The Effects of Long-Term Habitat Fragmentation on Ant Communities and Their Contributed Ecosystem Functions in an Australian Eucalyptus Forest

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THE EFFECTS OF LONG-TERM HABITAT FRAGMENTATION ON ANT COMMUNITIES
AND THEIR CONTRIBUTED ECOSYSTEM FUNCTIONS IN AN AUSTRALIAN
EUCALYPTUS FOREST

by

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The effects of long-term habitat fragmentation on ant communities and their contributed ecosystem functions in an Australian *eucalyptus* forest, written by Jeffrey L. McClenahan, has been approved for the Department of Ecology and Evolutionary Biology

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.
ABSTRACT

A crucial ecological question for the twenty-first century is how organisms will respond to the threat of habitat fragmentation. My dissertation is focused on determining the impacts of long-term experimental habitat fragmentation on ant communities in southeastern Australia. I use ants as a model organism because they play a crucial ecological role in Australian environments. My research was conducted at the Wog Wog Long-term Habitat Fragmentation Experiment in New South Wales, Australia.

First, I follow two ant species through 21 years of fragmentation to determine how their responses change over time. I found that *Leptomyrmex erythrocephalus* was not affected by fragmentation in the short term, but 21 years after fragmentation, it was less likely to occur in mature pine matrix and fragments than in continuous forest controls. *Aphaenogaster longiceps* was equally likely to occur in the fragments, controls and pine matrix early in the experiment but by year 21 post-fragmentation was less likely to occur in the pine matrix than fragments or controls. I conclude that changes in matrix suitability and specific habitat characteristics influence ant persistence in *Eucalyptus* fragments.

Next, I determine the relative importance of dispersal and selection by the environment for ant communities in which the spatial context of communities has been altered by experimental habitat fragmentation, compared to unaltered controls. I show that fragmentation increased the role of dispersal in the assembly of communities in small and medium fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments.
fragments. I demonstrate that the processes that determine community assembly are altered when the spatial context of a community changes.

Finally, I determine the impacts of habitat fragmentation on ant-mediated seed removal. Fragmentation increased the rate of seed removal in large fragments and fragment cores by changing the environment. Fragmentation reduced the number of seeds removed per ant in small fragments by reducing temperature and increased the number of seeds removed per ant in medium and large fragments by reducing grass coverage. This study shows that fragmentation can alter seed removal through changes to the environment that alter ant behavior.
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CHAPTER ONE

INTRODUCTION

The response of native flora and fauna to human activities poses one to the most pressing ecological concerns for the twenty-first century (Ellis and Ramankutty 2008). Human population is expected to increase from 7.3 billion in 2015 to 9.7 billion by the year 2050 (http://www.un.org/en/development/desa/news/population/2015-report.html) and a 2011 United Nations Environmental Program report estimated that a tripling of global resource extraction would be need to accommodate such population growth (Fischer-Kowalski et al. 2011). Current demand for natural resources has resulted in habitat fragmentation and loss to such a degree that habitat loss and fragmentation is now regarded as the greatest threat to global biodiversity (Pereira et al. 2010; Rands et al. 2010). Accompanying this threat is the emerging acknowledgement that crucial ecosystem functions are linked to resident communities and thus may also be threatened by habitat fragmentation (Loreau 2010; Tilman 2014). Given the two opposing trajectories of increased demand for natural resources and the potential for disruptions to biodiversity and ecosystem function it is crucial to understand how native organisms are affected by habitat fragmentation and the mechanisms by which habitat fragmentation may directly or indirectly impact ecosystem function.

The aim of my research is to determine the impacts of long-term habitat fragmentation on ant communities and their contributed ecosystem functions in a southeast Australian Eucalyptus forest. Specifically, I use the Wog Wog Long-Term Habitat Fragmentation Experiment (Wog Wog), located in southern New South Wales, Australia to understand, 1) how habitat fragmentation and a maturing pine matrix affects ant populations over 21 years, 2) the relative influence of spatial and environmental variables on ant community assembly in a fragmented
landscape, and 3) the direct and indirect pathways by which habitat fragmentation affects ant-mediated seed removal.

I study ants because ants are an important component of Australian ecosystems because of their diversity and biomass (Shattuck 1999). Ants are ubiquitous and are easy to collect. Additionally, there are broadly accepted sampling strategies, which make ants excellent organisms for study comparison between ecosystems (Agosti et al. 2000; Lach and Parr 2010). Ants play an important role in ecosystems, providing nutrient cycling functions, soil aeration, and seed dispersal (Benckiser 2010; Crist 2009; Palladini et al. 2007). Consequently, loss of ant biodiversity can have deleterious consequences such as slower rates of leaf litter decomposition and seed dispersal (Sanders and van Veen 2011; McGlynn and Poirson 2012).

Habitat fragmentation is the result of dividing once continuous native habitat into small, isolated remnants. This results in reduced habitat connectivity and decreases the amount of available suitable habitat for resident organisms. Habitat fragmentation can occur via urban development (Nufio et al. 2009), road construction, mining and resource extraction, and agriculture and forestry plantation establishment (Fahrig 1997; Fahrig 2003; Debuse 2007; Lindenmayer and Fischer 2007).

In chapter 2, I follow two ant species through 21 years after fragmentation at Wog Wog to determine how their responses to fragmentation changes over time as the matrix is first clear cut, then planted and eventually matures. I focus on the two ant species that represent the only remaining data for the early years of the experiment, *Leptomyrmex erythrocephalus* and *Aphaenogaster longiceps*. I found that *L. erythrocephalus* was not affected by fragmentation in the short term, but that 21 years after fragmentation, it was less likely to occur in both the mature pine matrix and fragments than in continuous forest controls. *A. longiceps* was equally likely to
occur in the fragments, continuous forest and pine matrix early in the experiment but by year 21 post-fragmentation was less likely to occur in the pine matrix than fragments or controls. I conclude that the response of ant populations to habitat fragmentation may take longer to detect than previously believed and that isolation of ant populations on fragments can be driven by the habitat characteristics of the matrix, which can change over time. This chapter is published as: McClenahan, J.L., Melbourne, B.A., Cunningham, S.A., Davies, K.D. (2016) Differential and delayed response to habitat fragmentation via the introduction of a pine matrix. *Ecological Entomology* 41: 554-561.

In recent decades, the effects of habitat fragmentation on community structure and persistence have been summarized by the metacommunity concept. A metacommunity is defined as a set of local communities connected by dispersal and consists of four fundamental scenarios; species sorting, mass effects, patch dynamics, and neutral theory. Each of these represents the varying influence of rate of dispersal, competitive ability, and suitability of habitat (Leibold et al. 2004; Holyoak et al. 2005). A recent community ecology synthetic framework identifies just four processes that structure communities: selection, dispersal, drift and speciation (Vellend 2010). I use this framework to understand how fragmentation changes ant community assembly. When landscapes are fragmented, the influence of dispersal and selection can be altered, resulting in changes to community assembly.

In chapter 3, I apply Vellend’s community ecology framework to understand the processes that determine ant community structure at Wog Wog. Specifically, I determine how the roles of dispersal and selection are altered, and how this results in significant changes to ant community assembly. I hypothesize that experimental fragmentation will alter community assembly on fragments compared to controls in two ways. 1) By changing the abiotic
environment, the spatial distribution of species’ niches, and thereby altering the distribution and abundance of species on fragments (changing the importance of selection). 2) By reducing dispersal between fragments and isolating populations of species on fragments. I show that fragmentation increased beta diversity, the spatial heterogeneity of species composition, and reduced the richness of fragments. I also demonstrate that compared to controls, fragmentation increased the role of dispersal in the assembly of communities in small fragments, and, to a lesser extent, medium fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments. I conclude that the processes that determine community assembly (selection, dispersal) are altered when the spatial context of a community is changed, and that fragment size can alter the relative roles of the processes that drive assembly.

An important extension to the understanding of the way habitat fragmentation can alter community assembly is the emerging focus on how fragmentation influences community contributed ecosystem functions. While there is broad acceptance of the link between biodiversity and ecosystem function, there is debate about the relative roles of different aspects of biodiversity (Vellend et al. 2013; Gonzales et al. 2016; Vellend et al. 2017) and the mechanisms by which habitat fragmentation affects ecosystem function (Oliver et al. 2015; Milligan et al. 2017). For example, does habitat fragmentation directly affect biodiversity, which then leads to changes in ecosystem function? Or does fragmentation alter the abiotic environment, which in turn leads to more or less favorable conditions for communities leading to changes in ecosystem function?

In chapter 4 I determine the pathways by which habitat fragmentation affects ecosystem processes. Specifically, I asked: 1) Does habitat fragmentation alter seed removal in forest fragments versus continuous forest, in fragments of different size and at fragment edges? If yes:
2) is the change in seed removal linked to the number of ant species at a site, which species are present, or how many ant individuals are present? 3) Do changes to the environment, that are the result of experimental fragmentation, affect the rate of ant seed removal? I show that habitat fragmentation increased seed removal in large fragments and fragment cores and that the number of seeds removed from a site was determined by the total number of ant individuals present at a site. Interestingly, fragmentation did not alter seed removal by directly altering the total number of ants at a site. Instead, fragmentation modified the environment so that more/fewer seeds were removed in different parts of the fragmented landscape, compared to continuous forest. Specifically, fragmentation reduced the number of seeds removed per ant in small fragments by reducing temperature there. Additionally, fragmentation increased the number of seeds removed per ant in medium and large fragments by reducing grass cover. More seeds were removed when grass cover was low. My results help disentangle which aspects of ant biodiversity are impacted by fragmentation and how these are linked to seed removal. I also highlight that fragmentation driven changes to seed removal can be the result of direct effects of fragmentation on the environment that alter ant behavior.
CHAPTER TWO

DIFFERENTIAL AND DELAYED RESPONSE OF TWO ANT SPECIES TO HABITAT FRAGMENTATION VIA THE INTRODUCTION OF A PINE MATRIX

Abstract

Ants are a ubiquitous and crucial component of Australian *Eucalyptus* forests, but responses to long-term habitat fragmentation remain poorly understood. We followed two ant species across a 21-year history of pine plantation establishment and maturation in a southeast Australian *Eucalyptus* forest. At Wog Wog in southeastern Australia, Native *Eucalyptus* forest was clear-cut to make way for plantation establishment and twelve remnant patches of forest were left intact and subsequently surrounded by a pine matrix. Pitfall traps were placed in continuous native forest, remnant *Eucalyptus* patches, and the pine matrix between fragments, and were stratified based on proximity to remnant patch edges and habitat type. We focus on two ant species that represent the only remaining data for the early years of the experiment.

While *Leptomyrmex erythrocephalus*, the rarer of the two species, was not affected by fragmentation in the short term, 21 years after fragmentation, it was less likely to occur in both the mature pine matrix and fragments than in continuous forest controls. *Aphaenogaster longiceps* was equally likely to occur in the fragments, continuous forest and pine matrix early in the experiment but by year 21 post-fragmentation was less likely to occur in the pine matrix than fragments or controls. Importantly, we only detected negative impacts of fragmentation on ant occurrence as the pine plantation matrix matured and isolated ant populations on fragments.

We conclude that changes in matrix suitability and specific habitat characteristics influence ant persistence in *Eucalyptus* fragments.
**Introduction**

Native habitats are crucial for the preservation of endemic organisms, yet they are increasingly threatened by habitat loss and fragmentation (Tscharntke et al. 2012; Ibáñez et al. 2014). The widely acknowledged negative impacts of habitat fragmentation on global biodiversity continue to grow with the ever-increasing demand for natural resources (Fahrig 1997; Tscharntke and Steffan-Dewenter 2002; Dauber et al. 2006; Cardoso et al. 2013; Haddad et al. 2015). Classic habitat fragmentation theory posits that isolation, habitat area, and edge effects are the primary drivers of biodiversity loss (Haddad et al. 2015). However, it is increasingly recognized that the type of matrix habitat surrounding fragments, and time since fragmentation both have large impacts on species survival in fragmented landscapes (Driscoll 2013; Haddad et al. 2015).

Habitat fragmentation occurs when land use change breaks up once-continuous habitat into smaller, isolated patches surrounded by a matrix that can consist of agriculture, road construction, housing developments, mining activities, and forest plantations (Lindenmayer and Fischer 2006; Ewers and Didham 2006). Remnant fragments of native habitat within this matrix may no longer support resident populations due to a reduction in food resources, nesting sites, or mate availability (Davies and Margules 1998; Nufio et al. 2009). Responses of species to fragmentation can include changes in the spatial distribution of populations within remnant patches and matrix (Debuse et al. 2007; Sobrinho and Schoereder 2007) and increased risk of population extinction for species with lower abundances within patches (Caughley 1994). Alternatively, species may be able to use the intervening matrix habitat, which may reduce their extinction risk on patches compared to species that are isolated on patches (Davies et al. 2004). This range of responses can be detected as within-patch changes in species occurrence (Davies
and Margules 1998) or different patterns of occurrence between remnant patches and surrounding matrix (Palladini et al. 2007).

Worldwide, only a handful of fragmentation experiments have been conducted for more than two decades (Haddad et al. 2015). These include the Biological Dynamics of Forest Fragments Experiment (Brazil, 34 years), the Kansas Old-Field Succession Experiment (USA, 29 years), the Wog Wog habitat fragmentation experiment (Australia, 28 years), the Savannah River Corridor Experiment (USA, 21 years), and the Canadian Boreal Forest Experiment (Canada, 20 years). With so few experimental studies lasting more than 10 or 20 years, our understanding of the long-term impacts of habitat fragmentation currently may be incomplete. The Wog Wog experiment in southeast Australia provides an excellent opportunity to investigate both short- and long-term population responses in a landscape fragmented as the result of land use change.

