

The effects of habitat fragmentation and wildfire on the presence of two ant species,  
*Aphaenogaster longiceps* and *Leptomyrmex erythrocephalus*

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## **Table of Contents**

<b>Acknowledgements</b>	<b>2</b>
<b>Abstract</b>	<b>3</b>
<b>Introduction</b>	<b>4</b>
<i>Questions and Predictions</i>	6
<b>Methods</b>	<b>7</b>
<i>Study system</i>	7
<i>Experimental design</i>	8
<i>Study species</i>	10
<i>Data collection</i>	11
<i>Data analysis</i>	11
<b>Results</b>	<b>12</b>
<b>Discussion</b>	<b>18</b>
<b>References</b>	<b>21</b>
<b>Supplemental figures</b>	<b>24</b>

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## Abstract

Anthropogenic changes to the environment, such as through habitat fragmentation and loss, can be detrimental to ecosystems. Habitat destruction resulting from such changes can degrade biodiversity and change ecosystem processes. Further, rising temperatures resulting from climate change have increased the occurrence of extreme disturbance events such as wildfires. In 2020, the Wog Wog Habitat Fragmentation Experiment in New South Wales, Australia, burned in the "Black Summer" wildfires. At Wog Wog, researchers study the effects of environmental changes on around 1,000 species of invertebrates. In this paper, I examine the combined effects of habitat fragmentation and wildfire on the presence of the two most abundant, generalist ant species at Wog Wog, *Leptomyrmex erythrocephalus* and *Aphaenogaster longiceps*. I examine differences in their presence pre- and post-fire. Previously, it was found that 12 years pre-fire, *A. longiceps* was equally likely to occur in *Eucalyptus* fragments and continuous *Eucalyptus* forest, and less in the non-native *Pinus radiata* (matrix) surrounding the fragments. On the other hand, *L. erythrocephalus* was most likely to occur in continuous forest, followed by fragments, then matrix. My prediction that post-fire, *A. longiceps* occurrence would not significantly decrease was supported by the results. This trend may be because *A. longiceps* have 30 cm deep nests, aiding them in surviving disturbance events. Previous research has also shown the species is not affected by fire severity. However, post-fire *A. longiceps* was significantly more likely to occur in continuous forest than fragments, possibly due to a decrease in occurrence in fragments directly pre-fire. My prediction that *L. erythrocephalus* occurrence would decrease post-fire was also supported. This may be due to the burning of their nests in logs, the base of trees, and other shallow soil areas. Future research should follow changes in both species' presence as succession continues, as fire can also have indirect effects on ants.

## Introduction

Habitat loss and fragmentation, which is the division of continuous habitat into smaller fragments, can result in biodiversity degradation (Haddad et al., 2015) and can affect ecosystem processes (Benitez-Malvido et al., 2008). Globally, we have lost one third of forests and 70% of what remains is within one kilometer of an edge (Haddad et al., 2015). The introduction of anthropogenic landscapes, also known as matrices, create edge effects in remnant habitat fragments that they surround. Edge effects are changes to the edges of remnant fragments, which can include changes to temperature, moisture, soil composition, predation, and species composition (Benitez-Malvido et al., 2008). Habitat fragmentation results in more isolated populations with weaker habitat connectivity, which can reduce the abundance of native species, like birds, plants (including old-growth trees), insects, and mammals (Haddad et al., 2015). This can impede processes like seed dispersal, plant herbivory, pollination, succession rates, and system carbon and nitrogen retention (Haddad et al., 2015). In order to conserve Earth's biodiversity, we must understand how species can continue to persist within altered landscapes.

At the Wog Wog Habitat Fragmentation Experiment (Wog Wog hereafter) in southeastern Australia, continuous *Eucalyptus* forest was cleared for the planting of a pine monoculture (matrix), leaving experimental *Eucalyptus* fragments. Researchers analyze how fragmentation alters species abundance, presence, and composition through time, depending on variables such as proximity to fragment edges, fragment size, and topography. They are then able to compare samples from fragments and the matrix to the continuous forest (controls hereafter). Ants are collected in invertebrate sampling here.

Ants are ecosystem engineers, meaning they are important to ecosystems due to their biodiversity, their role in altering their physical environment (Sanders & van Veen, 2011), and

their biomass – one estimate of global ant biomass being 12.3 million tonnes (Fayle & Kilmes, 2022). They affect their physical environment through their abundance, predation, herbivory, seed dispersal, and nutrient cycling (McClenahan, 2017; Sanders & van Veen, 2011). They also alter their environment through soil aeration, litter decomposition, and nest excavation and formation, which are examples of bioturbation, whereby living organisms contribute to soil turnover and the cycling of organic matter (Richards et al., 2011). Through changing the nutrient content of soil, they can increase decomposer density (Sanders & van Veen, 2011). Higher ant abundances also have greater effects on soil properties and food webs (Fayle & Kilmes, 2022). The loss of ant biodiversity would degrade these important ecosystem processes (McClenahan, 2017).

Previously, researchers at Wog Wog studied the responses of two ant species, *Aphaenogaster longiceps* and *Leptomyrmex erythrocephalus*, to habitat fragmentation. They found that after initial fragmentation (in years 1-4), *A. longiceps* was equally likely to occur in the fragments, controls, and the matrix (McClenahan, 2017). In the long-term post-fragmentation (after 21 years), *A. longiceps* was equally likely to occur in the fragments and controls and less likely to occur in the matrix (McClenahan, 2017). Whereas, *L. erythrocephalus* was most likely to occur in controls, followed by fragments, then matrix after both initial and long-term fragmentation (McClenahan, 2017). Further, topography affected each species, as each was less likely to occur in drainage sites than slope sites. This trend may be due to matrix and drainage sites having wetter soil and less light exposure. The two species likely prefer both drier soil and more light exposure (McClenahan, 2017). There was no effect on the occurrence of either species by proximity to fragment edge or fragment sizes (McClenahan, 2017).

