ON TAKING A THERMAL APPROACH TO FRAGMENTATION RESEARCH

by

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ABSTRACT

One of the most immediate and consistently documented effects of forest fragmentation is an increase in solar radiation at newly created edges, resulting in higher and more variable temperatures within remnant habitat patches. However, few studies address altered thermal conditions as a mechanism driving ecological change in fragmented landscapes, despite the understanding that fragmentation changes temperature, and that temperature strongly influences the behaviour, physiology, and interactions of animal species. The goal of my dissertation research was to tease apart the role of temperature change in ecological responses to forest fragmentation. I first developed a conceptual framework that integrates thermal biology into fragmentation research to better predict and understand species, community, and ecosystem-level responses to habitat fragmentation. I then applied this framework to two field studies. First, I used a morphometric analysis to provide some of the first evidence that fragmentation can lead to significant declines in body size in ectothermic organisms through its impact on thermal conditions. Second, I used species distribution models to show that thermal conditions, particularly thermal stress experienced at a site, provide even larger constraints on ectotherm distribution in fragmented landscapes than some of the main effects of fragmentation, including patch size and proximity to patch edge. These field studies center on a small, ground-dwelling lizard species (the common garden skink, Lampropholis guichenoti) within the long-term, largescale, controlled, and replicated Wog Wog Habitat Fragmentation Experiment. Together, these results demonstrate that temperature changes following fragmentation can have ecologically important impacts on organisms in remnant patches. Moreover, these results underscore the need for research efforts targeting temperature as a driver of ecological patterns in fragmented landscapes. Fragmentation remains one of the greatest contributors to biodiversity loss worldwide. Thus, understanding the future of global biodiversity relies on understanding the full spectrum of fragmentation's impacts.

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INTRODUCTION

For over forty years, the impacts of habitat fragmentation have captivated ecology and evolutionary biology researchers, and yet many questions in fragmentation ecology remain unanswered, including the strength and implications of the relationship between fragmentationdriven temperature increases and organismal responses to fragmentation. The goals of my dissertation research are to (1) call attention to the lack of thermal studies in the fragmentation literature, (2) provide ecologists with a fragmentation-temperature framework to integrate thermal biology concepts into fragmentation research to help close this gap in our understanding, and (3) to test concepts presented in the fragmentation-temperature framework to determine the tractability of its ideas. Throughout my dissertation, I argue that temperature increases following fragmentation are an important, underestimated driver of ecological change in fragmented landscapes, and that integrating thermal biology into fragmentation research provides novel insight into fragmentation's ecological consequences.

Fragmentation research incorporates a variety of ecological subfields, including invasion, disease, community, and ecosystem ecology. However, thermal biology has remained outside the scope of fragmentation research, despite a shared interest in the effects of warming on biological and ecological processes. Indeed, one of the most immediate and consistently documented effects of fragmentation is an increase in solar radiation at newly created edges, resulting in higher and more variable temperatures within remnant habitat patches (Murcia 1995, Chen *et al.* 1999, Laurance 2004). Yet few studies address altered thermal conditions as a mechanism driving ecological change in fragmented landscapes.

Both thermal biology and climate change research highlight the pervasive effects of warming on ecosystems. Temperature influences virtually all aspects of behavioral and

physiological performance in animal species (Huey 1982, Huey & Kingsolver 1989, Angilletta *et al.* 2002), and thus indirectly influences community and ecosystem-level processes dependent on animal community members, such as plant pollination (Traill *et al.* 2010) and carrion decomposition (Klein 1989). My dissertation highlights the impacts of thermal conditions and species' thermosensitivity on ecological processes in fragmented landscapes, at scales ranging from individuals to ecosystems.

In the first chapter of my dissertation, I present a fragmentation-temperature framework that integrates thermal biology and climate change findings into fragmentation research to predict the effects of fragmentation-driven warming on ecological systems. This framework first addresses how fragmentation changes thermal conditions in the landscape and then explores the relationships between temperature increases and organismal responses, starting with the smallest scale, individuals, and ending with the largest scale, ecosystems. The framework reviews the links between thermal conditions and organism fitness using thermal performance curves and presents new ways to estimate the impacts of fragmentation on species, including calculating reductions in physiological performance and increases in risk of mortality from overheating. I outline "What we know" and "Critical gaps" for each step of the framework in the hopes of guiding future research.

The second and third chapters of the dissertation use field studies to test the ideas presented in the fragmentation-temperature framework. My field studies target the response of a small, heliothermic lizard (the common garden skink, *Lampropholis guichenoti*) to the experimental fragmentation of its *Eucalyptus* forest habitat. *L. guichenoti* is a diurnal scincid species widely distributed in southeastern Australia (Cogger 2000) and the most abundance reptile species at our field site in southeastern Australia. My field studies are based within the

long-term, large-scale Wog Wog Habitat Fragmentation Experiment, one of the oldest and largest fragmentation studies in the world (Collinge 2009).

In the second chapter of the dissertation, I use *L. guichenoti* body size data spanning 30 years to test the prediction that skinks would be smaller in forest fragments relative to those in the non-fragmented control forest because of temperature increases following fragmentation. In addition, I predicted that the severity of temperature increase (i.e. amount of exposure to deforested areas) would affect the severity of body size decline, which I tested using body size differences among fragmented populations, compared across patch sizes and proximity to the edge of the patch. These predictions stem from the temperature-size rule, whereby higher incubation temperatures can lead to smaller body sizes in ectothermic individuals (Angilletta *et al.* 2004, Kingsolver & Huey 2008), and provide insight into the effects of fragmentation-driven warming on body size, and ultimately fitness, in ectothermic species.

In the third chapter of the dissertation, I developed a species distribution model to test the link between thermal conditions and *L. guichenoti* abundance patterns in the landscape. Species distribution models relate field observations of occurrence at a site with the underlying environmental variables of that site to estimate the species' environmental requirements (i.e. environmental niche) (Guissan & Thuiller 2005, Elith & Leathwick 2009, Kearney & Porter 2009). For this model, I built a database of 31 environmental variables, including fragmentation variables (e.g. *Fragmentation, Patch size, Proximity to edge*), habitat variables (e.g. *Leaf litter depth, Soil pH*), and climate variables (e.g. *Mean Temperature, Mean diurnal temperature range*) for each sample site at Wog Wog. I also included species-specific measures of thermal stress at each site (e.g. *% Peak activity time that temperatures exceed the species' thermal maximum*), which were derived from information on the thermal physiology of *L. guichenoti*. I then used generalized linear mixed models to determine the importance of each environmental variable to skink abundance, to provide insight into in the importance of thermal conditions for ectotherm persistence in fragmented landscapes.

Together, chapters two and three provide experimental evidence that temperature increases following fragmentation can have important impacts on organisms in remnant patches. In chapter two, I show that skinks declined in size precisely as predicted by the temperature-size rule after the fragmentation treatment was applied, such that the greater the exposure to deforested areas, the greater the decline in body size. This pattern was strongest in the first five years following fragmentation, during which body size was linearly and positively related to log patch size. To address alternative hypotheses for size declines, I compare body size patterns to two biological drivers: avian predator abundance and beetle prey biomass. However, neither variable showed patterns that explained body size declines in the fragmented forest.

In chapter three, I show that thermal conditions are important regulators of ectotherm distribution in fragmented landscapes. Specifically, I show that thermal stress had greater influence on skink abundance patterns than did *fragmentation*, *patch size*, or *proximity to edge*. I also show that there is a hump-shaped relationship between thermal stress and abundance at Wog Wog sites, suggesting a minimum, optimum, and maximum amount of thermal stress that individuals can endure to persist in remnant patches. Interestingly, the shape of the hump and location of the optimum depends on whether sites are found in the fragmented or continuous forest. These thermal stress thresholds can help predict future species distributions following fragmentation, offering a thermal approach to the conservation of *L. guichenoti* in fragmented landscapes.

Results from chapters two and three provide empirical evidence of temperature's role in ecological changes following fragmentation and underscore the need for further research efforts targeting temperature as a mechanism in fragmented landscapes. The field of thermal biology has

progressed tremendously in the last several decades, and topics once restricted to thermal biology—including thermal physiology—are finding new life in climate change research and new applications to ecological problems (Angilletta 2009). Here I present two field studies and a conceptual framework to integrate thermal biology into fragmentation research to advance our understanding of species persistence in an increasingly fragmented world.

CHAPTER 1

A FRAMEWORK FOR INTEGRATING THERMAL BIOLOGY INTO FRAGMENTATION RESEARCH¹

1.1 ABSTRACT

Habitat fragmentation changes thermal conditions in remnant habitat patches by increasing incoming and outgoing solar radiation at patch edges, and thermal conditions strongly influence species' distribution and activity patterns. However, few studies address how these altered thermal conditions might act as a mechanism driving ecological responses to fragmentation. Here we offer a conceptual framework that addresses how fragmentation changes temperature and how the effects of those temperature changes affect individual fitness, species distribution and activity patterns, community structure, and ultimately ecosystem functions. This fragmentation-temperature framework brings together findings from thermal biology, climate change, and fragmentation research to better understand the effects of fragmentation-driven temperature increases on organisms in remnant patches. We place a strong emphasis on future research directions by outlining "Critical gaps" for each step of the framework. Empirical efforts to apply and test this framework promise new understanding of fragmentation's ecological consequences and new strategies for conservation in an increasingly fragmented and warmer world.

¹ Tuff, K. T., Tuff, T. & Davies, K. F. (2016). "A framework for integrating thermal biology into fragmentation research." *Ecol. Lett.*, *19*, 361–374.

1.2 INTRODUCTION

Habitat fragmentation is one of the greatest contributors to biodiversity loss worldwide (CBD 2010) and increasing rates of fragmentation underscore the importance of understanding the full spectrum of its ecological consequences (Haddad *et al.* 2015). Fragmentation can be defined as the division of once-continuous habitat into smaller and more isolated patches separated by a matrix of human-transformed land cover (Haddad *et al.* 2015). Most fragmentation results in habitat patches surrounded by a matrix of low biomass and low structural complexity, such as pasture, cropland, or concrete, with thermal conditions unlike those of the remaining patches (Murcia 1995).

Studies on the effects of fragmentation in terrestrial systems abound, and many highlight the mechanisms underlying ecological changes following fragmentation, including altered dispersal dynamics (Templeton *et al.* 2011, Damschen *et al.* 2014) and changes in metapopulation and metacommunity dynamics (Jamoneau *et al.* 2012, De la Sancha *et al.* 2014). However, few studies explore temperature as a mechanism driving changes in fragmented landscapes, despite the understanding that fragmentation changes thermal conditions in remnant patches (Murcia 1995, Chen *et al.* 1999, Laurance 2004, Table 1), and that thermal conditions can strongly influence organism morphology, distribution, activity patterns, and evolutionary trajectory (Huey 1982, Angilletta 2009, Kingsolver 2009, Puurtinen *et al.* 2015).

Indeed, one of the most immediate and consistently documented effects of forest fragmentation is an increase in direct and diffuse solar radiation at newly created edges, often leading to hotter, drier, and more variable microclimate conditions within remnant patches (Murcia 1995, Chen *et al.* 1999, Laurance 2004). While fragmentation has important effects on a suite of microclimate variables, including light intensity, humidity, wind speed, and air pressure

(Murcia 1995, Chen *et al.* 1999, Laurance 2004), here we focus on the ecological consequences of temperature increases.

Specifically, we offer a conceptual framework that integrates thermal biology into fragmentation research to better understand the role of temperature in species, community, and ecosystem-level responses to fragmentation. Our framework addresses how fragmentation changes local and regional temperatures and how the effects of those temperature changes spread through the fabric of the ecosystem, from organism response via thermal sensitivity, to changes in species distribution and activity patterns, to shifts in community structure following species' responses, and ultimately to changes in ecosystem functions (Fig. 1). We focus on forest ecosystems because changes in thermal conditions are well documented and relatively consistent (Table 1). In section 2.1 we explore how the concepts might extend to non-forest ecosystems.

We also focus on diurnal species because they are more likely to encounter stressfully high body temperatures during their active period than are nocturnal species (Kearney *et al.* 2009). Nighttime temperatures are slightly lower at patch edges than at patch interiors, as areas near the edge lose higher amounts of long-wave radiation back to the atmosphere at night (Chen *et al.* 1995). Sites at the interior of tropical forest fragments, for example, were $0.2 \pm 0.1^{\circ}$ C warmer than in the pasture matrix at night, regardless of weather conditions (Daily & Ehrlich 1996). Thus, it is not likely that the responses of nocturnal species to fragmentation are heavily driven by thermal biology.

The effects of warming on organisms have come to the forefront of ecological research in the last several decades because of climate change projections (Huey *et al.* 2009, Kearney *et al.* 2009, Somero 2010, Gerick *et al.* 2014, Dohet *et al.* 2015). However, climate change is not the only factor increasing temperatures in landscapes throughout the world. Ground surface temperature is strongly dependent on vegetation cover (Hong *et al.* 1995) and fragmentation

replaces continuous vegetation cover with a mosaic of matrix and remnant habitat. These changes in vegetation cover can alter the circulation of heat, moisture, and momentum in the landscape (Hong *et al.* 1995), and fragmentation has been linked to warmer, drier climates across the globe, including Australia (McAlpine *et al.* 2007), the Amazon Basin (Cochrane & Laurance 2008), and West Africa (Garcia-Carreras & Parker 2011).

A recent trend in climate change research is to use species' thermal biology to predict their response to climate warming (Buckley 2008, Gvozdík 2012, Tattersall *et* al. 2012, Tunney et al. 2014). Through the integration of thermal biology, our understanding of the effects of climate change has seen several noteworthy advancements: 1) scientists can better predict range shifts because of an understanding of thermal preferences (Kearney & Porter 2009, Valladares *et al.* 2014); 2) scientists can better explain declines in body size because of temperature-size relationships (Sheridan & Bickford 2011); and 3) scientists can better understand the impacts of changes in air temperature on organisms in the landscape with the use of operative temperature, as opposed to air temperature alone (Sears *et al.* 2011, Hovick *et al.* 2014, Kearney *et al.* 2014). The integration of thermal biology into climate change research has led to huge developments in our understanding of extinction risk under global warming scenarios, and we predict that integrating thermal biology into fragmentation's effects.

Fragmentation produces its own signature warming, set apart from climate change by the short time scale and spatial arrangement within which temperature increases occur. The differences between climate change and fragmentation-driven warming can influence extinction predictions and, thus, warrant a unique framework that addresses temperature as a mechanism driving ecological changes in fragmented landscapes. We advocate for empirical efforts to apply and test the fragmentation-temperature framework, to improve our understanding of

fragmentation's ecological consequences by explicitly considering the impacts of temperature increases.



Figure 1: The cascade of effects that follow a thermal disturbance, such as fragmentation. Fragmentation leads to increased temperatures in remnant habitat patches, which will affect individuals, and ultimately species, according to their thermosensitivity. Broadly, species can respond to thermal stress by moving in space, adapting to new conditions, or going extinct. Different species will respond differently to the same temperature increase, and both symmetries and asymmetries in species' responses can lead to changes in community structure and dynamics. Shifts at the species and community level can even alter ecosystem functions in fragmented landscapes. We expect the intensity of the thermal disturbance and the thermal sensitivity of the organisms and interactions involved determine how far the effects cascade through the ecosystem. This framework offers a new tool to examine temperature as a mechanism driving ecological changes in fragmented landscapes.

1.3 FRAGMENTATION-TEMPERATURE FRAMEWORK

The fragmentation-temperature framework links thermal biology and fragmentation

research through a shared interest in understanding the effects of temperature change on

organisms. The framework is structured using classic scales of ecological organization:

individual, species, community, and ecosystem. We outline "Critical gaps" for each scale in the

hopes of guiding future research. The first step of the framework details patterns in fragmentation's effects on thermal conditions. The framework then reviews the relationships between temperature changes and organismal responses starting with the smallest scale, individuals, and ending with the largest scale, ecosystems.

1.3.1. THE EFFECTS OF FRAGMENTATION ON TEMPERATURE

Tree canopies intercept both incoming solar and outgoing long-wave radiation, creating cooler and more uniform thermal environments (Murcia 1995). When overstory vegetation is removed, such as during the fragmentation process, both incoming and outgoing radiation are increased, leading to hotter, drier, and more variable thermal conditions in remnant patches (Chen *et al.* 1999). Studies show daytime air temperatures average 2-5°C higher at patch edges than patch interiors, daytime soil temperatures average 7-9°C higher at patch edges than patch interiors, and maximum air temperatures at edges can average up to 10°C higher than patch interiors (Table 1). These thermal changes hold relatively constant across forest types and latitudes (Table 1) and rival the temperature increases expected from decades of climate change (IPCC 2014), although they occur over rapid time scales. Unlike mean and maximum temperatures, minimum temperatures (Ewers & Banks-Leite 2013, Table 1) and nighttime temperatures (Daily & Ehrlich 1996) rarely differ across edge, interior, and matrix areas.