A crucial, yet often neglected, consideration in fragmented landscapes is how temporal changes affect populations, both in remnant patches of native habitat and in the matrix (Debinski and Holt 2000; Driscoll et al. 2013). At Wog Wog, temporal changes began when the land surrounding the patches, the matrix, was clear-cut, removing forest habitat but also altering the environment of the remaining patches, most notably by altering fluxes of light, temperature and wind. Pine seedlings were planted and conditions within the matrix plantation changed rapidly over time: pine growth rate is typically between 1.0 and 1.5 m/yr with trees reaching maturity between 25 and 35 years (Waterworth et al. 2007). With a forest matrix, as the pines grow, the environment of both the matrix, and forest fragments, change: most often reported are changes in light availability, temperature, understory, and leaf litter (Driscoll et al. 2013). Changes to matrix habitat can, in turn, increase or decrease matrix permeability for a given species (Driscoll et al. 2013).
2013) so that this also changes with time. Thus, as the environment changes, the impact of the spatial effects of fragmentation and the environment on population persistence may vary (Debinski and Holt 2000; Tscharntke and Stoffan-Dewnteter 2002; Ewers and Didham 2006). In this study we investigate the impact of temporal changes by following the fates of two ant species over 21 years post-fragmentation in a native *Eucalyptus* fragment/pine plantation system.

Ants play an important role in ecosystems, providing seed dispersal, soil aeration, and nutrient cycling functions (Benckiser 2010; Crist 2009; Palladini et al. 2007). Loss of ant biodiversity can have deleterious bottom-up consequences such as slower rates of leaf litter decomposition and seed dispersal (Sanders and van Veen 2011). Ants are an especially important component of Australian ecosystems because of their diversity and biomass (Shattuck 1999), and we need to better understand how they respond to habitat fragmentation, including the effects of patch size, edges, and the matrix (Leal et al. 2012; Driscoll et al. 2013; Sweaney et al. 2014).

In this paper, we report results from the Wog Wog long-term habitat fragmentation experiment (Wog Wog) located in New South Wales, Australia. We examine the long-term responses of two species of ants (*Leptomyrmex erythrocephalus* and *Aphaenogaster longiceps*) followed through the first 11 years of a 24-year study and then again in year 24 of the study. These data represent the only surviving ant data for the early part of the Wog Wog experiment. Because the experiment represents one of just a handful of fragmentation experiments globally (Haddad 2015) the data presented here represent the only ant data collected that examine the experimental effects of fragmentation on ant populations in temperate forest that span decades. In year 24 and beyond, we have collected data on the entire ant community and the response of the community will be presented in future papers (Chapters 3 and 4). However, unlike for the two data sets presented here, it will not be possible to compare these data with data collected.
soon after fragmentation.

We asked: 1) Does occurrence probability of the two ant species change within remnant *Eucalyptus* patches, the pine plantation matrix, and continuous-forest controls across three post-fragmentation time periods? We predict that occurrence probability will decrease in the fragments and matrix through time. In the first four years, we expect occurrence to be lower in the fragments and pines compared to controls. Over time we predict that occurrence will rebound slightly in the pine sites and decrease slightly in the fragments as the pines mature and clear-cut areas recover from the disturbance of plantation establishment (Gómez and Abril 2011; Franklin 2012). 2) Is the occurrence of two ant species different in differently sized patches, in fragment edge versus core habitat, and in slope versus drainage line habitat, and does occurrence change relative to these features over time? We predict that occurrence will decline in patch edges relative to patch interiors and controls. We also predict that occupancy will decline in smaller patches relative to larger patches (Crist 2009; Brandão et al. 2011; Dohm et al 2011).

**Materials and methods**

**Study site**

The Wog Wog experiment is located in southeastern NSW, Australia, 17 km southeast of Bombala (37 degrees 04'30"S, 149 degrees 28'00"E; Fig. 1). Wog Wog was established in 1984 and was conceived as an experiment that would run over the course of a number of decades. The experimental design has been described by Margules (1993) and Davies and Margules (1998), and thus what follows is mainly a description of the methodology used in this particular investigation.

The layout of the experiment consists of six replicates, each of which is composed of three
differently sized patches (18 patches). The patch sizes are 0.25 ha (small), 0.875 ha (medium), and 3.062 ha (large), with each subsequently larger patch 3.5 times the size of the next smallest patch. The 18 patches were marked out during the southern hemisphere summer of 1984–1985 in what was then continuous *Eucalyptus* forest, and followed a randomized block design. Sampling began in 1985 and two years of data were collected before any clear-cutting. In 1987 the forest surrounding replicates 1–4 (Fig. 2-1) was clear-cut and planted with *Pinus radiata*, a non-native tree species. This created 12 remnant patches of *Eucalyptus* forest surrounded by a pine plantation. Replicates 5 and 6 (Fig. 2-1) were maintained in adjacent continuous *Eucalyptus* forest as control sites. The two control replicates serve as comparison against fragmented forest at both a seasonal and annual level.

Within each remnant patch eight monitoring sites were established, each containing two pitfall traps, for a total of 144 monitoring sites (288 traps). Sites were stratified into edge sites or core sites based on distance from remnant edge. Edge location was defined as those monitoring sites located within five meters of the patch edge. Because previous vegetation sampling by Austin and Nicholls (1988) had demonstrated an association between vegetation and topography, the eight sites were also stratified into either slope or drainage sites. The resulting mix of monitoring sites is 2 slope/edge sites, 2 slope/core sites, 2 drain/edge sites and 2 drain/core sites. An additional 44 monitoring sites (88 pitfall traps) were established within the pine matrix, stratified into either drainage or slope sites, for a total of 188 monitoring sites experiment-wide.

*Ant sampling*

Ant sampling occurred three times a year from 1985–1996 and again in 2009–2010. Sampling took place in November (Spring), February (Summer), and May (Autumn) with pitfall traps being opened for seven days during each sampling period. Traps were charged with 150 ml
Fig. 2-1. Map of the Wog Wog Long-Term Habitat Fragmentation Experiment showing forest remnants and control plots in continuous forest. Dots represent approximate locations for monitoring sites in the pine matrix.
of solution consisting of 73% ethanol (95%), 25% glycol, and 2% formalin poured into 16 oz (473 ml) plastic cups. The two traps associated with each monitoring site were pooled. Ants were filtered from pitfall solution and identified to species level using Shattuck (1999) and Wheeler (1934).

Data analysis

Data analysis was conducted in R (www.r-project.org) using the Ime4 package for mixed models. Since ants live in colonies, abundance in pitfall traps is likely biased by proximity of a trap to a colony. Therefore, I used ant presence-absence rather than abundance as the dependent variable in my models.

The fixed effects variables in my model were:

1) Treatment, three levels: i) fragments, ii) controls, iii) pines. This tests for the effects of forest fragmentation.

2) Patch size nested within fragments, three levels: i) small, ii) medium, iii) large. This tests for the effects of the size of remnant forest fragments.

3) Topography, two levels: i) slopes, ii) drainages: This test for the effects of topographic features which are known to have associated vegetation types.

4) Edge nested within fragments, two levels: i) edge, ii) core: This tests for the effects of edges within remnant patches.

5) Presence/absence before fragmentation: This is a covariate that controls for patterns in occurrence of the ant species in control sites and remnant patches before fragmentation. This covariate was not included in models including pines as no data were collected in what is now the pine matrix prior to clear cutting in 1987.

The experiment has a nested design, with occurrence probability being estimated at three
spatial scales: monitoring site, which is located within a remnant patch; remnant patch, which is located within a replicate; and replicate. To account for the residual variation associated with the spatial variable, two random effects variables were included in all models:

1) Replicate: six levels corresponding to the grouping of three remnant patches with one each of small, medium, and large.

2) Patch: 18 levels for models that did not include the pine matrix and 40 levels for models that did include the pine matrix.

Data were sparse and so I grouped data into four time periods: 1) the two years prior to fragmentation, 2) post-fragmentation years one through four, 3) post-fragmentation years five through eight, and 4) post-fragmentation year 21. Data for the two ant species was pooled within these time periods for each monitoring site. Year refers to biological year, which for the southern hemisphere starts in October. Pre-fragmentation presence/absence data were included in models as a covariate, as described above. The year of actual fragmentation was omitted from the analysis since this was the year of clear-cutting and debris was burned during establishment of the experimental fragments.

**Results**

Because data were aggregated I do not make comparisons of absolute occurrence between time periods but rather of relative occurrence among treatments within time periods.

The probability of occurrence of *Aphaenogaster longiceps* and *Leptomyrmex erythrocephalus* was influenced by time since fragmentation, treatment type (fragment/control/pine matrix) and topographic feature (slope/drainage; Figs 2-2 and 2-3) and before fragmentation presence/absence patterns in remnant patches did not change significantly
over time.

For *A. longiceps* (Fig. 2-2a, Fig. 2-3), there was no significant difference in probability of occurrence among the fragments, controls, and pine matrix in years 1-4 (p = 1.0). However, in years 5-8 there was a significant effect of treatment type (p = 0.0034), with *A. longiceps* more likely to occur in the fragments (p=0.001) and controls (p=0.048) than in the pine matrix. After 21 years the probability of occurrence of *A. longiceps* in the pine matrix remained lower than that in the fragments (p=0.0003) and controls (p=0.008; Fig. 2-2b). *A. longiceps* was equally likely to occur in the fragments and controls in each of the three time periods (p= 0.977, p=0.473, p=0.685 respectively; Fig. 2-2b. Effect sizes for all time periods appear in Fig. 2-3).

*Leptomyrmex erythrocephalus* was slightly more likely to occur in the fragments (p=0.0573) and significantly more likely to occur in the controls (p=0.0411) than in the pine matrix in years 1-4 (Fig. 2-2b). In years 5-8, *L. erythrocephalus* was more likely to occur in fragments (p=0.0078) and controls (p=0.0478) than in pines, with no difference in occurrence between fragments and controls (p=0.3738; Fig. 2-2b). Twenty-one years after fragmentation, *L. erythrocephalus* was significantly less likely to occur in the fragments than in the controls (p=0.0143), and significantly more likely to occur in the fragments (p=0.0183) and the controls (p=0.0001) than in the pine matrix (Fig. 2-2b; effect sizes for all time periods are shown in Fig. 2-3).

There was a significant effect of topographic feature (slope vs. drainage) on *A. longiceps* occurrence in years 1-4 averaged across all three treatments (fragments, controls and matrix; p=0.0001, Fig. 2-3), with occurrence consistently more likely in slope sites than in drainage sites. There was no interaction between treatment type and topographic feature (p=0.6975). The effect of topographic feature diminished in years 5-8 (p=0.4983). In year 21, *A. longiceps* was again more likely to occur on slopes than in drainages averaged across all three treatments (p=0.0011).
Fig. 2-2. Probability of occurrence of two ant species in fragments, continuous forest controls, and pine plantation matrix sites across three post-fragmentation time periods. Error bars represent 95% confidence intervals.
Fig. 2-3. Effect sizes for two species of ant *Aphaenogaster longiceps* and *Leptomyrmex erythrocephalus*. All error bars are 95 % confidence intervals. **Treatment:** closed circles represent the log odds ratio of occurrence in fragment sites compared to continuous forest control sites, while triangles represent the log odds ratio of occurrence in pine matrix sites compared to control sites. **Topography:** points represent the log odds ratio of occurrence in drainage-line sites compared to slope sites. **Size:** triangles represent the log odds ratio of occurrence in small fragment sites compared control sites, squares represent the log odds ratio of occurrence in medium fragment sites compared control sites, and circles represent the log odds ratio of occurrence in large fragment sites compared control sites. **Edge:** points represent the log odds ratio of occurrence in sites at fragment edges compared to sites in fragment interiors.
and there was no interaction between topographic feature and treatment type.

For *L. erythrocephalus*, there was no significant effect of topographic feature on occurrence probability in years 1-4 (p=0.6434, Fig. 2-2). However, in years 5-8 there was a significant effect of topographic feature (p=0.0013) averaged across all three treatments, with occurrence more likely in slope sites than drainage sites. There was no interaction between treatment type and topographic feature (p=0.3658). In year 21 post fragmentation, topographic feature again had a significant effect on *L. erythrocephalus* occurrence averaged across all three treatments (p=0.0148) with occurrence consistently higher in slope sites than drainage sites. However, there was no interaction between treatment type and topography (p=0.42).

Patch size had no significant effect on the probability of occurrence of either *A. longiceps* or *L. erythrocephalus* in any of the three post-fragmentation time periods across all treatments. Similarly, there was no significant effect of edge and core habitats on *A. longiceps* or *L. erythrocephalus* occurrence in any of the three time periods across all treatments. All effect sizes are shown in Figure 2-3.

**Discussion**

We examined the impacts of experimental habitat fragmentation on the occurrence of two Australian ant species, *A. longiceps* and *L. erythrocephalus*, over the course of 21 years. The establishment of pine plantation around fragments did not initially isolate populations on fragments. However, by year 21, both species occurred less frequently in the pine matrix than fragments or continuous forest, potentially isolating populations on fragments. As a result, the rarer of the two species, *L. erythrocephalus*, declined in occurrence in fragments compared to continuous forest, while the abundant species was unaffected. In the rarer species, the declining
suitability of the matrix habitat may have led to the isolation of small populations and an associated decrease in occurrence on fragments compared to continuous forest, while populations of the abundant species, which also became more isolated on fragments as the suitability of matrix habitat declined, may have been unaffected because it occurred at higher initial frequencies. The occurrence of neither species was affected by patch area or edges. However, both species were more likely to occur in open slope habitat than closed drainage-line habitat. Below we discuss the implication of our findings in more detail.