Wog Wog burned in the Australian 2019-20 “Black Summer” wildfires, creating an opportunity to examine the effects of an extreme disturbance driven by rising temperatures on ants and how that intersects with habitat fragmentation. This is important because most ecosystems globally are fragmented and impacted by multiple disturbances, and climate change has dramatically increased the frequency of extreme disturbance events like wildfire, drought, and heat waves (Stott 2016). The Black Summer wildfires burned 21% of of the temperate broadleaf and mixed (TBLM) forest biome in a single season, likely due to record breaking temperatures in the preceding summer, low rainfall, and widespread drought drying the *Eucalyptus* forest litter layer (Abram et al. 2021; Boer et al., 2020; Filkov et al., 2020). Studying the response of ants to wildfire in a fragmented landscape allows us to understand how the combined effects of these disturbances affect biodiversity and ecosystem processes. For example, in southeast Australia, Richards et al. (2011) found that following a wildfire, bioturbation through ant nest building could limit soil erosion by allowing areas in a water-repellent soil surface to take in overland flow to reach wettable soil underneath.

Understanding the impacts of multiple disturbances is important for biodiversity conservation. At Wog Wog, habitat fragmentation is now overlaid by wildfire, both human-sourced disturbances. Here, I ask how wildfire intersects with forest fragmentation to impact the persistence of these two ant species, *A. longiceps* and *L. erythrocephalus*. Through comparing pre- and post-fire occurrences of these species at Wog Wog, I study the response of each species to fire in a fragmented landscape.

### *Questions and Predictions*

Specifically, I ask: where will *A. longiceps* and *L. erythrocephalus* occur post-fire? How will this compare to pre-fire?

I predict that *A. longiceps* will not decrease in occurrence. I also predict there will be no decrease in occurrence due to fire severity, topography, fragment size, or proximity to fragment edge. Previous research suggests *A. longiceps* is not greatly affected by wildfire, with Richards et al. (2011) finding no reduction in *A. longiceps* bioturbation rates where wildfire was more severe. This may be because they have nests 30 cm deep, allowing them to survive various environmental stressors (McClenahan et al., 2017).

I predict that *L. erythrocephalus* will decrease in occurrence post-fire, especially where fire severity was greatest, such as in fragment cores. Their nests are shallower than *A. longiceps*, as they typically nest in roots, the base of trees, dead wood (standing or fallen), soil, and cavities left by small vertebrates such as lizards (Shattuck, 1999; Wheeler, 1915). This means the fire was more likely to burn their nests and reduce their occurrence. Although they tend to workers that store food in their gasters, known as repletes (Shattuck, 1999), these likely did not survive the fire. I also predict there will be no change in occurrence due to topography or fragment size.

## Methods

### *Study system*

The Wog Wog Habitat Fragmentation Experiment (Fig. 1) in southeastern Australia is a long-term experiment where researchers have studied the effects of habitat fragmentation on biodiversity and ecosystem processes. Wog Wog started in 1987 when the native *Eucalyptus* forest was fragmented by the introduction of non-native *Pinus radiata* for harvesting. The experiment consists of a fragmented *Eucalyptus* forest, a continuous undisturbed *Eucalyptus* forest, and a non-native *Pinus radiata* matrix surrounding the *Eucalyptus* fragments (Margules, 1992). *Eucalyptus* fragment replicates consist of small (0.25 ha), medium (0.87 ha), and large

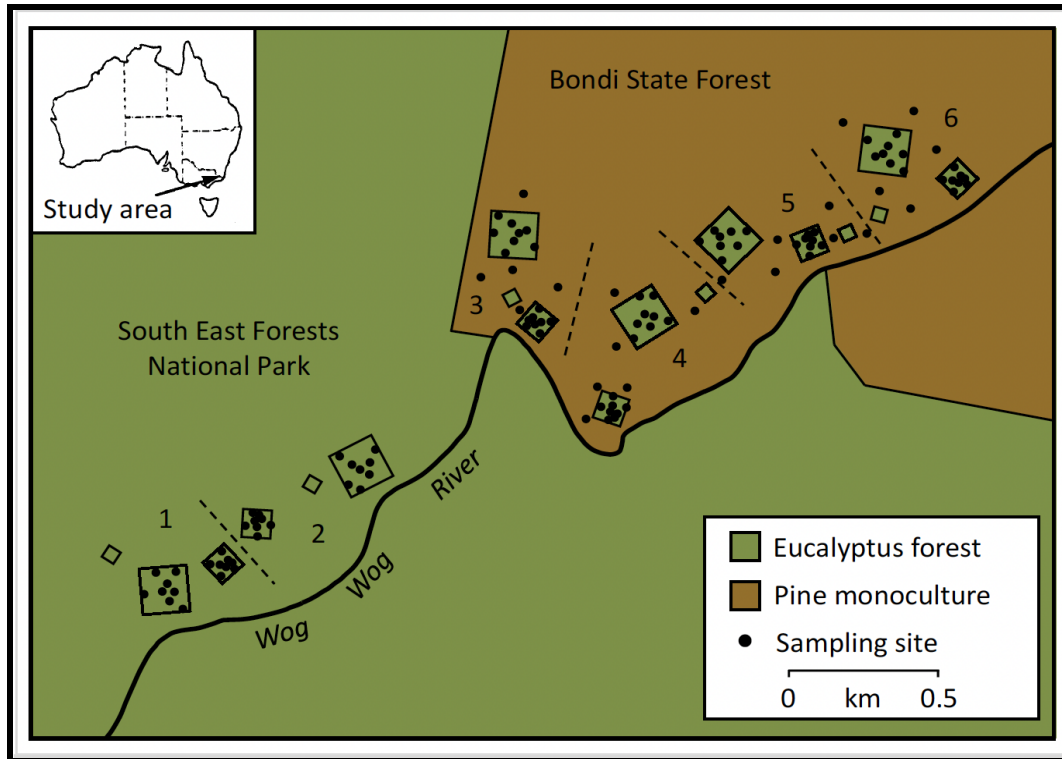


(3.06 ha) sizes. Fragmented replicates can then be compared to control replicates in adjacent, continuous *Eucalyptus* forest.

