The role of climate and tree nutrition on the occurrence of the southern greater glider (*Petauroides volans*) and its implications for conservation planning

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'The clearest way into the Universe is through a forest wilderness.'

John Muir – Scottish-American naturalist

This thesis is dedicated to Anu, my parents, aunt and grandmother

Abstract

The southern greater glider (*Petauroides volans)* is southeastern Australia's largest gliding marsupial and widely distributed, but the species has recently experienced drastic declines in population numbers. Its association with hollow-bearing trees, used for nesting, has made it an important flagship species for the conservation of old-growth forest ecosystems. Stand replacing or altering wild- or planned fires and timber harvesting have been identified as major threats to the greater glider, but individuals and populations have over time disappeared from areas that have experienced neither, raising questions about the role of other factors in their decline. Habitat suitability is determined by three distinct factors: A narrow thermotolerance makes greater gliders vulnerable to high ambient temperatures. A specialised diet consisting entirely of nutrient-rich *Eucalyptus* leaves confines them to certain forest types and the need for multiple large tree hollows for denning confines populations to mature forests. Therefore, different spatial scales need to be considered when determining likelihood of occupancy and habitat suitability for greater gliders.

Using high spatial and temporal resolution climate data, I identified that climate is driving greater glider occupancy across the landscape. At a stand scale, I developed new methods of remotely sensing feeding and nesting resources using field sampling and multispectral imagery collected by an unoccupied aerial vehicle (UAV). My findings have important implications for greater glider management and conservation of their habitat and associated forest types. At the landscape scale, I identified climatic refugia that may allow greater gliders to persist into a future under climate change if properly protected. At a stand scale, remotely sensed estimates of feeding and nesting resources may enable forest managers to better retain highly suitable habitat or assess remaining habitat suitability and likelihood of persistence after disturbance. The gathered knowledge enables us to spatially extrapolate field observations and model findings to test how different landscape, resource and disturbance configurations affect population density and persistence, which should further enhance our ability to protect southern greater gliders in southeastern Australia.

Declaration

This is to certify that

(i) the thesis comprises only my original work,

(ii) due acknowledgement has been made in the text to all other material used; and

(iii) the thesis is fewer than 80,000 words, exclusive of tables, illustrations, maps, bibliographies and appendices

Signed Benjamin Wagner Melbourne, 9th September 2021

Preface

This PhD thesis consists of four data chapters, one of which has been published in an international, peer-reviewed journal and two of which are either under review or submitted for publication. These papers were all primarily the work of me, Benjamin Wagner, who conceived, designed and implemented the research, collected and analysed the data in the field and laboratory, prepared the manuscripts and wrote this thesis. All co-authors supervised various stages of the PhD research, contributed data or knowledge or supported writing and revising the manuscripts.

The citations for these manuscripts are:

Chapter 2 - published in Ecosphere and the ESA Bulletin

Wagner, B., Baker, P. J., Stewart, S. B., Lumsden, L. F., Nelson, J. L., Cripps, J. K., Scroggie, M.P. & Nitschke, C. R. (2020). Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits. Ecosphere, 11(10), e03262

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Chapter 5 – under revision in Conservation Science and Practice

Wagner, B., Baker, P. J., & Nitschke, C. R. in review. The influence of spatial patterns in foraging habitat on the abundance and home range size of an arboreal marsupial in southeast Australia.

Data collection and surveys were carried out in National Parks and adjacent State Forests in East Gippsland, Victoria, Australia, approved under Department of Environment, Land, Water and Planning (DELWP) permit number 10008487. All drone flights were registered with Australia's Civil Aviation Safety Authority (CASA) under Aviation Reference Number (ARN) 1044739 and authorised by Parks Victoria with registered Unmanned Aerial Vehicles (UAVs) 11UCF720A40194 and 08QCEC2022034L.

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Much of the research in this thesis would not have been possible without the contribution of outstanding co-authors to chapters and publications and other experts that made the time to advise me. For Chapter 2, researchers and ecologists at the Arthur Rylah Institute (ARI) and the Victorian Department of the Environment, Land, Water and Planning (DELWP) provided valuable survey data and knowledge. Thank you to Lindy Lumsden, Jenny Nelson, Michael Scroggie, Jemma Cripps, Louise Durkin and Lucas Bluff. A special thanks goes to Jemma and Louise for inviting me to accompany their greater glider surveys in the Strathbogie Ranges early in my project, which greatly shaped my understanding of local fauna and flora and helped developing methodologies for later chapters. Their continuous support since I started my project was immensely valuable and I am grateful for their time and contributions. Stephen Stewart provided important climate data, which he developed from his own outstanding research and always had an open ear and great coding suggestions when I had questions, so many thanks go to him as well. For Chapters 3 and 4, Ben Moore was invaluable to the success of my aspirations to determine and map foliar nitrogen. Ben's immense knowledge in foliar and marsupial nutrition shaped much of the current chapter's structure and his invitation to teach me and conduct laboratory research at his institute at the Hawkesbury Institute (Western Sydney University) was a great and memorable experience. Thank you, Ben, for your amazing support! I would also like to acknowledge help and advice I received regarding *Eucalyptus* nutrition, remote sensing and greater glider foraging behaviour from Kara Youngentob. I would further like to thank Maria Cardoso, former biodiversity officer at VicForests Orbost, for her support of my project and introducing me to and guiding me in the beautiful forests of East Gippsland. Her help and experience were important for the site selection of my field study in the region.

Speaking of field studies, there are many people to acknowledge that helped collecting all the data in study sites spanning from the coast near Orbost to high-country around Bendoc, East Gippsland. Most importantly I would like to acknowledge the amazing work of Tim Willersdorf, former field technician in our working group. The field component of my research would have been impossible without his amazing field experience and his knowledge of the plants and forests of East Gippsland, and I will always remember how much I learned from him and the good times I enjoyed in the field with Tim. For field assistance I would also like to thank Anu Singh and Craig Nitschke, as well as Diego Torres, Ella Starkey, Steve Livesley, Edouard Sorin, Tom Ennes, and Floriane Bourrel. Project help was also provided in the office and lab. I

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1. Introduction and literature review

The loss of biodiversity is a concern of global scale and caused by climate change and anthropogenic disturbances (Stenseth et al. 2002, Walther et al. 2002, Butchart et al. 2010). Climate change is a result of an anthropogenically driven increase in greenhouse gases due to worldwide industrialization and globalization processes that lead to rising ambient temperatures and more frequent and extreme weather events (Chapin et al. 2000, Parry et al. 2007, Field 2014). Globally, climate has warmed by 0.6 °C in the 20th century alone, a rate double of that of an entire millennium before (McCarthy 2001). Seven out of the ten hottest years on record have occurred since 2010, with 2020 being the hottest thus far (National Center for Environmental Information 2021). The impact of climate change is likely to be exacerbated by anthropogenic disturbances and pressures on the natural environment such as land-use change (Stenseth et al. 2002), leading to alteration of ecological systems that drive losses in global biodiversity (Chapin et al. 2000, Walther et al. 2002). The rate of climate change and increases in occurrence of extreme events (Cai et al. 2014, Moran-Ordonez et al. 2018), has had noticeable impacts on global ecosystems such as the continual worldwide dieback of tropical coral reefs (Hoegh-Guldberg et al. 2007, Hughes et al. 2010, Cai et al. 2014, Iizumi et al. 2014, Eghbert et al. 2017) or increasingly severe droughts and forest fires leading to severe forest mortality (Ward et al. 2020, Geary et al. 2021). Decreases or losses of ecosystem functionality have been reported (Cramer et al. 2001), as well as changes in plant species physiology (Lawler et al. 1997, Cotrufo et al. 1998, Kanowski 2001, Rawal et al. 2015b, c) and to species composition and distributions around the world (Parmesan and Yohe 2003, Thomas et al. 2004). These changes are directly influencing terrestrial tree and plant species and indirectly impacting other species guilds, that use and rely on them for habitat (Thomas et al. 2004, Walther 2010). This trend, first reported by Parmesan et al. (1999) in their studies on range-shifts of European butterflies, has increasingly been observed and reported worldwide (see e.g.McCann et al. 2013, Rézouki et al. 2016, Hoffmann et al. 2019). Along with the impacts of climate change, human impacts on species are directly increasing the pressure on their populations through deforestation, timber harvesting, fire management, fragmentation or other forms of land management that reduce habitat area and/or quality leading to population declines, local extirpations, or extinctions (Diamond 1984, Lindenmayer et al. 2011, Youngentob et al. 2013, McLean et al. 2015).

As a response, it is often rare species that are the focus of conservation measures and public attention, due to their high vulnerability to extirpation or extinction if habitat and populations continue to decline (Rabinowitz et al. 1986, Gaston 1994). Research and conservation on common species is usually less directly targeted, using coarse filter management approaches,

while fine filter management is directly focusing on reducing the risk of extinction of critically endangered species (Noss 1987, Kohm 1990, Groves 2003, Hunter 2005). Nevertheless, many common species typically provide structure, function and services and play a major role in shaping our environment. As such, they are involved in main biotic interactions including predation, herbivory, seed dispersal or parasitism (Howe and Smallwood 1982, Gaston 2010). These species are also victims of habitat loss, fragmentation, degradation, overexploitation and invasion-pressure through factors such as land-use change, urbanisation, deforestation, overfishing, bushmeat collection or introduction of invasive species (Gaston 2008, Gaston and Fuller 2008, Gaston 2010). Continuous changes in climate and land-use pose a growing threat to flora and fauna and understanding how these factors affect species is important for conservation planning and sustainable land management. It is necessary to assess the habitat preferences and suitability of species to foster constructive conservation and management actions that can stabilize populations and react to threats dangers or pressures to these species. Detecting declines in population sizes and studying impacts of environmental change on common species is critical for understanding their decline and responding to possible extinction debts (Kuussaari et al. 2009, Gaston 2010). Based on the Principle of Determinism (Hoefer 2016), a qualitative understanding of a species' ecology is critical for informing management and inducing adaptive conservation to protect these threatened and associated species before they become rare and endangered (Tilman et al. 1994, Groom et al. 2006).

The greater glider (*Petauroides volans*)

Long considered common in Australia, the greater glider (*Petauroides volans*), the continents largest gliding marsupial (Jackson and Thorington 2012), has experienced a recent decline in population numbers (Lindenmayer et al. 2011, Youngentob et al. 2013). Greater gliders inhabit the *Eucalyptus* forests along the east coast of Australia, and have viable populations ranging from tropical Queensland in the north-east to temperate central Victoria in the south-east of the continent (Fig. 1.1, Lindenmayer et al. 1990a, van der Ree et al. 2004a). As an arboreal folivore, the greater glider relies exclusively on *Eucalyptus* for foraging and nesting in their hollows. It also satisfies most to all of its water requirements from their foliage, similar to the koala (Phascolarctos cinereus, Marples 1973, Foley et al. 1990, Kavanagh and Lambert 1990). Long-term greater glider habitat surveys have found population declines at annual rates of up to 9%, as well as local extinctions (Lindenmayer 2009, Lindenmayer et al. 2011), while climate modelling predicts substantial shrinking of greater glider habitats across eastern Australia in the future due to rising ambient temperatures (Kearney et al. 2010). The IUCN has classified the species as vulnerable (Burbidge and Woinarski 2016) and it is listed as threatened in parts

of its distribution under the Environment Protection and Biodiversity Conservation Act, and within Victoria under the Flora Fauna Guarantee Act (Woinarski et al. 2014, DELWP 2019). The decline in greater glider populations has typically been attributed to timber harvesting, land-use change, wildfires and planned burning, as these disturbances fragment habitat and reduce the amount of nesting- and foraging trees (Lindenmayer 1994, Possingham et al. 1994, McCarthy and Lindenmayer 1999, Kavanagh 2000, Lindenmayer et al. 2003, Lindenmayer et al. 2004, Pope et al. 2004, Lindenmayer 2009, Youngentob et al. 2013). Conservation recommendations and regulations at the state-level have set high priorities to the mitigation of assumed threats from logging and other forest management practices and proposed research priorities focus on the assessment of impacts of current forest and fire management practices (Woinarski et al. 2014, DELWP 2019).

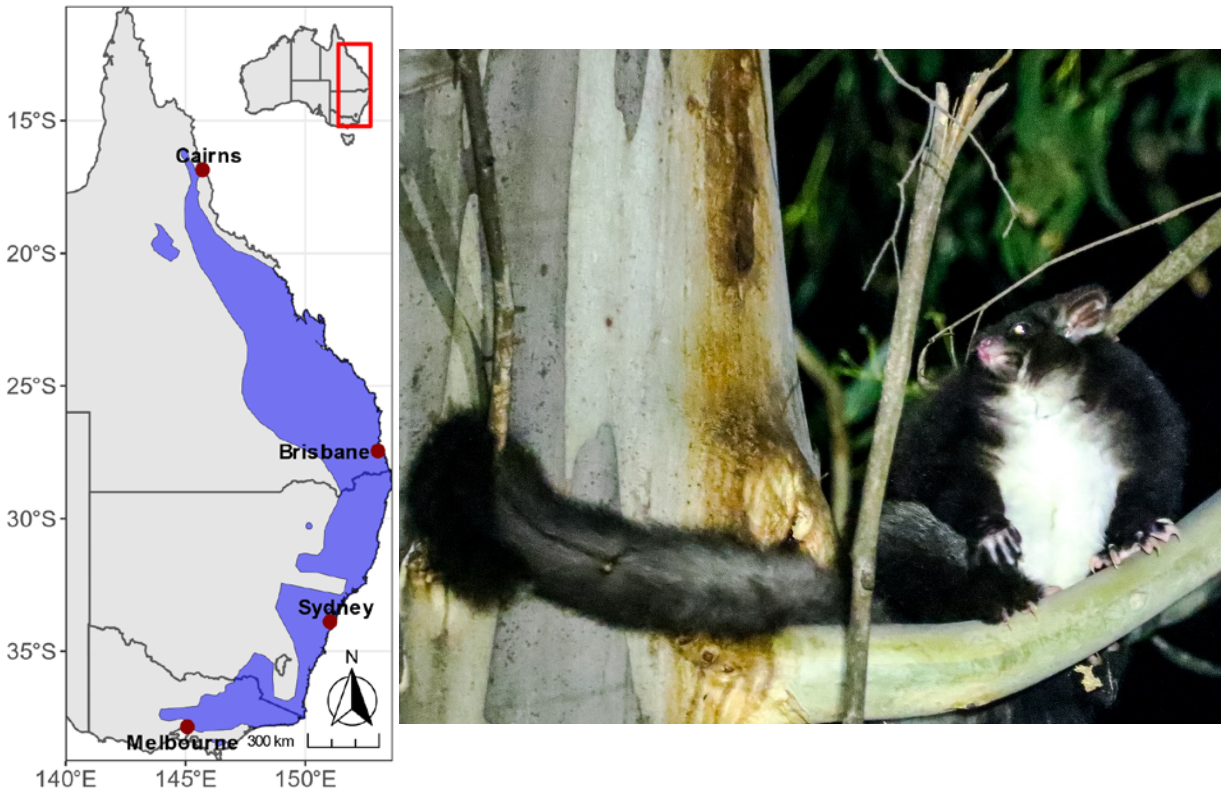

Figure 1.1. Left: Geographic range of the greater glider (blue shading) according to IUCN (2020). Right: a southern greater glider in its most common colour morph (black fur with a white chest) observed in a *Eucalyptus viminalis* on Granton Road near Narbethong, Victoria. Picture Credits: Christoph Parsch.

Taxonomy

The greater glider was first scientifically described in 1792 as *Didelphis volans* (Kerr.) and has since undergone many changes in both family and scientific name (see Maloney and Harris

2006, Harris and Maloney 2010). The greater glider is part of the family *Pseudocheiridae* (Winge, 1893 - see Jackson and Thorington 2012), which includes other arboreal marsupials such as the common ringtail possum (Jackson and Groves 2015). It is the largest gliding marsupial in Australia and is distinguished from other gliders by its gliding membrane attached to its elbow instead of hand (Johnson-Murray 1987), as well as its bushy, pendulous tail, which is longer than its body and has a small naked area at the tip (Fleay 1933, Jackson and Groves 2015). Greater gliders are currently divided into two subspecies: *P. volans minor* in northern Queensland and *P. volans volans* (the southern greater glider) in temperate and subtropical Victoria and New South Wales (Comport et al. 1996, Jackson and Thorington 2012). More recently, genetic evidence has been reported, that supports a population structure of three distinct greater glider species – Southern, Central and Northern – found in the temperate (mostly Victoria and southern New South Wales), subtropical (New South Wales and southern Queensland) and tropical regions (Queensland) of Australia (McGregor et al. 2020). Nevertheless, for conservation and management purposes, *Petauroides volans* has been legislated as a single species thus far (Woinarski et al. 2014, Burbidge and Woinarski 2016). The focus of this thesis will be the southern greater glider and its distribution in the state of Victoria, southeastern Australia.

Morphology

Petauroides volans is generally described in literature as a medium sized gliding possum with large gliding membranes, which increases the body-size appearance of the animal (Marlow 1965, Jackson 2012). Body lengths are reported between 39 – 43 cm and tail lengths from 43 – 52 cm at body masses between 1 – 1.7kg (700-900g for the northern subspecies, Rübsamen et al. 1984, Flannery 1994, Comport et al. 1996, Kavanagh and Wheeler 2004, Jackson and Groves 2015). While many possible colour-combinations of its fur that have been reported, two main colour morphs can be distinguished: brown-black pelt (Fig. 1.1) and a white-grey coating (Flannery 1994, Comport et al. 1996, McGregor et al. 2020).

Ecology and habitat

Greater gliders inhabit *Eucalyptus* forests along the east coast of Australia. A large variety of forest types suitable as greater glider habitat is reported in literature from open lowland forests along the coasts and plains to old-growth forests in high elevations and lower elevation woodlands west of the Great Dividing Range (Flannery 1994, Moore et al. 2004b). In south-eastern Australia they are found most commonly in tall high-elevation and wet forests, such as the Central Victorian Highlands or the high-country of East Gippsland (Fig. 1.2, Bennett et al. 1991, Kavanagh and Bamkin 1995, van der Ree and Loyn 2002, Eyre 2004, 2006,

Maloney and Harris 2006). Greater gliders have viable population densities from 0.5 – 3.8 animals per hectare and have a patchy distribution throughout the landscape (Kehl and Borsboom 1984, Henry 1985, Kavanagh and Lambert 1990, Comport et al. 1996). This patchiness may be explained with differences in foliar nutrition of different *Eucalyptus* species in their habitat (Braithwaite et al. 1984, Kavanagh and Lambert 1990, Cork and Catling 1996, Cork and Foley 1997), as well as nesting-space availability (Lindenmayer et al. 1990a), predator pressure (Kavanagh 1992), soil fertility, species, age and structure of the forest, disturbance history and climatic variables (Pausas et al. 1995, Cork and Catling 1996, Kearney et al. 2010). Average home-ranges sizes are between 1.2 and 4.1 ha, depending on sex of the animal and location, with male home-ranges being slightly larger (Kehl and Borsboom 1984, Comport et al. 1996, Kavanagh and Wheeler 2004, Pope et al. 2004). Individual animals have been observed to extend home range sizes to up to 18 ha, where habitat is fragmented or resources are scarce (Smith et al. 2007, Youngentob et al. 2013).

Figure 1.2. Two very different forest types forming greater glider habitat: On the left, dry lowland forests of Lake Tyers Reserve, East Gippsland, Victoria at ~50 meters above sea level. These landscapes are dominated by iron barks, boxes and silvertop ash (*Eucalyptus sieberi*). Population densities are low and greater gliders are confined to riparian areas with favourable climates and tree species such as *E. cypellocarpa*. On the right, a tall mature mixed stand of *E. viminalis* and *E. fastigata* on Mount Ellery, Errinundra Plateau, East Gippsland at ~1000 meters above sea level. These mixed species forests occur up to 1300 m elevation and have high densities of greater gliders in habitat that contains favourable tree species and are highly climatically suitable. Picture Credits: Benjamin Wagner.

Within their home-ranges, greater gliders usually occupy between four and 20 large tree hollows in branches or trunks of large-diameter, mostly mature or over-mature eucalypts, which are used for nesting (Henry 1985, Lindenmayer et al. 1990a, Comport et al. 1996, Cunningham et al. 2004, Kavanagh and Wheeler 2004, Lindenmayer et al. 2004, Lindenmayer et al. 2017). Greater gliders are mostly solitary, sharing a den rarely or during mating season from November to December (Fleay 1933, Kavanagh and Lambert 1990, Comport et al. 1996, Cunningham et al. 2004). They are strictly nocturnal, leaving tree-hollows to forage only after sunset and returning before dawn (Lindenmayer et al. 1990a, Cunningham et al. 2004). In the daytime greater gliders sleep in a curled posture, wrapping their tails around the body in a nest within a tree hollow and keep insulated from hot or cold temperatures outside (Rübsamen et al. 1984). The animal is reported to be able to glide distances up to 100 meters from the top of a tall tree to travel from its den-tree to a foraging tree (McKay 1983) and spends its entire diurnal and nocturnal cycle within the uppermost strata of the canopy, to which the greater glider is best adapted and where it is safest from predation by its main predator, the powerful owl (Ninox strenua, Kavanagh 1988, Kavanagh and Lambert 1990, Bennett et al. 1991, Cunningham et al. 2004).

Drivers of occupancy and habitat suitability

Greater glider habitat selection is strongly influenced by three main factors that operate over multiple spatial scales. At the landscape scale, climate can shape the distribution of the species due to its narrow thermotolerance, restricting populations to cooler and wetter parts of the landscape, predominantly found at higher elevations (Rübsamen et al. 1984, Kearney et al. 2010, Smith and Smith 2020). At the stand scale, a specialised diet consisting entirely of nutrient-rich *Eucalyptus* leaves and the need for multiple large tree hollows for denning, influences the establishment and spatial configuration of individual home ranges (Kavanagh and Lambert 1990, Lindenmayer et al. 1990b, Smith et al. 2007, McLean et al. 2015).

Physiology

Within the guild of arboreal folivores, it is especially the greater glider, that is most abundant at higher elevations with milder temperatures and more rainfall (Braithwaite 1983, Opie et al. 1990, Bennett et al. 1991, Kavanagh and Bamkin 1995, Braithwaite 1996, Smith et al. 2007, Taylor et al. 2017). Kavanagh and Bamkin (1995), studying greater gliders in southeastern New South Wales, concluded that elevation and the related vegetation community are the best predictors for the occurrence of greater gliders in some areas. In an early study on temperature tolerances of Australian mammals, Robinson and Morrison (1957) concluded, that

the guild of gliders have their thermal equilibrium at $2\,^{\circ}C > \Delta T > 1\,^{\circ}C$, a medium heat-regulatory ability and found a moderate respiratory response at 40 °C ambient temperature. Rübsamen et al. (1984) conducted studies on the thermoregulation of captive greater gliders from New South Wales and concluded that rather than having a thermoneutral zone covering several degrees like most homoeothermic species (Kingma et al. 2014), greater gliders have a thermoneutral point at 20 °C, above which the animal becomes hyperthermic. At these temperatures, they have to spend considerable amounts of water and energy to cool themselves through evaporative processes (Rübsamen et al. 1984). The study emphasizes the clear contrast between the greater glider's inefficient use of water for above described processes and the limited water availability within their arboreal habitat and main foraging resource – *Eucalyptus* leaves (Rübsamen et al. 1984). A preference for higher elevation forests may therefore exist because this particular thermoneutral point is less likely to be exceeded here, especially at night when greater gliders are active outside their insulated hollows. Other explanations include the occurrence of favourable forest communities in high elevations in combination with land clearing of suitable habitat in lowland regions (Gibbons and Lindenmayer 2002, Lindenmayer et al. 2011), as well as a nutritional relationship. In areas where nights are cold in comparison to daytime temperatures, plants metabolize less photosynthate, thus available foliage for gliders and other nocturnal folivores might be more nutritious in higher elevation ecosystems (Braithwaite 1996). Based on the results of the study in 1984 and including other factors as modelling parameters, such as food properties or metabolism of greater gliders, Kearney et al. (2010) created species distribution models (SDMs) to predict the habitat extent across the greater glider's range under climate change. They predicted habitat contractions of up to 94% which suggested the near loss of the northern subspecies *P. volans minor* in a 3 °C warming scenario (Kearney et al. 2010). In the south, populations were predicted to be more stable, but may also be affected by habitat loss associated with climate change (Kearney et al. 2010). These modelled findings are in line with field observation for greater gliders and other arboreal marsupials in response to high ambient temperatures. High mean annual temperatures and low precipitation rates, along with an increased forest fire frequency were found to be important in explaining greater glider density in the Blue Mountains, New South Wales (Smith and Smith 2020). For the koala – another eucalypt dependant folivore – similar distribution models have been used to predict its distribution under climate change and it was found that under a hotter and drier future, current distributions will shift and contract drastically (Adams-Hosking et al. 2011). Climatic effects on koala populations have been reported as early as the 1980s: In 1988 a severe local koala population crash was observed during a major drought and heatwave in the south-west of Queensland: 63% of the observed population died as a consequence of water deficiencies, while

most surviving animals were found in wetter gullies (Gordon et al. 1988). In an earlier drought in 1982 – 1983, large numbers of koalas reacted by moving into more suitable swamp- and manna gum forests (Hindell 1984). Similar behaviour in greater gliders has not yet been observed and may be restricted due to their smaller home-range sizes and limited dispersal ability, which are up to 100 ha in koalas (Moore et al. 2004b). Nevertheless, riparian areas with suitable climate have been found to act as important habitat refugia for greater gliders as well, where surrounding forests had been disturbed by timber harvesting and/or fire (Lindenmayer et al. 1993a, Kavanagh 2000, McLean et al. 2018).

Diet and foraging preferences

The greater glider is an arboreal folivore, the animal group among marsupials, that live and forage in trees and, in Australia, include the families *Phalangeridae*, *Pseudocheiridae* and *Phasocolarctidae* (Hume 1999, Jackson and Groves 2015). Other common examples of arboreal species feeding on foliage are common brushtail- and ringtail possums (*Trichosurus vulpecula*, *Pseudocheirus peregrinus*), as well as the koala (Phascolarctos cinereus, Flannery 1994). Most members of this group feed on a multitude of tree and plant products, such as fruits, flowers, buds, bark, leaves or invertebrates living within the same habitat (Smith and Winter 1997, Shipley et al. 2009). Only greater gliders and koalas forage exclusively on *Eucalyptus* and also satisfy all or most of their water requirements from their leaves (Marples 1973, Foley et al. 1990, Kavanagh and Lambert 1990, Moore et al. 2004b). Such specialisation is the rarest form of foraging among mammalian herbivores (Shipley et al. 2009). Greater gliders inhabit a variety of forests, express similar dietary patterns in all populations, even though situated in different climatic regions with different vegetation such as temperate Victoria or tropical north-eastern Queensland (Henry 1985, Comport et al. 1996, Hume 1999). The resulting adaption to this foraging preference and relatively stable environment of mature forests as habitats is a slow population turnover rate and a low reproductive output in populations of greater gliders, which is also observed in koalas (Tyndale-Biscoe and Calaby 1975). More opportunistic arboreal folivores, such as the common ringtail possum, have high reproduction rates with fast turnovers. While these traits allows such opportunists to respond to unstable habitat conditions more rapidly by e.g. colonization of another habitat, true folivores such as greater gliders and koalas are less resilient species when it comes to environmental change (Tyndale-Biscoe and Calaby 1975, Hume 1999, Shipley et al. 2009, Briscoe et al. 2015).

Eucalyptus leaves as a food resource

With almost 900 native species in Australia (Blakely 1965, Boland et al. 2006), *Eucalyptus* foliage is a widely available food resource in almost any climatic region of the continent. It is utilized by many animals in different ways, mainly by possums, as well as the koala (Flannery 1994). The characteristics of *Eucalyptus* foliage derived from their evolution on old and weathered soils limits their suitability as forage to a few adapted specialists such as the greater glider. Eucalypts have highly sclerophylly leaves, which are high in fibre content in most species (Attiwill and Leeper 1987). Two main factors characterize limitations as a foraging resource: (1) very low nutrient concentrations of *Eucalyptus* foliage; and, (2) the occurrence of plant secondary metabolites (PSMs), also referred to as anti-nutrients (Cork and Foley 1991, Moore et al. 2004b, Moore and Foley 2005, DeGabriel et al. 2009b, DeGabriel et al. 2009a, Youngentob et al. 2011). PSMs such as lignin or condensed tannins either hinders the digestive process or are toxic to live tissues of the animal or gut bacteria digesting it in the form of hydrolysable tannins or essential oils (Foley 1987, Foley et al. 1987). In comparison to other typical green foraging resources, *Eucalyptus* leaves, especially when mature, express low protein and carbohydrate availability, but are high in lipids and phenols, influencing the nutritional value and digestibility (Cork and Sanson 1990, DeGabriel et al. 2014). Eucalypt leaves are therefore a complicated food resource (Attiwill and Adams 1996, Hume 1999). Even though in comparison to other typical animal foraging resources, cellulose content is not significantly higher, the leaf fibre has a higher lignin content which contributes to its low digestibility (Moore et al. 2004a, Degabriel et al. 2008). An increased presence of condensed tannins in the leaves, which adhere to proteins, rendering them inactive and further decrease the digestibility of many components such as cell-wall carbohydrates adds complexity to eucalypt leaf digestions (Kavanagh and Lambert 1990, Degabriel et al. 2008, Wallis et al. 2012). This is especially problematic when they are consumed solely and without alternatives, such as flowers, buds or invertebrates, which are commonly used by other arboreal marsupials such as yellow-bellied- or sugar gliders (Petaurus australis, Petaurus breviceps, Cork 1984, Cork and Sanson 1990, Cork and Catling 1996, Cork and Foley 1997, Brown et al. 2006). The chemical make-up varies by *Eucalyptus* species and as a result has led to a foraging preference for certain species in greater gliders (Kavanagh and Lambert 1990, Youngentob et al. 2011).