In contrast to warming from climate change, warming in fragmented landscapes has a fixed, spatial arrangement, such that increased temperatures at forest edges create a thermal gradient that declines exponentially from edge to interior (Williams-Linera 1990, Didham & Lawton 1999, Saunders *et al.* 1999). Temperature gradients can extend variable distances inside a remnant patch, depending on forest structure at the edge ("Edge penetration distance," Table 1). However, the gradient itself can reverse over the course of the day, with temperatures

declining towards the interior during the day but increasing towards the interior at night (Chen *et al.* 1995). Consequently, the temporal range near an edge is also much higher than the natural variation within continuous habitat (Table 1).

			EDGE	EDGE	AIR TEMPERATURE INCREASES AT EDGE			EDGE
REFERENCE	FOREST TYPE	LOCATION	AGE (YRS.)	PENETRATION DISTANCE (M)	MEAN (°C)	MAX (°C)	MIN (°C)	RANGE (°C)
Kapos 1989	Tropical lowland rainforest with pasture matrix	Brazilian Amazon	1 month	20 - 60	1.4 - 2.8	NR	NR	NR
Williams- Linera 1990	Tropical pre-montane forest with pasture matrix	Panama	0.8-5	2.5 - 15	NM	1.5 - 3.1 M	0 – 1.0 M	NR
Matlack 1993	Oak-Chestnut forest with field matrix	Pennsylvania & Delaware, USA	1-5	24	0 - 5.3	NR	NR	ND
					3.1 - 5.8 M			INK
Chen et al.	Old-growth Douglas Fir forest with mixed-conifer matrix (<2 m tall)	Washington, USA	10-15	250	2.7 - 3.6	3.5	NR	3-5
1993					7.2 - 9.1			7 - 10
Chen et al.	Old-growth Douglas Fir forest with mixed-conifer matrix (<2 m tall)	Washington, USA	10-15	180 - 240	4.4 - 5.4	NR	NR	1.3 - 7.8
1995								1.7 - 15.5
Didham & Lawton 1999	Tropical lowland rainforest with pasture matrix	Brazilian Amazon	10-12	100 - 184	2.6 - 3.7	NR	NR	NR
Yan <i>et al.</i> 2007	Evergreen broadleaved forests	Jinyun Mountains, China	NR	15 - 25	NR	1.5 - 2	NR	2 - 6
								5 - 9
Sato <i>et al.</i> 2014	Alpine <i>Eucalyptus</i> forest with grassy ski-run matrix	New South Wales, Australia	NR	2	3.6	10.8	-0.5	11.3

Table 1: Findings from studies measuring differences in mean, maximum, and minimum air temperature and diurnal temperature range at patch edge versus interior sites within remnant patches in fragmented forests. For example, Kapos (1989) found mean air temperatures average 1.4 - 2.8°C higher at patch edges than interiors. Temperatures were measured using different methods across studies, so patterns are only broadly comparable. Soil temperatures (bold italicized) and air temperatures in the matrix ("M") were included when possible. "Edge penetration distance" is the distance into a patch at which temperature differences between edge and interior sites are no longer noticeable. NR = "not reported by author."

Ultimately, organisms near patch edges must cope with higher average temperatures, greater temperature maximums, and larger thermal variability throughout the day (Table 1). For small patches or those with high edge-to-interior ratios, these thermal changes may penetrate the entirety of the patch (Didham & Lawton 1999). However, the severity of thermal changes

depends on the season, weather conditions, and orientation of the patch, which control the amount of exposure to solar radiation (Chen *et al.* 1993, Chen *et al.* 1995, Didham & Lawton 1999). For example, the steepest thermal gradients occur on warm, sunny days and at edges receiving direct radiation (Chen *et al.* 1993).

The structure and thermal conditions of the matrix also influence thermal conditions within patches. For example, edge penetration distances for microclimate variables were two to five times greater at open edges than at closed edges in Amazonian forest patches (Didham & Lawton 1999). We suspect that the intensity of thermal disturbance following fragmentation influences how far the effects cascade through the ecosystem (Fig. 1). Although even modest temperature increases can generate a cascade of changing biotic interactions that affect the structural properties of the ecosystem (2.5°C, Barton & Schmitz 2009).

Differences in thermal conditions between patch and matrix habitat are largely the result of differences in structural complexity and biomass between the two habitat types (Murcia 1995). Thus, it is possible that fragmentation will not significantly alter thermal conditions or create thermal gradients in remnant patches when the contrast between patch and matrix habitat is low (e.g. grasslands, savannas, wetlands, arid, and semi-arid systems). In marine ecosystems, such as fragmented sea grass meadows, patch edges experience greater exposure to cooler, open-ocean currents (Fonesca & Fisher 1986), likely leading to reversed thermal gradients at patch edges and reversed spatial patterns in ecological responses. More research is needed to determine the impacts of fragmentation on thermal conditions in non-forest ecosystems to apply this framework. Consequently, the scope of this paper is largely limited to the fragmentation of forest ecosystems.

Fragmentation not only alters microclimates within remnant forest patches, it changes the state of the atmosphere locally and can influence circulation regionally (Dirmeyer & Shukla

1994). In continuous forest, differences in surface air temperatures are minimal because the canopy shields ground temperatures from high levels of solar radiation and buffers temperature flux, leading to a thermally stable surface condition (Hong *et al.* 1995). In fragmented forests, however, the mosaic of matrix and forest cover leads to anomalies in surface temperatures in the landscape. When these anomalies are large, it can induce novel air circulations (Hong *et al.* 1995). A notable example in fragmented landscapes is a heat-induced airflow known as the "vegetation breeze" (Cochrane & Laurance 2008).

The vegetation breeze stems from the juxtaposition of deforested and forested areas and is driven by the temperature differences between them (Cochrane & Laurance 2008). The air above forests tends to be cool and moist, whereas the air above clearings tends to be hot and dry. As a consequence, the air above clearings heats up and rises, reducing local air pressure and drawing moist air from the surrounding forest patches into the clearing. As the rising air gets cooler, the moisture it carries condenses into convective clouds that produce rainfall in the clearing. The air is then recycled—as hot, dry air—back into the forest patches (Cochrane & Laurance 2008).

The net effect of the vegetation breeze is that forest clearings receive more rainfall and forest patches receive less. In West Africa, for example, rainfall in warmer cropland areas was 46 times higher than cooler forest areas, and rainfall in forests decreased by more than 50% following land conversion to cropland (Garcia-Carreras & Parker 2011). Additionally, forest patches become increasingly desiccated, as moist air is actively drawn from the patches into clearings and hot, dry air is fed back in. Field observations and heat-flux simulations suggest that desiccating conditions can penetrate up to 100–200m into fragments from adjoining clearings (Didham & Lawton 1999, Laurance *et al.* 2011).

Temperature increases resulting from the fragmentation process can therefore lead to increased desiccation of forest patches, which may threaten patch persistence. In Brazilian Amazonia, where nearly 20,000 km of new forest edges are created each year, studies found sharply elevated rates of tree mortality, damage, and canopy-gap formation at patch edges, at least partially related to higher desiccation rates (Laurance *et al.* 2004, Cochrane & Laurance 2008, Laurance *et al.* 2011).

A prediction stemming from the vegetation breeze is that patches will erode over time, as degradation at patch edges perpetuates further degradation through increased exposure to cleared areas. Instead of maintaining their size, we expect forest patches to decline in area over time, leading to increased distance between patches and, in essence, further fragmentation. However, this shrinking-patch effect has never been described in fragmented landscapes, and it is possible that compensatory changes prohibit such shrinking from occurring. Studies in tropical forest fragments show that vines, secondary vegetation, and lateral branch growth typically "seal" patch edges within 5-10 years, making the patch less permeable to microclimate changes (Matlack 1993, Didham & Lawton 1999, Laurance *et al.* 2011). In forest types that regenerate more slowly, however, microclimate changes may persist at patch edges for longer (Table 1).

Critical gaps: A recent synthesis found that 20% of the world's remaining forests lie within 100 m of an edge and 70% lie within 1 km of an edge (Haddad *et al.* 2015), suggesting that a large portion of the world's remaining forests experience thermal conditions unlike those of continuous forest. We need more studies targeting thermal conditions in fragmented landscapes to better apply the concepts presented in this framework and more effectively tease apart temperature's role in species' responses to fragmentation.



Figure 2: A thermal performance curve describes the relationship between an organism's body temperature and its physiological performance. Middle panel: anatomy of a thermal performance curve, including the organism's critical thermal minimum (CT_{MIN}), critical thermal maximum (CT_{MAX}), optimal body temperature (T_{OPT}), performance breadth, and tolerance range. Top panel: comparing air temperature data to the thermal performance curve allows us to calculate 1) how much air temperature differs from the organism's optimal temperature (thermal safety margin) and 2) how much air temperature differs from the organism's thermal maximum (warming tolerance). Bottom panel: thermal performance curves vary with life history. A generic reference curve (dashed grey) is provided for comparison.

Specifically, future studies should focus on thermal conditions before and after fragmentation, between edge and interior areas, over time as matrix and edge structures change, and in habitats other than forests, where patterns may differ. Our understanding of fragmentation-driven warming will grow even more rapidly by incorporating innovative technologies into thermal studies, like infrared imagery, devices tracking field body temperatures, high-resolution thermal sensors, and biophysical models.

1.3.2. THE EFFECTS OF TEMPERATURE ON INDIVIDUALS

In the second step of the fragmentation-temperature framework, we explore the relationship between thermal conditions and fitness and present new ways to estimate the impacts of fragmentation on individuals.

Organisms regulate body temperature to stay within a preferred thermal range and away from thermal limitations, which can be quantified with a thermal performance curve. A thermal performance curve measures the relationship between body temperature and a physiological performance, such as metabolic rate, digestive efficiency, or sprint speed (Huey 1982, Huey & Kingsolver 1989, Angilletta et al. 2002; Fig. 2). From a thermal performance curve, we can determine the temperature at which the organism's performance is maximized (T_{OPT}) and the range of body temperatures over which the organism can perform relatively well (performance breadth) (Huey 1982, Huey & Kingsolver 1989; Fig. 2). Thermal performance curves also provide the critical thermal limits (CT_{MAX} and CT_{MIN}) beyond which the organism can no longer perform essential functions, such as the righting response or locomotion, and thus loses the ability to forage or escape from predators (Huey 1982, Sato *et al.* 2014; Fig. 2)

Researchers typically develop thermal performance curves for ectothermic species, but the same non-linear relationship between body temperature and physiological performance exists in endotherms (Angilletta *et al.* 2010, Huey *et al.* 2012). Ectotherms and endotherms differ in that body temperature in ectotherms mirrors environmental temperatures, allowing us to predict changes in performance using changes in environmental conditions (Kingsolver 2009).

Thermal performance curves prove vital for this framework because researchers can use them to calculate changes in physiological performance in fragmented landscapes, given known changes in thermal conditions. It is important to note that thermal performance curves are based on body temperature and not air temperature. However, air temperature is easier to measure than the body temperature of individuals, so researchers developed "operative temperature" models to gain access to thermal performance curves for making predictions (Porter & Gates 1969). Operative temperature is the temperature experienced by an organism, which is calculated from air temperature using a host of environmental and biophysical variables (Porter & Gates 1969, Kearney *et al.* 2014). Here we use air temperature as a proxy for body temperature in ectotherms to demonstrate concepts and calculations. Researchers applying the framework should use operative temperature or field body temperature data when possible to provide superior estimates of physiological performance at sites in fragmented landscapes.

To offer an example, air temperatures in recently fragmented forests average 2-5°C higher at patch edges than interiors (Table 1), which implies that ectotherms at newly created edges experience body temperatures approximately 2-5°C higher than before fragmentation. We can estimate the impacts of these higher temperatures on ectotherm fitness by measuring the degrees between new air temperatures and T_{OPT} (thermal safety margin) and the degrees between new air temperatures and T_{OPT} (thermal safety margin) and the degrees between new air temperatures and CT_{MAX} (warming tolerance) (Deutsch *et al.* 2008, Kingsolver 2009, Gerick *et al.* 2014) (Fig. 2). Because thermal conditions vary throughout the day and across seasons, researchers often calculate thermal safety margins and warming tolerance during peak activity time or during the warmest months to more accurately measure thermal stress. For example, to measure the effects of climate warming on sprint speed in diurnal lizards, Huey *et al.* (2009) focused on air temperature records between 10:00 and 14:00 in the summer season, while Gerick *et al.* (2014) used maximum summer air temperatures to measure thermal safety margins.

We predict that individuals with small thermal safety margins will exhibit lower fitness at patch edges and in small patches because thermal conditions following fragmentation are more likely to exceed the organism's thermal optimum, resulting in reduced physiological performance. For example, researchers often use the thermal performance curve for sprint speed as a proxy for the relationship between body temperature and predation success (Huey 1982). Crested anoles (*Anolis cristatellus*) sprint at greater than 90 percent of their maximal speed from sunrise to sunset in the current thermal conditions of their forest habitat (Huey *et al.* 2009). Huey *et al.* (2009) showed that a 3°C increase in air temperature—a conservative estimate for temperature increase following fragmentation—would result in elevated body temperatures that exceed the species' T_{OPT}, reducing sprint speed in *A. cristatellus* individuals to 40-80% of maximal during peak activity time.

We also predict that individuals with low warming tolerance will experience lower fitness at patch edges and in small patches because thermal conditions following fragmentation are more likely to approach the organism's critical thermal limit, increasing its risk of physiological shutdown. For example, Huey *et al.* (2009) showed that a 3°C increase in air temperature would push summer body temperatures in Puerto Rican ground-dwelling geckos (*Sphaerodactylus*) to only 3.5°C below the species' CT_{MAX}, resulting in severe thermal stress in individuals. The thermal extremes that often occur at patch edges (10°C higher than interiors, Sato *et al.* 2014) and in cleared areas (13°C higher than in forest patches, Currylow *et al.* 2012; 20°C higher than in forest patches, Boggs & McNulty 2010) will be especially problematic to individuals with low warming tolerance because of the high risk of overheating.

However, temperature increases following fragmentation may create more favorable thermal conditions for some individuals, allowing them to forage earlier and longer in remnant patches than in continuous forest (Saunders *et al.* 1991). For species with high thermal optima, for example, warming may confer a considerable advantage in terms of time spent within optimal limits (Kearney *et al.* 2009). In section 2.3, we identify some species for whom a positive response to warming is likely. Similarly, in the absence of thermal stress, higher temperatures should yield faster biochemical reactions, which could improve performance at the organismal level ("hotter is better" theory, Angilletta *et al.* 2009).

For individuals that can thermoregulate effectively, changes in air temperature may not extend to changes in body temperature through simple shifts in thermoregulatory behavior. For example, a common method for ectothermic organisms to thermoregulate is to "shuttle" between sun and shade or hot and cold microclimates (Huey 1974). Shuttling refers to the movement between hot and cold states to maintain an optimal temperature (Dreisig 1984). When environmental temperatures increase, individuals can adjust their shuttling behavior to reduce

risk of overheating, such as increasing the amount of time spent in thermal refugia (Sinervo *et al.* 2010, Kearney 2013) or shifting activity time to cooler parts of the day (Logan *et al.* 2006, Huey *et al.* 2012). However, activity restrictions can limit foraging time, constraining metabolic functions like reproduction (Sinervo *et al.* 2010). Thermoregulation in hotter forest patches therefore necessitates that individuals renegotiate the tradeoff between time spent foraging and time spent cooling down to avoid reductions in physiological performance.

Shuttling behavior also becomes more challenging following fragmentation because increased temperatures are coupled with declining availability of thermal refugia. Most fragmentation reduces structural complexity (Murcia 1995); thus, shade and cool microclimates become harder to find, and individuals must increase movement within a patch and/or disperse to larger patches to meet their thermoregulatory needs. These actions require increased energetic output and often increase predation risk (Huey 1974, Angilletta *et al.* 2002), making thermoregulation through shuttling behavior a longer, more energetically costly, and riskier process in fragmented landscapes.

These challenges can be exacerbated by a commonly observed phenomenon in remnant patches known as the 'crowding effect,' whereby population densities in remnant patches increase following habitat removal, as surviving individuals in the matrix crowd into the remaining habitat (Debinski & Holt 2000, Grez *et al.* 2004). When population densities increase, there will likely be higher competition for limited thermal refugia, leading to increased antagonistic interactions and higher competition for places to cool off.

Critical gaps: Ultimately, fragmentation will impact individuals according to their thermosensitivity and their capacity to buffer the impacts of warming through behavior, morphology, and physiology (Kearney *et al.* 2009). We can predict thermally driven reductions

or enhancement in fitness by calculating thermal safety margins and warming tolerance before and after fragmentation, in different patch sizes and shapes, and between edge and interior areas.

