The long-term and large-scale effects of the establishment of an exotic plantation on species of native forest beetles and butterflies

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Dedication

I dedicate this thesis to my parents Jayne Evans and John Macken.

Declaration

This thesis is my own work, except where otherwise acknowledged.

Maldwyn John Evans

February 2016

Preface

This thesis is presented as a series of connected papers that either have been submitted for publication in peer reviewed scientific journals, have been re-submitted following reviews or are in preparation for submission. Each paper is intended as a stand-alone piece of work. Repetition between papers has therefore been unavoidable. Each paper is preceded by a short paragraph of text that introduces the paper.

In accordance with The Australian National University's College of Medicine, Biology and Environment guidelines for submitting a 'Thesis by Compilation', this thesis also contains an Extended Context Statement. This statement is not intended as a comprehensive review of the literature relevant to this thesis; rather, its purpose is to demonstrate the relationship between all aspects of the research presented. It includes a brief introduction, outlines of experimental design, short summaries of each paper, and finally, a synthesis of the work of the entire thesis. The context statement is included at the start of the thesis as a stand-alone body of text. As a result, the thesis does not include a separate conclusion chapter after the main body of work; instead, all conclusions are presented in the context statement at the start of the thesis. Because of the data-rich nature of the research in the papers, it was necessary to include supplementary materials including extra tables and figures for papers I, II and III. These materials are included at the back of the thesis.

The majority of the work included in this thesis is my own. I received considerable guidance throughout from my supervisors Don Driscoll, Sam Banks and Kendi Davies and also gained assistance from a number of collaborators. My supervisors and collaborators form the co-authors on my papers and their contributions are fully acknowledged in the paper list below. All co-authors have agreed in writing with the author contribution statements provided. I

supply details of any other assistance in the acknowledgements section in this thesis, and in the acknowledgements for each individual paper.

Paper I. Evans, M. J., Banks, S.C., Davies, K.F., McClenahan, J., Melbourne, B.A., Driscoll, D.A. The use of traits to interpret responses to large scale edge effects – a study of epigaeic beetle assemblages across a *Eucalyptus* forest and pine plantation edge. *Landscape Ecology*. Re-submitted following revisions.

Author contributions: ME led the conceptualisation with advice from SB, KD, BM and DD; ME and JM collected the data; ME led the analysis with advice from SB, KD, BM and DD; ME led the writing; and SB, KD and DD made substantial contributions to manuscript revision.

Paper II. Evans, M. J., Banks, S.C., Davies, K.F., King, A.J., Sweaney, N., Driscoll, D.A. When the matrix isn't a matrix. A pine plantation provides new habitat for butterflies in a long term fragmentation experiment. In prep.

Author contributions: ME led the conceptualisation with advice from SB, KD, NS and DD; ME and AK collected the data; ME led the analysis with advice from SB, KD and DD; ME led the writing; and SB, KD, AK, NS and DD made contributions to manuscript revision.

Paper III. Evans, M. J., Banks, S.C., Driscoll, D.A., Melbourne, B.A., Davies, K.F. Short-term effects do not predict long-term impacts of fragmentation in a long-term fragmentation experiment. *Ecology*. Revisions currently underway.

Author contributions: ME led the conceptualisation with advice from SB, DD, BM and KD; ME, BM and KD collected the data; ME led the analysis with advice from SB, DD, BM and KD; ME led the writing; and SB, DD, BM and KD made substantial contributions to manuscript revision.

Paper IV. Evans, M. J., Banks, S.C., Barton, P.S., Davies, K.F., Driscoll, D.A. A long-term habitat fragmentation experiment leads to morphological change in two carabid species. In prep.

Author contributions: ME led the conceptualisation with advice from SB, PB, KD and DD; ME and KD collected the data; ME led the analysis with advice from SB, PB, KD and DD; ME led the writing; and SB, PB, KD and DD made contributions to manuscript revision.

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I would like to thank Brett Melbourne for his advice throughout, in particular when it came to matters of statistical significance. I also thank the helpful folk at the Australian National Insect Collection, especially Cate Lemann, Beth Mantle, Tom Weir, Nicole Fisher and Robyn Meier. I have spent a large chunk of my time in the collection and without their help and advice, I could not have completed this PhD. Thanks to Mauro Davanzo and Pier Bairstow for their field support and blokey conversations. Thank you to Saul Cunningham for allowing the extensive use of his lab facilities and for his extremely helpful advice.

I thank the many people that have been involved in establishing and maintaining the Wog Wog Habitat Fragmentation Experiment, including Chris Margules, Mike Austin and A. O. (Nick) Nicholls. I am also grateful to all of the people who have helped with fieldwork over the history of the experiment, particularly George Milkovits. Thanks to the Forestry Corporation of New South Wales for their cooperation and assistance in the day-to-day running of the experiment. I would also like to acknowledge the incredible work of John

Lawrence and Andy Hicks in identifying and mounting the beetles caught in the fragmentation experiment.

There are many friends that have helped me in many different aspects of my PhD. These include Philip Barton, Marwan El Hassan, Nic Engerer, Brad Farmilo, Claire Foster, Brett Howland, Karen Ikin, Andrew King, Mandy King, Pia Lentini, Jeff McClenahan, Laura Rayner, Chloe Sato, Ben Scheele, Ingrid Stirnemann, Dejan Stojanovic, Nici Sweaney, Kika Tuff and Martin Westgate. A special thanks goes to Brett Howland for his help in the field, including his demonstration of superb manskills involving a winch (!) and a 4WD. Thanks also to my volunteer Dave Portway – such good quality help has never come so cheap. Thank you to my good friend Philip Barton, whose advice, encouragement and clarity have been a constant source of motivation.

A big thank you goes out to all of my family and friends. This includes my amazing parents Jayne Evans and John Macken. A special thanks also goes to Jane and Simon McMillan who have provided unwavering support throughout. My two gorgeous boys Maldwyn and Aneirin Evans have been a source of delight, humour, fatigue and motivation. Finally, and most especially, I thank my partner, Joanne McMillan – without her help, love and support I would simply not have been able to do this.

Abstract

The influence of the land type between patches of remnant vegetation on species' survival is now widely acknowledged. From the species' perspective, this land could be hostile (defined as a matrix) or amenable (defined as new habitat). In this thesis, I was interested in whether species were favoured or hindered by fragmentation of their natural *Eucalyptus* forest habitat into remnants surrounded by a pine plantation and the mechanisms behind their responses. I took advantage of the Wog Wog Habitat Fragmentation Experiment, in Australia, to investigate the response of beetles and butterflies to this landscape change.

In a large scale edge effects study, I demonstrated that the effect of a *Eucalyptus* forest-pine plantation edge was widespread for the beetle community and that phytophagous beetles respond predictably to vegetation change along the edge gradient. Furthermore, I highlighted that many species responded to edge effects up to and beyond the scale tested (1000 metres).

In a study of butterflies at the Wog Wog Habitat Fragmentation Experiment, I demonstrated that butterfly species were richer in the pine plantation than the remnants and continuous forest. This suggested that the pine plantation offers new and possibly preferable habitat for butterflies than the corresponding native *Eucalyptus* forest. Furthermore, there was evidence for a mass effect within the remnants, with the pine plantation potentially boosting species richness and abundance of common species in the remnants when compared with the controls.

Revisiting carabid beetle species studied originally between 1985 and 1992, I found that responses in the long term (more than 25 years post-fragmentation) contrasted with those in the short term (five years post-fragmentation). Long-term species' responses were driven by the changing pine plantation matrix, which offers additional habitat resources and a habitat

structure favourable to carabid populations both in and around remnant native *Eucalyptus* forest fragments.

I used specimens of two carabid beetle species collected at Wog Wog to measure morphological change through the history of the experiment. Changes implied that one species increased its dispersal ability in response to the plantation landscape. This change was likely in response to the different ground structure in the pine plantation in tandem with the increased habitat that it provides.

Collectively, the papers in this thesis demonstrate that plantations can have both positive and negative effects for species. Species' responses to plantations changed over time as a result of a number of interacting factors such as changes in habitat resources and structure and species interactions. The trees at the Bondi State Forest are currently reaching maturity and are due for harvesting over the next few years. This suggests that many beetle and butterfly species will lose access to resources in the plantation resulting in their decline. This will likely impact species at over 1000m beyond the edge of the plantation, which includes those in the cores of the remnants. For this reason, caution should be applied when extrapolating any short term species responses to environmental disturbance, whether positive or negative, as they are liable to change in the future.

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Extended Context Statement

Introduction

The loss and fragmentation of native habitat are major threats to biodiversity worldwide (McCallum 2007; Stone 2007; Rands *et al.* 2010). There is a considerable body of ecological research that tracks how species, populations and communities respond to this threat (Fahrig 2003; Didham *et al.* 2012; Fahrig 2013). The impacts of habitat loss and fragmentation depend on a host of factors which include the spatial arrangement of remaining habitat, remnant patch size, distance to patch edges and habitat quality (Mortelliti *et al.* 2010). Furthermore, the land use type (e.g. urban (Ikin *et al.* 2012), agriculture (Foley *et al.* 2005), plantation forestry (Lindenmayer *et al.* 2003; Kröger 2012)) that replaces native habitat has significant effects on species and communities.

Species and community survival within fragmented landscapes is in large part determined by the type of land that is between the remnant patches (Ricketts 2001; van Halder *et al.* 2008; Taki *et al.* 2010; Driscoll *et al.* 2013; Sweaney *et al.* 2014). This land in-between the remnants is often the most extensive and connected part, and plays a major role in determining the ecosystem function within the landscape (Forman 1995). In the ecological literature, this land is often termed 'the matrix' with an assumption that it is hostile to the species studied (Driscoll *et al.* 2013). However, this term can be misleading when the human altered portion offers benefits for native species in the way of new or expanded habitat (Chase and Leibold 2003; Poulin and Villard 2011). The additional resource that this novel land type brings can increase the flow of individuals between the remnant patches (Åberg *et al.* 1995; Fischer *et al.* 2006; Mouquet *et al.* 2006; Davies *et al.* 2009; Venail *et al.* 2010; Livingston *et al.* 2013). Furthermore, it could potentially be used as extra resource for species in the patches (Ewers and Didham 2006), or even provide new habitat for species to establish

self-sustaining populations. In these cases the land that surrounds the remnant habitat is beneficial to species and is, therefore, not a matrix (Driscoll *et al.* 2013).

One replacement land type that causes major changes to species within fragmented landscapes is plantations (Stephens and Wagner 2007). Plantations constitute an estimated ten percent of the total worldwide forest area, or 264 million hectares, (FAO 2010); a figure which is projected to increase (FAO 2010). Undoubtedly, this will lead to many impacts on species within the habitat that it replaces. Minimising the impacts to biodiversity in plantations relies on understanding which species are affected and the mechanism behind their responses (Brockerhoff *et al.* 2008; Felton *et al.* 2010; Mortelliti *et al.* 2015).

In this thesis, I was interested in whether and why species were favoured or hindered by fragmentation of their natural *Eucalyptus* forest habitat into remnants surrounded by a pine plantation. I was particularly interested in the mechanisms behind species responses and whether responses changed over time as the pine plantation developed. I took advantage of the Wog Wog Habitat Fragmentation Experiment, in south-eastern Australia, one of the longest running fragmentation studies worldwide, to investigate the responses of beetles and butterflies to this landscape change over a period spanning 28 years.

In tandem with the Wog Wog Habitat Fragmentation Experiment, I established another sampling study within close proximity of the original experiment which I called the Wog Wog Edge Effects Study. What follows are detailed descriptions of both the Habitat Fragmentation Experiment and the new Edge Effects experiment. After this, I summarise each paper individually, before synthesising the results of the work in each paper.

The Wog Wog Habitat Fragmentation Experiment

The Wog Wog habitat fragmentation experiment was established in 1985 (Margules 1992) in what is now called the Bondi State Forest in south-eastern New South Wales, Australia (37°04'30"S, 149°28'00"E) (Figure 1). It was established to quantify the effects of habitat fragmentation on biodiversity, particularly ground dwelling invertebrates, and has revealed many important findings on habitat fragmentation (e.g. Davies and Margules 2000; Davies *et al.* 2000; Davies *et al.* 2001; Davies *et al.* 2004). Furthermore, apart from the Wog Wog Fragmentation Experiment, there are no other fragmentation experiments world-wide where the matrix has been converted to a completely novel vegetation type in a forested ecosystem, and only two that extend over a similar time period (Debinski and Holt 2000).

The Wog Wog habitat fragmentation experiment was created in a valley which was previously covered by open *Eucalyptus* forest with a grassy to shrubby understory. The experimental design is based around six replicates of three different sized square plots (0.25 ha, 0.875 ha and 3.062 ha) (Margules 1992); with four replicates established in the (to be) fragmented forest and two established in continuous undisturbed *Eucalyptus* forest. In 1987, the native *Eucalytpus* forest surrounding plots in four replicates was cleared and planted with a *Pinus radiata* plantation while two replicates remained in continuous native *Eucalyptus* forest, acting as controls.

In each plot, sample sites were stratified by topography (shallow slopes and steeper drainage lines) (Davies and Margules 1998). Slopes contain an understory of tussock grasses, forbs and scattered shrubs; moist drainage lines contain an understory of thick shrubs of *Kunzea ericoides* and wet drainage lines contain an understory of the narrow-leaved forb *Lomandra longifolia* (Austin and Nicholls 1988; Margules 1992). Further to this, each plot was also stratified by proximity to the edge (core and edge) (Davies and Margules 1998). There are a

total of 144 monitoring sites comprised of four edge and four core sites per plot. Following fragmentation of the four treatment replicates in 1987, the pine plantation was established in winter 1988. During this time, 44 addition sites were established in pairs of slopes and drains in the pine plantation. This makes a total of 188 sites across all treatments.

By the time of the field work for my research, the pines within the plantation had reached approximately 30 m in height and the understory was characterised by a layer of pine needle litter and occasional shrubs, tussock grasses and forbs in the slopes and the narrow-leaved forb *Lomandra longifolia* in the drainage lines. In 2010, the whole plantation within the fragmentation experiment was thinned resulting in a lighter and more open canopy and a temporary reduction in pine needle litter.

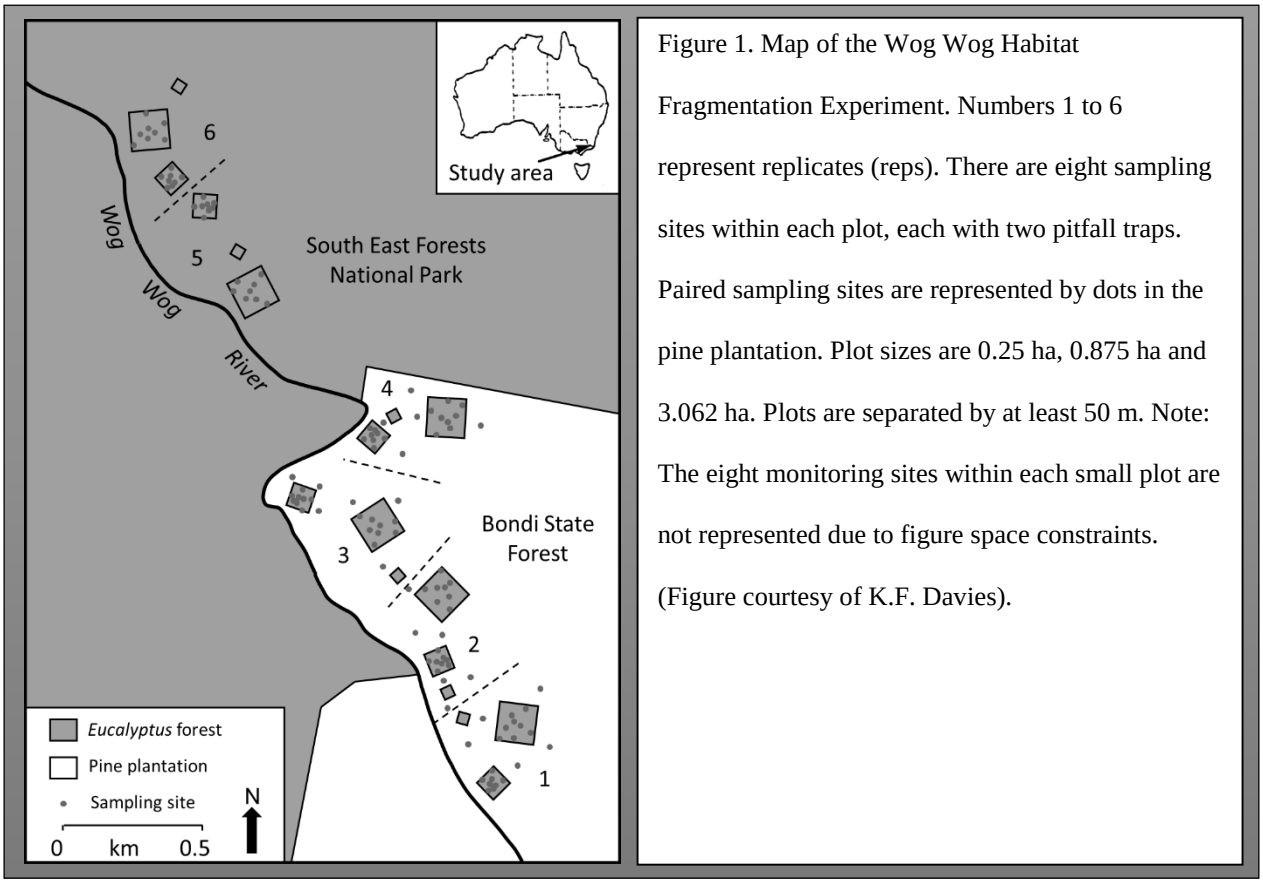

Figure 1. Map of the Wog Wog Habitat Fragmentation Experiment. Numbers 1 to 6 represent replicates (reps). There are eight sampling sites within each plot, each with two pitfall traps. Paired sampling sites are represented by dots in the pine plantation. Plot sizes are 0.25 ha, 0.875 ha and 3.062 ha. Plots are separated by at least 50 m. Note: The eight monitoring sites within each small plot are not represented due to figure space constraints. (Figure courtesy of K.F. Davies).

The Wog Wog Edge Effects Study

I established the Wog Wog Edge Effects Study (Figure 2) to test the impacts of edge effects beyond the spatial scale studied at the Wog Wog Habitat Fragmentation Experiment. By establishing the edge effects experiment within close proximity and with similar habitat types to the fragmentation experiment, my intention was to be able compare the results between the two experiments. My experimental design consisted of three blocks, each containing up to seven transects reaching from native *Eucalyptus* forest to the pine plantation forest across the intersection of the two forest types, termed the edge (Figure 2). Using a logarithmic scale, I located sampling sites along the transects at distances of 0 m (on the edge of the forest and road or firebreak), 10 m, 31.6 m, 100 m, 316 m and 1000 m into the eucalypt forest and 0 m, 10 m, 31.6 m, 100 m and 316 m into the pine forest (Figure 1). I established a total of 148 sampling sites consisting of 84 in native eucalypt forest and 64 in the pine plantation forest. A key feature of the edge effects experimental design is that sites at the same distance from the edge are placed at varying distances apart (see Figure 2). This novel anisotropic design allowed me to calculate background spatial autocorrelation between sites which in turn allowed me to control for the possible confounding effects of spatial autocorrelation across the edge.

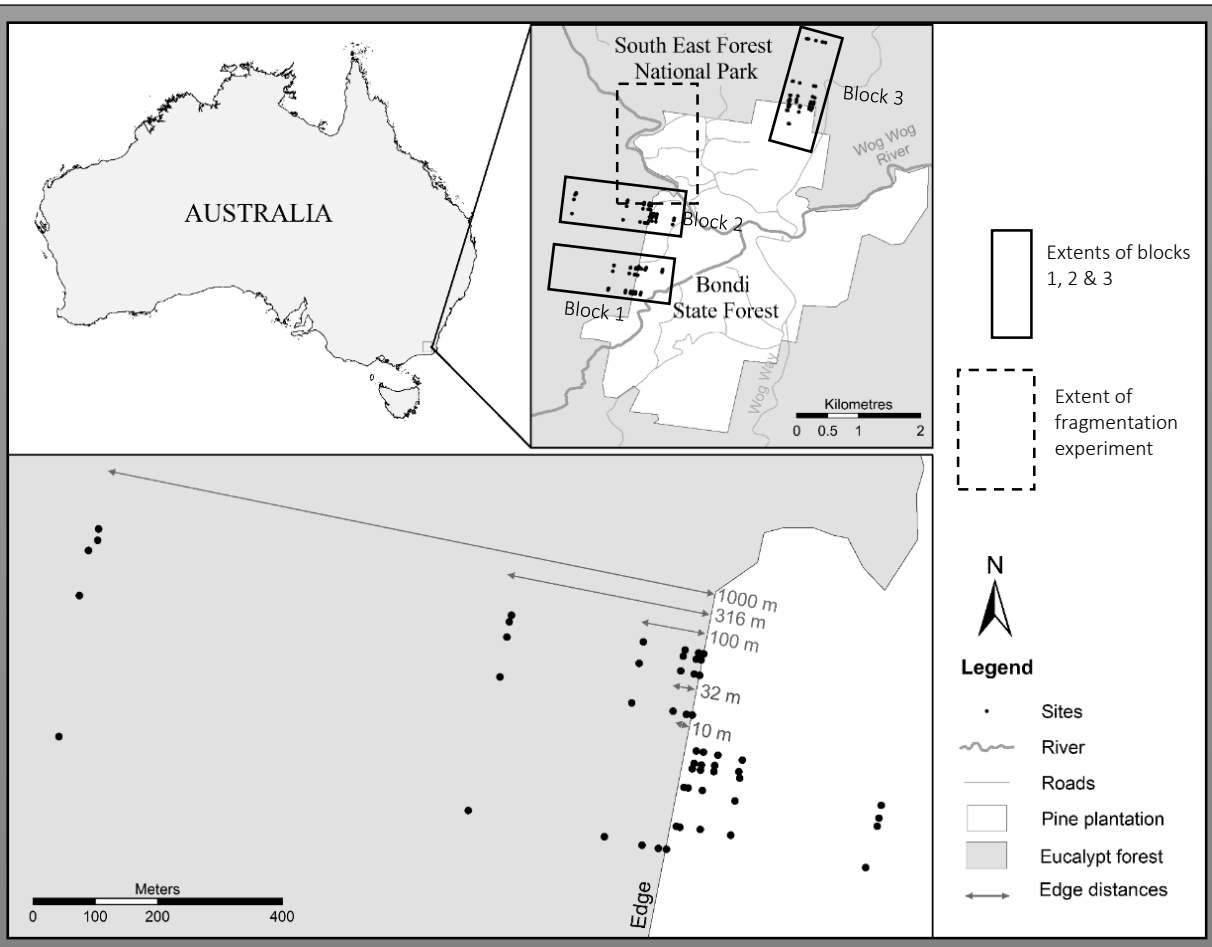

Figure 2. Map of Wog Wog Edge Effects Study. Figure includes the location and extent of the Wog Wog Fragmentation Experiment.

Overview of paper objectives, methodologies and summary of outcomes

Paper I. Beetles exhibit complex responses to edge effects.

In Paper I, I established the Wog Wog Edge Effects Study to research the responses of the Wog Wog beetle assemblage to large-scale edge effects. The edge created between adjoining habitats in a fragmented landscape has many effects on species and communities (Murcia 1995; Ries *et al.* 2004; Ewers and Didham 2008). Because species traits, such as feeding guild, dispersal ability or size, mediate their response to environmental disturbance, relating traits to edge responses can help give greater understanding to the mechanisms behind species' responses and offer predictability for other species in other systems (Lavorel and Garnier 2002; McGill *et al.* 2006; Webb *et al.* 2010; Langlands *et al.* 2011; Barnes *et al.* 2014; Ikin *et al.* 2014).

In this paper, I examined beetle species' responses to a two-sided large scale edge gradient between the native *Eucalyptus* forest and pine plantation. I used species' traits in tandem with existing predictive models of edge effects (Ries and Sisk 2004; Villaseñor *et al.* 2014) with the aim of understanding species' responses in relation to easily measured habitat variation along the edge. I showed that phytophagous species richness was directly related to vegetation changes across the edge. I also showed an association between native *Eucalyptus* forest and flying beetle species and exotic pine plantation and flightless beetles; a response most likely related to contrasting canopy and litter resources and structure between the two forest types. Individual species exhibited complex edge profiles indicating that the study was impacted by a road which created multiple edges. This study highlighted the need to examine species' responses from the species' perspective. It also demonstrated the need to study edge effects at appropriate scales.

Paper II. When the matrix isn't a matrix. A pine plantation provides new habitat for butterflies in a long term fragmentation experiment.

In Paper II, I used the Wog Wog Habitat Fragmentation Experiment to research the responses of species of common butterflies to the modified plantation landscape. I found that butterflies responded positively to pine plantations. The plantation therefore is not a matrix from the point of view of common butterfly species. In addition to this, the plantation offered new and possibly even more preferable habitat for butterflies than native *Eucalyptus* forest. A likely key factor that determines the positive responses shown for butterflies is the plantation management employed at Wog Wog. More specifically, thinning in the plantation has provided more light for butterflies and their host plants to thrive. However, plantation management also entails the harvesting of the pines, which is due in the next few years. This suggests that many of the beneficial resources that have developed in the pine will be lost, potentially leading to a decline in butterfly species.

Paper III. Short-term effects do not predict long-term impacts of fragmentation in a long-term fragmentation experiment.

Although studies that track either short- or long-term responses to fragmentation are common (e.g. Bell *et al.* 2001; Collinge and Palmer 2002; Vasconcelos *et al.* 2006; Thornton *et al.* 2010; Korfanta *et al.* 2012; Nijman 2013), those that compare responses between short and long timescales are rare. Addressing this knowledge gap is important as short-term responses are often used as a basis to make theoretical projections of long-term responses (Heywood *et al.* 1994; Tilman *et al.* 1994; Pimm *et al.* 1995; Brown *et al.* 2001; Brook *et al.* 2003; Hastings 2004; Triantis *et al.* 2010; Halley *et al.* 2014). In Paper III, I used data from the Wog Wog Habitat Fragmentation Experiment to compare short-term and long-term beetle responses to fragmentation. I re-visited the carabid species studied by Davies and Margules

(1998) with more recent data from 2011 and 2012, 24–25 years after fragmentation (26–27 years after the commencement of the study).

I found that, for carabid beetles, long-term responses to fragmentation differed from those over the short term. Carabid responses were driven by temporal variation in the pine plantation, which offers differing habitat resources and a habitat structure over time. In the long term, the plantation offers habitat to carabid populations both in and around remnant native *Eucalyptus* forest fragments. My findings have highlighted that the risk that much of the large body of work tracking short-term responses to fragmentation does not necessarily give an accurate indication of the true responses of species and communities to fragmentation.

Paper IV. The morphological responses of two carabid species to long-term habitat fragmentation experiment.

The morphological changes experienced by animals in response to environment change can potentially offer an extra level of information (Vanhooydonck *et al.* 2009; Desrochers 2010; Heidinger *et al.* 2010; Laparie *et al.* 2010) to help understand the mechanisms behind species responses to environmental change. I measured specimens of adult carabids of two species caught throughout the history of the Wog Wog Habitat Fragmentation Experiment to research the effects of the experimental changes at Wog Wog on their morphology. I was able to test whether these beetles responded morphologically to the experimental treatments and link these morphological responses to the population responses outlined in Paper III.

I showed that the two carabid species expressed contrasting morphological variation over time. Morphological traits related to dispersal ability implied that one species increased its dispersal ability in response to the plantation landscape. The other species, however, showed

contrasting morphological variation over the history of the experiment. When comparing these results with the population responses of these species, as outlined in Paper III, it is possible to infer that these two species have different inherent dispersal abilities. One species can disperse further than the other resulting in less resource constraints being posed on this species than on the other. The resource constraints posed on this second species resulted in a reduction in size. The morphological changes I demonstrated aided the inferences made about the drivers of the two carabid beetles' population responses and vice versa.

Synthesis

The pine plantation is new habitat for many species

Most of the species studied in this thesis were present in some numbers in the pine plantation. Furthermore, many of the species showed positive responses to the pine plantation, indicating that it is new habitat for these species. The butterflies researched in Paper II do not see the landscape as patches surrounded by an inhospitable matrix. Instead, the pine plantation provides supplementary habitat for these species. Furthermore, it is even possible that the plantation provides preferential habitat for butterflies over and above the *Eucalyptus* forest. The same could be said for the carabids in Papers I, III and IV, with the pine plantation even appearing to drive positive responses in the remnants. This concurs with previous studies that show that pine plantations can benefit carabid species (Bonham *et al.* 2002; Berndt *et al.* 2008; Lange *et al.* 2014).

Habitat resources drive responses

Habitat resource and structure in the pine plantation were clear drivers behind the positive responses of species studied. The butterfly species studied in Paper II responded positively to the provision of grass species in the pine plantation. The carabids in Paper I, III and IV also

seemed to benefit from the resources in the pine plantation. Pine plantation litter has been shown to contain high microarthropod abundances (Springett 1976) including high densities of collembola (Niemelä *et al.* 1996; Koivula *et al.* 1999) and amphipoda (Richardson 1980; Friend and Richardson 1986; O'Hanlon and Bolger 1993; O'Hanlon and Bolger 1999), which are known food sources for carabids (Kotze *et al.* 2011). This is somewhat confirmed by the Paper IV, which showed variation in relative head size; a trait that can be directly related to a carabid's ability to consume food items of certain sizes (Pearson and Stemberger 1980; Laparie *et al.* 2010).

Habitat structure also drives responses

The structure of the pine plantation also seems to offer favourable aspects to the species studied in this thesis. The pine plantation, despite offering slightly shadier habitat that the *Eucalyptus* forest still contained enough space for butterflies comfortably fly through. Carabids respond to increased canopy cover (Niemela and Halme 1992; Koivula *et al.* 1999; Lange *et al.* 2014), a fact that was consistent with the carabids studied here. Furthermore, the pine matrix forest floor is a much less complex environment than the eucalypt forest floor, and might be more favourable for carabid dispersal. The positive morphological responses related to dispersal for one species of carabid in the plantation shown in Paper IV suggested that some species are able to move more easily through it. Any increase in movement in the pine would serve to increase predator-prey interactions (Johnson 2006; Jana and Bairagi 2014), allowing the carabids to encounter their prey more often.

Many of the structural elements favourable to the species studied in the plantation are also available in the *Eucalyptus* forest. These include a closed canopy of similar heights and the provision of native grasses and shrubs. The similarity in structure between surrounding landscape and remnant habitat, the more favourable this landscape is for organisms in the

remnants (Prevedello and Vieira 2010; Campbell *et al.* 2011; Driscoll *et al.* 2013). Furthermore, low contrast edges can have less of an impact on a number of taxa (Ries and Sisk 2008) when compared with a higher contrast edges (e.g. native forest adjacent to farm land) (Desrochers *et al.* 2003; Reino *et al.* 2009; Brearley *et al.* 2010; Campbell *et al.* 2011; Noreika and Kotze 2012) and can influence the connectivity between the patches (Eycott *et al.* 2012). In comparison with more contrasting landscape types (e.g. grazing or urban land), the pine plantation might be considered low contrast and offer many of the habitat factors needed for species to thrive.

I also found that loss of habitat resource in the pine plantation is detrimental to the survival of some species. In Paper I, I found that phytophagous (herbivorous) species were more diverse in the *Eucalyptus* forest than the pine plantation, particularly towards the edge. My results confirmed that the vegetation diversity drives phytophagous beetle diversity at Wog Wog, as it does elsewhere (Lin *et al.* 2015).

Habitat is not the only factor.

The edge effects study (Paper I) showed that habitat alone was not the sole predictor of species occurrence across the edge. This indicated that species interactions at edges (Ewers *et al.* 2013) such as predation (Suarez *et al.* 1997; McGeoch and Gaston 2000; Lahti 2001; Ries and Fagan 2003; Leighton *et al.* 2008; Frost *et al.* 2015), parasitism (McGeoch and Gaston 2000; Cronin 2003), mutualism or commensalism (Schwarz and Huck 1997; Zelikova and Breed 2008; Ewers *et al.* 2013) are likely to be influential mechanisms behind the responses of species to environmental change.

Dispersal is influential

In Paper III, I discussed that dispersal in the pine plantation might have a large part to play in determining how the carabid species respond to it. Paper IV suggested that this was indeed the case, with contrasting dispersal related morphological responses echoing contrasting population responses. One species, *Notonomus resplendens*, showed an increase in relative leg and metatrochanter (muscle for locomotion) length in the pine plantation (Paper IV) which corresponded with an increase in occurrence (Paper III). However, the other species, *Eurylychnus blagravei,* responded only with decreasing metatrochanter length. Because the function of the metatrochanter is as a muscle to push or run and differs in morphology according to which the species uses most in its life-history, increases in metatrochanter size could suggest that *Notonomus resplendens* was able to colonise the new plantation habitat more quickly than *Eurylychnus blagravei,* an explanation that would be consistent with their respective population responses.