Foraging preferences of Petauroides volans

Studies, to understand the food selection preferences of possums and gliders in Australia, dating back to as early as the 1950s, all acknowledge the poor nutrient and especially low nitrogen status of *Eucalyptus* foliage (Andrewartha and Birch 1954, White 1978, Mattson 1980). It has been established that greater glider abundances are variable among forest

communities (Braithwaite 1983, Braithwaite et al. 1984, Kavanagh 1984, Lindenmayer et al. 1993a, McIlwee 2001, Eyre 2006, Lindenmayer et al. 2011, White 2012) and their small body-sizes and home-ranges should constrain them from using highly fibrous food and thus make greater gliders a highly selective species when it comes to foraging selection (Youngentob et al. 2011, Au et al. 2019a). This behaviour maximizes energy and nutrient intake, similar to other folivore species (Kay 1978, Parra 1978, Smith and Ganzhorn 1996). Research thus started to focus on the nutritional values of eucalypt leaves in relation to greater glider occurrence and it has been found that foraging species selection can be explained by total or available/digestible nitrogen as well as fibre contents: Those species that express higher nutrient availability are generally preferred by greater gliders and other marsupial folivores (Moore et al. 2004b). A study in southeastern New South Wales found that greater gliders preferred species high in foliar nitrogen and young leaves over mature ones if available, which show lower levels of lingo-cellulose and had higher digestibility (Kavanagh and Lambert 1990). Further research into foraging preferences found that it is not only nutrient availability, but the leaf chemical composition of certain species, that dictates the food selection (Cork and Foley 1991, Cork and Catling 1996, Youngentob et al. 2011, Jensen et al. 2015). Youngentob et al. (2011) described the differences in foliar chemistry of eucalypt subgenera and how they influenced greater glider feeding. Greater gliders prefer monocalypts over symphomyrtles. Monocalypt leaves have lower available nitrogen, due to high tannin concentrations binding nitrogenous compounds (Wallis et al. 2010), but do not contain formylated phloroglucinol compounds (FPCs), which can cause toxicosis and reduce the level of digestibility of plant nutrients (Cork and Foley 1991, Moore et al. 2004b, DeGabriel et al. 2009b). In line with this are the findings of Kavanagh and Lambert (1990): Three out of four commonly used feeding species in their study area were monocalypts that were high in foliar nitrogen (*Eucalypts fastigata, E. obliqua and E. radiata)*. Youngentob et al. (2011) proposed that greater gliders would be able to feed more, if both monocalypts and symphomyrtles occur within their home-ranges. Animals would be able to build up toxin levels and take up more nitrogen while feeding on symphomyrtles and then switch to monocalypts to detoxify their digestive system when needed, while still taking up (comparatively less) nitrogen from monocalypts (Youngentob et al. 2011). A switch back to symphomyrtles would then occur, before debilitating amounts of tannins are digested (Marsh et al. 2006). They furthermore proposed that for greater gliders, gliding could be an evolutionary adaption to energy and detoxification requirements and the scarcity of nutrients within their habitats: Gliding between trees reduces movement energy consumption drastically and allows the swift change between subgenera and to find favoured juvenile leaves within the forest (Johnson-Murray 1987, van der Ree et al. 2004b, Youngentob et al. 2011). The first assumption, which is proposed according to the detoxification limitation

hypothesis, was also observed by Cunningham et al. (2004) and later confirmed for greater gliders by Jensen et al. (2015). In their study on captive greater gliders from Tumut, New South Wales, they described concentrations of FPCs as the main factor determining how much individuals eat of either *Eucalyptus viminalis* or *E. melliodora* (both subgenus *Symphomyrtus*), which differ greatly in amounts of both available nitrogen and FPCs. When only fed with *E. viminalis*, the individual concentration of available nitrogen was decisive for feeding (Jensen et al. 2015). The surveyed gliders would balance their diet between potential gain and costs (available nutrients and FPCs) when presented with alternate food resources (Jensen et al. 2015).

Tree hollow formation

Most arboreal marsupial species nest in hollows and cavities in large mature trees (Lindenmayer et al. 1991a) which protect them and their offspring from environmental dangers and predation (Fig. 1.3, Smith and Lindenmayer 1988, Lindenmayer et al. 2017).

Figure 1.3. Left: A large mature messmate (*Eucalyptus obliqua*) observed near Mount Jack at intermediate elevation in East Gippsland's mixed species forests. These forests have not been disturbed for at least 70 years and at 63 meters in height and >2 meters in diameter, forest giants such as this tree, provide habitat for a wide range of forest-dependent fauna including large hollows for arboreal marsupials. Right: a typical tree hollow, suitable for arboreal marsupial occupation, with an entrance hole of ~30 cm in diameter. The hollow likely developed from the breaking of a branch fork after a storm and deepened through consecutive insect or fungal attack on the rotting timber. Mechanical disturbance and decay are major factors in hollow formation in Australian eucalypts. Picture Credits: Benjamin Wagner.

The formation of hollows in eucalypts depends on tree dimensions, form, age and mechanical disturbance (Lindenmayer et al. 1991b, Lindenmayer et al. 1993b). Trees with large diameters, shorter heights and/or irregular crown forms often express hollow occurrence in the temperate forests of southeastern Australia (Bennett et al. 1994, Gibbons et al. 2000, Fox et al. 2009). Due to the absence of excavating species such as woodpeckers, hollow formation requires long time-frames in Australia and therefore tree hollows mainly occur in mature trees that may have been exposed to different sources of damage or decay (e.g. fire or fungal attacks, Fox et al. 2008, Lindenmayer et al. 2017). Climate may play a role in these processes as well and can foster hollow formation in drier parts of the landscape through influences on species composition and growth form (Bennett et al. 1994). Strong positive relationships between stand age and the proportion of living trees with hollows in forests of the same landscape have been reported (see Gibbons et al. 2000) and unlogged or unburnt sites usually have more hollow bearing trees than forests that have been disturbed (McLean et al. 2015). Timber harvesting and forest fires negatively affect hollow occurrence and abundance by removing old hollow-bearing trees, which can lead to population declines in greater gliders (Lindenmayer et al. 1991b, McLean et al. 2015).

For greater gliders, the need for favourable foraging- and mature trees with hollows for nesting is assumed to drive habitat selection at the stand scale (Kavanagh and Lambert 1990, Lindenmayer et al. 1990a, Jensen et al. 2015). And, as preferred *Eucalyptus* species high in foliar nitrogen and digestibility are associated with certain climatic and topographic conditions that facilitate higher site productivity, greater gliders are typically found in higher abundance at higher elevations (Henry 1984, van der Ree et al. 2004a, Koch et al. 2008, Youngentob et al. 2011). These climatic conditions also favour their limited thermoregulatory abilities and likely act at broader (landscape) scales (Rübsamen et al. 1984, Smith and Smith 2020, Youngentob et al. 2021). Additionally, disturbances, which can be exacerbated by climate change or certain management practices may affect these drivers of habitat suitability and limit occurrence or decrease habitat suitability (Fig. 1.4).

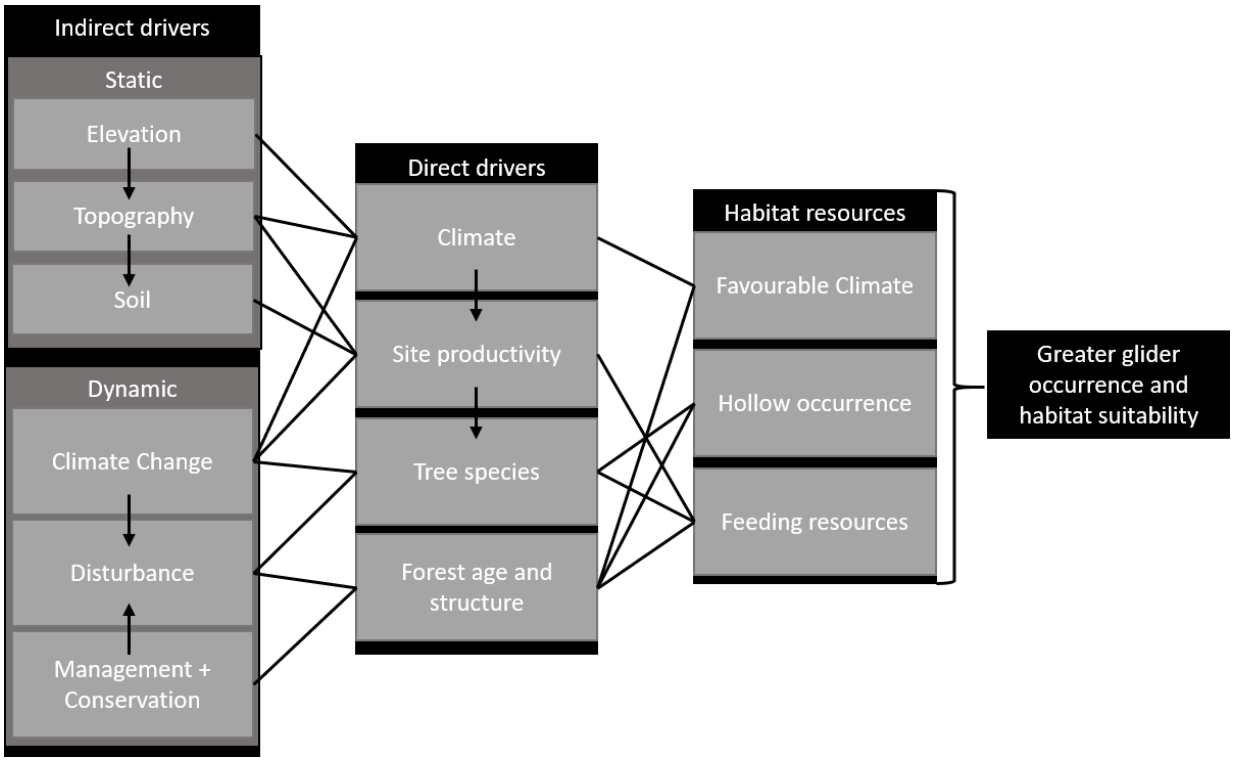

Figure 1.4. Conceptual framework of drivers in greater glider occurrence and habitat suitability. The three main habitat resources required to form populations (favourable climate, hollow occurrence and feeding resources) are affected by direct drivers such as site productivity and forest composition, which in turn can be affected by indirect drivers such as topography or climate change (indicated by connected boxes). Some drivers influence other drivers (indicated by arrows): For example, a changing climate increasing temperatures and reducing precipitation may increase the number and severity of disturbances from forest fires, or site productivity drives the tree species composition growing in a particular part of the forest landscape.

Greater Glider population declines

There is a conservation concern for the greater glider because of reported declines across its distribution. Surveys in long term study sites found populations declining at severe rates or being extinct locally (Lindenmayer et al. 2011, Lindenmayer and Sato 2018, Smith and Smith 2018). It was found, that populations in managed forests of southeastern Australia were declining at estimated annual rates of 8.8%, while a population in the Booderee National Park, New South Wales, became extinct by the year 2007 (Lindenmayer 2009, Lindenmayer et al. 2011). Greater glider populations in the Blue Mountains National Park, New South Wales have declined and shifted to mostly higher elevations since the 1980s, with declines in low elevation forests, where the species is now considered rare (Smith and Smith 2018). Surveys in forest remnants surrounded by *Pinus radiata* plantations in Tumut, New South Wales, revealed that glider densities were significantly lower in small remnants of eucalypt forests and patches surrounded by pines that had been harvested recently (Lindenmayer 2009,

Lindenmayer et al. 2011, Youngentob et al. 2013). Since most studied forests had been exposed to multiple disturbances such as harvesting operations, plantation establishment or planned- and wildfires, it is assumed that greater gliders, specialized on prevailing widespread environmental conditions, are at high risks of population decline when the formerly stable environmental conditions of their habitat change through disturbance (Taylor et al. 2007, Lindenmayer et al. 2011, Taylor et al. 2017). Additionally, a period of prolonged drought and above-average temperatures in the first years of the 21st century in southeastern Australia may have been influencing greater glider populations in those parts, adding climate as a potential agent in shaping occurrence (Moore et al. 2004b, Cai and Cowan 2008, Lindenmayer et al. 2011). A result of these disturbance events is the reduction of nesting space (large mature and hollow-bearing eucalypt trees) and feeding resources (leaves from preferred foraging species), landscape and habitat fragmentation, as well as an opening of the forest for predators. These factors lead to a loss or reduction of habitat suitability of prior greater glider habitats (Cunningham et al. 2004, Kavanagh and Wheeler 2004, Lindenmayer et al. 2004, Pope et al. 2004, Eyre 2006, Smith et al. 2007, Lindenmayer 2009, Woinarski et al. 2014, Berry et al. 2015, Burbidge and Woinarski 2016, Taylor et al. 2017). Earlier studies in southeastern Australia report the greater glider being the most vulnerable arboreal marsupial to logging in southeastern New South Wales (Kavanagh and Webb 1998) and the north-east coast of the state (Kavanagh et al. 1995). Another study by Kavanagh and Bamkin (1995) in southern New South Wales found the occurrence of greater gliders strongly associated with unlogged forests. It was reported that a high level of tree retention is needed for greater gliders to survive in forests subject to timber harvesting (Kavanagh 2000) and that population density decreases with harvesting intensity (McLean et al. 2018). While these findings help explain population declines of greater gliders in managed environments such as the Central Highlands of Victoria or the fragmented landscape of Tumut, such factors cannot adequately explain the complete extinction of greater gliders in Booderee National Park (Lindenmayer et al. 2018) and population declines in the Blue Mountains National Park (Smith and Smith 2020). Here, forests are not managed for timber or subject to land-use change due to the protected status of forests within National Parks in Australia since 1975 (see National Parks and Wildlife Conservation Act 1974). Furthermore, severe fires leading to habitat fragmentation did not occur in Booderee within the timeframe of the population collapse (Lindenmayer et al. 2011, Lindenmayer and Sato 2018). Proposed explanations revolve around an extinction debt from past urbanization activities (Tilman et al. 1994) or increased predator pressure by owls as a result of control measures for invasive species such as the red fox (Vulpes vulpes, Lindenmayer et al. 2011, Lindenmayer et al. 2018). Both explanations are not very likely, as: (1) greater gliders in Booderee seem to have declined there in many small subpopulations separately across

the reserve and very swiftly, arguing against an extinction debt (Tilman et al. 1994); and, (2) the implications made from a released competition for prey within different owl species in the reserve as a result of reduced fox numbers, seems unanticipated, although owl predation can create severe pressure on greater glider populations (Kavanagh 1988). Population declines and the slow disappearance of greater gliders from lowland forests in the Blue Mountains National Park was also statistically explained by increases in ambient temperatures, decreases in rainfall and associated increases in fire frequency (Smith and Smith 2020).

Management and conservation

Much of the above described observations and research have had influence on conservation planning and decisions for greater gliders over time. These are mainly described and recommended in the 2012 Conservation Advice for *Petauroides volans* from the 'Action Plan for Australian Mammals 2012' as well as the Flora Fauna Guarantee Act (FFGA), issued by the Threatened Species Scientific Committee (Woinarski et al. 2014, DELWP 2019). The Action Plan, acting on a federal level, states: "Cumulative effects of clearing and logging activities, current burning regimes and the impacts of climate change are a major threat to large hollow-bearing trees on which the species relies" and sets a vulnerable conservation status, with the option of listing greater gliders as threatened under State and Territory legislation (Woinarski et al. 2014, Department of the Environment and Energy 2016). This has happened in 2018 as an update to the FFGA, under which the greater glider is now considered threatened in Victoria (DELWP 2019). Findings and conclusions in the Action Plan are based on scientific literature and unpublished government or third-party reports and personal communications. On the federal level, 'severe' or 'catastrophic' consequences to population sizes are expected from habitat loss through timber harvesting, as well as prescribed burning, intense and frequent forest fires, timber production, climate change and predation by owls (Woinarski et al. 2014). It is suggested to "reduce the frequency and intensity of prescribed burns", emplace proper patch- and habitat-tree retention strategies, adapt logging rotation periods and "protect and retain hollow-bearing trees, suitable habitat and habitat connectivity" (Woinarski et al. 2014, Department of the Environment and Energy 2016). In parts of Victoria, regulations are in place to establish a special protection zone (SPZ) of 100 ha if greater gliders are found in densities of greater than 2/ha, 15/hour or >10/km of spotlighting survey (Nelson et al. 2018). A higher rate of tree retention must occur where timber harvesting is permitted in areas of medium greater glider densities across all of Victoria (Woinarski et al. 2014, DELWP 2019). Recommendations are to retain at least 40% of eucalypt basal area, where animal densities of five or more per spotlighting kilometre are observed (DELWP 2019). Although not part of the current mandatory 'Code of Practice for Timber Production 2014', these recommendations

are currently followed voluntarily by the state's forest management agency VicForests (DELWP and ARI staff, personal communication, April & May 2021 & DEPI 2014). The state's overarching goal for the protection of native forest-dependent fauna was ending timber harvesting in old-growth forests in late 2019 and the gradual phase-out of native forest timber harvesting by the year 2030, which was agreed on by the state government in November 2019 (DEPI 2014, DELWP 2019). In addition, ~100,000 ha of mature forest habitat across the entire state have been placed under immediate protection (Immediate Protection Areas – IPAs) at the same time (see DELWP 2019). In the federal conservation advice for the greater glider, high priorities are given to the active mitigation of threats through planned burns, timber production, clearfelling practices and fragmentation, while assessing relative abundances and the viability of populations across the entire species range is given a lower priority (Department of the Environment and Energy 2016). High valued research recommendations are the assessment of numbers, densities and types of hollow-bearing trees to retain, the assessment of fire management impacts on greater glider habitat and nesting space availability and in general, the effectiveness of threat mitigation methods (Woinarski et al. 2014). The Victorian Action Statement specifically mentions the need for focussed research programs to assess the impacts of climate change and heat stress on greater gliders and their habitat, the identification of climatic refugia and an investigation of foliar nutritional value and feeding behaviour (DELWP 2019).

Recent research and research gaps and opportunities

Although factors such as nutrient and water availability, plant productivity, tree-species preferences and vulnerability to high ambient temperatures or climate change have become part of the discussion around decline and the conservation of greater gliders and other arboreal marsupials (Adams-Hosking et al. 2011, Nelson et al. 2018, Au et al. 2019b, DELWP 2019, Reside et al. 2019, Smith and Smith 2020, Youngentob et al. 2021), how these affect greater glider habitat suitability and population persistence is still poorly understood. Until now, what may be least understood and considered in greater glider population dynamics is the effect of climate change on their habitat. While it has been modelled that an increase in ambient temperatures under climate change scenarios could affect populations (Kearney et al. 2010), distinct climatic requirements due to its physiology remain unknown. Additionally, the distribution of *Eucalyptus* foliar nutrients over a landscape and within and between stands and species has not been investigated deeply. The ability to predict climatic refugia at the landscape- and feeding and nesting resources at a stand-scale is still missing for large parts of the greater gliders' distribution. These could provide important improvements to management and reserve design, not only for the greater glider but many species associated with its old-

growth forest habitat. Earlier modelling approaches considering foliage and soil nutrients show that it is mainly the availability of nutrients and quality of leaves that determine the occurrence of arboreal marsupials such as the greater glider (Pausas et al. 1995). Forest stand condition and composition, nutrients and topography were the best predictors for explaining greater glider population densities in models based on survey data (Stockwell et al. 1990, Cork and Catling 1996). This is in line with preferences of gliders for favouring cool climates and nutrient rich tree species, thus more productive sites within forests (Cork 1992). What is missing, is the ability to predict these resources at relevant scales.

Spatial scale is an important factor in studies on the ecology of any species as it influences the relationship between environmental energy availability and species richness and abundance (Gaston and Blackburn 1996, Blackburn and Gaston 2002, Evans et al. 2008, Sreekar et al. 2018). Long-term ground-based surveying and monitoring approaches might not be able to provide quick enough assessments of certain populations and abundances, whose current conservation status may be in question. Detecting changes swiftly and across scales is important in the face of the current rapidly changing climate and methods have to be able to avoid lag times common in wildlife monitoring programs (Doak 1995). As such, methods of remotely sensing habitat distribution and suitability would be well suited to address current management and conservation concerns regarding the greater glider and close research gaps (Turner et al. 2003, Jensen 2007, Jones and Vaughan 2010, Briscoe et al. 2016). Remote sensing can be used for estimating plant productivity and nutrition, as well as climatic variables using means such as visible light imagery or spectroradiometers (Ustin et al. 2004, Asner and Vitousek 2005, Marvin et al. 2016, Fedrigo et al. 2019, Lepczyk et al. 2021, Stewart et al. 2021). Important correlations have been reported between the nutrient-, especially nitrogen-, status of plants and optical parameters including canopy and leaf spectral reflectance, leaf transmittance, chlorophyll and polyphenol fluorescence (Foley et al. 1998, Curran et al. 2001, Kokaly 2001). These can provide a swift and non-destructive method of assessing foliar nutrition and environmental energy availability as key determinants in wildlife population dynamics (Pettorelli et al. 2011, Munoz-Huerta et al. 2013). Progress in the field of Australian wildlife ecology has especially been made using different multi- and hyperspectral sensors to estimate total and available nitrogen in plants and correlating these towards animal abundance (Youngentob et al. 2012, DeGabriel et al. 2014, Wu et al. 2019) as well as providing a tool to estimate nutrient availability in high resolution in forest habitat over large landscapes (Dury and Turner 2001, Coops et al. 2003, Asner et al. 2009, Youngentob et al. 2012). Youngentob et al. (2012) and Wu et al. (2019) were successful in mapping total and available nitrogen to assess arboreal folivore habitat with aerial or satellite multispectral and hyperspectral imagery using different reflectance bands and vegetation indices. Other studies used direct leaf

reflectance from satellite imagery to determine eucalypt foliage nitrogen levels and crown conditions (Coops et al. 2003, Coops et al. 2004, Sims et al. 2013). Advances in animal ecology have also been made through linking primary productivity estimates from the vegetation indices, with species abundances and distribution (see e.g. Running 1990, Bro-Jørgensen et al. 2008, Evans et al. 2008, Mueller et al. 2008, Willems et al. 2009). This has been utilized not only for larger herbivores, for example in explaining African buffalo (*Syncerus caffer*) habitat selection and forage quality in relation to body conditions (Ryan et al. 2006, Ryan et al. 2012), but also in small mammals such as primates, whose home ranges, habitat selection- and use are closely related to elevated plant productivity (Willems et al. 2009). Plant productivity has recently been statistically linked to greater glider abundance and habitat suitability: Youngentob et al. (2015) found positive relationships between remotely sensed measures of forest productivity based on the normalized difference vegetation index (NDVI) in eucalypt forests of New South Wales. Remote sensing and aerial imagery have therefore proven to be useful in estimating nutrient- and especially nitrogen-status, as well as plant productivity and promise approaches for remotely detecting greater glider habitat suitability at multiple scales (Coops et al. 2003, Huang et al. 2004, Munoz-Huerta et al. 2013, Wang and Wei 2016).

Research questions and thesis chapters

This thesis aims to add to the understanding of the role of key factors influencing greater glider habitat selection, abundance and population persistence within southeastern Australia and to develop management and conservation recommendations for improving reserve design and forest management practices. The following research questions are addressed:

1. *What are the main climatic, forest-structural and nutritional determinants and drivers of greater glider habitat suitability in southeast Australia?*

2. *What is the role of forest nutrition and hollow occurrence on southern greater glider occurrence and abundance?*

3. *Can high resolution remotely sensed imagery be used to predict and map forest nutrition in mature southeastern Australian* Eucalyptus *forests?*

4. *What are the relationships between spatial patterns of habitat resources and greater glider abundance, density and population persistence?*

The thesis is organized around four data chapters (Chapters 2-5) addressing these research questions. While this introduction chapters serves as a general literature review and introduction to the study complex, each data chapter will have its own literature review related to the respective research topic in its chapter introduction. The thesis chapters are structured as illustrated in Figure 1.5. Each chapter addresses a different aspect of greater glider habitat requirements, occurring at different spatial scales:

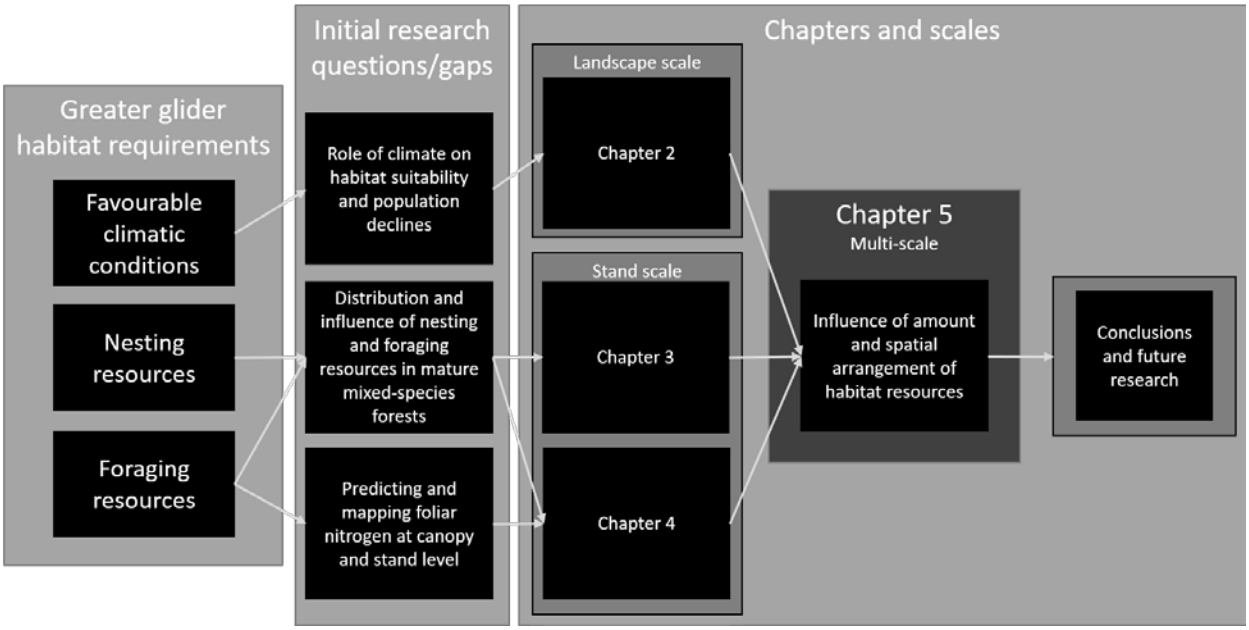

Figure 1.5. Thesis structure and chapters illustrating which greater glider habitat requirement is related to which research question in this thesis and which chapter is addressing which research question. Chapter 5 is based on findings from chapter 2-4 and addresses a research question that evolved from these chapters' findings and combines the scales studied.

The data chapters address the following topics:

Chapter 2: *Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits*

This chapter investigates drivers of greater glider presence and absence at the landscape scale with a focus on climatic conditions and how these have changed over time. Using remote sensing data and machine learning modelling, a spatial greater glider distribution model for the three major areas of distribution in Victoria, Australia is developed, and habitat suitability evaluated.

Chapter 3: *Habitat for gliders: Determining hollow availability and foliar nitrogen across a mixed-species forest landscape*

For Chapter 3, I conducted flora and fauna surveys in the mature mixed-species *Eucalyptus* forests of East Gippsland, Victoria and carried out leaf and soil chemistry analyses and

collected aerial imagery. These data were used to evaluate differences in two important stand-scale determinants of greater glider habitat suitability: hollow availability and foliar nitrogen. With linear and structural equation models, I identified important covariates to estimate both elements.

Chapter 4: *Mapping canopy nitrogen-scapes to assess foraging habitat for a vulnerable arboreal folivore in mixed-species Eucalyptus forests*

Chapter 4 builds and extends on data collected in the same forests as Chapter 3. I used high-resolution multispectral imagery, collected by a lightweight and low-cost commercial unoccupied aerial vehicle (UAV) to predict and map total and digestible foliar nitrogen from leaf-scale chemistry analyses. The ability to spatially quantify feeding habitat using UAV-acquired imagery allows for a swift and low-cost assessment of greater glider habitat.

Chapter 5: *The influence of spatial pattern in foraging habitat on the abundance and home range size of an arboreal marsupial in southeast Australia*

The final data chapter draws on findings from all previous chapters and acts as a synthesis to the thesis. Using properties and habitat configuration of the real landscapes and climatic conditions observed across East Gippsland, I created neutral landscapes of feeding habitat to test the effects of gradual decreases in habitat suitability. At the landscape scale (1000 ha), I studied impacts of decreasing climatic suitability on the accessibility of feeding habitat. At the stand scale (100 ha), I tested how different habitat configurations drive population density and how disturbances (e.g. fires or timber harvesting) may affect population persistence.

Chapter 6: Conclusion

A conclusion chapter summarises major findings of each chapter, compiles important implications for management and conservation of the greater glider and outlines future research opportunities.

2. Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits

Introduction

The effects of climate change and anthropogenic disturbances, such as land-use change, are negatively impacting biodiversity and altering ecological systems around the world (Stenseth et al. 2002, Walther et al. 2002). The increasing impacts of humans on natural ecosystems are leading to reductions in habitat area and quality for flora and fauna, which, in turn, lead to population declines, local extirpations, or extinctions (Diamond 1984, Lindenmayer et al. 2011, Youngentob et al. 2013). The rate of climate change and the increase in occurrence of extreme events has had noticeable impacts on many global ecosystems and species (Hoegh-Guldberg et al. 2007, Cai et al. 2014, Iizumi et al. 2014, Moran-Ordonez et al. 2018). In Australia, the climate is projected to change drastically with increases in mean annual temperatures of up to 4°C by the end of the 21st century (CSIRO and Bureau of Meteorology 2015) and shifts in the amount and frequency of precipitation, as well as increases in the frequency of extreme events (Orlowsky and Seneviratne 2012). For south-eastern Australia, these extreme events manifest as extended droughts and more frequent heat waves associated with increases in diurnal and nocturnal temperature maxima (Murphy and Timbal 2008).

Climate change is already having profound effects on the populations and distributions of native fauna (Cork and Catling 1996, Fischer et al. 2001, Welbergen et al. 2007, Kearney et al. 2010) and flora (Hughes et al. 1996, Mok et al. 2012, Rawal et al. 2015c, b). Habitat suitability models that include climate variables can provide insights into how species may respond to future climate change (Zimmermann et al. 2009, Briscoe et al. 2016, Mathewson et al. 2017). These models however rarely account for local weather patterns and extremes, which can have important influences on species' populations and distributions (Reside et al. 2010, Bateman et al. 2012, Moran-Ordonez et al. 2018). As such, it is important to assess the climatic preferences and tolerances of species to identify potential refugia and to develop effective conservation strategies that can maintain stable populations in these areas over time. This requires understanding not only the direct and indirect impacts of climate variability, but also their interactions with other factors; however, these have not been widely studied. Understanding how these various factors can affect species demography and habitat suitability are central to conservation planning and sustainable land management.

The greater glider (*Petauroides volans*), Australia's largest gliding marsupial, was once considered common but has recently experienced range-wide declines and local extinctions (Lindenmayer et al. 2011, Youngentob et al. 2013). The IUCN has classified the species as vulnerable (Burbidge and Woinarski 2016) and the species is listed as threatened nationally under the Environment Protection and Biodiversity Conservation Act, and within Victoria under the Flora Fauna Guarantee Act (Woinarski et al. 2014). In response, ~100,000 ha of

old-growth forest in Victoria was protected in late 2019 (DELWP 2019). The conservation of these old-growth forests was due to its association with hollow-bearing trees that it uses for nesting (Lindenmayer et al. 1990a). A range of studies have identified multiple factors that influence the habitat suitability of greater gliders at different scales, such as forest structure (Smith et al. 2007), disturbance (McLean et al. 2018), nutrient availability (Youngentob et al. 2011), and climate (Kearney et al. 2010). While the decline in greater glider populations has been variously attributed to timber harvesting, land-use change, bushfires and planned burning (Possingham et al. 1994, Kavanagh 2000, Pope et al. 2004, Lindenmayer et al. 2013, Youngentob et al. 2013), declines and extinctions have also been observed in protected reserves, where forests have not been subject to logging nor have experienced recent fire (Lindenmayer et al. 2011). The broader decline in the species' populations in some parts of its distribution is likely the result of other environmental factors. Climate and weather are potential factors (see Kearney et al. 2010); however, few studies have explored how recent climate change and extreme weather events impact the species. Changes to climate and weather patterns represent a potential systemic risk to greater gliders across their distribution as they have limited physiological flexibility - in particular, a narrow range of thermal tolerance (Rübsamen et al. 1984).