The experiment burned in the Australian 2019-20 "Black Summer" wildfires. Fire severity was measured as char height, measured as the height of fire char marks on *Eucalyptus* tree trunks, and topkill, the absence of epicormic resprouting on *Eucalyptus* trees. There was higher char and topkill rates in fragments compared to controls (Spiers et al. in prep). Further, topkill was more likely in fragment cores than along edges, likely due to fragment cores being drier from having a sparser canopy and therefore more ground-light availability than along edges (Spiers et al. in prep). Fire severity was not measured in the pine matrix, as remnant pine trees had been harvested by the lumber company shortly following the fire (Spiers et al. in prep). The fragments and matrix burned in a crown fire (Spiers et al. in prep).

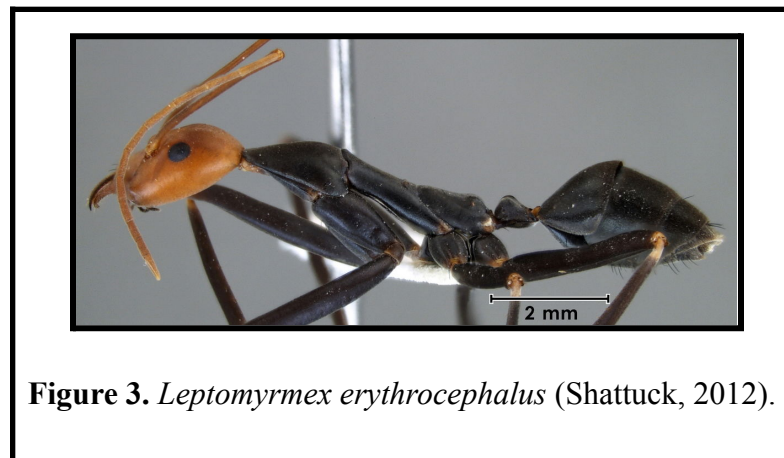
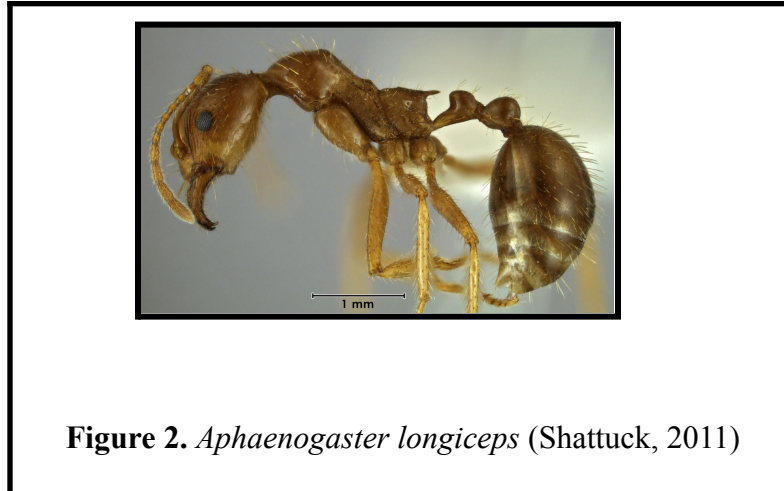
#### *Experimental design*

There are a total of 188 pitfall traps, with 144 in the continuous and fragmented *Eucalyptus* forest (8 per experimental patch) and 44 traps in the matrix. Pitfall traps are classified by their topography, and pitfall traps in small, medium, and large fragments are also classified by their distance to fragment edges. Each pitfall trap collects various small invertebrates, samples which are then separated into vials. Permanent pitfall traps consist of plastic cups inserted into PVC sleeves. Inside each cup is a metal cage to prevent vertebrates from falling in. A 150 mL solution of ethanol and glycol is placed in the bottom of the cups, and a 200 x 200 mm cover is placed on top to help prevent flooding. The covers contain legs that are set into the ground during each 7-day sampling period.



**Figure 1.** Map of the Wog Wog habitat fragmentation experiment in Southeastern Australia.

Green represents the continuous *Eucalyptus* forest, whereas brown represents the Pine monoculture, or matrix. *Eucalyptus* fragments, represented by green squares within the matrix, consist of small (0.25 ha), medium (0.87 ha), and large (3.06 ha) sizes. Each fragment contains eight sampling sites, and there are also sampling sites in the continuous forest and matrix (represented by black points). Map from (Resasco et al., 2017).

*Study species*

*Aphaenogaster longiceps* (Fig. 2), also known as the “funnel ant,” and *Leptomyrmex erythrocephalus* (Fig. 3), also known as the “spider ant,” are the most abundant generalist ant species at Wog Wog and there is a long series of pre-fire data available for them. This allows species viability and extinction rates to be measured.

The *Aphaenogaster* genus contributes greatly to bioturbation through nest excavation and the building of surface mounds, affecting soil processes and properties (Richards et al., 2011). *A. longiceps* lives in approximately extremely dense, 30 cm deep nests, which can allow for survival even when exposed to extremely high temperatures (Shattuck, 1999; Richards et al.,

2011). Colonies have high worker density and a queen that lives deep within the nest (McClenahan et al., 2017). Although nests contain large worker density, there are typically few workers seen at the surface, as the funnel-shaped nest entrances may trap foraging arthropods, reducing the need to forage above the ground (Shattuck, 1999).

*L. erythrocephalus* have shallower nests than *A. longiceps*, as they typically nest in roots, the base of trees, dead wood (standing or fallen), soil, and cavities left by small vertebrates such as lizards (Shattuck, 1999; Wheeler, 1915). They likely do not excavate their nests (Wheeler, 1915). However, they contain living storage workers, also known as repletes, which store liquid food in their gasters (Shattuck, 1999). This food is transferred to repletes from returning foragers, and replete abdomens become too extended for them to leave the nest (Shattuck, 1999). This aids in protection of the colony, and likely in food distribution during periods of environmental stress (McClenahan et al., 2017). Colonies average about a few hundred workers with a single queen (Shattuck, 1999).

#### *Data collection*

First, I identified the ant species *A. longiceps* and *L. erythrocephalus*, sorted them, and counted them. I analyzed and compared this data to past data, which shows the presence of each species in year 21 post-fragmentation. By comparing post-fire data to pre-fire data, I was able to examine differences in the presence of each species in the controls, the matrix, the small, medium, and large fragments, and where tree char height and topkill, topography, and proximity to fragment edge differed.