Scale

In Paper I, I showed that edge effects for many of the species studied can reach scales far beyond the immediate environs of the edge. When the Wog Wog Habitat Fragmentation Study was established, it was acknowledged that the experiment was restricted by its size (Margules 1992), and therefore the most appropriate suite of organisms to study were those acting at smaller scales, such as the ground dwelling invertebrates (Margules 1992). The butterfly responses shown in Paper II could indicate that the experiment is too small for highly mobile species. I showed no responses to the nested treatments of edge and size. Furthermore, it was not clear that the controls and treatments were completely independent of each other – e.g. I showed that butterflies were much less abundant in the native forest than the pine plantation, possibly as they were drawn to the pine plantation. The findings in Paper

I also suggest that even the smallest species can be affected by environmental change at scales of over 1000 metres with some species of beetle seemingly affected by the edge at these scales. Finding suitably undisturbed habitat to study edges and habitat fragmentation at larger scales, however, is becoming more difficult as undisturbed habitat is becoming rarer and other environmental gradients are often present (Haddad *et al.* 2015). Our study showcases the reality that considering such large edge effects is difficult due to the rarity of uniform habitat at scales with deep edge effects (Ewers and Didham 2008).

Other landscape elements

The human derived view of the landscape does not take into consideration other landscape elements that have effects on species at Wog Wog. One significant factor could be that the landscape contains many forestry roads. Resources on road edges can be increased due to runoff (Forman and Alexander 1998). Because increased nutrient loads can increase the size of beetle populations (Larsen *et al.* 1996), it follows that the road could be having a direct impact on beetle abundance. Furthermore, these roads can be barriers to dispersal for certain species (Weidemann *et al.* 1996; Keller and Largiader 2003; Lambert *et al.* 2014) including forest specialist beetles (Koivula and Vermeulen 2005) or can aid dispersal for others types of beetle (Vermeulen and Opdam 1995; Koivula *et al.* 2005; Noordijk *et al.* 2011; Knapp *et al.* 2013). In Paper I, I proposed that the road creates multiple edges: plantation against road, eucalypt against road and the interaction of these edges. Since I also demonstrated that edge effects as a result of these edges can reach scales far beyond the immediate environment of the edge, it is very possible that these roads have impacts on the species within the experiment. Despite the roads being comparitely small in area at Wog Wog, it is possible that their impacts are relatively large (Koivula and Vermeulen 2005; Yamada *et al.* 2010; Noordijk *et al.* 2011).

Species' responses change over time

Papers I and II have highlighted species' responses to habitat change at one snap-shot in time. In contrast, Papers III and IV demonstrated that any response can change over time. In Paper III, species that initially follow trajectories towards extinction seemed to have survived in the long-term. Species' responses to plantations change over time as a result of a number of interacting factors such as changes in habitat resources and structure and species interactions. The trees at the Bondi State Forest are currently reaching maturity and are due for harvesting over the next few years. This will result in reduction of many of the resources that these species rely on in the plantation which will impact those species' abilities to survive. For this reason, caution should be applied when extrapolating any short term species' response to environmental disturbance in forestry operations, whether positive or negative, as they are liable to change in the future.

Patch Matrix model

The Wog Wog Habitat Fragmentation Experiment is defined as 'fragments' surrounded by a pine plantation and was set up to test theories of island biogeography (MacArthur and Wilson 1967) in relation to isolation of populations in the fragments driven by an inhospitable matrix (Margules 1992). In reality, however, this human-derived patch-matrix interpretation of the landscape is probably only appropriate for a small subset of species (Betts *et al.* 2014). Each species perceives the landscape in a way that is directly related to its habitat requirements, life history and prey distributions (Fischer *et al.* 2005). This is not always in the same way as humans perceive the landscape (Betts *et al.* 2014). This is reflected in the literature, with effects related to patch size and isolation, those effects that Island Biogeography Theory predicts will be widespread, only weakly related to species responses, if at all (Connor *et al.* 2000; Prugh *et al.* 2008). The species that I studied also demonstrate this, as underscored by

the lack of responses to the nested treatments of edge and remnant size in Papers II, III and IV and the positive response to the pine plantation of many of the species studied. Simply put, for a majority of the species I studied, the "matrix" isn't a matrix.

Not all species will respond in this way

My thesis underlines the importance of a species-specific view of the landscape (Betts *et al.* 2014). This point should not only serve to highlight that many species are positively affected by the habitat change at Wog Wog, but also remind us that many species are adversely impacted by it. All of the studies in this thesis exhibit bias towards common species as a necessity. Common species are easiest to study because they appear in large enough numbers to provide good data for research. However, common species, in particular those studied in this thesis, are also more likely to be generalists able to adapt to a wide range of habitats. Specialists, on the other hand, by their very nature, are more restricted to specific habitat requirements and are therefore more likely to be affected by habitat change (Devictor *et al.* 2008), a point highlighted by the larger species richness of phytophagous beetles in the *Eucalyptus* forest in Paper 1. Therefore, it is important that the positive responses observed in common species should not be assumed to reflect the response of all species at Wog Wog.

Wog Wog Habitat Fragmentation Experiment in context and in the future.

My thesis identifies a substantial knowledge gap in understanding why some species changed over time, regardless of treatment. The changes could be a response to climate change during the time of the experiment. However, it is also be possible that some species, including some beetles, are impacted at scales larger than the assumptions of the experiment (i.e. that beetles in the controls are impacted by the landscape change). The scale of most beetle populations at Wog Wog been estimated to be an area roughly 10-25 m in diameter (Davies *et. al.* 2005). The morphological changes demonstrated in Paper IV could indicate that some species

populations change the scale at which they operate in response to the plantation. It would be useful to determine the distances which beetle species at Wog Wog disperse in this new landscape – This could be examined directly through tracking studies (Ranius and Hedin 2001; Hedin and Ranius 2002; Ranius 2006), perhaps selecting a subset of species with differing life-histories to test, given the technical constraints of tracking such small species. Population genetics studies (Brouat *et al.* 2003; Matern *et al.* 2008) would also reveal a great deal of information on the scale at which individuals of certain species operate as well as patterns of dispersal across the landscape over many generations.

A key strength of the Wog Wog Habitat Fragmentation is its longevity. As one of the longest running experiments of its type worldwide, it offers data that are simply impossible to get anywhere else. The experiment has produced a valuable collection of beetles, gathered from the field throughout the experiment's history, starting in 1985. As demonstrated by Papers III and IV, this collection has the potential to offer many novel insights into species' responses to landscape change. This includes further studies on morphology and new studies on the population genetics of species within the collection – studies that will become easier in the future, as technologies improve and costs decline. The fact that the collection offers the rare opportunity to study samples collected before the environmental changes took place, as well as specimens collected at different times during the plantation landscape cycle, means that it is of considerable value to science.

The Wog Wog experiment's unique and long history, means data collected at the site is extremely valuable and important for understanding impacts of environmental change on species and communities. The plantation at Wog Wog has not yet been through a complete harvesting cycle. It is crucial that work at the site continues into the future, so that we can understand the long-term impacts of this type of landscape on species through its whole cycle

and beyond. Considerable and ongoing investment will be essential to ensure that the vital work taking place at Wog Wog continues into the future.

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Paper I: The use of traits to interpret responses to large scale edge effects – a study of epigaeic beetle assemblages across a *Eucalyptus* forest and pine plantation edge.

In Paper I, I established the Wog Wog Edge Effects Study to research the responses of the beetle assemblage to large-scale edge effects of up to one kilometre. My intention was to see if changes in easily measurable habitat variation across an edge can help explain beetle responses in the context of their feeding guild and flying ability. I was also interested in the scale at which edge effects occur in the landscape. This information would complement the data collected in the Wog Wog Habitat Fragmentation Experiment which was not designed to research species responses to edge effects at this scale.

Evans, M. J., Banks, S.C., Davies, K.F., McClenahan, J., Melbourne, B.A., Driscoll, D.A. The use of traits to interpret responses to large scale edge effects – a study of epigaeic beetle assemblages across a *Eucalyptus* forest and pine plantation edge. *Landscape Ecology*. Re-submitted following revisions.

Abstract

Edge effects due to habitat loss and fragmentation have pervasive impacts on many natural ecosystems worldwide. We aimed to explore whether, in tandem with the resource-based model of edge effects, species feeding-guild and flight-capacity can help explain species responses to an edge.We used a two-sided edge gradient that extended from 1000 metres into native *Eucalyptus* forest to 316 metres into exotic pine plantation. We used generalised additive models to examine the continous responses of beetle species, feeding-guild species richness and flight capable group species richness to the edge gradient and environmental covariates. Phytophagous species richness was directly related to variation in vegetation along the edge gradient. There were more flight capable species in *Eucalyptus* forest and more flightless species in exotic pine plantation. Many individual species exhibited multiple-peaked edge-profiles. The resource based model for edge effects can be used in tandem with traits such as feeding-guild and flying ability to understand drivers of large scale edge responses. Some trait groups can show generalisable responses that can be linked with drivers such as vegetation richness and habitat structure. Many trait group responses, however, are less generalisable and not explained by easily measured habitat variables. Difficulties in linking traits with resources along the edge could be due to unmeasured variation and indirect effects. Some species' responses reached the limits of the edge gradient demonstrating the need to examine edge effects at large scales, such as kilometres.

Introduction

Fragmentation and loss of natural ecosystems reduces biodiversity and disrupts ecological communities (Krauss *et al.* 2010; Fahrig 2013). Loss and fragmentation of native vegetation creates 'edges', or abrupt changes in habitat type and quality between adjoining ecosystems, which have many effects on species and communities (Murcia 1995; Ries *et al.* 2004; Ewers and Didham 2008) including arthropods (Tóthmérész *et al.* 2014; Lacasella *et al.* 2015; Ohwaki *et al.* 2015). Identifying the mechanisms behind the effects that edges have on species is a significant challenge because species can respond in a number of contrasting ways (Ries and Sisk 2004). A challenge for improving our understanding of edge effects is to identify general patterns of responses to environmental change that can be transferred across species and ecosystems (Ikin *et al.* 2012; Barnes *et al.* 2014). Determining these general patterns would lead to a better understanding of the ecological mechanisms that underlie the responses of species to environmental change.

The conceptual resource-based model (Ries and Sisk 2004) proposes a framework for understanding mechanisms of edge effects. The model, which is based on resource distribution, assumes that abundances of species are determined by their resource associations. A feature of the model is that species may demonstrate positive, negative and neutral edge responses, depending on the context of the edge (Ries and Sisk 2004). It also allows for temporal and spatial variation of edge response within the same species and edge type (Ries and Sisk 2004).

An approach that has helped gain a better understanding of the underlying mechanisms behind environmental change, is to relate traits of species, such as feeding-guild and dispersal ability, to the observed disturbance response (Davies *et al.* 2000; Zurita *et al.* 2012). Traits can mediate the response of species to environmental change by influencing how species

interact with their habitat (Williams *et al.* 2010; Salmon *et al.* 2014). Examining edge responses of species with regard to their traits might therefore help to understand the processes driving their responses (McGill *et al.* 2006; Ikin *et al.* 2014). For example, if coarse woody debris was highest at the edge, then we might expect to see a positive edge response for saproxylic (dead wood associated) species (Lassauce *et al.* 2011; Bouget *et al.* 2014). Similarly, if leaf-litter increases along the edge gradient, we might expect more mycetophagous species (species that feed on fungi) (Franc 1997), one of the main decomposers of leaf-litter (Den Boer *et al.* 2005). Edges can increase predator prey interactions for some bird taxa (Leighton *et al.* 2008), and can result in spillover of predators into neighbouring habitat for some invertebrates (Frost *et al.* 2015). If this were true for epigaeic beetle species, we might expect an increase of predators at the edge with spillover into the non-preferred habitat.

According to the resource-based model, the variation in resources from edge to interior drives changes to species' abundances across that edge. If species with relevant traits such as feeding-guild or dispersal ability respond in a consistent and generalisable way to the habitat across the edge, then the resource-based model could be used to predict the responses of other species with the same traits in similar edge types. In this study, we used an edge between native forest and plantation forest to determine whether species traits help to explain beetle species responses to the edge. We tested the hypothesis that different species will respond to the edge according to their habitat resource requirements and that these species' feeding-guild or flight-ability classes help predict how they might respond, given how habitat resource changes across the edge.

Materials and methods

Study area

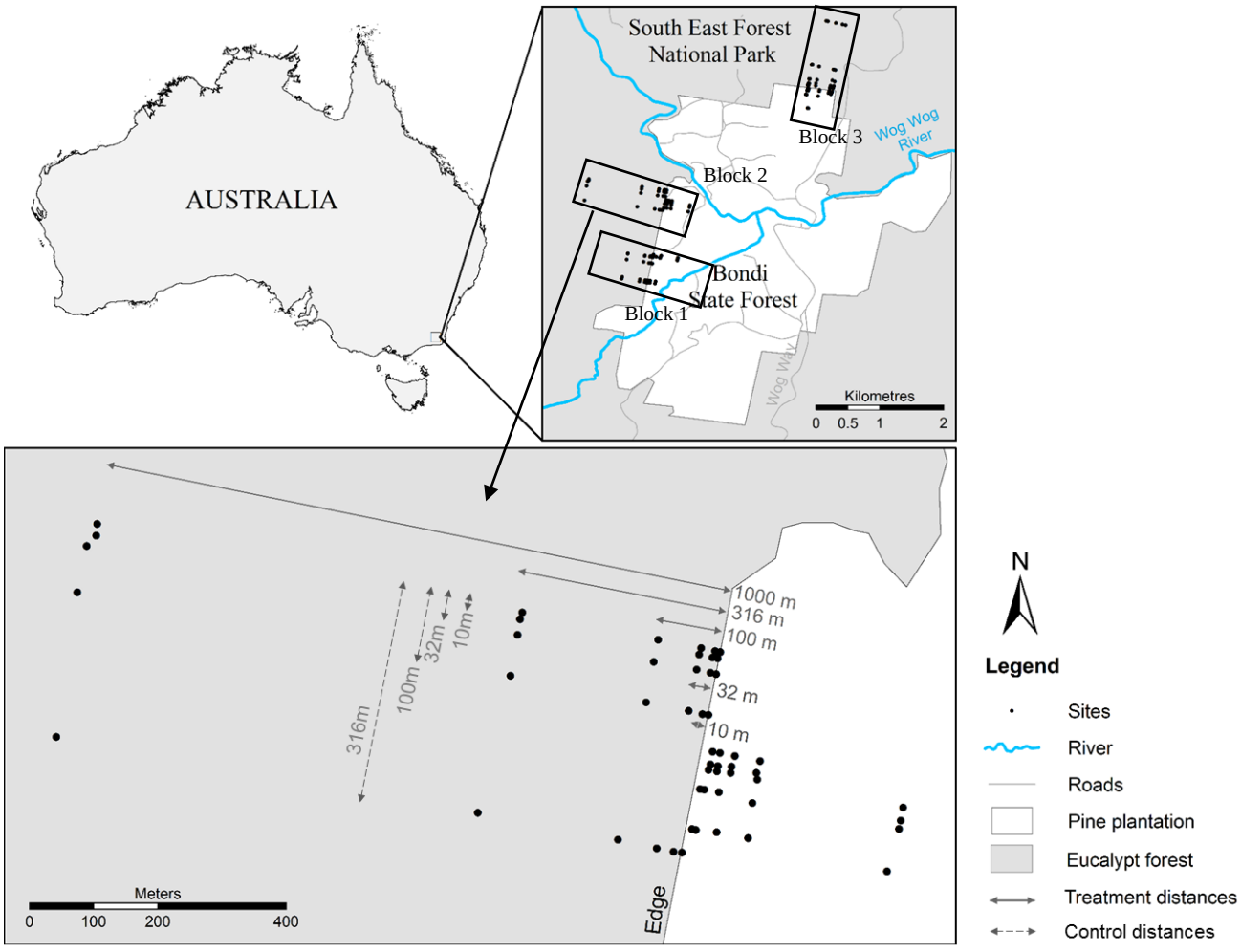
We conducted our research in the region of the Wog Wog Habitat Fragmentation Experiment (Margules 1992; Davies and Margules 1998) in the Bondi State Forest and South East Forests National Park in south eastern New South Wales, Australia (37°04'30"S, 149°28'00"E; Figure 1). The area was formerly continuous native grassy to shrubby open *Eucalyptus* forest characterized by tussock grasses, forbs and scattered shrubs (Austin and Nicholls 1988; Margules 1992). A large area was cleared in 1987 and planted with *Pinus radiata* for timber (Figure 1). At the time of data collection (2011), the pines were mature trees of around 30 m height. At full maturity, the *Pinus radiata* forest is taller and more dense with a more closed canopy than the native *Eucalyptus* forest (Baker *et al.* 2007). Its understory contains a dense layer of pine needles with occasional shrubs, tussock grasses and sedges.

Experimental design

Our experimental design consisted of three blocks of up to seven transects spanning the native *Eucalyptus* forest-pine plantation edge (Figure 1). The edge between the *Eucalyptus* and pine forests is intersected by a dirt road of about 10 m in width and (in one block) a cleared fire break of about 100 m in width. Sampling points were located along the transects at 0 m (on the edge of the forest and road or firebreak), 10 m, 31.6 m, 100 m, 316 m and 1000 m into the *Eucalyptus* forest and 0 m, 10 m, 31.6 m, 100 m and 316 m into the pine forest (Figure 1). We used a logarithmic scale, assuming that changes in abundances of species would be strongest near the edge (Didham *et al.* 1998; Ewers and Didham 2008). We did not use sampling points at 1000 m into the pine, as the pine forest at 1000 m is of a different stand age to all the other pine forest in the study. To avoid confounding the design with environmental variation not related to the edge, we kept the environmental conditions

between sampling points as similar as possible. Using geographical information software, we created a spatial topographic wetness model which allowed us to exclude sampling points in gullies and ridge tops. As a result of this, many transects did not have the full complement of sampling points at all distances. This left us with a total of 148 sampling points (84 in native *Eucalyptus* forest, 64 in pine forest) consisting of 296 pitfall traps arranged along 25 transects. A key feature of the design is that sampling points at the same distance from the edge are placed at varying distances apart (see Figure 1). This novel anisotropic design allowed us to calculate background spatial autocorrelation between sampling points allowing us to control for the possible confounding effects of spatial autocorrelation across the edge.

Figure 1.Map of study area.



Beetle sampling

We followed the beetle sampling protocol outlined in Margules (1992). At each sampling point, two pitfall traps, each consisting of a 90 mm wide and 100 mm deep cup, a 600 mm x 50 mm high fence and a 200 mm x 200 mm roof, were placed 3 m apart in a randomised direction. Pitfall traps containing pitfall fixative (94% ethanol, 5% glycol, 1% distilled water) were left open for one week in February 2011. The two pitfall trap catches at each sampling point were pooled to create one sample per sampling point. Beetles from each sample were sorted to species level. Where possible, we matched species caught to those in the Wog Wog beetle collection stored at the Australian National Insect Collection at CSIRO Ecosystem Sciences in Canberra, Australia. Each species in the CSIRO collection has a unique voucher code and we retained these codes for our collection. Other species that we were not able to match were given another unique code. Our resulting collection consists of species and morphospecies (all hereafter referred to as species). Some species within the collection were undescribed. In these cases, morphospecies were named to their highest known taxonomic rank. We categorised our species into feeding-guilds (Predator, Saproxylic, Phytophagous, Mycetophagous, Myrmecophylous, Xylophagous) and whether species were flightless or flight capable by referring to data used in previous work at the Wog Wog Fragmentation Experiment (Margules 1992; Davies *et al.* 2000) for the same species in the same area. For species that we were not able to match to the Wog Wog beetle collection, we measured their length, determined whether they had functional wings and assigned them to a feeding-guild according to other similar species in the same genus that had already been assigned a feeding-guild.

Environmental variables

We collected environmental variables to assess resource-based determinants of beetle composition in the study, as well as to measure possible confounding effects in the design. Firstly, we recorded slope and altitude. We then used a 3 m diameter plot around each sampling point in which to visually estimate covers of rock, bare ground, small woody debris, litter, moss, forb, grass, sedge, shrub and fern, and litter depth. We also recorded coarse woody debris (CWD) by measuring the diameter at the centre and end points of logs over 7.5 cm long, and the percentage of each log within the plot. We created an index for CWD at each sampling point by summing the length*average width (two endpoint widths plus centre width) of each piece of CWD recorded and multiplying it by the percentage inside the plot.

Analysis

Throughout our analysis, we used the distance from edge as an explanatory variable and treated this variable as a gradient (hereafter referred to as the edge gradient) from -316 m (316 m into the pine forest) to 1000 m (1000 m into the *Eucalyptus* forest). We transformed the absolute values of these edge distances by the natural log (d+1), and then classified the transformed pine forest distances as negative and kept the *Eucalyptus* forest distances as positive.

To determine the responses of beetle species to the edge gradient, we modelled species sampling point abundances using generalized additive models (GAMs) using the gamlss package (Rigby and Stasinopoulos 2005) in R version 3.1.1. (R Core Team 2014). GAMs allow any shape ranging from a straight line to a range of non-parametric curves, providing an ideal approach for exploring the continuous function along an edge gradient (Leighton *et al.* 2008). Other authors have used non-linear models of increasing complexity grounded in mechanistic edge effect theory (e.g. Ewers and Didham 2006; Porensky 2011). These

approaches allow the determination of quantitative edge-effect parameters which can then be used in further analysis (Porensky 2011). However, in order to model variation according to environmental change across the edge, we could not constrain the models to predefined shapes, which could potentially miss some of the variation we wished to describe.

For all of our GAMs, we included block as a random term. We tested a number of distributions for our models, and concluded that the negative binomial distribution was the best fit for the species in our data (Zuur *et al.* 2009).

To account for spatial autocorrelation, we calculated a distance-weighted autocovariate (Dormann *et al.* 2007) for each of our species. This required the calculation of a neighbourhood distance, or the maximum distance of autocorrelation. To calculate the neighbourhood distance, we first calculated an anisotropic non-parametric correlation function (Humston *et al.* 2005) using the 'ncf' package (Bjornstad 2013) in R version 3.1.1. (R Core Team 2014). We required only the distance for spatial autocorrelation of pairwise sampling points parallel to the edge, therefore using our anisotropic design to determine background spatial autocorrelation without the potentially confounding effect of distance from edge. Using the resultant correlation function we extracted the distance at which regional correlation is reached as our neighbourhood distance. Using the 'spdep' package (Bivand 2014) in R version 3.1.1. (R Core Team 2014), we then calculated the autocovariate assuming an inverse distance relationship between 0 m, where spatial correlation is at its maximum, and the calculated neighbourhood distance, where spatial autocorrelation is zero.

For all of our models, we controlled for possible confounding effects of edge distance by altitude, slope and spatial autocorrelation by modelling all combinations of edge distance,

slope, altitude and the calculated autocovariate in all of our models, treating slope, altitude and the autocovariate as linear terms.

We applied our GAM modelling approach to the 21 most numerous species with the remaining species not providing enough data for meaningful analysis (n>13). To test whether species had a significant response to the edge, we compared the AICc score of GAMs of species' responses to the edge and that of the null model that did not include the smoothed edge term (Burnham and Anderson 2002). If the model containing edge remained in the top ranked model, or was below ΔAICc =2 and therefore deemed a competitor, we interpreted that the species modelled responded to the edge gradient. If the null model was ranked higher and the corresponding edge model's score was ΔAICc>2, we interpreted that the species modelled did not respond to the edge gradient.

To test whether beetles within certain feeding-guilds or groups of dispersal ability (hereafter referred to as trait groups) would respond in generalisable ways, we ran the same modelling procedure as for our individual species. Firstly, we modelled trait group species richness across the edge using GAMs including slope, altitude, a calculated autocovariate and the random term of block. Again, we tested a number of distributions for our models, and concluded that the negative binomial or Poisson distributions were the best fits for the data (Zuur *et al.* 2009). We then compared the AICc score of trait group responses to the edge and that of the null model that did not include the smoothed edge term (Burnham and Anderson 2002). To determine any patterns common across trait groups and individual species with the same traits, we categorised their edge responses broadly into species or groups that inhabit pine or *Eucalyptus* forest in the interior or edge and whether they responded to the edge or not.

To determine whether measured habitat variation may have influenced the beetle responses to the edge, we repeated our models but included a set of linear habitat variables. First, we performed a principal components analysis (PCA) on the environmental variables using the package FactoMineR (Le *et al.* 2008) in R version 3.1.1. (R Core Team 2014) to retrieve a set of new principle component variables that explained major gradients in environmental variation. For those species and trait groups that were shown to have an edge response, we tested whether the principle components explained this response by running a model selection procedure with all combinations of the principle components and smoothed edge component. Again, we controlled for altitude, slope, and spatial autocorrelation in all models. We ranked the resultant models using AICc to see whether the inclusion of the PCA components overrode the smoothed edge term or increased the rank of the models. We removed those models where ΔAICc <2 and contained one additional parameter compared with the top ranked model, because these additional parameters are not considered to explain enough variation to justify their inclusion in the model and hence have negligible ecological effect (Arnold 2010). Our aim was to determine whether, in each model, the edge effect as reflected by distance from the edge, is negated by these habitat variables. Finally, to aid our interpretation of the environmental variables with regard to the edge, we modelled the principal components as a response to the edge gradient using GAMs assuming a normal distribution. We compared the edge model to the null model with the edge component omitted, comparing the AICc score of the two models, to see whether the PCA components showed a significant response to the edge gradient.

Results

We caught 5395 beetles consisting of 238 species from 38 families (Table S1). The most speciose family was Staphylinidae (98 species, 3409 individuals), followed by Curculionidae

(21 species, 111 individuals), Carabidae (16 species, 225 individuals) and Leiodidae (15 species, 76 individuals). The most common species caught were the Staphylinidae beetles *Anotylus cribriceps* (2265 individuals) and *Aleochara sp.* (468 individuals) and the Nitidulidae beetles *Thalycrodes pulchrum* (926 individuals) and *Th. australe* (256 individuals) (see Table S2 for breakdown of trait group relative abundances).

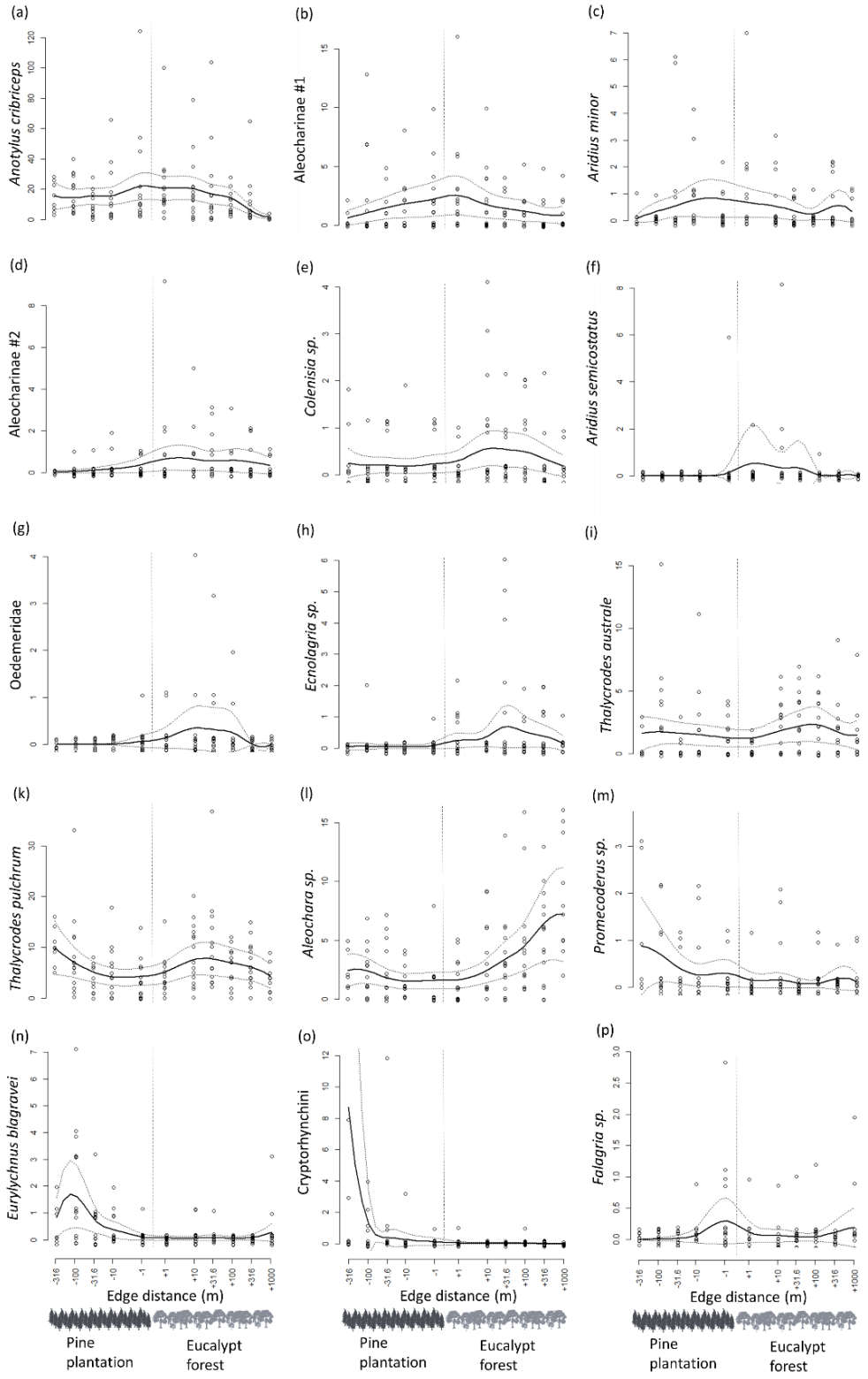
Species' responses

Fifteen of the 21 species modelled demonstrated a response to the edge gradient, with highly ranked models that included the smoothed edge term out-competing, or as in the case for two species, ranked as a competitor to, the null model (Table 1 & Figure 2). *Anotylus cribriceps*, Aleocharinae #1, and *Aridius minor* showed increases at the edge compared with *Eucalyptus* and pine interiors (Figure 2 (a) to (c)). Aleocharinae #2, *Colenisa sp.*, *Aridius semicostatus*, *Oedemeridae sp.*, *Ecnolagria sp.*, *Thalycrodes australe* and *Th. pulchrum* all increased on the *Eucalyptus* side, and up to 100 metres from the edge (Figure 2 (d) to (k)), with *Th. pulchrum* also increasing in the interior of the pine (Figure 2 (k)). *Aleochara sp.* showed a significant increase in the interior of the *Eucalyptus* forest (Figure 2 (l)). *Promecoderus sp.*, *Eurylychnus blagravei* and Cryptorhynchini showed a similar increase in the interior of the pine forest (Figure 2 (m) to (o)). *Falagria sp.* increased on the pine side of the edge and the interior of the *Eucalyptus* forest (Figure 2 (p)).

Table 1. Summary of results of model selection procedure for species responses to the edge. '✓' signifies that the model containing the edge term was ranked higher than the null model. * denotes that the edge model was ranked below the null model but was considered a competitor as its AICc score fell below ΔAICc = 2. A more detailed summary of the analysis is presented in the supplementary material (Table S3).

Species	n	ΔAICc (Edge)	Edge Term
Anotylus cribriceps	2265	0.00	✓
Thalycrodes pulchrum	926	0.00	✓
Aleochara sp.	468	0.00	✓
Aleocharinae (#1)	224	1.76	*
Aridius minor	74	0.00	✓
Thalycrodes australe	256	0.00	✓
Aleocharinae (#2)	59	0.00	✓
Notonomus resplendens	56	4.34	
Eurylychnus blagravei	55	0.00	✓
Colenisia sp.	49	0.00	✓
Promecoderus sp.	42	0.00	✓
Ecnolagria sp.	40	0.71	*
Cryptorhynchini	39	0.00	✓
Calodera sp.	28	12.87	
Sepedophilus sp.	22	4.53	
Acrotrichis sp.	22	3.82	
Prosopogmus oodiformis	21	3.54	
Aridius semicostatus	20	0.00	✓
Prosopogmus sp.	16	2.59	
Oedemeridae	16	0.00	✓
Falagria sp.	14	0.00	✓

Figure 2. Beetle species responses to the edge gradient based on the top ranked model including edge, altitude, slope, species specific autocovariate and random factor of block. Species that showed a neutral response to the edge are omitted. Each plot represents the GAM smooth component on the response scale. The x axis values were transformed (log(d+1)) for analysis. Dotted lines represent 95% confidence intervals. Dotted vertical lines represents the edge. Responses are jittered along the y-axis to avoid stacking of points.