We first sought to determine whether species occurrence varied among the three treatments (fragments, controls, and pine matrix) at three different post-fragmentation time periods. In the first post-fragmentation time period (years 1–4), neither species exhibited a difference in probability of occurrence among fragments, controls, and pine matrix (although *L. erythrocephalus* occurred more infrequently in the matrix than controls). Given the structural disturbance to soil associated with clear-cutting and the establishment of a pine plantation, we expected to see lower occurrence probability for ants in both the matrix and fragments. The use of heavy machinery to fell and remove trees, accompanied by the mechanical planting of saplings, involves considerable soil turnover. However, *A. longiceps* and *L. erythrocephalus* may be able to avoid local extinction under these conditions through their nest construction and life history traits. *A. longiceps* lives in large, deep nests with high worker density and a single queen that is protected deep in the nest. *L. erythrocephalus*, while living in smaller nests, tends repletes that are also protected deep in nests. A replete is a member of a group of workers that accept liquid food from returning foragers. Repletes will store large amounts of food in their gasters for long periods of time, serving both as food storage and distribution, thus protecting the survival of the colony (Shattuck 1999). Like our study, a survey in the Sonoran Desert showed
that scrub habitat conversion to non-native grass pasture had little impact on ant communities and the authors also suggested that life history traits associated with food provisioning may contribute to population persistence in disturbed habitats (Franklin 2012). We hypothesize that soil disturbance, while destroying the upper-most portion of a nest, may not directly impact workers and queens residing lower in the nest (Gordon 2010). This would allow for the persistence of ant colonies in the matrix and immediate re-colonization. Then, because both ant species continued to occur in the matrix between fragments, populations on fragments were not isolated or small, and thus were not at greater risk of extinction than populations in continuous forest.

In the second post-fragmentation time period (years 5–8), both *L. erythrocephalus* and *A. longiceps* were less likely to occur in the pine matrix sites than in the fragments and controls (which were not different from each other). This reduction in occurrence could be the result of a synergistic interaction between life history traits and a change in environment (Davies et al. 2004). For example, *L. erythrocephalus* is a solitary forager and rare. The combination of these two traits may have reduced the rate of food resource encounter in the non-native pine matrix. Red harvester ants (*Pogonomyrmex barbatus*) adjust their level of foraging activity in response to food availability—specifically, when food resources are abundant, returning successful foragers induce more foragers to leave the nest (Schafer et al. 2006; Pinter-Wollman et al. 2013). If this type of feedback is present in *L. erythrocephalus* and *A. longiceps*, conditions in which there is lower food availability may contribute to insufficient numbers of foragers leaving the nest in order to find food. Despite *L. erythrocephalus* tending repletes, reduced effort in foraging may ultimately contribute to smaller populations and/or fewer colonies in both species.

A second possibility is that the maturing pine-plantation altered soil characteristics and
these alterations proved deleterious to nest construction. *A. longiceps* nests are typically short-lived (3-12 months) and in sclerophyll forests are constructed in large grain, loose soil (Richards 2009). Maturing pine plantations alter ground-level light availability, which likely has an impact on soil moisture. Neither ant species studied does well in drainage sites, suggesting that higher levels of soil moisture may have a negative impact on colony persistence. Other studies also found that pine plantations support both fewer ant species and lower ant abundance (Corley et al. 2006; Sinclair and New 2004) most likely because maturing pines, coupled with undeveloped understory within managed plantations, provide fewer resources to ants (Sinclair and New 2004). Our results agree with these earlier investigations and suggest that the intermediate successional age of pine plantations might be a pivotal time for the conservation of ants, and a time during which management may want to focus efforts on mitigating the impacts of monoculture establishment.

By 21 years post-fragmentation, the occurrence of both species had declined further still in the pine matrix (Fig. 2-2). In *L. erythrocephalus*, the rarer of the two species, this may have led to the isolation of small populations at increased risk of extinction, and an associated decrease in occurrence on fragments compared to continuous forest. However, fragment populations of *A. longiceps* remained unaffected, potentially because this species occurred at higher initial frequencies than *L. erythrocephalus*. In other studies, ant worker numbers were lowest in old-growth closed-canopy forests, similar in structure to our pine plantation matrix, compared to young clear-cut areas (Palladini et al. 2007) and ant species richness was negatively impacted by fragment isolation through the increased distance between fragments (Paolucci et al. 2012). In contrast to this second finding, in our study, it is likely the lack of suitability of the matrix habitat that is isolating rather than the distance between fragments. Similar results were obtained in
tropical rainforest fragments, where it was the type of matrix habitat, oil palm plantations, rather than the distance between fragments that isolated predatory ant species (Hill et al. 2011, Tawatao et al. 2011). Our findings and those of these other studies suggest that 1) the habitat structure of the matrix is a key determinant of ant persistence in the matrix and as a result also determines ant persistence in embedded fragments, and 2) the succession of a forest matrix alters matrix permeability and ultimately ant colony persistence. Thus, succession decreases matrix permeability with time.

Edge and patch-size effects often impact species responses in fragmentation studies (Cunningham et al. 2005), and our second question was whether this is the case for two ant species at Wog Wog. We report the absence of both edge and patch-size effect on *A. longiceps* and *L. erythrocephalus* occurrence and argue that this further indicates that the remnant *Eucalyptus* patches are no different from control sites as suitable habitat for ants. This result contradicts previous studies that found significant edge effects in ant communities (Sobrinho and Schroereder 2007; Pinheiro et al 2010). Farmilo et al (2013) provide what might be an explanation for my result. These authors sampled the vegetation structure and litter depth at Wog Wog and concluded that any effects of edge were only seen within fragment corners.

With respect to our lack of fragment size affect, we propose three potential explanations. The first is that we only examined two generalist species of ants. Despite the decrease in occurrence of these two ant species in the matrix over time, the two species are clearly hardy enough to withstand disturbance events. Second, even though populations are relatively isolated on fragments, fragments are potentially large enough to support robust populations of these species. Finally, both *L. erythrocephalus* and *A. longiceps* were able to tolerate the matrix environment for a period of time, at least up until year eight post fragmentation. Thus, fragments
may not have been isolated long enough to drive population declines within fragments (e.g. Brühl et al. 2003; Bickel et al. 2006).

In contrast to edge and patch-size effects, topography (slope vs. drainage line) did play a role in species occurrence. Occurrence probabilities of both ant species were consistently lower in drainage sites than slope sites, which are associated with distinct plant understory communities (Austin and Nicholls 1984). L. erythrocephalus and A. longiceps may occur in response to differences in understory plant community composition, or may be responding directly to soil moisture or light levels--drainage lines are likely to have both higher soil moisture and lower light levels. Regardless, habitat has a greater influence on ant occurrence than does remnant size or edge effects.

In conclusion, the responses of A. longiceps and L. erythrocephalus to fragmentation took many years to manifest. Young pine plantation matrix habitat did not isolate ant species on fragments, so that initially fragmentation did not affect the persistence of these ant species. However, both species occurred infrequently in mature pine plantation matrix. In L. erythrocephalus, the rarer of the two species, this led to the isolation of small populations and an associated decrease in occurrence on fragments compared to continuous forest. In contrast, the more abundant species, A. longiceps, was equally likely to occur in fragments and controls. Our study demonstrates the importance of considering time since fragmentation, the habitat characteristics of both fragments and the matrix, and how the changing suitability of matrix habitat can alter ant persistence with time. Our results hint at a mechanism that may explain the complexity of ant responses to habitat fragmentation. While within fragment dynamics may play a pivotal role in influencing ant persistence we show that matrix type, whether based on temporal changes or overall structural differences, can determine whether certain ant species persist or go
extinct. From a conservation perspective, our study suggests that management strategies within a forest plantation matrix that help support ant persistence, could be implemented in a manner that still allows for economic success yet delays or mitigates the impacts of matrix introduction. The Wog Wog experiment is at a spatial scale that parallels the scale of many conservation and land-use change scenarios in which insect conservation is important. We advise caution in using ants as biological indicators without considering matrix type, the time period over which ant occurrence is being considered and the type of environmental changes that have taken place during the process of fragmentation.
CHAPTER THREE

WHICH PROCESSES DRIVE ANT COMMUNITY ASSEMBLY IN EXPERIMENTALLY FRAGMENTED FOREST?

Abstract

Understanding the processes that determine community structure is a fundamental problem in ecology, with potential to directly affect the management and conservation of ecosystems. When landscapes are fragmented, the roles of dispersal and selection by the environment can be dramatically altered, resulting in significant changes to community assembly. I use a long term, large scale fragmentation experiment to study the relative importance of dispersal and selection by the environment for ant communities in which the spatial context of communities has been experimentally altered, compared to unaltered controls. I hypothesize that experimental fragmentation will alter community assembly by: 1) changing the environment (the distribution of species’ niches) and thereby altering the distribution and abundance of species on fragments; 2) reducing dispersal between fragments and isolating small populations on fragments, thus reducing the number of species on fragments either deterministically or stochastically. Here I show that fragmentation reduced ant richness but increased beta diversity of fragments. The increased beta diversity of fragments was driven by both increased environmental heterogeneity in large fragments (variance in litter depth: 64% contribution to effect size) and a reduction in dispersal between fragments (29% contribution to effect size), with a minor role for other direct effects of fragmentation (6% contribution to effect size). Finally, compared to controls, fragmentation increased the role of dispersal in the assembly of communities in small fragments, and, to a lesser extent, medium fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments. Thus, I show experimentally that the
processes that determine community assembly (selection, dispersal) are altered when the spatial
context of a community is altered, and that fragment size can alter the relative roles of the
processes that drive assembly, increasing the role of dispersal in small fragments and selection in
large fragments. Like other temperate systems, selection is an important driver of community
assembly at Wog Wog but is subordinate to dispersal on small patches where there is more
dispersal from the matrix and where litter depth is less variable.
Introduction

Global habitat loss continues at a fast and accelerating rate and accounts for most biodiversity loss (Pereira et al. 2010; Rands et al. 2010). One third of forest, globally, has been cleared (Hansen et al. 2013), and of the remaining forest, 20% is within 100 m of an edge, and 70% is within 1 km of an edge (Haddad et al. 2015). A critical consequence is that the only remnants of many ecosystems are fragments of once continuous habitat, and so the fate of biodiversity, globally, depends on the survival of intact communities, and the processes that maintain them, in these fragments of habitat. Thus, understanding the fate of communities in habitat fragments is critical.

Understanding the processes that determine community structure, including species diversity and beta diversity, is a fundamental problem in ecology, with application to the management and conservation of ecosystems. For example, identifying the relative importance of dispersal for the maintenance of community structure could inform the design of landscapes. Here I define a metacommunity as a set of local communities that are connected by dispersal. Leibold et al. (2004) proposed four metacommunity paradigms (species sorting, mass effects, patch dynamics, and neutral theory. While oversimplified, these four paradigms focused attention on three key processes in community assembly: dispersal, selection by the environment (biotic and abiotic), and stochastic drift. Vellend (2010) formalized this focus on process, and added a fourth process, speciation. Recent work focuses on comparing the roles of these processes as a way to organize the empirical study of community assembly (Myers and Harms 2011) including understanding how community assembly changes in response to human disturbance (Vellend et al. 2007; Davies et al. 2009; Logue et al. 2011; Moritz et al. 2013; Püttker et al. 2015). I define community assembly as the construction and maintenance of
community structure (community: richness, composition, biomass, heterogeneity in species composition).

When landscapes are fragmented, the influence of dispersal (spatial processes) and selection can be dramatically altered, resulting in significant changes to community assembly (Davies et al. 2001; Püttker et al. 2015). Thus, the study of the relative importance of dispersal versus selection by the environment for communities for which spatial context has been experimentally altered (compared to unaltered controls) can provide insight into both the processes that alter community structure when landscapes are fragmented, and the relative roles of these processes in community assembly more generally. Here I determine how experimental fragmentation alters the relative roles of dispersal and selection in community assembly.

I specifically focus on dispersal and selection because speciation is outside of the ecological timeframe and spatial scale of our study, and neutral processes, or drift, continue to prove difficult to quantify ((Chase 2010; Myers et al. 2013) see examination and discussion of methods in (Vellend et al. 2014; Tucker et al. 2016)).

The relative importance of dispersal and selection in the assembly of ant communities can be altered by fragmentation in at least two significant ways. 1) Fragmentation can physically alter fragment habitat, which can reduce or increase niche opportunities for species, depending on the environmental dimensions of their niches – with potential to increase or decrease the role of selection in community assembly. 2) Fragmentation may reduce dispersal to, and colonization of, fragment communities if the matrix is a barrier to dispersal, or if the matrix is poor quality habitat. Reduced dispersal can lead to stochastic extinctions by preventing demographic rescue (Brown and Kodric-Brown 1977; Caughley 1994; Hufbauer et al. 2015). Conversely,
fragmentation may increase the colonization of fragments when matrix habitat provides better habitat than original fragment habitat by acting as a source. Thus, by providing novel habitat, the matrix can influence both dispersal and selection. Fragmentation likely modifies community assembly simultaneously by many or all of these mechanisms and therefore may increase or reduce the roles of dispersal and selection.

My study system is a large scale forest fragmentation experiment in southeastern Australia, Wog Wog, with a speciose ant fauna. In this system 81 ant species coexist on the forest floor. Many of these species are rare and many species appear to be functionally similar. I ask: does altering the spatial context of ant communities on fragments via habitat fragmentation change the importance of dispersal and selection in ant community assembly (Fig. 3-1A)? I note that there have been few experimental tests of the factors that determine the relative roles of dispersal and selection in community assembly (e.g. Chase 2007; Chase 2010; Myers and Harms 2011). I hypothesize that experimental fragmentation will alter community assembly on fragments compared to controls in two ways. 1) By changing the abiotic environment, the spatial distribution of species’ niches, and thereby altering the distribution and abundance of species on fragments (Figure 3-1A: path A and B, changing the importance of selection). 2) By reducing dispersal between fragments and isolating populations of species on fragments (Figure 3-1A: path C). This will reduce the number of species on fragments either deterministically, if which species are lost can be predicted (declining population paradigm (Caughley 1994)), or stochastically, if species are lost at random (small population paradigm (Caughley 1994)). I examine beta diversity, as well as alpha and gamma diversity, in fragments compared to controls and use linear mixed models that describe the structural relationships in Figure 3-1 to determine how the relative roles of dispersal and selection change (Vellend 2010; Vellend et al. 2014).
Changes in beta diversity can provide fundamental insights into the processes that create and maintain biodiversity (Tuomisto et al. 2003; Chase 2010; Anderson et al. 2011; Kraft et al. 2011; Myers et al. 2013) by describing the scaling relationship between local (alpha) and regional (gamma) diversity disturbance (Davies et al. 2001; Chase 2007; Vellend et al. 2007; Leprieur et al. 2011; Püttker et al. 2015). Thus, I can understand how habitat fragmentation changes the processes that drive assembly by linking changes in the relative importance of selection and dispersal to changes in beta diversity.