Unlike other mammals that have a thermoneutral zone of several degrees, the greater glider has a fixed thermoneutral point at 20 °C, above which it becomes hyperthermic (Rübsamen et al. 1984). This makes it particularly sensitive to changes in ambient temperature and water availability (Cork and Catling 1996, McIlwee 2001). Consequently, greater gliders are commonly found in areas with mild, cool temperatures and high rainfall. In south-eastern Australia, this is typically in mountainous areas >300 m a.s.l., although greater gliders are most abundant above 700 m (Bennett et al. 1991). They are nocturnal animals that emerge at night-time to feed; during the day they shelter in tree hollows to remain cool and protected from predators. At temperatures >20 °C, greater gliders expend considerable energy and water to cool themselves (Rübsamen et al. 1984). When nights are too hot, they remain in their insulated and cooler dens to conserve energy; however, this limits their ability to feed on *Eucalyptus* leaves, which are their primary source of nutrients and water (Marples 1973, Foley et al. 1990, Kavanagh and Lambert 1990). This physiological sensitivity suggests that a warming and drying climate poses a threat to the greater glider at the warmer and drier margins of its distribution (Kearney et al. 2010).

In addition to the direct physiological effect of temperature on the greater glider, climate change is also predicted to alter the nutritional value of one of their primary food resources (Lawler et al. 1997). *Eucalyptus* leaves have high levels of fiber, lipids, and phenols (Attiwill

and Leeper 1987), but low protein and carbohydrate availability. This limits their nutritional value and reduces digestibility (Cork and Sanson 1990). Nitrogen is the primary source of protein for arboreal folivores; however, it typically only comprises 0.8-2% of dry matter in *Eucalyptus* leaves (Moore et al. 2004b). Greater gliders have evolved a dietary preference for certain eucalypt species; they are found in greater abundance where eucalypt species with higher nitrogen content and digestibility are found at higher densities (Braithwaite et al. 1984, Kavanagh and Lambert 1990, Cork and Catling 1996, DeGabriel et al. 2009c, Jensen et al. 2015). Foliar nutrition is influenced by topography and climate (Attiwill and Adams 1996). As ambient CO_2 levels rise, the C:N ratio of *Eucalyptus* foliage has been observed to increase, which results in lower levels of available nitrogen in the leaves (Lawler et al. 1997, Cotrufo et al. 1998, Kanowski 2001) and increasing leaf toxicity (Cork and Foley 1997, Moore et al. 2004b), which could lead to further negative impacts on the greater glider.

In this study we evaluated the influence of climate, disturbance, topography, edaphic and forest structure variables on greater glider occupancy patterns within the south-eastern part of its distribution. The primary aim was to identify the key variables associated with their habitat selection and the role that they may have played in the observed decline of the species. These variables were used to develop a species distribution model to predict areas of potentially suitable habitat to help guide landscape-scale forest management and conservation planning. Given the physiological constraints of the greater glider and their decline in areas where their main assumed threat, disturbance, is not a direct issue, we hypothesized that landscape-scale changes in habitat suitability are driven more by climate, topography and edaphic factors, than disturbance.

Material and Methods

Study areas

Our study focused on three areas within the known distribution of the greater glider in Victoria, south-eastern Australia: East Gippsland, the Central Highlands, and the Strathbogie Ranges. These areas were chosen due to the availability of presence and absence records and strong gradients of topography, climate and vegetation communities across which the greater glider is known to occur (Appendix 1: Fig. S1).

East Gippsland includes approximately 1,200,000 ha of forests in far eastern Victoria (Dept. of Agriculture and Water Resources 2018). The vegetation ranges from open lowland forests dominated by a mix of *Eucalyptus* species (including *E. sieberi, E. tricarpa, E. globoidea)* and

Banksia spp. to dense, high-elevation (>1000 m a.s.l.) sites dominated by *E. delegatensis* and other 'high elevation mixed species' (Opie et al. 1990, Sebire and Fagg 2009). *Eucalyptus obliqua* is the most abundant species, occurring across the entire elevational range of the region (Dept. of Conservation and Natural Resources 1995). Elevation ranges from sea level to ~1300 m a.s.l. Annual rainfall across the region ranges between 648 - 1178 mm (average for 1981–2014, Stewart et al. 2020a) and mean annual temperature between 6 - 15.8°C (average for 1981–2014, Stewart and Nitschke 2017a). Greater gliders have been recorded at varying levels of abundance across the full range of elevation and in a variety of forest types. However, they are more abundant at higher elevations and in more closed forests (Henry 1984, Bennett et al. 1991, van der Ree et al. 2004a). Conservation-based prescriptions have been in place for over 20 years in East Gippsland to protect areas with high densities of greater gliders from timber harvesting (Dept. of Conservation and Natural Resources 1995, Dept. of Natural Resources and Environment 1997).

The Victorian Central Highlands includes ~860,000 ha of forest to the east of Melbourne. Elevation ranges from 75 to 1600 m a.s.l. Annual rainfall ranges between 564 - 2089 mm (Stewart et al. 2020a) and mean annual temperatures from 5.8 - 15.2°C (Stewart and Nitschke 2017a); however, local climate conditions are heavily influenced by topography in this complex landscape. The main canopy tree species in the Central Highlands forests are *E. regnans, E. delegatensis*, and *E. obliqua* (Dept. of Natural Resources and Environment 1998). Surveys of arboreal marsupials, including the greater glider, have been conducted in the Central Highlands since the 1980s and have recently documented significant declines in their occurrence (Incoll et al. 2001, Lindenmayer et al. 2011, Lindenmayer and Sato 2018). Until late 2019, there were no timber harvesting prescriptions for conserving the species' habitat in the Central Highlands. The recently updated and implemented *Petauroides volans* Action Statement stipulates that a higher rate of tree retention must now occur where timber harvesting is permitted in areas of medium greater glider densities across all of Victoria. In addition, ~100,000 ha of key habitat across the entire state has been placed under immediate protection (see DELWP 2019).

The Strathbogie Ranges is an isolated landscape of approximately 44,000 ha of forest northeast of Melbourne. This is an area of typically steep slopes with native forests surrounded by agriculture and pine plantations in the lowlands. Elevation ranges from 300 to 1033 m a.s.l.; mean annual rainfall ranges from 718 - 1245 mm (Stewart et al. 2020a) and mean annual temperatures from 10.4 – 15°C (Stewart and Nitschke 2017a). The main tree species in the region are *E. radiata*, *E. globulus*, *E.dives*, and *E. dalrympleana* (Marshall 2007). Recent government and citizen science surveys for nocturnal fauna have identified an abundance of greater gliders in the region. A comparison with historical data from the 1980s provides no

indication of population decline in the region suggesting that this isolated forest landscape may be an important refuge for the species (Nelson et al. 2018).

Datasets and survey design

Observations from four surveys for arboreal, nocturnal fauna in mature forest, carried out between 2012 and 2019 in the three study areas, were combined into a dataset consisting of 725 sites. The survey dataset includes 233 sites where greater gliders were present. The survey sites ranged in elevation from 9 to 1508 m a.s.l (Table 2.1). All surveys were conducted at night using standard spotlighting survey methods to detect nocturnal fauna while walking along forest tracks or through the forest, recording all species sighted using high-powered spotlights (Lumsden et al. 2013). The 2012 survey used 100 m transects to spotlight for arboreal species (Lumsden et al. 2013). The 2015 - 2019 surveys used transects of 1 km length on track or 500 m off-track (Nelson et al. 2018). The 2012 surveys were surveyed twice by a single observer, while all the other surveys were surveyed at least once using two observers (Table 2.1). Double observer distance sampling has been found to increase detection probabilities (Kissling and Garton 2006). The different survey methods represent different levels of survey effort, which could influence detectability at non-presence sites (Watson et al. 2008). If one or more individuals of greater glider were spotted, the site was considered a presence site. Sites where gliders were not detected were classified as absence sites; however, because detection is imperfect for greater gliders (see Wintle et al. 2005), some absence sites may represent false-negative observations. The inclusion of too many false-negative sites can impact the performance of species habitat models by diluting or overestimating the influence of the predictor variable (Tyre et al. 2003).

Table 2.1. Overview of surveys used for this study. Survey effort = number of surveys per site.

Region and year	Contributor	Sites	Greater glider presences	Elevational gradient (m. a.s.l.)	Survey effort	Minimum number of surveyors per survey
Central Highlands, 2012	Arthur Rylah Institute for Environmental Research	421	71	123 - 1508	2-3	1-2
East Gippsland, 2015	Department of Environment, Land, Water & Planning	164	94	9 - 1132	4	2
Strathbogie Ranges + Central Highlands, 2017-2018	Arthur Rylah Institute for Environmental Research	110	59	100 - 1400	1	2
East Gippsland, 2018 - 2019	This study	30	9	42 - 1200	1-2	2

Greater gliders have high detectability given their small home ranges, low mobility and high densities (Wintle et al. 2005). Wintle et al. (2005) found that two surveys had a greater than 60% detectability yielding low false-negative rates ($< 40\%$). Tyre et al. (2003) stated that for species with false-negative rates $< 50\%$, more sites should be sampled, as opposed to more visits to the same sites, to improve precision and reduce bias in habitat models. The approach used for the surveys considered in this study balanced multiple surveys to improve detectability at each site while increasing the number of independent sites to reduce potential bias in model estimates from false-negative observations. Other data recorded in all surveys included: location of observation, tree species on which an animal was observed, height on tree, behavior, fur color, time of observation, and distance and bearing to the animal.

Species distribution models built with balanced presence and absence points are more accurate and less likely to contain biases that may lead to model overfitting (McPherson et al. 2004, Liu et al. 2005). To ensure a balanced study design and avoid overrepresentation of absence sites from a single study region, we randomly selected absences from the 2012 Central Highlands surveys, where the target species was recorded at a lower proportion of sites. We

did this to match the presence:absence ratio of the other two landscapes, which was 53%. Random sampling of absences was selected to avoid biasing the selection of absence sites under the assumption that, given the survey effort, the absence sites are true absences that represent a range of potential habitat suitability within areas of mature forest. All presences were used in the analysis. After balancing the presence:absence ratio, the final dataset used for modelling included 437 sites (233 presences and 204 absences).

Independent variables

For all presence and absence sites, variables describing climate, topography, geology, forest structure, productivity and soil chemistry, as well as past management and disturbance records were compiled. The initial modelling dataset contained >150 variables across these categories, although climate variables were most common (Appendix 1: Table S1). We reduced the total number of variables by first removing highly correlated variables and then low or non-significant variables through generalized linear models (GLM, see below). Our final analysis included 12 variables.

Climate data

All climate variables were generated using daily gridded datasets. Variables used in the modelling were extracted at ~250 m resolution by interpolating weather station observations (Stewart and Nitschke 2017b, 2018, Fedrigo et al. 2019, Stewart et al. 2020a, b, c) and combining pre-existing datasets (McVicar 2011). The generated data span the period from 1981 to 2014 (33 years). These long, high-resolution time series of climate data were developed specifically for ecological modelling across the state of Victoria and were used to calculate derived variables describing aridity, weather events, and climate. Variables used for modelling included daily maximum, minimum and mean temperatures, diurnal temperature range, precipitation, potential evapotranspiration, vapor pressure deficit, and saturation vapor pressure (svp, Alduchov and Eskridge 1996), Equation 1, e_s = saturation vapor pressure, T = temperature.)):

(Equation 1) $e_s(T) = 6.1094 \times exp^{\frac{17.625 \times T}{243.04+T}}$

From these data, the number of nights with temperatures >20°C (hot nights) and days with ≥25 mm of precipitation (wet days) were calculated. In addition, a daily Condensation Index (CI, Equation 2, svp tmin = saturation vapor pressure at minimum temperature, vp9am = vapor pressure at 09:00 AM.) was derived, with CI values <0 used to calculate the number of days that condensation occurred. Climatic aridity for each site was calculated using the mean Annual Heat Moisture Index (AHMI, Equation 3, MAT = mean annual temperature, MAP =

mean annual precipitation. (Wang et al. 2006, Paudel et al. 2016)). A total of six climate variables were used in the final model.

(Equation 2) $CI = svp\ tmin - vp9am$

(Equation 3) $AHMI = \frac{(MAT+10)}{\left(\frac{MAP}{1000}\right)}$

Topographic, edaphic and vegetative data

We used static variables describing topography (elevation, slope, aspect, geology), edaphic conditions (pH, soil type, Terrain Wetness Index [TWI]), ecological context (ecological vegetation classes [EVC]), disturbance history, including number of past fires (both bushfires and planned burns) and number of timber harvesting operations, as well as the Normalized Difference Vegetation Index (NDVI) at survey date. These were collated for each site. All data are publicly available through open-source data portals DATA VIC (data.vic.gov.au) and TERN (portal.tern.org.au) or derived from freely available satellite imagery through NASA and USGS data portals (glovis.usgs.gov). For all sites, these data were extracted as spatial vector or raster layers in QGIS 3 (QGIS Development Team 2020). The spatial resolution of these data varied between 30 x 30 m (e.g. NDVI from Lansdat 8) to 100 x 100 m (e.g. TWI).

Data preparation

All statistical analyses were conducted in R (R Core Development Team 2020) and the packages *caret, dismo*, *effects*, *gbm, landscapemetrics, MuMIN, raster*, *ROCR,* and *SDMTools* (Sing et al. 2005, Hijmans et al. 2017, Fox and Weisberg 2018, Barton 2019, Greenwell et al. 2019, Hesselbarth et al. 2019, Hijmans 2019, VanDerWal et al. 2019, Wing et al. 2019). Cumulative data for climatic events such as the total number of hot nights or condensation days across all 33 years observed were divided by the total number of years (n = 33 for most variables) in the dataset to estimate mean annual values. Additionally, separate 11-year datasets were developed, where the total number of cumulative events across the eleven years observed was divided by n = 11. This allowed for comparisons of climate at approximately decadal time intervals. All variables were standardized prior to analysis.

Variable selection

The initial dataset included a wide range of variables that have been hypothesized to influence greater glider occupancy (Appendix 1: Table S1). To reduce the number of variables for analyses, we used a multi-step procedure. We first excluded variables when the Pearson's correlation coefficient was $\geq|0.7|$. The variable within a correlated pair that had more ecological relevance was kept. Variables that had multiple high intercorrelations with other variables of

ecological meaning were also removed. This was particularly the case with elevation, which was correlated with most climatic variables. Elevation also represents a static proxy of climate making its inclusion for understanding the role of climatic variability relatively uninformative. We grouped the variables into seven categories (extreme events, climate normals, structure/vegetation, topography, climatic indices, disturbance history, and soil) and used binomial GLMs to identify the strongest variables for predicting presence or absence of greater gliders within each group. Only variables with significance of $p \leq 0.01$ were selected for inclusion in the final analyses. In cases where all variables within a given group had $p \leq 0.01$, the *dredge* function in *MuMIN* was used to build multiple models on all possible combinations of variables within that group. Only the significant variables in models with the highest AIC and delta ≤ 2.5 were selected for use in the machine-learning modelling (Anderson and Burnham 2004, Burnham and Anderson 2004). This process reduced the initial number of variables to 12 for further analysis (Table 2.2).

Table 2.2. Final modelling variables, their groups and significance when fitted using GLM. Significance codes (p-value): 0 '*' 0.001 '**' 0.01 '*'. Variables such as hot nights are cumulative over the 33-year period, averaged per year.**

Group	Variable	Explanation	p
Extreme events	Hot nights	no. of nights with tmin ≥20°C	**
	Wet days	no. of days with P ≥25mm	***
	Condensation events	no. of days with CI<0	*
Climate normals	Potential evapotranspiration	mean et0 of site	***
	Vapor pressure deficit	mean vpd of site	*
Structure/Vegetation	Forest type	EVC	***
	NDVI	NDVI value at survey date	*
Topography	slope	slope in degrees	***
	TWI	Terrain Wetness Index	***
Climatic indices	AHMI	Annual Heat Moisture Index	***
Disturbance history	Fires	Number of past fires at site	***
Soil	pH	soil pH of organic layer	*

Statistical Modelling

We used boosted regression trees (BRT) to identify variables associated with the occurrence of greater gliders and model habitat suitability. A machine-learning technique was selected because, unlike linear models, it allows for nonlinearities and interactions to be considered

simultaneously (De'ath 2007, Elith et al. 2008). BRTs also allow for precise parameter control (such as learning rates and tree complexity) and an evaluation of interactions and variable thresholds within the final model. A learning rate of 0.001 was used with a bag fraction of 0.5 and a tree complexity of 5, to allow for interactions to be considered. The number of trees was chosen by error rate with minimum error as the selection criterion for model complexity (De'ath 2007). The full dataset was randomly split into training (70% of the data) and validation (30%) subsets. The models were built on training data only; model fit was tested using cross-validation (CV) and independent-validation using the full dataset and the validation dataset respectively. Multiple statistics were used to test model fit including CV correlation, deviance, accuracy, area under the curve (AUC), sensitivity (true positive rate, TPR) and specificity (true negative rate, TNR) and the true skill statistic (TSS), which, as compared to kappa, is not dependent on prevalence affecting predictive accuracy (Allouche et al. 2006). Cohen's kappa was instead used to determine the probability of occurrence threshold used to represent suitable habitat of the final habitat suitability model that maximized model fit (Elith et al. 2006, De'ath 2007, Elith et al. 2008). Additionally, the most important variable interactions were extracted. Interactions were based on the residual variance of a linear model fitted to determine the influence of the variable interaction on model variance. The interaction size expresses the relative strength of the interaction. If residual variance is 0, no interaction has occurred; the larger the interaction value, the stronger the observed interaction (see Elith et al. 2008).

Modelling spatial and temporal changes in greater glider habitat

We used the relationships between greater glider occurrence and environmental predictors to explore how these variables have changed over the last three decades and how this may have impacted the distribution of the species within the study landscapes. To do this, we developed rasterized data layers for each of the variables included in the final habitat suitability model. Important climatic variables were extracted for each ~250 m grid cell over the State of Victoria for two timeframes. The first timeframe was the entire 33 years of climate data; this was used to visualize the species distribution model. The second timeframe was a series of 11-year windows, which represented climate within the periods 1981-1992, 1992-2003, and 2003-2014 (climate years were calculated from July to June). These 11-year windows were used to test for changes in climate and variable patterns over time. Non-climatic variables were transformed into rasters and rescaled to 250 m resolution where necessary. Due to the lack of cloud-free satellite imagery for the entire State of Victoria for all survey periods, rasters were cropped to the forest areas of the three study landscapes. For these, all variable rasters were compiled into raster stacks using *raster*. Partial variable dependence plots were used to identify

thresholds (i.e., variable values that lead to positive or negative impacts on habitat suitability) and extracted for each of the significant climate predictors (i.e., AHMI, wet days, hot nights, VPD, and condensation). Using averaged rasters, we identified areas of suitable climatic conditions. Rasters representing all climatic variables for each 11-year window were used to calculate the % change in each climate variable included in the model between the first (1981 – 1992) and last (2003 – 2014) period. We then analysed the extent of currently suitable area by extracting area percentages and inter-period changes in habitat suitability using niche overlap and % area of habitat suitability in either period, defined by variable thresholds according to Schoener and Gorman (1968) and Warren et al. (2008). The number and size of patches of suitable and unsuitable habitat were extracted by reclassifying prediction rasters based on the identified suitability threshold defined by Cohen's kappa and elevation to create landscape classes. These were then analyzed using *calculate_lsm* from the *landscapemetrics* package. We also used the data to identify changes in the area with suitable climatic conditions for greater gliders based on climate variable-specific thresholds. Additionally, we used confirmed and verified historical records matching the earliest 11-year window from the Victorian Biodiversity Atlas (VBA, vba.dse.vic.gov.au/vba) to explore whether the modelled declines in climatically suitable conditions for greater gliders were consistent with observed spatial patterns of declines in greater glider observations.

Results

Model performance

Cross-validation and independent validation data sets suggest that the final boosted regression tree model performed with high classification accuracy in both evaluations. AUC was 0.93 for cross-validation and 0.82 for independent validation, respectively, and TSS were 0.71 and 0.5 (Table 2.3). In cross-validation, 90% of all presences and 81% of all absences were predicted correctly, while in independent validation, the model predicted 81% of all presences and 69% of all absences correctly. The best true positive (TP) and true negative (TN) predictions were achieved for the East Gippsland study region (Appendix 1: Fig. S2 + S3). These results show that the models are robust and can be used as a predictive tool for greater glider occupancy across the studied landscapes.

Table 2.3. Summary of model evaluation. Both validations were based on a BRT model of 3300 trees with a deviance of 0.68.

Test	Kappa	Accuracy	AUC	Correlation	Sensitivity	Specificity	TSS	P
Cross-validation	0.71	0.86	0.93	0.74	0.81	0.90	0.71	<0.001
Independent validation	0.49	0.75	0.82	0.56	0.69	0.81	0.5	<0.001

Variable importance

Aridity, weather events, and climate were the most important predictors of habitat suitability (Fig 2.1). Non-climatic variables had less influence, although they still contributed to the model performance. Of the five most important variables, four were related to climate: AHMI (22% variable influence), number of wet days (12.1%), number of hot nights (11%), and vapor pressure deficit (8.7%).

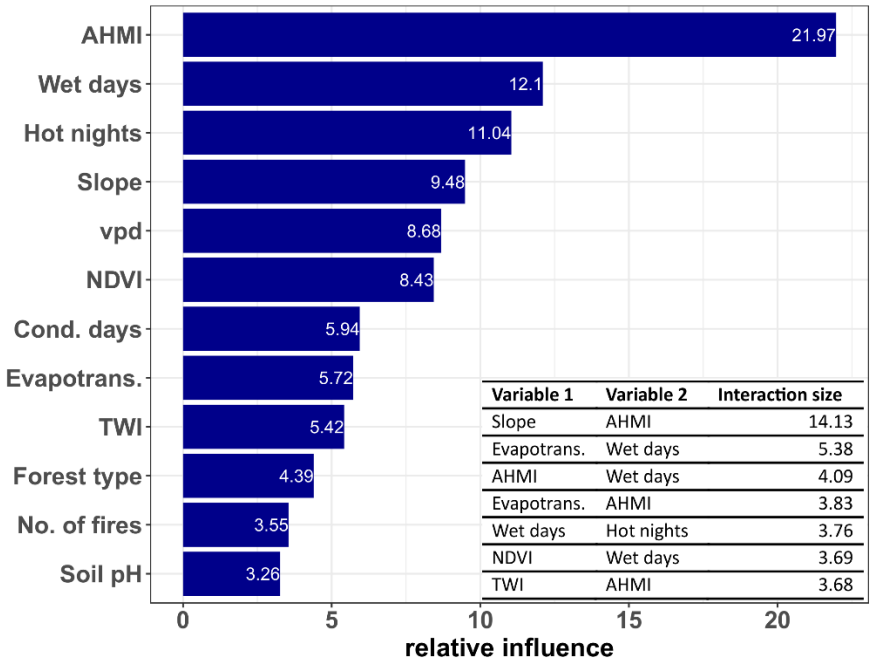

Figure 2.1. Variable importance in % and main interactions of final boosted regression tree (BRT) model for greater glider occupancy in eastern Victoria. See Table 2.2 for variable explanation.

Non-climatic variables had less influence, although they still contributed to the model performance. Of the five most important variables, four were related to climate: AHMI (22% variable influence), number of wet days (12.1%), number of hot nights (11%), and vapor

pressure deficit (8.7%). Other climatic variables had 5.9% (days with condensation) and 5.7% (evapotranspiration) variable influence, respectively. The performance of non-climatic variables in ranked order was: slope (9.5%), NDVI (8.4%), TWI (5.4%), EVC forest type (4.4%), number of fires (3.5%), and soil pH (3.3%). Partial dependencies were used to evaluate the influence (positive or negative) each variable had on presence or absence of greater gliders (Fig. 2.2). Interactions were detected between both climatic and non-climatic variables. The strongest interaction was observed between slope and AHMI (interaction size: 14.13, Fig. 2.1 + Appendix 1: Fig. S4).

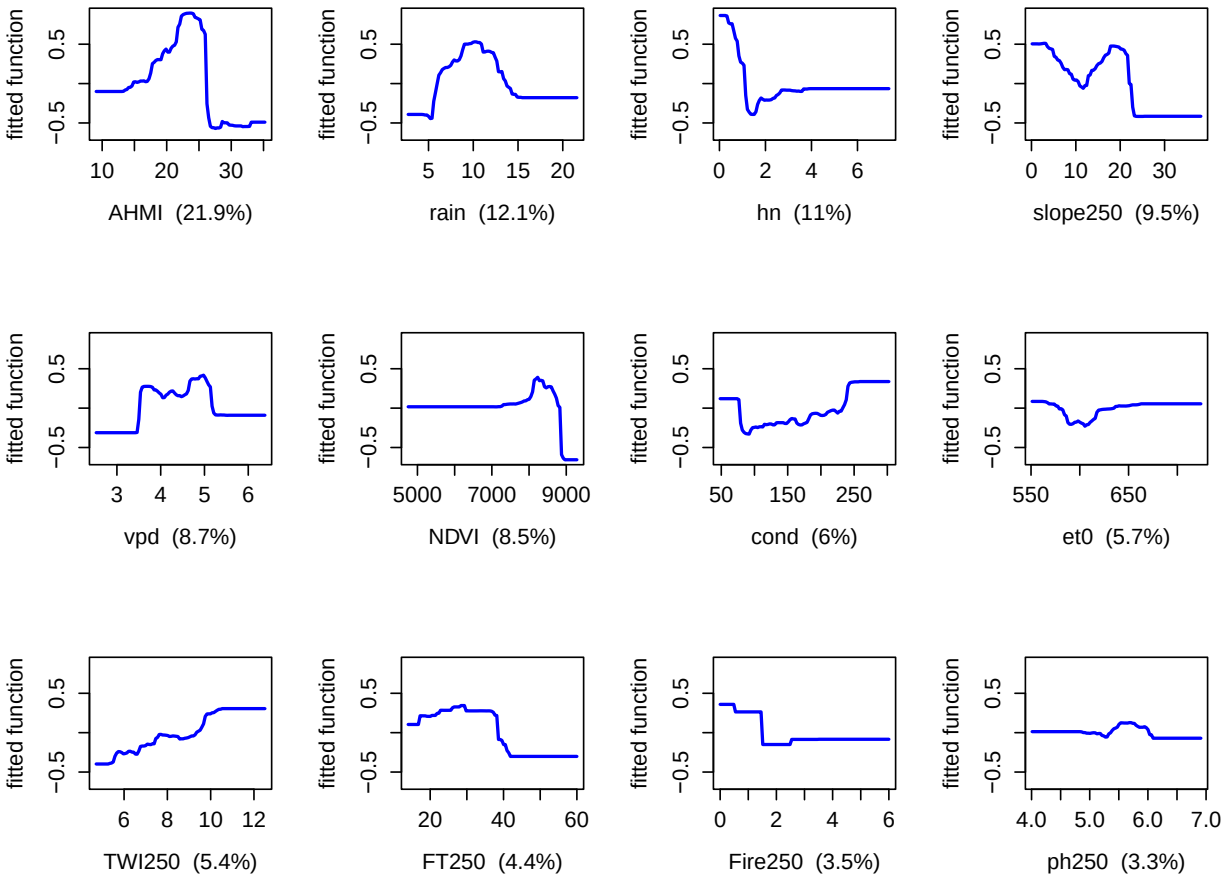

Figure 2.2. Partial variable dependence for all 12 modelling variables and their variable importance. AHMI = annual heat moisture index, rain = number days with P ≥ 25mm, hn = number of nights with tmin ≥ 20°C, slope250 = slope in degrees at 250 m resolution, vpd = vapor pressure deficit, NDVI = Normalized Difference Vegetation Index, cond = number of days with condensation index (CI)<0, et0 = potential evapotranspiration, TWI250 = Terrain Wetness Index at 250 m resolution, FT = forest type according to EVC, Fire250 = number of forest fires at 250 m resolution, ph250 = soil pH at 250 m resolution.

Species distribution models

We predicted the location of high suitability habitat — areas most likely to have greater gliders present — in all three study regions (Fig. 2.3). High habitat suitability was defined based on the probability that maximized the kappa statistic (maximum TPR+TNR at 0.47). Areas below the threshold were considered unsuitable and unlikely to support greater gliders based on the model parameters. In East Gippsland, 16% (~200,000 ha) of the forest area was found to be high suitability habitat. In the Central Highlands and Strathbogie Ranges, 47% and 49% were high suitability habitat (~400,000 ha and ~20,000 ha, respectively; Table 2.4, Fig. 2.3). Elevations above 700 m were predominately classified as highly suitable across all regions (Appendix 1: Fig. S5); elevations above 500 m make up more than 50% of the total suitable area in all study regions (Appendix 1: Fig. S6).