Effect of altitude, slope and autocovariate in models

Altitude and slope affected many of the species' responses, and there was spatial autocorrelation in the patterns observed for many species (Table S3). All effect sizes demonstrated by altitude and slope were comparatively small and did not appear in direct conflict with the edge gradient (Tables S3, S5, S6, S7). The calculated neighbourhood distances for individual species ranged from 0 metres to 756.46 metres (Table S3).

Trait group responses

The phytophagous feeding-guild demonstrated a response of richness to the edge (Table 2). This group showed a clear association with the *Eucalyptus* side of the edge, however it declined in the *Eucalyptus* core (Figure 3 (a)). Both flightless and flight capable sampling point richness exhibited an edge response (Table 2). Flight capable species exhibited a gradual increase from the interior of the pine continuing over the edge and tapering flat in the *Eucalyptus* forest (Figure 3(b)). Flightless species appeared to follow the opposite trajectory, and were more clearly associated with the pine plantation (Figure 3(c)).

Figure 3. Beetle trait group responses to the edge gradient based on the top ranked model including edge, altitude, slope, group specific autocovariate and random factor of block. Trait groups that showed a neutral response to the edge are omitted. Each plot represents the GAM smooth component on the response scale. The x axis values were transformed (log(d+1)) for analysis. Dotted lines represent 95% confidence intervals. Dotted vertical lines represents the edge. Responses are jittered along the y-axis to avoid stacking of points.

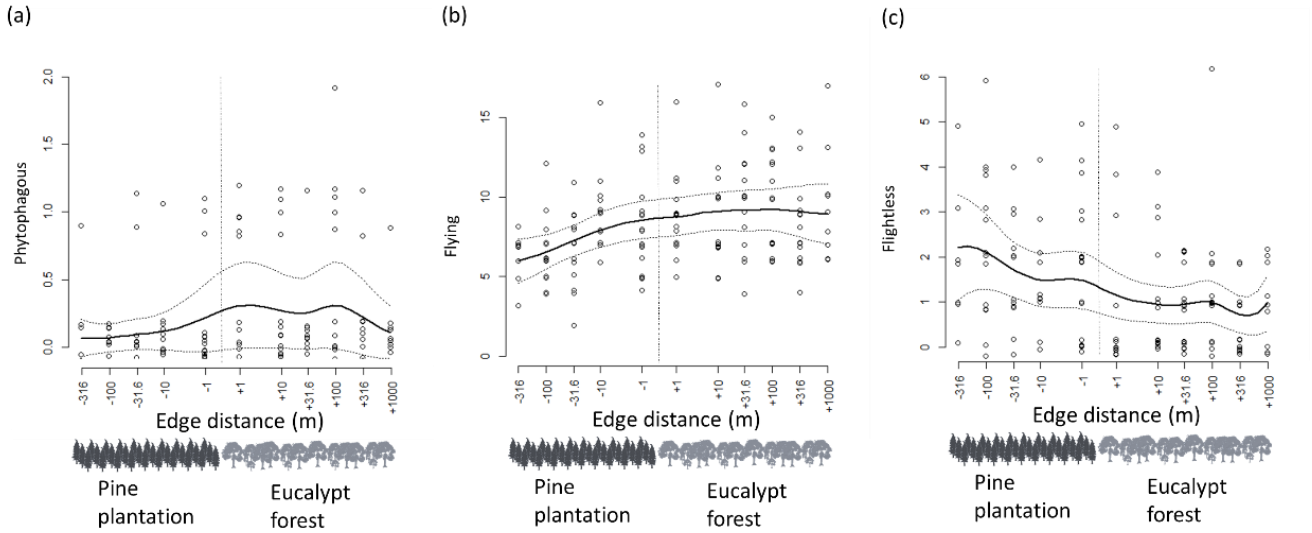


Table 2. Summary of results of model selection procedure for trait group responses to the edge. '✓' signifies that the model containing edge was ranked higher than the null model. * denotes that the edge model was ranked below the null model but was considered a competitor as its AICc score fell below ΔAICc = 2. A more detailed summary of the analysis is presented in the supplementary material (Table S6).

Species	ΔAICc (Edge)	ΔAICc (Null)	Edge Term
Xylophagous	2.43	0.00	
Predatory	6.06	0.00	
Mycetophagous	5.31	0.00	
Phytophagous	1.17	0.00	*
Saproxylic	6.07	0.00	
Flight capable	0.00	7.38	✓
Flightless	1.81	0.00	*

Generalisability of responses across traits

We found no consistent patterns across individual species according to traits. Flightless beetles were either mostly associated with the pine or were non-responsive to the edge. The exception to this was *Eurylychnus blagravei* which showed a small increase in the *Eucalyptus* forest interior.

Principal components analysis

The first five dimensions of the PCA explained just under 65% of variation in our environmental variables (PCA1=20.63, PCA2=14.69%, PCA3=12.08%, PCA4=9.00%, PCA5=8.35%). (Table 4). We interpreted the variations as decreasing litter and litter depth, increasing bare ground, grass and forb (PCA1), increasing forb and grass and decreasing bare ground and rock (PCA2), increasing woody debris (including coarse woody debris) (PCA3), increasing moss (PCA4) and increasing fern (PCA5) (Table 5). All environmental PCA variables showed a response to the edge gradient, although PCA4 and PCA5 were not significantly different to the null model (Table S4, Figure 4). PCA 1 responded to the edge with a unimodal peak at the edge (Figure 4 (a)). PCA 2 responded with a unimodal trough on the *Eucalyptus* side of the edge and also increased from the interior of the pine to the interior of the *Eucalyptus* forest (Figure 4 (b)). PCA 3's response comprised a peak on the pine side of the edge and a trough at around 100 m into the *Eucalyptus* forest (Figure 4 (c)).

Table 4. Correlation matrix of PCA components according to environmental variables. The first five dimensions of our PCA explained just over 65% of variation in our environmental variables (PCA1=20.63, PCA2=14.69%, PCA3=12.08%, PCA4=9.00%, PCA5=8.35%). Correlations of over 40% were used for interpretation (highlighted in grey).

Habitat variable	PCA1	PCA2	PCA3	PCA4	PCA5
Bare ground	0.52	-0.60	0.34	0.15	0.17
Coarse woody debris	0.16	0.23	0.73	-0.15	-0.20
Fern	0.09	0.32	-0.28	0.11	0.79
Forb	0.68	0.50	0.06	-0.13	0.05
Grass	0.67	0.47	-0.13	0.13	0.05
Litter	-0.77	0.14	-0.27	0.19	-0.06
Litter depth	-0.62	0.08	0.37	-0.08	0.24
Moss	0.20	0.16	-0.24	0.73	-0.37
Rock	0.29	-0.55	0.23	0.36	0.22
Sedge	0.24	0.32	-0.07	-0.30	-0.15
Shrub	0.30	-0.41	-0.39	-0.25	-0.18
Woody debris	-0.18	0.40	0.47	0.37	-0.03

Figure 4. GAMs of environmental variable principal components PCA1, PCA2 and PCA3 responses to the edge gradient. Dot-dash line represents the edge. PCA4 and PCA5 are not plotted as their edge responses were not significant.

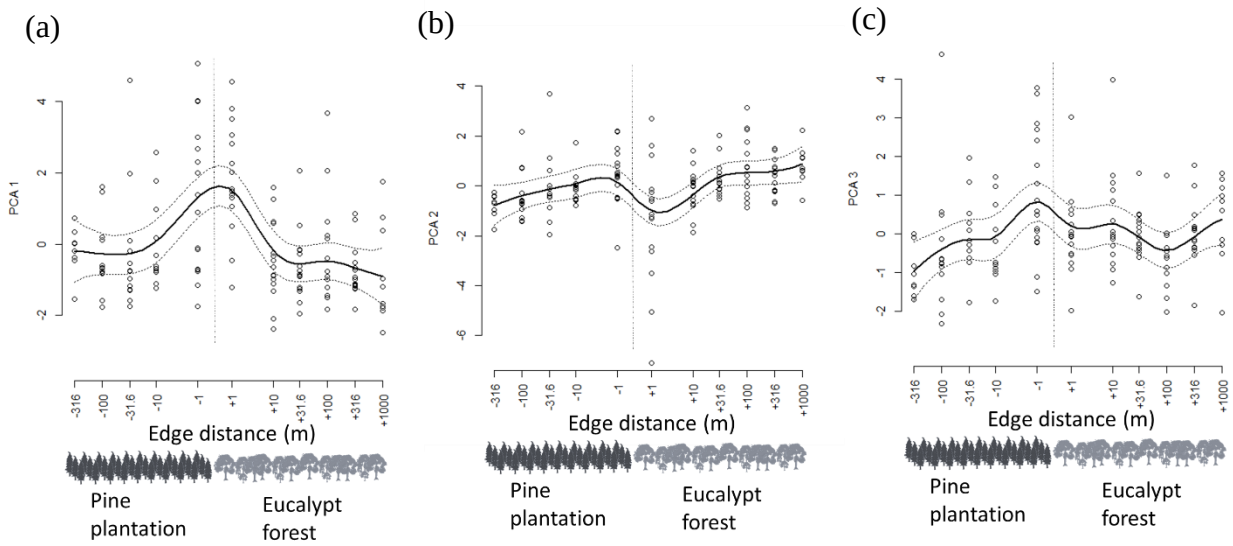


Table 5. Summary of results of model selection procedure for individual species to the edge, and environmental PCA components. Competing models appear below the top ranked model. Those competing models that exclude edge are highlighted. '✓' = edge term is included in the model. A more detailed summary of the analysis is presented in the supplementary material (Table S5).

Species	ΔAICc	Terms					
		Edge	PCA1	PCA2	PCA3	PCA4	PCA5
Anotylus cribriceps	0.00	✓		0.14			
Thalycrodes pulchrum	0.00	✓	-0.19	-0.10			
	0.70	✓	-0.20				
Aleochara sp.	0.00	✓		0.15	0.17		
Aleocharinae (#1)	0.00				0.22		
	1.00	✓			0.23		
Aridius minor	0.00	✓	-0.42	-0.36			
	1.45	✓	-0.48	-0.36	-0.20	0.27	
Thalycrodes australe	0.00		-0.19				
Aleocharinae (#2)	0.00	✓					
Eurylychnus blagravei	0.00	✓					
	1.94				-0.19	-0.15	-0.20
Colenisia sp.	0.00		-0.32			-0.65	0.29
	0.70		-0.33			-0.51	
	1.11	✓	-0.32			-0.50	0.27
	1.33	✓	-0.31			-0.40	
	1.51	✓	-0.31				
Promecoderus sp.	0.00	✓		0.37			
Ecnolagria sp.	0.00		-0.24			0.43	
						0.35	
Cryptorhynchini	0.00	✓				0.68	
	0.00	✓					
Aridius semicostatus	0.00	✓				-1.64	
Oedemeridae	0.00	✓	-0.95	0.57		0.85	
	0.31	✓	-1.20			0.72	

	0.41	✓	-1.24		0.96	0.33
	1.21	✓	-1.03			
Falagria sp.	0.00	✓				
	1.98			0.05	-0.47	-0.28

Species with edge responses correlated with PCA components.

Of the fifteen species exhibiting edge effects, six species produced competing models that did not include edge, indicating in these cases that the habitat covariates explained the response equally well (Table 5). Aleocharinae #1 responded positively to PCA3. *Thalycrodes australe's* edge response appeared to be negatively related to PCA 1. A competitive model that did not include edge for *Eurylychnus blagravei* showed negative responses to PCA3, PCA4 and PCA5. *Colenisia sp.* responded negatively to PCA1 and PCA4 and positively to PCA5. *Ecnolagria sp.* responded negatively to PCA 1 and positively to PCA4. Finally, *Falagria sp.*, responded positively to PCA 3 and negatively to PCA 4 and PCA5. The remaining species with edge responses, still exhibited this response when adding the environmental PCA terms (Table 5). Furthermore, their responses changed very little in profile shape (Figure S1).

Trait group responses correlated with PCA components.

The phytophagous feeding-guild was the only trait group of the three that responded to the edge that demonstrated a competing model that excluded edge (Table 6). The highest ranking model included only PCA2 and did not include edge, however, both PCA1 and PCA3 were also included in models that excluded edge (Table 6). Both the flight capable and flightless models were improved following the inclusion of the PCA variables, however, no highly ranked models excluded edge. Including environmental terms changed the edge profiles very little.

Table 6. Summary of results of model selection procedure for trait richness groups to the edge, and environmental PCA components. Competing models appear below the top ranked model. Those competing models that exclude edge are highlighted. '✓' = edge term is included in model. PCA numbers indicate effects sizes. A more detailed summary of the analysis is presented in the supplementary material (Table S7).

Trait group	ΔAICc	Terms					
		Edge	PCA1	PCA2	PCA3	PCA4	PCA5
Phytophagous	0.00			0.30			
	0.24	✓		0.35			
	1.38	✓		0.34	-0.27		
	1.62						
	1.79		0.11	0.24	-0.21		
	1.87		0.16				
	1.97				-0.23		
Flight capable	0.00	✓	-0.05				
Flightless	0.00	✓		0.28			
	1.24			0.27			
	1.70	✓	-0.10	0.35		-0.08	

Discussion

Edge effects were widespread for the beetle assemblage in our study, with the majority of species examined showing a response to the edge. Three of the trait groups: phytophagous, flight capable and flightless beetles, showed edge responses. Six of the species and phytophagous site richness were consistent with the set of predictions under the resource-based model, as demonstrated by the result that the environmental variables explained these species' responses more or equally as much as the edge gradient.

Generalisable edge responses according to traits.

The phytophagous, also known as herbivorous (Bernays and Chapman 1994), feeding-guild showed predictive promise using the resource based model. The association of a more diverse phytophagous species assemblage with the *Eucalyptus* forest side of the edge was associated with this group's overall negative responses to rock, bare ground and litter and positive responses to forb, grass, woody debris and ferns (PCA1, PCA2 and PCA3). *Eucalyptus* forests are likely to support more herbivorous beetle species than pine forests because of the availability of flowering plants which have richer beetle assemblages than leaves (Wardhaugh *et al.* 2014). Diversity of plant species, including between different species of *Eucalyptus* (Barton *et al.* 2010), drives species richness of phytophagous insects (Lin *et al.* 2015). This is in large part driven by host specificity of phytophagous species (Novotny and Basset 2005; Barton *et al.* 2010). The *Eucalyptus* forest contains multiple species of *Eucalyptus*, forbs and shrubs, whereas the pine plantation consists mainly of *Pinus radiata*, *Kunzea ericoides* and *Lomandra longifolia*. It follows, therefore, that the richer vegetation assemblage in the *Eucalyptus* forest, when compared with the pine planation, would drive the phytophagous species richness we see here.

Flight-capacity

The responses of flightless and flight capable species richness, despite not being easily explained by the vegetation variables, showed patterns of broader habitat associations; i.e. *Eucalyptus* forest or pine plantation. Canopy beetle assemblages are very distinct from understorey assemblages (Stork and Grimbacher 2006; Maguire *et al.* 2014) and species richness of flight capable beetles can be significantly higher in the upper canopy of the forest than its understory (Schroeder *et al.* 2009). This may be because flight capable beetles are more likely than flightless beetles to use canopy resources, simply as a result of their better vertical mobility. Therefore, we might expect to see more flight capable beetles in the canopy of the *Eucalyptus* forest, simply because they can gain access to its resources more easily. However, as we sampled ground beetles, we might only expect a small number canopy beetles to be sampled in our traps.

The same principle of resource association can be applied to the increased richness of flightless species in the plantation. Firstly, it must be noted that a large number of the species within the flightless group were carabids; a family of beetles known to be associated with pine plantations in countries other than Australia (Berndt *et al.* 2008; Lange *et al.* 2014). A factor in this association is thought to be that pine plantation litter (Springett 1976; Das and Ramakrishnan 1985), contains prey suitable for carabids such as microarthropods (Kotze *et al.* 2011). Forest understory structure might also be a driver for the dispersal related response we observed. Habitat complexity reduces predation success by decreasing the encounter rates between predator and prey (Scharf *et al.* 2006; Jana and Bairagi 2014). The pine plantation has a less complex forest floor than in the *Eucalyptus* forest. This might be more favourable for dispersal by flightless species allowing them to increase movement (Wiens *et al.* 1997) to

exploit more resources, including allowing them to encounter their prey more often (Johnson 2006; Jana and Bairagi 2014).

Some of our results suggest spillover, when individuals disperse into non-habitat (Shmida and Wilson 1985), has occurred for certain species groups. Flight-capable beetles were associated with the *Eucalyptus* side of the edge, however, the decline of these species in the pine plantation does not reach its lowest level until 316metres from the edge (Figure 3(b)). Flightless species, however, seemed to decline more closely (within 100metres) to the edge of their non-preferred habitat (*Eucalyptus*) (Figure 3(c)). Increased dispersal allows species to reach further into non-habitat (Wamser *et al.* 2012) and spillover occurs for flying species more readily than flightless (Lucey and Hill 2012). Therefore, our results could indicate that, due to increased dispersal ability, and hence further dispersal into non-habitat, spillover is greater for flight capable species than flightless species.

Species interactions

Our results suggest that indirect mechanisms might have a larger effect than habitat variables alone imply. Edges can result in many novel interactions between species that would not ordinarily interact, including predation (Ries and Fagan 2003; Leighton *et al.* 2008; Frost *et al.* 2015), parasitism (McGeoch and Gaston 2000; Cronin 2003) , mutualism or commensalism (Zelikova and Breed 2008; Ewers *et al.* 2013). Interactions can occur at the guild level, where species within the same feeding-guild, for example, are in direct competition for the same resource (Reitz and Trumble 2002). This would mean that many species would not necessarily have equal access to suitable resources, despite those resources being present in the landscape. To combat this, phytophagous species adopt resource partitioning (Kaplan and Denno 2007), a divergent strategy leading to differences in phenology and feeding location within the same resource (e.g. location on food plant)

(Connell 1980; Kaplan and Denno 2007). Therefore, making predictions based on species traits and the perceived available resources might be more challenging for groups other than phytophagous beetles (i.e. those that are known to adopt resource partitioning).

Accounting for the relevant resource variation

The lack of correlation between most of the species' and trait groups' edge responses and habitat change across the edge could simply mean that habitat requirements are diverse and difficult to measure for beetle species, and as a result, we were not able to measure resource requirements accurately enough. The one exception, phytophagous species, might be considered the most amenable trait group because their needs are simple and relatively easy to measure: i.e. vegetation. However, in the resource-based model, 'resources' are defined as provisions such as nest sites, service providers or abiotic resources (Ries and Sisk 2004), many of which are more difficult to measure. The suite of habitat variables we used is possibly not comprehensive enough to catch all resources relevant to the species studied here.

Multiple-peaked species responses

Our results indicate that positive species' responses are possible not only directly at the edge, but also at any given point along the edge gradient. For example, the responses of *Colenisia sp.*, *Aridius semicostatus*, *Oedemeridae*, *Ecnolagria sp.*, *Thalycrodes australe*, *Thalycrodes pulchrum,* and *Falagria sp.*, all showed peaks in abundance at different points along the transect. It is possible that each point offers a certain level of suitability for species, influenced by factors such as habitat resources (Ries and Sisk 2004) and interactions between species (Murcia 1995; Wimp *et al.* 2011).

Another factor that could contribute to the multiple-peaked edge responses is that the edge between the *Eucalyptus* and pine plantation forests is intersected by a dirt road, albeit one that

receives extremely low volumes of traffic. The gap between the two environments on either side of the road can aid dispersal for some beetle species (Noordijk *et al.* 2011; Knapp *et al.* 2013) and inhibit it in others (Koivula and Vermeulen 2005; Lambert *et al.* 2014). Roads can change abiotic components of the landscape such as light, wind and hydrology (Coffin 2007; van der Ree *et al.* 2011). At the study site, the road has resulted in changes in microclimate at its immediate environs, including increased light, more exposure to wind and changes in hydrology. In this regard, the road could result in multiple edges: plantation against road, *Eucalyptus* against road and the interaction of these two edges. If we were to consider the gradient in this way, then the resource based model allows some of the responses we see here (Ries and Sisk 2004). For example, the response of *Thalycrodes pulchrum* (Figure 2(a)) could be interpreted as habitat supplementation or complementation at the immediate environs of the edge on the eucalypt/road edge and habitat avoidance on the pine/road edge. Despite the road being comparatively small in area, it is possible that its impact is relatively large (Ingham and Samways 1996; Koivula and Vermeulen 2005; Yamada *et al.* 2010).

Other studies on edge effects and ground dwelling beetles have shown contrasting results to ours. For example, Tóthmérész *et al.* (2014) showed that at a forest-grassland edge, carabid species richness was greatest at the edge than in the forest or grassland, and Lacasella *et al.* (2015) found a similar response with an increase in arthropod species richness in the grassland. However, these studies followed the responses of arthropods across edges with a larger contrast than the eucalypt-pine forest boundary studied here (i.e. forest-grassland). This difference in responses highlights the need to consider the context of the edge including the resources provided on either side (Ries and Sisk 2004).

Temporal effects at a number of scales including season (Young and Mitchell 1994) and year (Chalfoun *et al.* 2002), can influence the responses of species to edges (Ries *et al.* 2004;

Ohwaki *et al.* 2015). However, these temporal effects, in consistence with the habitat resource model, are most likely linked to changes in resources across the edge through time (Ries *et al.* 2004). If we had sampled at different times of the year it is possible that different edge patterns would have been observed.

Edge effects scales

Our results highlight the need to establish an appropriate scale to study edge effects in order to determine how far edge effects reach into habitat and how this varies for different species. We found that some of our species showed responses to the edge that reached the limit of the scale of the experiment (1000m in the *Eucalyptus* and 316m in the pine). Other studies on ground dwelling invertebrates show similar large scale effects (Ewers and Didham 2008; Lacasella *et al.* 2015). Finding suitable areas to study edge effects at such scales, however, is becoming more difficult as undisturbed habitat is becoming rarer (Haddad *et al.* 2015). Considering such large edge effects is difficult due to the rarity of uniform habitat at the scales of deep edge effects (Ewers and Didham 2008).

Conclusions

We have demonstrated that, in some cases, the resource based model for edge effects (Ries and Sisk 2004) can be used in tandem with traits such as feeding-guild and flying-ability to understand drivers of large scale edge responses. Phytophagous species richness is determined by the variation of vegetation along an edge gradient and that simple measures of vegetation cover revealed these responses. We suggest that widening the scope of the vegetation measurements to include the heterogeneity and composition of vegetation would demonstrate more detailed correlations with phytophagous species richness. We also demonstrated a clear pattern of association between the core of *Eucalyptus* forest and flight capable beetle species and the core of the exotic pine plantation and flightless beetles. This is

possibly as a result of differences in litter resources and structure. However, many other responses were less easily explained by measured variables and feeding-guild. This could be a result of indirect effects such as interactions between species and guilds or because of environmental variation that we did not measure. Many of the individual species modelled showed complex responses to the edge gradient which included multiple peaks at differing regions along the edge gradient, not necessarily directly associated with the pine vs *Eucalyptus* edge. Our study also demonstrates the need to establish appropriate scales to study edge effects; a task which is becoming more difficult as undisturbed native habitat is becoming increasingly rare worldwide.

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Paper II: When the matrix isn't a matrix. A pine plantation provides new habitat for butterflies in a long-term fragmentation experiment.

In Paper II, my intention was to investigate the responses of common native Australian butterfly species to the landscape change at the Wog Wog Habitat Fragmentation Experiment. I wanted to determine how butterflies reacted to the establishment of an exotic pine plantation in a *Eucalyptus* forest landscape.

Evans, M. J., Banks, S.C., Davies, K.F., King, A.J., Sweaney, N., Driscoll, D.A. When the matrix isn't a matrix. A pine plantation provides new habitat for butterflies in a long-term fragmentation experiment. In prep.

Abstract

The influence of the land type between patches of remnant vegetation on species' survival is now widely acknowledged. This part of the landscape is often the most extensive and spatially contiguous part of the landscape, and plays a large role in determining species' responses to fragmentation. From the species perspective, this land could be hostile (defined as a matrix) or amenable (defined as new habitat). We collected butterfly abundance data in a long-term experiment in native *Eucalypt* remnants surrounded by a pine plantation. We ask 1) what is the occurrence and diversity of butterflies in the pine plantation and fragments? And 2) do habitat characteristics determine these responses? Butterfly species were richer in the pine plantation, suggesting that it offers new and possibly preferable habitat for butterflies than the corresponding native eucalypt forest. Furthermore, one species, *Geitoneura acantha*, was significantly more abundant in the remnants and plantation than the controls. This response was shown, in some part, to be driven by increasing grass cover and disturbance. We hypothesise that a combination of factors may drive our results, including the disturbed nature of the pine plantation that has allowed more resources such as grasses, sedges and shrubs to thrive. Disturbance includes thinning in the pine plantation that provides more light for butterflies and their host plants.

Introduction

Native habitat loss and fragmentation is a major threat to biodiversity worldwide (McCallum 2007; Stone 2007; Rands *et al.* 2010). The impact of habitat loss and fragmentation on biodiversity depends on a variety of factors including the spatial arrangement of remaining habitat, patch size, distance to patch edges and habitat quality (Mortelliti *et al.* 2010). When habitat is lost, it is replaced with a variety of other land uses such as urbanisation (Ikin *et al.* 2012), agriculture (Foley *et al.* 2005) and plantation forestry (Lindenmayer, Hobbs & Salt 2003; Kröger 2012) and these new land uses have significant effects on regional communities.

Plantations are a significant aspect of global environmental change (Stephens & Wagner 2007) constituting an estimated 7 percent of the total forest area, or 264 million hectares worldwide (FAO 2010). Furthermore, this figure is projected to rise following increases of 5 million hectares per year between 2000 and 2010 (FAO 2010). This has the potential to fragment species populations within the habitat that it replaces. Understanding which species are affected and the mechanisms behind their responses is important to minimise future biodiversity loss (Brockerhoff *et al.* 2008; Felton *et al.* 2010; Mortelliti, Michael & Lindenmayer 2015).

The land type between remnant patches strongly impacts species' survival in fragmentation landscapes (Ricketts 2001; van Halder *et al.* 2008; Taki *et al.* 2010; Driscoll *et al.* 2013; Sweaney, Lindenmayer & Driscoll 2014). The human-altered portion of the landscape is often the most extensive and connected part of the landscape, and plays a large role in determining the kinds and levels of ecosystem services present (Forman 1995). In the case of species that find this new part of the landscape hostile, it is termed the matrix (Driscoll *et al.* 2013). However, the human altered portion can offer many benefits for native species.

Resources within the modified areas may create new or expanded habitat for particular species (Chase & Leibold 2003; Poulin & Villard 2011). This additional resource availability can increase the flow of individuals between the remnant habitats (Åberg *et al.* 1995; Fischer, Lindenmayer & Manning 2006; Mouquet *et al.* 2006; Davies *et al.* 2009; Venail *et al.* 2010; Livingston, Philpott & Rodriguez 2013) and could potentially be used as a resource base for species that persist in the patches (Ewers & Didham 2006). If a species is able to establish self-sustaining populations in the modified land, the land surrounding remnant vegetation is new habitat and not a matrix (Driscoll *et al.* 2013).

We took advantage of an existing long-term fragmentation experiment to investigate how butterflies respond to fragmentation of their natural forest habitat into remnants surrounded by a pine plantation. More specifically, we asked 1) What is the occurrence and diversity of butterflies in the pine plantation and fragments? and 2) Do habitat characteristics influence butterfly occurrence in the pine plantation, and if so, which characteristics? We might expect that the conservation of butterflies in a pine plantation would benefit from the provision of larval food plants within the plantation which would complement habitat offered in the remnants.

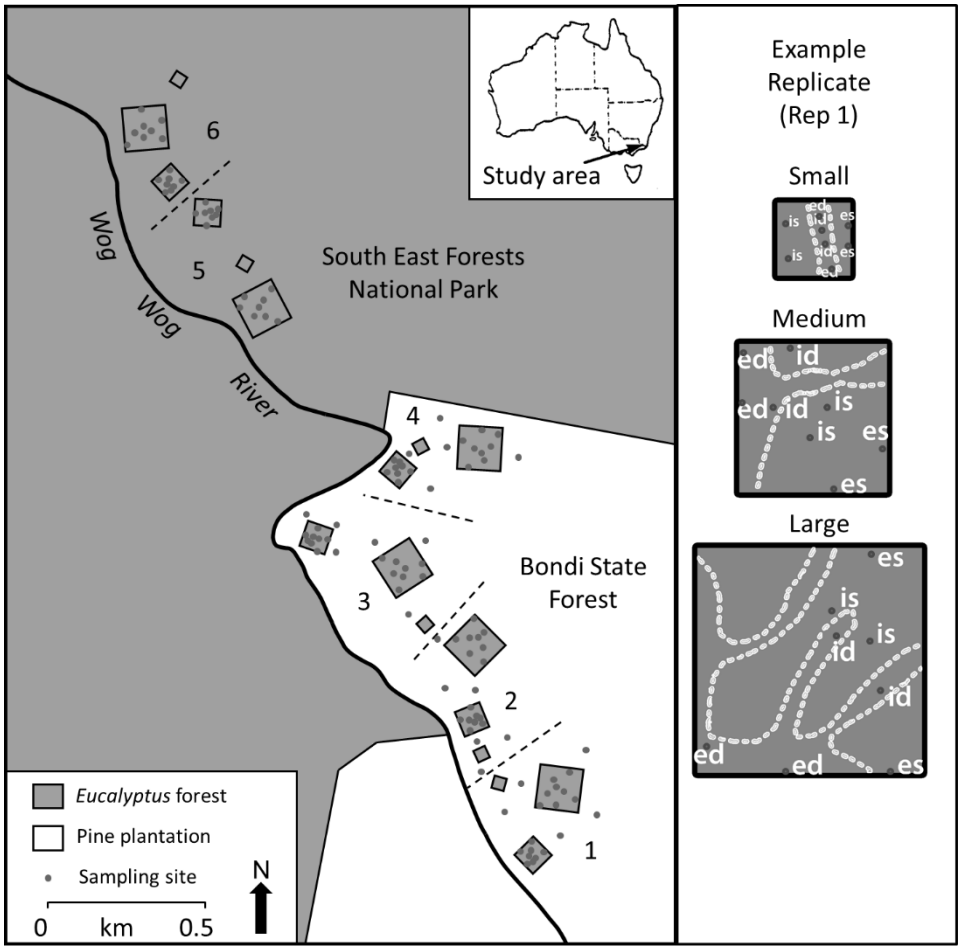
Materials and Methods

Study Site

The Wog Wog habitat fragmentation experiment was established in 1985 (Margules 1993) in the Bondi State Forest in south-eastern New South Wales, Australia (37°04'30"S, 149°28'00"E). It was created in a valley previously covered with open *Eucalyptus* forest containing a grassy to shrubby understory (Figure 1). The experiment consists of six replicates of square plots of three different sizes (0.25 ha, 0.875 ha and 3.062 ha) (Margules

1993). In 1987, the native *Eucalytpus* forest surrounding plots in four replicates was cleared and planted with *Pinus radiata* while two replicates remained in continuous native *Eucalyptus* forest, acting as controls.

Figure 1. Map of the Wog Wog Study area in South Eastern NSW. The internal site structure of replicate 1 is shown as an example of the arrangement of sites within small, medium and large patches. id = inner drain sites, ed = edge drain sites, is = inner slope sites, es = edge slope sites.



Within each plot, sample sites were stratified by proximity to the edge (core and edge) (Davies & Margules 1998) and topography (shallow slopes and steeper drainage lines). Slopes are characterised by an understory of tussock grasses, forbs and scattered shrubs; moist drainage lines are characterised by an understory of thick shrubs of *Kunzea ericoides* and wet drainage lines are characterized by an understory of the narrow-leaved forb

Lomandra longifolia (Austin & Nicholls 1988; Margules 1993). In each plot there are four edge sites and four core sites, resulting in a total of 144 monitoring sites across the 18 plots. There are an additional 44 sites in the surrounding pine plantation, again split equally between slope and drain sites. The pine plantation was established in winter 1988. By the time of our surveys in 2013-14, the pines were mature, and had reached approximately 30 m in height. The whole plantation within the experiment was thinned over a three month period in late 2010 and as a result, this environment is lighter, with less leaf litter.

Butterfly survey

We conducted summer surveys of all 188 sites three times, once in February 2013 and twice in January 2014. For each survey, we recorded the number of butterflies of each species that passed within a 20 m radius of the site over a five minute period. We conducted surveys during favourable weather conditions with no rain, low cloud and low winds (Douwes 1975). To account for observational level effects, we recorded the time, date, temperature and wind speed and estimated the percentage of cloud cover at each observation (Ricketts 2001). If butterflies could not be identified on the wing, they were caught using a butterfly net, identified and released. We did not consider that the different treatments (fragments, controls and plantation) posed any risk of detection bias – all treatments offered good visibility within 20 m radius of each site.