**Methods**

*The experiment*

The Wog Wog habitat fragmentation experiment is located in southeastern New South Wales, Australia (37°04'30"S, 149°28'00"E; Fig. 3-1B) in native, sclerophyll, *Eucalyptus* forest. It is named for nearby Mt. Wog Wog. The experimental design and the rationale for it were described by Margules (1993). I briefly reiterate the experimental design here (see also Davies et al. 2000; Davies et al. 2001; Davies et al. 2004; McClenahan et al. 2016; Tuff 2016; Evans et al. 2017). The experiment consists of three plot sizes: 0.25 ha, 0.875 ha, and 3.062 ha. Four replicates of each size (three plots, one of each size per replicate, for twelve plots total) became habitat fragments when the surrounding *Eucalyptus* forest was cleared in 1987 and planted to *Pinus radiata*, for plantation timber. Two replicates (three plots, one of each size per replicate, equals six plots total) remain in uncleared continuous forest, and serve as the unfragmented control plots.

Sites are stratified in two ways: first, by habitat type into slopes and drainage lines because the vegetation communities associated with these topographic features are different
Slopes are characterized by a grassy understory and scattered shrubs below open *Eucalyptus* forest. Drainage lines are dominated by *Kunzea*, a small shrubby tree that forms dense stands. Second, sites are stratified by proximity to the fragment edge (edge or interior). There are two monitoring sites in each of the four strata (slope edge, slope interior, drainage-line edge, drainage-line interior), totaling eight sites within each plot and a total of 144 sites over the 18 plots (fragments and controls). Following clearing, an additional 44 monitoring sites were established in the matrix between the habitat fragments (Fig. 3-1B), also stratified by habitat type. For the time period reported here the pine plantation was cleared land with rows of pine saplings. Two permanent pitfall traps are located at each monitoring site – 188 sites in total.

Ant sampling occurred in November (spring), February (summer), and May (autumn) in 2009–2010. Pitfall traps were opened for seven days during each sampling period. Traps were charged with 150 ml of solution consisting of 73% ethanol (95%), 25% glycol, and 2% formalin poured into 16 oz. (473 ml) plastic cups. The two traps associated with each monitoring site were pooled. Ants were identified to species level using Wheeler (1934) and Shattuck (1999).

Temperature data were collected using Onset Pendant temperature/light data loggers (UA-002-64) from November 2011 to May 2012 and from November 2012 to May 2013 in 20-minute intervals. Loggers were placed 1m north of the center of each site marker and attached to a plastic stake at 5cm off the ground. Temperature sampling spanned spring, summer, and fall to account for seasonal differences in thermal conditions and in two separate years to account for annual variation. I also collected % canopy cover from photographs taken at a height of 1 m and processed using ImageJ.
In February and May 2013, ground cover and fallen wood were surveyed at all 188 sample sites. I measured percentage ground cover of leaves, bark, grass, bare-ground, rock, wood, moss, and Lomandra sp., a large tussock-forming, grass-like plant (Xanthorrhoeaceae). I used a point intercept survey, running a 10 m long, 5 mm diameter cord in five directions (72 degrees apart) from the central point of each site. The cord was marked every 50 cm and the ground cover (bark, leaves, etc.) that the mark touched was scored, giving a total of 100 points at each site. Litter depth was measured in the same way. By running transects in five directions from a central point, the measures were deliberately biased toward the center of the site. This gave greater weight to habitat characteristics close to the pitfall traps.

The quantity of fallen wood at a site was also measured by walking the 10 m length of cord, in five directions from the central point, and scoring all wood under the cord. Fallen wood was scored for five categories with diameters of 1 cm, 2.5 cm, 5 cm, 20 cm, and 40 cm and over. Fallen wood was also scored as rotting or not.

**Data analysis**

*Fragmentation and community structure*

In one year of trapping, 25,000 individual ants were captured and identified, representing 81 species from seven sub-families.

*Community and experimental scales*

I defined alpha diversity as richness at the local community scale. This corresponds to the site scale (i.e. one pair of traps) in this experiment. Gamma diversity was defined as richness at
the whole fragment scale (or fragment-sized plots in controls), which is a metacommunity scale since it encompasses multiple local communities (Davies et al. 2005). This allowed us to consider how fragmentation affected the site scale (local) versus fragment scale (metacommunity) assembly, and to compare how beta diversity (variation in composition between sites within a fragment) varied between fragments. A third scale, replicate, accounted for experimental variation between the blocks of the randomized block design (Fig. 3-1). There is a fourth, larger, spatial scale encompassing the whole experiment, which defines the regional species pool (this scale is unreplicated and is not the subject of analyses). All statistical models are listed in Table 3-1.

**Alpha and Gamma diversity**

Species richness was calculated at either the site (alpha diversity) or fragment (gamma diversity) scale as the number of species observed over the year of study (three seasons). I used linear mixed models fitted by restricted maximum likelihood (REML) to test for the effects of habitat fragmentation *per se*, fragment size, and edge effects. Random effects consisted of up to three nested spatial scales: replicate, fragment, and site (described above).

The experiment has a nested design so that data are collected at three spatial scales. Individuals are trapped at pitfall *sites* (1-144), which are nested within *plots* (1-18), which are nested within *replicates* (1-6) (Fig. 3-1B). Thus, I included two random effects: *Replicate* and *Plot* in the alpha diversity analysis, and only *Replicate* in the gamma diversity analysis. Similarly, I could not test for edge effects in the gamma diversity analysis.
Table 3-1. List of statistical models.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Scale</th>
<th>Explanatory variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpha</td>
<td>Site</td>
<td>Fragmentation, fragment size, edge, topography</td>
</tr>
<tr>
<td>Gamma</td>
<td>Patch</td>
<td>Fragmentation, fragment size</td>
</tr>
<tr>
<td>Beta</td>
<td>Patch</td>
<td>Fragmentation, fragment size</td>
</tr>
<tr>
<td>Beta</td>
<td>Patch</td>
<td>Environmental variables including variance in litter depth. See Table 2 for list of variables.</td>
</tr>
<tr>
<td>Variance in litter depth</td>
<td>Patch</td>
<td>Fragmentation, fragment size</td>
</tr>
<tr>
<td>Proportion of species isolated</td>
<td>Patch</td>
<td>Fragmentation, fragment size</td>
</tr>
<tr>
<td>SEM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta</td>
<td>Patch</td>
<td>Variance in litter depth + proportion of species isolated + fragment size</td>
</tr>
<tr>
<td>Variance in litter depth</td>
<td>Patch</td>
<td>Fragment size</td>
</tr>
<tr>
<td>Proportion of species isolated</td>
<td>Patch</td>
<td>Fragment size</td>
</tr>
</tbody>
</table>
Figure 3-1 A. Hypotheses for how experimental fragmentation alters ant community assembly. Experimental fragmentation will alter community assembly in fragments compared to controls by: 1) changing the environment, species’ niches, and thereby altering the distribution and
abundance of species on fragments (path A and B, altering the importance of selection). 2) Reducing dispersal between fragments and isolating populations of species on fragments (path C). This will reduce the number of species on fragments either deterministically, if which species are lost can be predicted, or stochastically, if species are lost at random. B. Map of the experimental site showing *Eucalyptus* forest fragments and control plots in continuous forest. There are eight monitoring sites (represented by dots) within each fragment, each with two pitfall traps. Dots in the pine matrix between the fragments represent the location of a pair of monitoring sites (a slope site and a drainage-line site) established after fragmentation. Fragment sizes: 0.25 ha, 0.875 ha, and 3.062 ha. Fragments are separated by at least 50 m. Eight monitoring sites on each small fragment are not shown because of space constraints.
Table 3-2. List of environmental variables at the site scale.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter depth</td>
<td>Litter depth in cm</td>
</tr>
<tr>
<td>% canopy cover</td>
<td>% canopy cover from photographs</td>
</tr>
<tr>
<td>pH 2012</td>
<td>Soil pH from 2012 survey</td>
</tr>
<tr>
<td>Soil organic carbon</td>
<td>Soil organic carbon from soil survey</td>
</tr>
<tr>
<td>Soil wetness index</td>
<td>From 1985 soil survey</td>
</tr>
<tr>
<td>Mean temperature</td>
<td>Mean temperature in degrees Celsius</td>
</tr>
<tr>
<td>Leaves</td>
<td>% ground cover of leaves (area 10 m radius)</td>
</tr>
<tr>
<td>Bark</td>
<td>% ground cover of bark (area 10 m radius)</td>
</tr>
<tr>
<td>Grass</td>
<td>% ground cover of grass (area 10 m radius)</td>
</tr>
<tr>
<td>Roots</td>
<td>% ground cover of roots (area 10 m radius)</td>
</tr>
<tr>
<td>Bare ground</td>
<td>% ground cover of bare ground (area 10 m radius)</td>
</tr>
<tr>
<td>Rock</td>
<td>% ground cover of rock (area 10 m radius)</td>
</tr>
<tr>
<td>Wood</td>
<td>% ground cover of wood (area 10 m radius)</td>
</tr>
<tr>
<td>Moss</td>
<td>% ground cover of moss (area 10 m radius)</td>
</tr>
<tr>
<td>Lomandra</td>
<td>% ground cover of <em>Lomandra</em> (area 10 m radius)</td>
</tr>
<tr>
<td>Mean hard wood diameter</td>
<td>Mean diameter of fallen wood (area 10 m radius)</td>
</tr>
<tr>
<td>Mean rotting wood diameter</td>
<td>Mean diameter of rotting fallen wood (area 10 m radius)</td>
</tr>
</tbody>
</table>
**Beta diversity**

I calculated beta diversity (spatial heterogeneity of site-scale communities within fragments) for each fragment. I used the Jaccard metric to measure dissimilarity in species composition between all pairs of sites within fragments and then calculated the average dissimilarity to give a single value of beta diversity for each fragment. Jaccard is based on presence-absence data. I used linear mixed models (REML) to look for effects of fragmentation and fragment size on beta diversity using the same approach as for the analyses of gamma diversity.

**Does the environment alter community structure (path B)**

From my broad habitat survey and microclimate data I selected variables that I hypothesized might explain the distribution and abundance of ant species and therefore determine community structure: beta diversity. Nonetheless, this resulted in a large number of environmental variables that potentially explained community structure (Table 3-2). These variables grouped into four classes of variable: ground cover and structure, soil properties, canopy cover and temperature. I determined the change in deviance associated with each variable independently (p<0.05) using linear mixed models (REML). Models included the random effects Block and Plot. I assessed significance using likelihood ratio tests (p<0.05).

**Does fragmentation alter the environment (path A)**

I hypothesized that the habitat fragmentation treatment could 1) alter the environment of fragments, and thus, in turn 2) alter ant community structure via changes to the environment, as described in the section above (Fig. 3-1A). Once I had determined which environmental
variables predicted beta diversity (above), I backtracked to determine whether fragmentation had altered those environmental variables. That is, were they significantly different in fragments and continuous forest, in different sized patches, and at fragment edges versus interiors. I also looked for an interaction between fragmentation, patch size and edges. I used the same model fitting protocol as I used when determining the effects of fragmentation on alpha diversity described above.

There was one environmental variable that determined beta diversity: variance in litter depth. I fitted models using a linear mixed model (REML).

*Effects of isolation (path C)*

I looked at species occurrences in fragments, the matrix and continuous forest to understand 1) how the exchange of individuals between fragments and the matrix affected community assembly on fragments compared to controls and on fragments of different sizes compared to matched control patches, and 2) to gain insight into whether small patches were more likely to lose species than large patches by pairing a patch level isolation measure and the effect of fragmentation on gamma diversity.

I calculated a patch-level measure: the proportion of isolated species. I calculated this as the number of species on a patch that did not occur in the matrix divided by the total number of species on that patch. I used a linear mixed model (REML) to determine the effects of fragmentation and fragment size on the proportion of isolated species in a patch community. I also used the proportion of isolated species measure in the analyses below to understand the effect of dispersal on beta diversity.
Fragmentation alters the environment and reduces dispersal altering community assembly: SEM synthesis

My goal was to determine what proportion of the change in community structure driven by the fragmentation treatment could be attributed to either 1) path C: the direct effects of fragmentation on ant populations and in turn community structure (e.g. reduction in dispersal, isolation of populations on fragments with resulting increase in extinction risk); or to 2) paths A and B: fragmentation-driven changes to the environment that altered the distribution of species niches caused changes in the distribution and abundance of species within the community (Fig. 3-1). I developed an analysis that partitioned the total effect size of fragmentation into additive contributions from fragmentation per se (dispersal and unknown) and fragmentation-driven changes to the environment in the style of a structural equation modeling approach within a linear mixed effects model framework.