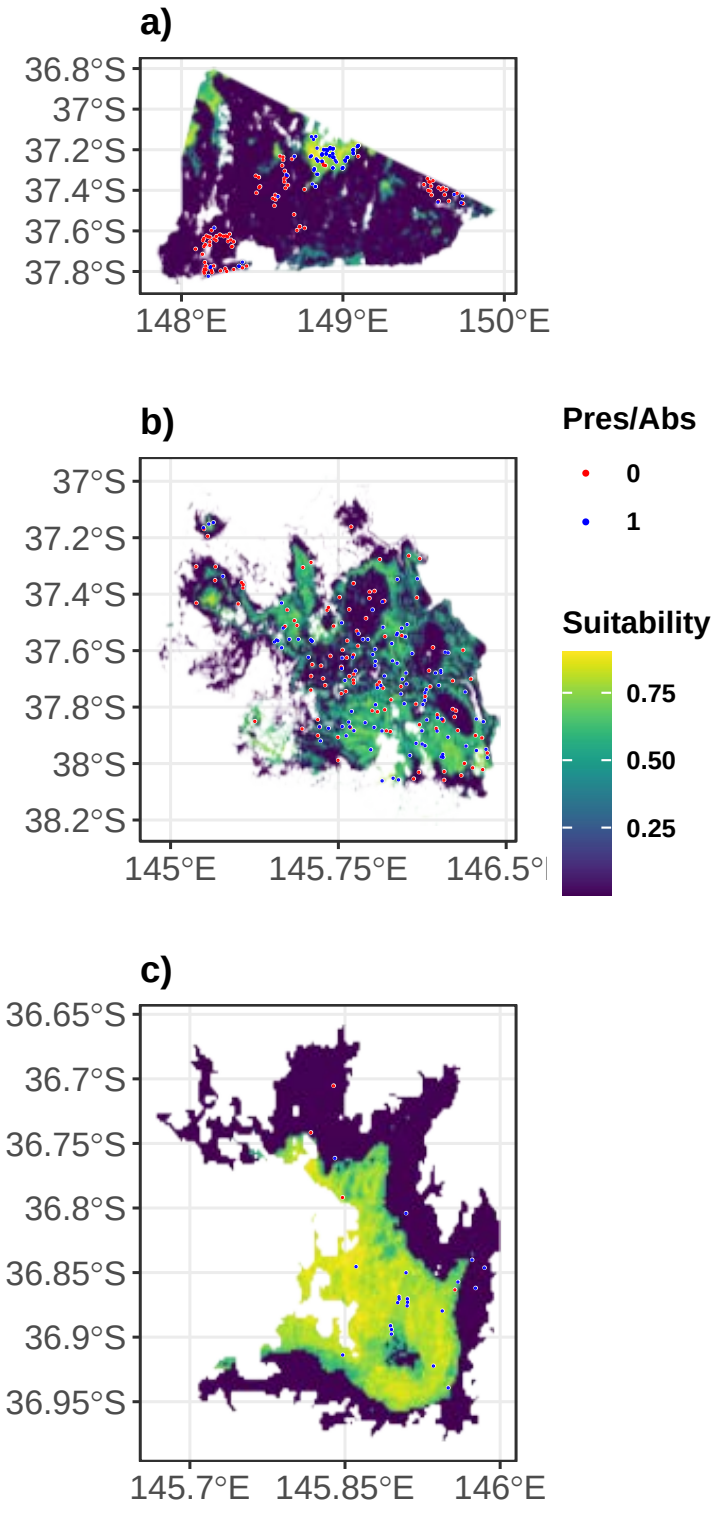

Figure 2.3. Mapped habitat suitability for greater glider over forest areas of a) East Gippsland, b) Central Highlands and c) Strathbogie Ranges with survey site overlay (0/red = absence, 1/blue = presence site.

Table 2.4. Habitat suitability statistics based on landscape predictions for the three study regions.

Study region	Area suitable (ha)	Area suitable	Mean suitability	Standard deviation	Standard error
East Gippsland	198,556	16%	0.64	0.14	0.0008
Central Highlands	403,462	47%	0.58	0.07	0.0003
Strathbogie Ranges	21,514	49%	0.75	0.08	0.0014

Changes in climatic predictors and suitable habitat over time

Analyses of the climate data and historic records suggested that climatic conditions over the past three decades have shifted, with extreme conditions such as hot nights increasing over time, particularly over the last five years of available data (Appendix 1: Fig. S7). In all sites within the three study regions, annual maximum summer night-time temperatures have exceeded the thermoneutral point of 20°C since 1996. Additionally, we observed a trend of rising mean annual night-time temperatures since the late 1980s across sites and regions (Appendix 1: Fig. S8). Analyzing changes in the area with suitable climatic conditions for greater gliders between 1981-92 and 2003-14 based on climate variable-specific thresholds, we found that the total area with suitable climatic conditions was highly responsive to decadal changes in climate across all three study regions and for all climate variables. The most striking response was a decline in the area of suitable conditions associated with changes in the number of hot nights. The increasing frequency of hot nights was associated with a reduction in area with suitable climatic conditions from 63% (across all three regions) to 10%. For three variables (AHMI, wet days, and condensation days) an increase in the suitable area was detected in some regions. However, in most cases these changes were marginal (Table 2.5 + Appendix 1: Fig. S9). Using single-variable suitable area extent and historic greater glider records from 1981-92, we found, across the study regions, that the total area with suitable climatic conditions and greater glider observations was much greater in the 1980s and that the changes in observed occurrences by the late 2000s are consistent with observed changes in climatic conditions (Fig. 2.4). Studying the % change in AHMI between the first and last 11-year period, we found that all study regions have generally become hotter and drier over time. These areas had higher average AHMI values in 2003-14 compared to 1981-92. Nevertheless, some areas in East Gippsland above 500 m elevation, experienced lower AHMI values between 2003-14, suggesting a decline in aridity during this time period (Fig 2.5).

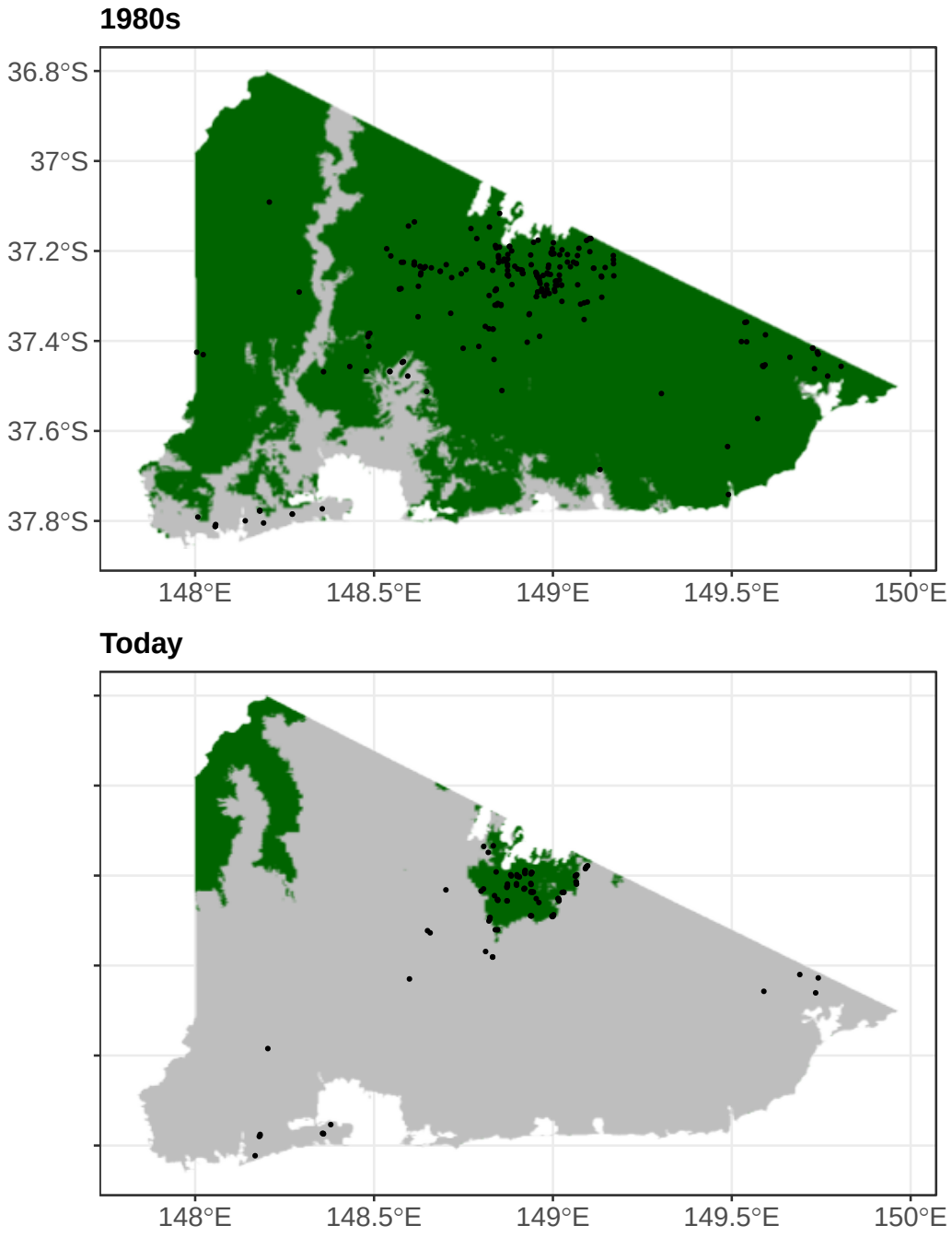

Figure 2.4. Example of suitable habitat decrease for variable 'hot nights' (number of nights reaching >20°C) according to variable threshold for 1981 - 1992 with historic records from the VBA and 2003 – 2014 ('Today') with presence records from this study in East Gippsland. Dark green represents suitable area, grey unsuitable, black dots are greater glider observations.

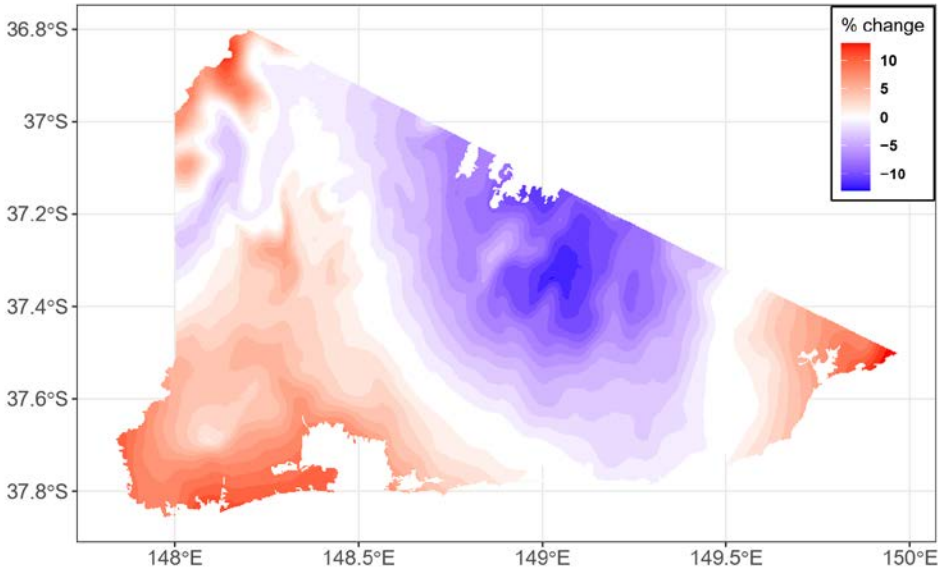

Figure 2.5. Percent change in AHMI between 1981-1992 and 2003-2014 in East Gippsland study region. Negative changes (blue colors) in AHMI indicate development of cooler and wetter conditions, pointing towards the formation of climatic refugia for the greater glide

Table 2.5. Area and overlap analysis results for each climate variable in the three study regions (EG = East Gippsland, CH = Central Highlands, SR = Strathbogie Ranges). Values marked in italics indicate (marginal) increases in suitable habitat, all others are declines, based on variable thresholds. See Table 2.2 for variable explanation.

Variable	Threshold	Region	% area suitable 1980s	% area suitable today	% niche overlap
AHMI	14 - 25	EG	*4.5*	*6.9*	*62.3*
		CH	50.4	43.4	73.2
		SR	46.5	15.7	33.8
Wet days	>100 occasions per decade	EG	84.3	61.3	72
		CH	54.3	51.3	89.2
		SR	*98.2*	*99.4*	*98.7*
Hot nights	<50 occasions per decade	EG	85	9.1	10.7
		CH	65	18.9	29
		SR	39.5	4.1	10.3
vpd	3.5 - 5	EG	59	36.8	53.1
		CH	64.1	54.8	81.6
		SR	10	6.3	63
Condensation days	>200 occasions per year	EG	25	19.6	65.6
		CH	*46.2*	*46.3*	*96.3*
		SR	*8.6*	*8.7*	*93.8*

Discussion

Climate change and weather extremes affect the quality and distribution of habitat for many animal species (Hughes et al. 1996, Reside et al. 2010, Bateman et al. 2012, Rawal et al. 2014, 2015a, Seidl et al. 2017). Using high-resolution, daily climate datasets we identified that the distribution of greater gliders in Victoria in south-eastern Australia is primarily influenced by climatic variables that relate to their unique physiology – areas with cool night-time temperatures and higher water availability were most suitable for greater gliders and areas with high night-time temperatures and arid conditions were least suitable. Importantly, we found that these climatic conditions have changed to such a degree over the last 30 years that it has precipitated a landscape-scale contraction of wetter and cooler conditions to higher elevations. Our results have important implications for understanding the recent declines of greater glider populations in the region (see Lindenmayer et al. 2011, Lindenmayer and Sato 2018).

The greater glider's unique physiology and diet make it particularly vulnerable to high temperatures and low water availability (Rübsamen et al. 1984). Higher temperatures lead to heat dissipation through more rapid—evaporation of saliva licked onto the animals' fur for cooling, as well as increased respiratory frequency and inefficient and excessive use of water for both processes. Foley et al. (1990) reported that free-living gliders obtained 58% of their water intake from water in leaves and only 18% from metabolic processes. Remaining water came from licking dew and rainwater on the surface of leaves, thus indirectly from their food source. Increasing aridity, more frequent hot nights, and decreasing numbers of wet days and days with condensation events all negatively impacted the area of potentially suitable habitat for greater gliders across a wide range of forests and forest conditions in southeastern Australia. Warmer nights (i.e., higher minimum temperatures) increase the water-holding capacity of the atmosphere (i.e., higher svp) and therefore reduce the amount of condensation available. When coupled with increasing aridity, these factors are likely to considerably reduce the amount of water available to the animal. Climate and weather variables accounted for ~65% of the variable influence in our model. Earlier studies demonstrated the influence of temperature on greater glider habitat suitability (Cork and Catling 1996) and suggested that climate is an important determinant of the species' future distribution (Kearney et al. 2010).

Aridity, represented by AHMI, was the most influential variable in our model. High values of AHMI indicate increased atmospheric aridity in response to either warmer temperatures and/or low precipitation, which in turn influence site-level moisture availability (Paudel et al. 2016). Higher AHMI values had a negative influence on occupancy (Fig. 2.2). This suggests that long-term shifts in regional hydroclimate have the potential to significantly alter the

distribution of the greater glider across the region. The observed change in aridity over the last 33 years is consistent with observed declines of the species within the region. Interestingly, our analyses found that some high elevation areas, particularly within East Gippsland, may have become *less* arid in recent years (Fig. 2.5). These areas were also modelled to be the most suitable for the greater glider. It is worth noting that AHMI does not account for the role of topography on water availability. To consider this, we included the Terrain Wetness Index (TWI), which accounts for fine-scale effects of landform on soil moisture. It explained 5.4% of the influence in the model. Higher TWI values are associated with greater upslope drainage and thus higher soil moisture (Beven and Kirkby 1979). Steeper slopes were also found to positively influence the occupancy of the greater glider (Fig. 2.2). This may be due to the influence of steepness on soil runoff and microclimate. Steeper slopes tend to connect to areas with high TWI values in riparian areas, which are also areas with increased condensation and lower temperatures due to cold air drainage (Stewart and Nitschke 2017a). Additionally, the strong interaction between AHMI and slope (Appendix 1: Fig. S4+S10), suggests that in drier parts of the landscape, areas with flatter slopes have a higher likelihood of occupancy. These areas have lower temperatures (see Stewart and Nitschke 2017a), higher terrain wetness indices, and higher levels of condensation. They are also typically dominated by riparian forests, where aridity is mediated by topographic influence. These results suggest that topographic complexity can provide microclimatic refugia in warmer and drier parts of the landscape, thus enabling the thermoregulatory threshold of greater gliders to be maintained. Many examples emphasize the importance of riparian and other stable habitat areas as refugia (Reside et al. 2019). Other species of Australian vertebrates, from the marsupial quokka (*Setonix brachyurus*) to woodland birds, are known to depend on these types of sites (De Tores et al. 2007, Bennett et al. 2014).

Several non-climatic variables relating directly or indirectly to vegetation quality were included in our final model of greater glider occurrence. The partial dependence plots of soil pH values suggest that sites with relatively neutral soils are preferred (Fig. 2.2). Soil pH may influence the nutritional content of the vegetation on which the species depends (Cork and Catling 1996). Soils with extreme pH values, whether too high or too low, generally have less plant-available nitrogen and other nutrients (Handreck et al. 2002). Cork (1992) showed that Australian eucalypt forests with leaf nitrogen content values below 10 mg/g are typically unfavorable for folivores. However, more research is needed to determine the relationship between soil pH and tree nutrition on greater glider habitat use. We also found that high NDVI values and certain forest types had a positive influence on occurrence (Fig. 2.2). In general, more productive forests (see Tucker 1979) with closed canopies were more likely to support the greater glider, which is consistent with early research by Kavanagh & Lambert

(1990). NDVI has previously been identified as a useful predictor of greater glider abundance (Youngentob et al. 2015). These variables may be capturing the influence of soil and vegetation patterns on forest nutrition, which in turn influences the occurrence of greater gliders and other marsupial folivores. Closed-canopy forests in general also have a microclimatic effect and typically have cooler temperatures and higher moisture retention than open canopy forests (Makarieva et al. 2006). These metrics may therefore represent a proxy for favorable microclimatic conditions within the landscape.

The lack of significant association with variables describing forest disturbance history (e.g., timber harvesting, forest fires, fire management practices) and the occurrence of greater gliders was surprising, as more than half of our sites had experienced some form of disturbance through fire or harvesting operations between 1980 and 2014 (Appendix 1: Fig. S11). Disturbance through fire and timber harvesting is generally considered the main threat to the species (Lindenmayer and Sato 2018, McLean et al. 2018). Timber harvesting in particular, changes the structure of the forest, reducing nesting and foraging resources by replacing hollow-bearing trees with young regrowth or leaving relatively few habitable trees through retention and thus poses a direct threat to the species at local scales (Lindenmayer and Sato 2018, McLean et al. 2018). However, the recently described local extinction of the greater glider at Booderee National Park, New South Wales, which has experienced neither logging nor severe fire over the period of observation, suggests that other factors may drive population fluctuations of the species (Lindenmayer et al. 2011). The lack of association between disturbance history and occurrence in our study may be, in part, due to the sampling design used to survey for greater glider and other arboreal marsupials. Typically, mature forests were targeted, and the survey technique detects animals when they are out foraging at night, rather than in their nesting habitat. However, the relatively small home ranges of greater gliders (Smith et al. 2007) may limit the importance of this as an issue. The species has often been detected adjacent to harvested areas. However, the harvested areas themselves are typically not directly targeted in arboreal marsupial surveys, nor are sites that have been recently burned. One reason for this is the dense vegetation that occurs in harvested and burnt areas, which limits detectability of animals in the forest canopy. Lindenmayer et al. (2013) found that the abundance of greater gliders declined when the amount of burned area around a survey point increased. The low importance of forest fires as a variable in our models suggests this response does not scale across the three study regions. Our analyses suggest that across mature forest stands, aridity and weather extremes are consistently more important than disturbance history in shaping the distribution of the species at the landscape-scale in southeast Australia.

Only recently have the potential effects of heat stress and drought been considered as threat to greater gliders (see DELWP 2019). Modelled future climate scenarios for southeastern Australia suggest that the climate will become warmer and drier with more extreme events in the coming decades (CSIRO and Bureau of Meteorology 2015). This may have important consequences for forests as habitat (Keenan and Nitschke 2016, Seidl et al. 2017). For the greater glider, predicted future climate conditions will likely lead to more hot nights and less available water from rainfall and condensation. Indirect effects on forest nutrition and eucalypt species composition, preferred for foraging, may also lead to a reduction in habitat suitability. Our results suggest that the species has already experienced the impacts of climate change and that these changes will be amplified as the climate becomes increasingly warmer and drier across southeastern Australia. Identifying and protecting bioclimatic refugia—that is, areas where suitable climatic conditions are likely to persist over the long term, within landscapes, is critical for the conservation of the greater glider. While many areas within the studied landscapes have become hotter and drier, some remained stable or have become less arid. Although observed aridity has increased throughout the entire Central Highlands and Strathbogie Ranges, mid- to high-elevation areas in East Gippsland have shown an opposite trend and may already be acting as climatic refugia for greater gliders (Fig. 2.5). These areas, where high densities of animals have been observed, are critical for the conservation of this species: In East Gippsland, more than 80% of suitable habitat lies above 500 m elevation and more than a third above 1000 meters (Appendix 1: Fig. S6). In contrast, low elevation sites, which have experienced the most drastic increases in AHMI, and which occur across all study regions, are likely to support fewer and fewer animals and will become increasingly unsuitable as habitat for the species. As the climate continues to change, low elevation sites and other areas where the AHMI is likely to increase may become habitat traps—fragments of low-quality habitat that will eventually be unable to support greater gliders. Here, patch size of suitable habitat is already smaller and clumpiness of patches is lower, indicating more isolated habitat. In higher elevation areas, fewer but larger patches with higher clumpiness (close to maximum aggregation) indicate intact and interconnected habitat for the greater glider (Appendix 1: Table S2). Developing a network of bioclimatic refugia across these landscapes would be critical to the long-term viability of their populations in the region. Identifying these areas and protecting them will not only foster greater glider populations, but with them a wide range of fauna and flora species relying on similar mature forest ecosystems and climatic conditions. All regions studied are covered by a complex and wide-ranging network of protected areas (Appendix 1: Fig. S12-S14). Recent conservation measures have added large areas to this protected network (DELWP 2019) and have led to the protection of additional crucial and climatically suitable habitat. As such, greater glider habitat in the Strathbogie Ranges

forests is now widely protected (Appendix 1: Fig. S14). Nevertheless, large areas of suitable habitat in both East Gippsland and the Central Highlands study regions still lie outside any protected area, while areas with low or no suitability contribute large percentages to the protected area network. We found ~360,000 ha of currently suitable habitat for greater gliders across all three study regions to still be outside the protected area network (Appendix 1: Fig. S12-14 + Table S3).

The sensitivity of greater glider physiology to changes in climate and the potential impacts of recent climate change on its distribution highlight significant challenges to the future conservation of some fauna. Conservation of these species is being challenged by both habitat loss and the direct impacts of climate change on their physiology. The latter process may drive a contraction in population size or range extent, independent of habitat availability. The number of examples of mammal species being challenged by climate change is increasing. Hoffmann et al. (2019) showed that the mountain pygmy possum (*Burramys parvus*) is increasingly threatened by the impacts of a warmer climate on its hibernation physiology, which may reduce overwintering survival. Rézouki et al. (2016) found that the recent trend to warmer winters and springs is increasing mortality rates in juvenile and older alpine marmots (*Marmota marmota*), due to interactions between marmot physiology, snow depth and social structures. Recent climate change is also considered as a potential cause in the contraction of moose (*Alces alces*) populations at the southern extent of their range due to heat stress (McCann et al. 2013). The broad conservation of habitat alone may not be enough to overcome the impacts of climate change for these species. Understanding where both climatic and habitat refugia co-occur is critical for conserving these species under warmer future climatic conditions. For the greater glider and other species that are being pushed up to and beyond their physiological limits, recognizing the systemic impact of recent climate change is critical to understanding and interpreting current population trends and designing conservation strategies that can facilitate their long-term protection. Although further work is needed to incorporate climate change predictions into assessments of future habitat suitability for the greater glider in the region (e.g. Nitschke et al. 2020), our results demonstrate that the fingerprint of climate change is already apparent across the warmer and drier portions of its distribution in south-eastern Australia.

Conclusion

Climatic aridity and heat stress are primary drivers of greater glider habitat suitability in the studied regions and likely contribute to observed changes in greater glider populations over

the past decade. Under a future of warming and drying climatic conditions, these observed declines are likely to continue as populations of greater gliders increasingly contract to bioclimatic refugia. Currently, the most suitable, stable, and least patchy habitat is found at higher elevations. However, these areas are not completely protected from future disturbances and climate change. Targeted protection of current and future bioclimatic refugia will be important to ensure that viable populations of greater gliders can persist in south-eastern Australia.

3. Habitats for gliders: Determining hollow availability and foliar nitrogen across a mixed-species forest landscape

Introduction

Human impacts on the habitat of species that rely on mature native forest ecosystems are directly increasing the pressure on their populations. Deforestation, timber harvesting, fire management, fragmentation due to land-use change or urbanisation reducing habitat area or quality, drive population declines, local extirpations, and, in some cases, extinctions (Diamond 1984, Lindenmayer et al. 2011, Youngentob et al. 2013, McLean et al. 2015). Climate change exacerbates these threats to habitat by increasing the frequency and severity of natural disturbances such as wildfires and droughts (Parry et al. 2007, Orlowsky and Seneviratne 2012). In the light of recent mega-fires, such as the 2019/20 'Black Summer' bushfires in eastern Australia that impact large parts of the distributions of many forest-dwelling fauna (Ward et al. 2020), there is an accelerating need for sound and effective methods for assessing and estimating habitat properties and suitability to quantify the amount of remaining high-quality habitat and adapt forest management to increase conservation efforts (Woinarski et al. 2014, Davey 2018b, DELWP 2019, Geary et al. 2021).

In Australia, the species most vulnerable to these increasing threats are those that occupy specific niches and have limited capacity of escaping or migrating from canopy- or stand-replacing disturbances as a result of small home-range sizes or specialized diets (Powell 2000, Smith et al. 2007, Shipley et al. 2009, Bowman et al. 2014, Davey 2018a). Arboreal marsupials are among those impacted most strongly by severe wildfires (Chia et al. 2016, McLean et al. 2018, Ward et al. 2020). However, amongst the arboreal marsupials, it is the folivores such as the greater glider (*Petauroides volans*) that are particularly vulnerable to stand- or crown-replacing disturbances (Kavanagh 2000, McLean et al. 2018). In complex forested landscapes, habitat suitability for forest-dependent species may rely on multiple features of the forest (Lindenmayer et al. 1990a, Lindenmayer et al. 1991c, Nitschke et al. 2020). These may be structural features, such as the occurrence of hollow-bearing trees (Smith and Lindenmayer 1988), or nutritional features, such as the presence of suitable prey or feeding species for foraging (Robbins 2012). Greater gliders prefer climatic conditions supporting their narrow thermoregulatory capacities and require large trees of their preferred *Eucalyptus* species, which have high foliar and digestible nitrogen (digN), while also being low in leaf toxins (Rübsamen et al. 1984, Kavanagh and Lambert 1990, DeGabriel et al. 2009a, Youngentob et al. 2011, Wagner et al. 2020). Furthermore, they require up to 14 nesting trees within their small 1-6 ha home ranges (Gibbons and Lindenmayer 2002, Smith et al. 2007). They are predominantly found at higher elevations with cooler and wetter climates (Smith and Smith 2020, Wagner et al. 2020). Favourable climatic conditions facilitate higher site productivity which leads to taller, mature forests dominated by *Eucalyptus* species with high foliar nitrogen and abundant

hollow-bearing trees (Smith et al. 2007, Koch et al. 2008, Kearney et al. 2010, Youngentob et al. 2011, Smith and Smith 2020, Wagner et al. 2020, Wagner et al. in review-a - Chapter 4). The formation of hollows in eucalypts is dependent on tree dimensions, form, age and mechanical disturbance (Lindenmayer et al. 1991b, Lindenmayer et al. 1993b). Trees with large diameters, shorter heights and/or irregular crown forms are important predictors for estimating hollow occurrence and abundance in the temperate forests of Australia (Bennett et al. 1994, Gibbons et al. 2000, Fox et al. 2009). The indirect nature of hollow formation due to the absence of excavating species (e.g., woodpeckers) means that hollow formation requires long time-frames and therefore mainly occurs in large and/or mature trees that have been exposed to different sources of damage or decay (e.g., fire or fungal attacks, Fox et al. 2008, Lindenmayer et al. 2017). Furthermore, climate plays a role in these processes and can foster hollow formation in drier parts of the landscape through influences on species composition and growth form (Bennett et al. 1994). Wetter climates drive the establishment of productive soils and large mature trees at high elevation (Lindenmayer et al. 1991b, Bennett et al. 1994). These high elevation forests support tree species with higher levels of foliar nitrogen due to higher soil fertility and temperatures and precipitation levels that foster forest productivity and tree growth (Attiwill and Leeper 1987, Attiwill and Adams 1996). Nevertheless, maturity (i.e. leaf age) may affect foraging suitability negatively. Mature leaves may contain more nitrogen but are also more fibrous, meaning that major parts the nutritional value can be indigestible, which is why arboreal folivores favour young foliage (Kavanagh and Lambert 1990, Hume 1999, Moore et al. 2004b). The factors driving these differences in hollow availability and foliar nutrition vary across landscapes as they are driven by templates of climate, soils, and topography (Turner and Gardner 2015).

One of the main areas of greater glider distribution in temperate Australia is the mixed-species *Eucalyptus* forests of southeastern Australia. The area was severely affected by the 2019/20 bushfires, burning vast areas of the greater glider's suitable habitat range (Ward et al. 2020). While climate has been identified as a landscape-scale driver of habitat suitability in the region (see Wagner et al. 2020), tree hollows and foliar nitrogen are locally more variable and may be more meaningful in determining the likelihood of occupancy at the stand scale in mature forests and after disturbance (Gibbons et al. 2000, Eyre 2006). In this study we aimed to test whether foliar nitrogen and hollow availability limits occupancy in the region and how these measures of stand-level greater glider habitat suitability can best be determined from methods of assessing forest structure and site productivity, often collected during forest inventory assessments. As greater gliders rely on a joint abundance of hollow-bearing trees and suitable feeding trees (Smith and Lindenmayer 1988, Kavanagh and Lambert 1990) and cannot occur

when either resource is sparse or absent (McLean et al. 2018), they should prefer a homogenous forest structure providing both old trees with hollows and a mix of preferred species and digestible, highly nutritious leaves (Youngentob et al. 2011). For this study we hypothesized that both low numbers of hollows or hollow-bearing trees and low levels of foliar nitrogen limit greater glider occupancy in the study region. We expect landscape-scale variability in these resources to greatly affect the presence or absence of greater gliders. Their occupancy should a complex spatial outcome of fire refugia (with large mature trees) and sites of high foraging suitability (containing favourable feeding species, Kavanagh 2000, Youngentob et al. 2011, McLean et al. 2018). Based on a review of the literature we expected that the occurrence and abundance of hollows would be related to tree dimensions, growth form, and age as well as forest structure and type (Gibbons et al. 2000, Fox et al. 2008, Koch et al. 2008). As foliar nitrogen is a function of available soil nutrients, climate, and site topography (Attiwill and Leeper 1987, Attiwill and Adams 1996), we explored the role and significance of these factors across a mature mixed-species forest landscape. Knowing what determines habitat suitability at across scales is crucial for assessing and conserving the remaining undisturbed habitat in a managed forest landscape impacted by a recent mega-fire (Ward et al. 2020, Geary et al. 2021).

Methods

Using flora and fauna surveys, leaf and soil chemistry analyses, spatial data, and linear and structural equation models, we tested a range of independent covariates to estimate landscape-scale variability in two important determinants of greater glider habitat suitability: hollow availability and foliar nitrogen.

Study area

The study was conducted in the approximately 1.2 million hectares (ha) mixed eucalypt forest landscape (Dept. of Agriculture and Water Resources 2018) of East Gippsland, Victoria, Australia. These forests range from open lowland forest along the coast (5-50 m a.s.l) to closed tall forest at high elevation (~1000–1300 m a.s.l.). The most common *Eucalyptus* species in these forests are *E. siebieri* in the lowlands, *E. globoidea* in mid-elevation sites, and *E. viminalis* at high elevations. *E. obliqua* is the most common species across the entire elevation gradient (Opie et al. 1990, Dept. of Conservation and Natural Resources 1995, Sebire and Fagg 2009). Average annual rainfall and temperature in the study region ranges from 648 to 1178 mm (average for 1981–2014, Stewart et al. 2020a) and 6–15.8°C (average for 1981–2014, Stewart and Nitschke 2017a), respectively. Across the study area greater gliders are most abundant at elevations >700 m in cool and wet forests, where their specific

thermoregulatory requirements are met (Henry 1984, Bennett et al. 1991, van der Ree et al. 2004a, Wagner et al. 2020).