Study species

The butterflies we observed in this study fall into four families: *Nymphalidae* (Browns and Nymphs), *Lycaenidae* (Blues and Coppers), *Pieridae* (Whites and Yellows) and *Hesperiidae* (Skippers). The *Nymphalidae* in our study consist of four species: *Heteronympha merope* (Common Brown), *H. metirius* (Wonder Brown), *Geitoneura acantha* (Ringed Xenica) and *Hypocysta metirius* (Brown Ringlet).

All of these butterflies rely on host plant species present at our site to lay eggs and provide food for their larvae (Field 2013). *Heteronympha merope, H. metirius, Geitoneura acantha, Hypocysta metirius* and *Zizina labradus* all use a variety of grass species as their larval food (Braby 2004; Field 2013). The only *Hesperiidae* species, *Trapezites symmomus*, relies mainly on one species of sedge, *Lomandra longifolia* and as a result likes the moist habitats where this plant thrives (Field 2013). *Jalmenus evagoras* uses mainly *Acacia* species and as a result prefers disturbed habitat where *Acacia* species are early colonisers (Braby 2004; Field 2013). The only *Pieridae, Pieris rapae* (Cabbage White), is a common and widespread species introduced from Europe in the 1920s preferring disturbed habitats where introduced larval food plants, such as forbs, are established (Braby 2004; Field 2013).

Habitat variables

We measured percentage of ground covered by leaves, bark, grass, bare-ground, rock, wood, moss, roots and *Lomandra* sp with a point intercept survey at each site. This allowed is to use these variables both as a proxy for differing habitats between treatments and to test directly the effect that host plants have on butterfly abundance. We ran a 10 m piece of rope in five directions, 72 degrees apart and recorded which of the above ground cover variables hit marks increasing at 50cm intervals along the rope. This resulted in 100 point intercepts per site. We also measured the quantity of wood at a site by scoring all wood under the rope according to one of five diameter categories: <1cm, 1-2.5cm, 2.5-5 cm, 5-20 cm and 20-40 cm and >40 cm. We created a fallen wood index for each site by summing all the diameters recorded. We also recorded an estimate of litter depth at each mark on the five ropes and created a litter depth index by summing all of the depths recorded.

Data Analysis

To test the effect of our treatments on butterfly observations, we used generalized linear mixed models (GLMMs) assuming a Poisson distribution using the 'lme4' (Bates *et al.* 2013) package in R (R Core Team 2014). For species that did not have sufficient data to run GLMMs, we performed Fisher's exact tests. This approach allowed us to test for significant independence of the responses to the factor levels with small sample sizes (Fisher 1922).

Question 1. What is the occurrence and diversity of butterflies in the pine plantation and fragmentation?

We ran two sets of models to answer, first, whether there was an effect on our response variables of the remnants, plantation and controls, and second, whether there was an effect on our response variables of the nested treatments of topography, edge or remnant size. Our response variables were species richness per site and individual species abundance per site.

In the first set of GLMMs, we modelled difference in butterfly communities between remnant, control, and pine plantation sites. As the plantation sites were not stratified by edge or size, we were not able to use these factors in our analysis. We were able to use patch as a random effect by applying patch numbers to plantation sites in spatially close pairs (within 20 metres of each other). This mimicked the spatial difference within remnant and control patches and avoided spatial autocorrelation errors in the data structure. To account for detection effects associated with the weather, we included the variables of cloud cover, temperature, wind level, date and time as fixed effects in all our models. All these observational effects were treated as continuous variables and rescaled to 0-100, where zero is the lowest value and 100 the highest.

The second set of GLMMs evaluated the effect of distance from edge, patch size and topography within the remnants compared to the controls. As these site strata were not available in the plantation, it was necessary to exclude the plantation sites from this analysis. We used patch as a random effect and, as in our plantation models, included date, time, cloud cover, temperature and wind level as fixed observational effects. We tested the effects of edge and size by including the interaction terms of treatment (remnants, controls) with edge and size.

For all of our response variables (richness, species abundances), we ran all possible subsets of the combinations of treatment effects (main treatments and their nested interactions, topography) present in the full model, including the null model (using the 'lme4' (Bates *et al.* 2013) and 'MuMIn' (Barton 2014) packages in R (R Core Team 2014)), whilst keeping our observational level effects (time, date, temperature, wind speed and cloud cover) in all models. We ranked the models using AIC_C (second order Akaike Information Criterion) scores, and examined those within two AIC_C units of the model with the lowest AICc score (Burnham & Anderson 2002). We excluded models that included uninformative parameters; those models within two AIC_C units of the higher ranked model with one additional parameter (Arnold 2010).

Question 2. What habitat characteristics might determine the butterfly responses?

To determine which habitat characteristics of the treatments explained butterfly responses, we ran another model selection procedure with a set of derived principal component habitat variables. We performed a principal components analysis (PCA), using the 'FactoMineR' (Le, Josse & Husson 2008) package in R (R Core Team 2014), on the habitat variables to retrieve a set of new variables that explained a substantial proportion of the environmental variation (>65%). We then added these new variables to the top ranked models previously

determined and followed the same model ranking and selection procedure outlined previously. We did this to determine whether the environmental variables recorded explain butterfly responses in tandem with, or in place of, the experiment treatment variables.

Results

We observed eight species of butterfly totalling 1645 individuals (. This will likely impact species at over 1000m beyond the edge of the plantation). Most of those individuals were either *Heteronympha merope* (n=1140) or *Geitoneura acantha* (n=420). We had sufficient data to examine these two species using GLMMs.

Question 1. How do butterflies respond to the pine plantation and fragmentation?

Main treatment responses

Butterfly richness was greatest in the pine plantation, followed by the remnants and then the controls (Table 2, Figure 2 (a)). The abundance of *Heteronympha merope* did not differ significantly between the main treatments of the controls, remnants and plantation (Figure 2(b)). The abundance of *Heteronympha merope Geitoneura acantha* was lower in the control sites than the plantation and remnant sites (Table 2, Figures 2(b & c)) Of the remaining six species, only the abundance of the two *Lycaenidae* showed a significant response to the treatments (Table 3), with both *Z. labradus* and *J. evagoras* being completely absent from the controls and most abundant in the pine (Table 1).

Table 1. Summary table of butterflies observed over two samples per site. Numbers in parenthesis represent the number of sites. *P* = Fisher's exact test of independence (Fisher 1922) for treatments of remnants, controls and plantation. Note: only those species with insufficient data for mixed modelling were tested using the Fisher's exact test.[+]introduced species. Mean and se columns are means and standard errors of butterfly abundance per sampling effort in each treatment.

Butterfly species	Remnants (96)			Controls (48)			Plantation (44)			Total	*p*
	n	Mean	se	n	Mean	se	n	Mean	se	n	
Heteronympha merope (Common Brown)	609	2.11	0.18	195	1.35	0.26	336	2.55	0.27	1140	
Geitoneura acanthi (Ringed Xenica)	268	0.93	0.09	34	0.24	0.12	118	0.89	0.13	420	
Heteronympha mirifica (Wonder Brown)	5	0.02	0.01	1	0.01	0.01	1	0.01	0.01	7	0.688
Hypocysta metirius (Brown ringlet)	3	0.01	0.01	1	0.01	0.01	4	0.03	0.01	8	0.504
Zizina labradus (Common grass blue)	6	0.02	0.01	0	0.00	0.01	9	0.05	0.01	13	0.028**
Jalmenus evagoras (Imperial Hairstreak)	2	0.01	0.01	0	0.00	0.02	8	0.06	0.02	10	0.034**
Trapezites symmomus (Splendid Ochre)	17	0.06	0.02	7	0.05	0.02	12	0.09	0.03	36	0.082*
Pieris rapae[+] (Cabbage White)	1	0.00	0.02	0	0.00	0.04	10	0.08	0.04	11	0.478
Totals	911			238			496			1645	

Table 2. Summary of results of AICc model selection for main treatments of remnant, controls and plantation and topography. '✓' signifies that the effect is included in the ranked model. df= degrees of freedom, Tp =main treatment (remnants/controls/plantation), Topo = topography (slopes or drains). See Table S1 for more detailed model summaries including uninformative parameters.

Response	ΔAICc	df	T_p	Topo
Richness	0.00	10	✓	✓
Heteronympha merope	0.00	8		✓
	0.97	10	✓	✓
Geitoneura acantha	0.00	10	✓	✓
	0.33	9	✓	

Figure 2.Predicted total species richness (a), and *Heteronympha merope* (b) and *Geitoneura acantha* (c) abundances in main treatments using poisson generalised linear mixed models. Error bars represent standard errors.

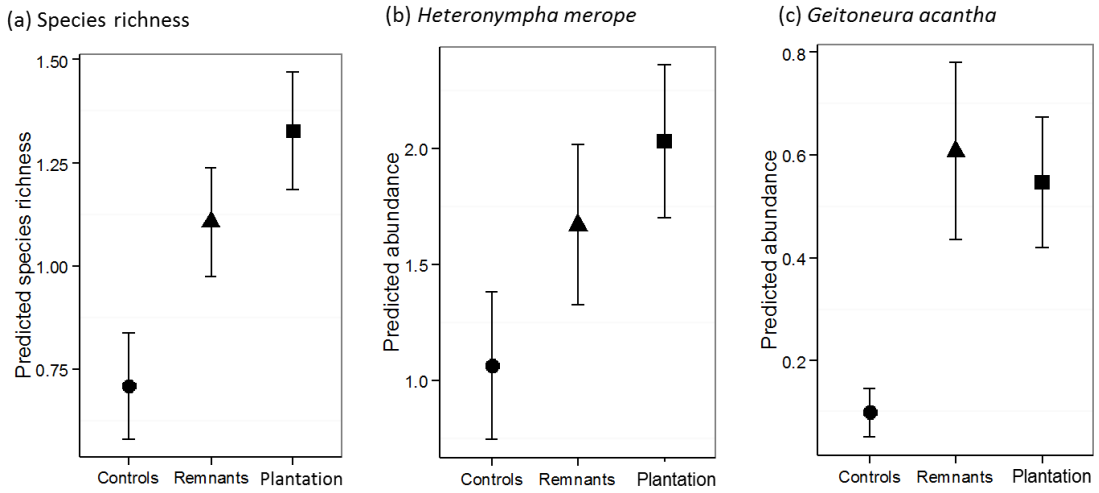


Table 3. Results of AICc model selection for main treatments of remnant and controls and nested treatments of edge, size and topography. '✓' signifies that the effect is included in the ranked model. df= degrees of freedom, T_F=main treatment (remnants/controls) , T_F:E=interaction effect of treatment and edge, Topo=topography. Terms that did not appear in any top ranked models are omitted. See Table S2 for more detailed model summaries including uninformative parameters.

Response	ΔAICc	df	T_F	T_F:E	Topo
Richness	0.00	9	✓		✓
Heteronympha merope	0.00	8			✓
	0.02	11	✓	✓	✓
Geitoneura acantha	0.00	9	✓		✓

Responses to remnant edge and size and topography

There was no effect of proximity to edge or size for any of the response variables. The only response variable to include the interaction of treatment and edge in the top ranked models was the abundance of *Heteronympha merope* (Table 3, Figure S2). Topography had a consistent effect on butterflies (Tables 2, 3, 5 and 6). Richness was lower in drainage sites than slope sites (Figure S1). The same pattern emerged for both *Heteronympha merope* and *Geironeura acanthi*.

Question 2. What habitat characteristics might determine the butterfly responses?

After performing a PCA on the environmental variables, we used the first five principal components as new variables in our models (Table 4 and Figure S3). These composite variables accounted for a total of 64.53 % of variation in the environmental dataset. We interpreted these components as gradients of decreasing disturbance including decreasing grass (PCA1), increasing growth form, decreasing woody debris and litter (PCA2), increasing moisture, decreasing leaf ground cover (PCA3), increasing disturbance (PCA4) and decreasing rock (PCA5).

The top ranked richness model dropped down the model ranks with the inclusion of PCA1 and PCA2 (Table 5). However, this effect was only apparent in the models that included the pine plantation (compare tables 5 and 6), with the environmental variables not improving the rank of the models that included the fragmentation data only. However, in both sets of models, richness responded negatively to PCA1 and PCA2 and positively to PCA3 and PCA5. Similarly to richness, adding the environmental components to the *Heteronympha merope* models improved the model rank in the models including the plantation data. This species responded positively to increased disturbance and decreasing moisture and rock cover and importantly, increasing grass cover (negatively to PCA1 and PCA3, positively to PCA5).

Geitoneura acantha, showed a similar response as richness, responding positively to increased disturbance, grass, litter cover and woody debris with decreasing litter depth (negatively to PCA1, PCA2 and PCA4).

Table 4. Correlation matrix of PCA components according to environmental variables. Correlations of over 40% were used for interpretation (highlighted in grey).

	PCA1	PCA2	PCA3	PCA4	PCA5
Bare ground	-0.05	0.39	-0.36	0.55	0.35
Bark	0.54	-0.39	0.19	0.19	0.28
Grass	-0.61	0.14	0.42	-0.45	0.27
Leaves	0.45	-0.19	-0.75	-0.18	-0.05
Lomandra	0.24	0.52	0.49	0.12	-0.37
Moss	-0.28	0.45	-0.51	0.02	-0.13
Water	0.17	0.36	0.22	0.59	0.18
Wood	-0.32	-0.66	-0.12	0.41	-0.18
Litter depth	0.66	-0.25	0.31	-0.18	0.19
Woody debris	-0.50	-0.52	0.23	0.40	0.03
Roots	0.15	0.22	0.13	0.20	0.16
Rock debris	0.15	-0.03	0.16	0.17	-0.73

Table 5. Summaries of results of AICc model selection for main treatments of remnant, controls and plantation with the added environmental PCA variables (PCA1-5). '✓' signifies that the effect is included in the ranked model. Observational level effects included in the models are omitted from the table. df= degrees of freedom, Tp =main treatment (remnants/controls/plantation). The previous top ranked model is highlighted in grey, unless its rank falls above ΔAICc = 2. See Table S3 for more detailed model summaries including uninformative parameters.

Response	ΔAICc	df	Tp	Topo	PCA1	PCA2	PCA3	PCA4	PCA5
Richness	0.00	11	✓	✓	-0.077				
	0.02	11	✓	✓		-0.059			
	0.73	10	✓	✓					
	1.74	12	✓	✓		-0.057	0.024		
	1.76	12	✓	✓		-0.061			0.025
Heteronympha merope	0.00	11		✓	-0.082		-0.091		0.062
	1.53	10		✓	-0.087		-0.100		
Geitoneura acantha	0.00	13	✓	✓	-0.117	-0.147		-0.187	
	1.20	12	✓	✓		-0.149		-0.199	

Table 6: Results of AICc model selection for main treatments of remnant and controls and nested treatments of edge, size and topography including the added environmental PCA variables (PCA1-5). '✓' signifies that the effect is included in the ranked model. df= degrees of freedom, T_F=main treatment (remnants/controls). The previous top ranked models are highlighted in grey, unless they fall above ΔAICc = 2. See Table S4 for more detailed model summaries including uninformative parameters.

Response	ΔAICc	df	T_F	T_F:E	Topo	PCA1	PCA2	PCA3	PCA4	PCA5
Richness	0.00	9	✓		✓					
	0.22	11	✓		✓		-0.066	0.077		
	1.84	11	✓		✓	-0.039		0.074		
	1.95	11	✓		✓	-0.030	-0.063			
Heteronympha merope	0.00	8			✓					
	0.02	11	✓	✓	✓					
	0.64	10	✓		✓	-0.055				
	1.02	12	✓	✓	✓	-0.045				
Geitoneura acantha	0.00	12	✓		✓		-0.171		-0.225	-0.094
	0.14	11	✓		✓		-0.191		-0.207	
	0.14	12	✓		✓	-0.113	-0.205		-0.193	

Discussion

Butterfly responses and mechanisms of response to eucalypt forest fragmentation

Butterflies were less abundant and species richness was lower in the continuous forest than the remnants or plantation. Our study suggests that pine plantations surrounding remnant eucalypt forest are not a matrix, but provide supplementary habitat for common butterflies. Furthermore, it is even possible that the plantation is providing preferential habitat for butterflies over and above the eucalypt forest.

The pine plantation at Bondi State Forest is a heavily disturbed environment and it appears that many of the butterfly species here take advantage of the plants that grow in these disturbed regimes. Butterflies benefit from improved understorey and maintenance of soil moisture levels in semi-natural habitats (van Halder *et al.* 2008), and our study demonstrates this. The two most common species, *Heteronympha merope* and *Geitoneura acantha* rely on a number of grass species for larval food plants (Orr & Kitching 2010; Field 2013). We found a positive relationship between grass cover and both of these species and also overall butterfly richness, a pattern which was mostly apparent in the pine plantation where grasses are available. Also, the preference for the pines shown by *Zizina labradus* and *Jalmenus evagoras* could indicate that these species use the plant species that grow in the relatively disturbed environment of the plantation. The road sides around the plantation and windrows inside it support many species including wattle species favoured by *Jalmenus evagoras.*

The management techniques employed in plantations have a strong influence on the species that are able to use that habitat, and are responsible in part for the mass effects we observed. The plantation at the Bondi State Forest is over 27 years old, and as a result has undergone thinning and pruning of the pines. Thinning increases forb and grass cover as a result of

decreased litter fall and increased light levels (Harrington & Edwards 1999), therefore increasing the resources available for these species. Furthermore, decreasing stand density, the result of thinning, has been shown to have a positive effect on species diversity, including butterflies (Kleintjes, Jacobs & Fettig 2004; Waltz & Wallace Covington 2004; Taki *et al.* 2010).

Our results could also be indicative of the effects of the low-contrast nature of the *Eucalyptus* forest when compared with the pine forest (e.g. when compared with forest vs cleared grazing or urban land). The more similar in structure that the surrounding landscape is to the remnants, the more favourable this landscape is for organisms in the remnants (Prevedello & Vieira 2010; Campbell *et al.* 2011; Driscoll *et al.* 2013). Studies have also shown that low contrast edges can sometimes mitigate the response of a number of taxa, including butterflies (Ries & Sisk 2008), when compared with a higher contrast edges (e.g. native forest adjacent to farm land) (Desrochers, Hanski & Selonen 2003; Reino *et al.* 2009; Brearley *et al.* 2010; Campbell *et al.* 2011; Noreika & Kotze 2012). A low contrast habitat can also influence the connectivity between the patches (Eycott *et al.* 2012), enabling butterflies to pass through the plantation more readily than otherwise. In this case, it appears that the plantation is preferable habitat. However, the similarity in structure that the plantation has with the continuous forest might, in part, explain why the plantation is favourable rather than hostile to butterflies.

In the case of the Bondi State Forest and most plantations worldwide, this system is dynamic and changing as the pines grow and management techniques, such as thinning and pruning are employed (Driscoll *et al.* 2013). It is possible that for a large section of the plantation's rotational lifespan, many butterfly species are not able to use the habitat as it does not provide the resources it may provide once thinning and pruning has been undertaken. For example, the stocking density of the young plantation might not allow as many butterfly larval food

plants to thrive and also prevent butterflies from dispersing through the plantation. This has been demonstrated by Kleintjes, Jacobs and Fettig (2004) who showed that decreasing overstory allowed increased dispersal of butterflies. Our results demonstrate that pine plantations in certain contexts help the persistence of some native species. Here, the use of thinning and pruning may have aided the growth of the larval food plants that the butterflies rely on; although perhaps only recently has this post-thinned plantation provided such a suitable habitat.

The finding that butterflies were far more abundant in the remnants and pines than the controls could indicate, not only is the habitat in the pine landscape more preferable than the continuous forest, that we could also be seeing landscape scale responses to the treatments, such as mass effects (Leibold *et al.* 2004; Lasky & Keitt 2013; Livingston, Philpott & Rodriguez 2013). Our data suggest that we have found evidence for a mass effect, or spill-over, within the remnants (Leibold *et al.* 2004; Lasky & Keitt 2013; Livingston, Philpott & Rodriguez 2013), with the pine plantation potentially boosting species richness and abundance of common species in the remnants when compared with the controls. It follows that we might also be seeing mass movement of butterflies from the continuous forest into the pine plantation. Butterflies are highly mobile, with distances previously recorded (Ovaskainen *et al.* 2008) for other species indicating that they could easily disperse the distances between the controls and plantation at Wog Wog (over 1.5 km). Furthermore, they are known to disperse towards preferable habitat rather than dispersing in random directions (Conradt *et al.* 2000), suggesting that they might actively move towards the pine plantation from the continuous forest. Further research is necessary to test this and a direct approach such as mark-recapture, as well as edge-effect studies to reveal any spill-over of butterflies either side of the edge between the eucalypt and plantation forests, would elucidate whether butterflies experience a landscape scale mass effect at Wog Wog.

Conclusions

We have shown that butterflies respond positively to pine plantations in a fragmented *Eucalyptus* forest landscape – i.e. that the plantation is not a matrix from the point of view of common butterfly species. Furthermore, the plantation offers new and possibly more preferable habitat for butterflies than the corresponding native eucalypt forest. Thinning in the pine plantation that provides more light for butterflies and their host plants is most likely a key factor in determining their positive response to the plantation.

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Paper III: Short-term effects do not predict long-term impacts of fragmentation in a long-term fragmentation experiment.

A major strength of the Wog Wog Habitat Fragmentation Experiment is its longevity. I wanted to take advantage of this and study the responses of species to the landscape change over the history of the experiment. The plantation has changed considerable since its establishment. Tracking species' responses through time reveals how species reacted to the various stages of the plantation rotation. What was particularly novel here was the availability of data showing not only how species occurred throughout the landscape after anthropogenic environmental change, but also before.

Evans, M. J., Banks, S.C., Driscoll, D.A., Melbourne, B.A., Davies, K.F. Short-term effects do not predict long-term impacts of fragmentation in a long-term fragmentation experiment. *Ecology*. Revisions currently underway.

Abstract

The lack of long-term fragmentation studies is a serious impediment to understanding species' responses to fragmentation. We took advantage of one of the longest-running fragmentation experiments to track species' responses over a timescale usually unavailable to ecologists. Revisiting carabid beetle species studied by Davies and Margules (1998), we find that responses in the long term (more than 25 years post-fragmentation) can contrast with those in the short term (five years post-fragmentation). Long-term species' responses were most likely driven by the changing matrix between remnants, which may provide new and preferred habitat for carabid beetles compared to native *Eucalyptus* forest, and increases the occurrence of many species, and carabid richness, within remnants. These findings highlight the risk that much of the large body of work tracking short-term responses to fragmentation may not accurately indicate the ultimate responses of species and communities to fragmentation.

Introduction

Habitat loss and fragmentation are a significant threat to biodiversity and to ecosystem processes worldwide (Mccallum 2007; Stone 2007; Rands *et al.* 2010; Haddad *et al.* 2015). There is a long history of ecological research on habitat fragmentation; many observational and experimental studies show effects of fragmentation on populations and communities (Fahrig 2003; Didham *et al.* 2012; Fahrig 2013). Although studies that track either short- or long-term responses to fragmentation are common (e.g. Bell *et al.* 2001; Collinge & Palmer 2002; Vasconcelos *et al.* 2006; Thornton *et al.* 2010; Korfanta *et al.* 2012; Nijman 2013), those that compare and contrast responses between short and long timescales are rare. Addressing this knowledge gap is important as short-term responses are often used as a basis to make theoretical projections of long-term responses (Heywood *et al.* 1994; Tilman *et al.* 1994; Pimm *et al.* 1995; Brown *et al.* 2001; Brook *et al.* 2003; Hastings 2004; Triantis *et al.* 2010; Halley *et al.* 2014). We address this gap by using data from a long-term field experiment to contrast short-term and long-term responses to fragmentation.

Because of the logistical difficulties of studying species' responses over long timescales, many studies have used a spatial framework as a substitute for long-term responses (Pickett 1989; Travis & Hester 2005). Many of these “space-for-time” substitution studies model the changes in species’ responses to future climate-driven change (Currie 2001; Elith & Leathwick 2009; Fitzpatrick *et al.* 2011; Blois *et al.* 2013). However, a recent study that empirically tested the effectiveness of space-for-time substitution recommended it should be used judiciously, as predictions for species’ responses performed comparatively poorly when compared with those resulting from “time-for-time” data (Blois *et al.* 2013).

Studies that have contrasted long- and short-term responses to environmental change suggest that short-term responses rarely or only weakly predict long-term responses (Hastings &

Caswell 1979; Ovaskainen & Hanski 2002; Briggs & Borer 2005; Hastings 2010; Smith *et al.* 2010; White *et al.* 2013). For example, Briggs and Borer (2005) used models to show that initial assumptions based on the short-term responses of intraguild predators and their competitors to new resources can result in incorrect predictions of the response over the long term, as models assume no immigration or ignore the efficiency of predators or prey to convert resources into new individuals. Similarly, long-term species composition of sown and naturally regenerating swards at agricultural field margins was not predicted by short-term responses to perennial weed invasion (Smith *et al.* 2010).

In fragmented systems, there are many possible drivers that might influence contrasting responses in the short and long term. The effects of fragmentation can change over time, particularly if there are major changes in the matrix, the environment between the remaining remnants (Driscoll *et al.* 2013). For example, in an agricultural matrix, the cycles of sowing, maturation, and harvesting of a crop change the structure and resources in the matrix through time (Holland *et al.* 2005). In particular, the conversion of a natural habitat into an agricultural or silvicultural landscape can decrease rates of productivity over multiple crop rotations (Keeves 1966; Kimetu *et al.* 2008; Tian *et al.* 2011), which can directly affect the abundance and richness of all species in the crop matrix and therefore fragments embedded in the matrix (Siemann 1998; Mittelbach *et al.* 2001). Other factors that could potentially change fragmentation effects on species over time include those at the population level such as crowding effects (Sharon & Forman 1998; Debinski & Holt 2000; Grez *et al.* 2004), genetic effects such as genetic drift and inbreeding (Saccheri *et al.* 1998; Frankham *et al.* 1999; Higgins & Lynch 2001; Fahrig 2003; Lopez *et al.* 2009; Bijlsma & Loeschcke 2012), and adaptive responses (Koskinen *et al.* 2002; Aguilar *et al.* 2004; Desrochers 2010; Laparie *et al.* 2010; Hendry *et al.* 2011; Somervuo *et al.* 2014), particularly if species are subject to

an adaptation lag (Burger & Lynch 1995; Hellmann & Pineda-Krch 2007; Aitken *et al.* 2008).

Given that most fragmentation studies are snapshots in time, but the effects of fragmentation may change over time, we question the value of short-term observations for predicting long-term consequences of fragmentation. To address this question, we take advantage of the Wog Wog Habitat Fragmentation Experiment in Australia. This study was established in 1985, before fragmentation took place, and therefore offers a timescale rarely seen in the fragmentation literature (Margules 1993; Davies & Margules 1998; Davies *et al.* 2000; Davies *et al.* 2001; Davies *et al.* 2004). Davies and Margules (1998) found that, five years post-fragmentation, carabid beetle species richness remained unchanged in remnants vs. continuous forest, while individual species responded in a variety of ways including increasing, decreasing, and remaining the same (Table 1). Given this variety of responses, along with the availability of data from before and after fragmentation, and over the short and long term, our study offers the ideal opportunity to ask how species respond to fragmentation over timescales rarely seen in the habitat fragmentation literature and large-scale experiments.

Revisiting species studied by Davies and Margules (1998) with new data from 2011 to 2012, 24–25 years after fragmentation (26–27 years after the commencement of the study), we asked: 1) what were the long-term responses of eleven individual carabid species, and carabid richness, to habitat fragmentation, and how did they compare with short-term responses? And 2) what were the long-term responses of these species, and carabid richness, in the matrix, and how did they compare with short-term responses? The experimental design allowed us to investigate not only how species and communities respond to fragmentation and the matrix, but also how they respond to factors such as remnant size and distance to remnant edge

(Didham *et al.* 2012; Fahrig 2013; Betts *et al.* 2014)—factors which had not been studied over longer time periods and about which there is ambiguity in the literature (e.g.Connor *et al.* 2000; Prugh *et al.* 2008).

A crucial factor at Wog Wog is that the matrix, a non-native pine plantation, changed considerably over time. Pine saplings were planted in 1987 but by 2011–2012, the pines were fully mature, reaching a height of over 30 m and enveloping the canopy to create a sheltered understory. We predict, therefore, that species that find mature pine forest favourable habitat will benefit from the additional habitat between remnants, whereas species negatively impacted will either become isolated in the remnants and/or decline. While question 1 allows us to test whether individual species, and the community, have responded to fragmentation differently over the long term, question 2, by measuring the response of individual carabids, and the carabid community, in the matrix, allows us to infer how the changing matrix influenced carabid species and communities in remnants.

Table 1. Responses of species richness and individual carabid species' probability of occurrence to fragmentation up to six year post fragmentation at the Wog Wog fragmentation experiment (summarised from Davies and Margules 1998).

Response variable	Fragmentation	Remnant size	Edge effects	Matrix
Species Richness	Neutral	Neutral	Neutral	Neutral
Notonomus resplendens	Declined	Reduced in all, particularly medium	Neutral	Present
Notonomus metallicus	Declined	Neutral	Insufficient data	Absent
Notonomus minimus	Declined	Neutral	Insufficient data	Absent
Notonomus variicollis	Increased	Increased in all, particularly in small. Least in medium	Increased core compared to edge.	Present
Eurylychnus blagravei	Increased	Increased in all, particularly in large. Least in medium	Increased in core, decreased in edge compared to controls	Present
Carenum bonelli	Increased	Neutral	Neutral	Present
Promecoderus sp	Neutral	Neutral	Neutral	Present
Helluo costatus	Neutral	Neutral	Neutral	Present

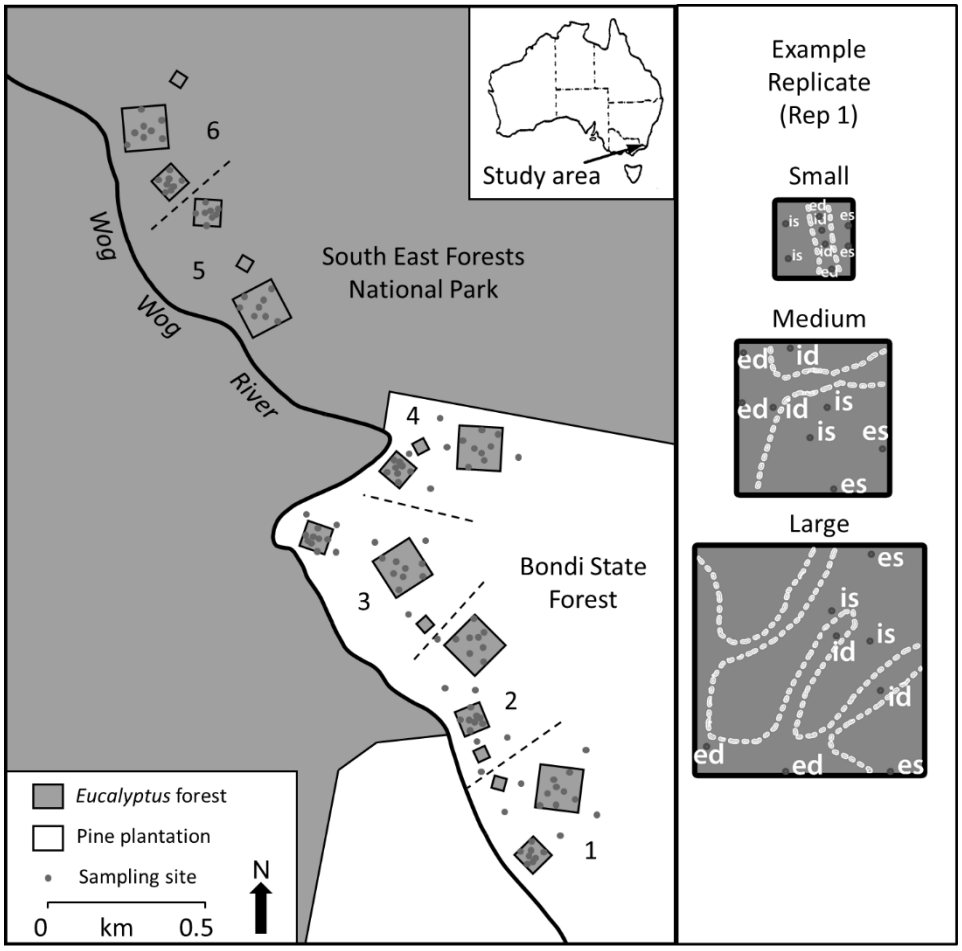
Predicting the long-term responses of these species based on their short-term responses is difficult given that initially, at Wog Wog, beetles were responding to an environment with a significantly contrasting matrix to that of today. Add to this the potentially confounding factors of population, genetic, and adaptive processes, and predicting species' responses becomes even more complicated. Furthermore, external effects such as climate change, which are known to affect species abundance and distribution (Thomas & Clarke 2004; Tylianakis *et al.* 2008; Moraal & Jagers Op Akkerhuis 2011; Buse *et al.* 2013; Salle *et al.* 2014), might interact with the effects of fragmentation complicating species' responses. Our study offers a unique opportunity to contrast short- and long-term responses to environmental disturbance without space-for-time substitution, and includes both spatial and temporal controls.