#### *Data analysis*

We used generalized linear mixed models (GLMM) with a binomial distribution to separately examine the pre-fire and post-fire difference in each ant species' presence in controls,

matrix, and fragments. We also examined the impact of fragment size, distance to edge, and topography on each ant species abundance. We used the R package lme4. We included the fixed effects for categorical variables 1) Fragmentation (controls, matrix, fragments), 2) Fragment size (small, medium, large), 3) Edge (edge, core), and 4) Topography (slope, drainage). The random effects Replicate (unique identifier for each replicate, 1-6) and Patch (unique identifier for each patch, 1-18) were included in all models.

We then used a Bayesian GLMM to look at the interaction between fragmentation and time. We considered only presence/absence data and used a Bayesian approach because of the small amount of data collected within each year. We included the fixed effects 1) Fragmentation, a categorical variable with three levels: controls, matrix, and fragments, and 2) Year, a numerical variable for years since fragmentation. We included the random effects Replicate (unique identifier for each replicate, 1-6), Patch (unique identifier for each patch, 1-18), and Site (unique identifier for each site, 1-188).

We used a bayesian GLMM to study the effects of fire on ant occurrence post-fire. Fire effects were measured as char height up *Eucalyptus* trees and *Eucalyptus* topkill. Char height (cm) along *Eucalyptus* trunks is a proxy measurement for flame height or residence time. *Eucalyptus* trees experience topkill if they do not resprout epicormically. Topkill is a binary variable where a tree either experiences topkill or resprouts epicormically. We included fragmentation (categorical: control, matrix, or fragment), char height (numerical) and topkill (binary) as fixed effects and replicate, patch, and site as random effects in our analysis.

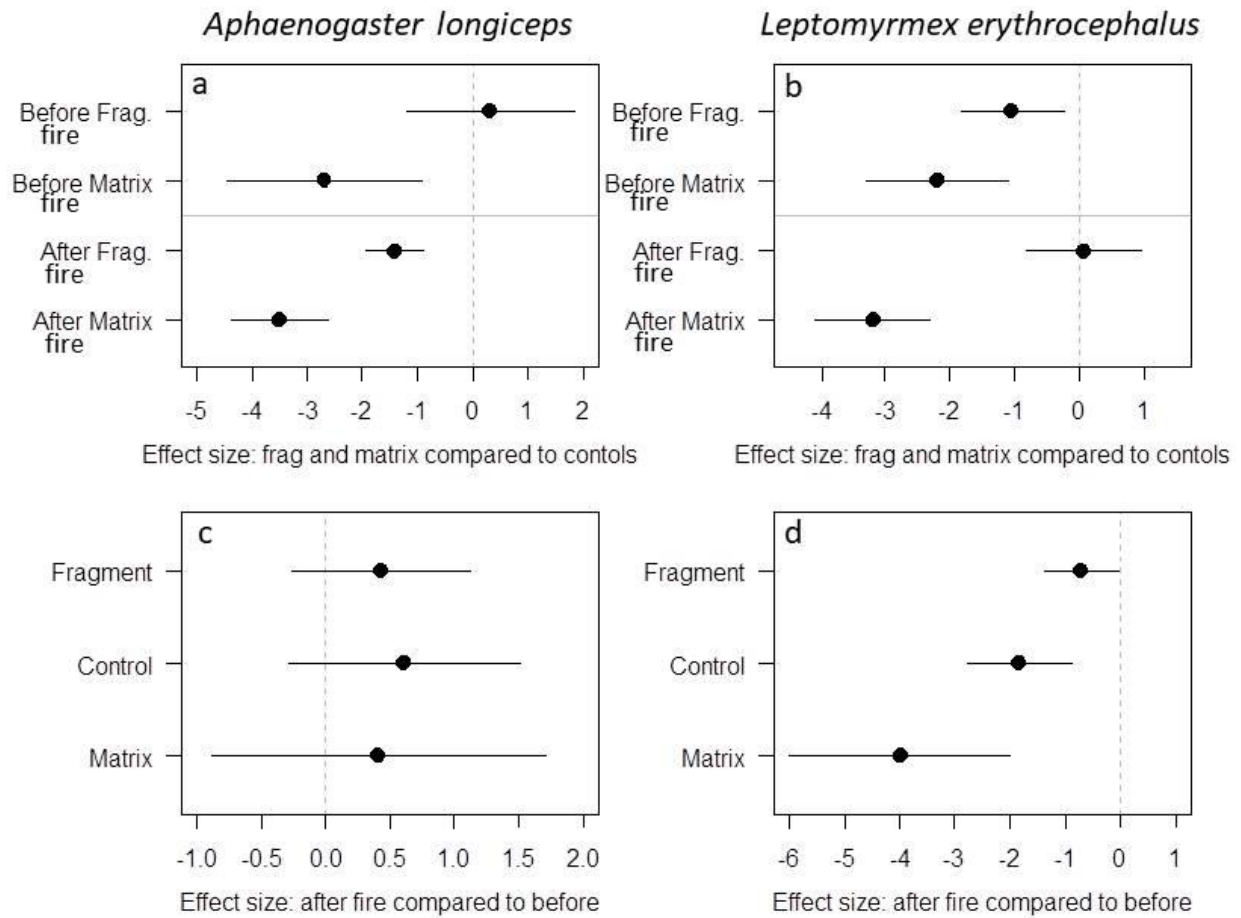
## Results

I compared the effect of fire and forest fragmentation on two abundant species of ant, *A. longiceps* and *L. erythrocephalus*. Overall, the fire impacted *A. longiceps* and *L. erythrocephalus*

