

# The response of dung beetles (Coleoptera: Scarabaeinae) to environmental stress correlates with nesting behaviour — an Australian study

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drought | fire | telecoprid | paracoprid | rainforest | wet sclerophyll | eucalyptus woodland | ecosystem services.

## **ABSTRACT**

Environmental stressors such as drought and fire can have detrimental effects on an ecosystem and its biodiversity. While invertebrates are an integral part of any ecosystem, there is limited data on how invertebrate populations are affected by environmental stressors, and how different species respond. This study surveyed dung beetle populations in Lamington National Park, south-east Queensland, Australia, that were affected by three years of drought, followed by bushfires in late 2019. Dung beetles were surveyed one year post-fire (2020–21) and the data were compared to data collected from an earlier dung beetle survey conducted in the same area in 2012–14 after a period of significant above-average rainfall. Changes to dung beetle abundance and community composition were observed in three different vegetation communities, even at sites that were not affected by fire. Several roller species (telecoprids) declined or were lost, while several tunnelling species (paracoprids) did not change or increased, suggesting that Australian rollers are less tolerant to drought and related environmental stressors.

Extensive and severe bushfires occurred in Australia in late 2019 through to 2020. These fires followed on from a multi-year drought that began in late 2017 and intensified throughout 2019 (Nguyen et al. 2021). Drought and fires affected many areas of eastern Australia, including subtropical regions of south-east Queensland. Concerns have been raised for many of the plants and animals impacted by these conditions, especially those species where most of their known distributions were affected (Ward et al. 2020). While impacts on vertebrate fauna and plants have been explored, there is limited knowledge about the impacts on invertebrate fauna in Australia (Saunders et al. 2021, Hyman et al. 2020, York & Lewis 2018). Invertebrates are important to ecosystem functions and services, yet there are many gaps in our understanding of how environmental stressors affect them. This is partly because of limited baseline survey data available, and the fact that around 70% of invertebrate fauna is yet to be described in Australia (Saunders et al. 2021).

Dung beetles are an ideal invertebrate taxon to study. They are easily sampled by standardised methods, taxonomically well characterised, ecologically important, and intrinsically linked to vertebrate fauna (Hill 1996, Spector 2006, Nichols et al. 2008). They are sensitive to changes in vegetation cover and soil moisture (Spector 2006, Nichols et al. 2007, Bicknell et al. 2014). Habitat disturbances, such as fire or deforestation, have been shown to affect dung beetle abundance and community composition (Andrade et al. 2014, Halffter & Arellano 2002). Additionally, dung beetles have been shown to respond differently in different habitats. For example, dung beetle abundance has been shown to increase after fire in fire-dependant tropical savanna (Carvalho et al. 2020, Gonçalves et al. 2022, Nunes et al. 2018). However, in some tropical forests, extreme dry seasons and associated fire events have been found to negatively affect dung beetle species richness, abundance and community composition, suggesting that drought and fire are direct drivers of change in dung beetle communities (França et al. 2020).

A dung beetle survey, conducted in 2012–14 by authors Monteith and Cully, covered the greater Beechmont area in southeast Queensland and included sites within the boundaries of Lamington National Park where the Beechmont Plateau joins the Lamington Plateau. This survey took place following a strong La Niña event (2010–2012) with significant above-average rainfall for the region (Bureau of Meteorology 2010, 2011, 2012). A total of 11,743 specimens from 1290 samples in 137 sites were collected from the target area over a two-year period, yielding 42 native and five introduced dung beetle species. Data from this first survey provided a baseline dataset to compare future surveys to.

Subsequently, 2017–2019 was recorded as the driest and hottest three-year period in subtropical eastern Australia since 2011 (Nguyen et al. 2021, Bureau of Meteorology 2017, 2018, 2019). Drought intensified in late 2019, creating conditions that led to the extensive bushfires that devastated parts of Lamington National Park in September 2019. The bushfire started in an area north of the park, then crossed the northern boundaries on 6 September. The fires affected rainforest, wet sclerophyll and eucalyptus woodland habitats. The low humidity and above-average temperatures meant that the fires continued to reignite until January 2020 (Hines et al. 2020).