Methods

Study site

The Wog Wog Habitat Fragmentation Experiment was established in 1985 with a proposed timescale of decades (Margules 1993). Located in southeastern New South Wales, Australia (37°04'30"S, 149°28'00"E) in a valley previously covered with open *Eucalyptus* forest. The experiment has a split plot design with six blocks. Two blocks are in the control forest and four blocks are in the fragmented forest. Within each block there are three square plots, one of each size (0.25 ha, 0.875 ha and 3.062 ha) (Margules 1993). In 1987, the forest surrounding 12 plots was cleared and planted with *Pinus radiata*, leaving remnant native *Eucalyptus* forest surrounded by a plantation matrix. The other six plots in continuous native *Eucalyptus* forest are controls (Figure 1). Each plot contains monitoring sites, stratified by topography into slopes and drainages (termed drains) and by proximity to the edge of the plot (edge or core). Topography primarily affects the understory. Slopes are characterised by tussock grasses, forbs and scattered shrubs, while drains are characterised by dense shrubs of *Kunzea ericoides* and moist areas containing the sedge *Lomandra longifolia* (Austin & Nicholls 1988; Margules 1993). Each of the 18 plots has two replicates of the four combinations of edge proximity and topography (core slope, edge slope, core drain, edge drain) (Margules 1993). This gives a total of 144 sites in the *Eucalyptus* forest plots across remnants and controls. Following clearing around the plots, an additional 44 sites were added in the pine matrix in spatially close pairs (one slope, one drain). Two permanent pitfall traps were placed at each sampling site. Traps were opened for seven days, four times a year from 1985 until 1992. Forest habitat fragmentation took place in 1987 with the pine plantation established in winter 1988. By 1992, the pines were ~5m in height.

Figure 1. Map of Wog Wog Habitat Fragmentation Experiment site. There are eight sampling sites within each plot, each containing two pitfall traps. Paired sampling sites are represented by dots in the pine matrix. Plot sizes are 0.25ha, 0.875ha, and 3.062ha. Plots are separated by at least 50m. Note: The eight monitoring sites within each small plot are not represented due to figure space constraints.



Traps were re-opened in 2010 and sampled three times per year until 2012, repeating the same sampling techniques as the earlier data collections. By 2012 the pines within the plantation were 30 m high. One recent study at the Wog Wog Habitat Fragmentation Experiment showed that small remnants, as a result of being surrounded by mature pines, are now characterized by increased canopy cover, increased soil moisture, and lower daily maximum temperatures (Farmilo *et al.* 2013).

Study species

Following on from Davies and Margules (1998), we analysed the effect of fragmentation on the carabid community as a whole, however, we focused on the responses of the eleven most abundant carabid species chosen in that study, three more than was studied in Davies and Margules (1998). These species are *Notonomus resplendens* (Castelnau), *N. variicollis* (Chaudoir), *N. minimus* (Sloane), *N. metallicus* (Sloane), *Eurylychnus blagravei* (Castelnau), *Promecoderus sp.* (Dejean), *Carenum bonelli* (Brulle), *Helluo costatus* (Bonelli), *Hypharpax peronii* (Castelnau), *Amblystomus sp.* and *Scopodes sp.*

Data Analysis

The experimental design is nested, requiring a number of models that incorporate the nested structure of edge/core and size. The data were combined into two-year blocks, i.e., years 1–2 (before fragmentation), and years 4–5, 6–7, and 26–27 (after fragmentation), allowing for a balanced design of year group factors. As data in years 26 and 27 were collected over three seasons rather than four, we excluded the winter samples from the earlier data so that the earlier data also only represented three seasons.

We used a series of generalized linear mixed and generalized linear models to estimate effects of treatment (remnant, control, matrix), year groups, topography (slope, drain) and the

nested factors of edge (edge, core) and size (small, medium, large). Response variables were species richness and the probability of occurrence of individual at sites. We modelled occurrence rather than abundance as many of our models exhibited complete separation. To overcome this, we were required to use Firth's correction (Firth 1993) which can only be used with binomial data. A comparison of carabid responses using abundance and occurrence revealed negligible differences between the two approaches. We assumed a Poisson distribution for species richness and a binomial distribution for occurrence.

Question 1: What were the long-term responses of eleven individual carabid species and carabid richness to fragmentation, and how did they compare with short-term responses?

To test the long-term effects of fragmentation, remnant size, edge, and topography, we used a model selection procedure using AICc (Burnham & Anderson 2002). As matrix sites do not have attributes of edge and size, it was necessary to exclude the matrix from this set of analyses. Using the 'lme4' (Bates *et al.* 2013), 'brglm' (Kosmidis 2013) and 'MuMIn' (Barton 2014) packages in R (R Core Team 2014), we fitted models with combinations of the interactions of year group, topography, fragmentation, edge, and size including the null model. To answer question 1, we were interested in the effects of:

- The interaction of year group and fragmentation, to a) test whether the initial responses to fragmentation remained the same or changed over the longer term.
- The three-way interactions of year group, fragmentation, and the nested treatments of edge and size, to test for changes in these treatments over time.

To account for spatial autocorrelation within the experiment, we used patch nested within replicate as random effects in the generalized linear mixed models. However, for the majority of the full species models, the data exhibited complete separation. Therefore, we applied Firth's correction (Firth 1993) and fitted models without random effects. For each species, we ranked all the resulting models, considering those within two AICc (second order Akaike Information Criterion) units of the lowest AICc score (Burnham & Anderson 2002), excluding models with uninformative parameters, i.e. those models that fell below $\Delta AICc = 2$ and included only one additional parameter as the top ranked model (Arnold 2010).

Question 2: What were the long-term responses of carabid species and species richness to the matrix, and how did they compare with short-term responses?

To investigate the effect of the matrix on long-term carabid responses, we fitted another set of models, this time with the main treatments of remnant, control and matrix. It was necessary to exclude the data from years one and two, as matrix sites were not included until after fragmentation. To answer question 2, we were interested in the effects of:

- The interaction of year group and the matrix treatments, to test whether the initial responses to the matrix remained the same or changed over the longer term.

To account for spatial autocorrelation, we used patch as a random effect in generalised linear mixed models by assigning patch numbers to matrix sites in the spatially close site pairs (within 20 metres of each other). Again, because many of the models exhibited complete separation, we applied Firth's correction (Firth 1993) and fitted models without random effects. We followed the same AICc model ranking procedure as we did with the first set of models.

Results

Over the course of the experiment we caught a total of 5017 individual carabid beetles from 45 different species (Table S1).

Question 1: What were the long-term responses of eleven individual carabid species and carabid richness to fragmentation, and how did they compare with short-term responses?

The interaction of year group and fragmentation appeared in the top ranked models for species richness and four of the eleven species (Table 2). Patterns of species richness in the long term were not predicted by those in the short term (Figure 2 (a)). In all years, carabid richness was always higher in the remnants than the controls, including even before fragmentation (Figures 2(a) and 4(a). However, the effect of fragmentation was slightly reduced in the short-term after fragmentation when compared with the before fragmentation data. However, richness in the remnants compared to the controls increased significantly in the long term (Figures 2(a) and 4(a)). However, during this period that was also a background decline in species richness (in the controls) (Figure 4(a)).

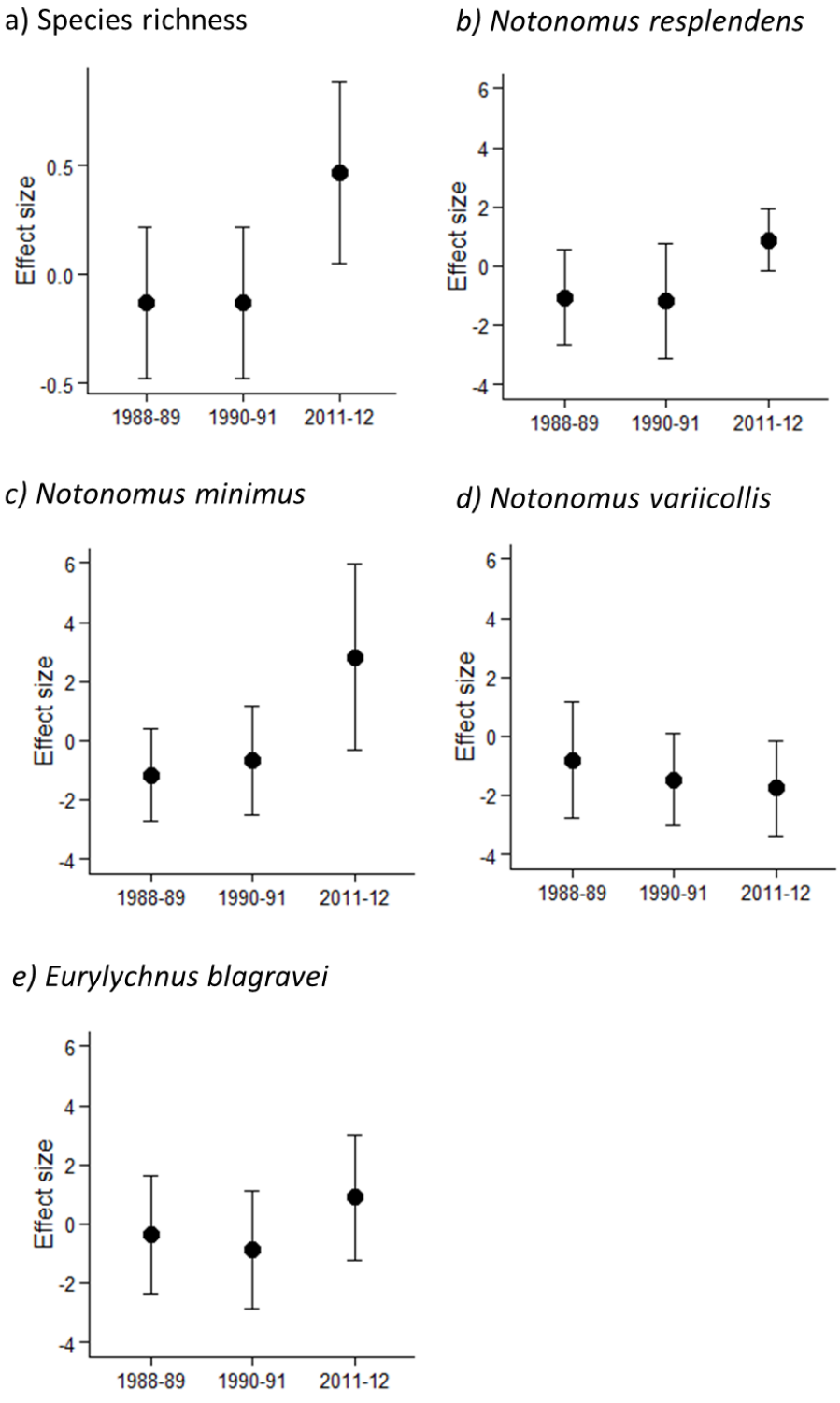
Fragmentation had a negative effect on *Notonomus resplendens* and *Notonomus minimus* over the short-term, however, over the long-term, by 2011-2012, there was a positive effect (Figures 2(b), 2(c), 4(b) and 4(c)). *Eurylychnus blagravei* showed a similar change in effect over time with years 2011-12 showing the greatest effect of fragmentation when compared to the controls (Figure 2(a)). However, this species was always more likely to occur in the remnants than the controls (Figure 4(e)). Fragmentation showed an increasing negative effect over time on *Notonomus variicollis* (Figures 2(d)), despite this species always being more likely to occur in the remnants than the controls (Figure 4(d)).

For all species and overall species richness, the interactions of year group, fragmentation, and edge and of year group, fragmentation, and remnant size did not appear in the top ranked models (Table 2). This indicates that the response to edge and size did not contrast over the short and long terms. There was, however, an interaction of treatment and size (F:S) for species richness and six of the eleven species (Table 2). There was also an interaction of treatment and edge (F:E) for species richness, *Eurylychnus blagravei*, and *Notonomus metallicus* (Table 2).

Table 2. Table showing top ranked models (ΔAICc<2) for responses of species richness and individual species occurrence to the effects of year group (Y), fragmentation (F), topography (T), remnant size (S) and edge (E). Terms separated by a colon indicate interaction terms. df = degrees of freedom, loglik = log likelihood, AICc = AICc score, ΔAICc = difference between model and top ranked AICc scores, (Int) = model intercept coefficient, '✓' = factor included in model. Response variables denoted with an asterisk were modelled using a generalized linear mixed model with patch as a random effect. All other models were generalized linear models using Firth's correction (Firth 1993).

Response	df	AICc	ΔAICc	(Int)	R^2	AdjR^2	Y	F	T	Y:F	Y:T	T:F	F:S	F:E
Species richness*	10	1949.8	0.00	0.29	0.20	0.21	✓	✓	✓	✓				
	14	1950.0	0.25	0.15	0.21	0.22	✓	✓	✓	✓			✓	
	13	1950.5	0.70	0.40	0.21	0.21	✓	✓	✓	✓	✓			
	17	1950.8	1.05	0.26	0.22	0.23	✓	✓	✓	✓	✓		✓	
Notonomus resplendens	12	535.8	0.00	0.08	0.28	0.40	✓	✓	✓	✓	✓			
	16	536.7	0.89	-0.13	0.29	0.41	✓	✓	✓	✓	✓		✓	
Notonomus minimus	14	267.6	0.00	-5.30	0.14	0.33	✓	✓	✓	✓	✓	✓	✓	
Notonomus variicollis	16	633.1	0.00	-2.02	0.25	0.34	✓	✓	✓	✓	✓		✓	
	12	634.2	1.09	-2.34	0.23	0.32	✓	✓	✓	✓			✓	
	13	634.6	1.54	-1.05	0.24	0.32	✓	✓	✓				✓	
Eurylychnus blagravei	11	571.8	0.00	-4.07	0.15	0.22	✓	✓	✓	✓				✓
	15	573.3	1.51	-4.86	0.16	0.24	✓	✓	✓	✓			✓	✓
Carenum bonelli	11	438.7	0.00	-3.58	0.15	0.26	✓	✓	✓			✓	✓	
Helluo costatus	7	316.0	0.00	-2.87	0.06	0.14	✓	✓	✓			✓		
	5	316.1	0.10	-3.45	0.06	0.13	✓	✓						
Promecoderus sp.	4	678.9	0.00	-1.16	0.04	0.06	✓							
Notonomus metallicus	9	232.2	0.00	-4.01	0.12	0.30	✓	✓	✓					
	11	233.6	1.46	-4.23	0.12	0.31	✓	✓	✓					✓
Hypharpax peronii	7	121.2	0.00	-6.36	0.04	0.17	✓	✓						
Amblystomus sp.	11	224.0	0.00	-3.66	0.10	0.28	✓	✓	✓			✓	✓	
Scopodes sp.	4	271.3	0.00	-2.20	0.03	0.07	✓							

Figure 2. Effect sizes (log odds ratios) of carabid species richness (a) and individual species ((b) to (e)) of the interaction of year and fragmentation. Bars represent 95% confidence intervals. Closed circles represent the log odds ratio of occurrence in remnant sites compared with control sites and before fragmentation data. Only those species where the interaction of year group and fragmentation was a factor present in the best fit models are shown.



Question 2: What were the long-term responses of carabid species and species richness to the matrix, and how did they compare with short-term responses?

The interaction of year group and treatments (controls/remnants/matrix) appeared in the top ranked models for species richness and six of the eleven species (Table 3). Time had a large effect on species richness in the matrix (Figure 3(a)). This was because, as the background richness declined over the long term (as indicated by the response in the controls), both matrix and remnant richness remained consistent (Figure 4(a)).

For three species, *Notonomus variicollis, Eurylychnus blagravei* and *Promecoderus sp;* the ageing matrix had an initial negative effect on occurrence when compared to the controls (Figures 3(d), 3(e) and 3(f)). However for all of these species this effect had climbed to be become neutral, as in the case of *Notonomus variicollis,* or positive, as in the cases of *Eurylychnus blagravei* and *Promecoderus sp*. Converting habitat to the matrix also had a positive effect on the likelihood of occurrence of *Notonomus resplendens, N. minimus* and *N. metallicus* over the long-term, with all these species demonstrating a neutral response to habitat conversion between 1988-89 and 1990-91.

In addition to the positive responses to the matrix and remnants, there were also some notable background short- to long-term responses (Figure 4). Species richness increased in the controls over the short term, only to decline back to pre-fragmentation levels in the longer term (Figure 4(a)). *Notonomus resplendens, N. minimus, Eurylychnus blagravei, Promecoderus sp.* and *N. metallicus* all showed a similar background temporal response (Figure 4). Our results, therefore, could indicate that there has been an environmental change across all treatments during the time of the experiment. For the duration of our study, from 1985 until 2012, temperatures (mean, maximum, minimum) increased in South East Australia, along with a decline in annual rainfall (Bureau of Meteorology 2014). The

temperature near Wog Wog followed a general rise from 1991 until 2013, with 2010 being a particularly warm year (Figure S2). Rainfall fluctuated throughout the time of the experiment, with 2008 and 2009 being particularly dry years (Figure S3). Changes in temperature and moisture are known to affect beetle development (Kitayama *et al.* 1979; Hagstrum & Milliken 1988), so it is possible, therefore, that the two drier years prior to the most recent surveys influenced carabid populations negatively across all treatments, resulting in lower probabilities of occurrence in 2011–2012.

Our results confirm that topography had a significant effect on carabid species (Tables 2 and 3). Species richness was higher, and eight of the eleven species were significantly more likely to occur, in the drain sites than the slope sites (Figure S1). Four species, *Carenum bonelli, Helluo costatus, Promecoderus sp.*, and *Scopodes sp.*, were more likely to occur in the slope sites than the drain sites.

Table 3. Top-ranked models (ΔAICc<2) testing for responses of species richness and individual species occurrence to the effects of the year group (Y), matrix (M), topography (T). A colon indicates an interaction term. df = degrees of freedom, loglik = log likelihood, AICc = AICc score, ΔAICc = difference between model and top ranked AICc scores, AdjR2 = adjusted R2, (Int) = model intercept coefficient, '✓'= factor included in model. Response variables denoted with an asterisk were modelled using a generalized linear mixed model with patch as a random effect. All other models were generalized linear models using Firth's correction (Firth 1993)

Response	df	AICc	ΔAICc	R^2	AdjR^2	(Int)	Y	M	T	Y:M	Y:T	T:M
Species richness*	9	1007.8	0.00	0.12	0.13	-0.22	✓	✓	✓		✓	
	13	1009.3	1.55	0.13	0.15	-0.10	✓	✓	✓	✓	✓	
*Notonomus resplendens**	11	509.0	0.00	0.33	0.46	2.73	✓	✓	✓	✓		
	13	510.1	1.02	0.33	0.47	2.92	✓	✓	✓	✓	✓	
	13	510.8	1.76	0.33	0.46	2.69	✓	✓	✓	✓		✓
Notonomus minimus	12	257.4	0.00	0.11	0.27	-1.86	✓	✓	✓	✓		✓
*Notonomus variicollis**	10	581.0	0.00	0.25	0.34	-3.42	✓	✓		✓		
	13	582.1	1.10	0.26	0.35	-3.68	✓	✓	✓	✓	✓	
Eurylychnus blagravei	10	585.4	0.00	0.18	0.26	-1.89	✓	✓	✓	✓		
	12	586.7	1.29	0.19	0.27	-2.23	✓	✓	✓	✓	✓	
Carenum bonelli	8	458.7	0.00	0.12	0.20	-1.07	✓	✓	✓			✓
	6	460.4	1.70	0.11	0.19	-0.82	✓	✓	✓			
Helluo costatus	5	299.6	0.00	0.06	0.13	-2.30	✓	✓				
	8	301.4	1.81	0.07	0.15	-1.73	✓	✓	✓			✓
*Promecoderus sp.**	10	627.9	0.00	0.09	0.13	-0.43	✓	✓		✓		
	13	629.4	1.52	0.10	0.14	-0.58	✓	✓	✓	✓		✓
Notonomus metallicus	10	230.3	0.00	0.11	0.29	-2.91	✓	✓	✓	✓		
Hypharpax peronei	5	207.9	0.00	0.34	0.63	-10.61	✓	✓				
*Amblystomus sp.**	9	225.5	0.00	0.09	0.25	-2.32	✓	✓	✓			✓
	13	227.3	1.82	0.10	0.28	-2.24	✓	✓	✓		✓	✓
Scopodes sp.	3	211.0	0.00	0.03	0.10	-4.83	✓					
	5	211.7	0.68	0.04	0.11	-5.14	✓	✓				
	6	212.4	1.39	0.04	0.12	-4.92	✓	✓	✓			
	8	212.5	1.56	0.05	0.14	-5.25	✓	✓	✓			✓

Figure 3. Effect sizes (log odds ratios) of carabid species richness (a) and individual species ((b) to (g)) of the interaction of year and the matrix sites. Bars represent 95% confidence intervals. Closed circles represent the log odds ratio of occurrence in remnant sites compared with control sites and years 1988-89. Closed triangles represent the log odds ratio of occurrence in matrix sites compared with control sites and years 1988-89. Only those species where the interaction of year group and the main treatments of remnants and matrix was a factor present in the best fit models are shown.

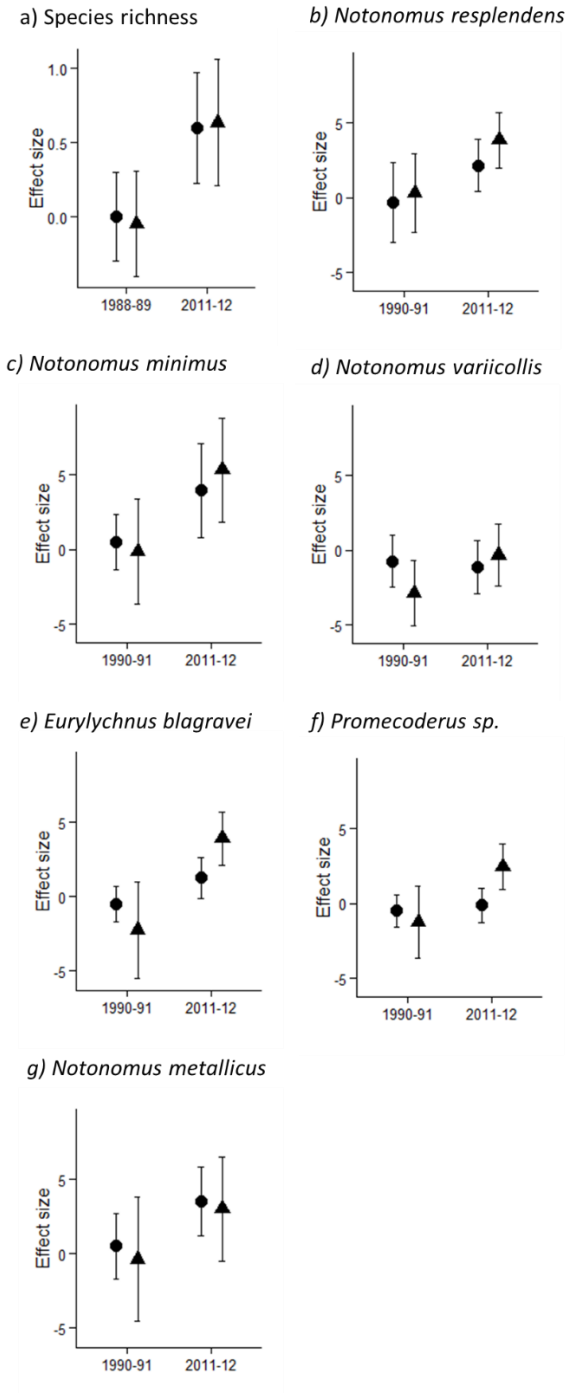
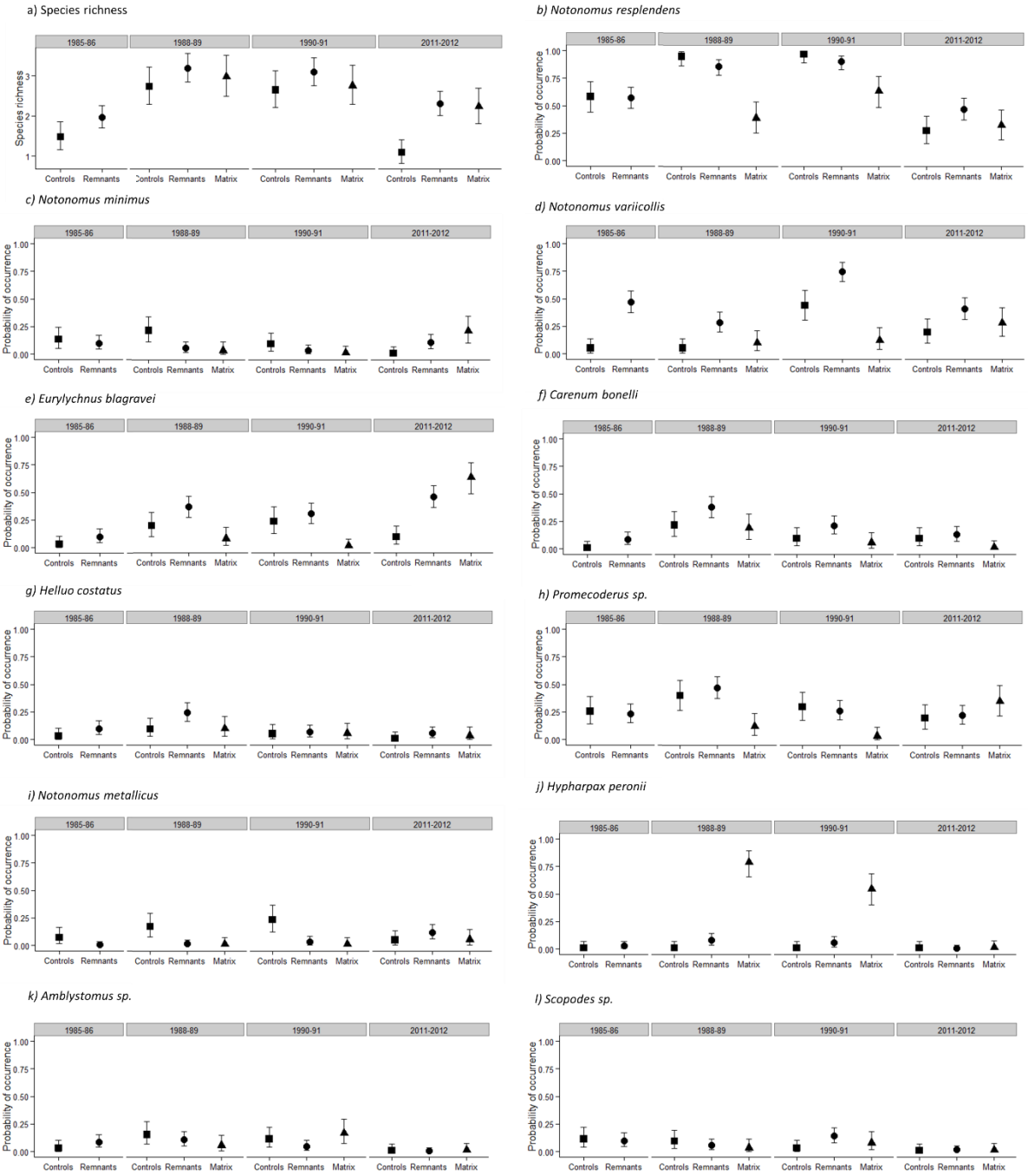


Figure 4. Responses of carabid species richness (a) and individual species ((b) to (l)) to the interaction of year and the main treatments of remnant and matrix. Bars represent 95% confidence intervals.



Discussion

By examining the responses of carabids to fragmentation over a timescale unusual in large field experiments, we show that long-term responses are not necessarily predicted by short-term responses. Two of the species (*Notonomus resplendens* and *N. minimus*) showed initial negative responses to fragmentation when compared to the controls only for this to become positive over the long-term. In contrast, species richness and the species *Eurylychnus blagravei* demonstrated a greater probability of occurrence in the remnants over the whole time of the experiment; a relationship that increased over the long-term. In this case, therefore, short-term responses predicted long-term responses. The contrasting results we have shown have implications for fragmentation research, highlighting the risk that much of the large body of work tracking short-term responses to fragmentation does not necessarily give an accurate indication of the ultimate responses of species and communities to fragmentation.

Species richness and the occurrence of nearly all of the species studied increased in the matrix over the long-term. This indicates that by 2012, the pines were habitat rather than a hostile matrix for these species. Pine plantations can provide suitable habitat for many carabid species (Bonham *et al.* 2002; Berndt *et al.* 2008; Lange *et al.* 2014), in particular mature pine plantations (Jukes *et al.* 2001; Lange *et al.* 2014), and this is clearly the case for many of the species considered, and the carabid community as a whole, in this study. Furthermore, an overall increase in occurrence of in *Notonomus resplendens, N. minimus, N. variicollis, Eurylychnus blagravei*, *Promecoderus sp.* and *Notonomus metallicus* in the matrix resulted in contrasting short- and long-term effects of habitat conversion to pine plantation. For three of these species, *Notonomus minimus, Eurylychnus blagravei* and *Promecoderus,* occurrence was less likely in the matrix than the controls and remnants over the short term,

but these species became most likely to occur in the matrix over the long term. The responses of these three species could indicate that their response in the remnants could be interpreted as a mass effect with source habitat for populations now being the pine matrix (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003; Lasky & Keitt 2013; Livingston *et al.* 2013). However, if a pure mass effect was the cause of this pattern, we might expect an accompanied change in edge effects in the remnants over the long-term, which we did not detect. However, mass effects cannot be completely ruled out here, as species of beetle are known to respond to edge effects over much larger scales than the distance to the core of the remnants at Wog Wog (Ewers & Didham 2008). One species, *Hypharpax peronii,* in contrast to most others, showed a positive response to the young pine plantation and little or no response to the mature plantation.

There are three reasons why the mature pine plantation could provide preferred habitat for the carabid species studied. First, the abiotic environment in the mature plantation might provide preferred habitat. Most carabids studied preferred the darker and moister microhabitat of drainage lines to drier and sunnier slopes (Figures S3 & S4). The mature pine plantation in 2011–2012, with its tall and closed canopy, provides cooler darker habitat than the younger, more open, plantation in the early years of the experiment. Further, this influence of the matrix could result in changes to the environment of the remnants (e.g. shading), and drive the positive responses to the remnants over the long-term. This offers an alternative explanation to mass effects described earlier and might be more likely as indicated by the lack of edge responses detected. In contrast, the only species to prefer slope to drain habitat, *Carenum bonelli,* did not respond positively to the plantation in the long term (although this relationship was not significant), suggesting that it preferred the younger pine forest because of its preference for more open and drier habitats. In other studies, similarly, different carabid

species have responded in positive and negative ways to increased canopy cover (Niemela & Halme 1992; Koivula *et al.* 1999; Lange *et al.* 2014).

Second, the mature plantation might benefit carabids by providing greater food availability. Most carabids are predators, therefore prey availability is a key habitat determinant (Niemelä 1993; Koivula *et al.* 1999). Pine plantation litter—despite having less diversity of microarthropod species, a key food source for carabids (Kotze *et al.* 2011), than native forest litter—has been shown to contain similar microarthropod abundances. Further, microarthropod abundance increases in older pine forests (Springett 1976), as pine litter accumulates with plantation age (Das & Ramakrishnan 1985). The addition of leaf litter in conifer plantations has been shown to change carabid communities through altered abiotic conditions and increases in prey items (Koivula *et al.* 1999; Magura *et al.* 2005). Springtails, a common food item for carabids, become more common with increasing litter (Koivula *et al.* 1999) and are correlated with carabid abundance (Niemelä *et al.* 1996; Koivula *et al.* 1999). Terrestrial amphipods, which are important in breaking down conifer leaf litter (O'hanlon & Bolger 1999), can reach high densities (Richardson 1980; Friend & Richardson 1986; O'hanlon & Bolger 1993) and therefore might offer a food source for the carabids.

A third potential benefit of the plantation is that the structure of the pine forest floor may positively affect the dispersal and movement of carabid species (Driscoll *et al.* 2013). Seven of the eleven species studied are flightless and ground dwelling. The pine matrix forest floor is a much less complex environment than the eucalypt forest floor, and might increase carabid movement in the matrix, potentially allowing the carabids to encounter their prey more often (Johnson 2006; Jana & Bairagi 2014).

Conclusions

We took advantage of one of the longest-running fragmentation experiments to track species' responses over a timescale usually unavailable to ecologists. We showed that long-term responses of more than 25 years post-fragmentation can contrast with shorter-term responses of up to five years. We attribute species' changing responses to temporal changes in the maturing pine plantation matrix, which potentially provides new and preferred habitat for some species, habitat structure that possibly favours dispersal in the matrix compared to native *Eucalyptus* forest, and might favourably alters habitat in remnants, via shading, increasing species occurrence for many species, and richness, within remnants. Our results highlight the need for caution in extrapolating long-term species' responses to landscape change from short-term data.