Thermal performance curves exist for a wide range of ectothermic species (Angilletta 2006), and thermal safety margins and warming tolerance can be easily calculated using estimated or known increases in environmental temperatures. However, more reliable projections of the impacts of fragmentation on performance can be developed by combining temperature data with information on the species' thermal physiology, ability to alter thermoregulatory behavior, and activity patterns (Huey *et al.* 2009). For many organisms in remnant patches, the negative consequences of warming will not result from increased exposure to lethal temperatures, but will instead result from sub-lethal effects, such as energetic imbalances and reductions in activity time (Gunderson & Leal 2016). Thermal constraints on activity is considered a mechanistic link between temperature increases and population processes (Kearney 2013, Gunderson & Leal 2016). Thus, studies targeting increases or reductions in activity time following fragmentation will provide new insight into population dynamics and persistence in remnant patches.

We suggest studies employ quantitative approaches, such as calculating body temperatures given behavioral scenarios, including (i) individuals sitting passively on the surface in matrix (full sun) conditions, (ii) individuals sitting passively on the surface in forest interior (deep shade) conditions, and (iii) individuals at the patch edge actively shuttling between forest and matrix habitat to thermoregulate (see Kearney *et al.* 2009 for details). Such models can shed new light onto the thermoregulatory value of different types of matrix habitat, patch configurations, and stage of matrix regrowth.

The relationship between body temperature and fitness is well established, but this knowledge has rarely been applied to individuals in fragmented landscapes. We need studies

targeting temperature-driven reductions and enhancements in physiological performance in remnant patches and the extent to which thermal performance curves can predict such outcomes. Few studies approach behavioral and physiological responses to fragmentation from a thermal biology perspective (Currylow *et al.* 2012, Stangler *et al.* 2014), but we think this line of research could yield important new insight into fragmentation's effects.

1.3.3. THE EFFECTS OF TEMPERATURE ON SPECIES

When populations of individuals experience thermal stress, then the species as a whole is more prone to local extinction. The third step of the fragmentation-temperature framework (Fig. 1) uses the same calculations presented in the second step of the framework to identify species at greatest risk of extinction following fragmentation (Table 2).

Fragmentation consistently reduces species richness (Haddad *et al.* 2015) but within this overarching pattern, species responses to fragmentation are notoriously idiosyncratic (Bregman *et al.* 2014). Predictions of species responses have been improved by explicitly considering life history traits, such as functional role (Bregman *et al.* 2014), dietary niche (Kennedy *et al.* 2010, Yong *et al.* 2011), and trophic level (Davies *et al.* 2000, Murphy & Romanuk 2012). We expect that including the thermal traits of species, such as thermal safety margin, warming tolerance, and performance breadth, will further improve our ability to predict and interpret their responses to fragmentation (Table 2). Thermal performance curves are developed for species by averaging the performance curves of intraspecific individuals. The fragmentation-temperature framework uses averaged performance curves for species-level measures of thermosensitivity.

THERMAL TRAIT	LOW RISK	HIGH RISK	EXTINCTION MECHANISM	HOW TO CALCULATE
Thermal safety margin	Large thermal safety margin (High T _{OPT})	Small thermal safety margin (Low T _{OPT})	Species with large thermal safety margins have a lower probability of new temperatures exceeding their optimum (and thus reducing performance) following an increase in temperature.	Measure the degrees between environmental temperatures and T_{OPT}
Warming tolerance	Large warming tolerance (High CT _{MAX})	Small warming tolerance (Low CT _{MAX})	Species with large warming tolerance have a lower probability of experiencing severe heat stress (and thus experiencing physiological shutdown) following an increase in temperature.	Measure the degrees between environmental temperatures and CT _{MAX}
Performance breadth	Low thermal specialization (wide performance breadth)	High thermal specialization (narrow performance breadth)	Every degree of temperature change will have a disproportionately larger impact on performance in species with narrow performance breadths (thermal specialists) than on performance in species with wide performance breadths (thermal generalists).	Measure the range of body temperatures that individuals maintain in the field or in the lab, when offered a thermal gradient

Table 2: Predictions for species at high and low risk of thermally driven extinction following fragmentation, based on three thermal traits (Thermal safety margin, Warming tolerance, and Performance breadth). The fourth column briefly explains the extinction mechanism related to the thermal trait, and the last column provides details on how to calculate the trait using the species' thermal performance curve and environmental temperature data. These predictions are derived from the climate change and thermal biology literature (for a full review, see Kearney *et al.* 2009, Somero 2010), and should be modified to address the unique temporal and spatial considerations of fragmentation-driven warming.

Broadly, we predict that species that can tolerate a large amount of temperature change

(wide performance breadth) and species with thermal safety margins and warming tolerance

greater than 2-5°C are more likely to persist in fragmented landscapes (Table 2). For example,

Saunders et al. (1991) hypothesize that ants of the Iridomyrmex genus will benefit from

fragmentation because *Iridomyrmex* species only forage at high temperatures, so elevated temperatures at patch edges following fragmentation allow the species to forage for a longer period of time. In contrast, temperature-driven reductions in foraging time are considered a major factor in the extinction of Carnaby's short-billed black cockatoos (*Calyptorhynchus latirostris*) following fragmentation (Saunders 1982).

Species with thermal safety margins and warming tolerance less than 2-5°C are less likely to persist in small and edge-dominant patches following fragmentation. Tropical ectotherms, for example, exhibit particularly small thermal safety margins and narrow performance breadths (Deutsch *et al.* 2008, Huey *et al.* 2009), which is alarming given that deforestation has increased significantly in the tropics over the past half century (Haddad *et al.* 2015). In the Brazilian Atlantic Forest, for example, the proportion of forest farther than 1 km from the forest edge has decreased from 90% (historical) to less than 9% (today) (Haddad *et al.* 2015). These high rates of deforestation, coupled with the sensitivity of tropical organisms to warming, raise new alarm regarding the future of ecosystems in some of our most biodiverse regions of the planet.

However, extinction is not the only response available to species experiencing thermal stress in remnant patches. Broadly, species facing higher temperatures have two possible compensatory responses: 1) given enough time and dispersal, populations can move to more favorable thermal environments in the landscape or 2) species can adjust to new conditions through behavioral plasticity, physiological plasticity, or adaptation (Sinervo *et al.* 2010). These responses can help mitigate thermal stress in hotter environments, and recent reviews suggest that species' capacity to buffer the impacts of warming through movement and adaptation can alter extinction trajectories (Kearney *et al.* 2009, Kearney *et al.* 2012, Valladares *et al.* 2014,

Buckley *et al.* 2015). Here we discuss how species might (A) move and (B) adapt to mitigate the impacts of elevated temperatures in remnant patches.

A. Movement: The thermal gradient present in remnant patches suggests that the distribution of species in remnant patches may be predictable if the thermosensitivities of the focal species are known. We expect individuals will disperse along the thermal gradient, spanning from patch edge to interior, to find areas with optimal thermal conditions. Because average temperatures are consistently higher at patch edges (Table 1), we expect different species to require different distances from the forest edge, depending on their thermal needs and according to their dispersal ability (Saunders *et al.* 1991) (Fig. 3). For example, in a network of boreal lakes, increased air temperatures produced steep thermal gradients at the water surface (Tunney *et al.* 2014). In response, temperature-sensitive lake trout (*Salvelinus namaycush*) shifted their habitat use to colder, offshore waters, where thermal conditions remained unchanged (Tunney *et al.* 2014).

Temperature-sensitive species (Table 2) should only occupy areas far from patch edges and are likely to contract their distribution towards patch interiors, where thermal conditions are perhaps unchanged. For small and edge-dominant patches, temperature increases may penetrate the entire patch (Didham & Lawton 1999), forcing thermally sensitive species to disperse to larger patches in search of cooler conditions. This increased emigration of species from small to large patches could spark a diversity of ecological cascades, and such movement may have important consequences for how individuals, species, communities, and ecosystems are affected by fragmentation.

Studies consistently document the replacement of forest specialist species with generalist species in small and edge-dominant patches (Lövei *et al.* 2006), but thermosensitivity provides a new mechanism underlying this pattern and further emphasizes the need to disentangle the

drivers of biodiversity changes in remnant patches. Many drivers of change in fragments will be co-linear with temperature increases, including desiccation and resultant vegetation changes, so identifying which of these is the "true" driver will take some disentangling.

B. Adaptation: Because of the immediacy with which temperature increases occur and constraints arising from the genetic architecture of thermal tolerance, many species cannot evolve rapidly enough to adapt to hotter thermal conditions following fragmentation (Sinervo *et al.* 2010, Somero 2010). However, studies suggest that plastic responses, such as shifts in thermoregulatory behavior and physiology, can mitigate thermal stress in hotter conditions (Kearney *et al.* 2009, Huey *et al.* 2012, Valladares *et al.* 2014) and might serve as an important mechanism underlying species persistence in remnant patches.

Terrestrial ectotherms often respond to warming by shifting activity patterns to reduce risk of overheating, such as increasing the amount of time spent in thermal refugia (Sinervo *et al.* 2010, Kearney 2013), shifting activity time to cooler parts of the day (Logan *et al.* 2006, Huey *et al.* 2012), or shifting seasonal activities, like reproduction, to cooler parts of the year (Kearney *et al.* 2009). Warming-driven shifts in activity time are considered a way for ectotherms to buffer the impacts of warming (Huey *et al.* 2009), but such shifts are more commonly linked to population declines than population persistence. For spiny lizards (*Sceloporus*), for example, heat-driven restrictions in foraging time during the breeding season led to local extinction events due to reductions in energy gain and ultimately lower fecundity (Sinervo *et al.* 2010). While studies have documented shifts in activity time in animals in remnant patches (Norris *et al.* 2010), such studies are rare and much needed.

The extent to which plastic responses (e.g. shifts in distribution or thermoregulatory behavior) help or hinder species persistence in fragmented landscapes remains an important and relatively unexplored question. Researchers should target changes in the spatial arrangement,

physiology, and thermoregulatory behavior of species in remnant patches to gain new insight into the potential for plastic responses to buffer species from the impacts of fragmentation or climate change-driven warming. Studies suggest that changes in thermoregulatory behavior can alter extinction outcomes in warming scenarios (Kearney *et al.* 2009, Huey *et al.* 2012, Valladares *et al.* 2014), and we think recently fragmented landscapes offer experiments primed to test these types of thermal questions.

Critical gaps: Evidence from the climate change literature suggests that thermal traits, including thermal safety margins, performance breadth, and warming tolerance, provide useful predictors of extinction risk in changing thermal environments (Deutsch *et al.* 2008, Somero 2010) (Table 2). We need a barrage of studies testing the predictive power of thermal traits for species' responses to fragmentation to determine the value of this approach in the context of fragmented landscapes. Future studies should compare the time spent in thermally stressful conditions before and after fragmentation, between edge and interior habitat, and over time as the matrix, vegetation density, and edge structure change (Fig. 3 presents an example). If predictions derived from thermal traits prove effective indicators of extinction risk, we can then offer a new, easy-to-use tool to guide biodiversity conservation in fragmented landscapes.

1.3.4. THE EFFECTS OF TEMPERATURE ON COMMUNITY DYNAMICS

No organism is an ecological island (Huey *et al.* 2012), and species' responses to warming can indirectly lead to shifts in community dynamics through direct changes in biotic interactions (Gilman *et al.* 2010). In step four of the framework, we explore how the thermal response of one species (movement, adaptation, or extinction) may cascade through the ecological community, altering interactions between competitors, predators, parasites, or mutualists in remnant patches (Peck *et al.* 2009, Gilbert *et al.* 2014, Dohet *et al.* 2015).



Figure 3: The spatial relationships between thermal conditions and performance along the edge of a remnant forest patch. Top row: illustration of a classic thermal gradient extending from a cleared matrix across the patch edge and into the forest interior. Middle row: hypothetical thermal performance curves for the same individual at three locations along the thermal gradient (patch interior, patch edge, and matrix). The range of body temperatures experienced by the individual at that location (green shaded area under the curve), the individual's preferred body temperatures (bracketed grey line), and the individual's optimal and maximum body temperatures (black and red dashed lines, respectively) are labeled. Bottom row: battery icons represent the relative amount of time the individual has available for activity (e.g. foraging and mating) at that location, based on the thermal conditions available. Activity time is reduced when the body temperatures experienced exceed the organism's optimal temperature.

For example, Tunney *et al.* (2014) show that when lake trout shifted their habitat use to combat warming, they developed a stronger dependence on deep-water resources, specifically phytoplankton production and cold-water prey. This shift lengthened the trophic pathways to lake trout and, ultimately, resulted in an increase in the food chain length of the entire ecosystem (Tunney *et al.* 2014), likely leading to further ecological cascades. The effects of the trout's shift on its warm-tolerant competitors and on the abundance of its prey are not yet known (Tunney *et al.* 2014), but it is possible that a variety of biotic interactions have been altered

Differences in thermosensitivity can also shift ecological communities via species loss (Peck *et al.* 2009), often through the replacement of cold-adapted or thermally specialized species by thermal generalist species taking advantage of warmer temperatures (Dohet *et al.* 2015). Extinctions from warming are hypothesized to shift communities towards dominance of smaller,

more active species, which typically have higher thermal tolerance and are more capable of making behavioral and physiological shifts (Peck *et al.* 2009).

These results suggest that if details about taxa thermosensitivity and changes in thermal conditions are known, changes in community dynamics following fragmentation may be predictable. In many cases, however, we do not know enough about individual sets of interactions between species or how temperature regulates the strength and direction of those interactions (Gilbert *et al.* 2014). In the hopes of making a generalizable statement, we predict that temperature-sensitive species (Table 2) will shift their habitat use to cooler, forest interior areas and develop a greater reliance on forest interior resources. We expect shifts in the behavior and habitat use of temperature-sensitive species to have broader impacts on community dynamics in remnant patches, such as lengthening or shortening trophic pathways and restructuring food web architecture.

Critical gaps: There has been a recent surge of interest in the relationship between temperature increases and biotic interactions (Gilman *et al.* 2010, Gilbert *et al.* 2014, Dohet *et al.* 2015), but few studies have applied these finding to interactions in fragmented landscapes (Stangler *et al.* 2014). We need studies targeting temperature-driven shifts in biotic interactions that consider the spatial structure of thermal conditions in remnant patches when developing hypotheses and predictions. Further, we need studies tracking subsequent changes in community structure and dynamics in remnant patches that emerge from shifts in biotic interactions. The relationship between temperature increases and altered biotic interactions in fragmented landscapes is relatively untested (Stangler *et al.* 2014) and presents a great opportunity for gaining new understanding of fragmentation's ecological consequences.

This relationship also presents an opportunity for insight into the overall impact strength of fragmentation events. We know very little about the connection between the severity of thermal disturbance following fragmentation and how far the effects of that fragmentation event

cascade through the ecosystem, but we expect better understanding of impact strength will be a key advancement of this framework.

1.3.5. THE EFFECTS OF TEMPERATURE ON COMMUNITY DYNAMICS

No organism is an ecological island (Huev *et al.* 2012), and species' responses to warming can indirectly lead to shifts in community dynamics through direct changes in biotic interactions (Gilman et al. 2010). In step four of the framework, we explore how the thermal response of one species (movement, adaptation, or extinction) may cascade through the ecological community, altering interactions between competitors, predators, parasites, or mutualists in remnant patches (Peck et al. 2009, Gilbert et al. 2014, Dohet et al. 2015). For example, Tunney et al. (2014) show that when lake trout shifted their habitat use to combat warming, they developed a stronger dependence on deep-water resources, specifically phytoplankton production and cold-water prey. This shift lengthened the trophic pathways to lake trout and, ultimately, resulted in an increase in the food chain length of the entire ecosystem (Tunney et al. 2014), likely leading to further ecological cascades. The effects of the trout's shift on its warm-tolerant competitors and on the abundance of its prev are not yet known (Tunney et al. 2014), but it is possible that a variety of biotic interactions have been altered. Differences in thermosensitivity can also shift ecological communities via species loss (Peck et al. 2009), often through the replacement of cold-adapted or thermally specialized species by thermal generalist species taking advantage of warmer temperatures (Dohet et al. 2015). Extinctions from warming are hypothesized to shift communities towards dominance of smaller, more active species, which typically have higher thermal tolerance and are more capable of making behavioral and physiological shifts (Peck et al. 2009).
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cascade through the ecosystem, but we expect better understanding of impact strength will be a key advancement of this framework.

1.3.6. THE EFFECTS OF TEMPERATURE ON ECOSYSTEM FUNCTION

Temperature indirectly affects ecosystem functions, such as food web stability, biomass accumulation, and carbon cycling, by directly changing species' activity and distribution patterns, biotic interactions, and community dynamics (Fagan *et al.* 1999, Chown & Gaston 2008, Traill *et al.* 2010, Nelson *et al.* 2013). In the final step of the fragmentation-temperature framework, we explore how warming-driven shifts at the species and community level can lead to changes in ecosystem function within remnant patches or across fragmented landscapes. We illustrate this concept using two important ecosystem functions: decomposition and pollination.

