruschke 2014). Our response variables were: the number of independent events for each species; species richness (i.e., count of all species detected at a site) of all species (total richness); native mammal species only; and native bird species only. Individual species were modeled if recorded by at least 10 camera traps.

We modeled our response variables as a function of whether the site was a burrow or a control ("site type"). Control sites were used as the reference category. If the 89% credible intervals of the mixed models did not overlap zero, it was considered evidence that the response variable at burrows was substantially different from the control sites (McElreath 2020). To test for compositional differences between species assemblages at burrows and control sites, we used a permutational multivariate analysis of variance (PerMANOVA). We used the Bray–Curtis index to calculate dissimilarities based on a square root transformation of our activity data. PerMANOVA was fit using the *adonis2* function from the *vegan* package (Oksanen et al. 2013). We permuted dissimilarities 999 times to assess significance. Community composition was visualized using nonmetric multidimensional scaling (nMDS: Legendre and Legendre 1998). To determine which species most influenced dissimilarities at burrows and control sites, we performed indicator species analysis using the *multipatt* function from the *indicspecies* package (De Cáceres et al. 2016).

Finally, to examine if associations were most pronounced in areas that experienced high-severity fires, we again used Bayesian models in *brms* (Bürkner 2017) to model response variables as a function of site type and fire severity class. We combined site type and fire severity to create a 6-level categorical variable (unburned burrow, unburned control, low–moderate burned burrow, low–moderate burned control, high severity burrow, high severity control) and used unburned controls as the reference category. Because some categories had few detections for some species, we used weakly informative priors with a Student's *t*-distribution to aid in model convergence. Specifying unburned controls as the reference allows both a comparison between burrows and control sites, which reveal whether burrows experience increased or decreased activity relative to controls—as well as a comparison between unburned and burned controls, which reveal the impacts of fire severity on each response variable. This allows the impact of burrows to be contextualized in terms of the background influence of fire.

Results

Camera traps recorded 746,674 images containing 370,845 wildlife images. Images were compressed into 14,580 events that represented 15,723 individual animals. Fifty-six species were identified (47 native species, 9 introduced), consisting of 19 mammal, 33 bird, and 4 reptile species. Common Wombat were present at all sampled burrows, which had an average burrow opening height of 19.18 cm (±2.77 SE) and width of 22.66 cm (±3.21 SE). Excluding Common Wombat, 48 species were identified at burrows and 43 at control sites (Supplementary Data SD1). Species found only at burrows included Common Ringtail Possum (*Pseudocheirus peregrinus*), Grey Fantail (*Rhipidura albiscapa*), Spotted Pardalote (*Pardalotus punctatus*), and White-throated Treecreeper (*Cormobates leucophaea*). Species only observed at control sites included Australian Raven (*Corvus coronoides*), Common Bronzewing (*Phaps chalcoptera*), and Eastern Rosella (*Platycercus eximius*). A total of 31 species were recorded interacting with burrows (Supplementary Data SD2), including several species inspecting (30 of 31 species), foraging (11/31), and entering and emerging (10/31) from burrows—while less common behaviors included drinking (4/31) and bathing (1/31) in flooded burrows, and geophagy (1/31; Supplementary Data SD2; Fig. 3). From 16,645 trap-days, images containing animals occurred over 8,384 trap-days, of which burrows contained pooled water for 207 days. From 28 burrows, 19 filled with water at least once for an average total time of 10.89 days (±3.74 SE). From 207 days where burrows were filled with water, 109 days occurred in spring, 54 in winter, and 44 in summer.