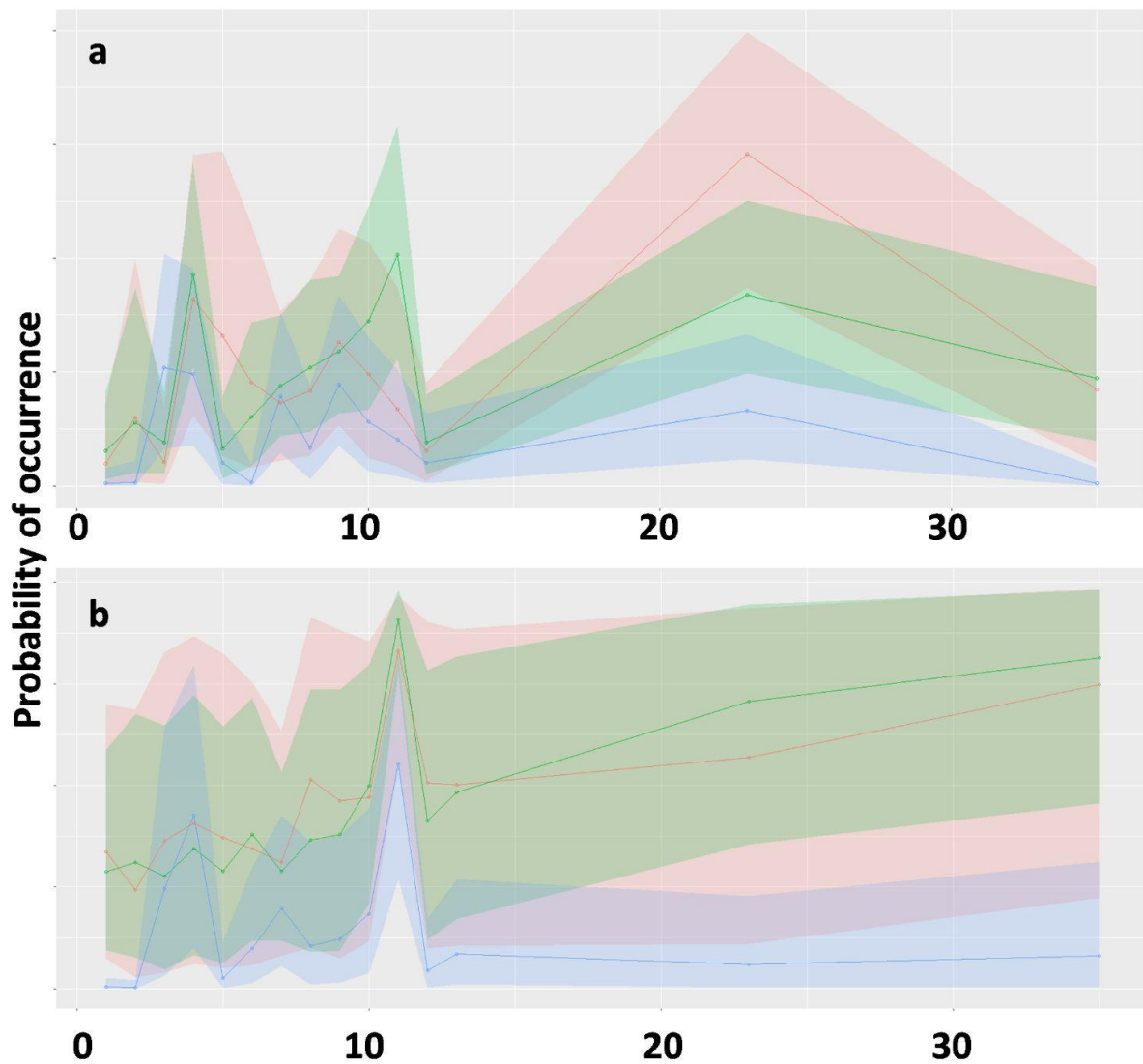
differently. Both species were rare in matrix habitat compared to controls before the fire and were absent from the matrix after the fire (Fig. 4 a and b). However, *A. longiceps* presence was not significantly reduced by fire in any given part of the landscape (fragment, matrix, controls) compared to before the fire (Fig. 4 c); in fact, *A. longiceps* had a tendency to increase in probability of occurrence in both fragments and controls after fire (Fig. 5 a). In contrast, *L. erythrocephalus* occurred less frequently in all parts of the landscape after the fire compared to before the fire (Fig. 4 d, Fig. 5 b). Compared to controls, fire homogenized the presence of *L. erythrocephalus* in fragments and matrix (Fig. 4 b) but reduced the presence of *A. longiceps* in fragments (Fig. 4 a).

After the fire, impacts of edge effects (AL: d.f. = 2, chisq = 0.07, P = 0.97; LE: d.f. = 2, chisq = 3.30, P = 0.19), and effects of topography (AL: d.f. = 3, chisq = 7.44, P = 0.06; LE: d.f. = 3, chisq = 0.22, P = 0.97) were not statistically significant for either species (see also Supplement Figures S1 and S2, Bayesian analyses). For *A. longiceps* there was a significant effect of fragment size, with ants most likely to occur in medium and small fragments and least likely to occur in large fragments (AL:d.f. = 3, chisq = 26.95, P = <0.001). There was no effect of size for *L. erythrocephalus* (LE: d.f. = 3, chisq = 3.94, P = 0.27).

Finally, *L. erythrocephalus* was less likely to occur in fragments than controls where fire severity was greatest, as measured by the char height of trees, and *A. longiceps* appeared unimpacted by fire severity (Fig. 6). Further, both species were less likely to occur in fragments where topkill was highest (Fig. 7).