Litter decomposition helps maintain the carbon cycle, and soil temperature exerts strong effects on litter composition rates due to the temperature sensitivities of soil biota (Chen *et al.* 1999, Laurance *et al.* 2002, Crockatt & Bebber 2015). Studies consistently show decomposition rates are lower at patch edges than patch interiors due to the hotter, drier conditions at patch edges (Laurance *et al.* 2002, Crockatt & Bebber 2015), and Chen *et al.* (1995) propose that we should see gradients in decomposition rate from the patch edge to interior driven by thermal conditions (e.g. Crockatt & Bebber 2015).

Klein (1989) also found lower rates of dung decomposition in Amazonian forest fragments compared to continuous forest, which he links to high rates of heat-driven mortality in dung and carrion beetles at patch edges. Klein (1989) proposes that extreme temperatures at forest-clearing boundaries desiccate dung beetle larvae in the soil at patch edges and overheat adults venturing into cleared areas. This increased mortality of beetles has been implicated in a compositional shift in the carrion-feeding guild, with heat-tolerant ants becoming more dominant

and heat-sensitive carrion beetles less dominant in small fragments and cleared areas (Klein 1989, Fagan *et al.* 1999).

Much like decomposition, pollination often relies on the temperature-sensitive behavior and activity patterns of animals. For example, orchids rely entirely on euglossine bees for pollination, and foraging behavior in euglossine bees is thermally driven, limited by low air temperatures in the morning and by overheating in the late afternoon (Armbruster & Berg 1994, Traill *et al.* 2010). Studies suggest that bees have less time available for pollen-collecting behavior in remnant patches following fragmentation, leading to lower food intake for the bees and eventually lower fecundity in orchids (Traill *et al.* 2010). Perhaps because of restricted activity time, studies also show that many euglossine species disappear entirely from remnant patches following fragmentation, further jeopardizing the future of orchids and other beepollinated plant species (Laurance *et al.* 2002).

Higher temperatures often result in general ecosystem instability, as temperature accelerates biological rates and can lead to cyclic or erratic dynamics (Laurance *et al.* 2002, Nelson *et al.* 2013). This phenomenon has been observed at patch edges in the form of hyperdynamism, whereby edges experience faster rates of ecological processes, including population and species turnover (Laurance *et al.* 2002). Hyperdynamism makes patch edges intrinsically less stable than patch interiors, and therefore ecosystem functions that rely on ecological processes at patch edges (e.g., soil respiration and seed production) are also less stable (Laurance *et al.* 2002). For example, small mammal abundances fluctuate more widely in forest fragments than in continuous forest, particularly in the first few years following fragmentation (Malcolm 1991 cited in Laurance *et al.* 2002). These fluctuations in abundance can lead to more dramatic fluctuations in broader forest functioning, as small mammals perform critical roles in forest ecosystems including predation on insect herbivores and seed dispersal.

Critical gaps: The impacts of fragmentation on ecosystem functions are not well understood (Peh *et al.* 2014), and we need more studies directly addressing temperature's role in altered ecosystem functions in fragmented landscapes to better predict the trajectories of ecosystems following fragmentation. We predict the magnitude and direction of fragmentation's effects on ecosystem functions will depend on both the severity of temperature change at patch edges and the thermosensitivity of the species on which the key functions depend. We expect ecosystem functions that rely on thermally sensitive species (Table 2) will consistently respond negatively to fragmentation, while functions influenced by a wider range of biotic and abiotic factors should exhibit more variable responses (Peh *et al.* 2014).

1.4. FRAGMENTATION-TEMPERATURE FRAMEWORK: UNTESTED CONNECTIONS

The fragmentation-temperature framework provides a skeleton for measuring temperature's influences on processes across ecological scales, ranging from individuals to ecosystems, but there are untested connections that emerge from this framework that must be addressed for a more comprehensive understanding of fragmentation's impacts. Here we present two untested connections: 1) the relationship between thermal biology and patch isolation and 2) confounding factors in determining temperature's role in ecological responses.

1.4.1 THERMAL ISOLATION

Patch isolation can lead to extinction in fragmented landscapes (Ricketts 2001, Prugh *et al.* 2008, Haddad *et al.* 2015), and increasing evidence suggests that the thermal conditions available and species' thermosensitivity play a role in determining patch isolation, particularly in ectotherms (Currylow *et al.* 2012, Munguia-Vega *et al.* 2013).

For lizards in a Eucalyptus forest fragmented within a pine plantation, for example, mode of thermoregulation was considered a potential driver of isolation pattern (Mortelliti *et al.* 2015). The eastern three-toed earless skink (*Hemiergis talbingoensis*) gains heat by direct contact with warm substrate (thigmothermy) and had increased colonization rates of eucalypt patches embedded within the plantation. The southern rainbow skink (*Carlia tetradactyla*) gains heat by direct solar radiation (heliothermy) and instead had decreased colonization rates of eucalypt patches. The authors suggest these differences in colonization rates may stem from thermal biology, such that the high levels of shade associated with pine plantations facilitated dispersal in the thigmothermic species but acted as a barrier to the heliothermic species, which could no longer meet its thermoregulatory needs during dispersal (Mortelliti *et al.* 2015).

From a thermal perspective, the challenge of surviving dispersal in fragmented landscapes is multifaceted. First, the extreme surface temperatures in cleared areas means species have an intrinsically higher risk of exceeding their CT_{MAX} . In the Central Hardwoods Region of the U.S., for example, monthly average temperatures in cleared areas can be 13°C warmer than in forest patches and reach over 40°C (Currylow *et al.* 2012). These high matrix temperatures require that eastern box turtles (*Terrapene carolina carolina*) traveling through the region maintain significantly higher body temperatures when in the clearings than when in the forest (Currylow *et al.* 2012).

Additionally, matrix habitat often lacks thermal refugia, which limits opportunities to thermoregulate during dispersal. Likely resulting from thermal stress in cleared areas, box turtles in the Central Hardwoods maintained generally smaller home ranges, concentrated their movement along forest edges, and ventured only short distances into forest clearings. The long-term implications of these changes in movement behavior are not yet known, but Munguia-Vega *et al.* (2013) found that, for *Urosaurus nigricaudus* lizards, the inability to disperse through or

use a thermally hostile matrix could result in frequent, time-delayed extinctions in remnant patches.

Patch isolation is typically measured using the distance between patches, presence of movement corridors, and resistance of the matrix to the interpatch movement of individuals (Ricketts 2001). We believe that thermal conditions and thermosensitivity can be easily integrated into matrix resistance to identify potential dispersal barriers. The greater the distance between patches, and the smaller the differential between the thermal conditions available and the species' CT_{MAX}, the more significant the barrier to dispersal becomes (i.e. the greater the "thermal isolation"). Thermal isolation can be easily integrated into metapopulation, metacommunity, and connectivity models via thermally driven changes in colonization and network flow rates.

1.4.2 CONFOUNDING FACTORS

An important question emerging from this framework is how important is warming relative to other fragmentation impacts, such as resource loss, in determining species responses to fragmentation? Similarly, changes in thermal conditions are often confounded with other abiotic edge effects, such as increased light levels, greater dessication and evapotranspiration rates, and decreased soil moisture and humidity (Murcia 1995, Chen *et al.* 1999; Didham & Lawton 1999; Laurance *et al.* 2004). How do we begin to disentangle the effects of changes in thermal conditions from other abiotic changes?

At this stage, we can only point to this gap in our understanding of temperature's role in ecological responses to fragmentation. Forest-interior species have multiple adaptations to their forest environment, and expanding our knowledge of thermal biology may not be useful if it is primarily resource availability, nesting sites, cover from predators, or low light levels that restrict

species to continuous forest stands. Manipulative experiments altering thermal conditions, while holding other abiotic and biotic variables constant, will be fundamental to teasing apart temperature's relative influence.

We expect that warming is a significant effect of fragmentation for diurnal, thermally sensitive (Table 2), ectothermic species in forest ecosystems, as well as for community dynamics and ecosystems functions dependent on such species. Thermal generalist, nocturnal, and endothermic species are presumably less affected by fragmentation-driven warming. We also expect the fragmentation-temperature framework is less relevant to species in ecosystems where fragmentation does not result in higher temperatures and greater thermal variability. However, much more research is needed to begin to address this untested connection.

1.5. CONCLUSION: TREATING TEMPERATURE AS A MECHANISM IN FRAGMENTATION RESEARCH

The field of thermal biology has progressed rapidly over the last 50 years, and topics once restricted to thermal biology—including thermal performance curves—are finding new life in climate change research and new applications to ecological problems (Angilletta 2009). The integration of thermal biology into climate change research has led to important advancements in our understanding of extinction risk under global warming scenarios, and we expect that integrating thermal biology into fragmentation research can lead to equally large advancements in our understanding of fragmentation's ecological consequences.

Temperature increases that result from the fragmentation process and increases that result from global climate warming differ in important ways, primarily the spatial arrangement and time frame over which the temperature increases occur. Fragmentation-driven temperature increases occur instantly, as opposed to gradually, limiting opportunities for genetic adaptation

and relying more heavily on behavioral and phenotypic plasticity (Sinervo *et al.* 2010, Somero 2010). Increases are also concentrated at patch edges, likely leading to species' responses that vary along fine-scale thermal gradients. These warming patterns remain an underexplored mechanism affecting individuals, species, communities, and ecosystems in fragmented landscapes.

The research methods used to study the effects of temperature in fragmented landscapes require the same tools used in climate change and thermal biology research. These include high-resolution temperature sensors, infrared imagery, field body temperature sensors, laboratory experiments measuring and manipulating thermosensitivity, as well as maps and models of thermal conditions. In particular, we suggest researchers apply these research methods to the long-term, large-scale fragmentation experiments that exist throughout the world (Debinski & Holt 2000, Haddad *et al.* 2015), many of which offer opportunities to study the effects of temperature in controlled, replicated, before-after experimental setups. Fragmentation experiments can further thermal biology research, which is historically laboratory based, because they provide an opportunity to test laboratory findings in a field system. Fragmentation experiments can also further climate change research because temperature increases following fragmentation provide opportunities to test models and predictions regarding species responses to warming.

Understanding the connection between fragmentation-driven temperature increases and ecological responses requires more than just additional experiments. It requires the development of new theory to deal with temperature as a mechanism driving change in fragmented landscapes. Here we presented two untested connections (thermal isolation and confounding factors), but countless connections remain to be explored, including defining climate space in fragmented versus continuous forests for niche modeling (Kearney & Porter 2009) and

developing quantitative models of restrictions in activity time in remnant patches that build upon those that exist for climate change (Kearney 2013, Gunderson & Leal 2016).

Scientific understanding advances most rapidly when theories and findings from multiple disciplines are integrated, and fragmentation research has succeeded in incorporating a variety of ecological subfields, including invasion, disease, community, and ecosystem ecology. However, thermal biology has remained outside the scope of fragmentation research, even though fragmentation changes temperature and thermal biology examines the effects of temperature change on biological and ecological processes.

Temperature is unique in its pervasiveness, influencing all levels of biological processes, from genes to interactions to energy flow. As Angilletta (2009, pg.1) explains, "Unlike many other variables that concern biologists, temperature is not just a property of life; it is a property of matter. Nothing escapes its control." We need to combine our understanding of the effects of fragmentation on temperature with our understanding of the effects of temperature on organisms to gain a more comprehensive understanding of the mechanisms behind biodiversity loss in remnant patches and to provide new strategies for habitat conservation in an increasingly fragmented and heated world.

CHAPTER 2

SHRINKING SKINKS: LIZARD BODY SIZE DECLINES IN A LONG-TERM FOREST FRAGMENTATION EXPERIMENT²

2.1 ABSTRACT

Increasing rates of habitat fragmentation underscore the importance of understanding the full spectrum of its ecological consequences. Here, we test the effects of fragmentation on body size using lizards collected over 29 years in the controlled and replicated Wog Wog fragmentation experiment. We found that lizards were smaller in forest fragments relative to those in the non-fragmented controls after the fragmentation treatment was applied. We also found that, for lizards within forest fragments, the greater the exposure to deforested areas, the greater the decline in body size. This pattern was strongest in the first five years following fragmentation and weakened or reversed over time as the matrix surrounding the fragments matured. Although it is not possible to unequivocally attribute size declines to temperature, our findings are consistent with predictions made under the temperature-size rule that ectotherms will be smaller in fragmented landscapes because of temperature increases at newly created edges. These results raise new concerns about the effects of fragmentation on organisms in remnant patches and offer new research priorities, as more evidence is needed to determine the generality of body size declines in fragmented landscapes. Results also question whether the widespread size declines, often attributed to climate change, may be caused or at least amplified by habitat fragmentation, which has been global in its impact.

² Tuff, K. T., Glidden, C. K., Nix, H. A., Melbourne, B. A., Meyers, J. A., Sarre, S. D. & Davies, K. F. (*in review*). "Shrinking skinks: lizard body size declines in a long-term forest fragmentation experiment."

2.2 INTRODUCTION

Habitat fragmentation is one of the greatest contributors to biodiversity loss worldwide (CBD 2010) and increasing rates of fragmentation underscore the importance of understanding the full spectrum of its ecological consequences. While a wealth of studies examine species and community-level responses to fragmentation (Ewers & Didham 2005, Hill *et al.* 2011, Fahrig 2013), few have focused on fragmentation-driven changes in individual morphology, such as body size (Lomolino & Perault 2007). This trend arises despite evidence from natural systems that changes in morphology can be rapid in response to novel selection pressures (Stuart *et al.* 2014, Salvidio *et al.* 2015) and the importance of morphological traits for organism survival.

Body size influences nearly all physiological and ecological processes (Sumner *et al.* 1999). According to the rules of allometric scaling, body size provides intrinsic constraints on many aspects of an individual's performance, such as foraging capacity, sprint speed, ingestion rate, immune function, and fecundity (Peters 1983, Brown *et al.* 1993). These restrictions extend beyond physiology to include constraints on an individual's success in biological interactions, such as competition for mates, predator avoidance, and territory acquisition and defense (Peters 1983, Mathis 1990). Thus, shifts in body size in response to fragmentation-driven changes in the physical and ecological environment could in turn influence the capacity for individuals to survive, compete, and reproduce in the landscape.

Studies on the effects of fragmentation on body size have found contrasting results. Some studies have found that individuals in fragmented habitat are larger than individuals in continuous habitat (butterflies, Norberg & Leimar 2002; grasshoppers, Heidinger *et al.* 2010; edible dormouse, Fietz & Weis-Dootz 2012), while others have found that individuals in fragmented habitat are smaller than individuals in continuous habitat (prickly skinks, Sumner *et al.* 1999; small mammals, Lomolino & Perault 2007; beetles, Henríquez *et al.* 2009; frogs,

Delgado-Acevedo & Restrepo 2008). These size differences have been attributed to differences in dispersal requirements (Norberg & Leimar 2002, Heidinger *et al.* 2010, Forsman *et al.* 2011), competitive or predatory pressures (Fietz & Weis-Dootz 2012), and the availability of resources (Sumner *et al.* 1999, Henríquez *et al.* 2009) between fragmented and continuous habitat. However, most studies emphasize that the mechanisms underlying body size patterns have not been rigorously tested.

There are two common shortcomings in fragmentation-body size studies: 1) most studies are conducted in non-manipulated habitats, which makes isolating fragmentation's effects from other confounded differences difficult and 2) most studies explore fragmentation-size relationships developed over long (200-1000 years) or unknown time scales. Here we attempt to overcome these shortcomings by examining body size patterns within a long-term, large-scale forest fragmentation experiment and as early as one year following the application of the fragmentation treatment.

In this study, we report on body size change in the heliothermic, ground dwelling common garden skink (*Lampropholis guichenoti*), within the Wog Wog habitat fragmentation experiment in southeastern Australia (Margules 1992). We use body size data spanning 30 years to experimentally test the prediction that lizards will experience morphological changes in forest fragments but not in the non-fragmented controls. In addition, we predict that the degree of fragmentation (i.e. patch size and proximity to edge) would determine the extent of morphological changes, which we tested by comparing differences among fragmented populations. Specifically, we tested whether 1) individuals in the smallest remnant forest patches would change more than those in the largest patches and 2) individuals at the edge of remnant patches would change more than those in patch interiors. In addition, we asked whether the

recovery of the pine plantation matrix habitat over time could foster a return to former skink



Figure 4: Map of the experimental site showing forest remnants and control plots. A) 1987 photo of a remnant Eucalyptus patch immediately after the fragmentation treatment was applied; B) 2011 photo of a slope site, which are generally warmer and drier; C) 2011 photo of a drainage site, which are generally cooler and wetter. body sizes as the effects of fragmentation ease.

Without additional experiments, it is not possible to determine whether morphological changes following fragmentation are genetic responses to altered selection pressures or the result of phenotypic plasticity (Sumner *et al.* 1999). We also cannot determine which of fragmentation's many effects drive body size changes. Here we explore the support for three possible mechanisms by comparing differences in body size observed between populations in fragmented and non-fragmented forest with differences in prey biomass, predator abundance, and thermal conditions, which can influence growth rates and/or survivorship in fragmented landscapes.