Several species showed increased activity around burrows when compared to control sites (i.e., 89% CIs did not overlap zero; Fig. 4; Supplementary Data SD3), including several native species such as Bush Rat (*Rattus fuscipes*), Agile Antechinus, Lace Monitor (*Varanus varius*), Painted Button-quail (*Turnix varius*), Grey Shrike-thrush (*Colluricincla harmonica*), and introduced Black Rat (*Rattus rattus*; Fig. 4; Supplementary Data SD3). Several native species including Swamp Wallaby, Red-necked Wallaby, Eastern Grey Kangaroo, Australian Magpie (*Gymnorhina tibicen*), Satin Bowerbird (*Ptilonorhynchus violaceus*), Crimson Rosella (*Platycercus elegans*), White-winged Chough (*Corcorax melanorhamphos*), and

introduced Feral Pig (*Sus scrofa*) were more active at control sites (Fig. 4; Supplementary Data SD3). The activity of all other species did not differ substantially between burrows and control sites. Native mammal richness was greater at burrows than control sites (Fig. 4; Supplementary Data SD3), whereas total richness and bird richness did not substantially differ (i.e., 89% CIs overlapped zero). For mammals, there was a tendency for smaller species to be positively associated with burrows and for larger species to be negatively associated with burrows (Fig. 5). A linear regression comparing the effect size from Bayesian mixed-effects models to the natural logarithm of body mass revealed a strong, negative relationship for mammals (Coefficient ± 89% CI = −0.494 [−0.638 to −0.350], $t = -6.026$, $R^2 = 0.784$). This relationship was far weaker when considering birds and reptiles in addition to mammals (Coefficient ± 89% CI = −0.295 [−0.502 to −0.089], $t = -0.621$, $R^2 = 0.052$), suggesting that this size-dependent relationship with burrows was specific to mammals.

Species composition varied between burrow and control sites (PerMANOVA, $F_{1,55} = 2.188$, $P = 0.003$; Fig. 6). Indicator species analysis identified several species associated with burrows: Bush Rat (*stat* = 0.849, $P = 0.001$); Agile Antechinus (*stat* = 0.773, $P = 0.001$); Lace Monitor (*stat* = 0.602, $P = 0.003$); White-throated Treecreeper (*stat* = 0.463, $P = 0.023$); and Yellow-footed Antechinus (*Antechinus flavipes*; *stat* = 0.463, $P = 0.026$). Indicator species for control sites were the Red-necked Wallaby (*stat* = 0.799, $P = 0.022$) and Feral Pig (*stat* = 0.639, $P = 0.037$; Fig. 6).

The association between Agile Antechinus and burrows was most apparent at burrows burned at high severity, remained evident at burrows burned at low–moderate severity, and was least evident (89% CIs overlapping zero) at unburned burrows (Fig. 7; Supplementary Data SD4). Bush Rat were more active at burrows burned at high severity, low–moderate severity, and unburned burrows. Painted Button-quail were more active around burrows that burned at high severity compared to unburned control sites (Fig. 7; Supplementary Data SD4). The association of Lace Monitor with burrows was only evident in unburned sites (Fig. 7; Supplementary Data SD4). Feral Pig, Spotted Quail-thrush, Common Brushtail Possum, and Australian Magpie were