The full structural equation model corresponding to Fig. 3-1B was the linear model:

\[ y_i = \beta_E \xi_{jKE} + \beta_D \xi_{jKD} + F_{jkR} + \beta_E \epsilon_{iE} + \beta_D \epsilon_{iD} + \epsilon_i, \]  

where \( y_i \) is the beta diversity of patch \( i, i = 1\ldots18 \), \( \xi_{jKE} \) is the mean environment (variance in litter depth) of a patch of size \( j = 1\ldots3 \) (small, medium, large), and type \( k = 1\ldots2 \) (fragmented, control), \( \xi_{jKD} \) is the mean dispersal index (proportion of isolated species) of a patch of size \( j \) and type \( k \), \( \beta_E \) and \( \beta_D \) are the slopes of the relationships of beta diversity to the environment and dispersal index respectively, \( F_{jkR} \) is the mean beta diversity of a patch of size \( j \) and type \( k \) (intercept of the linear model) and represents the remaining fragmentation effects after accounting for the effects of the environment and dispersal, \( \epsilon_{iE} \) and \( \epsilon_{iD} \) are the residuals from the
relationship of the environment and dispersal index to the fragmentation treatment respectively (see below), and $\epsilon_i$ are the remaining residuals. Equation 1 partitions the effect of patch size and type into three components, the environmental effect via fragmentation

$$ F_{jE} = \beta_E \xi_{jE}, $$

the dispersal effect via fragmentation

$$ F_{jD} = \beta_D \xi_{jD}, $$

and the remaining fragmentation effects, $F_{jR}$. For each component, I calculated the overall effect size, $\Delta \cdot$, as the difference between fragmented and control patches of the same size, averaged over the three patch sizes. Thus,

$$ \Delta E = \beta_E \frac{1}{3} \sum_j \Delta F_{jE}, $$

$$ \Delta D = \beta_D \frac{1}{3} \sum_j \Delta F_{jD}, $$

$$ \Delta R = \frac{1}{3} \sum_j \Delta F_{jR}, $$

where, $\Delta F_j = F_{j1} - F_{j2}$, that is, the difference between fragmented and control patches of a given size $j$.

To estimate the parameters in Eq. 1, I fitted three separate linear mixed effects models. The first model was for the effect of fragmentation on the environment (path A, Fig. 3-4)

$$ z_{iE} = \xi_{jE} + \epsilon_{iE}, $$

where $z_{iE}$ is the variance in litter depth in patch $i$. The second model was for the effect of fragmentation on dispersal (path C, Fig. 3-4)

$$ z_{iD} = \xi_{jD} + \epsilon_{iD}, $$

where $z_{iD}$ is the proportion of species isolated for patch $i$. Thus, the environment of patch $i$ or the dispersal characteristic of patch $i$ are determined by patch size and type (the effect of
fragmentation) and a residual due to random variation. The third model was for the combined
effects of fragmentation (i.e. patch size and type), environment, and dispersal on beta diversity
\[ y_i = \mathcal{F}_{jkr} + \beta E z_{IE} + \beta D z_{ID} + \varepsilon_i. \quad (5) \]

Substituting Eqs (3) and (4) into Eq. (5) gives Eq. (1). In all models, I assumed that the
residuals were normally distributed with two components of variance: a replicate-scale and a
patch-scale random effect.

Does fragmentation alter the roles of selection and dispersal in ant community assembly?

I plotted where each fragment/control plot sat in two dimensions defined by the variance
in litter depth (effect of selection) vs. proportion of isolated species on a patch (effect of
dispersal). I compared ellipses that enclosed replicate small, medium and large fragments to one
another and to continuous forest controls. I used a permutation test that compared the observed
overlap area of pairwise combinations of ellipses to those from 10,000 permuted ellipses where
labels were randomized.

Results

1. Fragmentation changed community structure

Fragmentation did not affect local richness (Alpha: Table 3-1, Fig. 3-2A). Local richness
also was not significantly different in small vs. medium vs. large fragments, or at fragment edges
versus interiors (Alpha diversity: Table 3-1). I also did not detect an overall difference between
fragments and controls in patch scale richness averaged over fragment sizes (Gamma diversity:
Table 3-2). However, fragmentation reduced patch scale richness in large fragments by 2.5
species compared large control patches, and also reduced richness by one species in medium
fragments compared to medium control patches (Fig. 3-2A; Gamma diversity: Table 3-2).
Fragmentation increased beta diversity in large fragments but not small fragments (Fig. 3-2B; Beta diversity: Table 3-3).

2. The environment on its own altered community structure (path B)

Only variance in litter depth predicted beta diversity, Jaccard dissimilarity, so that the spatial heterogeneity in species composition within a patch increased as the variance in litter depth increased (Fig. 3-3A, Fig. 3-1A, path B).

3. Fragmentation altered the environment (path A)

After establishing that variance in litter depth altered beta diversity, I determined whether fragmentation had altered variance in litter depth. Fragmentation increased the variance in litter depth, and more so in large than medium or small fragments (Fig. 3-3B, Fig. 3-1A, path A).

4. Dispersal: Proportion of species in a patch that occur in the matrix (path C)

To understand the role of dispersal and the effect of isolation, I examined the proportion of species within a patch that were isolated (did not occur in the matrix) and determined that small and medium fragments had a lower proportion of isolated species than small and medium patches, respectively, in continuous forest (Fig. 3-3C). This means that small fragments had communities that were more similar in composition to matrix communities suggesting 1) a greater exchange of individuals between matrix and small fragment sites but also, 2), that small fragments have likely lost some isolated species, otherwise would expect an increase in small fragment richness as the number of matrix species increases there compared to small control patches.
5. SEM synthesis: selection was a bigger driver of changes in community assembly than dispersal

Figure 3-4A summarizes the contribution of selection and dispersal to fragmentation driven change in beta diversity. Experimental fragmentation increased the variability in species composition in fragments (beta diversity), compared to continuous forest, by increasing the variability of leaf litter depth, and increasing the loss of species from fragments via reduced dispersal (Fig. 3-4A). 64% of the increase in beta diversity effect size could be attributed to fragmentation driven changes to the environment that then drove changes in beta diversity (selection; Fig. 3-4A, path B), and 29% to the effects of increased dispersal (dispersal; Fig. 3-4A path C). Six percent of the change in beta diversity in fragments compared to controls was due to unexplained effects of fragmentation (Fig. 3-4A path D).

6. Fragmentation altered the roles of selection and dispersal in ant community assembly

Fragmentation increased the role of dispersal and reduced the role of selection in the assembly of communities in small fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments. When I ordinated the beta diversity response space of communities in different sized fragments and controls by selection and dispersal, I find that dispersal had a large role and selection had a small role in the assembly of small patches (Fig. 3-4B). In contrast, in large fragments, selection had a large role in community assembly and the effect of dispersal ranged from low to high. The roles of dispersal and selection were intermediate in both the controls and medium fragments (Fig. 3-4B).
Figure 3-2. Effect sizes and 95% confidence intervals for the effects of experimental fragmentation of *Eucalyptus* forest on: A) local richness (alpha diversity) in fragments compared to controls, fragment scale richness (gamma diversity) in small fragments compared to small patches in continuous forest, medium fragments and medium patches in continuous forest, large fragments and large patches in continuous forest, and B) beta diversity in small medium and large fragments compared to control patches (Jaccard dissimilarity).
Figure 3-3. A. The relationship between the variance in litter depth and beta diversity (Jaccard dissimilarity). Each point represents the average beta diversity for one fragment/patch in continuous forest. B. Variance in litter depth in different sized fragments and continuous forest controls. Error bars represent 95% confidence intervals. C. Effect sizes: differences between fragments and controls in the proportion of species within a fragment that did not occur in the matrix grouped by fragments size. Small and medium fragments had fewer species that never occur in the matrix – isolated species -- than small and medium patches, respectively, in continuous forest controls. Error bars represent 95% confidence intervals.
Discussion

I asked, does altering the spatial context of ant communities on fragments via habitat fragmentation change the importance of dispersal and selection in ant community assembly? I investigate, first, the contributions of selection and dispersal in determining changes in fragment beta diversity, and second, how fragmentation alters the relative roles of selection and dispersal in community assembly, and in different sized fragments. I discuss my findings in turn below.

Selection is a bigger driver of changes in community assembly than dispersal

Fragmentation increased beta diversity (the heterogeneity in species composition) in fragments compared to continuous forest, and more so in large fragments than small. This increase in beta diversity was mostly driven (64%, Fig. 3-4A) by differences in the abiotic environment between fragments and controls – specifically an increase in the variance in litter depth that was most pronounced in large fragments (Fig. 3-3B). This increase in the variance in litter depth was driven by fragmentation (Fig. 3-3B, 3-4A) and is most likely a result of an increase in the productivity of trees in fragments (King et al. in review), resulting in increased canopy biomass and, as a result, increased litter depth (Figure 3-1). The resulting increase in variability in litter depth most likely provides a larger range of available ant niches (Chesson 2000; Chase and Leibold 2003) in large fragments, with litter acting as both habitat and a buffer to solar inputs. In tropical communities, ant species differ in litter depth niche preferences (Kaspari 1996), and light and microclimate are also important niche variables (Carvalho and
Vasconcelos 1999). In fragmented Amazonian forest, litter depth declined with distance from fragment edges, and, like our study, changes in ant community composition were linked to

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**Diagram:**

- **Environment**
  - Variance in litter depth 0.14
  - B) Selection/species sorting 0.015 (64%)
  - C) Dispersal 0.007 (29%)
  - D) Unexplained 0.0015 (6%)

**Spatial processes**

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A. Summary of effect sizes and their percent of the total effect size of fragmentation on beta diversity. Experimental fragmentation increased the variability in species composition in fragments (beta diversity), compared to continuous forest, by increasing the variability of leaf litter depth, and increasing the loss of species from fragments via reduced dispersal. 64% of the increase in beta diversity could be attributed to fragmentation driven changes to the environment that then drove changes in beta diversity and 29% to the effects of reduced dispersal. Six percent of the change in beta diversity in fragments compared to controls was due to unexplained effects of fragmentation. B. Space represented by the selection (variance in litter depth) and dispersal (proportion of isolated species in a fragment community) axes. Dots represent fragments. Fragmentation altered the roles of selection and dispersal in different ways in different parts of the landscape. Compared to controls, fragmentation increased the role of dispersal in the assembly of communities in small fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments. In small fragments, and to a lesser extent medium fragments, matrix and fragment communities share more species. In contrast, on large fragments, the influence of the matrix is not different from controls. However, instead, there is a larger effect of selection, the environment, in shaping communities.
variability in litter depth (Carvalho and Vasconcelos 1999).

However, the change in ant community assembly on fragments -- increased beta diversity -- was also driven by increased dispersal between fragments (29%, Fig. 3-4A), especially in small fragments (Fig. 3-3C). The effect of dispersal on community assembly was measured as the proportion of species in fragment/patch communities that were isolated by the matrix (did not occur there). Small and medium fragment communities both contained more matrix species than controls (Fig. 3-3C) suggesting a greater influence of the matrix on small and medium fragments communities – a mass effect. However, there was no resulting increase in fragment-level richness, which suggests that small and medium fragments also lost isolated species, as theory would predict (MacArthur and Wilson 1967; Levins 1969; Caughley 1994). In classic metapopulation theory, sub-populations on isolated patches periodically go extinct and are recolonized by individuals migrating from other patches (Levins 1969). Metapopulations go extinct when the rate of extinction of individual patches is greater than the rate of dispersal among patches (Hanski 1991). Empirically, these predictions consistently play out: fragmentation frequently results in the loss of species from fragments.

Just 6% of the fragmentation-driven increase in beta diversity could be attributed to unexplained effects of fragmentation. Species may be lost deterministically from fragments if which species are lost can be predicted -- from their traits, for example. In our study, isolated species occurred less frequently on fragments, and fragment communities were composed of fewer isolated species (Figs. 3-3C). Thus, to some extent I was able to predict which species were lost from ant communities. The unexplained 6% may represent an unmeasured ant trait that
predicts risk of local extinction on fragments, unmeasured environmental factors, or detection error.

*Fragmentation changes the relative roles of selection and dispersal in community assembly*

These experimental results provide mechanistic insights into the assembly of communities highlighting the importance of synthetic analyses in community ecology that integrate effects of selection and dispersal. In the above paragraphs I discuss what proportion of the increase in beta diversity detected is driven by selection or dispersal but not whether the roles of selection and dispersal increased or declined in fragments. In this section I add this piece: here I discuss how my study provides some of the first experimental evidence that fragmentation alters community assembly by simultaneously modifying the relative roles of dispersal and selection compared to controls. Fragmentation altered the role of selection and dispersal in different ways in different parts of the landscape (Fig. 3-4B). Compared to controls, fragmentation increased the role of dispersal in the assembly of communities in small fragments, while at the same time increasing the role of selection in the assembly of communities in large fragments. In small fragments, and to a lesser extent medium fragments, matrix and fragment communities share more species as the result of a greater exchange of individuals between adjacent habitat (a mass effect, Leibold et al. 2004). Although I detected no edge effects, small fragments have a larger proportion of habitat that abuts an edge than, in turn, medium and large fragments. In contrast, on large fragments, the influence of the matrix is not different from controls (Fig. 3-3C). However, instead I see a larger effect of selection, the environment, in shaping communities.

In other studies that examined the roles of selection and dispersal in community assembly, niche-based processes were frequently the most important drivers of beta diversity,
and especially in temperate systems. For example, Gilbert and Lechowicz (2004) found that the environment was a more important driver than dispersal limitation in a temperate forest understory. Myers et al. (2013) determined that species sorting (i.e. selection) structured highly aggregated, low-diversity temperate forests, while dispersal limitation structured highly aggregated, high-diversity forests. In aquatic invertebrate communities, Chase (2010) experimentally demonstrated that niche-based processes (again, selection) were more important in structuring low productivity communities while stochastic processes became more important as productivity increased. Levine and HilleRisLambers (2009) show experimentally that niche differences (selection) structure temperate grassland communities.