Many of the sites surveyed for dung beetles in 2012–14 were affected by the bushfires in 2019, so the data from this first survey provided the fortuitous opportunity to compare dung beetle communities from two different time periods, under two very different climate scenarios. While the first survey took place during a time of above-average rainfall, the second survey took place after three years of drought, followed by fire. The data from a subset of sites from the first survey were selected and then the sites were re-surveyed using the same methods and at the same time of year to provide a one-to-one comparison between the two surveys. The aim of this study was to assess changes in the dung beetle community under two different climatic conditions to provide insights into how dung beetles respond to environmental stressors of drought and fire in different habitats, and to provide further data for baseline studies.

## MATERIALS AND METHODS

**Study area:** The Beechmont Plateau is a northern extension of the plateau systems formed by both basalt and rhyolite lava flows from the Tweed Shield Volcano that was active 23 mya on what is now the border between Queensland and New South Wales (Willmott 2004). The plateau is about 20 km long and up to 5 km wide and bounded to east and west, respectively, by the valleys of the Nerang and Coomera Rivers. It ranges from 300 m to 650 m altitude with its highest point at the southern end (Upper Beechmont), where it narrows and connects to the higher and more extensive Lamington Plateau through an eroded razorback ridge carrying the road between the two plateau systems. The first dung beetle survey covered the whole of the Beechmont Plateau as well as the southern transition area adjoining the Lamington Plateau and was conducted at various times over a two-year period. The second survey repeated collections at a subset of the original sites in the southern transition area of the Lamington Plateau at selected times to enable a site-to-site comparison.

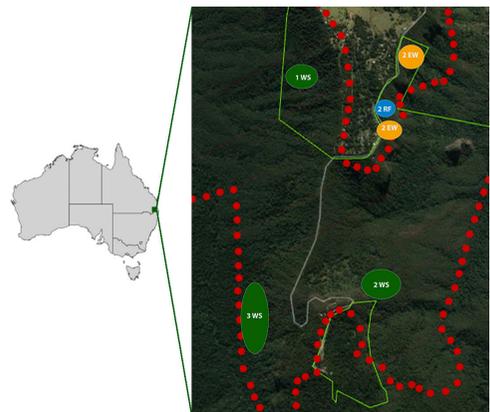
**Site selection:** A subset of twelve sites were selected from the 2012–14 dung beetle survey to be re-surveyed. They were chosen based on their location within the national park, and their accessibility. Every effort was made to re-survey as close as possible to the original survey sites. Sites were located in three different habitats: 1) four in eucalyptus woodland (EW) at 600–650 m elevation, 2) six in wet sclerophyll (WS) at 560–630 m elevation, and 3) two in a small rainforest (RF) patch (approximately 1.4 hectares in size) at 650 m (Fig. 1).

**Site locations/descriptions:** The four EW sites were located on the east side of Binna Burra Road in upper Beechmont (Fig. 1). They were characterised by widely spaced eucalyptus trees with an understory of grass and fern covering the soil surface, and few shrubs. The EW sites had undergone a controlled burn by National Park staff in August 2019 just prior to the bushfires, so did not burn further during the bushfire in September.

Of the six WS sites, four were located to the west of Binna Burra along the westward-facing slope: two sites along the Illinbah circuit track, one further

south along the Gwongoorool track and one was located north of the Illinbah sites, accessed via upper Beechmont. The two remaining WS sites were east of Binna Burra, accessed from the Lower Bellbird track. These sites were located on a slight easterly slope (Fig. 1). The WS sites originally had densely spaced trees of many species, including emergent eucalypts and rainforest trees with an understory of shrubs and herbs covering the soil surface. These sites experienced moderately severe fire during the bushfire in September 2019 (defined by partial canopy and sub-canopy damage) with the tall shrub, vine and small tree layer mostly destroyed (Hines et al. 2020).

Two RF sites were located in a small, isolated remnant of complex notophyll vine rainforest adjacent to Binna Burra Road in upper Beechmont, just to the north of the EW sites (Fig. 1). Neither of these rainforest sites were burned in the 2019 fire.



**Figure 1.** Map of Australia showing region of survey in south-east Queensland. Area expanded to show location of sites within Lamington National Park area. Red lines indicate area burned by bushfire. Green lines indicate national park boundary. Site localities are marked by ovals with numbers representing the number of sites at each locality. WS = wet sclerophyll, EW = eucalyptus woodland, RF = rainforest. Map of Australia credit: Lokal Profil, CC BY-SA 2.5 via Wikimedia Commons; expanded map taken from Google Earth ©2023 Google Earth.