Fig. 3. Examples of animals and behaviors observed at Common Wombat burrows: (A) a Lace Monitor foraging in the burrow entrance; (B) a Short-beaked Echidna inspecting the lip of the burrow; (C) a Swamp Wallaby drinking from a burrow full of water; (D) a Red-necked Wallaby inspecting the burrow entrance; (E) a Grey Shrike-thrush foraging at the burrow entrance; and (F) a Pied Currawong drinking from a partially filled burrow.
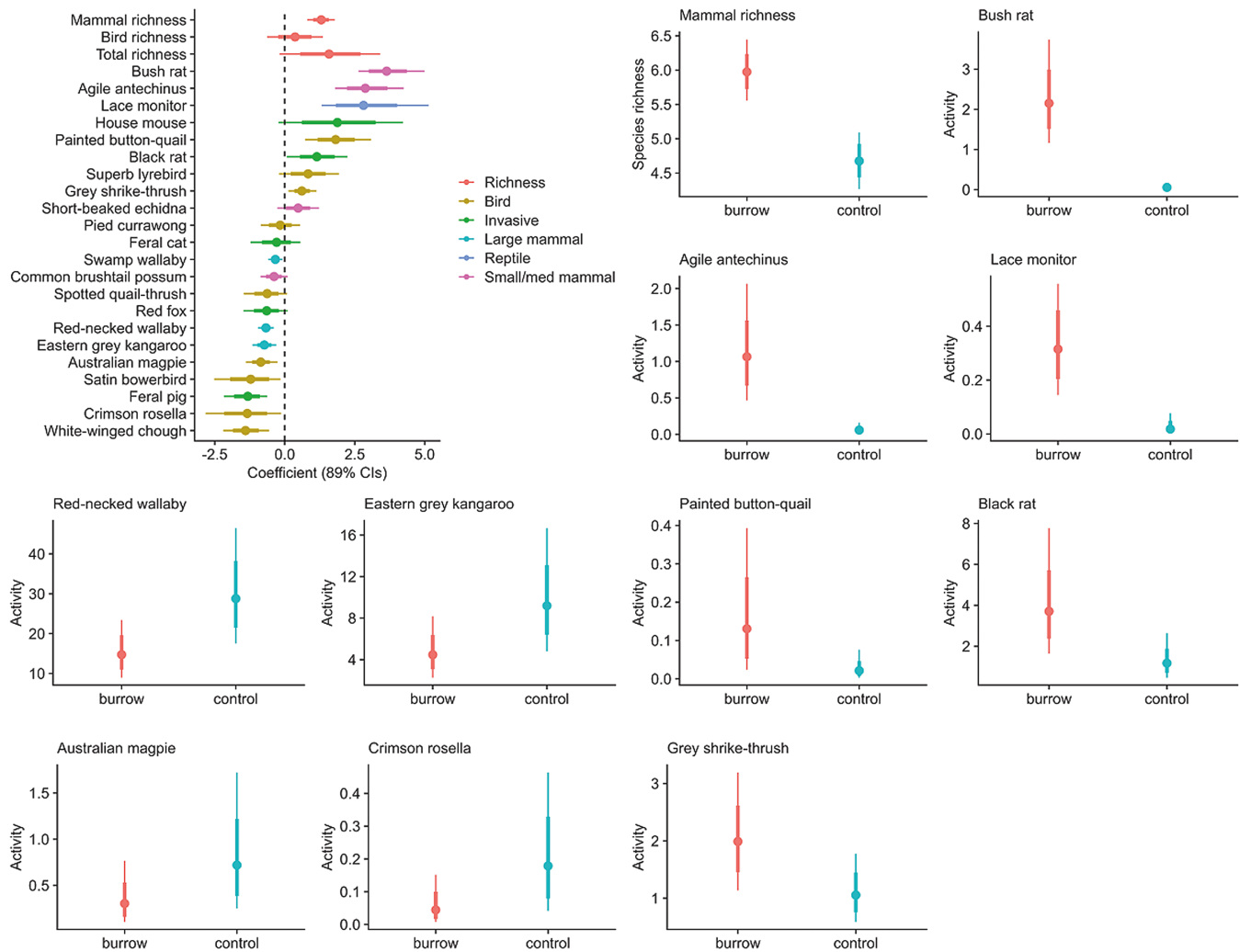
Fig. 4. Coefficients and credible intervals from Bayesian models comparing species activity in burrows versus control sites (controls specified as the reference category), and examples of species activity predicted from those models. In activity plots: colored dot = point estimate; thick bars = 66% CIs; and thin bars = 89% CIs.

all less active around unburnt burrows (Fig. 7; Supplementary Data SD4). Native mammal richness was higher at burrows that were either burned at high severity or remained unburnt (Fig. 7; Supplementary Data SD4). Swamp Wallaby, Feral Pig, and feral Domestic Cat (*Felis catus*) were the only species for which activity varied depending on fire severity, all being more active in areas that burned at high severity during the 2019–20 bushfires (Fig. 7; Supplementary Data SD4).

Discussion

Ecological facilitation by Common Wombat increases the activity of numerous native species, alters community composition, and boosts native mammal richness. Body size determined whether mammals were positively or negatively associated with burrows, with smaller species being more active and larger species being less active around burrows. The association of several species with burrows persisted—and in some instances was strengthened—after severe wildfire, consistent with the stress-gradient hypothesis. Our results add to a growing literature underscoring the significance of burrowing engineers as ecological facilitators.

Wombat burrows affect animal community composition.