My study adds an important dimension to this literature by experimentally demonstrating two things. First, that increased dispersal can override selection as a driver of community assembly in temperate systems on small fragments. Given that the earth’s forests are fragmented -- 20% of forest is within 100 m of an edge and 70% is within 1 km of an edge (Haddad et al. 2015) -- this is an important finding for understanding and managing assembly in forest communities. Second, the role of selection in assembly can be amplified when a key niche variable, in this case, litter depth, becomes more variable in space.

Conclusion

What does this large-scale habitat fragmentation experiment teach us about the processes that determine community assembly that we did not know? First, I determine that landscape fragmentation drives changes in community assembly through both selection, by changing the environment, and dispersal, by increasing the interchange of ant species between small fragments and the matrix. Both changes to the environment and increased dispersal are recognized as
significant drivers of community and population change in fragmented landscapes (Didham et al. 1998; Davies et al. 2004; Laurance et al. 2011; Damschen and Brudvig 2012; Didham et al. 2012; Arroyo-Rodríguez et al. 2013; Damschen et al. 2014; Haddad et al. 2015; Püttker et al. 2015). However, here I was able to determine their relative importance in altering community assembly in an experimental setting. I show that selection is a larger overall driver of the increased heterogeneity in species composition of fragments than dispersal but that increased dispersal also contributes. Second, I show that fragmentation alters the relative roles of selection and dispersal in different parts of the landscape, increasing the role of dispersal in small fragments, while at the same time increasing the role of selection in large fragments, compared to controls. Thus, fragmentation not only alters the relative roles of the processes that determine community assembly but does so in different ways in different sized fragments.

Future work at Wog Wog should examine how the upcoming harvesting of the pine plantation matrix further alters the roles of dispersal and selection in ant community assembly on fragments, given the already altered state of fragment communities. Matrix clearing should reduce dispersal between fragments increasing the degree of isolation of populations. I predict that we will see extinctions on small fragments and an increased role of selection in all fragments as fluxes of temperature and solar radiation increase.
CHAPTER FOUR
DIRECT AND INDIRECT INFLUENCE OF HABITAT FRAGMENTATION: ANT-MEDIATED SEED REMOVAL IN A LONG-TERM HABITAT FRAGMENTATION EXPERIMENT

Abstract

Ecosystem processes are dependent on the interaction between biotic and abiotic elements of a system. Global biodiversity is currently under severe threat from habitat fragmentation and loss. While there is consensus that processes associated with fragmentation have direct impacts on biodiversity, we are just now beginning to understand how fragmentation affects ecosystem functions. Myremecochory is a crucial ecosystem function that limits intraspecific tree competition and locates seeds in habitat that helps facilitate germination. Since ants are a ubiquitous component in Australian ecosystems, I sought to determine the impacts of habitat fragmentation on seed removal. I asked: 1) Does habitat fragmentation alter seed removal in forest fragments versus continuous forest, in fragments of different size and at fragment edges? If yes: 2) is the change in seed removal linked to the number of ant species at a site, which species are present, or how many ant individuals are present? 3) Do changes to the environment, that are the result of experimental fragmentation, affect the rate of ant seed removal?

My focus was the ant community at the Wog Wog Long-term Habitat Fragmentation Experiment in New South Wales, Australia. I conducted a seed removal experiment with Eucalyptus sideroxylon seeds and used linear mixed models and structural equation models for data analysis. Habitat fragmentation increased seed removal in large fragments and fragment cores. The number of seeds removed from a site was determined by the total number of ant individuals present at a site. However, fragmentation did not alter seed removal by directly
altering the total number of ants at a site. Rather, fragmentation modified the environment so that more/fewer seeds were removed in different parts of the fragmented landscape, compared to continuous forest, when the same number of ant individuals was present. Specifically, fragmentation reduced the number of seeds removed per ant in small fragments by reducing temperature there. Further, fragmentation increased the number of seeds removed per ant in medium and large fragments (and potentially fragment cores) by reducing grass cover there. More seeds were removed when grass cover was low. My study helps to disentangle which aspects of ant biodiversity are impacted by fragmentation and are linked to seed removal. Our study also highlights that fragmentation driven changes to seed removal can be the result of direct effects of fragmentation on the environment that alter ant behavior.
Introduction

Ecosystem processes are the result of complex interactions between the biotic and abiotic components of a given system (Grace et al. 2010; Tilman et al. 2014). Habitat loss is the greatest threat to global biodiversity (Pereira et al. 2010; Rands et al. 2010) with approximately 50% of terrestrial environments having been converted to agriculture or urban development (Ellis and Ramankutty 2008). Forest habitat has been reduced by one third (Haddad et al. 2015) with 90% of remaining forest within 1km of non-native habitat (Hansen et al. 2013). An alarming consequence is that small, isolated habitat fragments are all that remain of once continuous ecosystems. Therefore, the preservation of both biodiversity and ecosystem functions depends on understanding how they are connected and how they respond in fragmented landscapes (Crist 2009; McConkey et al. 2012). Key ecosystem functions can include processes like seed dispersal, productivity, nutrient cycling and litter decomposition. Here I focus on ant mediated seed dispersal.

Theoretical and empirical research suggests a link between biodiversity and ecosystem processes (Traill et al. 2010; Haddad et al 2015). However, it is not always clear which quality of “biodiversity” is key for a given ecosystem function. For example, some studies focus on the number of species present and link reductions in a given ecosystem function to reductions in local richness (Tilman et al 2014; van der Plas et al. 2016). Alternatively, the number of individuals present, or the presence of a numerically dominant species may have the greatest influence on a given ecosystem function (Hillebrand et al. 2008; Warren and Giladi 2014; Tanaka and Suzuki 2016).

Abiotic factors also drive ecosystem processes both directly (e.g. wind, water and fire all act to disperse seeds; McConkey et al. 2012; Pascov et al. 2015) and indirectly by determining
the number of species or individuals present and their behavior (Debuse et al. 2007; Ribas and Schoereder 2007). Thus, when fragmentation alters abiotic conditions on fragments (Fischer and Lindemayer 2007; Farmilo et al. 2013; Chávez-Pesqueira and Núñez-Farfán 2016) it can alter seed dispersal both directly, by changing fluxes of wind, water and fire, and indirectly, by altering the frequency, distribution and/or behavior of key biotic seed dispersers. For small, ground-dwelling ectotherms, like ants, changes to the abiotic environment can lead to changes in species richness and evenness (Debuse et al. 2007; Gibb et al. 2015) and impact foraging activity and encounter rate (Kaspari et al. 2003; Shafer et al. 2006; Pinter-Wollman et al. 2013; Ewers et al. 2015).

Globally, an estimated 11,000 plant species rely on ant-mediated seed dispersal (Leal et al. 2015; Pascov et al. 2015). Australia has approximately 1500 mymrecocchorous species (Bell 1994). Seed removal rates range from 65-100% (Wellington and Noble 1985; Grimbacher and Hughes 2002) and thus ants play a crucial role in soil seed-reserves, germination rates, and local plant diversity and abundance (Bell 1994, Yates et al. 1996; Lomov et al 2009; Mucina and Majer 2012). Reductions in dispersal rate are likely to result in decreased richness and abundance of plants, which may result in decreases in system resilience (McConkey et al 2012; Pigot et al. 2016) and changes to interaction networks (Dátilo et al. 2014). When ants were excluded from artificial seed banks, seeds germinated but resulting seedlings did not survive to adulthood (Yates et al 1996). For shade intolerant species, like *Eucalyptus* trees, seed dispersal can reduce parent-offspring competition and allow establishment within suitable habitat (Cordeiro and Howe 2003).

In this study, I examine the effects of forest fragmentation on seed dispersal in a long-term, landscape-scale habitat fragmentation experiment in southeastern NSW Australia. I ask: 1) Does
habitat fragmentation alter seed removal in forest fragments versus continuous forest, in fragments of different size and at fragment edges? If yes: 2) is the change in seed removal linked to the number of ant species at a site, which species are present, or how many ant individuals are present? 3) Do changes to the environment, that are the result of experimental fragmentation, affect the rate of ant seed removal (Fig. 4.1)?

Previously, I detected relatively small changes in local, site level, richness at Wog Wog as the result of fragmentation – just one species per site or a reduction of about 9 percent (Vellend et al. 2013; Chapter 3). Therefore, I hypothesized that if fragmentation alters seed dispersal, ant species richness is unlikely to be a significant driver (Vellend et al. 2013). Instead, the total number of ant individuals at a site or the presence of key seed disperser species may be important (Lassau and Hochuli 2004; Beaumont et al. 2011; Warren and Giladi 2014). Finally, I hypothesize that changes to the environment, as the result of fragmentation, may alter the per capita rate of seed dispersal (Ribas and Schoereder 2007; Fergnani et al. 2010) by, for example, altering ant activity levels (e.g. changes to temperature, Yates et al. 2011; Lima and Antonialli-Junior 2013; Barbieri et al 2015; Blight et al. 2016), or by providing alternative sources of seeds (e.g. increases in the frequency of understory plants, like grasses, that produce many seeds as the result of changes to understory light regimes; Sipos and Kindlmann 2013; Chen and Robinson 2014; Dátillo and Dyer 2014) (Fig. 4.1).

Methods

The experiment

The Wog Wog long-term habitat fragmentation experiment is located in southeastern New South Wales, Australia (37°04'30"S, 149°28'00"E; Fig. 4-2) in native, dry sclerophyll,
Eucalyptus forest. It is named for nearby Mt. Wog Wog. The experimental design and the rationale for it were described by Margules (1993). Briefly, it consists of three plot sizes: 0.25 ha, 0.875 ha, and 3.062 ha. Four replicates of each size (three plots, one of each size, per replicate equals twelve plots total) became habitat fragments when the surrounding Eucalyptus forest was cleared in 1987 and planted to Pinus radiata, for plantation timber. Two replicates of each size (three plots, one of each size, per replicate equals six plots total) remain in uncleared continuous forest, and serve as the unfragmented control plots.

Sites are stratified in two ways: first, by habitat type into slopes and drainage lines because the vegetation communities associated with these topographic features are different (Austin and Nicholls 1988). Slopes are characterized by a grassy understory and scattered shrubs below open Eucalyptus forest. Drainage lines are dominated by Kunzea, a small shrubby tree that forms dense stands. Second, sites are stratified by proximity to the fragment edge (edge or interior). There are two monitoring sites in each of the four strata (slope edge, slope interior, drainage-line edge, drainage-line interior), totaling eight sites within each plot and a total of 144 sites over the 18 plots (fragments and controls). Following clearing, an additional 44 monitoring sites were established in the matrix between the habitat fragments (Fig. 4-2), also stratified by habitat type. Two permanent pitfall traps are located at each monitoring site – 188 sites in total.

Ant sampling occurred in February (summer) 2009 and 2010. Pitfall traps were opened for seven days during each sampling period. Traps were charged with 150 ml of solution consisting of 73% ethanol (95%), 25% glycol, and 2% formalin poured into 16 oz. (473 ml) plastic cups. The two traps associated with each monitoring site were pooled. Ants were identified to species level using Wheeler (1934) and Shattuck (1999).
Seed traps were constructed from plastic petri dishes (Fisherbrand, 100mm x 15mm). A Dremel tool was used to drill two holes on the side of the base and lid 180 degrees from each other in order to restrict animal entry but allow ants to move freely in and out of the traps. Eight seeds of *Eucalyptus sideroxylon* and eight seeds of *Lomandra longifolia* (www.Australianseed.com), were placed in each trap and traps, including lids, were placed on the ground one meter south of the monitoring site star pickets and anchored to the ground with two aluminum tent stakes. Traps were set out in February (summer) 2015 and 2016 for seven days. *Lomandra longifolia* seeds were rarely removed and I do not consider them further in this paper. The number of *E. sideroxylon* seeds removed was recorded on day seven. Ant data were not collected in the same years that seed traps were set but the experiment was stable during this time as trees in the pine plantation were mature.

Temperature data were collected using Onset Pendant Temperature/Light Data Loggers (UA-002-64) from November 2011-May 2012 and from November 2012-May 2013 in 20-minute intervals. Loggers were placed 1m north of the center of each site marker and attached to a plastic stake at 5cm off the ground. Temperature sampling spanned spring, summer, and fall to account for seasonal differences in thermal conditions and in two separate years to account for annual variation. I also collected percent canopy cover data at each site from photographs taken at a height of 1 m and processed using ImageJ.

In February and May 2013, ground cover and fallen wood were surveyed at all 188 sample sites. I measured percentage ground cover of leaves, bark, grass, bare-ground, rock, wood, moss, and *Lomandra* sp., a large tussock-forming, grass-like plant (Xanthorrhoeaceae). I used a point intercept survey, running a piece of rope, 10 m long, in five directions (72 degrees
apart) from the central point of each site. The rope was marked every 50-cm and the ground cover (bark, leaves, etc.) that the mark touched was scored, giving a total of 100 at each site. Litter depth was measured in the same way. By running transects in five directions from a central point, the measures were deliberately biased toward the center of the site. This gave greater weight to habitat characteristics close to the pitfall traps.

The quantity of fallen wood at a site was also measured by walking the 10 m length of rope, in five directions from the central point, and scoring all wood under the rope. Fallen wood was scored for five categories with diameters of 1 cm, 2.5 cm, 5 cm, 20 cm, and 40 cm and over. Fallen wood was also scored based on whether it was rotting or not.

**Data Analysis**

1. **Effects of fragmentation treatments on Eucalyptus seed removal**

   I combined data from February 2015 and February 2016. I fitted generalized linear mixed models (binomial distribution) to determine the effect of fragmentation, edges, fragment size and the matrix on the probability of seed removal, weighted by the number of seeds in the trial (16 but occasionally one seed was lost before the traps were opened). The explanatory variables were defined as follows. *Fragmentation* was a factor with two levels, fragments and controls. *Size within fragmentation* was a factor with four levels, small, medium and large and controls. *Edge within fragmentation* was a factor with three levels, core sites, edge sites and controls. The experiment has a nested design so that data are collected at three spatial scales. Seed trials were set up at pitfall sites (1-144), which are nested within plots (1-18), which are nested within replicates (1-6). Thus, I included two random effects: *Replicate* and *Plot*. I also considered the
interaction between size and edges but there were no significant effect sizes and so it is not presented here.