**Survey period:** Trapping for the second survey was conducted monthly from October to February, which corresponds with the period of maximum dung beetle activity in the region. The twelve sites were sampled over a 24-hour period, once a month, from late October 2020 to late February 2021,

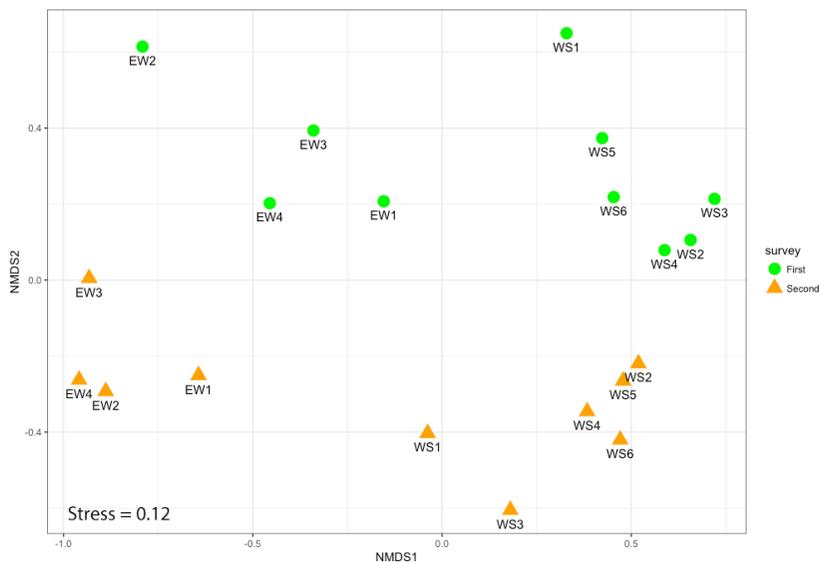
resulting in five sampling times. In the first survey, although sites were sampled multiple times over a two-year period from 2012–14, the only data used for comparison was data collected from the same five survey times from late October to February, to enable a direct comparison with the second survey.

**Survey methods:** Sampling methods were the same for both surveys. Both surveys used pairs of baited pitfall traps — one with mushroom and one with grey kangaroo dung — set at each site for 24 hours per sampling period. Two different baits were used to ensure that a range of dung beetles were collected (Ebert et al. 2019). Traps were 500 ml plastic cups (9 cm diameter) sunk in the ground and part-filled with detergent water. Baits were 6 cm diameter balls of dung or crushed mushroom, wrapped in gauze cloth and suspended from a metal grid placed over the cup. The pair of traps at each site were set approximately 5 m apart. Traps were emptied after 24 hours, then closed until the next sampling period. Dung beetles were extracted from the samples, then identified to species level. Dung beetle species were classified in three different groups based on their nesting behaviour: 1) tunnellers, which bury dung

directly under the dung deposit, 2) rollers, which move the dung away from the dung deposit or 3) nest parasites (kleptoparasites), which occupy the nest of other dung beetles.

There were two traps per site at each of the twelve sites, sampled monthly for five months to result in 120 samples for the second survey. Data from 120 samples from the first survey were used for direct comparison and differences in abundance were assessed for each nesting behavioural group.

**Statistical methods:** Data from the mushroom and kangaroo-baited traps at each site were pooled to arrive at a single sample per site for both the first and second surveys. Non-metric multidimensional scaling (NMDS) was used to examine community dissimilarity based on raw species abundance in each sample using Bray-Curtis dissimilarity. Analysis of similarities (ANOSIM) was used to test if differences in the beetle community composition were significant between each habitat and again between each survey time. Statistical analyses were conducted in R (R Core Team 2017) using the vegan package (Oksanen et al. 2018).



**Figure 2.** Non-metric multidimensional scaling (NMDS) ordination plot comparing the dung beetle communities from the first and second surveys at each of the twelve surveyed sites. Green circles represent the first survey and orange triangles represent the second survey. Analysis of similarities (ANOSIM) confirmed that the eucalyptus woodland (EW) and wet sclerophyll (WS) habitats had significantly different species composition ( $R=0.8009$ ,  $p<0.001$ ), and the two survey times also had significantly different community composition ( $R=0.3162$ ,  $p<0.01$ ). The closer the points are on the ordination, the more similar the communities. Based on the clearly separated ordination, interactions between survey time and habitat were assumed to be unlikely.