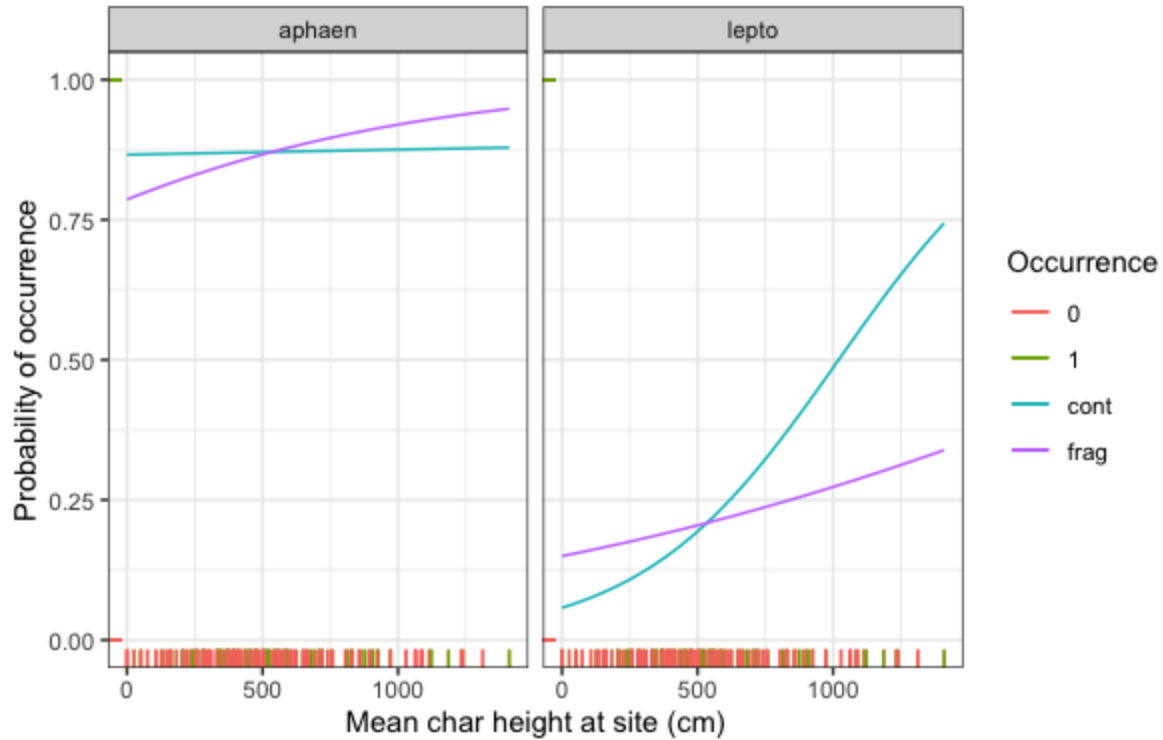
**Figure 4.** Effect size plots of *Aphaenogaster longiceps* and *Leptomymex erythrocephalus* occurrence: **a and b**) before and after fire in fragments and the matrix compared to controls. In these plots the gray, hashed line represents the probability of occurrence in the controls. Error bars are 95 % CI and where they do not cross the gray line, the difference in probability of occurrence is significant. **c and d**) in fragments, controls and the matrix after the fire compared to before the fire. In these plots the gray, hashed line represents the probability of occurrence in that part of the landscape before the fire. Error bars are 95 % CI.



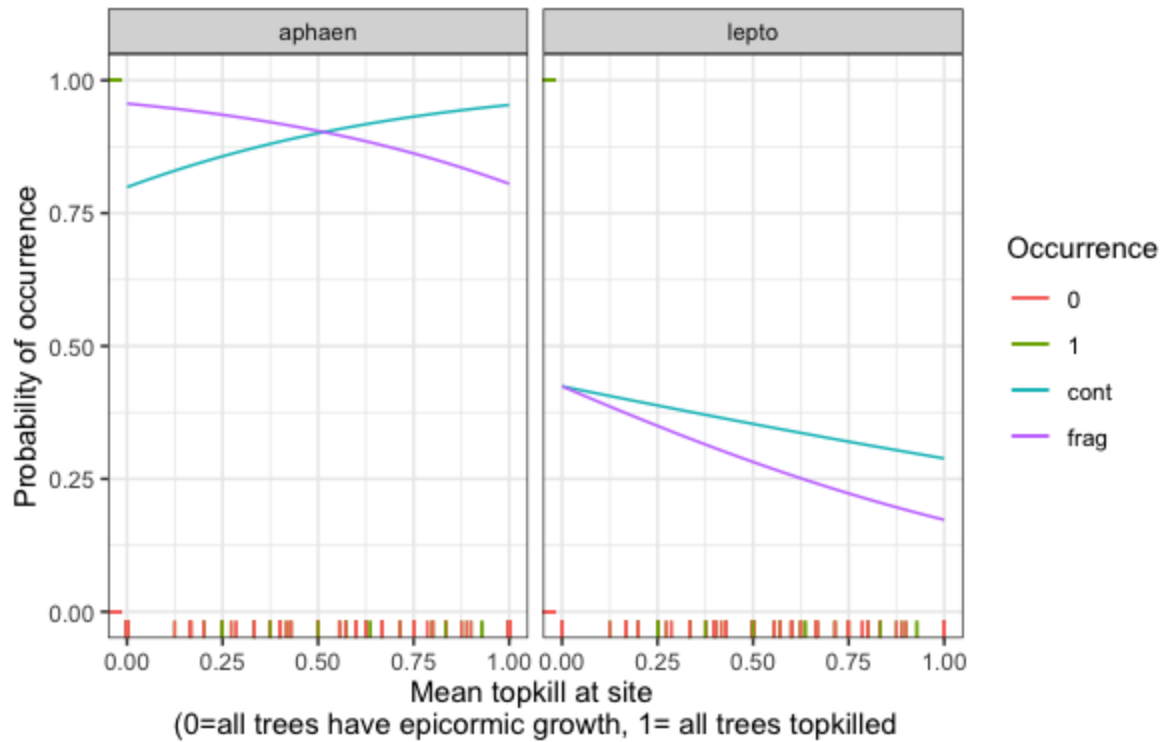
**Figure 5.** Probability of occurrence of a) *Leptomyrme erythrocephalus* and b) *Aphaenogaster longiceps* across biological time (years) in fragments (green), matrix (blue) and controls (red).

The fire occurred in January-February, 2020.





**Figure 6.** Impact of *Eucalyptus* char height and forest fragmentation on *L. erythrocephalus* (right) and *A. longiceps* (left) presence in controls (blue) and fragments (purple). Red and green bars represent presence and absence.



**Figure 7.** Impact of *Eucalyptus* topkill and forest fragmentation on *A. longiceps* (left) and *L. erythrocephalus* (right) presence in controls (blue) and fragments (purple). Red and green bars represent presence and absence.