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Paper IV: A long-term habitat fragmentation experiment leads to morphological change in two carabid species.

Historical beetle specimens, collected from the fragmentation experiment site since 1985, provided an opportunity to test for morphological changes in response to the environmental change that occurred during that time. I wanted to look at the morphology of two species' of carabid with known responses to landscape change, as documented in Paper III. This study of morphological responses dovetailed neatly with Paper III, and offered the opportunity to gain extra insights into the mechanisms behind species responses to landscape changes that a study of population responses would not reveal.

Evans, M. J., Banks, S.C., Barton, P.S., Davies, K.F., Driscoll, D.A. A long-term habitat fragmentation experiment leads to morphological change in two carabid species. In prep.

Abstract

Most understanding of species' responses to environmental change is based on studies of populations and communities. The morphological changes experienced by animals in response to environment change might offer an extra level of information to understand the mechanisms behind species' responses to it. We used specimens of two flightless carabid beetle species (*Notonomus resplendens* and *Eurylychnus blagravei*) collected over the 28 years history of the Wog Wog Habitat Fragmentation Experiment, Australia, to measure carabid morphological change as a responses to time and fragmentation of their native habitat into remnants surrounded by an exotic pine plantation. The mature stage of the pine plantation selected for individuals of bigger size and longer legs of *Notonomus resplendens*; traits associated with increased dispersal ability. The direct contrast in size and trochanter length changes shown for *Eurylychnus blagravei,* in tandem with the population response differences for both species suggests that the two species might adopt differing dispersal strategies. *Eurylychnus blagravei* demonstrated changes associated with resource constraints, which possibly resulted in a reduction in size. *Notonomus resplendens* exhibited male-biased dispersal, with relative trochanter lengths increasing for males in the mature pine plantation, which demonstrated that the plantation drove divergence between the sexes. Tracking studies and population genetics would improve our understanding of why these species respond to habitat change with differing population and morphological responses. Furthermore, population studies might benefit from determining the relative abundances of each sex in experimental treatments in order to highlight the possibility of genetic impacts that could threaten the future viability of the species.

Introduction

Most of our current understanding of species' responses to environmental change originates from studies of populations and communities (Jackson and Overpeck 2000; Thomas *et al.* 2004; Williams *et al.* 2010). Yet, many organisms also express phenotypic variation in response to environmental change (Pigliucci 2001; DeWitt and Scheiner 2004; Miner *et al.* 2005). This includes changes in behaviour, morphology, growth, life history and demography, which can occur across or within generations (Black and Dodson 1990; Black 1993; Agrawal *et al.* 1999; Miner *et al.* 2005). Morphology is a dominant feature of an organism's phenotype and is directly linked to how it interacts with its environment (Salmon *et al.* 2014). Knowledge of morphological responses has the potential to complement knowledge of population and community responses by providing additional insight into the mechanisms behind species' responses to environmental change.

Habitat change imposes selection pressure on morphology through effects of (Kingsolver and Pfennig 2007; Da Silva and Tolley 2013; Vergilov and Tzankov 2014) changing habitat factors such as food quality, competition with other species, vegetation structure and microclimate (e.g. Desrochers 2010; Laparie *et al.* 2010; Marnocha *et al.* 2011). For example, a reduction in population density, which increases the amount of food available to remaining individuals, can lead to larger individuals in deer (Ashley *et al.* 1998). Conversely, a reduction in prey items results in smaller individuals in terns (McLeay *et al.* 2009). The morphology of species can also change according to the type of food resources in new habitat. For example, the width of the head of insect species can be directly related to its ability to consume larger food items (Pearson and Stemberger 1980; Laparie *et al.* 2010). Also, many species exhibit sexual dimorphism related to how they exploit food resources (Atchley 1971; Fairbairn 1997; Laparie *et al.* 2010). Phenotypic selection pressures, such as

those associated with habitat change, can also result in a number of different effects on the variability of individuals within a population (Sorensen and Hill 1982; Sorensen and Hill 1983; Price *et al.* 1988; Albertson *et al.* 2003; Estes and Arnold 2007; Kingsolver and Pfennig 2007; Landi *et al.* 2015). Studying how species respond morphologically to environmental change may therefore offer insights into the mechanisms leading to population change.

Changes to morphology in response to landscape can reflect adaptations associated with dispersal ability. Better dispersers are more likely to colonise and establish populations in fragmented habitats (Travis and Dytham 2002; Fahrig 2003) resulting in selection pressure for individuals with improved dispersal ability in landscapes experiencing fragmentation of habitat (Travis and Dytham 2002; Holt 2003; Desrochers 2010). This same mechanism can also result in selection pressures for increased dispersal ability when a species is exposed to new habitat which it is able to colonise. For example, carabids (Laparie *et al.* 2013), butterflies (Hill *et al.* 1999) and damselflies (Anholt 1990) have all shown that exposure to more habitat can result in individuals that have changed morphologically for increased dispersal ability (Taylor and Merriam 1995; Hill *et al.* 1999; Laparie *et al.* 2013).

Research that examines morphological changes within species in response to landscape change and over time is rare (but see Desrochers 2010; Marnocha *et al.* 2011). One of the reasons for this is that there are very few long-term studies globally that have sufficient data to address this problem. This limits our ability to ask questions about long-term phenomena, such as climate change. Here, we used a long-term fragmentation experiment (over 25 years old), one of the longest running of its kind (Farmilo *et al.* 2013; Haddad *et al.* 2015), to research the effects of anthropogenic landscape modification on the morphology of two flightless carabid beetle species (Coleoptera: Carabidae). This landscape consists of native

Eucalyptus forest which was fragmented into experimental remnants with the cleared part of the landscape replaced with a *Pinus radiata* plantation forest. During the time of the experiment, from 1985 until 2013, South East Australian mean, maximum, and minimum temperatures increased, and annual total rainfall declined (Bureau of Meteorology 2014). The temperature near Wog Wog followed a rise from 1991 until 2013, with 2010 being a particularly warm year. Throughout the time of the experiment rainfall fluctuated, with 2008 and 2009 being particularly dry years (see Paper III for more information). One of the carabids, *Notonomus resplendens* became more abundant in pine plantation relative to the patches and controls. The second carabid, *Eurylychnus blagravei*, showed no response to fragmentation in the first five years of the experiment, but in the long term, became more likely to occur in the remnants and the pines than the controls (see Paper III for more information).

Using specimens of adult stage carabids sampled between 1985 and 2013, we measured key aspects of beetle morphology linked to size and dispersal ability across fragmentation treatments over the timescale of the experiment. We tested for morphological variation over time in response to the establishment of a pine plantation establishment around remnant native *Eucalyptus* forest patches and related changes to those in control sites located in continuous *Eucalyptus* forest. Many species can adapt over relatively short evolutionary timescales of decades (Berthold *et al.* 1992; Vanhooydonck *et al.* 2009; Desrochers 2010), and this is especially true for insects such as beetles which have rapid life cycles and demonstrate strong phenotypic plasticity (Moczek 2010).

We asked if landscape change led to morphological changes in both species. We might expect that both species could respond with an increase in traits related to dispersal ability as their occurrence increases in the pine plantation as it matures over the timescale of the

experiment (Laparie *et al.* 2013). Furthermore, if the beetles had changed their primary food resource, we might also expect to see variation in head width as they adapt to different food items (Pearson and Stemberger 1980; Laparie *et al.* 2010). We might also expect a sexually dimorphic response, depending on how males and females adapt to this new resource (Atchley 1971; Fairbairn 1997; Laparie *et al.* 2010).

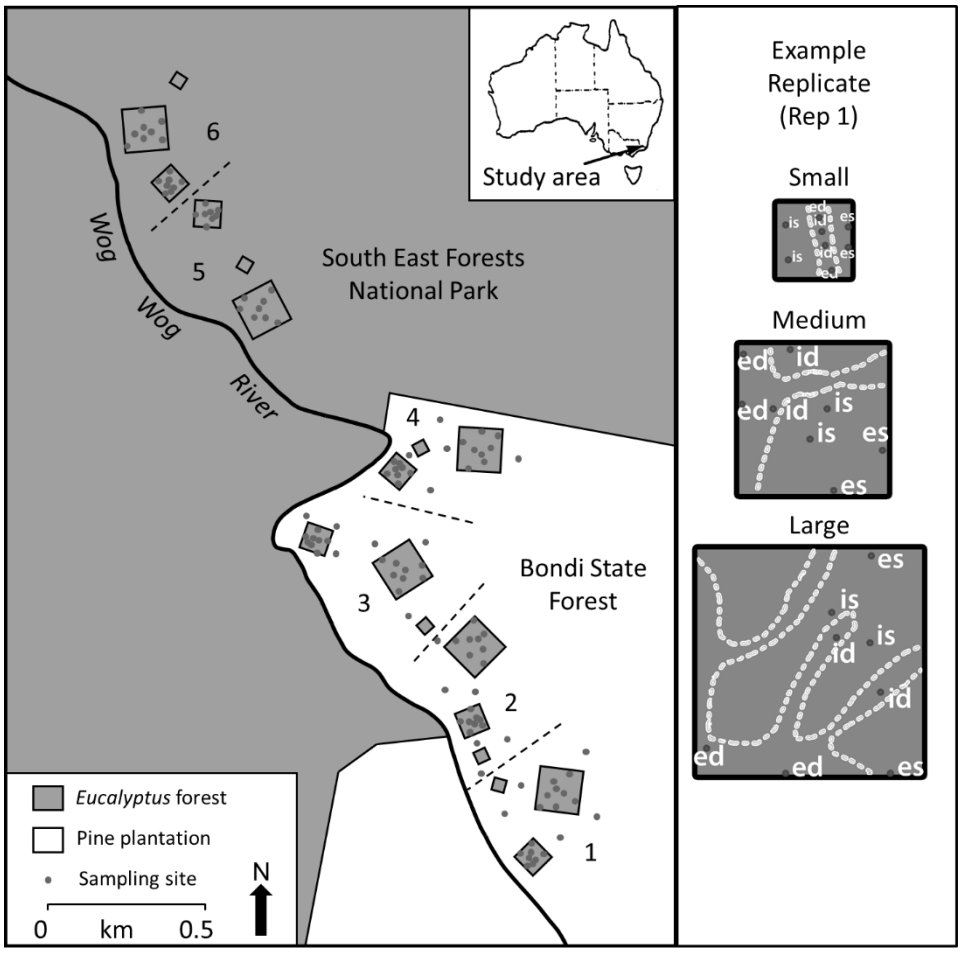
Methods

Study site

Our study was conducted in the Wog Wog Habitat Fragmentation Experiment (Margules 1992), which is a long-term and landscape scale experiment (Davies and Margules 2000). This long-term experiment offers the ideal opportunity to research the morphological changes of species in response to landscape change. Located in south-eastern NSW, Australia (37°04'30"S, 149°28'00"E), the experiment was established in 1985 (Margules 1993) in a valley previously covered with open *Eucalyptus* forest. It consists of six replicates of square plots of three different sizes (0.25 ha, 0.875 ha and 3.062 ha) (Margules 1993). In 1987, the forest surrounding four of these replicates was cleared and planted with a plantation of *Pinus radiata* (Figure 1). Each plot contains a number of monitoring sites, stratified by topography into slopes and drains and by proximity to the edge of the plot (edge or core). Each of the 18 plots was divided into four combinations (core slope, edge slope, core drain, edge drain) (Margules 1993) and replicated twice giving a total of 144 sites. Following clearing around the plots, an additional 44 sites were added in the pine plantation. Each site, contains two permanent pitfall traps which were opened for seven days, four times a year from 1985 until 1992. Traps were re-opened in 2009 and sampled three times per year until 2013, by which time the pines within the plantation were approximately 30m high. Throughout the history of

the experiment, a random subset of the adult beetles were pinned and stored at the Australian National Insect Collection in Canberra, Australia.

Figure 1. Map of the experimental site. There are eight sampling sites within each plot, each with two pitfall traps. Paired sampling sites are represented by dots in the pine plantation. Plot sizes are 0.25ha, 0.875ha and 3.062ha. Plots are separated by at least 50m. Note: The eight monitoring sites within each small plot are not represented due to figure space constraints.



Study species

We chose two species of common but similar flightless carabid beetle species with known contrasting population responses to the experiment: *Notonomus resplendens* and *Eurylychnus blagravei* (Paper III). Both of these species were suitable size for morphological work given the equipment available for this study and were also available in large enough numbers spread across the time of the experiment to offer sufficient data for analysis. We included samples from 1985-1987 (before fragmentation), 1988-92 (short-term after fragmentation) and 2009-13 (long-term after fragmentation).

Measurements

We made morphological measurements using images taken with a SmartDrive SatScan Collections v2.0.10 scanner at the Australian National Insect Collection. The SatScan enables high resolution images of invertebrate sample drawers to be taken. We used these drawers to take multiple images of several beetles at the same time, being careful to accompany each beetle with labels containing data on site and date of collection. Each resultant composite image contained 40 individual carabid adults which we then cut into individual beetle images. Digital landmarks were placed on each image using the software programs tpsUtil (Rohlf 2013a) and tpsDIG (Rohlf 2013b) (Figure 2). We then used the coordinates of the landmarks to calculate the linear distance between the landmarks. Using images taken of both the dorsal and ventral sides of the two species, we took linear measurements on each individual of both species (Table 1 & Figure 2). As a proxy for overall size, we measured elytra width and length and derived an area metric by multiplying these two metrics. We chose the elytra, as opposed to body length, for this index, to minimise variation due to orientation or as a result of parts of the body, such as the head, protruding out more in some individuals than others. To obtain a measure relevant to dispersal capacity, we measured femur length and

metatrochanter length. Leg length is considered to indicate dispersal ability in flightless species (Laparie *et al.* 2013). We measured metatrochanter length because carabid species that run typically have shorter trochanters than species that use pushing to move through their environment (Evans 1977). If a carabid species has adapted to an environment where dispersal requirements have changed, then the metatrochanter could change in size. We also measured the distance between eyes (fore inter-ocular width) as a proxy for head width (Laparie *et al.* 2010). This allowed us to examine whether the beetles have responded to different food items that require a smaller or larger head width to consume food effectively. We were only able to determine the sex for *Notonomus resplendens.* For this species, we also measured the last abdominal sternite, a trait that has shown to be larger in females than males in carabids and is thought to be as a result of female investment in fecundity in new habitats (Laparie *et al.* 2010).

Figure 2. Examples of dorsal (a) and ventral (b) images of *Eurylychnus blagravei* (a) and *Notonomus resplendens* (b) including landmarks as hollow circles and linear measurements as arrows.

(a) (b)

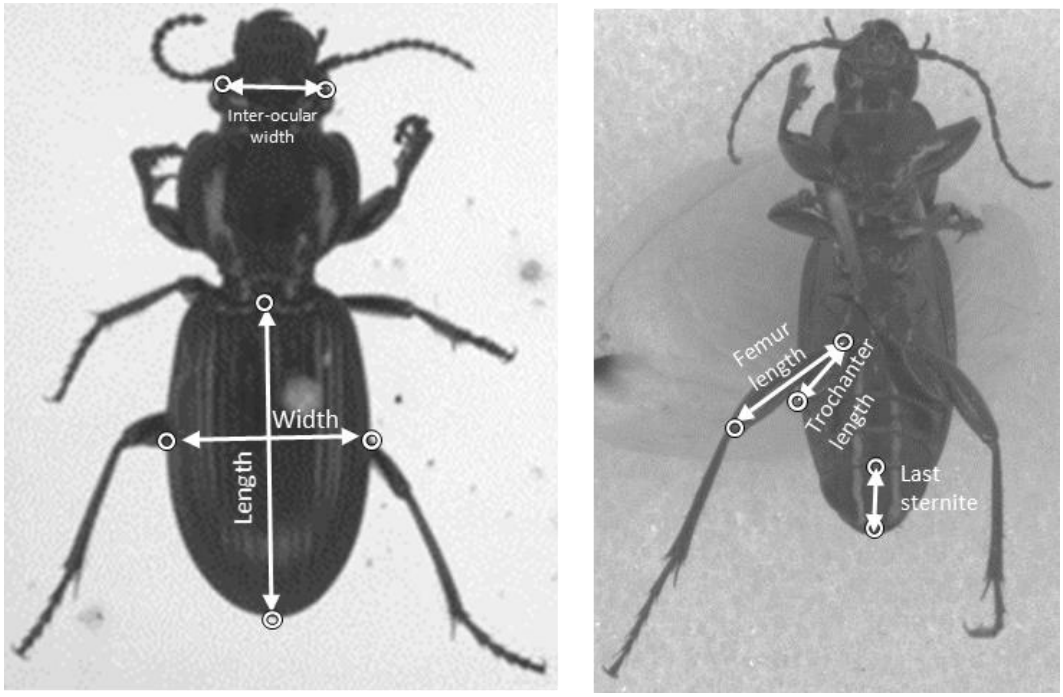


Table 1. Summary of measured morphological traits, their relevant ecological function and possible predictions and interpretations of their responses.

Morphological trait	Relevant ecological function	Prediction/Interpretation
Elytra area (width*length)	Proxy for overall size.	Size might increase in new habitat.
Femur length	Walking and dispersal.	Longer leg length indicates an increased movement capacity.
Metatrochanter length	Walking and dispersal.	Longer metatrochanter indicates a shift to running instead of burrowing.
Inter-ocular width	Food items.	Wider head indicates a switch to larger food items.
Last ventral sternite	Reproductive potential.	Longer sternite indicates increased investment in reproduction.

Data Analysis

As size is the dominant morphological trait among animals (Peters 1983), we needed to first determine patterns of variation in other morphological traits beyond that which is correlated with body size (Barton *et al.* 2011). We calculated residuals from linear regressions of $\log_{10}$(trait) against $\log_{10}$(elytra area), for each separate trait of femur length, metatrochanter, and inter-ocular width of both species. This allowed us to characterize traits relative to the static allometry inherent in the beetles (Ribera *et al.* 1999; Shingleton *et al.* 2007; Barton *et al.* 2011).

To address our questions, we used linear mixed effects models using the 'lme4' (Bates *et al.* 2013) and 'MuMIn' (Barton 2014) packages in R (R Core Team 2014) assuming a Gaussian distribution. To account for spatial autocorrelation within the experiment, we fitted patch as a random effect in the models. To test for the effect of time, we combined data into year blocks, i.e. 1985-87 (before fragmentation), 1988-92 (immediately after fragmentation), and 2009-2013. We tested for differences in morphological traits across the experimental

treatments in two steps (model steps #1 and #2). This is because the pine plantation sites were not established until after fragmentation, and it was necessary to run sets of models (#1) including pine plantation sites, but excluding all data from before fragmentation, and (#2) including all data years but excluding the pine plantation sites.

Model set #1 (Including pre-fragmentation data, excluding plantation data)

We tested whether there was an effect of time in general and (morphological trait ~ Y) and an interaction between time and treatment (control vs remnants in fragmented landscape) (morphological trait ~ Y*F). We also tested for effects of the nested treatments of fragment size (morphological trait ~ Y*F*S) and edge (morphological trait ~ Y*F*E) and for effects of topography (i.e. slopes and drainage lines) (morphological trait ~ T), its interaction with year group (morphological trait ~ Y*T), treatments (morphological trait ~ F*T) and the further interaction of time (morphological trait ~ Y*F*T). For *Notonomus resplendens* we also included sex (Sex) as an interacting factor in the models (See Table 2 for full models). We ranked all the resulting models, including the null model, considering those within two AICc (second order Akaike Information Criterion) units of the lowest AICc score (Burnham and Anderson 2002), excluding models with uninformative parameters (Arnold 2010).

Model set #2 (Including plantation data, excluding pre-fragmentation data)

For the data that included the pine plantation sites, we repeated the same model selection procedure as the models with the pre-fragmentation data, however, we excluded the nested treatments of size and edge (Table 2).

Table 2. Summary of full models used for variable selection using AICc model ranking. 'Y' = Year group, 'F' = main treatments, 'T' = topography, 'S' = size, 'E' = edge. '*' = denotes interaction.

Species	Data used		Full model
	Pre-fragmentation (model set #1)	Plantation (model set #2)	
Notonomus resplendens	✓		Morphological trait ~ Y + F + T + Y*F + Y*F*S + Y*F*E + Y*T + F*T + Y*F*T + Y*Sex + F*Sex + T*Sex + Y*F*Sex + Y*F*S*Sex + Y*F*E*Sex + Y*T*Sex + F*T*Sex + Y*F*T*Sex
Notonomus resplendens		✓	Morphological trait ~ Y + F + T + Y*F + Y*T + F*T + Y*F*T + Y*Sex + F*Sex + T*Sex + Y*F*Sex + Y*T*Sex + F*T*Sex + Y*F*T*Sex
Eurylychnus blagravei	✓		Morphological trait ~ Y + F + T + Y*F + Y*F*S + Y*F*E + Y*T + F*T + Y*F*T
Eurylychnus blagravei		✓	Morphological trait ~ Y + F + T + Y*F + Y*T + F*T + Y*F*T

Results

We measured 374 individuals of *Notonomus resplendens* and 265 individuals of *Eurylychnus blagravei* (Table 3). In both species, log(traits) were weakly correlated with log(elytra area), indicating variation in morphology regardless of elytra area (Table 4).

Notonomus resplendens

Model set #1: Temporal changes in the remnants and controls

Notonomus resplendens showed a strong morphological change over time (Table 5, Figures 3-4), but no fragmentation effect. From 1985 until 2013, this species became larger in all treatments, but with males being relatively smaller than females (Figure 3(a)). Relative femur length of males increased over the time of the experiment (Figure 3 (b)) and by 2009-13, males had larger relative trochanters than females (Figure 3 (c)). By 2009-13, Males and females had diverged in inter-ocular width with males having significantly less inter-ocular width than females (Figure 3(d)). The only relationship shown for sternite length was that males had larger last sternite in 2009-13 than in 1988-92 (Figure 3(e)). There was no interactive effect of the nested treatments of edge and size for this species.

Table 3. Summary of individual carabids caught and from which of the main treatments of year block and treatment of (a) *Notonomus resplendens* and (b) *Eurylychnus blagravei.*

(a) *Notonomus resplendens*

	1985 to 1987	1988 to 1992	2009 to 2013	Total
Remnants	32	76	71	179
Controls	9	66	44	119
Pine	NA	33	43	76
Total	41	175	158	374

(b) *Eurylychnus blagravei*

	1985 to 1987	1988 to 1992	2009 to 2013	Total
Remnants	8	99	73	180
Controls	2	26	6	34
Pine	NA	1	50	51
Total	10	126	129	265

Table 4. Summary statistics of morphological traits, and allometric regressions with elytra area for (a) *Notonomus resplendens* and (b) *Eurylychnus blagravei.*

(a) *Notonomus resplendens*

	Trait statistics (mm)				Allometry		
Trait(Y)	Min	Max	Mean	SE	R^2	a (SE)	b (SE)
Elytra width	3.60	5.26	4.45	0.013	0.88	-0.59 (0.04)	0.54 (0.01)
Femur length	4.22	6.77	5.55	0.022	0.19	0.38 (0.14)	0.34 (0.04)
Trochanter length	1.73	3.78	2.94	0.014	0.22	-0.65 (0.18)	0.44 (0.04)
Inter-ocular width	1.82	3.01	2.57	0.010	0.35	-2.06 (0.14)	0.51 (0.04)
Last sternite	1.16	3.39	1.95	0.012	0.10	-0.87 (0.23)	0.39 (0.06)

Allometric equation: $\log_{10}(Y) = a + b \log_{10}(\text{elytra area})$

(b) *Eurylychnus blagravei*

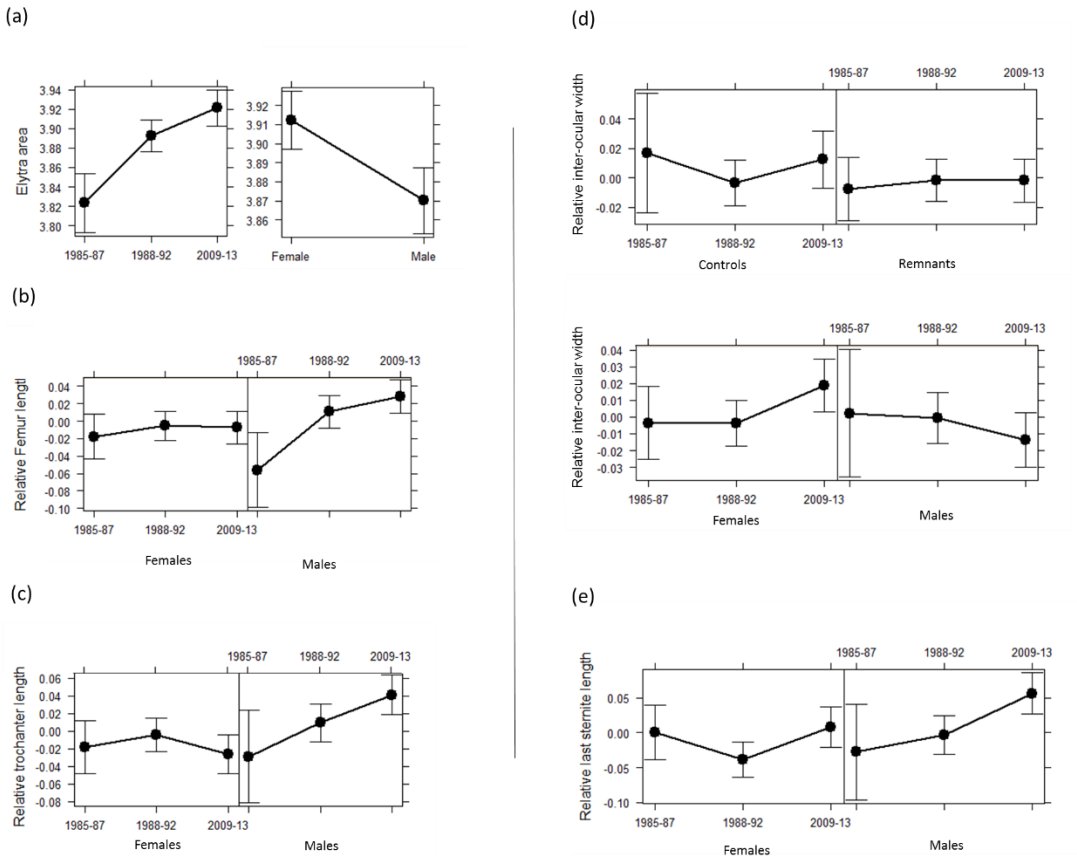
	Trait statistics (mm)				Allometry		
Trait(Y)	Min	Max	Mean	SE	R^2	a (SE)	b (SE)
Elytra width	5.90	7.31	6.61	0.017	0.87	-0.20 (0.05)	0.49 (0.01)
Femur length	3.30	4.84	4.17	0.019	0.16	-0.21 (0.23)	0.39 (0.06)
Trochanter length	1.50	2.80	2.01	0.012	0.18	-1.55 (0.29)	0.53 (0.07)
Inter-ocular width	2.61	3.70	3.22	0.012	0.42	-1.10 (0.16)	0.54 (0.04)

Allometric equation: $\log_{10}(Y) = a + b \log_{10}(\text{elytra area})$

Table 5. Table showing top ranked models (ΔAICc<2) testing for responses of morphological variables of *Notonomus resplendens* to the effects of year block (Y), main treatment of remnants (F), topography (T), sex (Sex), remnant size (S) and edge (E) and a selection of their interactions. Predictor variables that did not appear in the top ranked models are not included in the table (e.g. size). df = degrees of freedom, loglik = log likelihood, AICc = Akaike's information criterion adjusted for small sample size score, ΔAICc = difference between model and top ranked AICc scores, (Int) = model intercept coefficient, '✓' = factor included in model.

Trait	df	AICc	ΔAICc	(Int)	Y	F	T	Sex	Y:F	Y:Sex	T:Sex
Elytra area	6	-540.7	0.00	3.84	✓			✓			
Elytra width	6	-1508.0	0.00	-0.011	✓			✓			
	9	-1507.8	0.18	0.002	✓	✓		✓	✓		
	8	-1507.1	0.88	-0.009			✓	✓			✓
	5	-1507.0	0.99	-0.010	✓						
	11	-1506.3	1.64	0.003	✓	✓	✓	✓	✓		✓
	8	-1506.3	1.70	0.003	✓	✓			✓		
	9	-1506.0	1.98	-0.01	✓	✓	✓	✓			✓
Femur length	8	-730.1	0.00	-0.018	✓			✓		✓	
Trochanter length	8	-622.4	0.00	-0.020	✓			✓		✓	
	4	-620.5	1.96	-0.018				✓			
Inter-ocular width	3	-809.5	0.00	0.003							
	6	-809.5	0.06	0.003		✓				✓	
	7	-807.7	1.87	0.006		✓			✓	✓	
Last sternite	6	-461.6	0.00	-0.019	✓			✓			
	8	-460.3	1.33	-0.004	✓			✓		✓	

Figure 3. Responses of *Notonomus resplendens* morphology to year block using the pre-fragmentation data. Only those factors that were present in the best fit models are shown. Bars represent 95% confidence intervals.



Model set #2: Temporal changes in remnants, controls and plantation

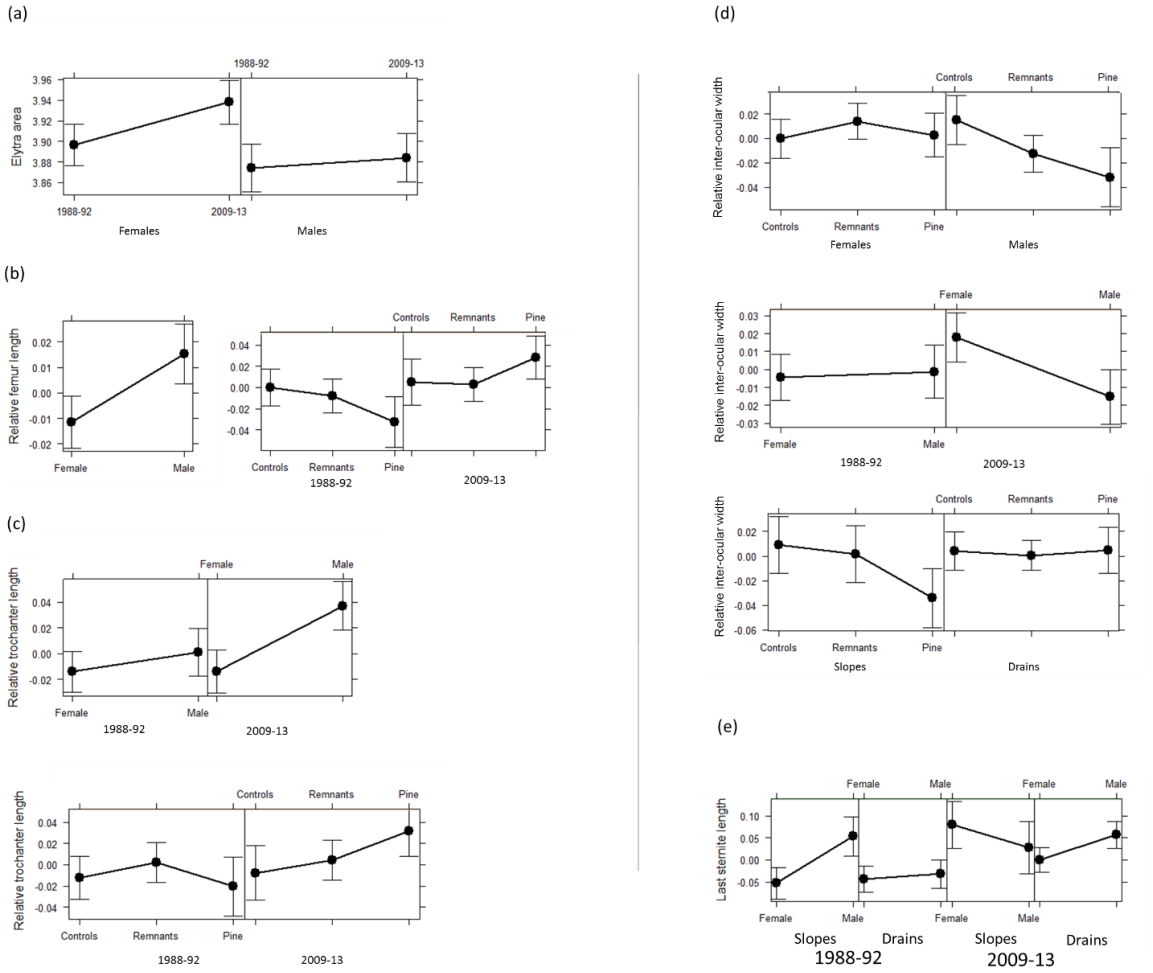
In parallel with the pattern revealed in the first set of models, *Notonomus resplendens* became larger from 1988-92 to 2009-13, however, this relationship was revealed to be the response of females only (Table 6, Figure 4 (a)). Relative trochanter length diverged across the main treatments over the long-term among the sexes, with males developing longer trochanters than females by 2009-13 (Figure 4(c)).