Species	Notes	Eucalyptus woodland (EW)		Wet sclerophyll (WS)		Rainforest (RF)	
		First survey	Second survey	First survey	Second survey	First survey	Second survey
		<i>Amphistomus macphersonensis</i> Matthews, 1974	Flightless	0	1	1	1
<i>Amphistomus</i> NSW1		0	0	175	22	93	63
<i>Aulacopris maximus</i> Matthews, 1974		0	0	4	0	2	0
<i>Cephalodesmius armiger</i> Westwood, 1842	Flightless	0	0	0	0	3	0
<i>Cephalodesmius quadridens</i> Macleay, 1871	Flightless	0	1	10	16	17	33
<i>Diorygopyx incomptus</i> Matthews, 1974	Flightless	163	73	36	9	2	0
<i>Diorygopyx simpliciclunis</i> Matthews, 1974	Flightless	1	2	139	9	199	16
<i>Lepanus australis</i> Matthews, 1974		10	0	4	3	2	0
<i>Lepanus meierae</i> Gunter & Weir, 2019		2	0	2	7	1	1
<i>Lepanus</i> NSW4		0	0	0	0	1	0
<i>Lepanus ustulatus</i> (Lansberge, 1874)		21	0	58	5	248	1
<i>Monoplistes leai</i> Paulian, 1934		5	0	33	0	110	2
<b>Total</b>		<b>202</b>	<b>77</b>	<b>462</b>	<b>72</b>	<b>704</b>	<b>124</b>

**Table 1.** Species list showing the rollers collected in the first and second surveys in three habitats: eucalyptus woodland (EW), wet sclerophyll (WS) and rainforest (RF) in Lamington National Park. **Note:** Some species are currently undescribed but are listed using the nomenclature coding system devised by Geoff Monteith (Queensland Museum, Brisbane, QLD) and Tom Weir (Australian National Insect Collection, Canberra ACT).

## RESULTS

In the first survey, 1,875 dung beetles were collected from the twelve selected sites, representing 28 different species. In the second survey, overall dung beetle abundance declined by more than half with only 852 beetles collected from the same sites, representing only 24 species. Five species were lost and one was gained (Tables 1 & 2). However, the overall decline in abundance was due to large declines in abundance in WS and RF habitats, whereas in EW, abundance slightly increased

(Tables 1 & 2). Most species occurred in more than one habitat but with marked differences in abundance (Tables 1 & 2).

To test for differences between dung beetle communities, we used an analysis of similarities (ANOSIM). Ordination showed that the EW and WS habitats had different community composition ( $R=0.8009$ ,  $p<0.001$ ), and there were significant differences between the first and second surveys ( $R=0.3162$ ,  $p<0.01$ ) (Fig. 2). Based on the clearly separated ordination, interactions between survey time and habitat were assumed unlikely.

Species	Notes	Eucalyptus woodland (EW)		Wet sclerophyll (WS)		Rainforest (RF)	
		First survey	Second survey	First survey	Second survey	First survey	Second survey
<i>Demarziella interrupta</i> (Carter, 1936)	Nest parasite	5	66	2	12	0	0
<i>Demarziella metallica</i> (Carter, 1936)	Nest parasite	0	5	3	51	2	3
<b>Total</b>		<b>5</b>	<b>71</b>	<b>5</b>	<b>63</b>	<b>2</b>	<b>3</b>
<i>Onthophagus arrilla</i> Matthews, 1972		5	0	28	41	11	2
<i>Onthophagus auritus</i> Erichson, 1842		3	22	1	1	1	0
<i>Onthophagus australis</i> Guérin-Méneville, 1838		3	1	0	0	0	0
<i>Onthophagus bornemisszai</i> Matthews, 1972		8	10	8	1	4	5
<i>Onthophagus capella</i> Kirby, 1818		6	41	0	0	1	6
<i>Onthophagus</i> CQ2		6	3	39	17	32	2
<i>Onthophagus dunningi</i> Harold, 1869		24	35	0	0	0	0
<i>Onthophagus leanus</i> Goidanich, 1926		0	3	0	0	0	0
<i>Onthophagus mamillatus</i> Lea, 1923		0	0	3	0	0	0
<i>Onthophagus neostenocerus</i> Goidanich, 1926		0	12	2	1	14	0
<i>Onthophagus pugnax</i> Harold, 1868		2	1	99	12	21	18
<i>Onthophagus rubicundulus</i> Macleay, 1871		1	25	0	0	0	1
<i>Onthophagus</i> SEQ2		0	1	1	0	0	0
<i>Onthophagus sydneyensis</i> Blackburn, 1903		17	25	96	63	57	93
<i>Onthophagus turral</i> Matthews, 1972		0	0	2	0	0	0
<b>Total</b>		<b>75</b>	<b>179</b>	<b>279</b>	<b>136</b>	<b>141</b>	<b>127</b>