## Discussion

My predictions that *A. longiceps* would not significantly decrease in occurrence post-fire due to habitat type, fire severity, topography, or proximity to fragment edge were supported by the results; although *A. longiceps* had a tendency to occur less frequently in fragments where topkill was highest. In fact, they had a slight overall increase in occurrence in fragments and especially in controls, possibly because the fire made soil conditions more preferable. *A. longiceps* often resides in sandy, dry soil (Shattuck, 2008) and are common in *Eucalyptus* forests and semi-arid regions, which are suggestions that would improve survival through wildfires (Richards, 2009). This survival is likely aided through their deep tunnels (Richards, 2009). Further, fire can positively affect species that prefer open or disturbed areas and/or species who forage on seeds, like *A. longiceps* (Matsuda et al., 2011). My prediction that fragment size would not affect *A. longiceps* occurrence was not supported, as they were most likely to occur in medium and small fragments and least likely to occur in large fragments. Their occurrence was not measured directly pre-fire (32 years post-fragmentation), so it is possible they may have further decreased in the matrix and subsequently in fragments compared to controls. This would explain why post-fire they increased in occurrence the most in controls.

*A. longiceps*' response to fire is similar to findings regarding *A. sutherlandi*, the funnel web spider, also at Wog Wog. The funnel web spider was resilient to fire, possibly by burrowing underground (Wyatt, 2022). Species that can go beneath the soil surface may survive fire more by evading direct mortality. However, *A. longiceps* long-term response may change as succession continues, especially because fire can affect ant diversity and occurrence indirectly, through interspecific competition, food resources, and habitat changes (Farji-Brener et al., 2002).

My predictions that post-fire *L. erythrocephalus* would be less likely to occur, and that topography or fragment size would not directly change their occurrence, were also supported by the results. My prediction that they would be less likely to occur where fire severity was greatest was partially supported, as they were less likely to occur in fragments than controls; char height and topkill were greatest for trees in fragments compared to controls. 12 years pre-fire (21 years post-fragmentation), *L. erythrocephalus* were less likely to occur in fragments than controls, likely due to decreased occurrence in the matrix and associated population isolation and extinction in fragments (McClenahan et. al., 2016). This was likely also the case directly pre-fire, which would explain their reduced occurrence in fragments where fire severity was greater. However, proximity to fragment edges did not affect their occurrence, despite topkill and char height being greater in fragment cores. *L. erythrocephalus*' overall decrease in occurrence post fire is likely due to their niche preference. Because they reside in shallow nests (Shattuck, 1999; Wheeler, 1915), their colonies likely directly burned in the fire.

The contrasting occurrences of *A. longiceps* and *L. erythrocephalus* post fire are likely determined by their niches. The same disturbance can have different impacts on species due to factors such as habitat openness (Anderson, 2018). Therefore, the composition of ant biodiversity directly after a fire often depends on the levels of direct mortality caused by the fire (Arnan et al., 2006). Ants that reside above or shallowly below ground, like *L. erythrocephalus*, are the most susceptible to direct disturbance impacts (Anderson, 2018). For instance, one leaf-nesting ant species, *O. smaragdina*, is sensitive to fire as it directly burns nests that are close to the ground (Anderson, 2018). For our results, nesting habits explains the decrease in occurrence of *L. erythrocephalus* and the lack of decrease in occurrence of *A. longiceps*.

In summary, I examined the response of *A. longiceps* and *L. erythrocephalus* to habitat fragmentation and wildfire. I found that while *A. longiceps* was largely resilient to fire, *L. erythrocephalus* was not. I suggest that *A. longiceps* may have survived better due to their deep nests, whereas *L. erythrocephalus* may have been negatively impacted because of their shallow nests. Examining the responses of different ant species to wildfire can help us to understand how niche preference changes species occurrence. It can also help with future predictions as to how ant species may respond to fire in a fragmented landscape. Subsequently, it can allow us to understand how various important ecosystem processes that are provided by ants, like bioturbation and seed dispersal, are affected.