The presence of Common Wombat burrows alters the local environment sufficiently to elicit clear changes in local animal communities. Of particular interest is an apparent size dependency in species interactions with burrows, with smaller mammals being more active and larger mammals less active at burrows. The capacity of a species to enter Common Wombat burrows appears to be linked to the size of the species, with larger animals being excluded from utilizing the available shelter and foraging potential due to the size of the burrow openings. We detected numerous examples of smaller species using Common Wombat burrows, including Bush Rat, Black Rat, Short-beaked Echidna, Grey Shrike-thrush, White-throated Treecreeper, and Lace Monitor. Our survey method may have even underestimated the activity of some of these species, as camera traps are often less effective at capturing smaller species of mammals, birds, and reptiles (Jumeau et al. 2017). Other researchers have documented small mammals entering and exiting burrows: Triggs (2009:33) mentions antechinus and bush rats seen "scurrying away from burrow entrances," that antechinus "emerge from small crevices in the walls of Bare-nosed
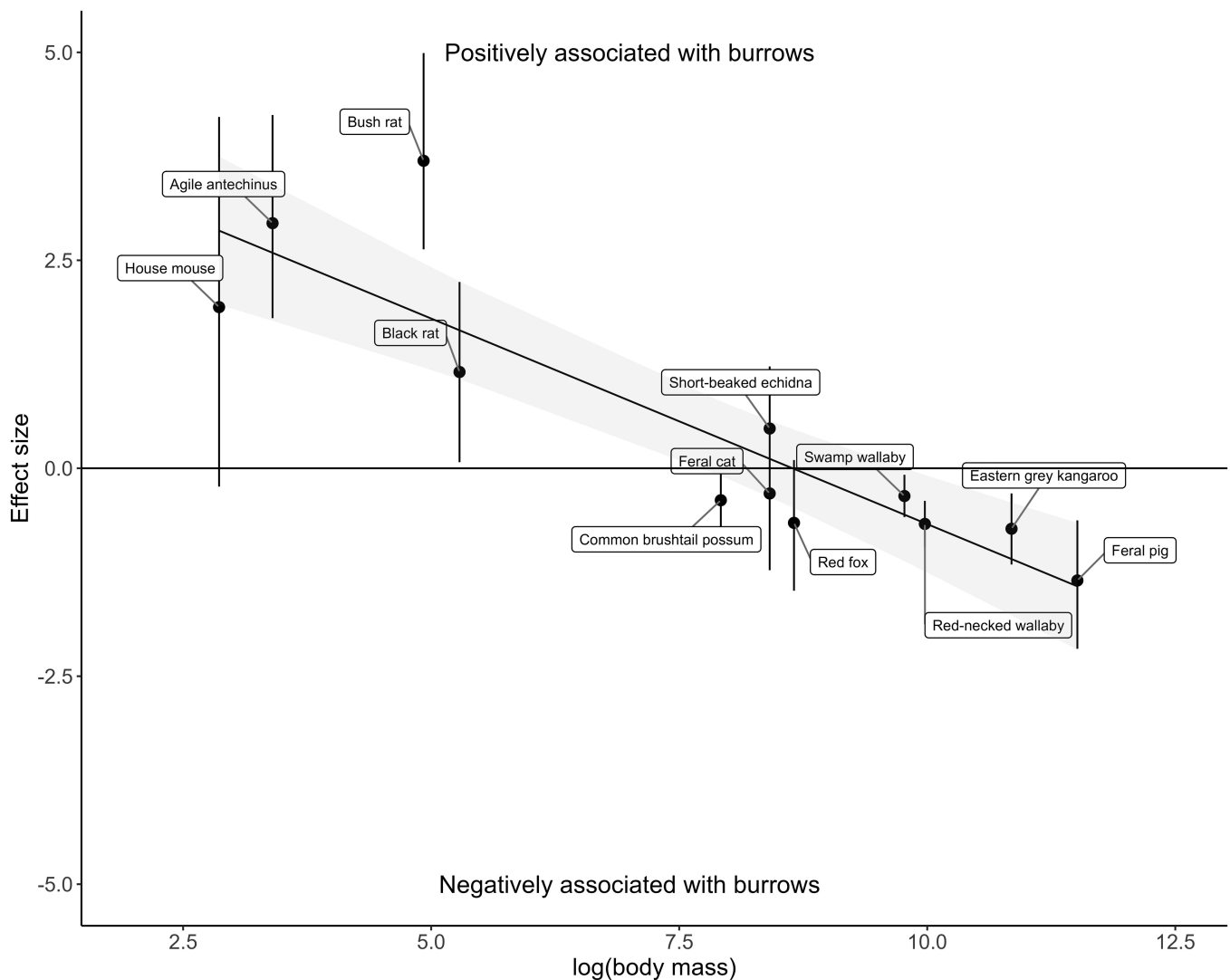
Fig. 5. Effect size from Bayesian mixed-effects models of treatment (burrow vs. control) against the natural logarithm of body mass for mammals at Woomargama National Park: black line = fitted relationship from linear regression model; black dots = coefficients ± 89% credible intervals; effect sizes > 0 indicate a positive association with burrows, and effect sizes < 0 indicate negative associations.