**Table 2.** Species list showing the tunnelling species and kleptoparasitic species (which also tunnel) collected in the first and second surveys in three habitats: eucalyptus woodland (EW), wet sclerophyll (WS) and rainforest (RF) in Lamington National Park. **Note:** Some species are currently undescribed but are listed using the nomenclature coding system devised by Geoff Monteith (Queensland Museum, Brisbane, QLD) and Tom Weir (Australian National Insect Collection, Canberra ACT).

Although the RF habitat did not have enough replicate sites to analyse statistically, most species were more abundant in the first survey (Tables 1 & 2). Overall, the abundance of roller species greatly declined in all three habitats (Table 1). Details for each habitat follow.

**Eucalyptus woodland (EW):** Abundance in EW sites increased slightly in the second survey, but the community composition changed noticeably (Fig. 4). The most abundant species in the first survey was a flightless roller, *Diorygopyx incomptus* (Fig. 3C, Fig. 4). Although this species was still the most abundant roller collected in the second survey, it decreased from representing 58% of total dung beetle abundance to 22% (Fig. 4). Four other roller species found in the first survey were absent from the second survey. In contrast, tunnellers and nest parasites increased from 30% to 76% of total

abundance, although a large portion of this was due to the increased abundance of *Demarziella interrupta* (Fig. 3G, Fig. 4).

**Wet sclerophyll (WS):** WS sites showed a large decrease in abundance in the second survey (Fig. 5). Most noticeable were the declines of two previously dominant rollers species, *Amphistomus NSW1* and *Diorygopyx simpliciclunus* (Fig. 3A & D, Fig. 5). Another roller, *Monoplistes leai* (Fig. 3F) was present in all WS sites in the first survey but was not collected at all in the second survey (Fig. 5). Tunnellers also declined overall, but their proportion within the community increased due to the decline of formerly more abundant roller species (Fig. 5). A large percentage (17%) of the increase in the tunneller population in the second survey was attributed to *Demarziella metallica*.

**Rainforest (RF):** Although the RF sites were not affected by fire, there was still a marked decline in abundance and species richness compared to the first survey (Fig. 6). The most notable species declines were the rollers *Lepanus ustulatus*, *Diorygopyx simpliciclunus* and *Monoplistes leai* (Fig. 3E, D & F, Fig. 6). These three species together made up 66% of the community in the first survey but dropped to 7% of the community in the second survey. The most abundant tunneller, *Onthophagus sydneyensis* (Fig. 3I, Fig. 6) increased in the second survey.



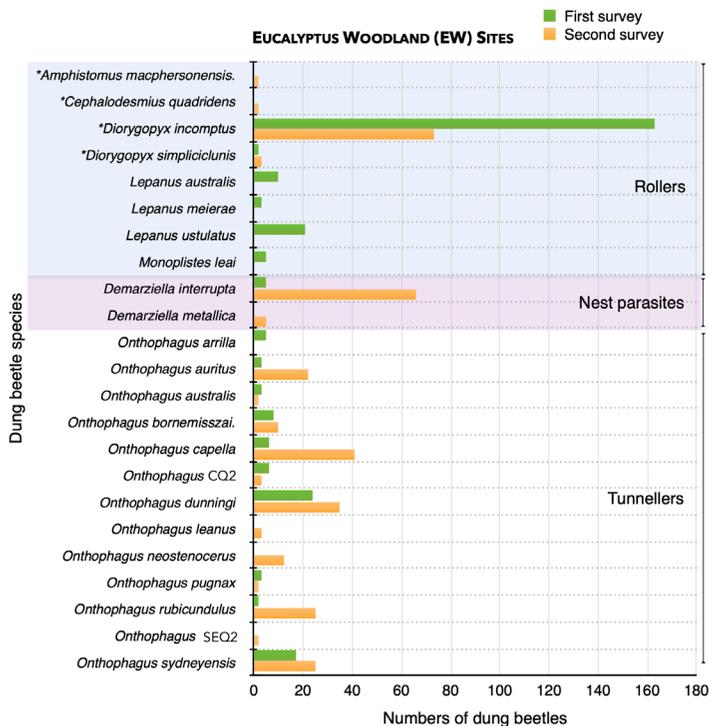
**Figure 3.** A selection of some of the dung beetle species collected during the surveys: **A** *Amphistomus NSW1* **B** *Cephalodesmius quadridens* **C** *Diorygopyx incomptus* **D** *Diorygopyx simpliciclunus* **E** *Lepanus ustulatus* **F** *Monoplistes leai* **G** *Demarziella interrupta* **H** *Onthophagus arrilla* **I** *Onthophagus sydneyensis*. A–F are rollers, G is a nest parasite and H–I are tunnellers. Photo credits: Geoff Thompson and Andy Wang, Queensland Museum.