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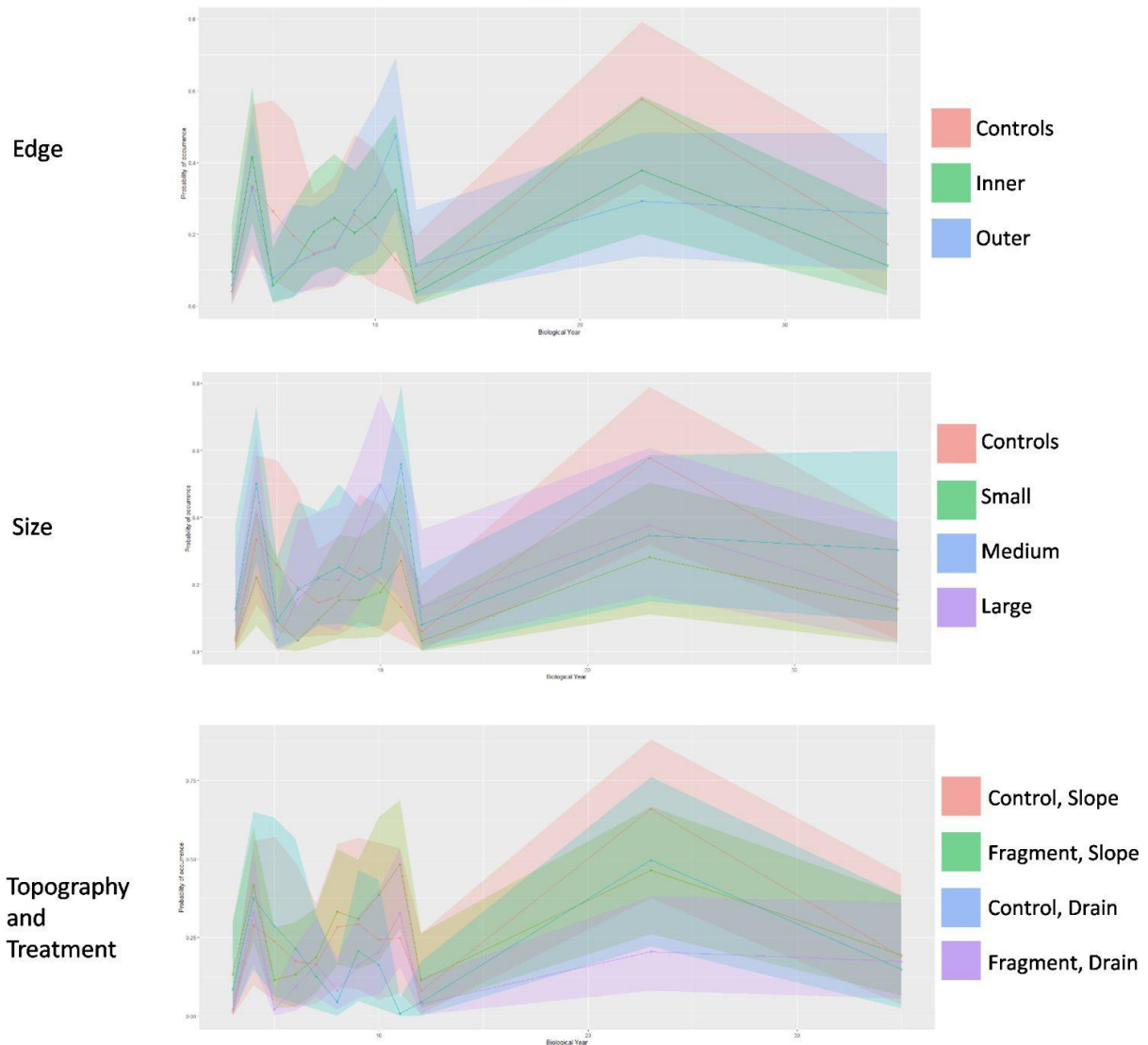
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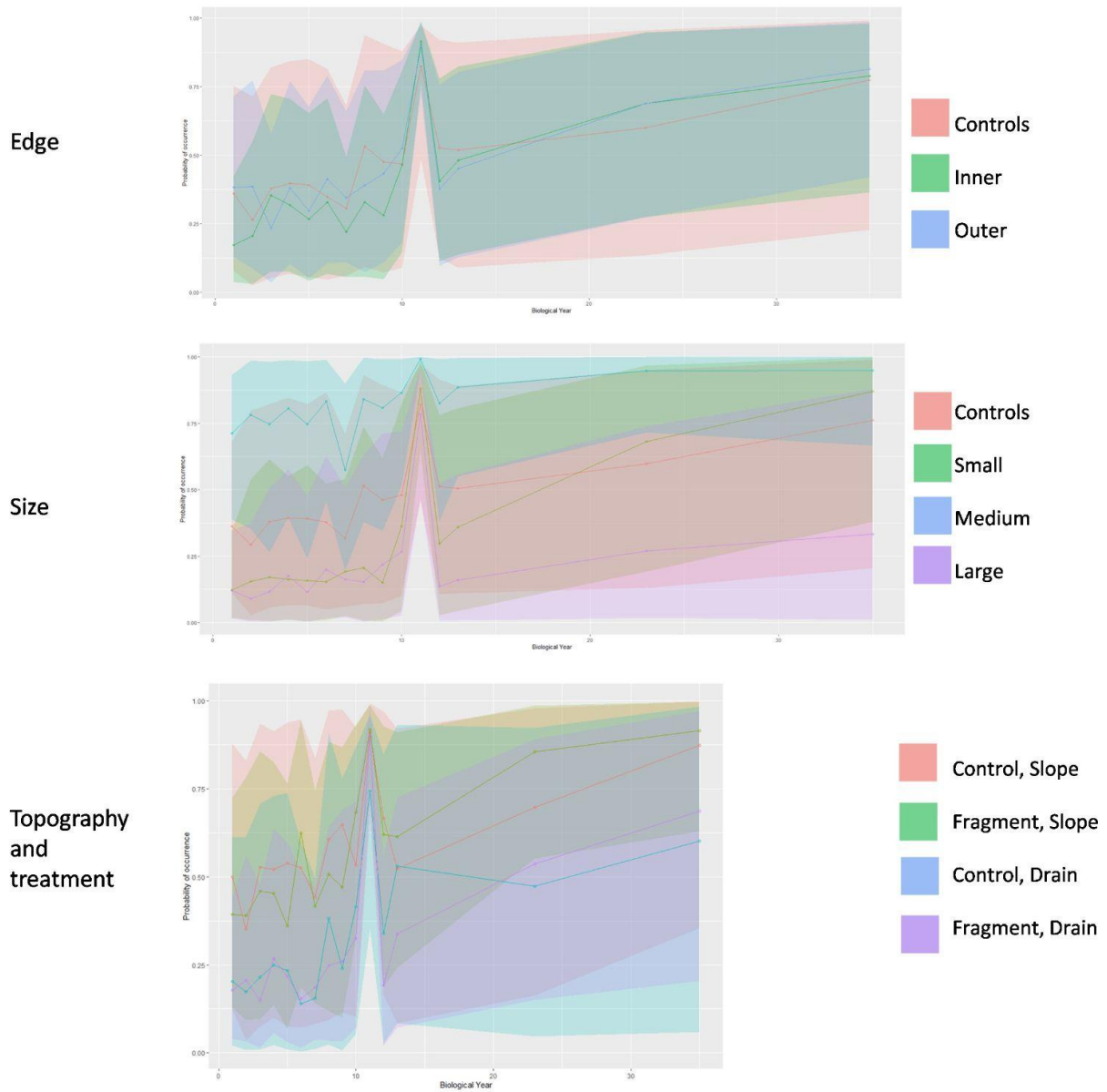


## Supplemental figures



**Figure S1.** Probability of occurrence of *Leptomyrmex erythrocephalus* across biological time for different treatments: edge effects, size effects and a topography-fragmentation interaction.

Analyses are Bayesian GLMM and error bars are 95% credible intervals.



**Figure S2.** Probability of occurrence of *Aphaenogaster longiceps* across biological time for different treatments: edge effects, size effects and a topography-fragmentation interaction.

Analyses are Bayesian GLMM and error bars are 95% credible intervals.