Male relative inter-ocular width was different across the main treatments with males having narrower inter-ocular width in the pines than the controls (Figure 4 (d)). Males also had reduced inter-ocular width when compared with females in 2009-13 (Figure 4(d)). Relative inter-ocular width also showed a response to the interaction of the main treatments and topography, however, the factor levels were shown not to be significantly different (Figure 4(d)). The last sternite length varied between sex and the interacting treatments of topography and year group (Figure 4(e)). A close inspection of the resultant plot of these interactions reveals that the significant variation was between sex and year group, rather than topography.

Table 6. Table showing top ranked models (ΔAICc<2) testing for responses of morphological variables of *Notonomus resplendens* to the effects of fragmentation including the pine plantation sites (F), year block (Y) and topography (T) and a selection of their interactions. Predictors including interactions that did not appear in the top ranked models are not included in the table. df = degrees of freedom, loglik = log likelihood, AICc = Akaike's information criterion adjusted for small sample size score, ΔAICc = difference between model and top ranked AICc scores, (Int) = model intercept coefficient, '✓' = factor included in model.

Trait	df	AICc	ΔAICc	(Int)	Y	F	T	Sex	Y:F	T:Sex	F:Sex	Y:Sex	F:T	Y:T	Y:T:Sex
Elytra area	6	-609.1	0.00	3.90	✓			✓				✓			
	5	-609.0	0.12	3.90	✓			✓							
Elytra width	7	-1684.7	0.00	-0.005	✓	✓		✓							
	6	-1684.3	0.46	-0.004	✓	✓									
	5	-1684.2	0.54	-0.006				✓							
	6	-1683.8	0.98	-0.008	✓		✓	✓							
	7	-1683.3	1.41	-0.005	✓	✓	✓								
	4	-1683.1	1.62	-0.005	✓										
	9	-1683.1	1.65	-0.005	✓	✓		✓			✓				
	9	-1683.1	1.67	-0.005	✓	✓	✓	✓		✓					
	7	-1683.0	1.75	-0.007	✓		✓	✓		✓					
	5	-1682.8	1.91	-0.007	✓		✓								
Femur length	9	-839.0	0.00	-0.010	✓	✓		✓	✓						
Trochanter length	10	-734.8	0.00	-0.015	✓	✓		✓	✓			✓			
	6	-733.1	1.68	-0.011	✓			✓				✓			
Inter-ocular width	13	-880.6	0.00	-0.003	✓	✓	✓	✓			✓	✓	✓		
	10	-878.9	1.68	-0.010	✓	✓		✓			✓	✓			
Last sternite	10	-514.5	0.00	-0.052	✓		✓	✓		✓		✓		✓	✓

Figure 4. Responses of *Notonomus resplendens* morphology to year block using the data including the pine plantation sites. Only those factors that were present in the best fit models are shown. Bars represent 95% confidence intervals.



Eurylychnus blagravei

Model set #1: Temporal changes in the remnants and controls

Eurylychnus blagravei showed a strong morphological change over time (Tables 7 and 8). In contrast to *Notonomus resplendens*, *Eurylychnus blagravei* became smaller over the course of the experiment (Figure 5(a)). However, in common with *Notonomus resplendens*, *Eurylychnus blagravei* showed an increase in relative femur length including an increase in the controls and not the remnants over the time of the experiment (Figure 5(b)). *Eurylychnus blagravei's* relative trochanter length, however, decreased over the time of the experiment (Figure 5(c)), in contrast to *Notonomus resplendens. Eurylychnus blagravei's* relative inter-ocular width did not change significantly (Figure 5(d)). *Eurylychnus blagravei* did not respond morphologically to the nested treatments of remnant size and edge. *Eurylychnus blagravei* showed an increase in relative femur length in the slopes over the time of the experiment; a pattern that was not reflected in the drains, where relative femur length remained unchanged (Figure 5(b)).

Model set #2: Temporal changes in remnants, controls and plantation

Eurylychnus blagravei varied in overall size between the main treatments, however, any variation was not significant (Figure 6(a)). *Eurylychnus blagravei's* femur length increased from 1988-92 to 2009-13 (Figure 6(b)), but was accompanied by a decrease in trochanter length, as in the first set of models for this species (Figure 6(c)). In all models for *Eurylychnus blagravei,* the fact that we were unable to determine this species' sex may have meant that we masked some of the effects to the treatments.

Table 7. Table showing top ranked models (ΔAICc<2) testing for responses of morphological variables of *Eurylychnus blagravei* to the effects of fragmentation, year block (Y), topography (T), remnant size (S), edge (E) and a selection of their interactions. Predictor variables that did not appear in the top ranked models are not included in the table (e.g. size, edge). df = degrees of freedom, loglik = log likelihood, AICc = Akaike's information criterion adjusted for small sample size score, ΔAICc = difference of AICc score between model and top ranked AICc scores, (Int) = model intercept coefficient, '✓' = factor included in model.

Trait	df	AICc	ΔAICc	(Int)	Y	F	T	Y:F	Y:T	F:T
Elytra area	5	-481.9	0.76	4.33	✓					
Elytra width	3	-1203.0	0.00	0.00						
Femur length	9	-536.4	0.00	-0.10	✓	✓	✓	✓		
	8	-536.0	0.32	-0.10	✓	✓		✓		
	5	-536.0	0.34	-0.03	✓					
	8	-535.8	0.56	-0.10	✓		✓		✓	
	6	-534.9	0.58	-0.02	✓		✓			
	11	-534.9	1.48	-0.09	✓	✓	✓	✓		✓
Trochanter length	5	-466.6	0.00	0.04	✓					
	8	-466.1	0.48	0.01	✓	✓	✓			✓
Inter-ocular width	5	-707.7	0.00	0.03	✓					
	8	-705.8	1.94	0.06	✓	✓		✓		

Figure 5. Responses of *Eurylychnus blagravei* morphology to year block using the fragmentation only data. Only those factors that were present in the best fit models and with factor levels are shown. Bars represent 95% confidence intervals.

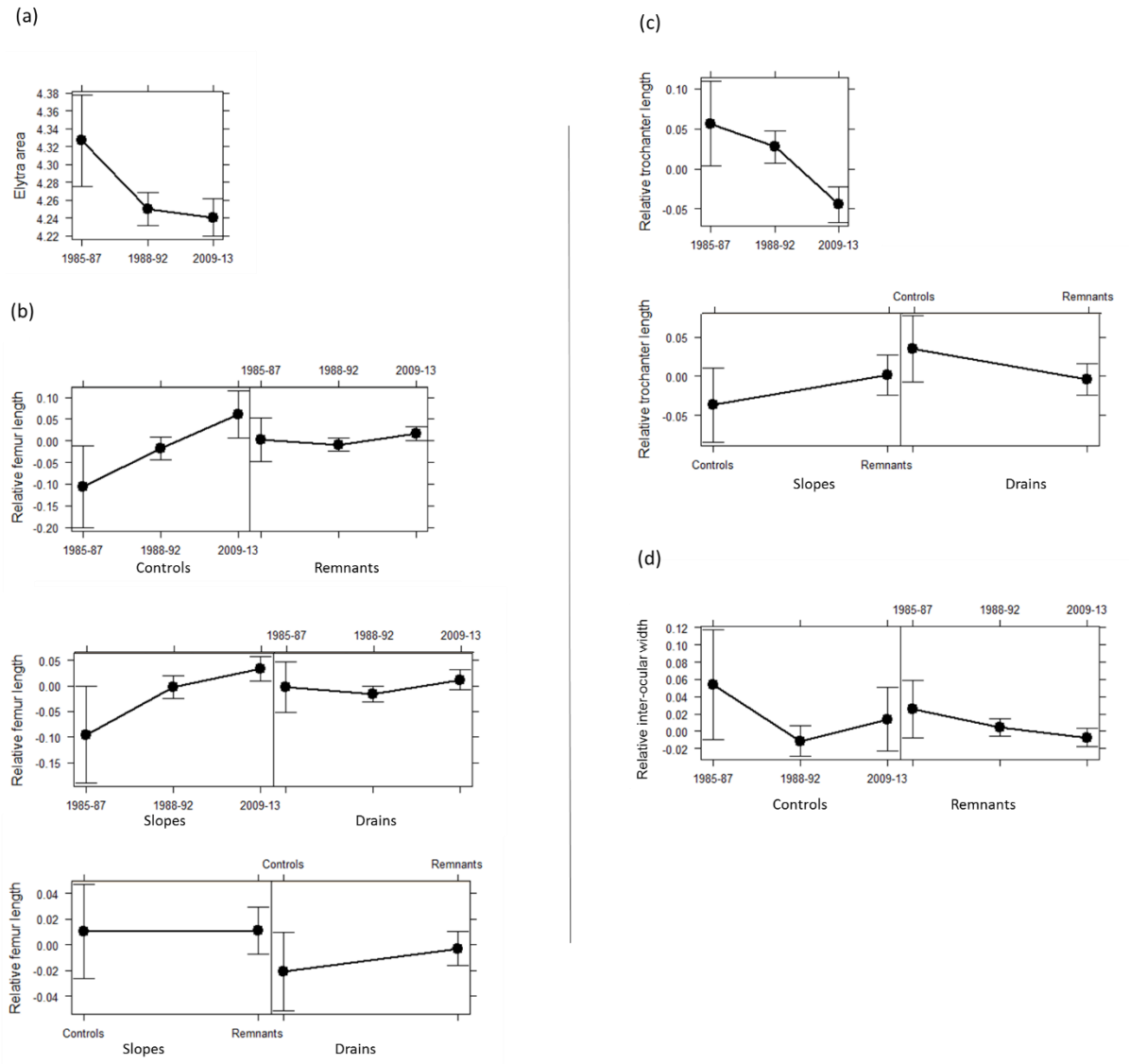
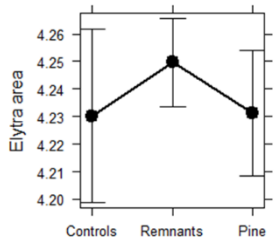


Table 8. Table showing top ranked models (ΔAICc<2) testing for responses of morphological variables of *Eurylychnus blagravei* to the effects of fragmentation including the pine plantation sites (F), year block (Y) and topography (T) and their interactions. Predictors that did not appear in the top ranked models are not included in the table. df = degrees of freedom, loglik = log likelihood, AICc = Akaike's information criterion adjusted for small sample size score, ΔAICc = difference between model and top ranked AICc scores, (Int) = model intercept coefficient, '✓' = factor included in model.

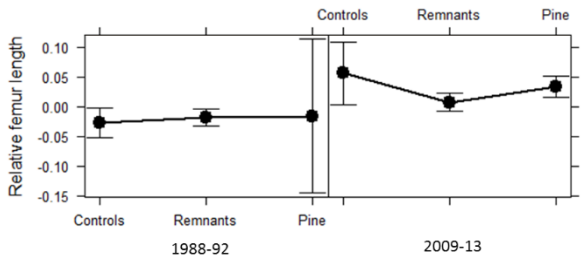
Trait	df	AICc	ΔAICc	(Int)	Y	F	T	Y:F	F:T
Elytra area	3	-585.2	0.00	4.24					
	5	-583.6	1.60	4.23		✓			
Elytra width (relative)	3	-1430.0	0.00	0.00					
	5	-1428.0	2.00	0.00	✓		✓		
Femur length (relative)	4	-654.5	0.00	-0.02	✓				
	6	-654.0	0.49	-0.02	✓	✓			
	7	-653.3	1.17	-0.01	✓	✓			
	8	-653.2	1.24	-0.03	✓	✓		✓	
	9	-652.6	1.93	0.01	✓	✓	✓		✓
Trochanter length (relative)	4	-549.0	0.00	0.03	✓				
	6	-548.2	0.78	0.02	✓	✓			
Inter-ocular width (relative)	3	-816.2	0.00	0.00					

Figure 6. Responses of *Eurylychnus blagravei* morphology to year block using the data including the pine plantation sites. Only those factors that were present in the best fit models are shown. Bars represent 95% confidence intervals.

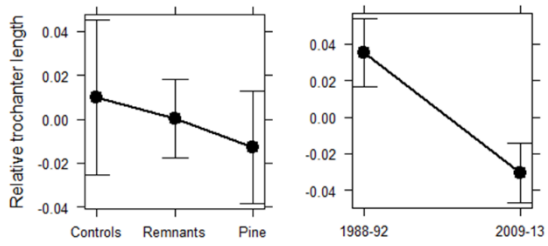
(a)



(b)



(c)



Discussion

New habitat promotes dispersal related traits

The most compelling morphological responses were those of *Notonomus resplendens*, which showed an increase in relative leg length in the mature pine plantation compared with the remnant or control sites. This change could indicate that it has responded by increasing its dispersal ability in this new habitat. One proposed mechanism for such a response in fragmented habitat is that there is selection for individuals with greater dispersal capability that can access fragmented patches of habitat (Desrochers 2010). However, these species become increasingly common in the pine plantation over time. Many animals, including carabids, exhibit promotion of dispersal related traits at an invasion front (Anholt 1990; Heidinger *et al.* 2010; Laparie *et al.* 2013). The individuals that move into the plantation as it becomes more amenable for carabids during the timescale of the experiment might be considered invaders and dispersal related traits such as leg length, could be promoted as a result. Another aspect of the pine plantation that could be selecting for dispersal related traits is its floor structure. The pine plantation floor is a much less complex environment when compared with the eucalypt forest floor. In ants, a decrease in leg length is associated with a more complex habitat (Parr *et al.* 2003; Farji-Brener *et al.* 2004; Sarty *et al.* 2006; Gibb and Parr 2010; Wiescher *et al.* 2012). If this were the case with carabids, then we might expect that a simpler habitat structure, such as the pine forest floor, would drive and increase in leg length.

Additional habitat drives a sexually dimorphic response

Extra clues to the mechanisms behind the leg length response might be revealed by the clear sexually dimorphic response of *Notonomus resplendens* which suggests that this species might exhibit sex-biased dispersal (Pusey 1987); as used by some beetles (Dubois *et al.* 2010;

Tanahashi 2014), including carabids (Lagisz *et al.* 2010). Many species exhibit sex-biased morphological changes related to dispersal (Travis and Dytham 2002; Heidinger *et al.* 2010; Laparie *et al.* 2013) with changes in dispersal ability often offset by lower reproductive rates, thought to be related to size (Crawley 1989). Our results have demonstrated that the addition of the pine habitat has driven divergence in movement related traits among the sexes. This could mean that females might respond less to selection pressures for increased dispersal as a necessity in order to invest in reproduction.

Male-biased dispersal could have long term consequences for species in the modified landscape at Wog Wog. If species with sex biased dispersal find the plantation marginal (which is possible, particular at early stages in the plantation rotation), it might experience a loss of genetic diversity and genetic adaptive potential (Hebert and Luiker 1996; Lagisz *et al.* 2010). This would in turn threaten its viability in the landscape over the long term, particularly in the face of more environmental disturbances throughout the plantation's harvesting cycle. Future population work at Wog Wog and studies like it, might benefit from determination of both species and sex (if reasonably possible). Populations with differences found in sex ratios according to treatments might highlight not only sex-biased dispersal but also sink habitat in the landscape; which would alter interpretations on the viability of the plantation as habitat for the species studied.

Along with the sexually-dimorphic response to the treatments evident for *Notonomus resplendens*, there was also broad-scale sexually-dimorphic size response for this species. In agreement with previous studies of carabids (Laparie *et al.* 2010), we found that females of *Notonomus resplendens* were significantly larger than males over all treatments. This is thought to be a reflection of the resource requirements of females being greater than males as a result of higher energetic cost of reproduction (Atchley 1971; Fairbairn 1997; Laparie *et al.*

2010). We also found that females of *Notonomus resplendens* had increased inter-ocular width than males by 2009-13. A larger head width can be related to the ability to consume larger food items (Pearson and Stemberger 1980; Laparie *et al.* 2010). Because food is a major part of the resources used for reproduction in arthropods (Juliano 1985; Sota 1985), this could indicate that females, under pressure from a novel environment, i.e. the plantation, have adapted to different food resources to be able to invest in reproduction. However, we also found that males of this species had significantly smaller inter-ocular width in the plantation than the controls, whereas females did not demonstrate any response of this measure to the main treatments. Nevertheless, this pattern could still indicate a response in the face of changing resources, with males responding to smaller food sources, but females mitigating this response by eating a wider size range of food resources in order to consume more energy for reproduction.

Contrasting dispersal responses between species

It is unclear whether there was any response related to dispersal for *Eurylychnus blagravei*. This species was smaller, regardless of treatment, had very little change in femur length, but showed an overall reduction in trochanter length from pre-fragmentation to the long-term after fragmentation. This species' population response (Paper III) indicated that the mature plantation constituted new habitat, but in the years during its establishment following fragmentation, was unsuitable. Therefore, *Eurylychnus blagravei* has either not experienced selection for increased dispersal ability in the plantation, or any changes have yet manifested because it only began to increase in the plantation more recently than *Notonomus resplendens.*

Resource constraints possibly leading to cannibalism

The resource constraints imposed on *Eurylychnus blagravei* could result in cannibalism, something that carabids adopt in the face of resource pressures (Currie *et al.* 1996; Laparie *et al.* 2010). Adults cannibalise the larval stage, with smaller individuals possibly being less prone to cannibalistic predation than larger individuals (Laparie *et al.* 2010), simply as a result of the reduced time it takes them to develop from the larval to the adult stages (Blanckenhorn 1998). Thus, cannibalism could drive *Eurylychnus blagravei's* reduction in size over the time of the experiment as a result of this species' resource constraints which include is comparatively poor ability to move and increase its interactions with prey.

The differing response of the study species' trochanter length could imply they have different dispersal strategies. The size and shape of carabid metatrochanters relates to how species move: longer metatrochanters are thought to be related to running and further dispersal, whereas shorter and fatter metatrochanters are thought to relate to wedge-pushing whilst burrowing (Evans and Forsythe 1984). If this mechanism is the cause of the contrasting metatrochanter size changes, then this might possibly indicate that *Notonomus resplendens* moves through the landscape more quickly than *Eurylychnus blagravei.* In turn, this could suggest that *Notonomus resplendens* is able to colonise new habitat more quickly than *Eurylychnus blagravei,* which would correspond with the population responses detailed earlier and also suggest a reason why morphological changes related to dispersal are apparent in *Notonomus resplendens* and not in *Eurylychnus blagravei.*

Morphological responses, regardless of treatment

We found that both species exhibited morphological changes over time, regardless of the landscape treatments. A possible reason for these morphological changes, is that the landscape as a whole has had significant impacts on these species. The scale at which

environmental disturbance has effects on species is now known to be much greater than first thought (Ewers and Didham 2008; Berges *et al.* 2013; Bennett *et al.* 2014). More specifically, for beetles, Ewers and Didham (2008) have shown that impacts of landscape change can reach distances of up to 1km or possibly more beyond the scale of disturbance. At Wog Wog, the distances between the controls and remnants and matrix sites ranges from 700 m to 3 km, meaning that such large scale landscape effects are possible and could be influencing the carabids in the control sites. The pine matrix might be effecting change in the controls via mechanisms such as those induced by novel predation (Suarez *et al.* 1997; McGeoch and Gaston 2000; Lahti 2001; Ries and Fagan 2003; Leighton *et al.* 2008) and parasitism (McGeoch and Gaston 2000; Cronin 2003).

Conclusions

Carabid species express morphological variation over short time scales in response to landscape change. The landscape presented at the mature stage of the pine plantation selects for individuals of *Notonomus resplendens* with increased dispersal ability which is exhibited as an increase of overall size and leg length. Furthermore, the plantation seems to have driven divergence in dispersal ability between the sexes, probably as a result of the need for reproduction in females offsetting the selection pressures for increased traits related to movement. The direct contrast in size and trochanter length changes shown for both species suggests that the two species might adopt differing dispersal strategies. *Notonomus resplendens* might be able to disperse further than *Eurylychnus blagravei* resulting in *E. blagravei* perhaps experiencing comparatively more resource constraints, which in turn could result in a reduction in size. Evidence that tests the dispersal strategies of these species using tracking studies (Ranius and Hedin 2001; Hedin and Ranius 2002; Ranius 2006) or population genetics (Brouat *et al.* 2003; Matern *et al.* 2008) would improve our

understanding of why these species respond to habitat change with differing population and morphological responses.

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Paper I supplementary materials

Table S1. Summary of beetles caught.

Beetle Family	No. Species	No. individuals	*Eucalyptus* Richness	*Eucalyptus* Abundance	Pine Richness	Pine Abundance
Anthicidae	5	30	5	26	3	4
Bostrichidae	1	2	1	2	0	0
Brentidae	1	1	1	1	0	0
Byrrhidae	1	1	1	1	0	0
Cantharidae	1	2	1	2	0	0
Carabidae	16	225	12	83	12	142
Cerambycidae	3	5	0	0	3	5
Chrysomelidae	3	4	3	4	0	0
Cleridae	2	2	1	1	1	1
Coccinellidae	1	3	1	2	1	1
Corylophidae	7	21	6	9	3	12
Cryptophagidae	1	3	1	3	0	0
Curculionidae	20	111	15	22	14	89
Elateridae	3	7	2	4	2	3
Endomychidae	1	1	1	1	0	0
Histeridae	5	6	5	6	0	0
Hydraenidae	1	1	1	1	0	0
Laemophloeidae	2	12	2	4	1	8
Latridiidae	6	108	5	62	5	46
Leiodidae	15	76	10	50	10	26
Lucanidae	1	1	1	1	0	0
Melandryidae	1	1	1	1	1	1
Melyridae	1	1	0	0	0	0
Mordellidae	2	2	1	1	1	1
Mycetophagidae	1	1	0	0	1	1
Myraboliidae	1	1	1	1	0	0
Nitidulidae	6	1196	6	720	4	476
Oedemeridae	1	16	1	15	1	1
Passalidae	1	1	0	0	1	1
Phalacridae	2	2	1	1	1	1
Ptiliidae	2	24	2	14	1	10
Ptinidae	6	18	6	6	1	12
Salpingidae	1	1	0	0	1	1
Scarabaeidae	6	14	5	9	3	5
Silvanidae	4	18	3	16	2	2
Staphylinidae	98	3409	81	2000	66	1409
Tenebrionidae	8	65	4	50	7	15
Zopheridae	1	1	1	1	0	0
Grand Total	238	5393	188	3120	146	2273

Table S2. Table showing number of species in each trait group.

Trait group	n
Saproxylic	28
Mycetophagous	45
Predatory	116
Xylophagous	27
Phytophagous	16
Myrmecophagous	6
Flying	204
Flightless	34

Table S3. Results of model selection procedure for species responses to the edge, slope, altitude, block and the autocovariate. Competing models appear below the top ranked model.'✓' = term is included in model. Df = degrees of freedom. LogLik = Log likelihood. Int = Intercept. Alt = Altitude. Ac = Autocovariate. A_n = Calculated neighbourhood distance.

Response variable	n	Model selection scores				Linear coefficients				A_n	Smooth	
		AICc	ΔAICc	Df	LogLik	Int	Alt	Slope	Ac		Edge	
Anotylus cribriceps	2265	1086.79	0.00	8.99	-533.75	5.34	-0.01	-0.05	0.33	125.89	✓	COL065
		1090.01	3.22	5.00	-539.80	5.70	-0.01	-0.05	0.52			
Thalycrodes pulchrum	926	841.05	0.00	11.36	-408.13	-2.49	0.01	-0.01	-0.01	756.46	✓	COL090
		853.52	12.47	5.00	-421.55	-0.17	0.00	0.00	0.75			
Aleochara sp.	468	618.00	0.00	11.86	-296.01	4.28	-0.01	0.01	0.13	130.14	✓	COL041
		645.04	27.04	7.11	-314.99	-8.48	0.02	0.02	0.36			
Aleocharinae (#1) (undescribed species)	224	474.78	0.00	7.40	-229.54	6.05	-0.01	-0.09	0.26	490.07		COL058
		476.54	1.76	11.64	-225.54	3.24	-0.01	-0.08	-0.01		✓	
Aridius minor	74	265.80	0.00	10.75	-121.23	-7.51	0.01	0.05	1.53	159.10	✓	COL095
		266.34	0.54	6.00	-126.87	-5.15	0.01	0.03	1.87			
Thalycrodes australe	256	531.64	0.00	8.00	-258.31	4.08	-0.01	-0.01	NA	0	✓	COL244
		533.64	2.00	4.00	-261.68	4.62	-0.01	-0.02	NA			
Aleocharinae (#2) (undescribed species)	59	232.19	0.00	10.0	-105.29	0.15	0.00	-0.15	-0.35	136.20	✓	COL054
		237.06	4.84	6.00	-112.23	-3.28	0.01	-0.18	-0.21			
Notonomus resplendens	56	196.27	0.00	6.00	-91.84	-6.36	0.01	0.05	2.88	636.03		COL272
		200.61	4.34	10.00	-89.50	-10.09	0.02	0.06	2.58		✓	
Eurylychnus blagravei	55	194.59	0.00	9.00	-87.64	-3.12	0.00	0.06	0.71	82.64	✓	COL326

		210.76	16.17	5.00	-100.17	2.38	-0.01	0.07	2.12			
Colenisia sp.	49	224.69	0.00	8.16	-103.64	-7.33	0.02	-0.03	NA	0.00	✓	COL025
		226.50	1.81	4.48	-108.60	-5.76	0.01	-0.04	NA			
Promecoderus sp.	42	185.68	0.00	9.00	-83.19	-21.02	0.05	-0.02	-2.48	179.05	✓	COL327
		202.41	16.73	5.00	-95.99	-4.92	0.05	0.05	0.67			
Ecnolagria sp.	40	164.85	0.00	5.00	-77.21	-2.27	0.00	0.03	2.81	119.26		COL105
		165.56	0.71	9.00	-73.13	4.53	-0.02	0.04	1.78		✓	
Cryptorhynchini (undescribed species)	39	125.44	0.00	9.00	-53.07	-0.27	0.00	-0.18	3.02	115.44	✓	COL125
		126.57	1.13	7.44	-55.39	22.73	-0.07	-0.06	4.38			
Calodera sp.	28	126.12	0.00	5.00	-57.85	-7.33	0.01	-0.06	2.25	75.94		B204
		138.99	12.87	9.00	-59.85	1.23	-0.03	-0.04	2.14		✓	
Sepedophilus sp.	22	137.79	0.00	5.00	-63.68	3.29	-0.01	0.00	0.69	91.16		COL140
		142.32	4.53	9.00	-61.51	0.75	-0.01	0.00	0.37		✓	
Acrotrichis sp.	22	131.84	0.00	5.00	-60.71	1.10	-0.01	0.01	1.42	73.31		COL570
		135.66	3.82	9.00	-58.18	7.27	-0.03	0.03	1.19		✓	
Prosopogmus oodiformis	21	134.19	0.00	4	-62.96	-5.31	0.01	-0.02	NA	0.00		COL343
		137.73	3.54	8.00	-60.35	-1.79	0.00	-0.02	NA		✓	
Aridius semicostatus	20	76.12	0.00	9.00	--28.41	-40.60	0.09	0.25	-0.37	202.53	✓	COL284
		79.54	3.42	5.00	-34.56	-16.55	0.03	0.35	2.97			
Prosopogmus sp.	16	112.44	0.00	4.00	-52.08	-0.54	0.00	-0.05	NA	0.00		COL339

		115.03	2.59	8.00	-49.00	-2.24	0.00	-0.03	NA		✓	
Oedemeridae	16	85.45	0.00	9.00	-42.59	-3.82	0.00	0.05	4.36	87.93	✓	COL507
		88.57	3.12	5.00	-39.08	3.58	-0.02	0.05	5.13			
Falagria sp.	14	90.05	0.00	11.66	-32.28	-15.49	0.03	-0.02	-6.41	526.33	✓	COL043
		94.92	4.87	7.52	-39.48	-13.24	0.03	-0.08	-5.34			

Table S4. Habitat PCA variables as responses modelled against the edge gradient. .'✓' = term is included in model. Df = degrees of freedom.
LogLik = Log likelihood. Int = Intercept.

Environmental variable					Terms	
	AICc	ΔAICc	Df	LogLik	Int.	Edge
PCA1 (Edge)	526.79	0.00	6	-257.10	0.05	✓
PCA1 (Null)	558.27	31.48	2	-277.10	2.29e-16	
PCA2 (Edge)	492.74	0.00	6	-240.07	-0.07	✓
PCA2 (Null)	508.03	15.29	2	-251.97	1.21e-16	
PCA3 (Edge)	470.03	0.00	6	-228.72	-0.02	✓
PCA3 (Null)	479.03	9.00	2	-237.47	-1.54e-16	
PCA4 (Edge)	434.40	1.12	6	-210.90	-0.04	✓
PCA4 (Null)	435.52	0.00	2	-215.72	2.47e-16	
PCA5 (Edge)	426.04	1.74	6	-206.73	-0.04	✓
PCA5 (Null)	424.30	0.00	2	-210.11	-1.28e-16	

Table S5. Results of model selection procedure for individual species to the edge, slope and altitude and environmental PCA components. Competing models appear below the top ranked model. Refer to Figure 3 for interpretation of the PCA components. '✓' = term is included in model. Df = degrees of freedom. LogLik = Log likelihood. Int = Intercept. Alt = Altitude. Ac = Autocovariate.