## DISCUSSION

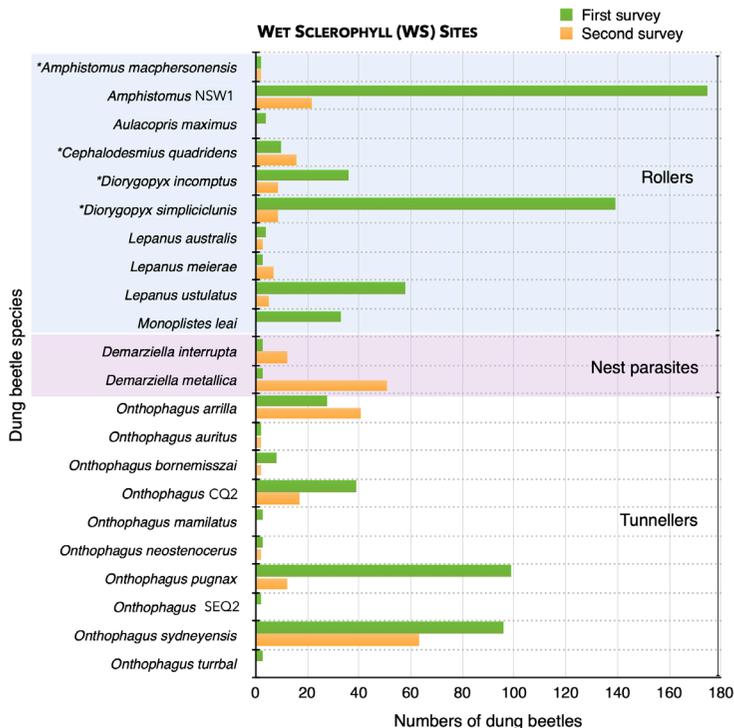
The different habitats in this study each supported a different community of dung beetle species, although there was some overlap. This was not unexpected since vegetation structure has been shown to influence dung beetle communities, as it is linked to microclimate and vertebrate fauna (Louzada et al. 2010). Other Australian dung beetle studies have also found that different habitats and soil types support different dung beetle communities (Matthews 1971, 1974, 1976, Hill 1996, Monteith 2003, Monteith & Kenyon 2011, Monteith & Ebert 2016).

Although species richness did not change markedly from the first survey to the second survey, there were significant changes in community composition and abundance in all three habitats.

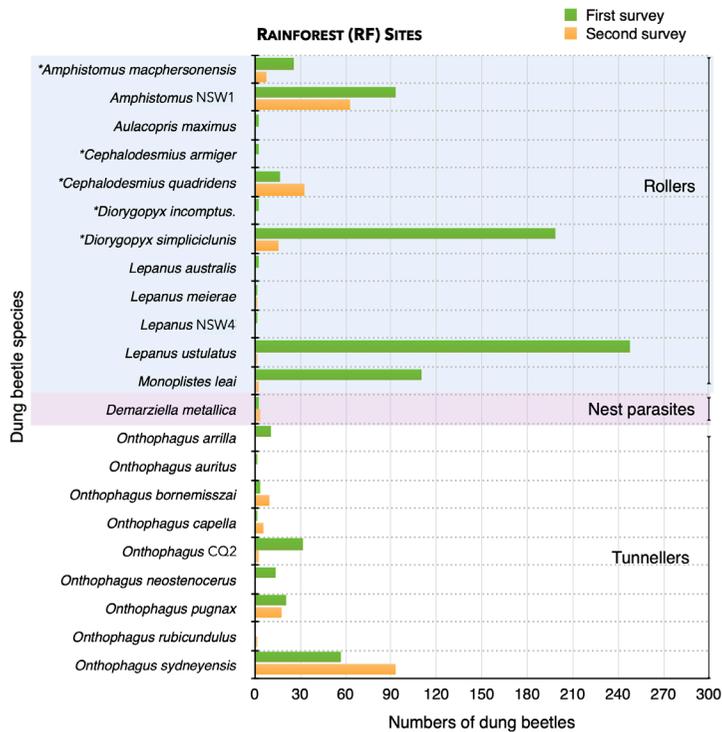
**Note for Figs 4, 5 and 6.** Nesting behaviour is indicated by colour: blue denotes rollers, purple is for tunnelling nest parasites, and white denotes tunnellers. An asterisk before the species name indicates flightlessness.