Wombat burrows," and that goannas "have also been found in wombat burrows," while McIlroy (1973) found Bush Rat in Common Wombat burrows. One of our authors (DRM) has observed antechinus and bush rats escaping to Common Wombat burrows not far from our study region. Even relatively larger species, like the Swamp Wallaby and Red-necked Wallaby, were observed entering burrows, although these were rare events (relative to other behaviors). Common Wombat are large-bodied and stocky mammals with occasional displays of aggression, and they are known to compete with macropods for resources (Tamura et al. 2021). Thus, it is plausible that Common Wombat actively deter larger competitors away from their burrows, or that macropods avoid burrows to reduce the risk of a negative encounter, as Common Wombat vigorously defend their territories against unwanted intruders (Triggs 2009).

Aside from providing shelter, Common Wombat burrows could affect animal communities via changes in soils, vegetation, and topography around the burrow. Soil around Common Wombat burrows has greater nitrogen than surrounding soil due to the deposition of wombat feces, while vegetation in the vicinity of burrows typically includes more bare ground and herbaceous plants, with less shrub cover (Guy and Kirkpatrick 2021). These variables could affect the foraging opportunities for small herbivores and carnivores alike. Common Wombat burrows may increase the activity of ground-dwelling insectivores and omnivores such as Bush Rat, Agile Antechinus, Grey Shrike-thrush, and Painted Button-quail, by providing increased foraging opportunities. While little is known of invertebrate communities present at Common Wombat burrows (and was not a specific subject of our research here), high diversities of invertebrates have been recorded at the burrows of other species. For instance, Gopher Tortoise burrows support hundreds of arthropod species (Jackson and Milstrey 1989), while burrows and mounds from Gunnison's Prairie Dog (*Cynomys gunnisoni*), Black-tailed Prairie Dog (*C. ludovicianus*), and Banner-tailed Kangaroo Rat (*Dipodomys spectabilis*) increase arthropod abundance and richness compared to surrounding areas without mounds and burrows (Davidson and Lightfoot 2007). Additionally, native Australian predators including Western Quoll (*Dasyurus geoffroii*), Sand Goanna