I then estimated effect sizes as the log odds ratio of a given treatment to the controls, as follows:

\[
\text{logit}(p_{\text{fragments}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{matrix}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{fragment interiors}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{fragment edges}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{small fragments}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{medium fragments}}) - \text{logit}(p_{\text{controls}})
\]

\[
\text{logit}(p_{\text{large fragments}}) - \text{logit}(p_{\text{controls}})
\]

where \( p_{\text{fragments}} \), \( p_{\text{controls}} \), \( p_{\text{matrix}} \) are the probabilities of occurrence in fragments, controls, and matrix respectively, and so on for edges and different fragment sizes. The logit function is \( \ln(p/(1-p)) \). Confidence intervals were calculated by profiling.

2. Do ants determine seed removal?

I hypothesized that ant richness, the total number of individual ants, and the abundance of particular individual ant species at a site could all determine the number of seeds removed at that site. I fitted generalized linear mixed models (binomial distribution) weighted by the number of seeds in the trial to determine the effect ant richness, the total number of individual ants, and the abundance of the eleven most abundance ant species on seeds removed. I included \textit{Replicate} and \textit{Plot} as random effects. I first considered each explanatory variable individually. I then considered whether the effects of total ant abundance, richness and \textit{Rhytidoponera metallica}
abundance (the only species to explain seed removal) on seed removal were additive rather than being correlated by looking at all pairwise combinations of explanatory variables as well as a model that contained all three explanatory variables. I compared models using model selection.

**Figure 4-1.** Map of the experimental site. There are eight sampling sites within each patch, each with two pitfall traps. Paired sampling sites are represented by dots in the pine matrix. Patch sizes are 0.25ha, 0.875ha and 3.062ha. Patches are separated by at least 50m. The eight sampling sites within each small patch are not represented because of space constraints. Right panel, i=inner fragment, e=fragment edge, s=slope, d=drainage line.
Figure 4-2. Potential mechanisms determining the effect of fragmentation on seed removal. Fragmentation potentially affects the total abundance of ants at a site both directly, by reducing population sizes and isolating them, placing populations at risk of stochastic extinction, and indirectly by altering fragment habitat and thereby increasing/decreasing the presence of a given ant species’ habitat. Further, the total abundance of ants at a site determines seed removal but the number of seeds removed for a given number of ant individuals present at a site could be modified by the environment at that site.
3. Direct and indirect effects of fragmentation on seed removal

I hypothesized that fragmentation affected the total abundance of ants at a site both directly, by reducing population sizes and isolating them, placing populations at risk of stochastic extinction, and indirectly by altering fragment habitat and thereby increasing/decreasing the presence of a given ant species’ habitat (Fig. 4-1).

In turn, I hypothesized that the total abundance of ants at a site determines seed removal but that the number of seeds removed per ant could be modified by the environment of a site. For example, two sites might have the same number of ant individuals present but one site is cooler than the other, which results in fewer seeds being removed there (Fig. 4-1).

I constructed a quantitative version of Figure 4-1 by both investigating specific relationships where informative and finally by partitioning effect sizes to determine the relative contributions of 1) spatial process and the environment on total ant abundance, and 2) total ant abundance and the environment on seeds removed, as follows:

4. Effects of fragmentation and the environment on total ant abundance

I first asked whether there was a total effect of fragmentation, fragment size and edge effect (including the environment and spatial processes) on log ant abundance using logistic regression mixed models. I constructed models as described in 1. and 2. above.

I next worked to decompose the effects of the environment and spatial effects of fragmentation.

First I asked whether the environment determines log total ant abundance. From my broad habitat survey and microclimate data I selected variables that I hypothesized might explain the distribution and abundance of total ant abundance. This resulted in a large number of
environmental variables that potentially explained total ant abundance (Table 4-1). These variables grouped into four classes of variable: ground cover and structure, soil properties, canopy cover and temperature. I determined the change in deviance associated with each variable independently (p<0.05) using linear mixed models (REML). Models included the random effects Block and Plot. I then fitted a full model containing all variables that were significant individually. I dropped and added variables, iteratively, until I reached a final model containing only significant variables (Table 4-2).

Once I had determined which environmental variables predicted log total ant abundance (above), I backtracked to determine whether fragmentation had altered those environmental variables. That is, were they significantly different in fragments and continuous forest, in different sized patches, and/or at fragment edges versus interiors. I also looked for an interaction between fragmentation, patch size and edges. I used the same model fitting protocol as in 1. but used linear mixed models (REML) rather than generalized linear mixed models. I then estimated effect sizes as the log odds ratio of a given treatment to the controls, as in 1. Confidence intervals were calculated by profiling.

Finally, I decomposed effect sizes to determine the relative roles of spatial processes versus the environment on log total ant abundance (Fig. 4-1), using the same method described in Chapter 3, Methods, Data analysis, SEM synthesis.

5. Effects of ant abundance and the environment on seed removal

Having determined that the total number of ants drives the number of seeds removed at a site (see results), finally, I investigate whether the number of seeds removed per ant is modified by environmental conditions at that site (Fig. 4-1) by partitioning the effects of log total ant abundance and the environment, using the same method described in Chapter 3, Methods, Data
analysis, SEM synthesis. I first established that temperature and percent grass cover were the only environmental variables linked to the number of seeds removed, using the same protocol as in 4 above.

Table 4-1. List of environmental variables at the site scale.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter depth</td>
<td>Litter depth in cm</td>
</tr>
<tr>
<td>% canopy cover</td>
<td>% canopy cover from photographs</td>
</tr>
<tr>
<td>pH 2012</td>
<td>Soil pH from 2012 survey</td>
</tr>
<tr>
<td>Soil organic carbon</td>
<td>Soil organic carbon from soil survey</td>
</tr>
<tr>
<td>Soil wetness index</td>
<td>From 1985 soil survey</td>
</tr>
<tr>
<td>Mean temperature</td>
<td>Mean temperature in degrees Celsius</td>
</tr>
<tr>
<td>Leaves</td>
<td>% ground cover of leaves (area 10 m radius)</td>
</tr>
<tr>
<td>Bark</td>
<td>% ground cover of bark (area 10 m radius)</td>
</tr>
<tr>
<td>Grass</td>
<td>% ground cover of grass (area 10 m radius)</td>
</tr>
<tr>
<td>Roots</td>
<td>% ground cover of roots (area 10 m radius)</td>
</tr>
<tr>
<td>Bare ground</td>
<td>% ground cover of bare ground (area 10 m radius)</td>
</tr>
<tr>
<td>Rock</td>
<td>% ground cover of rock (area 10 m radius)</td>
</tr>
<tr>
<td>Wood</td>
<td>% ground cover of wood (area 10 m radius)</td>
</tr>
<tr>
<td>Moss</td>
<td>% ground cover of moss (area 10 m radius)</td>
</tr>
<tr>
<td>Lomandra</td>
<td>% ground cover of <em>Lomandra</em> (area 10 m radius)</td>
</tr>
<tr>
<td>Mean hard wood diameter</td>
<td>Mean diameter of fallen wood (area 10 m radius)</td>
</tr>
<tr>
<td>Mean rotting wood diameter</td>
<td>Mean diameter of rotting fallen wood (area 10 m radius)</td>
</tr>
</tbody>
</table>
Table 4-2. Summary of the effects of environmental variables on total ant abundance. The significance of a variable was determined by the change in deviance (Deviance) associated with dropping that variable. A variable was considered significant when the change in deviance associated with it exceeded the chi-squared critical value, at $p < 0.05$, for the number of degrees of freedom (d.f.) that the variable conferred. The level of significance, the Chi-squared probability, is listed in the p-value column.

<table>
<thead>
<tr>
<th>Variable</th>
<th>d.f.</th>
<th>Deviance</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replicate stratum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>1</td>
<td>10.214</td>
<td>0.001</td>
</tr>
<tr>
<td>Percent cover of grass</td>
<td>1</td>
<td>7.2856</td>
<td>0.007</td>
</tr>
<tr>
<td>Litter depth</td>
<td>1</td>
<td>6.1797</td>
<td>0.013</td>
</tr>
</tbody>
</table>
Figure 4-3. Effect sizes and 95% confidence intervals of the probably of a *Eucalyptus* seed being removed -- from generalized linear mixed models (logistic). The effect size is the difference from controls on the log odds ratio scale. Confidence intervals were calculated by profiling. The solid vertical grey line represents a doubling of the probability of a seed being removed.
Results

1. Effects of fragmentation treatments on Eucalyptus seed removal

I hypothesized that fragmentation, fragment size and edge effects all could affect seed removal. I determined that fragmentation increased the probability of seed removal in fragment cores and in large fragments (Fig. 4-3). I used logistic regression mixed models.

2. Do ants determine seed removal?

I hypothesized that ant richness, the total number of individual ants, and the abundance of particular individual ant species at a site could all determine the number of seeds removed at that site. From logistic regression mixed models I determined that the total number of ant individuals at a site (logged) was the best predictor of the number of seeds removed (AIC = 864, p<0.001) compared to species richness, logged (AIC=871, p<0.001). I also individually considered the effect of the eleven most abundant ant species on seed removal. The logged abundance of only one species, *R. metallica* (ANT067), positively predicted the rate of seed removal (AIC=866, p=0.004). The abundances of two other species, *Solenopsis* sp. (ANT068) and *Prolasius* sp. (ANT061), negatively predicted the number of seeds removed. These species are likely competitors of *R. metallica*. I also looked at whether the effects of total ant abundance, richness and *R. metallica* abundance on seed removal were additive rather than being correlated. While log total ant abundance is the single best predictor of the number of seeds removed, log total ant abundance and log abundance of *R. metallica* together are the best model (AIC=862) suggesting that while total ant abundance best predicts the number of seeds removed, for a given number of ants at a site, the greater proportion of those ants that are *R. metallica*, the more seeds are
removed. For completeness AIC for the other models are: log total abundance, log richness, log \( R. \) metallica: AIC=865; log total abundance, log richness: AIC=866; log richness, log \( R. \) metallica: AIC=866.

3. Direct and indirect effects of fragmentation on seed removal

I hypothesized that fragmentation affected the total abundance of ants at a site both directly, by reducing population sizes and isolating them, placing populations at risk of stochastic extinction, and indirectly by altering fragment habitat and thereby increasing/decreasing the presence of a given ant species’ habitat (Fig. 4-1).

In turn, I hypothesized that the total abundance of ants at a site determines seed removal but that the number of seeds removed per ant could be modified by the environment of a site. For example, two sites might have the same number of ant individuals present but one site is cooler than the other, which results in fewer seeds being removed there (Fig. 4-1).

I constructed a quantitative version of Figure 4-1 by both investigating specific relationships where informative and finally by partitioning effect sizes to determine the relative contributions of 1) spatial process and the environment on total ant abundance, and 2) total ant abundance and the environment on seeds removed. I describe these findings in turn.

4. Effects of fragmentation and the environment on total ant abundance

I first asked whether there was a total effect of fragmentation, fragment size and edge effect (including the environment and spatial processes) on log ant abundance using logistic regression mixed models. In total, fragmentation did not affect total ant abundance (Fig. 4-4), although, total ant abundance is reduced in pine plantation matrix habitat.

I next worked to decompose the effects of the environment and spatial effects of fragmentation. First I determined, from a linear mixed model, that log total ant abundance is a
function of three environmental variables: litter depth, percent cover of grass and, temperature (Table 4-2, Fig. 4-5). Further, that fragmentation affects each of these environmental variables but in different, and sometimes opposing, ways (Fig. 4-6).

Finally, I decompose effect sizes to understand the relative roles of spatial processes versus the environment on total ant abundance. Spatial processes and the environment almost equally determine ant abundance (Fig. 4-7). However, the effect of spatial processes is positive. Total ant abundance was reduced in the matrix, which means that fragmentation increased the isolation of populations on fragments. Thus, I should expect the effect of fragmentation to be negative. The positive effect I see likely represents the effects of unmeasured factors on ant abundance (e.g. competitive dynamics between species, unmeasured environmental variables).

Looking at these relationships more closely, fragmentation increases litter depth, which negatively affects total ant abundance, fragmentation reduces the percent cover of grass, which positively affects the number of ants, and finally that fragmentation reduces temperature, which negatively affects the total ant abundance (Fig. 4-7). Relatively, the effect of litter depth on ant abundance is much larger (32%) that either grass cover (6%) or temperature (4%).

5. Effects of ant abundance and the environment on seed removal

I already determined that the total number of ants drives the number of seeds removed at a site. Here I determine that the number of seeds removed per ant is modified by environmental conditions at that site – the percentage grass cover and temperature (Table 4-3, Fig. 4-7). Fragmentation reduces temperature in small fragments (Fig. 4-6), and this is turn reduces the number of seeds removed in fragments compared to controls for a given number of ants presents (Table 4-3, Fig. 4-7). In addition, fragmentation reduces the cover of grass in medium and large fragments (Fig. 4-6) and this positively affects the removal of seeds in fragments compared to
controls (Table 4-3, Fig. 4-7). More seeds are removed per ant when less grass is present. There is also a trend (but CIs encompass zero) for fragmentation to reduce grass cover in fragment cores, potentially positively affecting seed removal there for a given total abundance of ants.

**Table 4-3.** Summary of the effects of environmental variables and total ant abundance on seeds removed. The significance of a variable was determined by the change in deviance (Deviance) associated with dropping that variable. A variable was considered significant when the change in deviance associated with it exceeded the chi-squared critical value, at $p < 0.05$, for the number of degrees of freedom (d.f.) that the variable conferred. The level of significance, the Chi-squared probability, is listed in the $P$-value column.