**Figure 4.** Bar graph showing the abundance of dung beetle species at eucalyptus woodland (EW) sites for each survey. Rollers made up 72% of the community in the first survey, declining to 24% in the second survey.



**Figure 5.** Bar graph shows the abundance of dung beetle species at wet sclerophyll (WS) sites for each survey. Rollers made up 62% of the community in the first survey, declining to 27% in the second survey.



**Figure 6.** Bar graph shows the abundance of dung beetle species at rainforest (RF) sites for each survey. Rollers made up 83% of the community in the first survey, declining to 49% in the second survey.

These changes to the dung beetle community are likely linked to changes in habitat but it is difficult to discern how much was due to drought and how much was due to fire or other factors. Dung beetle populations have been shown to take one to three years to recover following drought, but this was with no other stresses (Beiroz et al. 2017). Recovery after bushfire, in addition to drought, would likely take even longer. In a similar study, dung beetle species richness and abundance were shown to decrease after drought, but even more so when exacerbated by fire (França et al. 2020).

The rainforest sites did not burn during the 2019 bushfires, yet still showed a dramatic change in abundance and community composition. This would suggest that although fire certainly had an impact on the other habitats, drought is likely to be the underlying cause of community change overall. Several years of drought prior to the fires would have affected the vertebrate populations that many dung beetle species rely on for food and brood material. The extreme drought was also associated with above-average levels of evaporative stress,

indicating the soil moisture was extremely low (Nguyen et al. 2021). Larval mortality would likely increase since the brood balls are vulnerable to desiccation (Beiroz et al. 2017). Resistance to desiccation has been shown to vary among dung beetle species, with those living at higher elevations being more sensitive to drier conditions (Nervo et al. 2021). It has been observed that dung beetle species that are more sensitive to disturbance are replaced by more tolerant species (Gonçalves et al. 2022), altering community composition.

The added effects of fire on the other study sites would also contribute to changes seen in dung beetle community composition. A study compared dung beetle assemblages between burned and unburned areas of closed canopy forest in Brazil found that abundance and species richness did not change significantly, but the dung beetle community structure and composition changed, with smaller species becoming more predominant (Andrade et al. 2014). Another recent study surveyed dung beetle species in northern New South Wales that had at least 50% of their range impacted by the 2019

fires and found that although the targeted species were still present in burned areas, numbers were less abundant than in unburned sites (Reid et al. 2022). Our results concur with these studies and emphasise that different species respond differently to environmental stressors.

The WS sites exhibited greater changes in community composition than the EW sites. This may be attributed to greater severity of fire at these sites. In the WS sites, the bushfire damaged portions of the canopy, decimating most of the vining plants and rainforest understory plants. Although herbaceous regrowth was present in the second survey, the habitat was not restored to its pre-fire state. Since dung beetle communities respond to changes in vegetation structure and microclimate (Halffter & Arellano 2002, Nichols et al. 2007), a more open canopy, less understory and drier microclimate post-fire would be more favourable for some species, though not others (Schowalter 2012, Halffter & Arellano 2002). Species such as *Diorygopyx simpliciclunis* and *Amphistomus* NSW1 were abundant in the first survey, yet absent or greatly reduced in the second survey, while other species such as *Onthophagus arrilla* (Fig. 3H), *Demarziella metallica* and *Cephalodesmius quadridens* increased.

In contrast, fires in the EW sites were part of a controlled burn so were less intense than the bushfire affecting the WS sites. Canopy was not damaged, and regrowth of native grass and ferns was evident. Furthermore, eucalyptus woodlands are more fire-adapted, so dung beetle species living in this habitat are likely to adapt better to understory changes, similar to what has been seen in other comparable habitats (Carvalho et al. 2020, Gonçalves et al. 2022, Nunes et al. 2018). Yet changes still occurred to the community composition, suggesting that other factors are affecting the community.