2.3 MATERIALS AND METHODS

Wog Wog:

Wog Wog is the name of a mountain, a river, and a former cattle property on the coastal side of a tableland escarpment in southeastern New South Wales, Australia (37°04'30" S, 149°28'00" E). The experiment is situated in *Eucalyptus* forest, which was being cleared for a softwood (*Pinus radiata*) plantation (Margules 1992). The Wog Wog habitat fragmentation experiment (hereafter referred to as "Wog Wog") was established by CSIRO and remains one of the oldest and largest fragmentation studies in the world (Collinge 2009).

The full experimental design is provided in Margules (1992). Briefly, sampling at Wog Wog began in February 1985 when six replicates were delineated. Each replicate consists of three plots: one small (0.25 ha; $50m^2$), medium (0.875 ha; $93.5m^2$), and large (3.062 ha; $175m^2$). Dispersal distance between plots has been controlled for, as all plots are approximately 50m apart (Margules 1992). Four of the six replicates became habitat fragments when the surrounding *Eucalyptus* forest was cleared two years later in 1987. Two replicates remain in adjacent continuous forest and serve as non-fragmented control plots (Fig. 4). Each plot has eight monitoring sites, giving a total of 144 sites across the six replicates. Each monitoring site has two permanent pitfall traps (90 mm wide x 100 mm deep). We combine captures from the two traps into a single sample before processing. Traps are opened for seven days, four times a year, once during each season.

Sites are further stratified by proximity to the edge of a plot (edge vs. interior). Edge sites are located within 5.4 ± 0.4 m (mean \pm S.E.) of plot edges; interior sites are located as close to plot centers as possible (Margules 1992, Farmilo *et al.* 2013). In the continuous forest, plot size and proximity to edge are artificial boundaries but control plots were designed to match the spatial arrangement of sampling plots in fragments as much as possible. The overstory at Wog Wog is a mixture of *Eucalyptus* species and sites are additionally stratified by type of understory vegetation associated with topography (slope vs. drainage lines). Slope sites are warmer and drier, characterized by a grassy understory, native plant litter, and herbaceous vegetation. Drainage line sites are cooler and wetter, characterized by dense shrub thickets of *Kunzea ericoides* and *Lomandra* species (Austin & Nicholls 1988, Farmilo *et al.* 2013).

Skink morphometrics:

The garden skink is a small, heliothermic lizard widely distributed in southeastern Australia (Cogger 2000). They are active, opportunistic feeders and forage widely within relatively small home ranges (20m², Anderson & Burgin 2002). *L. guichenoti* populations exhibit a rapidly maturing, high-turnover demographic pattern (average lifespan of 2-3 years) (Cogger 2000, Hutchinson 1993). Adults average 40 mm in snout-vent length (SVL), which is measured from the tip of the nose to the cloaca and excludes the tail. Juvenile skinks grow rapidly until sexual maturity is reached within one year, after which growth continues but at much slower rates (Hutchinson 1993). Most skinks do not survive long enough to reach an age where growth has ceased completely (Hutchinson 1993).

Over 2500 skinks have been trapped at Wog Wog since 1985 and are maintained at the Australian National Wildlife Collection, CSIRO. To controls for differences in the age of individuals, we restricted samples for this study to adult specimens. Because males and females attain equivalent body lengths and generally lack sexual dimorphism (Torr & Shine 1993), we did not control for gender in this study. This resulted in a sample size of 1,199 adult *L. guichenoti* individuals.

To measure SVL, skink specimens were flattened between two plates of glass to form a slide. Glass plates helped reduce curvature and minimize measurement bias across individuals. Each slide was then photographed using the SatScan imaging system (SmartDrive Limited, Huntingdon, Cambridgeshire, UK; for details, see Mantle *et al.* 2012). SatScan uses a combination of hardware and software that captures a series of 200-400 images at precisely monitored positions. These images are then stitched together to create a high-resolution final image with minimum distortion (Mantle *et al.* 2012) (Fig. 5). SVL served as a proxy of overall body size because all other measured traits (head width, body width and femur length) were



Figure 5: Skink specimens pressed between glass plates and photographed using the SatScan imaging system. SatScan captures a series of 200-400 images at precisely monitored positions and stitches the images together into a single, high-resolution image. Insert shows a single individual from a SatScan image, in order to highlight the precision with which individuals can be measured.

linearly correlated (r(1159)=0.70, p<0.001; r(1159)=0.67, p<0.001; r(1172)= 0.51, p<0.001, respectively). Hereafter, SVL is referred to as "body size."

Body size was measured three times per individual using the ImageJ software (Version 1.44o, Rasband 2011). We used the mean of the three repeated measurements as the sample unit in analyses that compare population means across treatments. Using a variance components analysis, we estimated the standard deviation of repeated measurements on an individual to be 0.279 mm. Thus, the standard error of the mean for three repeated measurements was 0.16 mm or

less than half a percent of the mean snout vent length.

Time blocks:

Individuals were binned into five time blocks to ensure sample sizes were sufficient for analyses across treatments. Time blocks correlate with increased growth of the pine matrix surrounding the patches and represent distinct thermal conditions. Individuals were binned according to the year of their capture: *pre-fragmentation* (two years before the fragmentation treatment was applied), *bare forest* (first five years following fragmentation), *seedling forest* (six to nine years post fragmentation), *sapling forest* (ten to thirteen years post fragmentation), and *young forest* (23 to 26 years post fragmentation). Years refer to biological years, which, in the southern hemisphere, begin in the spring (September) of one calendar year and end in the winter (August) of the following calendar year. Fragmentation was applied over the course of nine months in 1987, so individuals trapped in year three were not included in the analysis.

Data analysis:

The experimental design at Wog Wog is highly structured and requires an analysis that incorporates the nested treatment structure applied to the fragments and controls (Davies & Margules 1998). We used a linear mixed model for body size analyses. We included four fixed effects in the model (Davies & Margules 1998): **1**) *Fragmentation*: a variable with two levels: (i) fragmented forest and (ii) continuous forest, that tests for the effect of forest fragmentation. **2**) *Patch size within fragmentation*: a variable that describes the interaction between fragmentation and size. It has four levels: (i) small, (ii) medium, (iii) large, and (iv) controls, and tests for an effect of plot size nested within the fragmentation treatment.

We modeled patch size in two ways: first as a continuous variable and additionally as a categorical variable to check for a nonlinear or non-monotonic response. When treated as a continuous variable, patch size was logged and centered, while controls were set to zero (the center) and only the interaction of *Fragmentation:Patch size within fragmentation* was fitted together with the main effect of *Fragmentation*. This parameterization of the linear model correctly estimates separate parameters for the main effect of fragmentation and an effect of patch size within fragments only. Fitting patch size as a categorical variable did not reveal any nonlinear responses. **3**) *Edge within fragmentation*: a variable that describes the interaction between fragmentation and edges. It has two levels: (i) edge and (ii) interior. All sites in the continuous forest are categorized as interior. **4**) *Habitat*: a variable nested within plots with two levels: (i) slope and (ii) drainage lines.

Because of the experiment's nested design, data are collected at three spatial scales. Individuals are trapped at pitfall *sites* (1-144), which are nested within *plots* (1-18), which are

nested within *replicates* (1-6). Thus, we included three random effects: *Replicate, Plot,* and *Site*. For each of the five time blocks, we tested for the effects of *Fragmentation, Patch size, Edge,* and *Habitat* on mean body size, as well as the interactions between *Fragmentation: Habitat* and *Patch size: Edge,* while accounting for body size variance associated with *Replicate, Plot* and *Site.* Models were fitted in R (Version 3.1.1, R Development Core Team 2008) using the lmer function in the lme4 package (Version 1.1-7, Bates *et al.* 2014). Significance of fixed effects was assessed using likelihood ratio tests. Plots of residuals suggested that assumptions of normality and homogeneity of variance were satisfied.

Beetle biomass:

To address the alternative hypothesis that body size changes in forest fragments were due to changes in food availability, we compared body size patterns to changes in beetle biomass. While *L. guichenoti* is an opportunistic feeder, beetles are frequent prey items (comprised 15-25% of gut contents (Lunney *et al.* 1989) and occurred in >66% of stomachs examined (Crome 1981)). Thus, beetle biomass served as a rough measure of food availability. We first measured beetle abundance by recording the number of beetles trapped at each site. Records of beetle species have so far been processed up until 1991 (five years post-fragmentation), over which time 655 beetle species were captured. Body length (mm) was measured for every species. We included all beetle species in prey abundance measurements, except species \geq 20 mm in length. Lunney *et al.* (1989) found no prey items \geq 20 mm in the stomach contents of *L. guichenoti*, suggesting prey of this length are too large for consumption. This resulted in the inclusion of 654 species (54,727 individuals), ranging from 0.6 to 19 mm.

We converted beetle abundance to beetle biomass using the length-weight allometries provided in Sample *et al.* (1993). In our calculations, we used family-specific parameter values to account for the variety in body shape within the order Coleoptera. For species in which

family-specific values were not available, we used a value generalized for Coleoptera. We used the values derived from Model 2 in Sample *et al.* (1993), which includes both length and width as independent variables.

Predator abundance:

To address the alternative hypothesis that body size changes in forest fragments were driven by changes in predation pressure, we compared body size patterns to changes in the abundance of avian predators. Birds are primary predators of *L. guichenoti* (Anderson & Burgin 2008), so their abundance served as a rough measure of predation pressure. Only species that consume small reptiles, as gleaned from the literature (Parsons 2007, Slater *et al.* 2006), were included. This resulted in the inclusion of 31 species (1,449 individuals).

Avian species richness and abundance were surveyed in each plot. However, the number and levels of transects differed according to plot size. Small plots were sampled as a single transect. Medium plots were sampled as two transects, stratified according to topography: upslope or downslope. Wog Wog is located in a river basin, so transects on the plot side nearest the river are downslope and transects on the side furthest from the river are upslope. Transects in large plots are further stratified by orientation (east or west). Thus, large plots have four transects: east-upslope, west-upslope, east-downslope, and west-downslope. This gave a total of 42 transects.

Species and abundance counts were based on sight and call. Species occurring inside of plots were scored and abundance recorded. Species occurring outside of plots were excluded. Sampling was conducted as an asymptotic count (successive additions of five-minute intervals until an asymptote of species richness was reached for each transect). Plots were sampled during the peak plant growth period (last week of October/first week of November) from 1985-1999 and again in 2009.

Temperature measurements:

Temperature data were not collected at Wog Wog until 2011. Thus, to address body size trends in the initial time blocks, we rely on well-documented pattern in mean and maximum temperatures (Tuff *et al.* 2016). Regional weather data were available but could not explain size differences between populations in patches only 50 m apart.

2.4 RESULTS

Pre-Fragmentation time block (2 years pre-fragmentation): We trapped few individuals in the two years before the fragmentation treatment was applied so there were insufficient data to test for differences between control and fragment plots (fragment plots were still in continuous forest at this time). For completeness, a density plot is shown for pre-treatment body sizes (Fig. 6). Overall body size mean was 38.26 mm (s.e. 1.03 mm).

Bare forest time block (1 to 5 years post-fragmentation): Skinks in the fragmented forest were 7.62% smaller than those in the continuous forest (effect size = -2.76mm, s.e. = 0.66, p<0.001) (Fig. 3). Body size within fragments declined from large to small patches with a slope of 0.688 (s.e. = 0.30, p = 0.023) for the relationship between body size and log patch size. Relative to the controls, individuals were 4.36% smaller in large patches, 6.36% smaller in medium patches, and 9.84% smaller in small patches. Skinks were also smaller at the hotter edge sites than cooler interior sites but the effect of edge was not significant (effect size = 0.02mm, s.e. = 0.49, p = 0.949). Skinks were significantly smaller at hotter slope sites than cooler drainage sites (effect size = -1.10mm, s.e. = 0.43, p = 0.021). Beetle biomass was 19.44% higher in the fragments than in the control plots (Fig. 7). Avian predator abundance was 37.33% lower in the fragments than in the control plots (Fig. 7).



Figure 6: Skink body size (snout-vent length) in forest plots within the Wog Wog experiment in New South Wales, Australia. Data are binned into time blocks according to time since the fragmentation treatment was applied: *pre-fragmentation* (two years before fragmentation), *bare forest* (first five years following fragmentation), *seedling forest* (6-9 years post fragmentation), *sapling forest* (10-13 years post fragmentation), and *young forest* (23 to 26 years post fragmentation). Leftmost panels: kernel density plots; also shown are mean body size (solid vertical lines) and standard error (dotted vertical lines) for individuals in continuous and fragmented *Eucalyptus* plots. Sample sizes are shown. Right panels: body size means and 95% confidence intervals across fragmentation sub-treatments: plot size, proximity to edge, and habitat type. Sites in the continuous forest were categorized as interior sites (for proximity to edge) and as slope or drainage sites (for habitat type). Stars indicate level of significance of the treatment effect in linear mixed model analyses. Regression lines show the slope of the relationship between body size and log patch size.



Figure 7: Avian predator abundance (top row) and beetle biomass (bottom row) in fragmented versus continuous *Eucalyptus* forest plots within the Wog Wog experiment. Beetle abundance records have been processed from 1985-1991, so only the *Pre* and *Bare* time blocks are shown. Bird survey data spans 1985-1999 and 2009, so all time blocks are shown. Barplots show mean, 95% confidence intervals, and sample size.

Seedling forest time block (6 to 9 years post-fragmentation): Skinks in the fragmented forest were 8.26% smaller than those in the continuous forest (effect size = -3.15mm, s.e. = 0.43, p<0.001). Body size varied less across patch size, although individuals remained smallest in the smallest patches. Size declined from large to small patches with a slope of 0.19 (s.e. = 0.14, p = 0.149) for the relationship between body size and log patch size. Skinks varied little between edge and interior sites (effect size = -0.43mm, s.e. = 0.27, p = 0.127). Skinks were again significantly smaller at slope sites than drainage sites (effect size = -0.86mm, s.e. = 0.25, p<0.001). Avian predator abundance was 35.20% lower in the fragments than in the control plots.

Sapling forest time block (10 to 13 years post-fragmentation): Many patterns associated with fragmentation and body size disappeared by the later two time blocks. Skinks were only slightly and not significantly smaller (3.42%) in fragmented versus continuous forest (effect size

= -1.31mm, s.e. = 0.76, p = 0.072). The relationship between body size and log patch size had a slope of 0.02 (s.e. = 0.32, p = 0.951). Edge trends reversed, such that skinks were significantly smaller at interior sites than edge sites (effect size = -1.04mm, s.e. = 0.46, p = 0.024). Skinks were again significantly smaller at slope sites (effect size = -1.09mm, s.e. = 0.42, p = 0.008). Avian predator abundance was 97.98% lower in the fragments than in the control plots.

Young forest time block (23 to 26 years post-fragmentation): Skink body size no longer differed between fragmented and continuous forest (effect size = -0.07mm, s.e. = 0.89, p = 0.922) and overall mean body size was only 0.19 mm different than when the experiment began (mean = 38.45 mm, s.e. = 0.32). Body size no longer varied across patch edge (effect size = -0.69mm, s.e. = 0.87, p = 0.317). The relationship between body size and log patch size had a slope of 0.26 (s.e. = 0.49, p = 0.627). The effect of habitat was no longer significant (effect size = -0.68mm, s.e. = 0.66, p = 0.318) but skinks remained smaller at slope sites. Avian predator abundance was 43.65% lower in the fragments than in the control plots.

There were no significant interactions between *Fragmentation: Habitat* or *Patch size*: *Edge* in any time blocks. Random effects accounted for little of the variance in body size: *Replicate* (0% in all time blocks), *Plot* (ranged from 0.97-6.94%), and *Site* (ranged from 0-5.26%). For a summary of body size means, standard error, and sample size, see Table 3.

		Pre-fragmentation		Bare forest			Seedling forest			Sapling forest			Young forest			
Variable	Level	n	Mean	s.e.	n	Mean	s.e.	n	Mean	s.e.	n	Mean	s.e.	n	Mean	s.e.
Fragmentation	Controls	3	34.61	3.34	61	38.02	0.54	73	39.33	0.43	28	37.80	0.73	44	38.34	0.46
Fragmentation	Fragments	11	39.25	0.82	222	35.30	0.24	518	36.35	0.12	160	37.14	0.21	66	38.77	0.41
Patch Size	Large				59	36.40	0.47	175	36.65	0.21	42	37.42	0.38	25	38.77	0.70
Patch Size	Medium				60	35.67	0.44	152	36.38	0.22	51	36.65	0.37	26	38.86	0.66
Patch Size	Small				103	34.45	0.33	191	36.06	0.20	67	37.35	0.34	15	38.61	0.85
Edge	Interior				186	36.18	0.30	338	36.85	0.18	108	37.00	0.30	75	38.32	0.40
Edge	Edge				97	35.32	0.34	253	36.56	0.18	80	37.59	0.26	35	39.18	0.46
Habitat	Drainage	8	38.79	1.66	130	36.52	0.34	277	37.18	0.20	92	37.81	0.29	58	38.95	0.41
Habitat	Slope	6	37.54	1.02	153	35.35	0.30	314	36.34	0.16	96	36.71	0.29	52	38.21	0.46

Table 3: Summary of skink body size data across forest fragmentation treatments: 1) *Fragmentation*: a variable with two levels: (i) Controls and (ii) Fragments; 2) *Plot size*: a variable nested within the fragmentation treatment with three levels: (i) Large, (ii) Medium, (iii) Small; 3) *Edge*: a variable nested within plots which has two levels: (i) Interior and (ii) Edge; and 4) *Habitat*: a variable nested within plots which has two levels: (i) Drainage and (ii) Slope. Table includes sample size, mean snout-vent length (mm), and standard error calculated from the raw data for each time block.