<table>
<thead>
<tr>
<th>Variable</th>
<th>d.f.</th>
<th>Deviance</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Replicate stratum</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>1</td>
<td>12.351</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percent cover of grass</td>
<td>1</td>
<td>7.6391</td>
<td>0.006</td>
</tr>
<tr>
<td>Log total ant abundance</td>
<td>1</td>
<td>1.399</td>
<td>0.237</td>
</tr>
</tbody>
</table>
Figure 4-4. Effect sizes and 95% confidence intervals for the effects of fragmentation on the log of total ant abundance in fragments, fragment cores and edges, and small medium and large fragments (from linear mixed models). The effect size is the difference from controls on the log scale. Confidence intervals were calculated by profiling. The solid vertical grey lines represent a 10% increase/decline in log total ant abundance.

Results summary

Habitat fragmentation increases seed removal in large fragments and fragment cores. The number of seeds removed from a site is determined by the total number of ants present.

Fragmentation does not alter seed removal by directly altering the total number of ants at a site.
Rather, fragmentation modifies the environment so that more/fewer seeds are removed in different parts of the fragmented landscape, compared to continuous forest, when the same number of ants is present. Specifically, fragmentation reduces the number of seeds removed per ant in small fragments by reducing temperature there. Further, fragmentation increases the number of seeds removed per ant in medium and large fragments (and potentially fragment cores) by reducing grass cover there. More seeds are removed when grass cover is low.

**Discussion**

Debate rages about the importance of the link between biodiversity and ecosystem function (Vellend et al. 2013; Oliver et al. 2015; Gonzales et al. 2016; Milligan et al. 2017; Vellend et al. 2017). While experimental evidence that links reductions in biodiversity to reductions in ecosystem function abounds (García and Martínez 2012; Hooper et al. 2012), outside of diversity experiments, disturbance driven reductions in local diversity are almost never of the same magnitude as these experiments (Vellend et al. 2013). Further, most studies focus on productivity as a key ecosystem process. While some other ecosystem processes are likely predicted by productivity, for example carbon sequestration, other key processes may not be linked and are understudied.
Figure 4-5. Relationships between environmental variables and log total ant abundance from a linear mixed model.
**Figure 4-6.** Effect sizes and 95% confidence intervals for the effects of fragmentation on three environmental variables in fragments, fragment cores and edges, and small, medium and large fragments (from linear mixed models). The three environmental variables are key variables that predict total ant abundance at Wog Wog. The effect size is the difference from controls on the log scale. Confidence intervals were calculated by profiling. The solid vertical grey lines, where present, represent a doubling or halving of litter depth (cm) and percent grass cover.
Figure 4-7. Summary of effect sizes and their percent of the total effect size of fragmentation on log total ant abundance and seed removal. Spatial processes and the environment almost equally determine ant abundance. The positive effect of spatial processes likely represents the effects of unmeasured factors on ant abundance (e.g. competitive dynamics between species, unmeasured environmental variables). For effects of the environmental on ant abundance, fragmentation increases litter depth, which negatively affects total ant abundance, fragmentation reduces the percent cover of grass, which positively affects the number of ants, and finally that fragmentation reduces temperature, which negatively affects the total ant abundance. Relatively, the effect of litter depth on ant abundance is larger than grass cover and temperature. The total number of ants at a site determines the number of seeds removed. However, the number of seeds removed per ant is modified the environment at a site. Fragmentation reduces temperature in fragments, and fewer seeds are removed per ant at cooler sites. In addition, fragmentation reduces the cover of grass and more seeds are removed per ant when grass cover is lower.
Myremecochory is a crucial ecosystem function that limits intraspecific tree competition and locates seeds in habitat that helps facilitate germination (Farwig and Berens 2012; Almeida et al. 2013). Changes to seed dispersal rates have great potential to alter understory and tree communities (Cordeiro and Howe 2003; Gómez and Espadaler 2013), and in turn impact light, temperature and water regimes. Since ants are a ubiquitous component in Australian ecosystems, and have been shown to respond to habitat fragmentation, I sought to determine the impacts of habitat fragmentation on seed removal and to understand the role changes in ant communities might play. I also consider that components of ant communities, other than ant diversity, that might drive changes to seed dispersal.

Habitat fragmentation changed seed removal rates so that the probability of seed removal increased in fragment cores and large fragments compared to controls. This is not a novel result (Cordeiro and Howe 2003; Magrach et al. 2011; Leal et al. 2014). However, this finding contributes to mounting evidence that fragmentation impacts not only biodiversity but also entire ecosystems (Didham et al. 1996; McConkey et al. 2012; Oliver et al. 2015). While an important result, I sought to understand the mechanistic link between habitat fragmentation and seed removal by asking: 1) Does habitat fragmentation directly affect ant communities and if so do those changes drive changes in seed removal? 2) Do changes to the environment, that are the result of experimental fragmentation, affect the rate of ant seed removal (Fig. 4-1)?

The total number of ant individuals at a site, not local ant richness or the abundance of any one ant species, predicted the probably of seed removal (and see Lomov et al. 2009; Aranda-Rickert and Fracchia 2011). However, more seeds were removed when the total number of ants at a site contained a larger proportion of \textit{R. metallica} individuals. Nonetheless, total ant
abundance alone was a better predictor of probability of seed removal than *R. metallica* abundance alone.

These results are consistent with other studies in two ways. The first is that the presence of a single ant species can significantly drive removal rates (Zelikova et al. 2008; Fayle et al. 2011). The second is that *R. metallica* is consistently found to play a large role in seed removal in Australian ecosystems (Drake 1981, Thomas 2003; Gove et al. 2007; Lubertazzi et al. 2010; Beaumont et al. 2011; Majer et al. 2011). This builds on an emerging consensus that just a few ant species can make disproportionately high contributions to seed dispersal. For example, in the Great Smoky Mountains of the United States, seed dispersal was best predicted by the abundance of *Aphaenogaster rudis* (Zelikova et al. 2008) and in northwestern Argentina, *Pogonomyrmex cunicularius* accounted for 84% of the seeds removed at experimental sites (Aranda-Rickert and Fracchia 2011).

While total ant abundance predicted the probably of seed removal, fragmentation’s direct and indirect effects on ant abundance worked in opposite directions so that, in sum, local total ant abundance was not modified on fragments (Fig. 4-4). While the direct effects of fragmentation on total ant abundance were positive, fragmentation induced changes to the abiotic environment, which affected ant abundance negatively. I found that fragmentation increased litter depth, reduced the percent cover of grass in larger fragments, and lowered average temperature in small fragments and that these variables best predicted ant abundance (Fig. 4-6 and 4-7). Previous work has linked litter depth and grass cover to ant abundance (Yates et al. 2011; Moyano and Feener 2014; Jacquemin et al. 2016) and this link may be explained by the size-grain hypothesis, which suggests that more complex environmental conditions (e.g. deeper litter and more grass coverage) may make it harder for larger ant species to navigate and forage
That lower average temperature in small fragments, as compared to medium and large fragments, had an impact on ant abundance is not surprising since ants are ectothermic. Above ground foraging activity has been shown to be reduced in cooler environments (Holldobler and Wilson 1990; Stuble et al. 2013; Caldato et al. 2016), which likely explains why I captured fewer ants in cooler fragments.

While my study lends support to previous work, which highlights the response of ant community structure to changes in abiotic conditions (Debuse et al. 2007; Ribas and Schoederer 2007; Sipos and Kindlmann 2013; Arnan et al. 2014; Chen and Robinson 2014) I provide an important discovery, which extends this understanding and shows that ant-mediated seed removal can be affected by changes in abiotic conditions.

Fragmentation did not alter the number of seeds removed from large fragments and fragment cores by altering the total number of ant species at a site but rather by changing the per capita rate of seed removal by changing the abiotic environment. In other words, fragmentation modified the environment so that more/fewer seeds were removed in different parts of the fragmented landscape, compared to continuous forest, when the same number of ant individuals was present. Specifically, fragmentation increased the number of seeds removed per ant in medium and large fragments (and potentially fragment cores) by reducing grass cover there. More seeds are removed when grass cover is low, likely because grasses produce a large number of seeds, which may compete with eucalypts for dispersers. Additionally, as small, ground dwelling organisms, ants are also subject to a variety of structural environmental challenges, such as increased ground rugosity, when foraging. Structural challenges affect ants in both the encounter phase and retrieval phase and therefore may limit foraging success (Kaspari and Weiser 1999; Gibb and Parr 2010).
Further, fragmentation reduced the number of seeds removed per ant in small fragments by reducing temperature there. As ectothermic organisms, ants rely on temperature cues to induce activity (Holldobler and Wilson 1990). Empirical evidence indicates that foraging success is predicted by temperature such that lower temperatures result in lower resource acquisition and encounter rate (Barbiere et al. 2015; Sagata and Gibb 2016) and this may be compounded by temperature of a food resource itself (Pettit and Latty 2016). Future experiments should examine ant preference for arboreal and understory seeds to determine whether resource availability or environmental complexity is driving dispersal rates.

In summary, I provide two critical clarifications to the biodiversity-ecosystem function debate (Vellend et al. 2013; Oliver et al. 2015; Gonzales et al. 2016; Milligan et al. 2017; Vellend et al. 2017). First, our study helps to disentangle which aspects of ant biodiversity are impacted by fragmentation and are linked to seed removal. Like many other studies, reductions in local diversity were modest, even for a dramatic impact like habitat fragmentation, where a number of ant populations are isolated on fragments or have significantly reduced abundances in the matrix (Chapter 2). Nonetheless, our results highlight the importance of other measures of community structure as important drivers of seed dispersal: here the total number of ants and presence of _R. metallica_. Second, a key driver of seed removal was fragmentation driven changes to the environment that altered ant per capita seed removal. The environment was altered in different ways in fragments of different sizes so the probability of a seed being removed changed in different parts of the fragmented landscape. Future habitat fragmentation-ecosystem function studies involving ants should describe ways in which abundantly dominant species affect rates of
seed removal and determine the relative contributions of ant communities to various ecosystem functions within fragmented landscapes. I caution that the effects of habitat fragmentation on seed removal are complex and suggest that larger-scale, controlled experiments will be the best setting in which to draw conclusions regarding human impacts on ecosystems.
CHAPTER FIVE
CONCLUSIONS

The aim of my research was to determine the impacts of long-term habitat fragmentation on ant communities and their contributed ecosystem functions in a southeast Australian *Eucalyptus* forest. I approached this research from a holistic perspective by first examining the impacts of a changing matrix on two species of ants (population level). Next, I considered the relative influence of spatial and environmental components in ant community assembly (community level). Lastly, I applied the approach from my community analysis to an analysis of the impacts of fragmentation on ecosystem function (ecosystem level). I summarize my conclusions below.

I found that the establishment of a pine plantation matrix around *Eucalyptus* fragments did not initially (years 1-4) isolate populations of *A. longiceps* and *L. erythrocephalus* on fragments, with both species equally likely to occur in controls, fragments, and pine matrix. However, by years 5-8, when pine seedlings had matured to samplings, both species were less likely to occur in the pine matrix than in fragments and controls indicating population isolation as a result of fragmentation. In year 21, when the pine matrix had matured, both species occurred less frequently in the pine matrix than fragments or continuous forest and the rarer of the two species, *L. erythrocephalus*, declined in occurrence in fragments compared to continuous forest with the more abundant species being unaffected.

The different long-term responses of *A. longiceps* and *L. erythrocephalus* to fragmentation took many years to manifest and this study demonstrates the importance of considering time since fragmentation, the habitat characteristics of both fragments and the matrix, and how the changing suitability of matrix habitat can alter ant persistence with time. My
results especially highlight the pivotal role that matrix type can have on ant persistence in a fragmented landscape.

Next, I determined how habitat fragmentation affects ant community assembly. Specifically, I asked, does altering the spatial context of ant communities on fragments via habitat fragmentation change the importance of dispersal and selection in ant community assembly? I found that fragmentation increased beta diversity in fragments compared to continuous forest. The majority of the change in beta diversity was driven by selection as measured by abiotic environmental variables and this was particularly notable in large fragments.

Dispersal between fragments also played an important yet smaller role. Interestingly, dispersal between fragments was dependent on fragment size, with small and medium fragments containing more matrix species than control sites. However, despite the increase in dispersal between the matrix and small and medium fragments, this was not accompanied by an increase in patch level species richness. While these results suggest a mass effect, they also indicate a greater influence of pine matrix on small and medium fragments since these fragments have likely experienced the loss of isolated species.

This study emphasizes the importance of using a synthetic approach to understanding community assembly in fragmented landscapes. By partitioning the relative contributions of selection and dispersal I provide insight into the mechanisms by which habitat fragmentation can alter community assembly. I also demonstrate that habitat fragmentation can alter the importance of selection and dispersal in different parts of a fragmented landscape.

Finally, I focused on the influence of habitat fragmentation on ecosystem function. I found that habitat fragmentation led to an increased probability of seeds being removed in both large fragments and core habitat. The increase was driven by ant abundance and was influenced
by the proportion on *R. metallica* individuals present. However, fragmentation did not alter seed removal by directly altering the total number of ants at a site. Rather, fragmentation modified the environment such that more/fewer seeds were removed in different parts of the fragmented landscape when the same number of ants was present.

I show that fragmentation can lead to different per capita rates of seed removal in different parts of a fragmented landscape. These results underscore the potential for fragmentation to alter ecosystem function by altering environmental variables, which then affect ant behavior.

My research contributes three important advances to our understanding of the impacts of habitat fragmentation. First, I demonstrate the impacts that a maturing matrix environment can have on population response over time and show that population isolation may take longer to detect than previous thought. Second, I illustrate how fragmentation can alter the roles of dispersal and selection and how this influences community assembly. And last, I demonstrate links between habitat fragmentation and ecosystem function by demonstrating how fragmentation alters environmental variables which lead to changes in ant behavior.
REFERENCES