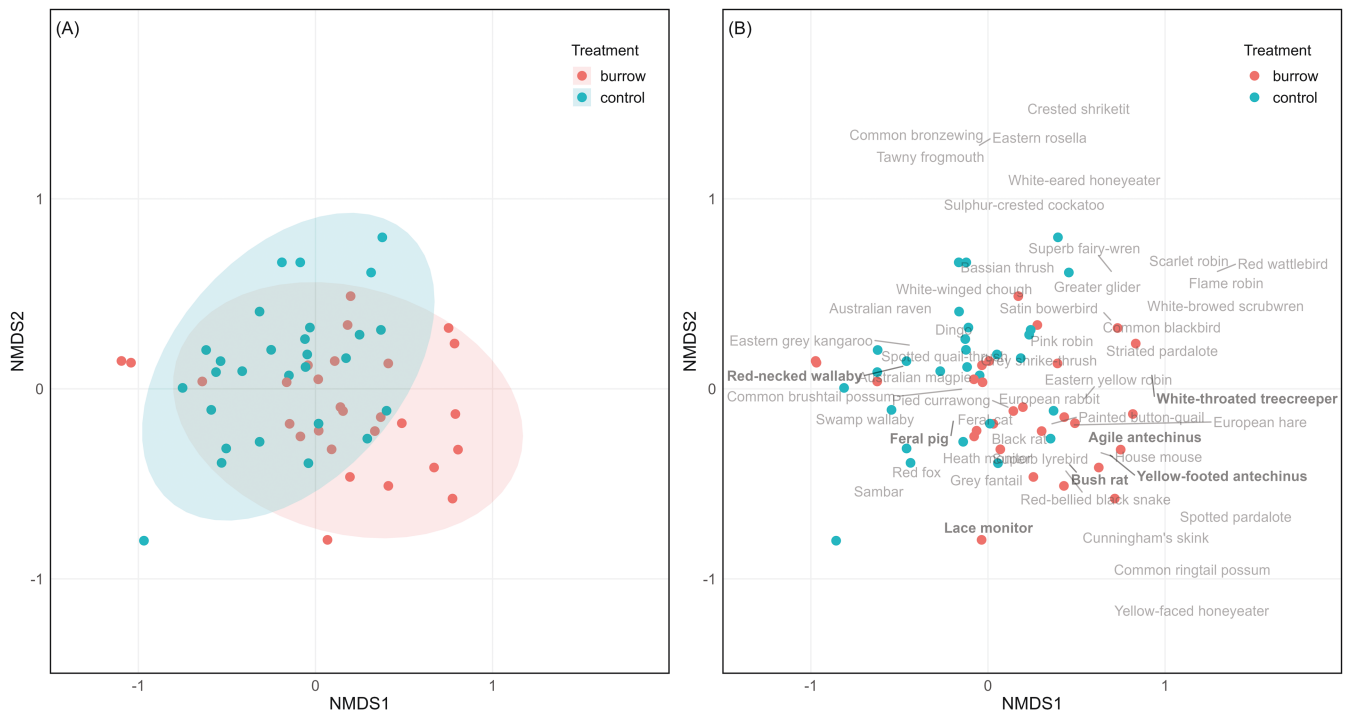
Fig. 6. The difference in species composition at burrows and control sites in Woomargama National Park. Ordinations show nMDS plots of square root transformed activity indices: (A) sites (points) colored by treatment (burrow vs. control)—distances between sites indicate community dissimilarity, and shaded areas are ellipses based on a multivariate *t*-distribution; and (B) the location of species in ordination space with indicator species highlighted in bold.

(*V. gouldii*), and Mulga Snake (*Pseudechis australis*) use burrows from European Rabbit (*Oryctolagus cuniculus*) that concentrated prey species (Dean et al. 2023). The increase in activity of small vertebrates around Common Wombat burrows may cascade through the system, as these species attract and are exploited by larger native predators such as Lace Monitor. These large, generalist, ectothermic carnivores may also derive additional benefits from Common Wombat burrows, because burrows provide a thermal refuge, buffering against extreme environmental conditions (Pike and Mitchell 2013).

Finally, we observed several instances of Common Wombat burrows filling with water including during summer, signaling that water provision may be another ecological role that they provide. Macropods including Eastern Grey Kangaroo, Red-necked Wallaby, and Swamp Wallaby were all captured drinking from burrows, and Pied Currawong were observed bathing. These observations suggest that burrows could provide an important water resource to animals, although they may only provide critical services during periods of low water availability. For example, well-digging by feral equids in North American deserts increases water availability and, probably due to the scarcity of water in this system, vertebrate richness (Lundgren et al. 2021). While water was not scarce during our study period, or compared to other drier ecosystems, it does play a vital role in regulating and maintaining ecosystem services, especially in the drier months (Pepper et al. 2008). As such, water provision via Common Wombat burrows, especially during warmer periods, presents an interesting observation that warrants further investigation.

Wombat burrows as fire refuges.