Random effect	Pre	Bare	Seedling	Sapling	Young
Site		0	5.02	5.26	0
Plot		0.97	1.53	3.53	6.94
Replicate		0	0	0	0
Residual		99.03	93.45	91.21	93.06

Table 4: Summary of the percent variance in body size (MSV) explained by random effects in linear mixed model analyses in each time block.

2.5 DISCUSSION

Fragmentation is a primary threat to biodiversity worldwide (CBD 2010) but the effects of fragmentation on body size remain unclear. In this study, we used lizards captured over 29 years in a large-scale forest fragmentation experiment to test predictions related to body size changes following fragmentation. We found that lizards were smaller on average in forest fragments relative to those in the non-fragmented controls after the fragmentation treatment was applied. We also found that lizards within forest fragments declined in size according to exposure to fragmentation's effects. This pattern was strongest in the first five years following fragmentation, during which body size was linearly and positively related to log patch size (Fig. 6), but it continued into the *seedling forest* time block.

However, the edge and size trends observed in the early time blocks weakened and sometimes reversed over time. By the *sapling forest* time block (10-13 yrs. post fragmentation), the differences in body size between individuals in the continuous forest and fragments had lessened considerably. By the *young forest* time block (23 to 26 yrs. post fragmentation), skinks were no longer smaller in the fragments, while skinks had become larger at patch edges than interiors. It is likely that the absence and/or reversal of patterns in the later time blocks is related to regrowth of the pine plantation surrounding the patches, which could weaken fragmentation's

effects. By the *young forest* time block, the native forest was shorter than the pine plantation (mean height: 25.0 ± 0.6 m compared with 28.9 ± 1.1 m) and patches were often overtopped and shaded by the matrix surrounding them (Farmilo *et al.* 2013).

Understanding the relationship between landscape structure and body size is an important component of conservation planning because body size influences both the performance and long-term survival of individuals (Kingsolver & Huey 2008). In our study, individuals in the fragmented forest ranged from 7-8% (~3 mm) smaller than those in the continuous forest in the first two time blocks following fragmentation. While small, this difference is likely ecologically significant. A study on red-backed salamanders (*Plethodon cinereus*; ~38 mm SVL), for example, found that a 3 mm difference in SVL conferred a competitive advantage in contests over resources (Mathis 1990). Additionally, the linear relationship between body size and most fitness correlates suggests that smaller individuals are inevitably less fit (Brown *et al.* 1993, Kingsolver & Huey 2008).

Size differences in individuals between habitat types may reflect differences in growth rate, survivorship, or both. Food availability has strong proximate effects on growth rates of lizards (Sinervo & Adolph 1989) and reductions in food resources following fragmentation have been linked to declines in mean body size in fragments (Sumner *et al.* 1999, Bucher & Entling 2011). To explore this hypothesis, we compared body size patterns to changes in beetle biomass. Although *L. guichenoti* is an opportunistic feeder, beetles are important and frequent components of their diet (Lunney *et al.* 1989, Crome 1981) and thus provide an estimate of invertebrate prey availability. However, mean beetle biomass increased 69% in forest fragments immediately following fragmentation (Fig. 7), suggesting initial size declines were not due to decreased availability of prey items.

Changes in the size of individuals may also result from differences in selective pressures in fragmented habitat. For example, changes in habitat structure due to forest removal can increase vulnerability to predation and lead to a related decline in mean body size in remnant patches (Sumner *et al.* 1999). To explore this hypothesis, we compared body size patterns to changes in the abundance of avian predators. However, mean predator abundance in the fragments decreased by 28% immediately following fragmentation and remained lower than the controls across all remaining time blocks (Fig. 7), suggesting that size declines in the fragments were not due to increased predation pressure. Notably, skinks are also a major prey item for many elapid snakes (Downes & Shine 2001), which were not included in this study. Effects of fragmentation on snake populations will be investigated in future studies at Wog Wog.

An alternative explanation is that differences in thermal conditions underlie size differences between populations in fragmented and continuous forest. Body size in ectotherms often depends on the temperature experienced during development (Angilletta *et al.* 2004, Kingsolver & Huey 2008). An increase in incubation temperature causes a decrease in adult body size in >83% of ectothermic species studied to date (Atkinson 1994, Forster *et al.* 2012). This thermal plasticity of body size—termed the temperature-size rule—has long been recognized (Standfuss 1895) and has been shown to apply extensively among ectothermic animals (Atkinson 1994).

While the mechanisms underlying the temperature-size rule are difficult to determine, much of the literature points to a temperature-driven decoupling of an individual's growth rate (increase in weight per time) and developmental rate (increase in life stage per time) (Forster *et al.* 2011, Sheridan & Bickford 2011). The incubation period for *L. guichenoti*, for example, decreases from 150 to 27.8 days following a 15°C increase in incubation temperature (Shine1983). In addition, individuals were smaller at the hotter slope sites than at the cooler

drainage line sites in all time blocks, and the difference was significant in three out of four time blocks. While this relationship exists largely outside the context of fragmentation, because habitat categories are based on understory vegetation and topography, it is suggestive of a temperature-size rule relationship in *L. guichenoti*.

Higher temperatures at forest edges following fragmentation (Murcia 1995, Chen *et al.* 1999, Ewers & Banks-Leite 2013) suggest that reduced body size in ectothermic species is likely in fragmented landscapes because of the temperature-size rule. Indeed, one of the most immediate and consistently documented effects of forest fragmentation is an increase in direct and diffuse solar radiation at newly created edges, resulting in higher surface temperatures within remnant forest patches (Tuff *et al.* 2016). Studies show daytime air temperatures average 2-5°C higher at patch edges than patch interiors, daytime soil temperatures average 7-9°C higher at patch edges than patch interiors, and maximum air temperatures at edges can average up to 10°C higher than patch interiors (citations in Tuff *et al.* 2016). Although it is not possible to unequivocally attribute size declines to temperature, three lines of evidence support this interpretation: (i) the decrease in body size within fragments corresponded with reforestation, which decreases temperature; and (iii) the direction of the phenotypic change is consistent with physiological knowledge.

While we cannot conclusively say that biological factors were not responsible for the observed size trends, these results raise an interesting question: What is the relative influence of abiotic versus biotic drivers of body size in natural systems? In this study, body size trends were opposite to those expected if they were driven by the biological factors we examined, i.e. body size declined in fragments, despite an increase in prey biomass and a decrease in avian predators. If these biological drivers were operating at the same time as temperature, this suggests that

changes in temperature have the potential to trump biological drivers in terms of influence on body size. More studies—particularly manipulative experiments—are needed to begin to answer this question.

This study provides strong experimental evidence that forest fragmentation can lead to body size declines in ectothermic organisms. Further, the convergence of body size in the continuous and fragmented forest following matrix reforestation suggests that the consequences of fragmentation on body size might be mitigated or reversed through conservation strategies that target restoration of the structural environment. Experimental studies linking reforestation and phenotypic change will provide critical information on the generality and strength of this relationship.

As a final note, there has been a surge of correlative studies in the last five years linking global climate trends to body size declines across taxa and often in terrestrial systems (Sheridan & Bickford 2011, Gardner *et al.* 2011, Caruso *et al.* 2014). Our results raise the possibility that the widespread body size declines attributed to climate change may be caused, partially caused, or at least amplified by habitat fragmentation, which has been equally global in its impact (Haddad *et al.* 2015). We suggest studies control for temperature increases driven by land cover change when correlating body size declines and long-term climate trends in terrestrial species. Such information will help improve projections of future size declines and other thermally driven responses in the context of both habitat fragmentation and climate warming.

CHAPTER 3

COMPARING DIRECT AND INDIRECT EFFECTS OF FRAGMENTATION ON LIZARD ABUNDANCE WITHIN THE WOG WOG EXPERIMENT

3.1 INTRODUCTION

Understanding the factors that determine a species' spatial distribution is a central objective in ecological research, with applications to predicting range shifts, extinctions, and biological invasions following changes in environmental conditions (Guissan & Thuiller 2005, Buisson *et al.* 2008, Elith & Leathwick 2009, Xiaojun *et al.* 2011). In recent years, studies have turned to the mechanisms underlying distribution patterns and, specifically, to the power of environmental variables, such as air temperature or habitat structure, to predict where species might occur in their current range and in the future given changes in environmental conditions (Reino *et al.* 2013, Brown & Yoder 2015, Willis *et al.* 2015). Species distribution models (SDMs) relate field observations of occurrence at a site (abundance or presence/absence) with the underlying environmental variables of that site to estimate the species' environmental requirements (i.e. environmental niche) (Guissan & Thuiller 2005, Elith & Leathwick 2009, Kearney & Porter 2009).

Studies suggest that landscape factors that influence dispersal (e.g. habitat fragmentation) can be even stronger determinants of distribution patterns than environmental factors that regulate eco-physiology, such as thermal conditions (Warren *et al.* 2001, Guissan & Thuiller 2005, Buisson *et al.* 2008, Reino *et al.* 2013). This is because species distributions are determined not only by environmental suitability, but also by the species' ability to disperse through the landscape to reach suitable habitat patches (Pearson & Dawson 2003, Svenning & Skov 2004, Guissan & Thuiller 2005, Reino *et al.* 2013, Willis *et al.* 2015). Habitat

fragmentation reduces connectivity in the landscape via habitat removal, which can prevent species from reaching optimal habitat even when present.

Habitat fragmentation (hereafter: fragmentation) can be defined as the division of oncecontinuous habitat into smaller, more isolated patches separated by a matrix of humantransformed land cover (Haddad *et al.* 2015). Most fragmentation results in patches surrounded by a matrix of low biomass and low structural complexity, such as pasture, cropland, or concrete, with environmental conditions unlike those of the remaining habitat patches (Murcia 1995, Tuff *et al.* 2016). In this study, we explore the effects of fragmentation on species distribution in a low-habitat-contrast setting: native *Eucaplytus* forest patches surrounded by 28-year old, nonnative *Pinus radiata* timber plantation. Despite the low contrast in patch and matrix types, structural and compositional differences between pine and *Eucalyptus* forests still lead to differences in environmental conditions that can affect how species move through and use matrix habitat (Davies *et al.* 2001, Taylor *et al.* 2007, Farmilo *et al.* 2013).

Because fragmentation can influence a species' ability to access optimal habitat, dispersal ability provides an important consideration when comparing the strength of fragmentation versus environmental variables on distribution patterns. For example, Warren *et al.* (2001) found that fragmentation had a much stronger influence on distribution in dispersal-limited butterfly species than did environmental conditions. Specifically, distribution declined in 26 out of 28 dispersal-limited species in fragmented habitat, despite warmer thermal conditions that promoted faster larval growth rates, earlier flight periods, and increased abundance (Warren *et al.* 2001). However, nine out of 18 butterfly species that were not dispersal limited increased their distribution over the same time period, as predicted by favorable environmental conditions (Warren *et al.* 2001). Here we compare the impacts of fragmentation and environmental variables on the distribution of a small, generalist lizard species (the common garden skink,

Lampropholis guichenoti). We presume *L. guichenoti* has at least partial dispersal ability in the landscape, given the high correlation between mobility and generality (Warren *et al.* 2001, Komonen *et al.* 2004) and that individuals were trapped in the pine matrix in six out of eleven sampling seasons.

While there have been a number of studies exploring the relative influence of fragmentation and climate conditions on species distribution (Warren *et al.* 2001, Yates *et al.* 2010, Renton *et al.* 2011, Fordham *et al.* 2012, Reino *et al.* 2013), few consider the potential confounding effects between the two. Fragmentation limits dispersal in the landscape but also changes environmental conditions in remnant patches and in the matrix surrounding them (Ewers & Didham 2005). Generally, fragmentation increases solar radiation at newly created edges, leading to higher and more variable temperatures, greater light intensity, and lower air and soil moisture within remnant habitat patches (Murcia 1995, Chen *et al.* 1999, Didham & Lawton 1999, Laurance 2004, Laurance *et al.* 2011, Tuff *et al.* 2016). The aim of this study was to determine the relative influence of fragmentation and environmental factors on the abundance of *L. guichenoti*, while considering the confounding effects of fragmentation-driven changes in environmental conditions.

This study takes place within one of the world's few large-scale, manipulative fragmentation experiments—the Wog Wog Habitat Fragmentation Experiment in southeastern Australia (Margules 1992). The detailed objectives were 1) to measure the effects of fragmentation (fragmentation, patch size, proximity to edge, and their interactions) on skink abundance; 2) to measure the effects of local environmental conditions, including habitat structure and microclimate, on skink abundance; 3) to examine how fragmentation affects the environmental conditions of remnant patches; and 4) to broadly compare the strength of fragmentation versus environmental regulators of skink abundance within Wog Wog (Fig. 8).



Figure 8. Conceptual model of the hypothesized effects of fragmentation and environmental variables on species distribution in a fragmented landscape. Fragmentation can directly influence distribution patterns by altering spatial processes (reduction in dispersal, isolation of populations on fragments with resulting increase in extinction risk) (path A). Environmental variables can directly influence distribution patterns by limiting the physiological suitability of habitat patches (path B). Fragmentation can also indirectly influence distribution patterns by directly altering the environmental conditions of remnant patches (patch C).

We predict that fragmentation will have significant effects on both skink abundance and local environmental conditions. However, we expect that environmental variables will provide overall stronger determinants of abundance patterns than fragmentation variables, given evidence that skinks can disperse through the landscape and, thus, can respond directly to environmental conditions. In meeting these objectives, this study will improve our understanding of the strength of fragmentation and environmental regulators of species distribution in fragmented landscapes.

Additionally, this study contributes to discussions regarding the impacts of fragmentation in forest landscapes fragmented within tree plantations. The establishment of tree plantations for commercial purposes is an emerging cause of fragmentation globally (Brockerhoff *et al.* 2008, Farmilo *et al.* 2013). In Australia, more than two million hectares are now dedicated to forestry plantations, with over one million plantation hectares comprised of *P. radiata* (Australian Bureau of Rural Sciences 2010). Thus, it becomes increasingly important to understand the variables underlying species distributions, and ultimately persistence, in landscapes fragmented by timber plantations.

3.2 MATERIALS AND METHODS

Ecology of Lampropholis guichenoti

Scincidae comprises the largest, most diverse reptile family in Australia (Cogger 2000). *Lampropholis guichenoti* is a small (2.1 g body mass), diurnal, heliothermic scincid lizard widely distributed in southeastern Australia (Cogger 2000). They are active, opportunistic feeders that take in a wide variety of invertebrate prey (Lunney *et al.* 1989). Individuals forage widely and exhibit little territoriality, maintaining communal clutches and natural densities of 85-90 individuals per hectare (Milton 1980). Adults average 40 mm in snout-vent length, with the tail adding 60-70 mm (Torr & Shine 1993). While males have slightly larger heads than females, the sexes generally attain similar body lengths and lack sexual dimorphism (Simbotwe 1985, Torr & Shine 1993). *L. guichenoti* is a habitat generalist, thriving in both natural and highly modified habitats, including burned and logged forests (Lunney *et al.* 1991) as well as urban gardens (Torr & Shine 1993, Prosser *et al.* 2006). They maintain relatively small home ranges (20m², Anderson & Burgin 2002; < 30m², Turner *et al.* 1969) and exhibit a rapidly maturing, high-turnover demographic pattern (average lifespan of 2-3 years) (Cogger 2000, Hutchinson 1993).

Species dataset

L. guichenoti were trapped within the Wog Wog Habitat Fragmentation Experiment over eleven sampling periods between summer 2010 and fall 2013. Because trapping success was low (189 individuals total), we summed skink abundances at each site from the eleven sampling periods. We compared our models of summed skink abundance with models in which the data were analyzed by year and season, and the models were not qualitatively different.

The Wog Wog Habitat Fragmentation Experiment

The Wog Wog habitat fragmentation experiment (hereafter referred to as "Wog Wog") was established by CSIRO in 1985 and remains one of the oldest and largest fragmentation

studies in the world (Collinge 2009). The experiment is situated in *Eucalyptus* forest embedded within a commercial *P. radiata* timber plantation located in southeastern New South Wales, Australia (37°04'30" S, 149°28'00" E). For full experimental design details, see Margules (1992). Briefly, the experiment contains six replicates, and each replicate consists of three *Eucalyptus* forest plots: one small (0.25 ha; 50m²), medium (0.875 ha; 93.5m²), and large (3.062 ha; 175m²) (Fig. 2). Four of the six replicates became habitat fragments when the surrounding *Eucalyptus* forest was cleared in 1987 and planted with *P. radiata* seedlings. Two replicates remain in adjacent continuous forest and serve as non-fragmented control plots (Ch. 2, Fig. 4).