Plot design

Our survey plot network was designed to include a range of *Eucalyptus* species that are utilized by greater gliders as a foraging resource, as well as species that the gliders are known to avoid (Kavanagh and Lambert 1990, Comport et al. 1996, Cunningham et al. 2004). Study sites were established across the topographic gradient of the greater gliders' known range in the region. To ensure only mature forests were captured in the study design, we stratified the landscape to eliminate forests that had been disturbed by fire or logging in the previous 40 years, using publicly available spatial layers on forest fire and timber harvesting history from the Victorian State government (https://www.data.vic.gov.au/). We established 30 plots in three elevation bands – lowlands (0–420 m), mid-hills (420–840 m), and high elevation (840–1260 m a.s.l). Within each elevation band, we established 10 plots of varying elevation, aspect, and slope. In each band, four plots were in flat or gully locations, four in mid-slope positions (north- and south-facing) and two on the ridge, close to the maximum elevation of the respective band (Appendix 2 Fig. S1). This design captured the wide range of elevation, topographical position, forest types and tree species diversity present in the East Gippsland distribution range of the greater glider (Fig. 3.1).

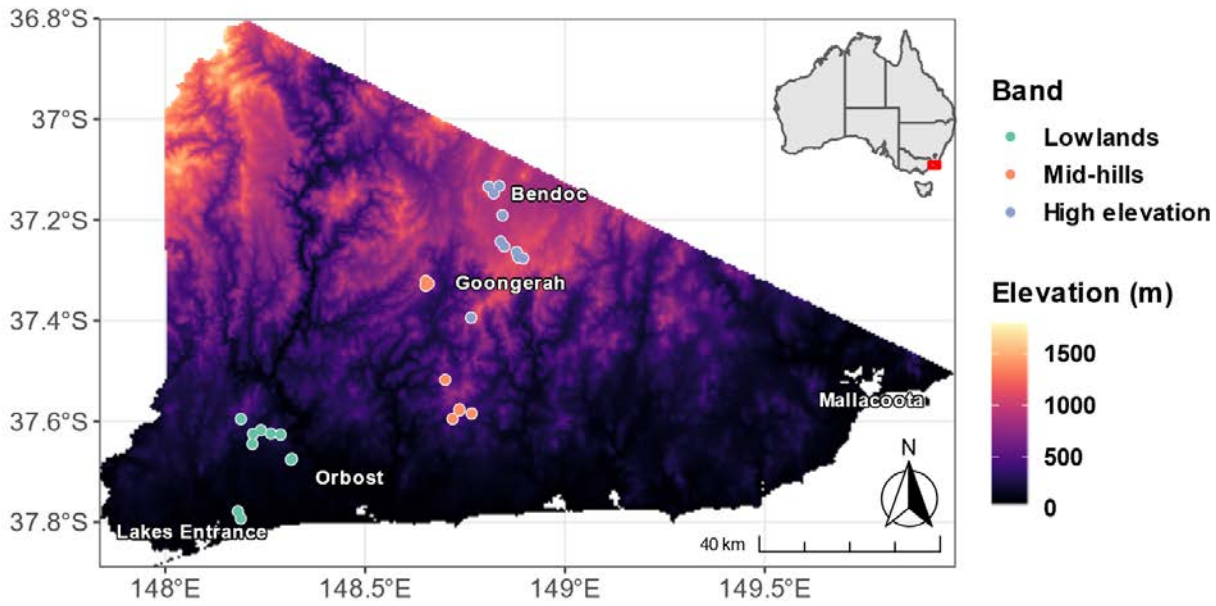

Figure 3.1. Study area map of East Gippsland, Victoria, showing elevation gradient and plot positions

Assessing forest structure

Each plot centre location was recorded using a handheld Garmin® GPS and waypoint averaging for the duration of the ground survey. In each survey plot, we recorded site attributes (elevation, slope, aspect, crown cover and basal area of dominant tree species), then established a variable radius plot using a Kramer's dendrometer with a basal area factor (BAF) of four. This ensured the sampling would capture large, mature, and dominant trees that form the canopy, and which are the preferred nesting and foraging habitat for greater gliders. For each tree in the variable radius plot sample, we recorded the species, diameter at breast height (DBH), height, crown width, foliage cover, vigour (health status in categories), age class, structural layer the tree belonged to, and the occurrence, number, and type of major hollows (for details on these variables see Appendix 2 Table S1). The presence of ground-level flora was recorded in a 100 m^2 subplot around the plot centre.

Leaf and soil sample collection

To determine the nutritional value of the *Eucalyptus* foliage within each plot, leaf samples were collected from five trees per plot, representative of the mixture of *Eucalyptus* species recorded there. One tree was sampled in each quadrant of the plot (i.e., northwest, northeast, southeast, southwest), while an additional dominant tree was selected subjectively to ensure a reasonable representation of the dominant species (Appendix 2 Fig. S2). Foliage samples were collected with a throw-line launcher, as described by Youngentob et al. (2016). We collected ~100 g of fresh leaf samples from a total of 150 trees across all of our plots. Soil samples were collected to a depth of 10 cm from 30 locations within each survey plot, using a tube corer. Leaf and soil samples were sealed in individual air-tight bags, frozen (leaves) or cooled (soils) and transported to the laboratory for further processing.

Wildlife surveys

To determine occupancy of greater gliders, spotlighting surveys on 1-km transects proximate to the plot centre were carried out at all sites. For these surveys, an average pace of 10 minutes per 100 m was used by a minimum of two observers walking 10 minutes apart, scanning tree canopies for eyeshine reflectance using strong torchlights. This pace and setup maximized the probability of detection (Wintle et al. 2005, Kissling and Garton 2006, Nelson et al. 2018). Any detected animal's location was recorded using a handheld GPS. Further observation data of the tree species on which the animal was observed, height of the tree, animal behaviour, fur colour phase, time of observation, and distance and bearing to the animal were also recorded. Any spotlighting transects with one or more detected greater gliders were considered

occupied for the purpose of this study. All observations were submitted to the Victorian Biodiversity Atlas (VBA, vba.dse.vic.gov.au/vba).

Data processing and variable selection

Chemical analyses

Collected fresh leaves were frozen after collection and dried in the laboratory using a VirTis® BenchTop Pro© freeze-dryer. We used a pressure of 50 microbars and condenser temperature of -70°C for 24-72 hours (Julkunen-Tiitto and Sorsa 2001). Dried leaf samples were ground to pass a 1-mm screen using a Foss® Cyclotec 1093© mill and frozen at -20°C until further analysis. Total nitrogen (N) was determined according to the Dumas procedure using a Leco® TruMac© CN analyser. Digestible nitrogen (digN) was quantified by *in vitro* digestion with cellulose and pepsin according to Degabriel et al. (2008). We reported N, digN and digestible dry matter (DDM) as % dry mass (% DM). Soil samples were dried at room temperature, sieved to pass a 2-mm screen, composited by plot, and analysed for soil nutrients. The following soil chemical properties were considered: soil pH ($CaCl_2$), nitrate nitrogen (NO_3 in mg/g), phosphorous (P in mg/g), potassium (K in mg/g), total nitrogen (soil N in percent) and total carbon (C in percent). Soil N and C were derived using dry combustion, while other elements were determined colorimetrically or via spectroscopy at an external laboratory.

Additional spatial variables

In addition to structural variables, fauna survey records, and leaf and soil chemical values, we included variables related to climate and topography as modelling candidates from spatial layers. These had previously been identified as important for determining greater glider habitat suitability at the landscape scale (see Wagner et al. 2020). They include the Annual Heat Moisture Index (AHMI), number of days with condensation (1981 – 2014), the Terrain Wetness Index (TWI), and average site Normalized Difference Vegetation Index (NDVI) along with further topographic variables such as slope and aspect (Table 3.1).

Table 3.1. Model groups and variables related to tree hollows and foliar nutrition with

Hollow occurrence and abundance		
Group	**Variable**	**Details**
Structural	Height	Tree height in meters
	DBH	Tree diameters at 1.3m above ground in cm
	Volume	Tree volume from DBH + height (see Eq.1)
	Crown area	Crown area in m2 from crown widths
	Health category	Categorical variable describing tree health (Appendix 2 Table S1)
	Age class	Categorical variable describing tree age (Appendix 2 Table S1)
	Structural layer	Categorical variable defining the structural layer a tree belonged to (see Appendix 2 Table S1)
Site-level	Slope	Slope of site in degrees
	Aspect	Aspect of site in degrees
	Soil type	Soil type according to Australian soil classification
	AHMI	Annual heat moisture index (AHMI = (MAT+10)/(MAP/1000)
	TWI	Terrain wetness index
	NDVI	Normalized difference vegetation index
	Condensation days	Number of days with condensation according to Stewart et al. (2020b), Wagner et al. (2020)
	No. of forest fires	Number of fires a site received since 1980
Nutrients	Soil pH	Soil pH (CaCl2)
	Soil total nitrogen	Total soil nitrogen in %
	Soil total carbon	Total soil carbon in %
	Soil nitrate nitrogen	Soil nitrate nitrogen (NO_3) in mg/kg
	Soil phosphorous	Soil phosphorous (P) levels in mg/kg
	Soil potassium	Soil potassium (K) levels in mg/kg
	Average foliar nitrogen	Averaged foliar nitrogen (% DM) of site
Foliar total nitrogen, digestible nitrogen and DMD		
Soil properties	Soil pH	Soil pH (CaCl2)
	Soil total nitrogen	Total soil nitrogen in %
	Soil total carbon	Total soil carbon in %
	Soil phosphorous	Soil phosphorous levels in mg/kg
	soil potassium	Soil potassium levels in mg/kg
	Slope	Slope of site in degrees

Site-level	Aspect	Aspect of site in degrees
	Soil type	Soil type according to Australian soil classification
	Soil sub-type	Soil sub-type according to Australian soil classification
	AHMI	Annual heat moisture index (AHMI = (MAT+10)/(MAP/1000)
	TWI	Terrain wetness index
	NDVI	Normalized difference vegetation index
	Condensation days	Number of days with condensation according to Stewart et al. (2020b), Wagner et al. (2020)
	No. of forest fires	Number of fires a site received since 1980
	Foliage cover	Projected foliage cover at site
Structural	Height	Tree height in meters
	DBH	Tree diameters at 1.3m above ground in cm
	Volume	Tree volume from DBH + height (see Eq.1)
	Crown area	Crown area in m2 from crown widths
	Health category	Categorical variable describing tree health (Appendix 2 Table S1)
	Age class	Categorical variable describing tree age (Appendix 2 Table S1)
	Structural layer	Categorical variable defining the structural layer a tree belonged to (see Appendix 2 Table S1)
	Number of trees per ha	Extrapolated number of trees per hectare
	Number of hollows	Number of hollows observed on tree

Modelling hollow availability and tree nitrogen

Structural data and differences between occupied and unoccupied or elevational bands were evaluated using F and p statistics from one-way analysis of variance (ANOVA) and Tukey Honest Significant Differences (HSD) tests. We used a multi-step modelling procedure to determine meaningful predictors for both hollow occurrence (presence or absence of hollows) and abundance (number of hollows), as well as N, digN, and DDM. First, we split all available modelling variables into logical groups (Table 3.1). For hollows, we used structural, site level, and nutrient data for analyses; for foliar nutrition, we used structural, site, and soil data groups (Table 3.1). Within these groups we tested for intercorrelation between variables. We reduced the number of initial predictor variables in each group by removing pairs with Pearson's correlation coefficient $r \geq |0.8|$. All variable candidates were then standardized to a mean of zero and standard deviation of one. We built a generalized linear model (GLM) with all uncorrelated variables per group as predictors with hollow or foliar nutrition metrics as the response variable. Using every possible variable combination in separate models (i.e., model

dredging), we identified the best variable combinations based on model performance as represented by the Akaike Information Criterion (AIC) and delta values ≤ 2. The predictor variables in the best models were then used in a combined model of hollow availability or foliar nutrition that drew the best variables from each group. All models were evaluated using AIC, model R^2, and variable significance (p). We were also interested in variable relationships within the models. To further analyse and interpret different interaction effects between and on model variables, we developed structural equation models (SEMs) to conduct path analyses (Bollen and Stine 1992, Rosseel 2012). Path analyses on the final combined models revealed important model interactions and indirect effects. All statistical analyses were conducted in R (R Core Development Team 2020) using the packages *MuMIn*, *lavaan* and *caret* (Rosseel 2012, Barton 2019, Wing et al. 2019). SEM performance was evaluated using each path's R^2 value.

Results

Our 30 study sites ranged in elevation from 32–1185 m a.s.l., covering slopes from 1–55% and aspects from 26–355°. We measured a total of 463 individual *Eucalyptus* trees from 17 species. Common and dominant canopy species included *Eucalyptus consideniana, E. globoidea*, and *E. sieberi* at low elevation, *E. obliqua, E. cypellocarpa*, and *E. fastigata* in the mid-elevation sites, and *E. corajingolensis and E. viminalis* at high elevation. We recorded 239 individual animal observations during night-time spotlighting surveys across all sites. Of these, 160 observations were arboreal marsupials, including 44 greater gliders, which we found at nine sites. Greater gliders occurred with the highest frequency and density in high elevation sites, where they were found at 6 out of 10 sites.

Tree hollows and forest structure

Tree hollows were abundant across our survey plots. The number of observed hollows ranged from 8 to 78 per plot, with similar ranges in occupied (8 – 73, mean = 34.6 ($\pm$ 19.4), n = 9) and unoccupied sites (9 – 53, mean = 25.6 ($\pm$ 14), n = 21). Although the average number of hollows measured per plot in the lowlands was the lowest (17.5 $\pm$ 5.62), a higher mean number of both hollow-bearing trees (70.9 $\pm$ 39.2) and hollows (294 $\pm$ 105) was found when extrapolating plot-level data to one hectare (Fig. 3.2). There were no differences between group means of hollows and hollow bearing-trees in elevation bands (F= 2.258, p = 0.124) or occupied and unoccupied sites (F = 1.273, p = 0.269), as determined by one-way ANOVA.

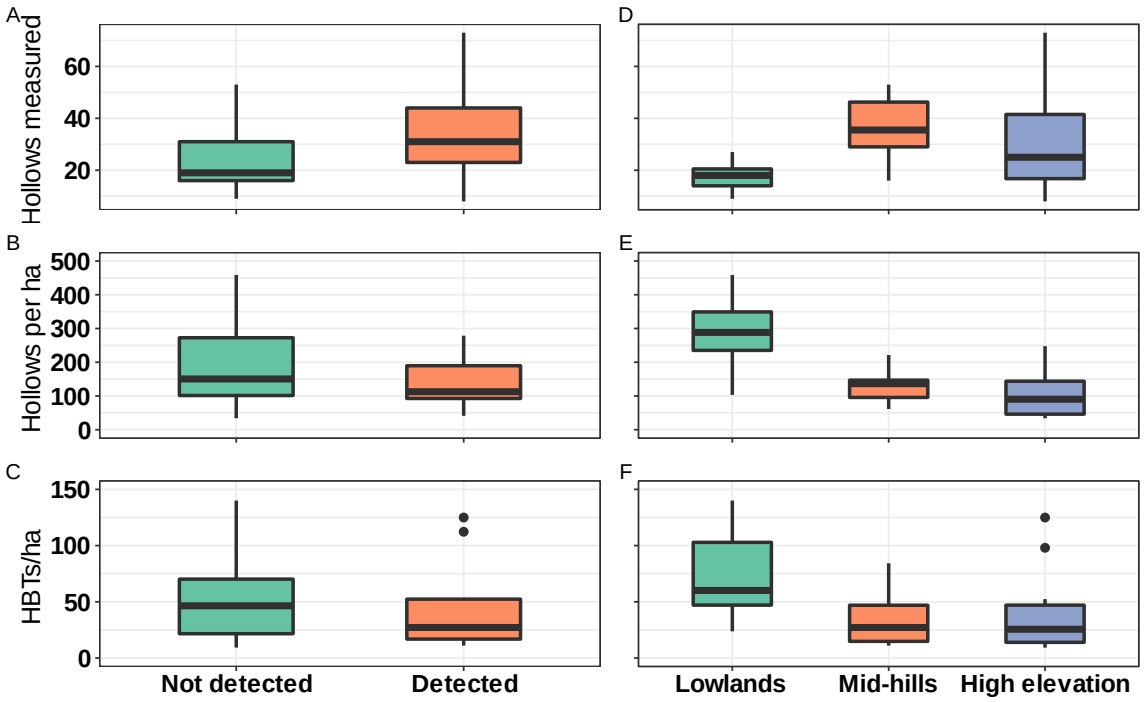

Figure 3.2. Observed hollow distribution for sites distinguished by greater glider detection (A-C) and elevational band (D-F). At the plot level, hollow occurrence differed significantly between elevation bands (A, F= 4.725, p = 0.0174). There were no statistical differences between occupied and unoccupied sites (F = 1.273, p = 0.269) or elevation bands (F= 2.258, p = 0.124) when extrapolating survey data to an area of 1 ha.

The largest tree diameters (DBH) within our variable radius plots were observed in high- and mid-elevation transects (mean DBH of 122 ± 60.8 cm, and 109 ± 60.2 cm, respectively, Fig. 3.3A). Unoccupied sites had a higher frequency of trees with DBH <100 cm, whereas occupied sites had higher average DBH (110 ± 56.5 cm for occupied sites, 90.5 ± 60.3 cm for unoccupied sites, Fig. 3.3B). Differences in mean DBH were significant between occupied and unoccupied sites ($F = 10.69$, $p = 0.00116$) and between lowland and mid to high elevation bands ($F = 71.52$, $p \approx 0$). DBH distribution did not differ between mid- and high elevation bands when analysing the ANOVA (Tukey HSD test $p = 0.07$). We observed similar patterns for tree height distribution and crown area. For example, lowland sites lacked trees >40 m in height and >200 m^2 crown area and the frequency of trees <30 m in height and <100 m^2 crown area was greater in sites where greater gliders were absent (Appendix 2 Fig. S3A-D). Tree heights were different between elevation bands ($F = 96.02$, $p < 0.001$), as were crown areas ($F = 58.88$, $p < 0.001$).

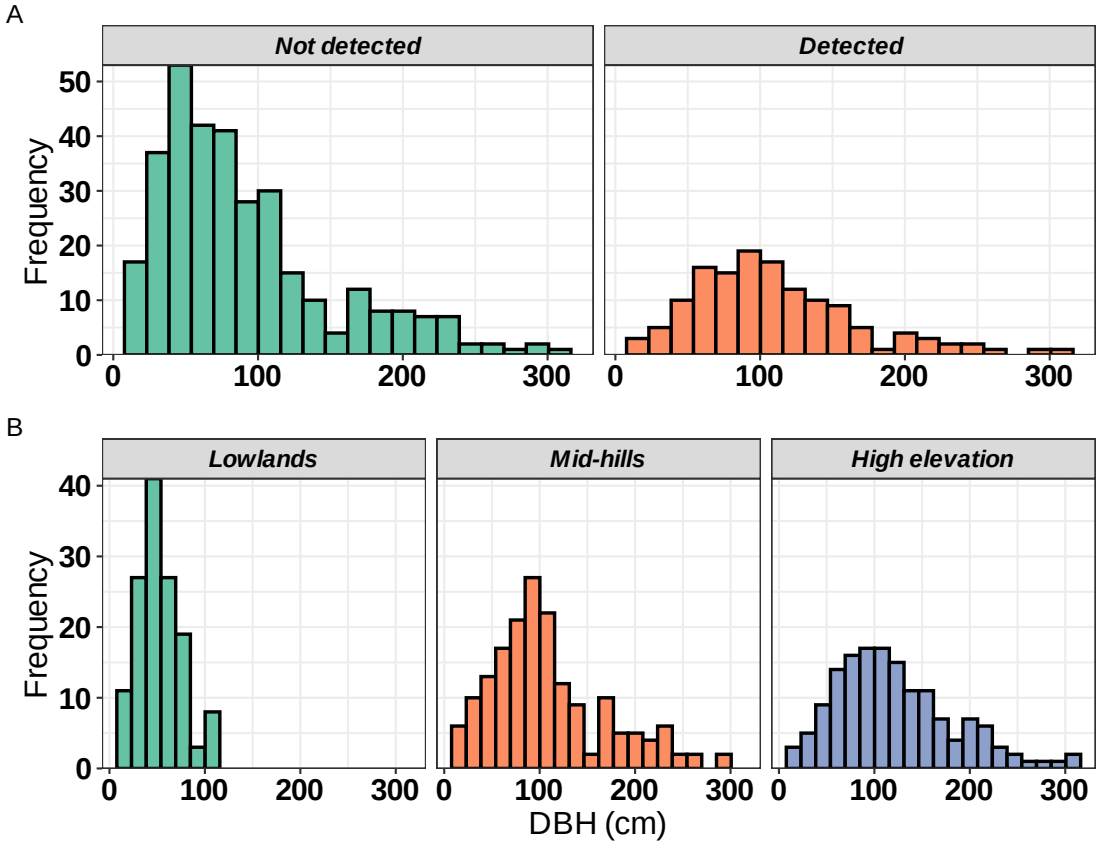

Figure 3.3. Observed diameter distribution for sites distinguished by greater glider detection (A) and elevational band (B)

Foliar and soil chemistry

The 150 sample trees from 17 *Eucalyptus* species varied in total leaf nitrogen (N) from 0.63-1.92% dry mass (% DM). Digestible nitrogen (digN) ranged from 0.45 to 1.73% DM and digestible dry matter (DDM) from 49.05-83.58 % DM (Appendix 2 Fig. S4A-C). Both average plot level N and digN increased with elevation, while DDM decreased. Nitrogen content was highest at high elevation and in sites with greater gliders present. We found that a mean plot N value of 1.1% DM was a reasonable threshold for greater glider occupancy across our sites. Greater gliders were not observed in plots with mean N values below this threshold. There was no difference between occupied and unoccupied sites in digN distribution ($F = 0.417$, $p = 0.52$), although it was slightly lower at low elevation sites. DDM was highest in the lowlands and higher in unoccupied sites (Appendix 2 Fig. S5A-F). DDM differed significantly between elevation bands ($F = 6.42$, $p = 0.00229$) and occupied or unoccupied sites ($F = 9.778$, $p = 0.00224$). N, digN, and DDM were on average slightly higher in the sub-genus *Symphomyrtus* ($n = 7$ species, Appendix 2 Fig. S6A-C) when all samples were pooled together, but did not differ ($p = 0.224$, 0.115 and 0.516 for N, digN and DDM respectively). Soil nitrogen (N)

ranged from 0.08-0.76 % and soil carbon (C) from 2.8-14.3%. Soil phosphorus (P) concentrations were between 1 and 20 mg/g and potassium (K) between 46-452 mg/g. The concentrations of these soil chemical elements increased with elevation.

Modelling hollow availability

Non-correlated and grouped candidate variables are listed in Table 3.1. In the forest structure variable group, DBH, tree height, age class, health (vigour) category and tree structural layer best explained hollow occurrence. When simplifying the model by calculating tree volume from DBH and tree height (H) (Eq. 1, assuming trees having a conical shape), model performance improved, and significant variables of the best model reduced to volume, age class, and tree structural layer (Table 3.2).

$$Tree\ volume\ (m^3) = \frac{\frac{DBH}{200}^{2*3.142}\ (m^2) * H\ (m)}{3} \quad \text{(Equation 1)}$$

Table 3.2. Model results for occurrence of hollows from the best model from the structural group

Variable	Estimate	95% CI[1]	p-value
(Intercept)	-1.9	-2.7, -1.2	<0.001
Age class	0.86	0.59, 1.2	<0.001
Structural layer	-0.38	-0.85, 0.06	0.10
Tree volume	0.07	0.04, 0.10	<0.001

[1]CI = Confidence Interval

The tree's age class (regrowth, mature, over-mature, late-mature or dead stag) was equally important as volume for hollow occurrence (both $p < 0.001$). In the site variable group, only AHMI had a significant ($p < 0.01$) effect on hollow occurrence, when using all uncorrelated site variables, as well as climate variables only. Finally, hollow occurrence was best explained by mean plot foliar and soil N in the nutrition group. Similar results were found when modelling hollow abundance (number of hollows per tree) by variable group, although some variables differed, especially in the site group, which also included soil-type, aspect, condensation days, and site NDVI in the final model (Appendix 2 Table S2). A final model that combined the best variables from each group indicated that hollow occurrence is best explained by tree volume, age class, structural layer, TWI, and foliar N (Fig. 3.4). The final model for hollow

abundance contained the same variables, but foliar N and TWI were replaced by AHMI, aspect, and condensation days (Table 3.3).

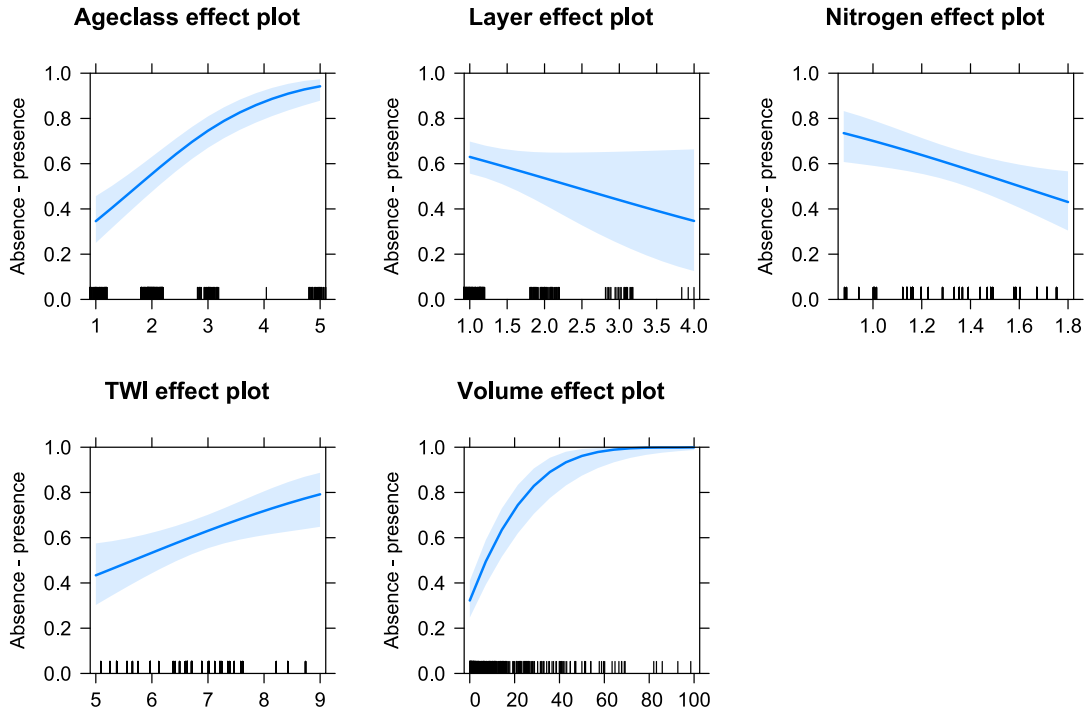

Figure 3.4. Partial variable dependencies of the final (combined) hollow occurrence model.

Table 3.3. Model results for combined final models of hollow occurrence and abundance

	Hollow occurrence			Hollow abundance		
Variable	**Estimate**	**95% CI[1]**	**p-value**	**Estimate**	**95% CI[1]**	**p-value**
(Intercept)	-2.9	-5.3, -0.57	0.017	1.8	1.6, 2.0	<0.001
Age class	0.86	0.60, 1.1	<0.001	0.60	0.41, 0.79	<0.001
Structural layer	-0.39	-0.85, 0.06	0.092	-0.16	-0.35, 0.03	0.10
Mean foliar N	-1.4	-2.5, -0.39	0.007	-	-	-
TWI	0.40	0.12, 0.69	0.006	-	-	-
Tree volume	0.08	0.05, 0.12	<0.001	1.3	1.1, 1.5	<0.001
AHMI	-	-	-	0.37	0.16, 0.57	<0.001
Aspect	-	-	-	0.22	0.03, 0.41	0.021
Condensation days	-	-	-	0.36	0.16, 0.56	<0.001

[1]CI = Confidence Interval

Modelling foliar nitrogen

For foliar nitrogen, the best models were dominated by measures of soil productivity. We observed strong linear relationships between total foliar nitrogen (N) and the plant nutrients NO_3, P, and K, as well as soil total nitrogen (soil N, Fig. 3.5, Table 3.4). Soil nitrogen and K were also highly correlated with digN and DDM. Nutrient models performed better for N than digN or DDM. Since soil total carbon (C) and soil N were highly correlated, we tested two GLMs in which either soil N or soil C was included in the soil variable group of predictors. For the group of predictors that included soil C, foliar N was best explained by soil NO_3 ($p < 0.01$), P ($p < 0.05$) and K ($p < 0.001$); whereas for the model containing soil N, soil N and K (both $p < 0.001$) were the strongest predictors (Table 3.4). Using site variables only, AHMI, TWI, aspect, condensation days, site NDVI, and soil subtype best explained foliar N. For the structural group the best predictors of foliar N were tree volume, tree age class, and trees and hollows per hectare (Appendix 2 Table S3). The best model using a combination of the most

significant variables from all groups included K, AHMI, TWI, NDVI, and tree age class (Fig. 3.5, Table 3.5). The best combined model for digN included soil N, age class, foliage cover and tree structural layer, while DDM was best explained by soil K, soil-type, slope and aspect, condensation days, and tree age class. Results for grouped models of both digN and DDM can be found in Appendix 2 Table S4.