We found that associations between species and burrows persisted, and often strengthened in fire-impacted habitat,

particularly in areas that burned at high severity. Smaller-sized animals including Agile Antechinus, Bush Rat, and Painted Button-quail all retained positive associations with burrows in areas that were subject to high-severity fire, and all 3 were most active at burrows subject to high-severity fire. By contrast, the association of Lace Monitor with burrows was only evident at unburned burrows. These findings suggest that the association of species with Common Wombat burrows is highly context-dependent, and that fire plays a significant role in determining the nature of this relationship in Australian forests.

For small vertebrates that are vulnerable to predators, many flammable refuges such as logs are consumed by severe fires (Bassett et al. 2015). Wombat burrows—which survive fire and can persist for decades (Taggart and Temple-Smith 2008)—potentially provide important postfire shelter. Our study suggested that the 2019–20 bushfires had relatively negligible impacts on the activity of species that were relatively similar between burnt and unburnt habitat. However, it did indicate that the impacts of fire might concentrate the activity of small vertebrates within the vicinity of burrows, providing a locus from which foraging and intraspecific interactions can occur in relative proximity to predictable shelter and protection from predators. Disturbances in other regions likely shape associations between other ecosystem engineers and the co-occurring species. Allospecific use of Gopher Tortoise burrows dramatically increases during and after a fire (Knapp et al. 2018), and European Rabbit warrens support greater densities of Mediterranean lizards in unfavorable habitat (Gálvez Bravo et al. 2009), further highlighting the context-dependent importance of burrows in disturbed landscapes.

Our results have important implications for conservation. The geographic range of Common Wombat has declined since European colonization of Australia (Buchan and Goldney 1998; Triggs 2009;
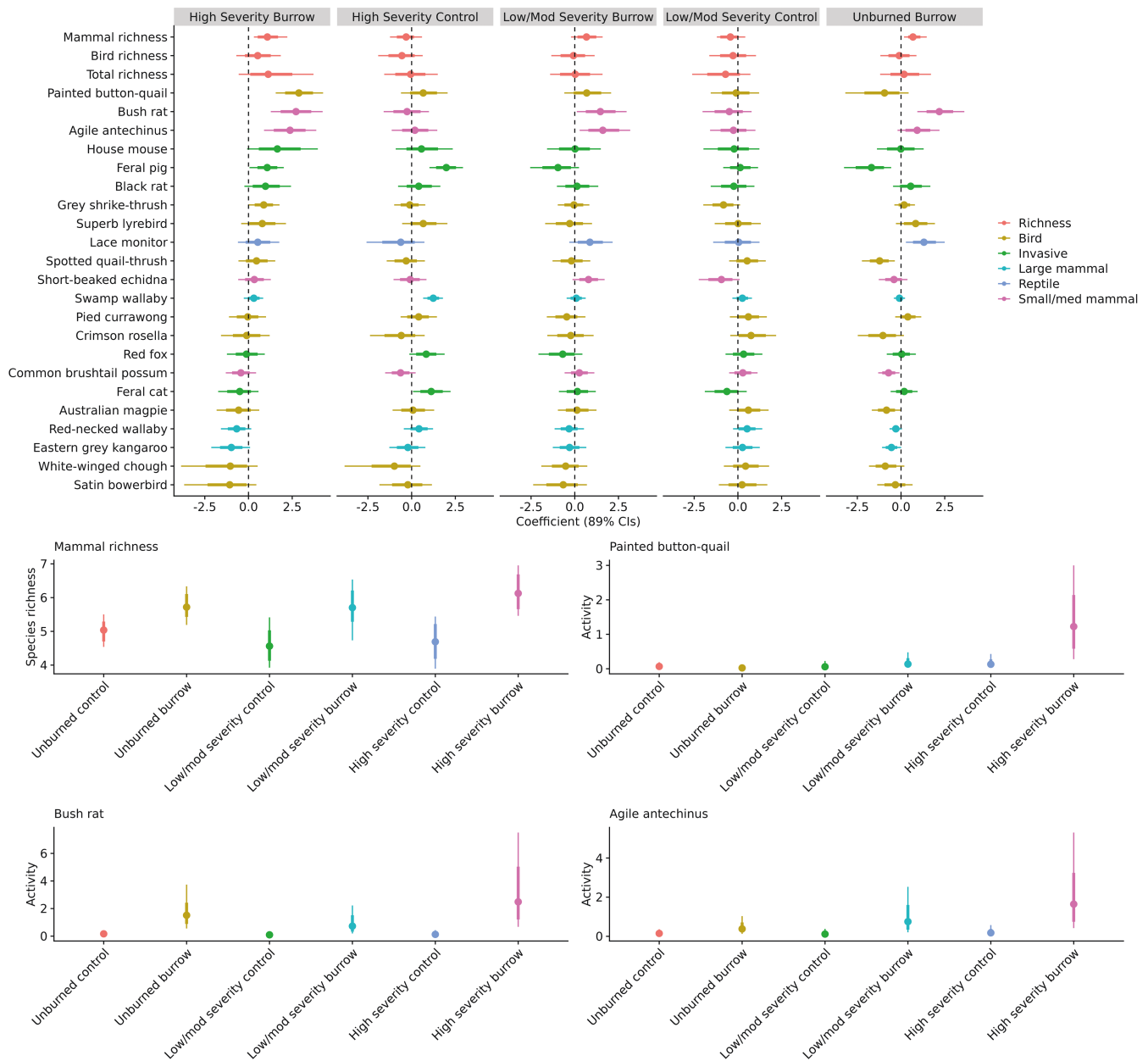
Fig. 7. Coefficients and credible intervals from Bayesian models comparing species activity in burrows versus control sites in sites that vary in fire severity (controls specified as the reference category), and examples of species activity predicted from those models. In activity plots: colored dot = point estimate; thick bars = 66% CIs; and thin bars = 89% CIs.