Response variable	Model scores				Linear coefficients				Environmental coefficients					Smooth
	AICc	ΔAICc	Df	logLik	Int	Alt	Slope	Ac	PCA1	PCA2	PCA3	PCA4	PCA5	Edge
Anotylus cribriceps	1083.74	0.00	10.00	-531.07	5.47	-0.01	-0.04	0.32		0.14				✓
Thalycrodes pulchrum	833.41	0.00	11.00	-404.74	-1.20	0.01	-0.01	0.15	-0.19	-0.10				✓
	834.11	0.70	10.00	-406.25	-1.24	0.01	-0.01	0.27	-0.20					✓
Aleochara sp.	611.54	0.00	13.83	-290.40	0.68	0.00	0.01	0.20		0.15	0.17			✓
Aleocharinae (#1)	471.40	0.00	8.55	-226.55	7.34	-0.02	-0.09	0.00			0.22			
	472.40	1.00	9.66	-222.13	4.02	-0.01	-0.09	-0.37			0.23			✓
Aridius minor	255.88	0.00	11.00	-115.97	-9.83	0.02	0.06	1.02	-0.42	-0.36				✓
	257.33	1.45	13.00	-114.31	-9.78	0.02	0.06	1.06	-0.48	-0.36	-0.20	0.27		✓
Thalycrodes australe	528.49	0.00	5.00	-259.03	3.88	-0.01	-0.03	NA	-0.19					
Aleocharinae (#2)	232.19	0.00	9.00	-105.29	0.15	0.00	-0.15	-0.35						✓
Eurylychnus blagravei	194.59	0.00	9.00	-87.64	-3.12	0.00	0.06	0.71						✓
	196.53	1.94	10.00	-85.52	2.15	-0.01	0.05	1.99			-0.19	-0.15	-0.20	
Colenisia sp.	220.15	0.00	7.00	-102.66	-5.19	0.01	-0.04	NA	-0.32			-0.65	0.29	
	220.85	0.70	6.00	-104.13	-5.21	0.01	-0.04	NA	-0.33			-0.51		
	221.26	1.11	11.00	-98.66	-7.06	0.02	-0.02	NA	-0.32			-0.50	0.27	✓
	221.48	1.33	10.00	-99.93	-6.31	0.01	-0.03	NA	-0.31			-0.40		✓

	221.66	1.51	9.00	-101.18	-7.60	0.02	-0.03	NA	-0.31					✓
Promecoderus sp.	183.27	0.00	10.00	-80.83	-22.12	0.06	-0.02	-2.51		0.37				✓
Ecnolagria sp.	160.96	0.00	7.00	-73.08	-0.89	0.00	0.04	2.64	-0.24			0.43		
	161.19		6.00	-74.30	-1.42	0.00	0.04	2.81				0.35		
Cryptorhynchini	124.91	0.00	10.00	-51.65	-3.21	0.00	-0.18	3.08				0.68		✓
	125.44	0.00	9.00	-53.07	-0.27	0.00	-0.18	3.02						✓
Aridius semicostatus	73.82	0.00	10.00	-26.10	-37.12	0.08	0.28	-0.03				-1.64		✓
Oedemeridae	81.85	0.00	12.02	-27.75	-8.56	0.01	0.08	4.07	-0.95	0.57		0.85		✓
	82.16	0.31	13.65	-25.93	-9.70	0.01	0.07	2.22	-1.20			0.72		✓
	82.26	0.41	14.61	-24.80	-7.82	0.01	0.09	2.19	-1.24			0.96	0.33	✓
	83.06	1.21	12.64	-27.61	-9.63	0.01	0.06	2.48	-1.03					✓
Falagria sp.	90.05	0.00	11.66	-32.28	-15.49	0.03	-0.02	-6.41						✓
	92.03	1.98	10.46	-38.37	-18.23	0.04	-0.04	-5.02			0.05	-0.47	-0.28	

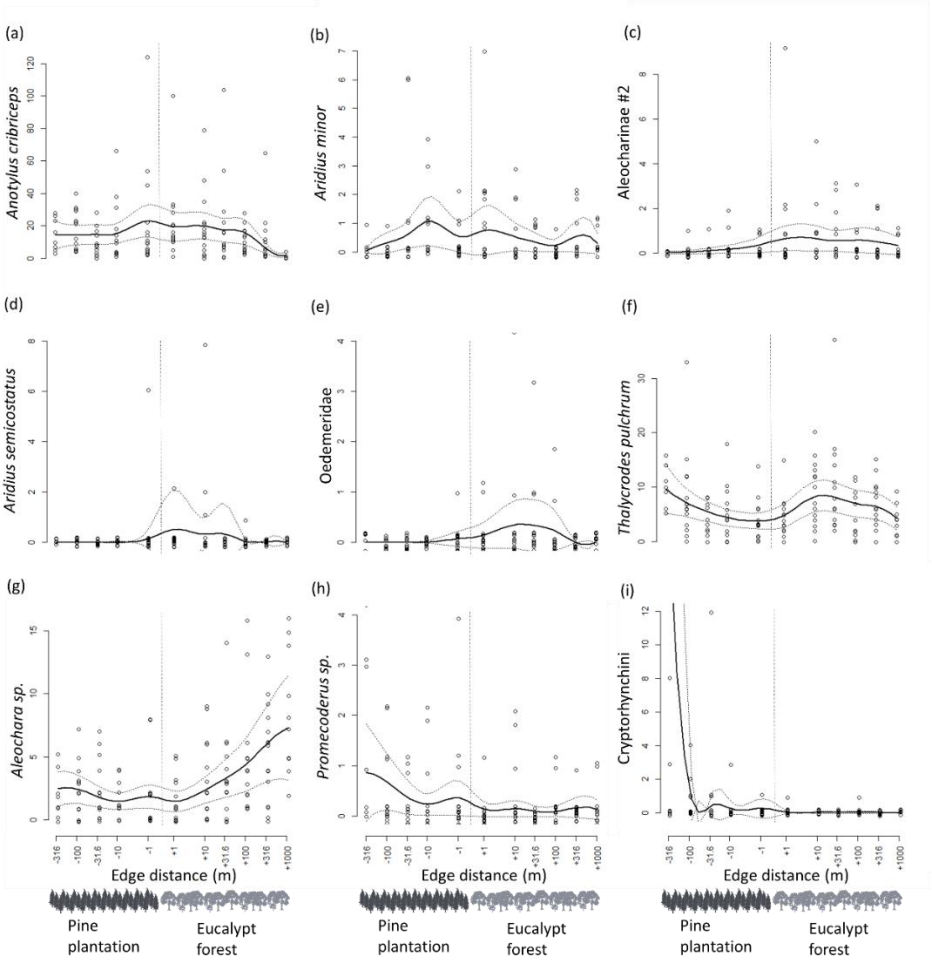
Table S6. Results of model selection procedure for trait group responses to the edge, slope and altitude. Competing models appear below the top ranked model. Refer to Figure 3 for interpretation of the PCA components. '✓' = term is included in model. Df = degrees of freedom. LogLik = Log likelihood. Int = Intercept. Alt = Altitude. Ac = Autocovariate. * denotes that models use the poisson distribution as opposed to the negative binomial distribution.

Response variable	Model selection scores				Linear coefficients				A_n	Smooth
	AICc	ΔAICc	Df	LogLik	Int	Alt	Slope	Ac		Edge
Xylophagous	270.33	0.00	6.00	-128.87	-2.47	0.00	0.04	0.72	229.52	
	272.76	2.43	10.00	-125.59	-4.14	0.01	0.04	0.47		✓
Predatory*	639.86	0.00	4.00	-315.79	-0.59	0.00	-0.01	0.69	748.55	
	645.92	6.06	8.00	-314.44	-0.66	0.00	-0.01	0.69		✓
Mycetophagous	535.47	0.00	5.00	-262.52	0.79	0.00	0.01	0.16	98.92	
	540.78	5.31	9.00	-260.74	1.66	0.00	0.01	0.13		✓
Phytophagous*	159.78	0.00	4.00	-75.75	-2.80	0.00	-0.07	0.21	138.64	
	160.95	1.17	8.00	-71.95	-2.70	0.00	-0.05	-0.78		✓
Saproxylic*	444.12	0.00	5.23	-216.60	0.63	0.00	-0.02	0.12	138.18	
	450.19	6.07	9.81	-214.51	1.47	-0.00	-0.02	0.03		✓
Flying	726.06	0.00	9.00	-353.38	1.89	0.00	-0.01	-0.05	88.75	✓
	733.44	7.38	5.00	-361.51	1.15	0.00	-0.01	-0.01		
Flightless	448.59	0.00	5.00	-219.09	-0.13	0.00	0.00	1.12	132.72	
	450.40	1.81	9.00	-215.55	-2.81	0.01	-0.01	0.77		✓

Table S7. Results of model selection procedure for trait group responses to the edge, slope, altitude, block, autocovariate and environmental PCA components. Competing models appear below the top ranked model.'✓' = term is included in model. Df = degrees of freedom. LogLik = Log likelihood. Int = Intercept. Alt = Altitude. Ac = Autocovariate. A_n = Calculated neighbourhood distance. * denotes that models use the poisson distribution as opposed to the negative binomial distribution.

Response variable	Model scores				Linear coefficients				Environmental coefficients					Smooth
	AICc	ΔAICc	Df	logLik	Int	Alt	Slope	Ac	PCA1	PCA2	PCA3	PCA4	PCA5	Edge
Phytophagous*	158.15	0.00	5.00	-73.86	-2.96	0.00	-0.06	-0.03		0.30				
	158.39	0.24	9.00	-69.54	-5.14	0.01	-0.04	-1.27		0.35				✓
	159.53	1.38	10.00	-68.58	-5.70	0.01	-0.04	-1.51		0.34	-0.27			✓
	159.77	1.62	4.00	-75.75	-2.80	0.00	-0.07	0.21						
	159.94	1.79	7.00	-72.57	-3.52	0.01	-0.06	-0.45	0.11	0.24	-0.21			
	160.02	1.87	5.00	-74.80	-3.47	0.01	-0.06	-0.14	0.16					
	160.12	1.97	5.00	-74.85	-3.06	0.00	-0.07	0.13			-0.23			
Flying	721.93	0.00	10.00	-350.16	1.82	0.00	-0.01	-0.05	-0.05					✓
Flightless	438.60	0.00	10.00	-208.50	-4.37	0.01	0.00	0.73		0.28				✓
	439.84	1.24	8.00	-211.49	1.78	-0.01	0.01	1.09		0.27				
	440.30	1.70	12.00	-206.99	-4.74	0.01	0.00	0.70	-0.10	0.35		-0.08		✓

Figure S1. Beetle species responses to the edge gradient based on the top ranked model including edge, altitude, slope, species specific autocovariate and random factor of block with the addition of the habitat covariates. Species responses that were explained by the habitat covariates are omitted. Each plot represents the GAM smooth component on the response scale. The x axis values were transformed (log(d+1)) for analysis. Dotted lines represent 95% confidence intervals. Dotted vertical lines represents the edge. Responses are jittered along the y-axis to avoid stacking of points.



Paper II supplementary materials

Table S1. Results of AICc model selection for main treatments of remnant, controls and plantation including those models deemed uncompetitive because of uninformative parameters. '✓' signifies that the effect is included in the ranked model. LogLik = log likelihood, df= degrees of freedom, Int= intercept, Tp =main treatment (remnants/controls/plantation), Topo=topography, Temp=temperature, Cloud=cloud cover, Wind=wind speed.

Response	AICc	ΔAICc	Wght	LogLik	df	Int	T_p	Topo	Temp	Cloud	Wind	Date	Time
Richness	1389.8	0.00	1.00	-684.69	10	-0.07	✓	✓	0.005	-0.002	-0.001	-0.004	0.005
Heteronympha merope	2361.8	0.00	0.62	-1172.78	8	-0.01		✓	0.012	0.000	-0.002	0.003	0.001
	2362.8	0.97	0.38	-1171.20	10	-0.46	✓	✓	0.012	0.000	-0.002	0.003	0.012
Geitoneura acantha	1267.9	0.00	0.54	-623.77	10	-2.03	✓	✓	0.024	-0.003	0.003	-0.006	-0.008
	1268.3	0.33	0.46	-624.97	9	-2.13	✓		0.024	-0.003	0.004	-0.006	-0.008

Table S2. Results of AICc model selection for main treatments of remnant and controls and nested treatments of edge, size and topography including those models deemed uncompetitive because of uninformative parameters. '✓' signifies that the effect is included in the ranked model. LogLik = log likelihood, df= degrees of freedom, Int= intercept, T_F=main treatment (remnants/controls) , T_F:E=interaction effect of treatment and edge, T_F:S=interaction effect of treatment and remnant size, Topo=topography, Temp=temperature, Cloud=cloud cover, Wind=wind speed.

Response	AICc	ΔAICc	Wght	LogLik	df	Int	T_F	T_F:E	Topo	Temp	Cloud	Wind	Date	Time
Richness	1018.0	0.00	1.00	-499.80	9	0.05	✓		✓	0.003	-0.005	-0.001	-0.005	0.001
Heteronympha merope	1688.5	0.00	0.35	-836.06	8	0.707			✓	-0.002	-0.002	-0.006	-0.001	0.003
	1688.5	0.02	0.34	-832.92	11	0.328	✓	✓	✓	-0.002	-0.002	-0.006	-0.002	0.003
	1688.6	0.19	0.31	-835.11	9	0.367	✓		✓	-0.002	-0.002	-0.006	-0.002	0.003
Geitoneura acantha	921.5	0.00	1.00	-451.55	9	-1.850	✓		✓	0.020	-0.002	0.004	-0.009	-0.009

Table S3. Results of AICc model selection for main treatments of remnant, controls and plantation with the added environmental PCA variables (PCA1-5) including those models deemed uncompetitive because of uninformative parameters. '✓' signifies that the effect is included in the ranked model. Wght = Model weight, LogLik = log likelihood, df= degrees of freedom, Int= intercept, Tp =main treatment (remnants/controls/plantation), Topo=topography, Temp=temperature, Cloud=cloud cover, Wind=wind speed. The previous top ranked model is highlighted in grey, unless it falls above ΔAICc = 2.

Response	AICc	ΔAICc	Wght	LogLik	df	Int	Tp	Topo	Temp	Cloud	Wind	Date	Time	PCA1	PCA2	PCA3	PCA4	PCA5
Richness	1389.1	0.00	0.21	-683.29	11	-0.047	✓	✓	0.004	-0.002	-0.001	-0.004	0.000	-0.077				
	1389.1	0.02	0.21	-683.30	11	-0.053	✓	✓	0.005	-0.002	-0.001	-0.004	0.000		-0.059			
	1389.3	0.26	0.18	-682.37	12	-0.040	✓	✓	0.004	-0.002	-0.001	-0.004	0.000	-0.063	-0.049			
	1389.8	0.73	0.15	-684.69	10	-0.068	✓	✓	0.005	-0.002	-0.001	-0.004	0.000					
	1390.8	1.74	0.09	-683.12	12	-0.061	✓	✓	0.005	-0.002	-0.001	-0.004	0.000		-0.057	0.024		
	1390.8	1.76	0.09	-683.13	12	-0.045	✓	✓	0.005	-0.002	-0.001	-0.004	0.000		-0.061			0.025
	1390.9	1.89	0.08	-683.19	12	-0.053	✓	✓	0.005	-0.002	-0.001	-0.004	0.000	-0.073		0.017		
Heteronympha merope	2349.8	0.00	0.42	-1163.64	11	-0.053		✓	0.012	0.000	-0.003	0.003	0.002	-0.082		-0.091		0.062
	2351.3	1.53	0.19	-1163.36	12	-0.061		✓	0.012	0.000	-0.003	0.003	0.002	-0.090		-0.091	0.023	0.062
	2351.3	1.53	0.19	-1165.45	10	-0.080		✓	0.012	0.000	-0.003	0.003	0.002	-0.087		-0.100		
	2351.3	1.54	0.19	-1163.36	12	-0.045		✓	0.012	0.000	-0.003	0.003	0.002	-0.079	-0.023	-0.088		0.066
Geitoneura acantha	1255.2	0.00	0.36	-614.27	13	-1.989	✓	✓	0.022	-0.003	0.002	-0.006	-0.008	-0.117	-0.147		-0.187	
	1256.0	0.81	0.24	-613.62	14	-2.011	✓	✓	0.023	-0.003	0.002	-0.006	-0.008	-0.120	-0.137		-0.198	-0.066
	1256.4	1.20	0.20	-615.92	12	-2.025	✓	✓	0.023	-0.003	0.002	-0.006	-0.008		-0.149		-0.199	
	1256.4	1.21	0.20	-613.82	14	-1.960	✓	✓	0.022	-0.004	0.001	-0.007	-0.008	-0.138	-0.160	-0.058	-0.201	

Table S4. Results of AICc model selection for main treatments of remnant and controls and nested treatments of edge, size and topography including the added environmental PCA variables (PCA1-5) including those models deemed uncompetitive because of uninformative parameters. '□' signifies that the effect is included in the ranked model. LogLik = log likelihood, df= degrees of freedom, Int= intercept, T_F=main treatment (remnants/controls) , T_F:E=interaction effect of treatment and edge, T_F:S=interaction effect of treatment and remnant size, Topo=topography, Temp=temperature, Cloud=cloud cover, Wind=wind speed. The previous top ranked models are highlighted in grey, unless they fall above ΔAICc = 2.

Response	AICc	ΔAICc	Wght	LogLik	df	Int	T_F	T_F:E	Topo	Temp	Cloud	Wind	Date	Time	PCA1	PCA2	PCA3	PCA4	PCA5
Richness	1018.0	0.00	0.18	-499.80	9	0.046	✓		✓	0.003	-0.002	-0.001	-0.005	0.001					
	1018.1	0.12	0.17	-498.81	10	0.036	✓		✓	0.003	-0.002	-0.001	-0.005	0.001		-0.065			
	1018.2	0.20	0.16	-498.85	10	0.015	✓		✓	0.004	-0.002	0.000	-0.005	0.001			0.075		
	1018.2	0.22	0.16	-497.80	11	0.006	✓		✓	0.004	-0.002	-0.001	-0.005	0.001		-0.066	0.077		
	1019.6	1.62	0.08	-499.56	10	0.055	✓		✓	0.003	-0.002	-0.001	-0.005	0.001	-0.039				
	1019.9	1.84	0.07	-498.61	11	0.024	✓		✓	0.004	-0.002	-0.001	-0.005	0.001	-0.039		0.074		
	1019.9	1.89	0.07	-499.69	10	0.039	✓		✓	0.004	-0.002	-0.001	-0.005	0.001				-0.020	
	1020.0	1.95	0.07	-498.67	11	0.044	✓		✓	0.003	-0.002	-0.001	-0.005	0.001	-0.030	-0.063			
	1020.0	1.96	0.07	-499.73	10	0.042	✓		✓	0.003	-0.002	-0.001	-0.005	0.001					-0.017
Heteronympha merope	1688.5	0.00	0.21	-836.06	8	0.707			✓	-0.002	-0.002	-0.006	-0.001	0.003					
	1688.5	0.02	0.20	-832.92	11	0.328	✓	✓	✓	-0.002	-0.002	-0.006	-0.002	0.003					
	1688.6	0.19	0.19	-835.11	9	0.367	✓		✓	-0.002	-0.002	-0.006	-0.002	0.003					
	1689.1	0.64	0.15	-834.28	10	0.365	✓		✓	-0.002	-0.002	-0.006	-0.002	0.003	-0.055				
	1689.3	0.83	0.14	-835.43	9	0.728			✓	-0.002	-0.002	-0.006	-0.002	0.003	-0.047				
	1689.5	1.02	0.12	-832.37	12	0.332	✓	✓	✓	-0.002	-0.002	-0.006	-0.002	0.003	-0.045				
Geitoneura acantha	910.2	0.00	0.28	-442.75	12	-1.934	✓		✓	0.021	-0.002	0.003	-0.008	-0.009		-0.171		-0.225	-0.094
	910.4	0.14	0.26	-443.87	11	-1.902	✓		✓	0.021	-0.002	0.003	-0.008	-0.009		-0.191		-0.207	
	910.4	0.14	0.26	-442.82	12	-1.879	✓		✓	0.020	-0.002	0.003	-0.009	-0.009	-0.113	-0.205		-0.193	
	910.8	0.54	0.21	-441.96	13	-1.909	✓		✓	0.021	-0.002	0.003	-0.008	-0.009	-0.100	-0.186		-0.212	-0.083

Figure S1. Predicted species richness (a), and two species' abundances (b & c) against slope using poisson generalised linear mixed models. Error bars represent standard errors.

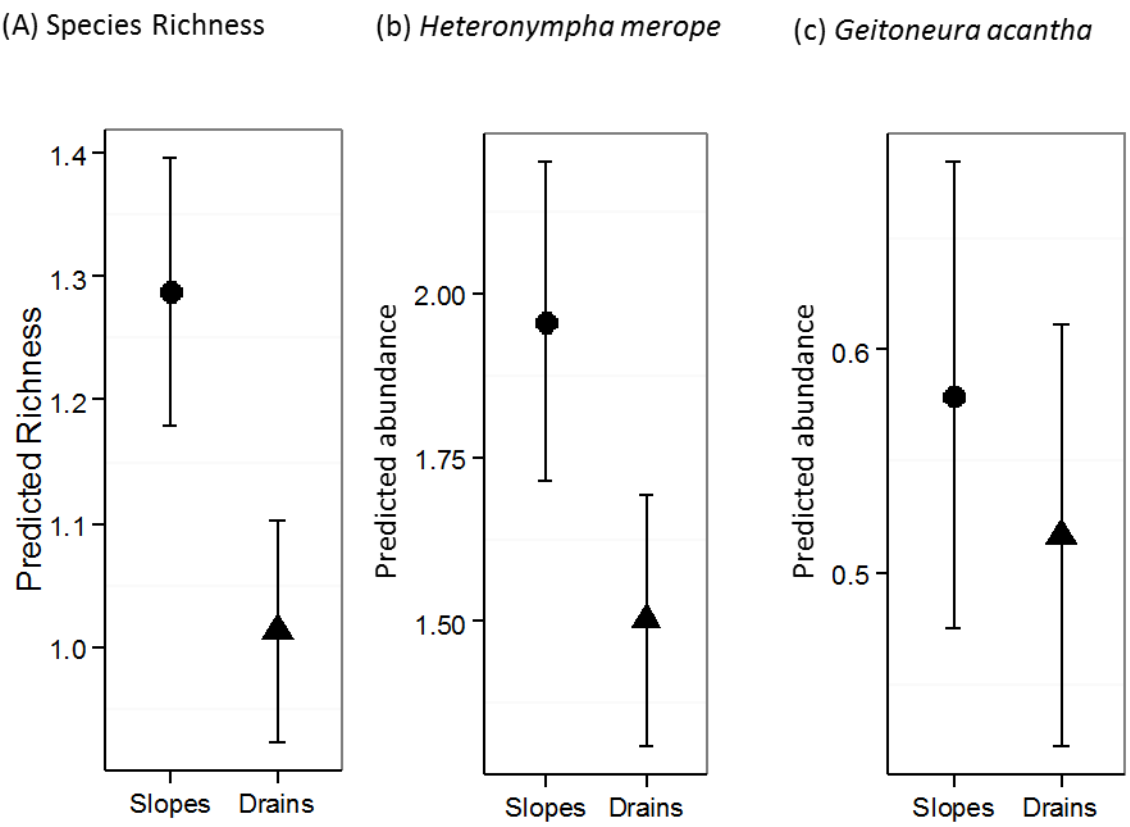


Figure S2. Predicted *Heteronympha merope* abundances in edge and core remnant sites using poisson generalised linear mixed models. Error bars represent standard errors.

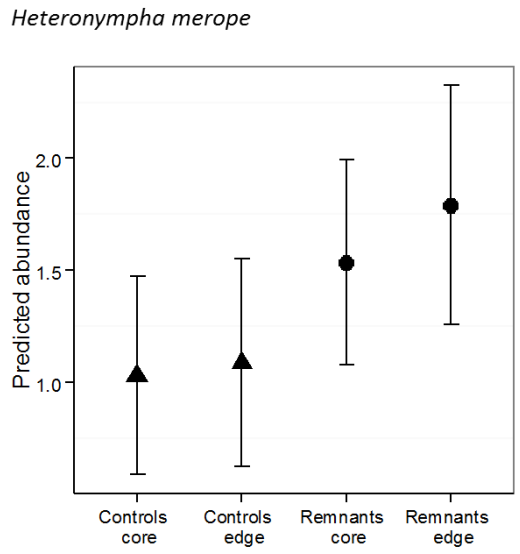
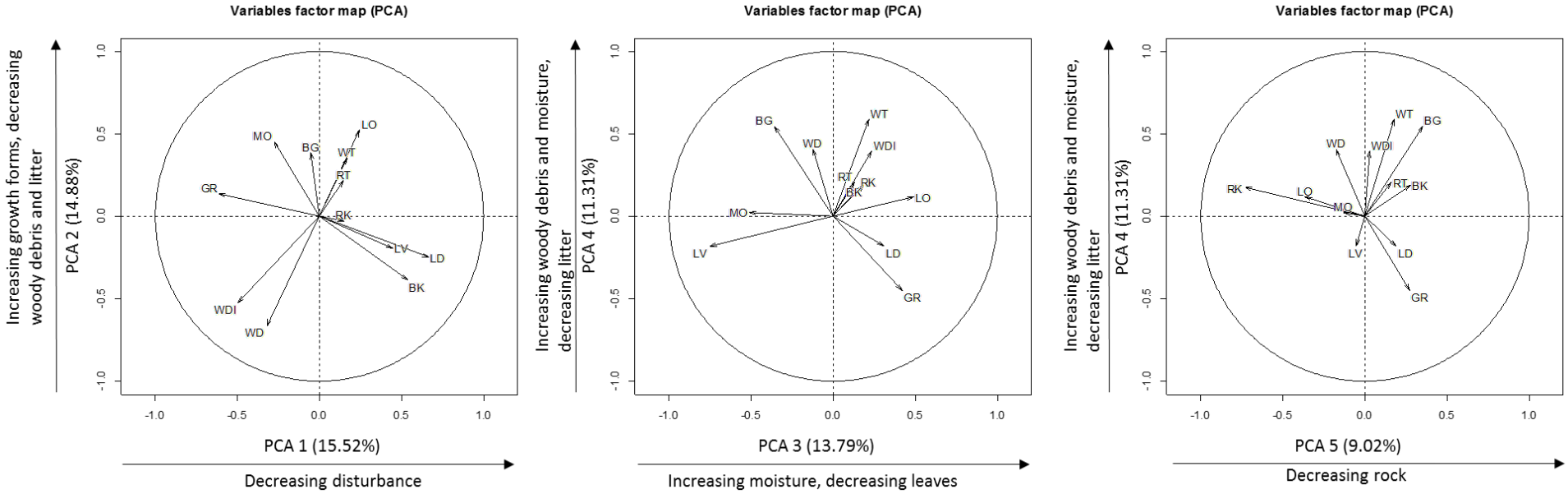


Figure S3. Results of principle components analysis (PCA) on habitat variables. Principle components 1-5 shown, which make up 65.78% of explained variation. GR=grass, MO=moss, BG=bare ground, LO=*Lomandra sp.*, WT=water, LV=leaves, LD=litter depth, BK=bark, WD=wood, WDI=woody debris, RT=roots,, RK=rock debris.



Paper III supplementary materials

Table S1. Carabid species. Number of individuals of each carabid species caught, by year group and treatment (number of sites in parentheses).

Carabid species	1985-1986 (144)	1988-1989 (188)	1990-1991 (188)	2011-2012 (188)	Remnants (96)	Controls (48)	Matrix (44)	Total
Notonomus resplendens	213	1058	1071	229	1300	1112	159	2571
Notonomus variicollis	152	48	409	145	647	62	45	754
Eurylychnus blagravei	12	120	87	175	279	36	79	394
Promecoderus sp.	48	117	74	62	175	98	28	301
Hypharpax peronii	2	134	50	0	16	0	170	186
Carenum bonellii	9	101	32	26	132	24	12	168
Notonomus minimus	23	20	7	27	38	22	17	77
Helluo costatus	15	42	10	7	58	7	9	74
Amblystomus sp.	11	26	22	0	32	15	12	59
Notonomus metallicus	3	10	23	17	16	34	3	53
Scopodes sp.	15	10	26	1	38	10	4	52
Mecyclothorax sp.	0	16	24	0	5	2	33	40
Prosopogmus sp.	4	2	3	30	23	5	11	39
Prosopogmus oodiformia	2	17	13	5	8	3	26	37
Euthenarus promptus	0	21	14	1	29	0	7	36
Hypharpax sp.	9	13	3	0	8	5	12	25
Anomotarus sp.	1	11	4	5	12	6	3	21
Gnathaphanus melbournensis	2	8	9	0	4	1	14	19
Microlestodes sp.	3	4	3	2	6	6	0	12
Anomotarus sp.	1	2	6	2	7	4	0	11
Lecanomerus sp.	0	6	2	1	3	1	5	9
Stenolophus piceus	0	5	4	0	0	0	9	9
Amblystomus sp.	0	0	7	1	1	1	6	8
Pericompsus sp.	0	4	2	1	2	1	4	7
Lecanomerus sp.	1	0	0	5	2	0	4	6
Agonocheila sp.	0	2	0	4	3	1	2	6
Lacordairia sp.	1	2	0	2	3	2	0	5
Moriodema mcoyei	1	0	0	4	4	1	0	5
Homethes elegans	0	1	3	0	3	0	1	4
Adelotopus sp.	1	1	0	2	2	1	1	4
Clivina sp.	0	2	2	0	2	1	1	4
Euthenarus sp.	0	2	1	0	3	0	0	3
Pseudoceneus sp.	0	0	3	0	0	0	3	3
Lecanomerus sp.	1	0	0	1	0	1	1	2
Mecyclothorax sp.	0	1	0	1	1	0	1	2
Notiobia sp.	0	1	0	0	0	1	0	1
Clivina basalis	0	1	0	0	0	0	1	1
Clivina sp.	0	1	0	0	0	0	1	1
Amblytelus sp.	0	1	0	0	1	0	0	1

Tachys sp.	0	1	0	0	0	0	1	1
Trechobembix sp.	0	0	1	0	1	0	0	1
Amblystomus sp.	0	0	1	0	0	1	0	1
Lestignathus sp.	0	0	1	0	0	1	0	1
Notiobia sp.	0	0	1	0	0	0	1	1
Tasmanitachoides sp.	0	0	1	0	1	0	0	1
Notiobia sp.	0	0	1	0	1	0	0	1
Totals	530	1811	1920	756	2866	1465	686	5017

Figure S1. Responses of carabid species richness (a) and individual species ((b) to (k)) to topography using all data combined. Bars represent 95% confidence intervals.

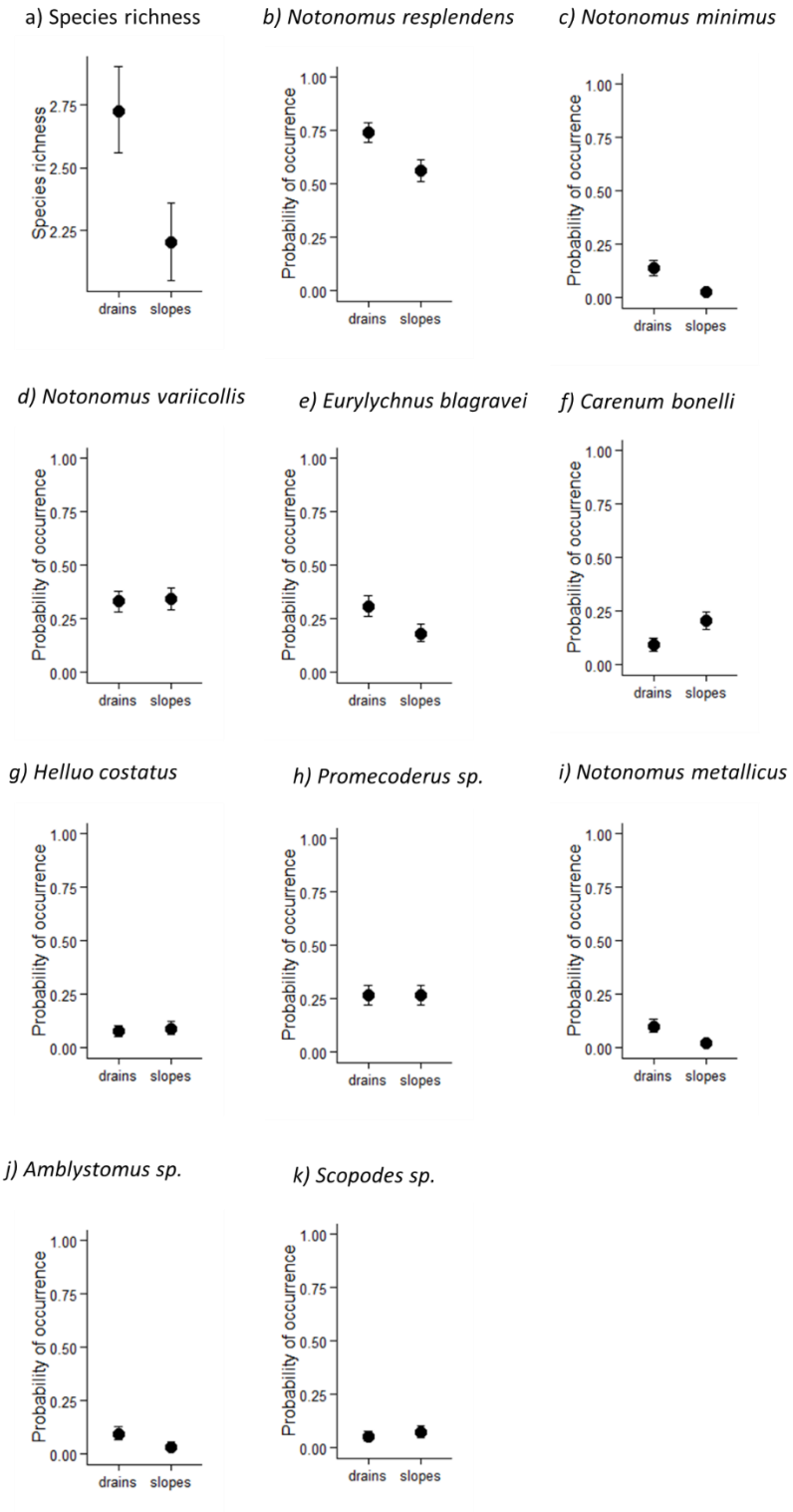


Figure S2. Mean and maximum average annual temperatures for region. Based on the Bombala Therry St weather data (Bureau of Meteorology 2014). Missing data reflects data not collected in those years.

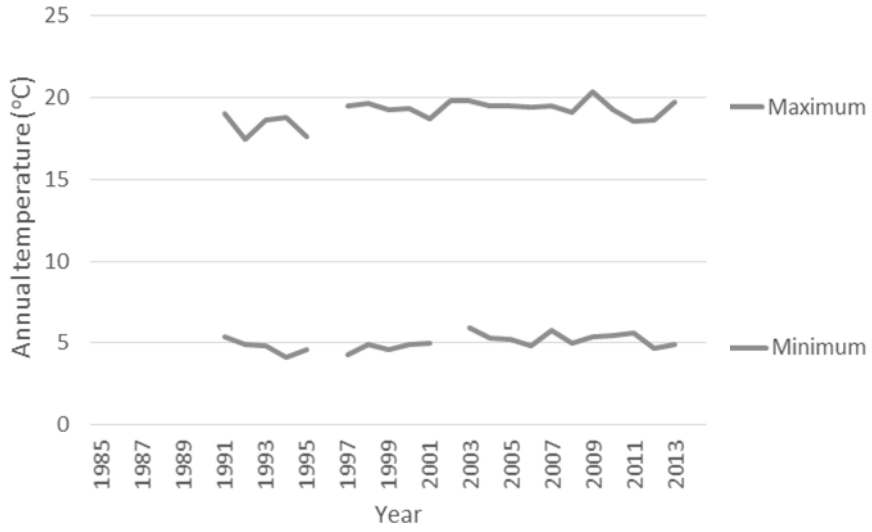


Figure S3. Total annual rainfall for region. Based on Bombala Therry St weather data (Bureau of Meteorology 2014). Missing data reflects data not collected in those years.