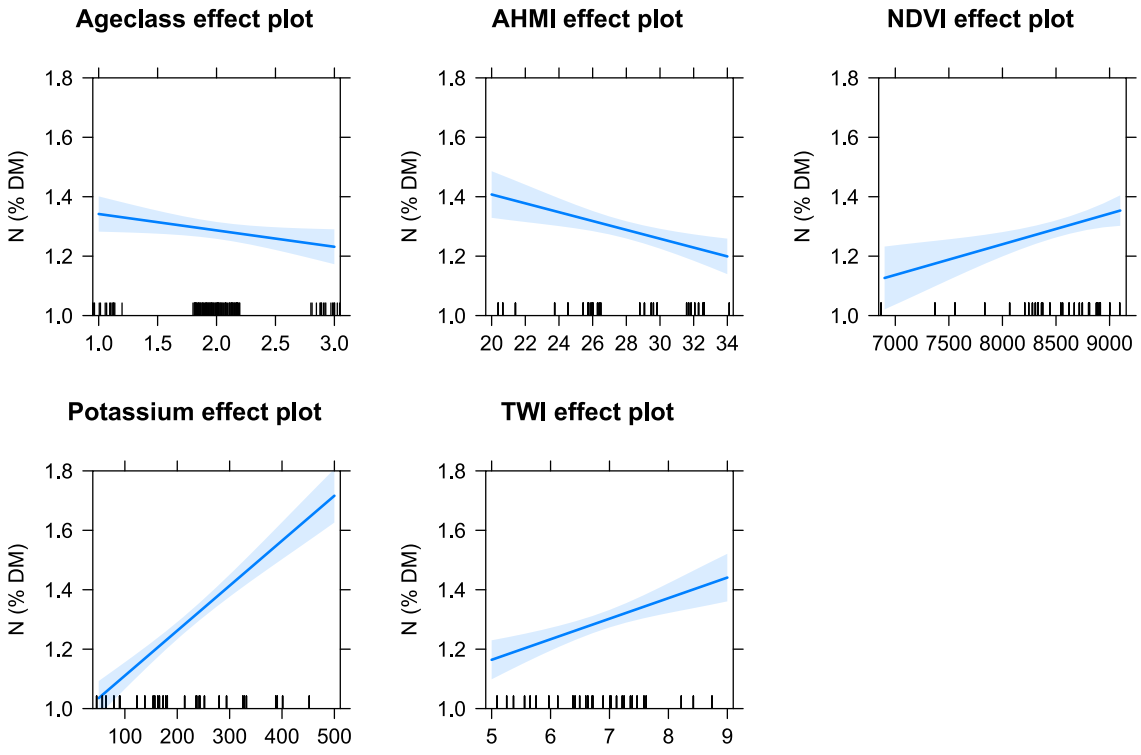

Figure 3.5. Partial variable dependencies of the final (combined) total nitrogen model.

Table 3.4. Model results for separate foliar nitrogen models, containing either soil total carbon (C) or soil nitrogen (N)

	Model containing C			Model containing N		
Variable	**Estimate**	**95% CI[1]**	**p-value**	**Estimate**	**95% CI[1]**	**p-value**
(Intercept)	0.80	0.69, 0.92	<0.001	0.88	0.81, 1.0	<0.001
Soil NO3	0.02	0.01, 0.03	0.005	-	-	-
Soil P	0.01	0.00, 0.01	0.036	-	-	-
Soil K	0.00	0.00, 0.00	<0.001	0.00	0.00, 0.00	<0.001
Soil N	-	-	-	0.60	0.36, 0.84	<0.001

[1]CI = Confidence Interval

Table 3.5. Model results for combined final model of foliar nitrogen

Variable	Estimate	95% CI[1]	p-value
(Intercept)	1.3	1.3, 1.3	<0.001
Age class	-0.03	-0.06, 0.00	0.037
AHMI	-0.06	-0.09, -0.02	0.001
NDVI	0.05	0.02, 0.09	0.002
K	0.17	0.13, 0.20	<0.001
TWI	0.06	0.03, 0.09	<0.001

[1]CI = Confidence Interval

Modelling variable relationships

Results from structural equation models (SEMs) are illustrated as path analyses in Figures 6 (for hollow occurrence) and 7 (for foliar nitrogen). Apart from playing a role in hollow occurrence, tree age class was also significant in describing foliar nitrogen, with mature ages being associated with less nitrogen, an effect observed in both SEMs. Age class, AHMI, and TWI were independent of other significant predictor variables of hollow occurrence or foliar N. Both number of fires and low values of NDVI had a significant negative effect on age class, while AHMI was influenced by elevation and TWI by topography (slope and aspect). In the hollow occurrence SEM, the structural layer in which a tree occurred was associated with the estimated stem volume of the tree, where canopy trees had the greatest volume. In the nitrogen SEM, NDVI, used as a measure of forest productivity, was also influenced by AHMI, whereas soil K, a measure of soil fertility, was influenced by TWI and AHMI, with cooler and wetter climates and topographic positions being associated with higher soil K and foliar N.

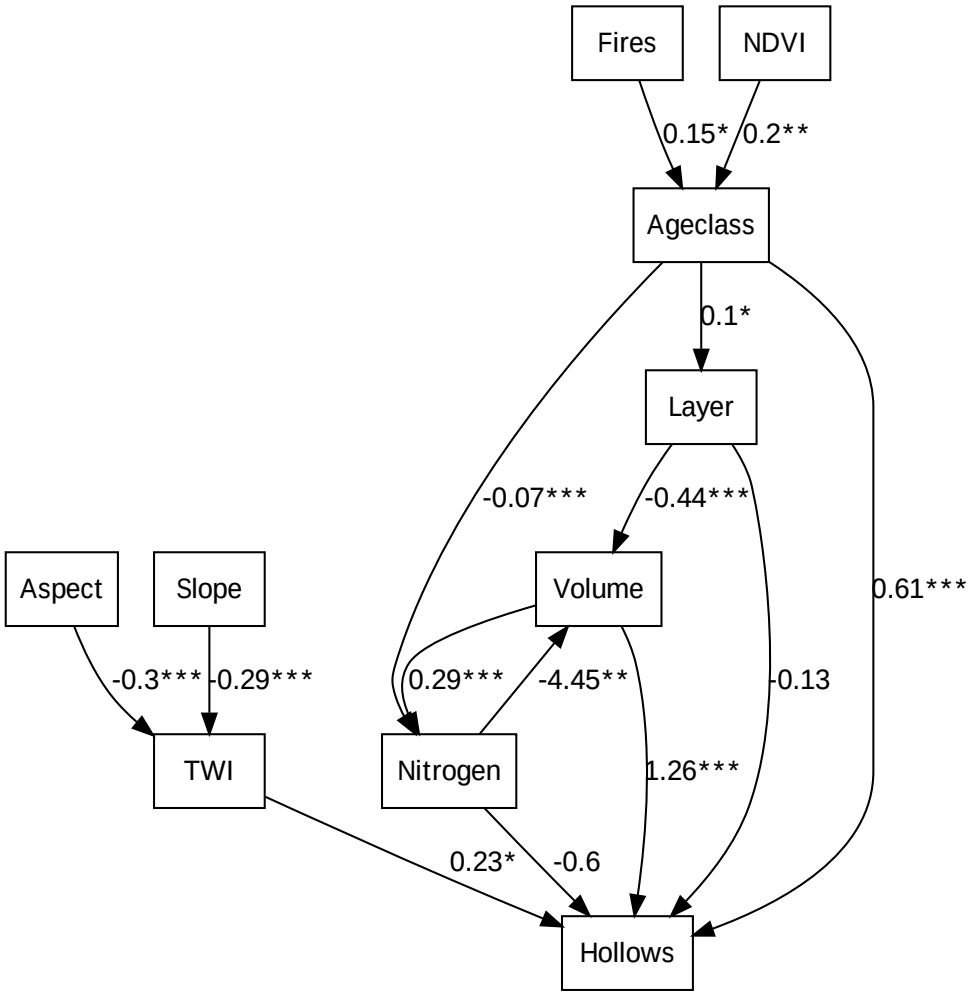

Figure 3.6. Structural equation model for response variable number of hollows (Hollows) illustrating variable relationships in the final hollow model with additional modelling variables used to show external influences. Numbers are estimates and (*) indicate significance (p = 0 (***), p < 0.001 (**), p < 0.01 (*)). R-squared for separate path models were 0.4 for hollows, 0.82 for volume, 0.1 for layer, 0.25 for age class and 0.53 for nitrogen.

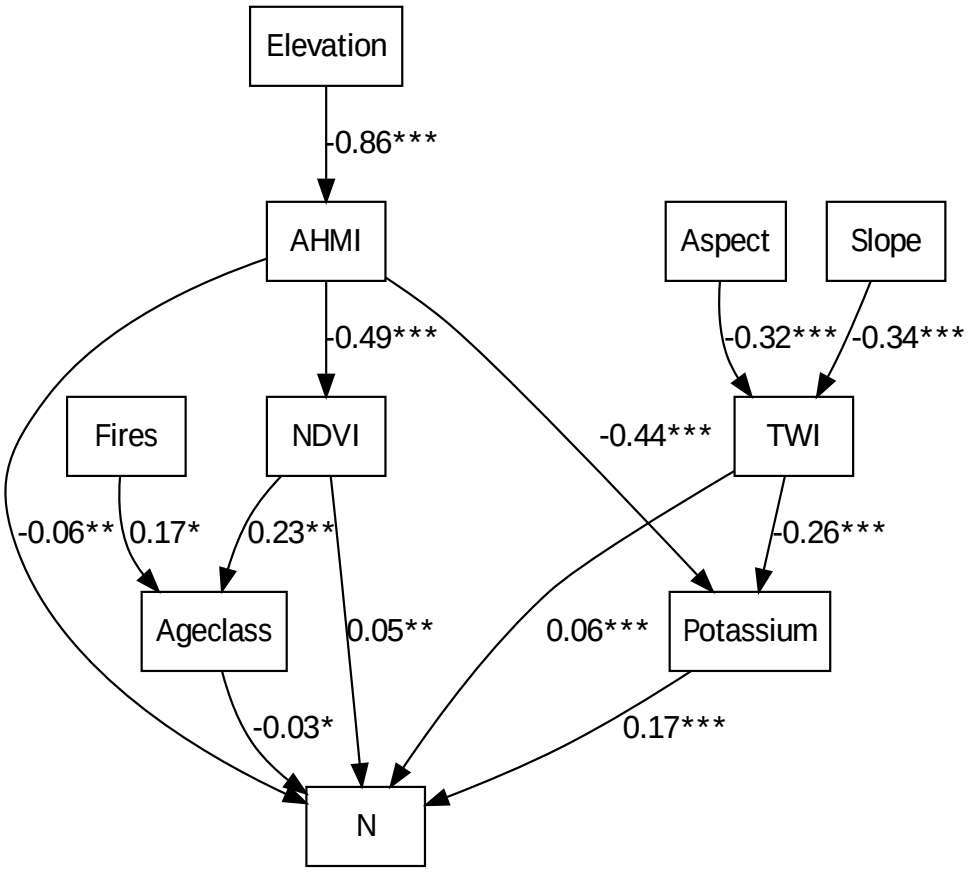

Figure 3.7. Structural equation model for response variable foliar nitrogen (N) illustrating variable relationships in the final nitrogen model with additional modelling variables used to show external influences. Numbers are estimates and (*) indicate significance (p = 0 (***), p < 0.001 (**), p < 0.01 (*)). R-squared for separate path models were: 0.61 for N, 0.24 for NDVI, 0.1 for age class, 0.27 for potassium, 0.24 for TWI and 0.74 for AHMI.

Discussion

In the study landscape of East Gippsland, hollow occurrence and abundance, foliage and soil chemistry and greater glider occurrence was driven by climate, topography and site productivity. The associated forest types and tree species found there showed significant differences in soil and foliar nitrogen, whereas hollows were abundant. Tree size, soil productivity and nutritional value of *Eucalyptus* leaves increased with elevation (Appendix 2 Fig. S7). The largest trees and most productive sites were found at elevations >840 m a.s.l. Here we also detected greater gliders in larger numbers, in sites with cooler climates (see Wagner et al. 2020), and where foliar total nitrogen (N) was highest among all sites.

Hollow availability and foliar nitrogen

Hollow occurrence and abundance were homogenous across sites and elevation bands. Although we recorded more hollows in mid- and high elevation sites, the average number of hollows and hollow bearing trees (HBTs) per hectare were higher in the lowlands (Fig. 3.2). This is often the case in drier parts of the landscape, where growth form and tree species composition is driven by the amount of rainfall and lower site productivity, leading to earlier hollow formation (Bennett et al. 1994, Fox et al. 2008). We recorded more hollows in sites where we also observed greater gliders, but when scaling up to the hectare, the mean number of hollows and HBTs/ha was higher in sites with no detections (Fig. 3.2). Our study focused on mature forests that had not been disturbed in at least the last 40 years. At most sites, we could only find signs of historical selective logging, which ceased in the 1950s and 60s (VicForests Orbost staff, personal communication, May 2018). Strong positive relationships between stand age and the proportion of living trees with hollows in forests of the same landscape have been reported (see Gibbons et al. 2000) and unlogged or unburnt sites regularly contain more HBTs than forests that were disturbed (McLean et al. 2015). Logging and fire history can negatively affect hollow occurrence and abundance (Lindenmayer et al. 1991b, McLean et al. 2015). We therefore assume that hollows are not a limiting factor for greater glider occupancy in mature forests of East Gippsland, Victoria. This is also supported by the number of other hollow-dependent fauna observed during spotlighting surveys. We frequently detected other arboreal mammals that also require hollows for nesting such as sugar gliders (*Petaurus breviceps*), ringtail possums (*Pseudocheirus peregrinus*), and yellow-bellied gliders (*Petaurus australis*) in all three elevation bands. For example, sugar gliders were most frequent in the lowlands (60% occupancy), where only one site had greater gliders present (10% occupancy, Appendix 2 Table S5). However, because hollow occurrence was high across all sites, we could not determine how much variation in greater glider abundance or presence:absence was actually explained by tree hollows.

Throughout the landscape and range of *Eucalyptus* species sampled, foliar N increased with elevation and the associated tree species found there (Appendix 2 Figs S4+S6C). Observations of greater gliders were only made where average N concentrations were ≥1% N DM (Appendix 2 Fig. S5). This nitrogen threshold has frequently been reported for greater gliders in landscapes with similar species mixture (Foley and Hume 1987, Kavanagh and Lambert 1990, Cork 1992, Youngentob et al. 2011). Additionally, the mixture of eucalypt subgenera within a site may play a role in observed occupancy patterns. Species of the *Monocalyptus* subgenus typically had lower levels of digestible nitrogen (digN), which may limit tree use by greater gliders (Wallis et al. 2010, Youngentob et al. 2011). Although all transects had more species

of *Monocalyptus* than *Symphyomyrtus*, the ratio in the lowlands was 7:4 in favour of *Monocalyptus*, while at high elevation it was a closer to 4:3. Foliar N concentrations in eucalypts are mostly driven by site productivity, which increases with elevation in these landscapes, and climate (Braithwaite et al. 1984, Attiwill and Adams 1996, Cork and Catling 1996). Higher levels of foliar N allow for higher levels of digN, which has been identified as a more meaningful measure of forage quality for folivores (DeGabriel et al. 2009b, Wallis et al. 2010, DeGabriel et al. 2014).

Climatic conditions at higher elevation are also favourable for greater gliders, which are vulnerable to high temperatures and low water availability (Kearney et al. 2010, Smith and Smith 2020, Wagner et al. 2020). The combination of high total and digestible nitrogen availability and favourable climate explains why the species was predominantly detected here. Digestible dry matter (DDM) is driven by phenol and lignin levels of the foliage and was therefore more closely related to digN (Appendix 2 Fig. S4, Choo et al. 1981, Youngentob et al. 2011), but was slightly lower at high elevations and occupied sites. This observed reduction of mean DDM with elevation and occupied sites may also be explained by the ratio of subgenera found at highly productive, high-elevation sites. Larger trees of the subgenus *Symphyomyrtus*, such as *Eucalyptus viminalis*, are known to have lower DDM (Youngentob et al. 2011) due to higher levels of indigestible fibre as leaves mature (Moore et al. 2004b).

Modelling hollow occurrence and abundance and foliar nitrogen

Both stand-level factors associated with greater glider habitat suitability – hollow-bearing trees and foliar N – could be modelled using a combination of structural variables from field surveys, soil nutrient data from chemical assessments, and topographic and climatic factors. This is encouraging as tree hollow availability as well as foliar nutrition can therefore be estimated from standard survey- and freely available topographic and climatic spatial data.

Hollow models

Among variable groups, tree structural metrics were most important in explaining both hollow occurrence (presence or absence of hollows) and abundance (number of hollows). We found tree volume, as calculated from tree height and diameter to be the most meaningful predictor of both hollow metrics. Other variables such as the structural layer a tree belongs to and tree age class additionally improved model performance. The proportion of canopy and subcanopy trees with hollows was ~60%, whereas the proportion dropped to <40% for mid-storey trees (Fig 3.4). The trees in lower strata containing hollows were often dead stags and thus likely former canopy trees. Large trees that form the canopy have the largest tree dimensions in terms of diameter and volume. As trees develop in the canopy, branch loss in the lower crown

due to self-pruning and side-shading from suppressed trees leads to the formation of hollows (Smith and Lindenmayer 1988, Fox et al. 2009, Lindenmayer et al. 2012a). Tree height was negatively correlated with hollow availability with shorter trees being more likely to have hollows. Shorter mature trees are often associated with a poorer form (e.g., a broken top that may lead to chimney hollow formation, Fox et al. 2008). A tree's volume or diameter and reduction in height as it matures can also be a proxy of its age (Ashton 1976), and it is assumed that most eucalypts start forming hollows only after reaching mature ages >100-150 years (Bennett et al. 1994, Gibbons et al. 2000, Koch and Baker 2011, Lindenmayer et al. 2017). Our structural equation models (SEMs) support the important association between hollow occurrence and tree size and age (Fig. 3.6, Lindenmayer and Wood 2010). Multiple studies have observed form and age (also associated with tree vigour) as an important indicator of hollow availability (see Lindenmayer et al. 1993b, Bennett et al. 1994, Owers et al. 2015). Tree diameter has frequently been identified as a good predictor of hollow abundance in *Eucalyptus* forests due to the often near-linear relationship between tree size and the formation of hollows (Lindenmayer et al. 1993b, Bennett et al. 1994).

The final hollow models contained either the annual heat moisture index (AHMI) or terrain wetness index (TWI), along with site aspect and number days where condensation occurred (Table 3.3). These variables were independent from the other covariates in our SEMs (Figs 3.6+3.7) as AHMI and TWI are driven by topography and can be described as a function of slope and aspect or altitude (Beven and Kirkby 1979, Paudel et al. 2016). The AHMI combines mean annual temperature and precipitation into an index expressing atmospheric aridity, while the TWI accounts for fine-scale effects of landform on soil moisture. Hollow number increased with AHMI values and aspects describing cooler and wetter sites, where more condensation took place. This may describe the positive effects these cooler and wetter conditions have on enhancing tree growth (Ashton 1976). TWI values associated with cooler and wetter conditions in gullies and riparian areas or lower levels of foliar nitrogen also positively affected hollow occurrence. Tree growth is largely influenced by site productivity, hydrology, and climate. AHMI and TWI are effectively proxies for these types of variables, where cooler and wetter conditions estimate higher site productivity. Foliar nutrient levels can reflect forest productivity as well, with highly productive sites having higher levels of foliar nitrogen and a higher amount of available and preferred young foliage (Moore et al. 2004b). More productive sites will have faster-growing and larger trees, which should form hollows at a younger age (Wormington and Lamb 1999). This should also reduce the susceptibility of individual trees to mortality in fires, which may promote the accumulation of more large trees, even in fire-prone areas (Chia et al. 2015, Trouvé et al. 2021). Low levels of foliar nitrogen are associated with mature trees in less productive sites in drier parts of the landscape (e.g., at low elevation sites, Attiwill and

Adams 1996). Here we also observed on average more hollows and hollow-bearing trees per hectare because the drier and lower productivity conditions at those sites seem to accelerate the development and support the accumulation of hollows in trees (Bennett et al. 1991, Bennett et al. 1994). These nitrogen and tree maturity relationships are also illustrated by the strong negative relationship between nitrogen and tree volume in the hollow occurrence SEM (Fig. 3.6). In addition, we found that the high elevation forests had more small diameter trees, which are less likely to have hollows, in the lower strata of the forest.

Nitrogen models

Constituents of soil chemistry such as soil nitrogen or potassium were most important in determining leaf N, digN and DDM. The final model of foliar nitrogen combined variables from all groups, describing the most important factors from soil properties, climate and forest structure in determining foliar nitrogen (Fig. 3.7). Our models also highlighted that nutrients such as soil K have the most significant effect on foliar nitrogen (Fig. 3.5). Our analyses also revealed relationships between climate, topography and soils, all of which influenced leaf N directly or indirectly, underlining the importance of site productivity and soil fertility in increasing foliar nitrogen in this landscape. Plant-available soil nutrients are associated with site productivity and foster the development of tall mature forests, which generally have higher foliar nitrogen and can therefore support arboreal species abundance (Turner and Kelly 1981, Braithwaite et al. 1984, Adams 1996). Our site-level group, final combined model and SEM found that site productivity is driven by climate and topography (Adams 1996, Attiwill and Adams 1996). Variables associated with cooler and wetter climates (AHMI, TWI, days with condensation), exposure to sunlight (aspect), and site productivity (high NDVI values, Tucker et al. 1981, and soils associated with higher levels of plant nutrients) were positively associated with foliar nitrogen (Appendix 2 Table S3). These conditions are predominantly found at higher elevation and favour conditions for *Eucalyptus* species associated with high foliar nitrogen (Kavanagh and Lambert 1990). We also found that tree age class (indicative of increasing tree age) had a negative influence on foliar nitrogen (Appendix 2 Table S3), as seen in both SEMs. As leaves mature, their fibre content increases, reducing digestibility (Moore et al. 2004b) and making them a less favourable foraging resource for folivores. Younger trees and foliage often have higher levels of nitrogen (Moore et al. 2004b). As such, maturing and ageing trees may increase habitat suitability through the formation of hollows but reduce habitat quality by decreasing the forage quality. Our SEM analyses also revealed that the number of fires and low NDVI values (a proxy for past disturbances such as timber harvesting that reduce crown cover, Yengoh et al. 2015) could estimate stand age (Figs 3.6+3.7). Tree and stand age are mainly determined by disturbances to the forest ecosystem (Attiwill 1994).

Our findings emphasize the important role disturbances can play in the loss of hollow-bearing trees (van der Ree and Loyn 2002) and recruitment of new growth, influencing nesting opportunities and providing young leaves that are more digestible and higher in foliar N in forest ecosystems (Chia et al., 2016). This highlights the need for a heterogenous forest structure to provide both favoured foraging and sufficient nesting opportunities for arboreal folivores.

Conclusion

We assessed mature, mixed-species *Eucalyptus* forests in East Gippsland, Victoria, to better understand the factors controlling the two key stand-scale habitat features of the greater glider - hollow-bearing tree occurrence and forage quality. Detection of greater gliders was highest in high elevation areas with cooler and wetter climates and high foliar nitrogen, whereas hollows were available across all elevations and forest types. We demonstrate that forest inventory data describing stand structure (e.g., tree diameter, height and age) combined with topographic, climatic, and site productivity data (e.g., AHMI, TWI and soil properties) can be used to estimate these habitat features at the stand level. This provides a useful tool for making forest management and conservation decisions for greater gliders and associated arboreal folivores in the region. As hollows were abundant throughout sites and not limiting site-level occupancy of the greater glider, foliar nitrogen appears to be the most important factor limiting stand-level habitat suitability within these landscapes. The successful conservation of greater gliders in the region now requires comprehensive methods to map high-quality habitat, which is primarily defined by the presence of trees with nitrogen-rich foliage. Remote sensing spectroscopy to foliar nitrogen in the canopy of *Eucalyptus* forests is a promising avenue for expanding our approach for identifying high-quality habitat from the plot level to the stand level and potentially whole landscapes.

4. Mapping canopy nitrogen-scapes to assess foraging habitat for a vulnerable arboreal folivore in mixed-species *Eucalyptus* forests

Introduction

The ability to determine and monitor habitat suitability for vulnerable wildlife populations is important for efficient conservation planning (Turner et al. 2003, Turner and Gardner 2015). Individual species may have multiple habitat requirements which typically differ across spatial scales (Shifley et al. 2006, Nitschke et al. 2020). As such, species-specific adaptations to a certain climate regime (e.g. fur length) may be determined at a relatively broad scale with low-resolution data (Turner and Gardner 2015), while certain habitat requirements (e.g., density of tree hollows for nesting) may require high-resolution data at much finer scales (Turner et al. 2003). This is often the case for arboreal fauna that rely on the occurrence of nesting and feeding resources, which may be influenced by many other environmental factors, including site productivity, disturbance history, forest structure, and tree morphology and physiology (Foley et al. 1999, Gibbons and Lindenmayer 2002, Dearing et al. 2005, Youngentob et al. 2011, Lindenmayer et al. 2017).

Herbivore foraging decisions are closely related to plant nutritional quality and their distributions and home-range sizes are often determined by the quality of forage, which is driven by foliar chemistry (Foley et al. 1999, Wallis et al. 2012, Au et al. 2019b, Martin et al. 2020). For arboreal folivores with specialized diets, such as the koala (*Phascolarctos cinereus*), the concentration and digestibility of protein and amino acids are primary determinants of nutritional adequacy (Cork and Catling 1996, Moore et al. 2004b, Moore et al. 2010). Protein digestibility can be strongly constrained by the actions of tannins, which form insoluble complexes with proteins (Hagerman and Butler 1978). Protein accounts for most of the nitrogen (N) found in plant tissue, and concentrations of N, and hence protein, can be limiting for herbivores due to its low concentration and poor digestibility in plant tissue (Kavanagh and Lambert 1990, Degabriel et al. 2008, Wallis et al. 2012).

The southern greater glider *(Petauroides volans, McGregor et al. 2020)* is both a threatened species and a folivore whose diet is limited to *Eucalyptus* leaves. Listed as Vulnerable by the IUCN (Burbidge and Woinarski 2016), it is threatened by anthropogenic disturbances such as climate change and timber harvesting, causing habitat contraction, fragmentation or loss (Lindenmayer et al. 2011, Youngentob et al. 2013, McLean et al. 2018, Wagner et al. 2020). The greater glider's protein and most of its water intake is obtained exclusively from the foliage of *Eucalyptus* trees (Foley et al. 1990). Such specialisation is the rarest form of foraging among mammalian herbivores (Shipley et al. 2009). Home range sizes are 1-4 ha for greater gliders inhabiting mature forests but can increase depending on resource availability (Kavanagh and Wheeler 2004, Pope et al. 2004, Smith et al. 2007). Different factors affect habitat selection and occupancy by greater gliders differ across scales: At a broader extent, a narrow

thermal tolerance confines its distribution to the cooler and wetter areas of the landscape (McIlwee 2001, Kearney et al. 2010, Wagner et al. 2020). At the spatial scale a greater glider's home range, its specialised diet and the need for mature trees with hollows for nesting, together drive habitat selection (Kavanagh and Lambert 1990, Lindenmayer et al. 1990a, Jensen et al. 2015). As such, southern greater gliders are typically found in higher abundance at higher elevations and in mature forests that are composed of favoured *Eucalyptus* species (Henry 1984, van der Ree et al. 2004a, Youngentob et al. 2011).

In Australia, forests dominated by tree species with average foliar N measures <1% of leaf dry mass (% N DM) are significantly less favourable as habitat for arboreal folivores (Cork 1992). Greater gliders prefer tree species with foliar N levels >1% N DM (Kavanagh and Lambert 1990, Youngentob et al. 2011). However, foraging exclusively on *Eucalyptus* foliage is constrained by high levels of plant secondary metabolites (PSMs) that may cause toxicosis or reduce foliage digestibility. This plays an important role in the regulation of feeding and in forage selection by arboreal folivores (Cork and Foley 1991, Moore et al. 2004b, Moore and Foley 2005, Youngentob et al. 2011). PSMs such as tannins bind to proteins, reducing N digestibility (Marsh et al. 2003), while formylated phloroglucinol compounds (FPCs), are powerful antifeedant defences against herbivory, that cause herbivores to reject or reduce their intake of defended tree foliage (Lawler et al. 1998b, Moore and Foley 2005). The amount of N in leaves that can be digested (digestible nitrogen, digN) can be a more meaningful measure of forage quality for folivore browsers, especially because N and digN are not always correlated (Degabriel et al. 2008, DeGabriel et al. 2014). Nevertheless, total N may provide a more general measure of site productivity and nutritional suitability for the herbivore community in forests (Cork and Catling 1996, Wallis et al. 2012). Both measures are important to assess feeding habitat: *Eucalyptus* leaves can be high in N and tannins, making the high levels of N unavailable or can be high in digN but also FPCs and therefore more resistant to herbivory (Lawler et al. 1998a, Marsh et al. 2003, Moore et al. 2004b, Wallis et al. 2012).

Determining foliar nutritional quality of potential habitat trees at the relevant scale presents a challenge. Techniques that require measuring individual leaves such as chemical analysis and digestions are impractical due to the enormous number of trees that would need to be sampled and the cost and time involved in processing the resultant leaf samples in the laboratory (Youngentob et al. 2012). However, foliar spectroscopy, which uses the light absorption features of leaves can quantify leaf chemistry at the scale of individual leaves, tree crowns, forest stands, or whole landscapes, depending on the equipment (Ebbers et al. 2002, Kerr and Ostrovsky 2003, Kokaly et al. 2009). Because the spectral signature of foliage is correlated with foliar chemical properties (Curran 1989), foliar spectroscopy has proven to be effective

for measurements of leaf chemistry that avoids the challenges imposed by scale. Variations in reflectance can be determined using multi- or hyperspectral sensors that are either laboratory based, hand-held, airborne or carried by satellites (Kokaly et al. 2009). Like chemical analyses, laboratory-based or hand-held sensors are impractical at the scale required for habitat assessments. Most satellite-based sensors collect data at coarser spatial grains than individual trees or animal home ranges and therefore lack the high resolution required to detect variability within leaf or canopy reflectance (Young et al. 2017). For example, current Landsat captures imagery at 30 x 30 m and Sentinel at 20 x 20 m spatial resolution. Consequently they cannot provide information on spectral variability at the scale of individual trees, at which arboreal folivore feeding decisions are made (Futuyma and Moreno 1988, Attiwill and Adams 1996, Hume 1999, Baldeck et al. 2015, Asner et al. 2017). High-resolution alternatives from air- or spaceborne hyper- and multispectral imagery can be costly, but have been successfully applied to determine N and digN from spectral reflectance, and therefore mapping potential of feeding habitat for southeastern Australian folivores (Youngentob et al. 2012), as well as koalas in western Queensland (Wu et al. 2019) by determining N and digN from spectral reflectance. Another promising tool for acquiring very high-resolution imagery at a fine scale are unoccupied aerial vehicles (UAVs), or drones. UAVs are a low-cost alternative to aerial or satellite imagery. They have been applied in the agricultural sector to estimate crop nutrients and the forestry sector to measure structural metrics of trees (Felderhof and Gillieson 2014, Adão et al. 2017, Mohan et al. 2017, Nevalainen et al. 2017). UAVs, fitted with sensors, are simple to operate, cost-effective, and highly mobile, making them useful for mapping areas at scales of tens to hundreds of hectares at sub-metric (<1m) resolutions. These platforms can carry multi- or hyperspectral cameras, LiDAR or thermal imagers, which increases their utility for ecological research (Anderson and Gaston 2013). For example, UAVs have been used to detect koalas (Beranek et al. 2020) and map herbivore feeding habitat (Olsoy et al. 2020) using thermal and multispectral imagery, respectively. While hyperspectral sensors fit for UAVs can be costly and may require larger and heavier platforms, newer-generation multispectral sensors are a fraction of the cost and can be readily integrated into small commercial UAVs that can be operated without specialist knowledge or certification (see CASA 2019). These sensors contain NIR and edge bands to capture reflectance >750 nm wavelength that are needed to distinguish absorption features related to foliar N (Curran 1989). These bands, along with the three visible-light bands (red, green, blue) are also useful for developing a range of vegetation indices associated with plant productivity and nutrition (Xue and Su 2017). High correlations have been reported between N levels of plants, plant productivity, and indices derived from spectral reflectance (Coops et al. 2003, Huang et al. 2004, Munoz-Huerta et al. 2013, Wang and Wei 2016). These can provide additional metrics alongside direct reflectance

for assessing environmental energy availability as a key determinant in wildlife population dynamics and habitat selection (Pettorelli et al. 2011, Munoz-Huerta et al. 2013). Plant productivity determined remotely by spectral indices has been linked to greater glider abundance and habitat suitability as well. Youngentob et al. (2015) found that animal detection and abundance increased with higher readings of the normalized difference vegetation index (NDVI), putting additional emphasis on the utility of vegetation indices and remote-sensing spectroscopy to identify high-quality feeding habitat for *Eucalyptus* folivores.