Baker and Gynther 2023), and is predicted to substantially contract from climate change (Graham et al. 2019). The 2 other species of wombat are vulnerable to extinction (Swinbourne et al. 2016a), and numerous other burrowing Australian marsupials have been driven to extinction since European colonization (Woinarski et al. 2019). Throughout the forests of eastern Australia, Common Wombat are the only extant species of native mammal capable of excavating wide, deep, and elaborate burrows, and our research suggests that they play a critical role for a host of other species. The importance of ecosystem engineers for providing critical shelter for other species highlights the often-overlooked risk of co-extinctions due to the loss of burrowers. For example, endangered pygmy Blue-tongued Skink (*Tiliqua adelaidensis*)—presumed extinct for 33 years (Armstrong and Reid 1992; Armstrong et al. 1993)—are entirely reliant on burrows

constructed by lycosid and mygalomorph spiders (Hutchinson et al. 1994). Changed land use has caused declines in these ecosystem engineering spiders and the near extinction of the lizards (Souter et al. 2007). The value of burrowers as providers of shelter and refuge likely increases after disturbance across a range of ecosystems. The occurrence of larger and more severe wildfires around the world has placed a premium on understanding how animals survive, persist, and recover following extreme wildfire events. Our research has revealed that Common Wombat burrows play a valuable and under-appreciated role in the fire-prone forests of Australia.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Species which were identified at burrows and controls.

Supplementary Data SD2.—Number of images per behavior observed from species interacting with wombat burrows.

Supplementary Data SD3.—Results of coefficients, with 89% confidence intervals, from Bayesian models comparing species activity in burrows versus controls.

Supplementary Data SD4.—Results of coefficients, with 89% confidence intervals, from Bayesian models comparing species activity in burrows versus controls in sites that vary in fire severity.

Author contributions

GDL helped conceptualize the study, collect data, curate the data set, wrote the original draft, and led the analysis; DGN conceptualized the study, provided analysis assistance, and assisted on the original draft; WLG played a pivotal role in the analysis of the data and editing and revising the manuscript; CJJ assisted with the analysis and played a significant role in editing and revising the manuscript; EES, KA, DRM, and DMW helped edit and revise the manuscript.

Conflict of interest

None declared.

Data availability

Data are available upon reasonable request.

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