Each plot has eight monitoring sites, giving a total of 144 sites across the six replicates. An additional 44 sites were established in the pine matrix in 1987 following fragmentation. Each monitoring site has two permanent pitfall traps (90 mm wide x 100 mm deep) that are combined into a single sample for processing. Traps are opened for seven days, three times a year, once during the spring, summer, and fall seasons.

Fragmentation variables

Sites at Wog Wog have three fragmentation attributes (Table 5): 1) *Fragmentation*: whether sites are located in fragmented or continuous forest; 2) *Patch size*: in the fragmented forest, sites are located in either small, medium, or large patches; 3) *Edge*: in the fragmented forest, sites are stratified by proximity to the edge of a plot (edge vs. interior). Edge sites are located within 5.4 ± 0.4 m (mean \pm S.E.) of plot edges; interior sites are located as close to plot center as possible (Margules 1992, Farmilo *et al.* 2013). To test for an interaction between *Fragmentation*, *Patch Size*, and *Edge*, we developed an additional variable (*Size_Edge*) that has seven levels: Small-edge, Small-interior, Medium-edge, Medium-interior, Large-edge, Largerinterior, and Controls. The overstory at Wog Wog consists of a mixture of *Eucalyptus* species and sites are additionally stratified by type of understory vegetation associated with topography (*Topo*: slope vs. drainage lines). Slope sites are warmer and drier, characterized by a grassy understory, native plant litter, and herbaceous vegetation. Drainage line sites are cooler and wetter, characterized by dense shrub thickets of *Kunzea ericoides* and *Lomandra* species (Austin & Nicholls 1988, Farmilo *et al.* 2013). To test for an interaction between *Fragmentation* and *Topo*, we developed the interaction term *Topo_Frag* (Table 5).

Environmental variables

Environmental variables were selected to cover the primary climate and habitat factors thought to affect skink distribution (Table 5). The variables described below focus on the most relevant factors.

Our climate variables focused on temperature because temperature frequently occurs in the literature as a predictor of both local and large-scale distributions, particularly of ectothermic organisms (Buckley 2008, Cunnington *et al.* 2008, Reino *et al.* 2013, Brown & Yoder 2015, Willis *et al.* 2015). Temperature data were collected using Onset Pendant® Temperature/Light Data Loggers (UA-002-64) from November 2011-May 2012 and from November 2012-May 2013 in 20-minute intervals. Loggers were placed 1m north of the center of each site marker and attached to a plastic stake at 5cm off the ground. Temperature sampling spanned spring, summer, and fall to account for seasonal differences in thermal conditions and in two separate years to account for annual variation.

We converted raw temperature data into ecologically targeted BIOCLIM variables (Booth *et al.* 2014). We selected BIOCLIM variables that reflect average conditions (e.g. mean temperature), range in thermal conditions (e.g. annual and diurnal range in temperature), and temperature extremes (e.g. maximum temperature). We also developed thermal physiology
variables that combine temperature data with physiology information for *L. guichenoti* for species-specific indicators of thermal stress *(TEO, TEM)* (Table 5).

Laboratories studies show *L. guichenoti*'s mean selected body temperature in a thermal gradient (thermal optimum) is 33.7°C (Fraser 1980) and the species' thermal limit (thermal maximum) ranges from 40-42°C (Spellerberg 1972, Greer 1980). For each site, we calculated the percent of peak activity time that temperatures exceed L. guichenoti's thermal optimum, set at 34°C, and thermal maximum, set at 40°C, over the course of the temperature sampling period. We set peak activity time at midday (10:00-14:00), as seen in other studies on thermal stress in diurnal, heliothermic lizards (Huey *et al.* 2009).

The habitat variables included in our model cover basic structural and compositional traits (Table 5). In February and May 2013, we surveyed habitat structure at all 188 sample sites. We used a point-intercept survey, running a piece of rope, 10 m long, in five directions (72 degrees apart) from the central point of each site. The rope was marked every 50 cm. At each mark, we scored the type of ground cover (leaves, bark, grass, etc.) and leaf litter depth (cm), resulting in 100 scores for each variable at a site. If the rope touched a piece of fallen wood, we also scored the diameter of the wood (1cm, 2.5cm, 5cm, 10cm, 20cm, 40cm, >40cm) and whether it was rotting or not (rotting vs. hard). By running transects in five directions from a central point, the measures were deliberately biased towards the center of the site, giving greater weight to habitat characteristics close to the pitfall traps. Because our species relies on direct solar radiation to thermoregulate, we also measured light availability (*Perc Cov*) at each site.

VARIABLE	LEVELS	CODE	DESCRIPTION	
Fragmentation	Fragmented, Continuous	F	Whether the site is in the fragmented or continuous forest	
Patch size	Small, Medium, Large, Control	F	Size of the remnant forest patch	
Edge	Edge, Interior, Control	F	Whether the site is at the edge or interior of the patch	
Торо	Slope, Drainage lines	F	1985 site classification based on understory vegetation and topography	
Size_Edge	S-E, S-I, M-E, M-I, L-E, L-I, Control	F	Interaction between patch size and edge. S=small, M=med, L=large, I=interior, E=edge	
Topo_Frag	F-S, F-D, C-S, C-D	F	Interaction between fragmentation and topography. S=slope, D=drain, F=frag, C=cont	
WetIndex	Scored from 1 (driest) to 5 (wettest)	Н	1985 site classification based on soil horizon, thickness, mottling, and % clay content	
Edge_Distance	Continuous	Н	Distance to the closest edge	
Edge_Direction	Cardinal and InterCardinal directions	Н	Which direction the closest edge faces	
DomCoverType	Leaves, Bark, Grass, Roots, etc.	Н	Most frequent ground cover type	
Litter depth	Continuous	Н	Mean litter depth (cm)	
DomWoodDiam	1, 2.5, 5, 10, 20, 40, >40	Н	Most frequent diameter (cm) of fallen wood	
DomWoodType	Rotting, Hard	Н	Most frequent decomposition stage of fallen wood	
Perc_Cov	0 – 100 %	Н	Percent canopy cover, measured from hemispherical fisheye photographs	
pH_2012	Continuous, 0-14	Н	Soil pH in 2012	
OrgC	Continuous	Н	Soil organic carbon content for 1985 samples	
MDR	Continuous	Т	Mean Diurnal Temperature Range (°C):	
MDR_summer	Continuous	Т	Mean Diurnal Temperature Range in summer (°C)	
MAR	Continuous	Т	Mean Annual Temperature Range (°C):	
MAR_summer	Continuous	Т	Mean Annual Temperature Range in summer (°C)	
MeanT	Continuous	Т	Mean temperature (°C)	
MeanT_summer	Continuous	Т	Mean summer temperature (°C)	
MaxT	Continuous	Т	Maximum temperature (°C)	
TEO	0 - 100 %	Т	% peak activity time that temperature exceeds thermal optimum	
TEO_s	0-100 %	Т	% peak activity time in summer that temperature exceeds thermal optimum	
TEM	0-100 %	Т	% peak activity time that temperature exceeds thermal maximum	
TEM_s	0-100 %	Т	% peak activity time in summer that temperature exceeds thermal maximum	

Table 5: List and description of the 21 environmental variables and 6 fragmentation variables included in our analyses of skink abundance data. Variables were measured at each of the 188 sample sites at Wog Wog. Variables are coded by type: F = Fragmentation variable, H = Habitat variable, T = Thermal variable.

Data Analysis

We used generalized linear mixed models (GLMMs) to investigate the effects of fragmentation and environmental variables on *L. guichenoti* abundance. Because we are modeling skink abundance, as opposed to presence/absence, our data are counts and therefore follow a Poisson distribution. Models were fitted in R (Version 3.2.0, R Development Core Team 2008) using the lmer function in the lme4 package (Version 1.1-7, Bates *et al.* 2014). Because we were most interested in comparing the effects of fragmentation and environmental conditions on skink abundance, our main analyses exclude data from sites in the pine plantation matrix, which lack the *Patch size* and *Edge* treatments. Here we present methods to address each of the four detailed objectives of the study.

Q1. Do *Fragmentation*, *Patch size*, *Edge* and their interactions affect skink abundance?

We included four fixed effects in the model (Table 5): **1**) *Fragmentation*: a variable with two levels, (i) fragmented forest and (ii) continuous forest, that tests for the effect of forest fragmentation. **2**) *Patch size*: a variable that describes the interaction between fragmentation and size. **3**) *Edge*: a variable that describes the interaction between fragmentation and edges. **4**) *Topo*: a variable nested within plots with two levels: (i) slope and (ii) drainage lines. We also included two interaction terms: **1**) *Topo_frag*: a variable that describes the interaction between fragmentation between fragmentation between fragmentation and topography, and 2) *Size_Edge*: a variable that describes the interaction between fragmentation between fragmentation, patch size, and edge.

Because of the experiment's nested design, data are collected at three spatial scales. Individuals are trapped at pitfall *sites* (1-144), which are nested within *plots* (1-18), which are nested within *replicates* (1-6). Thus, we tested for the effects of *Fragmentation*, *Patch size*, *Edge*, and *Topo* on skink abundance, as well as the two interaction terms *Topo_Frag* and *Size_Edge*, while accounting for variance associated with *Replicate*, *Plot* and *Site*. The significance of fixed effects was assessed using likelihood ratio tests.

Q2) Do the environmental conditions of remnant patches, including habitat structure and microclimate, affect skink abundance?

From our broad habitat survey and microclimate data, we selected variables that we hypothesized might explain skink abundance. This resulted in the inclusion of 21 environmental variables (10 describing habitat structure and composition, 11 describing thermal conditions) (Table 5). The change in deviance associated with each variable was assessed using Poisson GLMMs. Models included the nested random effects *Replicate*, *Plot*, and *Site*.

When examined independently, three habitat variables [mean litter depth (*Litter depth*), soil organic carbon (OrgC), and percent canopy cover ($Perc_Cov$)] and seven thermal variables [mean diurnal temperature range (MDR), mean diurnal temperature range in summer (MDR_summer), mean annual temperature range (MAR), mean summer temperature range (MAR_summer), mean temperature (MeanT), mean temperature in the summer ($MeanT_summer$), and maximum temperature (MaxT)] explained skink abundance. Variables within each category were highly correlated, so we used a combination of forward and backward selection to determine the relative strength of these ten environmental variables on skink abundance. We assessed significance using likelihood ratio tests (p<0.05).

Q3) Do fragmentation, patch size, proximity to edge, and their interactions affect the local environmental conditions of remnant patches?

Once we had determined which environmental variables most strongly predicted skink abundance (Q2), we wanted to determine the effects of fragmentation on those environmental variables. More clearly stated, were they different between fragmented and continuous forest, across differently sized patches, and at fragment edges versus interiors? We used the same model fitting protocol that we used to determine the effects of fragmentation on skink abundance (Q1) and included all of the same fixed effects, interaction terms, and random effects in the models. However, we used linear mixed models instead of GLMMs, as the environmental variables tested followed a normal, as opposed to Poisson, distribution.

Q4) Do fragmentation or environmental variables more strongly regulate skink abundance patterns at Wog Wog?

Our goal was to determine what proportion of *L. guichenoti*'s response to the fragmentation treatment could be attributed to the direct effects of fragmentation (e.g. reduction in dispersal, isolation of populations on fragments with resulting increase in extinction risk) versus the indirect effects of fragmentation (e.g. fragmentation-driven changes in abiotic conditions) (Fig. 8).

In our first approach to answering this question, we compared the performance of models with only environmental variables to models with both environmental and fragmentation variables (Table 6). To evaluate model performance, we used the Akaike information criterion (AIC) as a measure of information loss of each candidate model, with the best fitting model having the lowest AIC and consequently the highest Akaike weight (Burnham & Anderson, 2002). However, we realized that models with the fragmentation variables required significantly more parameter estimates than models with only environmental variables (compare Table 6, model 0 with Table 6, model 1). Thus, the models representing fragmentation were greatly reduced in power, with a larger penalty for number of parameters and many fewer degrees of freedom available, making this direct model comparison statistically unfair.

Instead, we developed an analysis that partitioned the total effect size of fragmentation into additive contributions from the effects of fragmentation per se and the effects of

fragmentation-driven changes in abiotic conditions. We used the style of a structural equation

Model	Df	AIC	logLik	LD	MeanT	F	F:LD	F: MeanT	F:S:E
m0	6	407.17	-197.59	Х	Х				
m1	7	407.98	-196.99	х	Х	Х			
m2	8	409.17	-196.59	х	Х	Х	х		
m3	8	407.75	-195.88	х	Х	Х		Х	
m4	12	414.29	-195.15	х	Х				Х

modeling approach within a GLMM framework.

Table 6. Comparison of AIC values for five models describing the relative importance of fragmentation treatments and environmental variables on skink abundance. Models include the environmental variables litter depth (LD), mean temperature (MeanT), as well as the variables fragmentation (F) and the interaction between fragmentation, patch size, and edge (F:S:E). Terms separated by a colon indicate interaction terms. Df = degrees of freedom, loglik = log likelihood, AIC = AIC score, x = term in model. The highest performing models are highlighted in grey.

3.3 RESULTS

Variable	d.f.	Dev.	P-value
Replicate stratum			
Fragmentation	1	0.306	0.580
Plot stratum			
Size	2	2.234	0.327
Site stratum			
Edge	1	0.087	0.768
Торо	1	3.150	0.076
Fragmentation: Topo interaction	1	0.796	0.372
Size: Edge interaction	2	5.338	0.069

Table 7. Summary of the Poisson generalized linear mixed model analyses of the effects of habitat fragmentation on skink abundance. The significance of a variable was determined by the change in deviance (Dev.) associated with dropping that variable. A variable was considered significant when the change in deviance associated with it exceeded the chi-squared critical value, at p < 0.05, for the number of degrees of freedom (d.f.) that the variable conferred. The level of significance, the Chi-squared probability, is listed in the p-value column.

		Litter depth		MeanT	
Variable	d.f.	Dev.	P-value	Dev.	P-value
Slope habitat <i>Replicate stratum</i> Fragmentation	1	1.987	0.159	0.000	0.988
<i>Plot stratum</i> Size	2	5.490	0.064	4.503	0.105
<i>Site stratum</i> Edge Size: Edge interaction	1 2	0.446 1.366	0.517 0.505	0.026 7.378	0.871 0.025
Drainage line habitat Fragmentation	1	4.859	0.028	7.639	0.006
<i>Plot stratum</i> Size	2	0.914	0.633	7.060	0.029
<i>Site stratum</i> Edge Size: Edge interaction	1 2	1.667 2.667	0.197 0.264	0.000 14.071	0.986 <0.001

Table 8. Summary of the linear mixed model (REML) analyses of the effects of fragmentation on leaf litter depth (*Litter depth*) and mean temperature (*MeanT*). Because topography had significant effects on both variables, we developed separate models for sites in the slope habitat and drainage line habitat. The significance of a variable was determined by the change in deviance (Dev.) associated with dropping that variable. The level of significance, the Chi-squared probability, is listed in the p-value column. d.f. = degrees of freedom. Significant variables (p<0.05) are bold faced.

(Q1) None of the fragmentation variables (Fragmentation, Patch size, or Edge) had a

significant effect on *L. guichenoti* abundance (Table 7). For the interaction between *Patch size* and *Edge*, although the omnibus statistic was not significant, skink abundance was significantly lower at the interior sites in small fragments than in continuous forest (p=0.017; Fig. 9).

(Q2) Skink abundance was explained by two environmental variables: mean litter depth (*Litter depth*) (d.f.=1, Δ Deviance = 5.503, p=0.019) and mean temperature (*MeanT*) (d.f.=1, Δ Deviance = 10.430, p=0.001) (Model 0 in Table 6). Both environmental variables have linear

relationships with skink abundance, such that skink abundance increases with increasing *Litter depth* and *MeanT* (Fig. 10).

(Q3) We then tested the effects of fragmentation on the two environmental variables that best predicted skink abundance: *Litter depth* and *MeanT*. Because topography had a significant effect on *Litter depth* (d.f.=1, p<0.001) and there was a significant effect of the interaction between topography and fragmentation on *MeanT* (d.f.=2, p=0.006), we developed separate models for sites in the slope habitat and drainage line habitat (Table 8). We found that *Fragmentation* had a significant effect on *Litter depth* and *MeanT* in the drainage line habitat but not in the slope habitat (Table 8, Fig. 11). In slope habitat, however, there was an apparent, although not statistically significant (p=0.064), relationship between patch size and litter depth, such that litter depth increased as patch size decreased (Fig. 12). In both habitat types, there was a significant effect of the interaction between *Patch size* and *Edge* on *MeanT*, such that *MeanT* decreased as patch size decreased at edge sites but not interior sites (Fig. 12).