With a continuing population decline and evidence of habitat contraction into the cooler and wetter areas of their distribution due to recent climate change (Kearney et al. 2010, Smith and Smith 2020, Wagner et al. 2020), conservation planning for the greater glider is calling for a better understanding of the factors that determine habitat suitability (DELWP 2019). Research has focussed on the impact of fires and timber harvesting on changes in greater glider occurrence (Lindenmayer et al. 2013, Taylor and Lindenmayer 2019); however, declines are also occurring in areas not impacted by these disturbances (Lindenmayer et al. 2011). Understanding the impacts of climate extremes and foliar nutritional value on habitat suitability is key to developing comprehensive conservation strategies for greater gliders and other arboreal folivores. Incorporating methods that can detect potential feeding habitat at finer scales such as a glider's home-range would enhance current management and conservation planning at an operational scale. The ability to map feeding habitat and identify highly nutritious trees will be beneficial for the management and conservation of arboreal folivores that have strict requirements for feeding and nesting resources (Kavanagh and Lambert 1990, Lindenmayer et al. 2004, Eyre 2006). In this study we tested whether high-resolution multispectral imagery, collected by a lightweight and low-cost commercial UAV, can be used to model and predict N and digN at the tree canopy level and identify feeding habitat for southern greater gliders at a home range scale (4 ha). We explore the potential for mapping feeding habitat and test for relationships between spatial feeding metrics such as potential feeding area and detectability.

Methods

Study area

The East Gippsland region in eastern Victoria, Australia, has a high diversity of *Eucalyptus* species and contains considerable areas of greater glider habitat. East Gippsland has ~1.2 million ha of mixed species eucalypt forests (Dept. of Agriculture and Water Resources 2018), ranging from open lowland forests dominated by *Eucalyptus sieberi, E. tricarpa,* and *E.*

globoidea to dense, high-elevation forests (~1000–1300 m a.s.l.) with *E. delegatensis, E. viminalis, E. cypellocarpa, E. croajingolensis* and other high-elevation species (Opie et al. 1990, Sebire and Fagg 2009). *Eucalyptus obliqua* is the most abundant tree species and occurs across the entire elevation gradient (Dept. of Conservation and Natural Resources 1995). Annual rainfall and temperature for the region are 648–1178 mm (1980-2020, Stewart et al. 2020a) and 6–15.8°C (1980-2020, Stewart and Nitschke 2017a), respectively. Greater gliders have been recorded across the elevational range and in a variety of forest types, making this area especially suitable to study inter- and intra-specific differences in leaf nutritional quality and their influences on greater glider habitat suitability. Greater gliders are most common above 700 m in closed cool and wet forests where their thermoregulatory requirements are consistently met (Henry 1984, Bennett et al. 1991, van der Ree et al. 2004a, Wagner et al. 2020).

Survey design

We selected study sites based on the region's elevational and topographic range (i.e., aspect and slope). Survey plots were located within three elevation bands (lowlands: 0–420 m, mid-hills: 420–840 m and high elevation: 840–1260 m a.s.l). In each of these three elevation bands, we established ten plots (total N = 30 plots, Appendix 3 Fig. S1, Tables 4.1 + Appendix 3 Table S1). Within each elevation band we captured variability in topography by establishing four plots in flat or gully floor locations, four in mid-slope positions (north- or south-facing), and two plots on ridges (Appendix 3 Fig. S2). We only selected study sites that had not been logged or burnt 30–40 years prior to sampling. We collected multispectral imagery using an unoccupied aerial vehicle (UAV) and leaf samples from individual trees in two years, early summer 2018 and 2019, to ensure that trees had full crowns. This reduced negative effects on model classification from mixed pixels of canopy and ground vegetation reflectance in the imagery (Hsieh et al. 2001). The plot network was designed to cover the range of eucalypts known to act as forage resources for the greater glider, as well as several species not known to be utilised (Kavanagh and Lambert 1990, Comport et al. 1996, Cunningham et al. 2004).

Forest structure

The position of each plot centre was recorded to an accuracy of ~5 m with a handheld GPS (Garmin, Olathe, USA) using waypoint averaging for a minimum of 90 minutes per plot. In each plot, we recorded elevation, slope, aspect, crown cover and basal area of dominant tree species. Basal area was measured using a Kramer's dendrometer and a basal area factor (BAF) of four. This variable radius approach ensured the sampling would capture the large, mature, and dominant trees that form the canopy, and which are the preferred nesting and feeding trees for greater gliders in occupied sites (Kavanagh and Lambert 1990). The largest plot size

resulting from this method was 4 ha, which is congruent with the home range size of greater gliders in mature forests (Lindenmayer et al. 2004, Pope et al. 2004). For trees within BAF = 4, we recorded the species, diameter at breast height (1.3m, DBH), height, crown widths (both measured using a Vertex IV, Haglof, Långsele, Sweden), estimated tree health, and counted number of hollows using binoculars. All other vegetation (i.e., ground-level vegetation) was recorded for presence only in a 100 m^2 subplot around the plot centre.

Sample collection

Leaf samples were collected from five dominant trees per plot. One tree was sampled in each quadrant of the plot (i.e., northeast, southeast, southwest, northwest) with an additional dominant tree selected randomly (Appendix 3 Fig. S3). These five sample trees represented the mixture of *Eucalyptus* species in the plot. Leaf samples were collected using a throw-line launcher and rope, creating a sling around a branch to break it (see Youngentob et al. 2016 for details). A total of 150 trees were sampled, with ~100 g fresh leaf sample material collected from each tree. Individual samples were put in an airtight zip lock bag and frozen after collection. The location of each sampled tree was recorded using GPS waypoint-averaging, as well as bearing and distance from the plot centre to later identify sample-trees in the aerial UAV imagery. Leaf samples were measured for average Normalized Difference Vegetation Index (NDVI) using a handheld GreenSeeker crop sensor (Trimble, Sunnyvale, USA) on a black tarp after collection. These index values were used as a mask before pixel extraction from multispectral imagery to distinguish leaves from other parts of the crowns (e.g., branches).

Capturing canopy reflectance

We collected aerial multispectral imagery for an area of ~20 ha around each plot centre using an autopiloted Phantom 4 Pro V2 multirotor UAV (DJI, Shenzhen, China), modified to carry a Rededge-M multispectral sensor (MicaSense, Seattle, USA, Appendix 3 Fig. S4). The sensor captures data on five separate spectral bands (red, green, blue, red-edge and near-infrared - NIR) at centre wavelengths 475, 560, 668, 717 and 840 nm, respectively. This range is associated with leaf absorption features for chlorophyll a and b, tannin, lignin and protein (Curran 1989, Peñuelas et al. 1994, Curran et al. 2001, Huang et al. 2004, Ferwerda et al. 2006). Flight paths were pre-programmed using Ground Station Pro (DJI, Shenzhen, China) and planned in accordance with Australian Civil Aviation Safety Authority regulations at a maximum flight altitude of 120 m above ground and within visible line of sight (CASA 2019). Due to the homogenous canopy structure in many plots, an image front- and side-overlap ratio of 90% was chosen and flights were executed between two hours before and after solar equilibrium of the survey day to avoid shadows and ensure consistent ambient light conditions

in all images (Dandois et al. 2015). To accurately map ground elevation, the UAV was launched from canopy openings or forest roads, which ensured sufficient reference ground imagery was captured for later processing. The aerial imagery had a ground resolution of ~2.5 cm.

Wildlife surveys

Spotlighting surveys on 1-km transects along a forest track adjacent to, or through the plot centre, were undertaken at all plots. An average pace of 10 minutes per 100 m was used by two observers walking 10 minutes apart to to maximize the probability of detection (Kissling and Garton 2006, Nelson et al. 2018). The locations of all arboreal fauna detected were estimated from distance and bearing to the observer position. In addition, we collected data on tree species on which an animal was observed, height in tree, behaviour (e.g., idle or feeding), colour morph and time of observation.

Sample and data processing

In vitro chemical analyses

Collected fresh leaves were frozen after collection and later dried using a VirTis BenchTop Pro freeze dryer (SP Industries, Stone Ridge, USA) for 24-72 hours. Dried samples were ground to pass a 1-mm screen using a Cyclotec 1093 sample mill (Foss, Hilleroed, Denmark) and kept frozen at -20°C until further analysis. Total nitrogen (N) was determined using combustion based on the Dumas procedure in a TruMac CN analyser (Leco, Castle Hill, Australia). Digestible nitrogen (digN) was quantified through *in vitro* digestion using cellulose and pepsin according to Degabriel et al. (2008). Briefly, duplicate 0.5 g samples were weighed into F57 fibre filter bags (Ankom, Macedon, USA) and sealed, before sequential digestion in buffer, pepsin, and cellulase over 5 days. Residues were weighed and residual N content determined as for N. Both N and digN were reported as % dry matter (% DM).

Multispectral imagery processing

UAV multispectral imagery was processed in Metashape (Agisoft, St. Petersburg, Russia) using Structure from Motion (SfM), a technique of photogrammetric range imaging to estimate 3D structure from 2D overlapping image sequences (Ullman 1979). First, all images were calibrated from raw pixel values to absolute spectral radiances for the day of image acquisition using images of a reflectance panel exposed to direct sunlight, recorded before and after each flight. The processing in Metashape produced 3D point clouds and georeferenced, multispectral stitched images of all photos (orthomosaics) for each plot and its surroundings (Fig. 4.1A). Orthomosaics were exported as multi-layer raster stacks with one band for each centre

wavelength, while point clouds were used to compute a canopy height model (CHM) of each plot. All spatial processing was carried out in R (R Core Development Team 2020) using the packages *raster, sf* and *lidR* and their dependencies (Pebesma 2018, Hijmans 2019, Roussel and Auty 2019).

Canopy height models and tree detection

To create CHMs for each plot, 3D point clouds were normalized to a 0 m ground elevation. During processing, a digital terrain model (DTM) and a digital surface model (DSM) were calculated, expressing both the ground elevation and point elevation above ground. The CHM is the difference between DSM and DTM ($CHM = DSM - DTM$) and extracted as a 2D raster, expressing each raster cells height above ground in meters (Fig. 4.1B). These were derived using *lidR*'s grid_canopy function with a resolution of 0.5 m and a sub-circle algorithm using a 0.5 m disk on each point return to close empty cells (pits) in the final output (Khosravipour et al. 2014). A tree detection algorithm was applied to each CHM, informed with a fitted function of tree height and mean crown width, derived from field measurements (see Popescu and Wynne 2004), to approximate the position of each dominant tree in the area covered by UAV multispectral imagery around the plot centre. Approximate crown outlines for each detected tree were then extracted using a tree segmentation algorithm based on marker-controlled watershed object detection, using the approximate tree positions extracted earlier as markers (Gaetano et al. 2014). These approximate crown outlines were used to aid in delineating sample trees from the orthomosaics for crown pixel reflectance extraction (Fig. 4.1C). Using the GPS positions of plot centres and sample trees, we cross-referenced both CHM and orthomosaics to confirm ground accuracy of <1 m.

Index calculation

To test the performance of UAV multispectral imagery in predicting measures of foliar nitrogen, we used direct reflectance (radiance band values), spectral indices, and simple ratios derived from the five initial bands. Indices matching available bands and wavelengths were chosen from studies testing different spectral bands and indices as predictors of plant chemistry (see Chen 1996, Pastor-Guzman et al. 2015, Xue and Su 2017, Wu et al. 2019). We derived a total of 14 indices using band calculation on raster stacks of each plot's orthomosaic (Appendix 3 Table S2). Together with the five initial spectral bands, a total of 19 variables were considered.

Canopy nitrogen data analysis

Extracting reflectance and index values for sample trees

The accuracy of tree positions and crowns from CHM delineation was assessed visually using true- and false-colour composites of plot orthomosaics. In cases where sample trees were not correctly delineated (~10% of all trees), the position and crown shape were corrected manually using image interpretation and distance and bearing from the plot centre, aided by the structural measurements collected in the field (e.g. height or crown width). From confirmed crown outlines, a vector polygon layer was created, covering the crown of each sample tree as extraction masks. Using *raster*'s extract function, we extracted all crown pixel values from the 19 band raster stacks of canopy reflectance and indices using the tree crown polygons (n = 150). To create a canopy dataset, we removed pixels not associated with foliage (e.g., branches or bare ground) by applying a NDVI mask using the minimum NDVI field value measured with the crop sensor (Appendix 3 Table S1). We then subsampled 1000 random pixels (pixel size = 2.5 cm^2) from each tree and calculated the mean value of each variable from the extracted pixels. This resulted in a dataset containing each tree's mean crown reflectance (n =150) of five multispectral bands and the mean value for each of the 14 indices.

Modelling total and digestible nitrogen

We used Random Forest (RF) to model canopy N and digN from spectral reflectance and indices. We chose this machine-learning method as it has been used for predicting leaf N from multispectral imagery in different vegetation types, accounts for interactions and non-linearities, and produces more reproducible outcomes compared to other machine-learning approaches (see Breiman 2001, Abdel-Rahman et al. 2013, Li et al. 2014, Ramoelo et al. 2015). RF modelling and model evaluation were carried out in R using the packages *randomForest* and *caret* (Liaw and Wiener 2002, Wing et al. 2019). We reduced the number of initial predictor variables to eight by removing highly correlated pairs (Pearson's correlation coefficient $r \geq |0.8|$). The dataset was separated into training and validation data using a 70:30 split based on the distribution of N and digN values. To find the best combination of variables, we tested multiple models on combinations of non-correlated spectral bands and indices and compared mean squared residuals and percent variance explained. The optimal number of decision trees was chosen by minimum error rate. To increase model performance, only variables that contributed ≥5% increase in mean square error (IncMSE) if removed, were considered. Models were built on training data only and performance was tested using cross- and independent-validation. We evaluated the predictive performance of the models by

calculating the R^2, root mean squared error (RMSE), mean absolute error (MAE) and correlation (p) between observed and predicted N and digN values. As model predictive performance varied depending on the random data split, we created 100 independent models based on 100 random splits and evaluated the standard deviation (SD), standard error (SE), and coefficient of variation (CV), as well as mean and median of R^2, RMSE and MAE amongst all models. The best models were chosen based on highest R^2 and lowest RMSE to report maximum predictive performance of canopy N from canopy leaf reflectance and vegetation indices. An outlier test assured that respective performances were not deviating markedly from other observations.

Home-range scale data analysis

We built models to predict spatial patterns of nutritional suitability and feeding habitat at the home range scale (4 ha) using a supervised classification RF model based on a pre-defined N threshold. For this, we used the same predictor variables we identified to be important in predicting canopy N.

Data extraction and compilation

For spatial predictions of nutritional suitability, we used the sampled 1000 pixels per tree (N = 150.000 pixels, pixel size = 2.5 cm^2) in a supervised classification model. Pixel values were classified into suitable (≥1% N DM, i.e., presence if feeding habitat) and unsuitable for folivore feeding (<1% DM, i.e., absence of feeding habitat), according to Cork (1992), based on the respective tree's estimated canopy N. We subsampled pixels based on the ratio of suitable to unsuitable points in the dataset (4:1, 25,000 pixels each) to ensure a balanced sample and reduce the chance of biases that may result in model overfitting (McPherson et al. 2004, Liu et al. 2005). The final plot-level dataset contained 50,000 value combinations of all bands and indices as predictor input for a binomial response variable describing nutritional suitability based on the nitrogen threshold (0 = absence of feeding habitat, 1 = presence of feeding habitat).

Modelling potential feeding habitat

The supervised classification dataset was also split into training and validation data (70:30%) and a binomial RF built on training data only. Model performance was assessed using accuracy, area under the curve (AUC), sensitivity, specificity and the true skill statistic (TSS, see Allouche et al. 2006) of the independent validation (15,000 pixels). Cohen's kappa was used to determine the threshold distinguishing presence and absence of feeding habitat. The value represents maximum model fit and was used to accurately classify spatial predictions into two classes (Elith et al. 2006, Elith et al. 2008).

Mapping potential feeding habitat

To analyse the spatial distribution and configuration of nutritional suitability adequacy based on N, we first cropped raster stacks for each plot to an equal area to enable inter-site comparisons. A square 4-ha area around each plot centre was chosen. This aligned with the maximum recorded plot area in the field based on the variable radius sampling using a BAF = 4 prism and documented greater glider homer range sizes in mature forests (Pope et al. 2004). We used the binomial RF model to predict the probability of finding feeding habitat in each pixel of the cropped raster stacks (Fig. 4.1C). As foliage sample collections were restricted to the upper canopy in order to ensure compatibility with the multispectral UAV imagery, we excluded all pixels below the minimum sub-canopy height measured in the field (Appendix 3 Table S1). We used each plot's CHM and field canopy height measures to crop the prediction rasters to the tree canopy layer and excluded all pixels that represented understory vegetation or ground and other non-canopy features. We calculated the mean and SD of predicted nutritional suitability (likelihood of a pixel being associated with ≥1% N DM) for each plot. To assess proportion of potential feeding habitat, we classified each raster into nutritionally suitable (≥1% N DM) or unsuitable (<1% N DM) areas, using Cohen's kappa (maximum sensitivity and specificity). We assigned a separate class (non-habitat) from previously removed pixels of non-canopy area to ensure inter-site comparability (Fig. 4.1D). We calculated the area and proportion of total area of each class and derived clumpiness, a measures of connectivity and spatial aggregation using the package *landscapemetrics* (Hesselbarth et al. 2019). These metrics were used to compare plot-specific configurations of feeding habitat with structural measurements, canopy N and digN measurements and to test for relationships with greater glider detection and abundance using linear models.

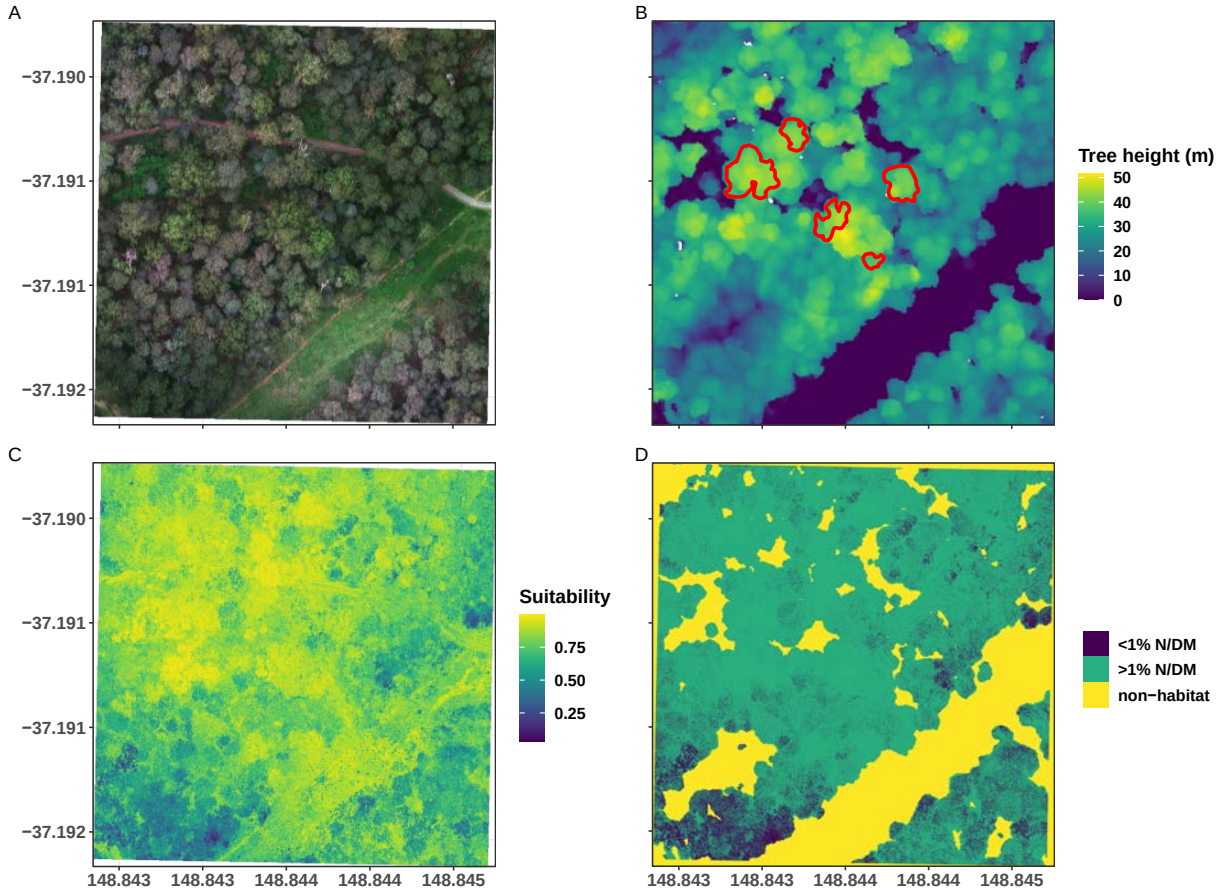

Figure 4.1. Examples of UAV imagery data products and spatial model prediction workflow. A) True-colour (RGB) orthomosaic of a plot centre (High elevation – Plot 6) and surrounding forest area (4 ha). B) Final canopy height model of the same plot with sample tree crown outlines in red. These crowns were detected using the point-cloud and CHM and corrected manually using aerial interpretation. C) Raw spatial predictions from the supervised classification RF model to the sample area of 4 ha indicating likelihood of finding >1% N DM in a pixel from 0-1, where 1 is 100% likelihood (suitability). D) Finalized spatial predictions after removing pixels not associated with the forest canopy using the CHM (B) and minimum subcanopy height measured as a mask, as well as classifying spatial predictions from % suitability to presence and absences of feeding habitat (≥1% N DM) based on Kappa (maximum true-positive and true-negative rate).

Results

Structural assessment and canopy nitrogen

Our 30 plots ranged in elevation from 32–1185 m a.s.l. and covered slopes from 1–55%, as well as aspects from 26–355°. Dominant canopy species were *Eucalyptus consideniana, E. globoidea*, and *E. sieberi* in the lowlands, *E. obliqua, E. cypellocarpa*, and *E. fastigata* in the mid-hills, and *E.* croajingolensis and E. viminalis in the high-elevation plots (Tables 4.1 + Appendix 3 Table S1). A total of 17 canopy Eucalyptus species were sampled. They varied in leaf total nitrogen (N) from 0.63–1.92% DM (Fig. 4.2). Mean plot-level nitrogen (meanN), based on averaging the five sample tree measurements in each plot, ranged from 0.87% DM in the lowlands to 1.74% DM at high elevation (Table 4.1). Due to sample loss, we could only analyse 116 samples from 15 Eucalyptus species (out of the original 150 samples from 17 species) for digestible nitrogen (digN). Digestions and/or chemical analyses created one true outlier, which was removed from further analyses. DigN ranged from 0.45–1.73 %DM (Appendix 3 Fig. S5).

Animal observations

We recorded 44 individual greater gliders while surveying nocturnal arboreal fauna across our plots. Greater gliders were found in 10% of lowland, 20% of mid-hill and 60% of high-elevation plots at varying densities. In the lowlands only two greater gliders were observed in a single plot. In contrast, we found up to 14 individuals during a single survey along a high-elevation plot (Table 4.1). Greater gliders were observed in seven *Eucalyptus* species, which were all measured to have leaf N $\geq$1% DM within our samples (Fig. 4.2).

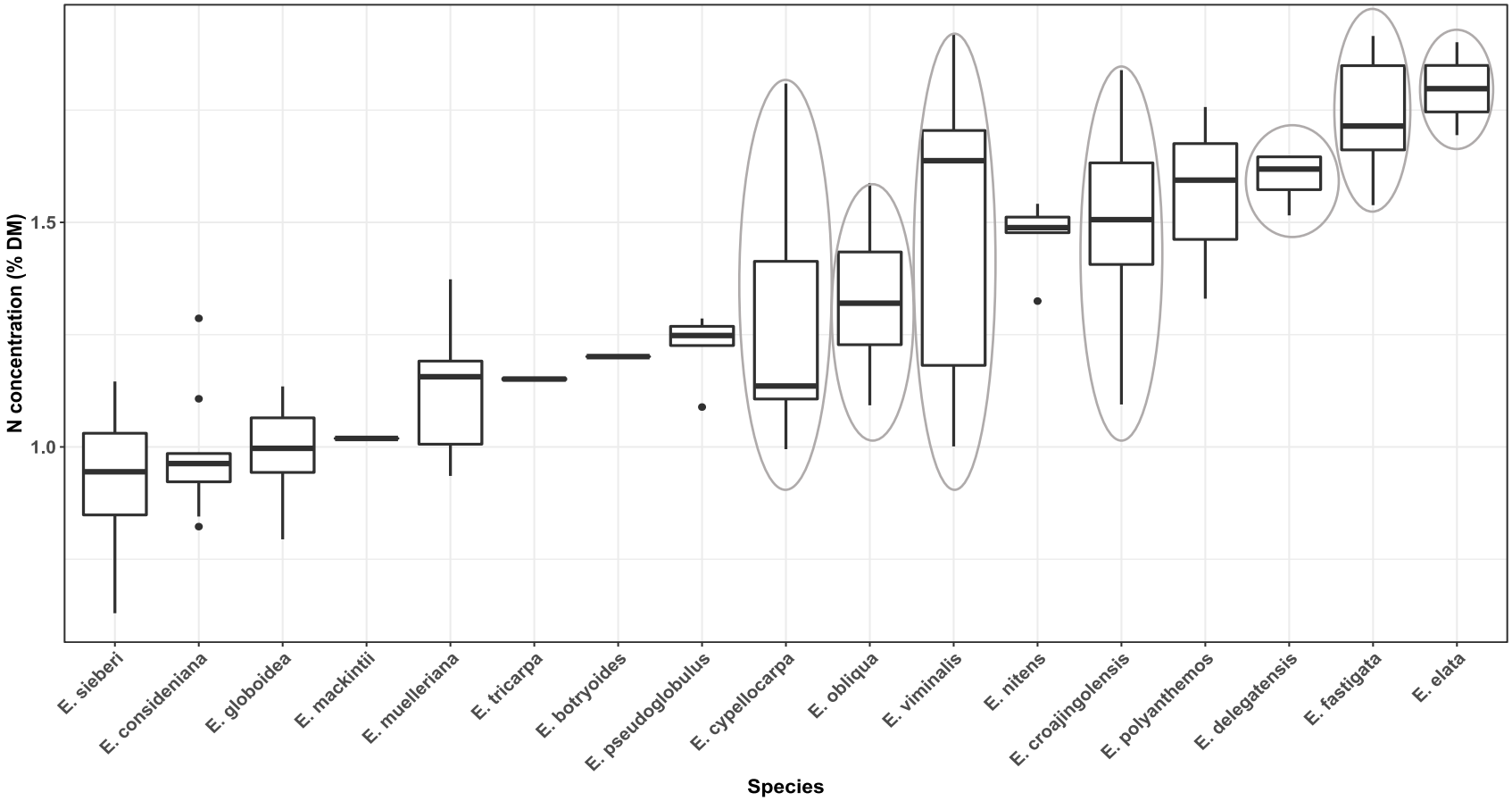

Figure 4.2. Nitrogen concentration of the 17 sampled *Eucalyptus* species. Species in which greater gliders were observed are circled.

Table 4.1. Description of each study plot

Position	Plot	Elevation (m.a.s.l)	Dominant canopy species	Measured meanN (% DM)	Measured meandigN (% DM)	No. of greater gliders observed	predicted meanN (% DM)	Mean nutritional suitability	Fraction of total plot area suitable (%)	Spatial aggregation (clumpiness metric)
Lowlands	1	120	*E. sieberi*	1.01	0.95	0	1.16	0.61	30.28	0.78
	2	181	*E. condensiana*	1.37	0.81	0	1.32	0.63	46.01	0.67
	3	397	*E. sieberi*	1.00	-	0	1.06	0.50	33.97	0.56
	4	222	*E. polyanthemos*	1.00	-	0	1.19	0.47	7.25	0.64
	5	126	*E. globoidea*	0.94	0.88	0	1.00	0.42	14.21	0.68
	6	61	*E. globoidea*	1.01	0.87	0	1.17	0.55	23.73	0.73
	7	159	*E. consideniana*	1.12	0.84	0	1.15	0.56	29.13	0.73
	8	203	*E. consideniana*	0.88	0.81	0	0.99	0.36	13.43	0.46
	9	282	*E. consideniana*	0.89	0.84	0	1.11	0.38	14.86	0.48
	10	32	*E. globoidea*	1.20	0.90	2	1.23	0.61	29.65	0.74
Mid-hills	1	439	*E. obliqua*	1.14	0.93	0	1.26	0.66	61.40	0.65
	2	661	*E. fastigata*	1.14	0.97	1	1.24	0.88	88.09	0.85
	3	777	*E. cypellocarpa*	1.39	0.92	1	1.30	0.64	25.11	0.78
	4	679	*E. sieberi*	1.29	0.91	0	1.32	0.63	59.72	0.64
	5	501	*E. muellerinia*	1.20	1.10	0	1.27	0.70	73.71	0.52
	6	448	*E. pseudoglobulus*	1.23	1.15	0	1.22	0.73	60.43	0.78
	7	692	*E. cypellocarpa*	1.49	0.98	0	1.41	0.75	70.78	0.74
	8	710	*E. sieberi*	1.16	1.16	0	1.31	0.86	87.74	0.75
	9	720	*E. fastigata*	1.71	1.13	0	1.56	0.76	79.57	0.60
	10	446	*E. obliqua*	1.44	-	0	1.39	0.82	84.22	0.80
	1	926	*E. croagingolensis*	1.60	-	2	1.44	0.67	61.61	0.56

High elevation	2	1001	*E. croajingolensis*	1.48	-	0	1.44	0.68	63.51	0.64
	3	1185	*E. delegatensis*	1.58	-	0	1.45	0.57	51.49	0.66
	4	1050	*E. nitens*	1.47	-	0	1.42	0.74	39.20	0.87
	5	907	*E. viminalis*	1.15	-	2	1.25	0.88	64.77	0.94
	6	937	*E. croagingolensis*	1.59	0.88	14	1.41	0.76	64.42	0.76
	7	1072	*E. cypellocarpa*	1.75	1.12	3	1.52	0.71	65.53	0.68
	8	920	*E. obliqua*	1.33	1.01	0	1.34	0.78	73.74	0.72
	9	1117	*E. obliqua*	1.35	0.95	3	1.24	0.50	37.64	0.58
	10	924	*E. viminalis*	1.67	1.20	5	1.54	0.64	57.33	0.60

Evaluating performance of canopy and spatial models

Out of 19 initial candidate variables, eight were selected as model predictors for both N and digN; the others were discarded due to high intercorrelations. All non-correlated bands and indices were found to improve model performance and contribute ≥5% increase in mean square error (incMSE) to the model. Five predictors were indices ($GDVI, VARI, NDI_{B-NIR}, NDI_{RE-NIR}, RI$, Table 4.2), while three were direct reflectance averages (green-, NIR-, and red-edge bands). Averaged crown $GDVI$ was the most important predictor with 19.3% incMSE. Overall, indices contributed more to model performance (~53%) than direct reflectance averages (~35%). The most important direct reflectance variable was the green band with 13.5% incMSE (Fig. 4.3).