The fires occurred in early spring when many species would potentially be preparing to breed. Dung beetles that survived the fire would find limited food resources to gather for their brood due to a potential reduction in vertebrate dung availability. This would be especially detrimental to species that are flightless. Even with vigorous regrowth to provide cover a year after the fire and improve the

microclimate, it would still take time for populations to fully recover after disrupted breeding cycles.

Nesting behaviour appears to be a significant factor influencing how individual species were affected by drought and fire. In the RF and WS habitats, the dung beetle species that were most often reduced or lost were the rollers. Genera such as *Amphistomus* and *Diorygopyx* situate their brood balls near the surface, slightly buried or under rocks and logs (pers. obs.). These brood balls would be especially vulnerable to increased temperatures and desiccation. The beetles themselves would also be more exposed to fire than tunnelling species. An exception to this is *Cephalodesmius quadridens* (Fig. 3B), an unusual roller species that lives in a permanent nest burrow and provisions its larvae in brood nests underground where the brood would be more protected from desiccation (Monteith & Storey 1981). *Cephalodesmius* are also generalist feeders so less reliant upon vertebrates for food resources than other species (Ebert et al. 2019), which may help to explain why their numbers increased at some sites in the second survey.

The roller species represent a relictual Gondwana lineage, adapted to an historically mesic habitat that has contracted considerably with the aridification of the Australian landscape over the millennia (Byrne et al. 2011, Gunter et al. 2019). The fact that several of the species are flightless suggests they are adapted to a stable and persistent microhabitat (Scholtz 2009). Insects from stable ecosystems are generally considered less tolerant than those from more variable ecosystems (Schowalter 2012), indicating that these species would be more susceptible to habitat disturbances. Five of the twelve roller species in this study are flightless and therefore limited in their ability to repopulate burned areas rapidly. The flightless species showed an overall decline in abundance in the second survey for all three habitats, but even those species that are capable of flight declined markedly. For example, *Lepanus ustulatus* and *Monoplistes leai* can fly and were found in all three habitats for the first survey, although most abundant in RF sites. However, these two species declined to almost nothing in the second survey. This would suggest that, although flightlessness would be a contributing factor to

roller decline, it is not the only factor. Small brood size and higher risk of brood desiccation would also contribute to the vulnerability of these species.

In contrast, tunnellers did not decline overall as much as rollers, and in fact, increased in EW sites. All tunnelling species surveyed are in the genus *Onthophagus*, which have a worldwide distribution, disperse over large distances and readily adapt to new environments (Breeschoten et al. 2016). Their fecundity is also very high compared to other native dung beetle genera (Halffter & Edmonds 1982). *Onthophagus* species lay their eggs in tunnels several centimetres below the surface, giving developing larvae a degree of protection from the immediate effects of drought and bushfire (Halffter & Edmonds 1982). Their increased numbers in the EW sites concurs with a study in the tropical savanna of the Australian Northern Territory (Carvalho et al. 2020). The only species collected in that study were *Onthophagus*, and abundance of smaller *Onthophagus* species increased as the habitat became more open (Carvalho et al. 2020). This may reflect their adaptability and their ability to readily disperse into burnt areas from unburnt habitat.

The other species that increased dramatically in the second survey, especially in WS and EW sites, were the very small *Demarziella interrupta* and *D. metallica* (3-4 mm in size). Some observations suggest that these species are nest parasites, i.e., they lay their eggs in other dung beetle nests (Matthews 1976), although very little is known of their behaviour. In the first survey, *Demarziella* represented a very small proportion of total dung beetle numbers. However, in the second survey, numbers increased to nearly 20% of the total in both EW and WS habitats. Why the increase in these species? Is it because there is an increase in tunnelling species and therefore more opportunity for nest parasitism? Could it reflect a dung beetle community under stress? It is difficult to say until we know more about the behaviour of these small species.

While these surveys are only a snapshot from two time periods, they provide evidence of changes to dung beetle communities under different environmental conditions. Dung beetles are present and active after prolonged drought and subsequent fire events, but community composition changes.

Nesting behaviour and flight ability appear to be important in discerning which species may be more sensitive or tolerant to climate extremes. If environmental stressors eliminate less tolerant species from these areas and cause local extinctions, how will this affect the ecosystem services these species provide? Longer term monitoring will be important to discover if these changes are temporary and the dung beetle communities are eventually restored to pre-drought composition.

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