(Q4) Environmental variables were stronger regulators of skink abundance than the fragmentation variables, regardless of the statistical approach taken. Two environmental variables, *Litter depth* and *MeanT*, comprised the most parsimonious model of skink abundance (Model 0 in Table 6). When the effects of fragmentation were added to the parsimonious model (Model 1 in Table 6), AIC scores either increased, suggesting lower model performance, or stayed the same. We suspect this is due to the model penalties described in the methods above. When we partitioned the effect sizes using the structural equation model approach, the effects of fragmentation per se (e.g. reduction in dispersal, isolation of populations on fragments with resulting increase in extinction risk) accounted for approximately 40% of the observed reduction in skink abundance on fragments, while fragmentation-driven changes in abiotic conditions accounted for approximately 60% of the reduction in skink abundance. The environmental

Figure 9. The effects of fragmentation on skink abundance (No. individuals effects were driven almost entirely by a reduction inpensive hat Wog Magn Bass while increased represent standard errors. litter depth had a small positive effect on skink abundante (Fogtinupus forest, L = large patches,While not included in the final model, the performance performance between the temperature S = small patches, exceeds the species' thermal optimum (TEO) had a hoteratorhiv territor, on skink abundance. When E = patch edge. Bottommodeled in place of MeanT (same structure as Modelanch: Tabandance Bointationhumped-shaped sites in small patches is relationship with skink abundance, such that abundasies if is antiker elister as the minoreases. abundance in continuous optimizes at an intermediate value (~18% in fragmeforestland at interiors) iterdithen declines as large and medium patches. TEO continues to increase (Fig. 13).





Figure 10. Predicted abundances from the top-performing model of the effects of fragmentation and environmental variables on skink abundance (Model 0 in Table 3). Skink abundance was explained by two environmental variables: leaf litter depth and mean temperature. Abundances are from Poisson GLMMs and are at the site scale. Dotted lines demarcate minimum values for persistence at a site (abundance = 1, Litter depth = 2.52cm; Mean temperature = 33.03°C).



Figure 11. Mean litter depth and mean temperature in fragmented (Frag) versus continuous (Cont) Eucalyptus forest plots at Wog Wog. Data are from sites in drainage line habitat, where the effects of the Fragmentation treatment are significant (p-values from linear mixed models are included). Bars represent standard error.



Figure 12. The effects of *Fragmentation*, *Patch size* and *Edge* on mean litter depth and mean temperature in fragmented (Frag) and continuous (Cont) forest plots. Bars represent standard error, and p-values are derived from linear mixed models. First panel: the effect of Patch size on litter depth. Data are from slope habitat only. Panel two: the effect of the interaction between Fragmentation, Patch size, and Edge on mean temperature. Data are from both slope and drainage line habitat. C = continuous forest, L = large patches, M = medium patches, S = small patches, I = patch interior, E = patch edge.



Figure 13. Predicted abundances from a model of the effects of Fragmentation and the environmental variables Litter depth and percent of peak activity time that temperature exceeds the species' thermal optimum (TEO). The model has the same structure as Model 0 in Table 3, but TEO has been substituted for MeanT. Abundances are from Poisson GLMMs and are at the site scale. Dotted lines demarcate the TEO values that maximize skink abundance in fragmented (Frag) and continuous (Cont) forest.

3.4 DISCUSSION

Understanding the factors that determine a species' spatial distribution is a central objective in ecological research, with applications to predicting range shifts, extinctions, and biological invasions (Guissan & Thuiller 2005, Buisson *et al.* 2008, Elith & Leathwick 2009, Xiaojun *et al.* 2011). Studies show that landscape factors that influence dispersal (e.g. fragmentation) can be stronger determinants of distribution than environmental regulators of eco-physiology because landscape factors can restrict movement between patches even if environmental conditions within patches are favorable (Warren *et al.* 2001, Ewers & Didham 2005, Buisson *et al.* 2008, Reino *et al.* 2013). In this study, we used skinks captured over eleven sampling periods in a large-scale fragmentation experiment to compare the relative influence of fragmentation and environmental variables on abundance patterns. To better understand the indirect impacts of fragmentation on abundance, we also tested for the effects of fragmentation on the strongest environmental regulators of skink abundance (Fig. 8).

We found that two environmental variables, mean leaf litter depth and mean temperature, largely determine skink abundance patterns at Wog Wog. These variables represent two types of eco-physical regulators: habitat structure and thermal conditions. Leaf litter depth and composition have been linked to small skink abundance in other studies (Mather 1989, Anderson & Burgin 2002, Howard *et al.* 2003) because leaf litter affects the ability of individuals to thermoregulate, feed, and avoid predators by offering retreat sites (Howard *et al.* 2003). Our results suggest that skinks prefer at least 2.52 cm of litter depth at a site but also that more leaf litter is favored (Fig. 10).

This litter depth threshold suggests that leaf litter may be part of the reason skinks are not trapped in the matrix more frequently, as the average litter depth in the matrix is only 0.76 cm (continuous forest = 1.61 cm, fragmented forest = 2.15 cm) and the maximum litter depth of any

matrix site was only 1.26 cm (continuous forest = 2.89 cm, fragmented forest = 3.44 cm). Similarly, a study on a congener species (*L. delicata*) found that litter type matters as much as litter depth, as skinks preferred to occupy native *Eucalyptus* leaf litter over non-native pine litter, even when the pine litter was supplemented with additional prey items (Howard *et al.* 2003).

Suitable thermal conditions are also an established environmental criterion for *L*. *guichenoti* (Greer 1980, Torr & Shine 1993), and ectotherms more broadly. The temperature regulation process helps animals gather food, reproduce, and avoid being eaten (Huey 1982). Thermal conditions thus indirectly influence fitness by directly regulating physiological, behavioral, and ecological performance (Huey & Kingsolver 1989, Kingsolver 2009, Dell *et al.* 2011). Surprisingly, of the seven highly correlated thermal variables that independently explained skink abundance, mean temperature was the strongest thermal predictor, outcompeting even the species-specific thermal stress variables *TEO* and *TEM*. Our results show that skinks favor warmer sites, preferring an average of at least 33.03°C (Fig. 10). As previously mentioned, laboratories studies found *L. guichenoti*'s mean selected body temperature in a thermal gradient was 33.7°C (Fraser 1980), so these findings were not surprising.



Figure 14. Summary of research findings. Environmental variables were the strongest determinants of skink abundance patterns at Wog Wog (patch B). Fragmentation variables did directly affect skink abundance (path A). However, the greater consequences were fragmentation's effects on the environmental variables regulating skink abundance (path C). Thus, fragmentation predominantly influenced abundance patterns by altering the conditions available in remnant patches.

Results from this study suggest that the impacts of fragmentation on abiotic conditions can have greater consequences for ectotherm distribution patterns than the impacts of fragmentation per se. Fragmentation per se accounted for approximately 40% of the reduction in skink abundance on fragments, whereas fragmentation-driven changes in litter depth and temperature accounted for approximately 60% of the reduction in skink abundance (Fig. 14). Sites in remnant forest patches had more leaf litter than those in continuous forest (Fig. 11) and, within slope habitat, litter depth increased as patch size declined (Fig. 12). Greater leaf litter in remnant patches is commonly observed in fragmented forests and often linked to lower rates of litter decomposition at patch edges (Laurance et al. 2002, Crockatt & Bebber 2015) as well as leaf shedding in drought-stressed tress at patch edges (Laurance et al. 2011). Remnant patches also experienced lower average temperatures than in continuous forests. Within edge sites, mean temperature decreased as patch size decreased (Fig. 12). This relationship between temperature and patch size likely stems from 1) increased canopy cover in smaller patches at Wog Wog (Farmilo et al. 2013) and/or 2) increased exposure to the closed-canopy pine matrix. Currently, the trees in the Eucaplytus forest patches are shorter than trees in the pine plantation (mean height: 25.0 ± 0.6 m compared with 28.9 ± 1.1 m) and remnant patches are often overtopped and shaded by the matrix surrounding them (Farmilo et al. 2013).

Ultimately for the skinks at Wog Wog, the greatest consequences of fragmentation are not the direct effects of reduced connectivity but instead fragmentation's indirect effects on the environmental conditions necessary for their persistence (Fig. 14). This importance of environmental conditions in remnant patches further emphasizes the role of matrix habitat in mitigating fragmentation's impacts. Remnant patches surrounded by a cleared or pasture matrix experience much greater changes in environmental conditions than patches surrounded by regrowth forest or commercial tree plantations (Didham & Lawton 1999, Denyer *et al.* 2006,

Wuyts *et al.* 2008, Wright *et al.* 2010, Ewers & Banks-Leite 2013). For example, loggers placed at sites in a recently cleared forest just outside of the Wog Wog experiment experienced mean temperatures upwards of 65.99°C, whereas sites in the current pine plantation matrix experience mean temperatures upwards of 40.45°C (Tuff *et al.* unpublished data). Studies comparing environmental and fragmentation predictors in landscapes with greater contrast between patch and matrix habitat, such as in recently fragmented forests, are therefore a necessary supplement to the findings presented here.

While not included in the final model of skink abundance, the percent of peak activity time that temperature exceeds the species' thermal optimum (*TEO*) set limits on skink abundance worth exploring. *TEO* is an indication of thermal stress at a site. Unlike mean temperature or litter depth, which had linear relationships with skink abundance, thermal stress provides a humped-shaped relationship with skink abundance, such that abundance first increases as *TEO* increases, optimizes at an intermediate value, and then declines as *TEO* continues to increase (Fig. 13). The relationship between thermal stress and skink abundance maintains the same shape as the relationship between body temperature and physiological performance, known as the thermal performance curve (Huey 1982, Angilletta 2002). A thermal performance, such as metabolic rate, digestive efficiency, or sprint speed (Huey 1982, Huey & Kingsolver 1989, Angilletta *et al.* 2002). From a thermal performance curve, we can determine the temperature at which the maximum performance of an organism occurs and the critical minimum and maximum thermal limits beyond which it cannot survive.

The hump-shaped relationship between *TEO* and skink abundance in remnant patches suggests that thermal stress, unlike litter depth and average temperature, may provide both upper and lower constraints on persistence, such that there is a minimum amount of thermal input

required to meet thermoregulatory needs, an optimal amount (TEO_{OPT}), and a threshold beyond which thermal stress leads to negative population growth. Interestingly, the shape of this abundance-*TEO* curve is dependent on the type of forest (fragmented or continuous) that the skink lives in. TEO_{OPT} is 18.18% in fragments and 11.92% in controls, suggesting that individuals in the fragmented forest prefer or require greater amounts of thermal input.

There are multiple hypotheses to explain these differences in TEO_{OPT}. One hypothesis is that skinks in the fragments require more thermal input due to the greater amount of leaf litter at sites, which can act as a thermal buffer (Howard *et al.* 2003). A second hypothesis is that differences in TEO_{OPT} stem from shifts in thermal tolerance in skink populations in the fragmented forest. As *L. guichenoti* individuals become reproductively active within one-year (Hutchinson 1993), it is possible that dramatic temperature increases following fragmentation (Tuff *et al.* 2016) fostered selection for increased thermal tolerance in populations in the fragmented forest. The high mobility of the species could negate this possibility. Regardless, studies exploring shifts in thermal tolerance following fragmentation can offer new insight into species adaptation and persistence in fragmented landscapes and should be pursued further.

In summary, this study shows that environmental variables can be stronger determinants of distribution than fragmentation variables, specifically for mobile species in a low-contrast setting. Results also show that fragmentation can have important indirect effects on distribution through its impacts on environmental conditions. There are limitations to our models, as we did not include biological factors, such as population dynamics or species interactions, and thus we have limited ability to predict future occurrence or extinction events (Buckley 2008, Elith & Leathwick 2009, Van der Putten *et al.* 2010). However, we can say that litter depth and thermal conditions provide important constraints on skink abundance in remnant patches and, thus,

should be considered when developing conservation strategies to maintain small reptile populations in fragmented landscapes.

Ultimately, more studies comparing the relative influence of environmental and fragmentation variables on species distribution patterns in fragmented landscapes are needed, particularly in recently fragmented forests where fragmentation-driven changes in environmental conditions are the most pronounced. Such studies will improve our understanding of species responses to fragmentation and lead to more comprehensive approaches to biodiversity conservation in fragmented landscapes.

CLOSING THOUGHTS

This dissertation offers ideas, research findings, and a conceptual framework designed to guide the ecological community in taking a thermal approach to fragmentation research. The contributions of this work center on (1) providing a framework that treats temperature as a mechanism behind species, community, and ecosystem-level responses to fragmentation (chapter one), and (2) testing concepts presented in the framework to determine the tractability of its ideas (chapters two and three). Ultimately, this dissertation provides evidence that warming is an important and underestimated mechanism operating in fragmented landscapes and lays the foundation for future studies targeting the ecological fallout of thermal disturbances.

Summary of key findings

Temperature is a known driver of animal behavior, physiology, and spatial distribution, and thermal conditions have been used to predict ecological responses to environmental change in many different contexts. Historically, temperature increases following fragmentation have been considered in the context of edge effects and are well documented as a consequence of fragmentation (Kapos 1989, Matlack 1993, Murcia 1995, Chen *et al.* 1993, Chen *et al.* 1999, Saunders *et al.* 1999, Laurance 2004, Sato *et al.* 2014). My research takes this understanding a step further by considering thermal changes not only as a consequence of fragmentation, but also as a mechanism driving species responses in fragmented landscapes.

In chapter one, I used the fragmentation-temperature framework to show that thermal biology can be easily and intuitively integrated into fragmentation research, offering new tools and hypotheses to address temperature as a driver of ecological changes in fragmented landscapes. For example, I show that thermal traits (thermal safety margin, warming tolerance,

and performance breadth) can be used to estimate the impacts of fragmentation on species and can help identify species at risk of thermally driven extinction in remnant patches.

In chapter two, I used morphometric analyses to show that fragmentation-driven temperature increases can lead to body size declines in ectothermic species because of the temperature-size rule. Specifically, I show that skinks declined in size precisely as predicted by the temperature-size rule after the fragmentation treatment was applied, such that the greater the exposure to deforested areas, the greater the decline in body size. I then used avian predator abundance and beetle prey biomass to show that patterns in classic biological drivers could not explain size declines.

In chapter three, I used a species distribution model to show that thermal conditions are important regulators of ectotherm distribution in fragmented landscapes. Specifically, I show that thermal stress had greater influence on skink abundance patterns than did patch size or proximity to edge. I also show that there is a hump-shaped relationship between skink abundance and thermal stress at Wog Wog sites, and that the shape of the hump depends on whether sites are located in the fragmented or continuous forest.

Together, results from chapters one, two, and three provide evidence that temperature can impact species in ways that are not often considered in fragmentation studies but that have important ecological consequences.

Future directions

As is often the case, this research has led to more questions than answers about temperature's role as a mechanism of change in fragmented landscapes. Many future research directions are highlighted in the "Critical Gaps" sections of chapter one, but I will mention additional pressing questions here. One of the most unexpected results of my dissertation research is that thermal variables had a greater influence on skink abundance than did

fragmentation variables. Consequently, a major question to address in the future is under what circumstances does this relationship hold? We tested the relative influence of fragmentation and thermal variables on abundance in a low-contrast setting, following 28-years of pine matrix regrowth. What would that relationship look like immediately after fragmentation, when both patch isolation and increases in temperature are more pronounced?

Results from chapter two suggest that size declines following fragmentation should be widespread in species that follow the temperature-size rule, and that declines should be highly predictable based on exposure to deforested areas. Major questions to address include how ubiquitous are size declines following fragmentation? Can they be reliably predicted by patch size and proximity to edge? To what extent are those declines driven by temperature increases as opposed to other fragmentation-related factors? Achieving answers to these questions will allow us to address the broader question of whether the widespread size declines attributed to climate change may be caused, partially caused, or at least amplified by habitat fragmentation, which has been equally global in its impact.

One of the broadest predictions of my dissertation is that temperature-driven changes at the species level should scale up to predictable, temperature-driven changes at the community and even ecosystem level. This prediction presents a great opportunity for gaining new understanding of the impacts of fragmentation, and these connections have only barely begun to be addressed. I expect that better understanding of "impact strength" (how far the effects of fragmentation-driven warming cascade through the ecosystem) will be a key advancement of my dissertation work.

Conclusion

Warming serves as a unifying phenomenon among climate change, thermal biology, and fragmentation research, but the work presented in this dissertation targets the unique spatial and

temporal considerations of temperature increases in fragmented landscapes. While I was able to draw from a wealth of studies in the climate change and thermal biology literature, I have gone to great lengths to distinguish this body of work as a method for advancing our understanding of ecological responses to fragmentation. The thermal challenges facing individuals in remnant patches have rarely been considered (Currylow *et al.* 2012), but in doing so, this dissertation contributes a new perspective to contemporary debates about the future of global biodiversity, including how to conserve species in an increasingly fragmented world. I hope that my work will be the foundation for future studies aimed at teasing apart the role of temperature in ecological responses to fragmentation and will help the broader ecological community understand how and why to take a thermal approach to fragmentation research.

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