Table 4.2. The five meaningful spectral indices in predicting total canopy nitrogen their formulae and literature reference.

Index	Full name	Formula	Reference
$\boldsymbol{GDVI}$	Generalized Difference Vegetation Index	$NIR - Green$	Wu (2014)
$\boldsymbol{NDI\ B/NIR}$	Normalized Difference Index - Blue/Near Infrared	$\frac{(Blue - NIR)}{(Blue + NIR)}$	Wu et al. (2019)
$\boldsymbol{NDI\ RE/NIR}$	Normalized Difference Index Red Edge/Near Infrared	$\frac{(Red\ Edge - NIR)}{(Red\ Edge + NIR)}$	Wu et al. (2019)
$\boldsymbol{RI}$	Redness Index	$\frac{(Red - Green)}{(Red + Green)}$	Escadafal and Huete (1991)
$\boldsymbol{VARI}$	Visual Atmospheric Resistance Index	$\frac{(Green - Red)}{(Green + Red - Blue)}$	Gitelson et al. (2002)

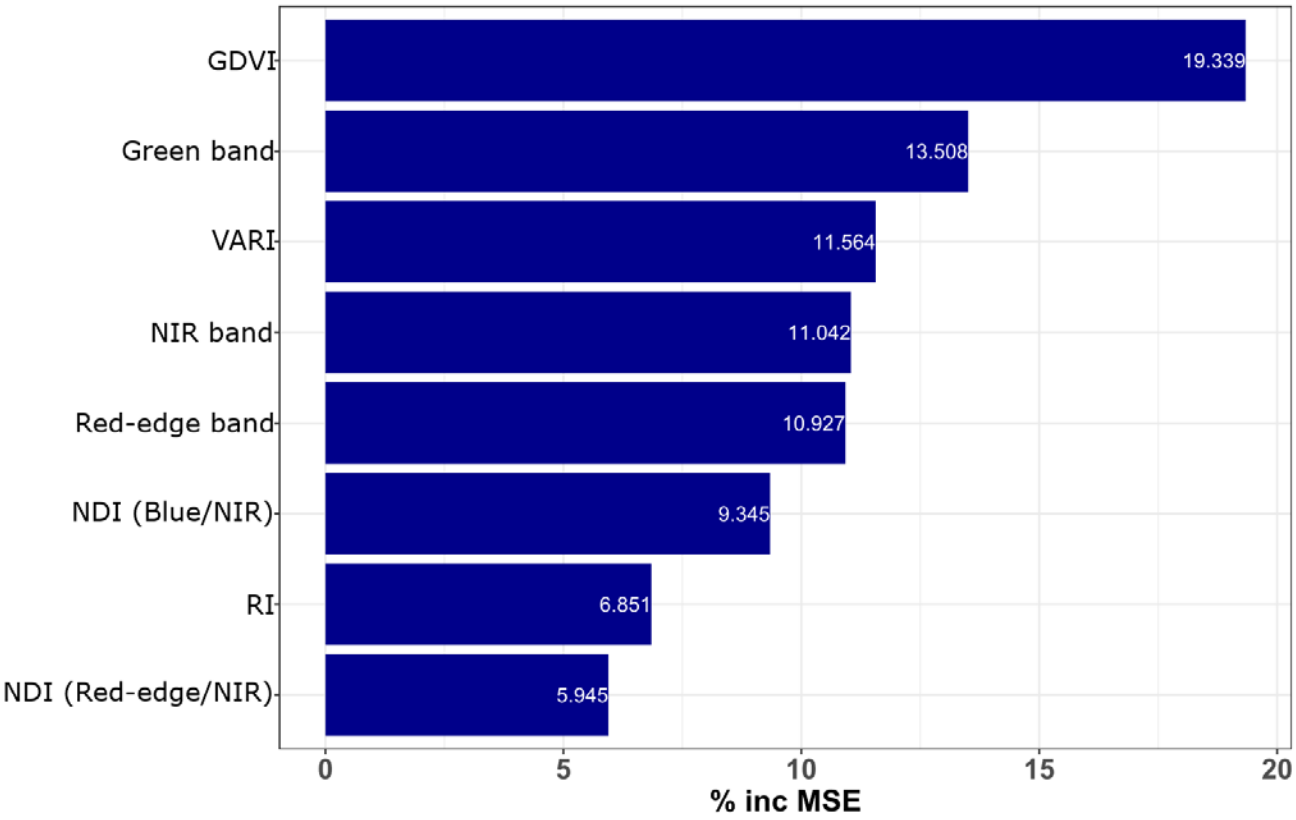

Figure 4.3. Variable importance plot of the final canopy nitrogen model. Variable importance is given as the percentage increase in model mean standard error (% inc MSE) that would occur of the respective variable was removed.

Best canopy nitrogen model predictions

Canopy-level predictive performance for both N and digN % DM across 100 independent models is reported in Appendix 3 Figure S6, Tables 4.3 and Appendix 3 Table S3. Model performance for N was good with mean cross-validation R^2 of 0.69 (±0.04). The highest R^2-model explained 79% of variability between predicted and observed N % DM in cross-validation and 49% in independent validation (Fig. 4.4). The lowest RMSE was found at 0.15 for cross-validation and 0.20 for independent validation (Appendix 3 Fig. S6).

Table 4.3. Average and median value of model evaluation metrics from 100 independent models of total nitrogen

Evaluation	Test	Mean	Median	Standard deviation	Standard error
MAE	Cross-validation	0.128	0.128	0.003	0.00029
	Independent validation	0.210	0.210	0.016	0.00163
RMSE	Cross-validation	0.169	0.169	0.006	0.00061
	Independent validation	0.256	0.255	0.018	0.00181
R^2	Cross-validation	0.687	0.688	0.038	0.00381
	Independent validation	0.203	0.194	0.088	0.00882

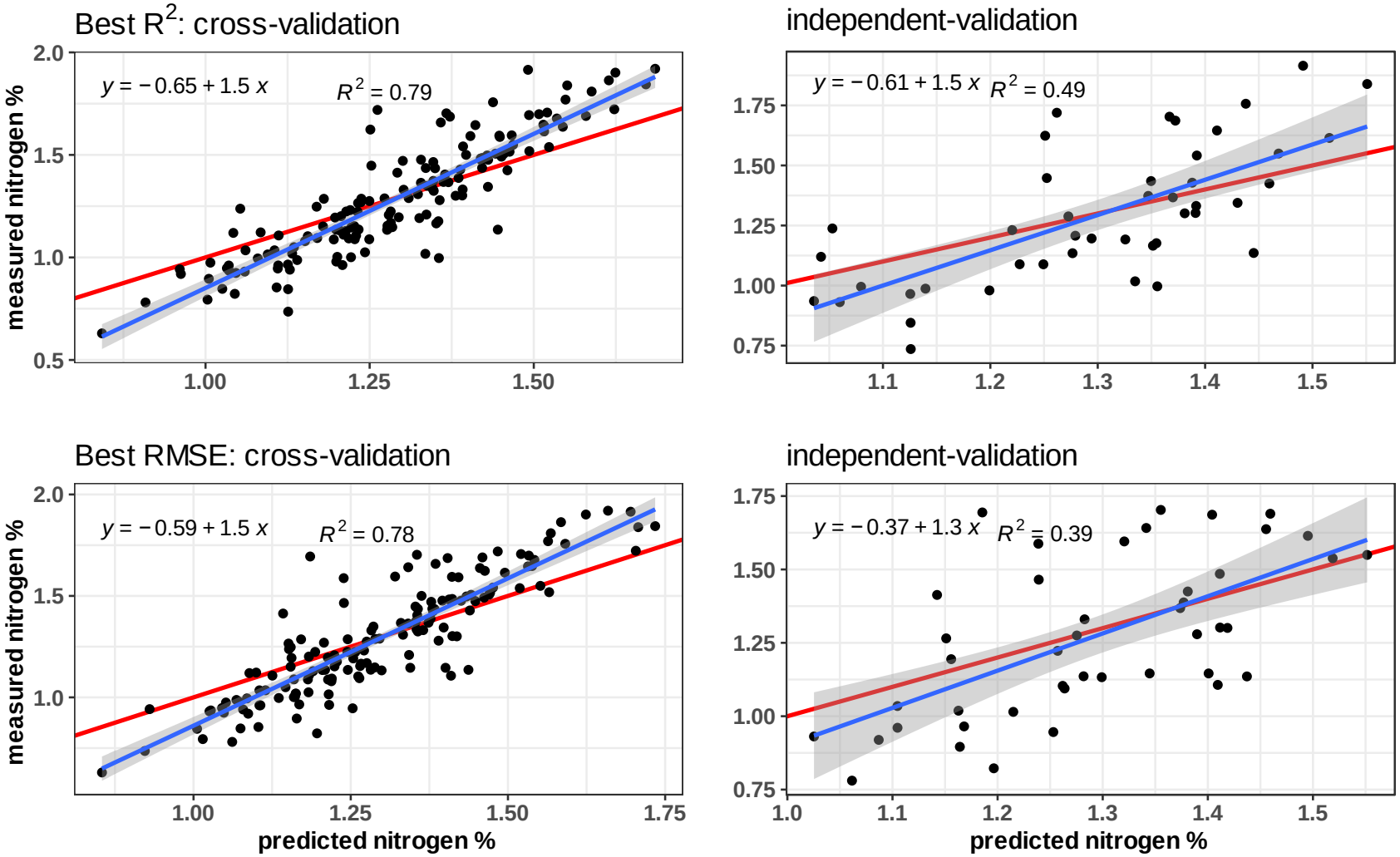

Figure 4.4. Regression of predicted and observed canopy nitrogen of the best models based on either R2 (top) or RMSE (bottom) for cross- (left) and independent validation (right). The red line illustrates a supposed 1:1 relationship (0 intercept).

For digN, cross-validation also resulted in 79% of the variability explained, but only 12% in independent validation, indicating that models for N yielded more robust relationships between canopy nitrogen levels and multispectral reflectance and indices than digN. As all uncorrelated variables available were used for predicting both N and digN, there was little scope to improve independent model performance for digN without adding additional spectra or developing new spectral indices. Therefore, total nitrogen (N) was used for developing the spatial models with supervised classification. Because the overall independent validation performance was better in the highest-R^2 model (R^2 = 0.49) at a similar RMSE (0.21), we chose this model for a regression of meanN (mean N of five sampling trees per plot) and the respective average of predictions. This model explained 90% of the variability between predicted and observed meanN %DM (Fig. 4.5).

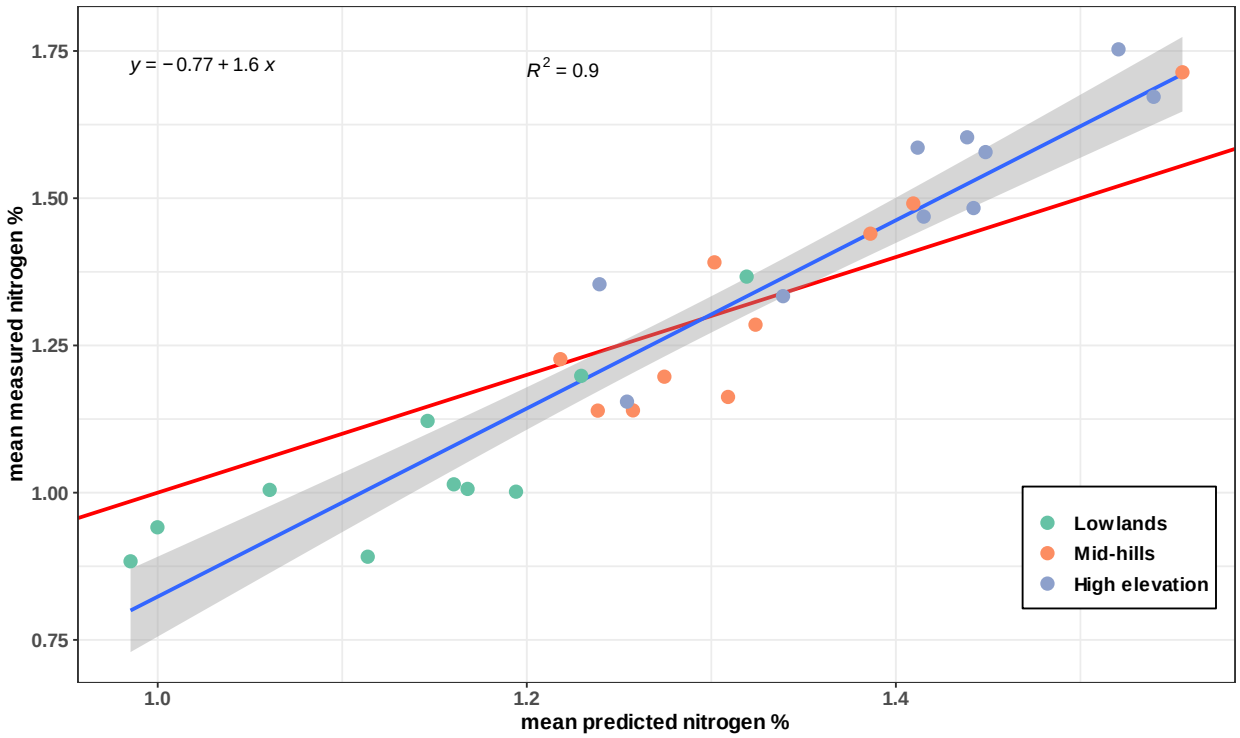

Figure 4.5. Regression of predicted and observed nitrogen, averaged on the plot level. The red line illustrates a supposed 1:1 relationship (0 intercept).

Spatial model performance

Both accuracy and area under the curve (AUC) of supervised classification models were 0.78 and 0.88, respectively, with sensitivity (true positive rate, TPR) and specificity (true negative rate, TNR) both at 0.79, resulting in a true-skill statistic (TSS) of 0.59. This performance indicated substantial agreement between observed and predicted N classes (Table 4.4). The model correctly predicted 78.6% (6133) of pixels associated with ≥1% N DM and 80.2% (6257) of pixels with <1% N DM (Appendix 3 Fig. S7). These metrics demonstrated that the spatial model was robust and could be used to map feeding habitat across all plots. Cohen's kappa (maximum TPR+TNR rate) was 0.49 and used as the threshold to classify spatial predictions into areas of <1% (not feeding habitat) and ≥1% N DM (feeding habitat).

Table 4.4. Model evaluation metrics for the supervised classification model to spatially classify feeding (≥1% N DM) and non-feeding habitat (<1% N DM).

Evaluation	Value
Accuracy	0.79
Kappa	0.59
Sensitivity (TPR)	0.79
Specificity (TNR)	0.80
True Skill Statistic (TSS)	0.59
Area under the curve (AUC)	0.88
Correlation	0.67
max TPR+TNR at	0.49
Number of pixels held-out for validation	15600
Correctly predicted absences	6257
Correctly predicted presences	6133
False presences	1543
False absences	1667

Detection thresholds and spatial distribution and aggregation of feeding habitat

An analysis of spatial predictions of N classes and feeding habitat area (Fig. 4.1C+D) at the home range scale identified mean nutritional suitability – the average likelihood (0-100%) of occurrence of ≥1% N DM in any given pixel - between 36% and 87%. The lowest suitability was observed in a lowland plot dominated by *E. consideniana* and the highest in a high-elevation plot dominated by *E. viminalis* and *E. croajingolensis*. The proportion of feeding habitat (areas classified as ≥1% N DM) as a fraction of the total 4-ha home-range scale considered here, varied from 7% to 88%, with largest available feeding habitat area in mid-hill plots, followed by high-elevation plots (Table 4.1). Across our plot network, greater gliders were not detected where meanN was <1.1% DM, mean nutritional suitability was below 50%, and the proportion of feeding habitat was below 25%. We found greater gliders in one-third of plots with meanN between 1.1-1.4 % DM and in two-thirds with meanN >1.4 % DM. Half of all plots in the highest nutritional suitability category had glider detections and plots with >25% of the area classified as feeding habitat, detections were made at one-third of all plots (Appendix 3 Fig. S8).

Large proportions of the plot area in the lowlands were classified as non-habitat (e.g., sub-canopy crowns or canopy gaps). In addition, non-feeding habitat (areas classified <1.1% N DM) was most aggregated at the lowland plots. Both feeding (areas classified ≥1.1% N DM) and non-feeding habitat were on average equally aggregated and covered equal areas in the lowlands, indicating an equal spatial distribution of similarly sized clumps of feeding- and non-feeding habitat in between large areas of non-habitat. A high aggregation and larger area of feeding habitat coupled with a lower aggregation of non-feeding habitat in the mid-hills and at high elevation indicated larger clumps of interconnected feeding habitat, interspersed with small areas of non-feeding habitat (Fig. 4.6D+E). When extrapolating structural and chemical measurements of the five leaf sample trees from the plot level to a hectare, we observed on average more suitable (canopy N ≥1.1% DM) and unsuitable trees (canopy N <1.1% DM) in the lowlands, but also lower crown area and tree basal area, indicative of more smaller trees with smaller leaf volume at lower densities. At high elevation there were almost no unsuitable trees per hectare and crown areas and tree basal areas were highest (Fig. 4.6A-C).

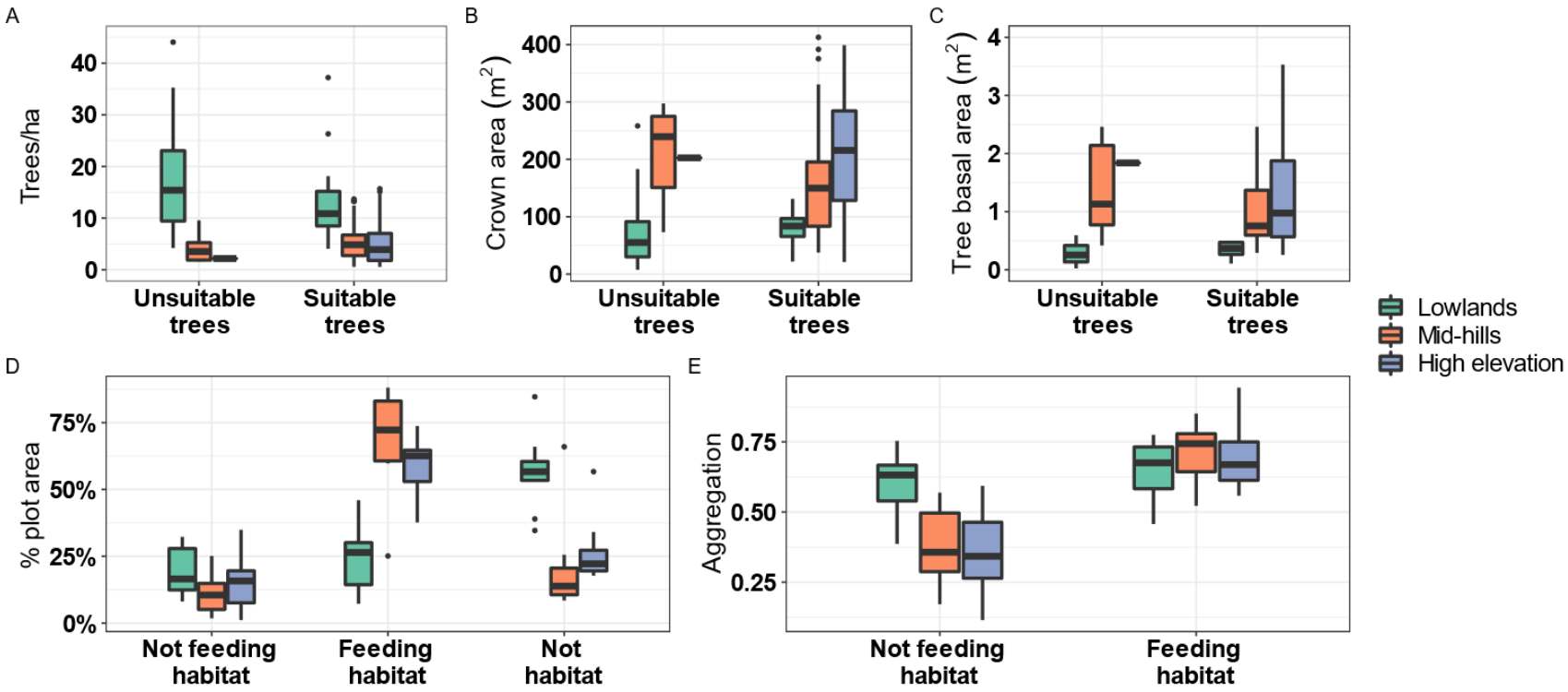

Figure 4.6. Structural (A-C) and spatial (D+E) differences between feeding and non-feeding trees (extrapolated from 5 sample trees to 1 ha) or habitat (on a home range - 4ha - scale) and elevational bands. Aggregation of non-habitat was not considered in figure 4.6E because it was mostly 100% aggregated through all three elevation bands.

When testing whether N influenced greater glider detection using binomial GLMs, we found a significant relationship between the occurrence of greater gliders and meanN % DM ($p < 0.05$, Table 4.5). Foliar Nitrogen concentration was positively associated with likelihood of greater glider detection (Appendix 3 Fig. S9), emphasizing the importance of the availability of foliar nutrition on folivore species occurrence.

Table 4.5. Model summary for a generalized linear model (GLM) describing the relationship between the detection of greater gliders and mean observed canopy nitrogen by plot.

Response	**Greater glider detection** (GLM)		
Variable	**Estimate**	**95% CI**[1]	**p**
(Intercept)	-5.6	-11, -1.0	0.030
Mean observed N	3.6	0.19, 7.7	0.05

[1]CI = Confidence Interval

Discussion

As remote-sensing technologies advance, there are many opportunities to use them in spatial ecology and conservation. Here we show that canopy total nitrogen (N), estimated using a commercial multispectral sensor mounted on an unoccupied aerial vehicle (UAV), can provide accurate high-resolution data on forest canopy nitrogen and that this is useful for identifying nutritionally suitable feeding habitat for a marsupial arboreal folivore of significant conservation concern. Our approach provides a mechanism for developing spatial models of potential feeding habitat to guide forest management and species conservation planning in forested landscapes.

Leading predictors of canopy nitrogen

While canopy N has long been recognized as an important component of the diet of arboreal marsupials and is often determined using laboratory-based or handheld spectroscopy (Cork and Catling 1996, Moore and Foley 2005, Marsh et al. 2014), direct estimates from remote-sensing platforms have only recently been developed. For example, Youngentob et al. (2012) integrated measures of *Eucalyptus* foliar N and digestible nitrogen (digN) from imaging spectroscopy using aerial hyperspectral imagery, while Wu et al. (2019) showed that digN can be predicted by spaceborne multispectral imagery. Both studies made use of spectral bands and/or vegetation indices derived from these bands, encouraging the application of

multispectral imagery in determining eucalypt foliar N as a measure of forage quality. Our eight uncorrelated predictor variables (Fig. 4.3) utilized all available bands and wavelengths covered by our multispectral sensor (475–840 nm). All bands and indices used in our modelling process reflect known nitrogen or associated biochemical absorption features. Three predictors were averaged band reflectances, while five were derived spectral indices. The most important predictor was the Generalized Difference Vegetation Index ($GDVI$, ~19% increase in mean-squared error, incMSE, Fig. 4.3, Table 4.2), which combines the near-infrared (NIR) and green band (Table 4.2). The index covers absorption features that have been detected at 570 nm (green) for chlorophyll and nitrogen (Peñuelas et al. 1994) and 800–900 nm (NIR) for tannins and chlorophyll (Ferwerda et al. 2006). $GDVI$ is also strongly associated with leaf area index (LAI) and shows greater sensitivity to lower vegetation cover than other frequently applied vegetation indices (Wu 2014). Its high importance in this study suggests that $GDVI$ is capturing crucial absorption features for estimating N, while also being able to distinguish the different vegetation types and associated *Eucalyptus* species we encountered from dry lowland to highly productive high-elevation sites.

The second most important predictor was the averaged green band reflectance (13.5% incMSE). Green reflectance is known to relate to N absorption features directly, rather than associated biochemicals (Peñuelas et al. 1994). This band is highly sensitive to foliar N levels (Thomas and Oerther 1972, Xue et al. 2004) and performs better than NIR- or red bands (e.g., used in the normalized difference vegetation index, $NDVI$) at distinguishing vegetation from other features (Gitelson et al. 1996). It may therefore combine the ability to directly determine nitrogen through high N sensitivity, while reducing errors arising from background reflectance.

The averaged NIR and red-edge bands were equally important (~11% incMSE each). NIR is associated with nitrogen between 800–~1000 nm (Curran 1989, Coops et al. 2003), while red-edge wavelengths at 700–800 nm correlate with chlorophyll and mesophyll absorption, as well as tannins (Filella and Peñuelas 1994, Curran et al. 2001, Ferwerda et al. 2006). Other important indices, such as the two normalized difference indices (NDI) used here (Table 4.2), were also found to be meaningful predictors of foliar N in other studies (see e.g. Wu et al. 2019). Both the Redness Index (RI) and the Visual Atmospheric Resistance Index ($VARI$) combine the green band's features with other bands associated with chlorophyll (red and blue band) and lignin (blue band) absorption (Curran 1989, Curran et al. 2001, Ferwerda et al. 2006).

Observed detection thresholds and imperfect detection

We observed higher detection rates for greater gliders with increasing amounts and quality of feeding resources (Appendix 3 Fig. S8). From canopy N measurements and spatial predictions, we derived three variables describing the quality of feeding habitat: mean plot nitrogen (meanN), nutritional suitability (likelihood of finding pixels associated with ≥1% N dry mass, DM), and the area of feeding habitat within a plot (as a proportion of the total area, 4 ha). Greater gliders were detected in plots that had ≥1.1% meanN (DM), ≥50% average nutritional suitability, and more than a quarter of the plot area as feeding habitat. The larger crown sizes observed at high elevation (Fig. 4.6B) also indicate a higher foliage volume, while the high aggregation of feeding habitat (Fig. 4.6E) suggests that this foliage is higher in nutritional quality. Our findings are in agreement with earlier studies demonstrating that greater gliders prefer sites with higher levels of foliar N (see e.g. Kavanagh and Lambert 1990). Braithwaite (1983) suggested and Cork (1992) later identified a nutritional threshold of 1% N DM for arboreal folivore habitat suitability. We found a similar, but slightly higher, nitrogen threshold (1.1% N DM) in our plots. Many studies have found that greater glider occurrence or abundance is higher where *Eucalyptus* species associated with high leaf N contents are present (Braithwaite et al. 1984, Cork and Catling 1996, Jensen et al. 2015). We found positive relationships between increasing meanN and detection across our sites (Table 4.5, Appendix 3 Fig. S9), providing further support for the importance of foliar nutrition on habitat selection of the greater glider in the study region.

Some plots exceeded all three of the identified thresholds but did not have greater glider detections (n = 14, Table 4.1). While these may be true absence sites, they may also reflect imperfect detection (i.e., gliders were present, but not detected) (MacKenzie et al. 2005). Detection rates for greater gliders at occupied sites are ~66% when surveyed twice or employing two observers per survey (Wintle et al. 2005, Nelson et al. 2018). The observed spatial and structural patterns of potential feeding habitat at different forest types and elevations may explain our detection rates. Although at low elevation the number of both feeding and non-feeding trees was higher when extrapolating from plot measurements to the hectare, both tree basal area and average crown sizes were much lower than at high elevation (Fig. 4.6B+C). At the same time, an equal aggregation of feeding- and non-feeding habitat within much larger areas of non-habitat indicates that foraging resources reaching levels ≥1% N DM were more dispersed and scarcer in the lowlands. Combined with lower tree density and less available feeding resources (i.e., lower crown area, smaller area of feeding habitat), it can be assumed that greater gliders need to move between trees more frequently and travel further distances to reach feeding habitat in suitable areas in the lowlands. The ability to glide allows

accessing favourable food resources at further distances while expending little energy (DeGabriel et al. 2009a). In fact, the scarcity of nutrients and occurrence of chemical anti-herbivory defences in *Eucalyptus* foliage has been proposed as a factor favouring the evolutionary development of gliding in greater gliders as the most energy-efficient type of movement between trees for continued feeding and detoxification (Youngentob et al. 2011). Nevertheless, fewer and more dispersed foraging resources may lead to lower population densities in folivores (Chapman et al. 2002, Chapman et al. 2004, Wallis et al. 2012). For greater gliders a combination of smaller areas of more dispersed feeding habitat and lower population densities may require an increase in exploratory movements to reach nitrogen rich foliage to forage on and find mating partners and may therefore lead to larger home ranges sizes (Pope et al. 2004, Smith et al. 2007) and therefore lower likelihood of detection when using a standardized survey method for a range of forest structures and configurations of feeding habitat. Even when assuming stable home range sizes (e.g. 2.6 ha, see Pope et al. 2004), a survey at a plot with only 30% feeding habitat (≈1.3ha) may only cover 50% of a greater gliders home range occupying the area (Fig. 4.7A). Only when the plot has about ~60% feeding habitat would an entire average home range be covered (Fig. 4.7B, Table 4.1). At high elevation, structural and spatial patterns such as larger crown sizes almost entirely consisting of feeding habitat (high spatial aggregation and larger areas), lower areas of non-habitat and higher basal areas would require less movement and may allow higher population densities and therefore smaller home ranges. Consistent with this, we detected up to 14 individuals per survey at high elevation plots, where animals were even observed in the same tree and often in close proximity (Fig. 4.7B). It is therefore likely they had either overlapping or smaller home ranges, supported by a higher abundance of feeding resources. Based on our findings, survey standards may need to be adapted for differences in spatial arrangement of feeding habitat, home range sizes and population density at different forest types. Our metrics may therefore be a useful guide where non-detections may require additional surveying efforts to ensure detection and confirm occupancy. Furthermore, the ability to map potential feeding habitat may help in planning survey transects and increase the likelihood of detection in habitats where foliage quality is limited. Depending on management prescriptions, this tool may then also be applied to protect or retain trees that are important to sustain nutritional suitability and connectivity within the greater glider's home range.

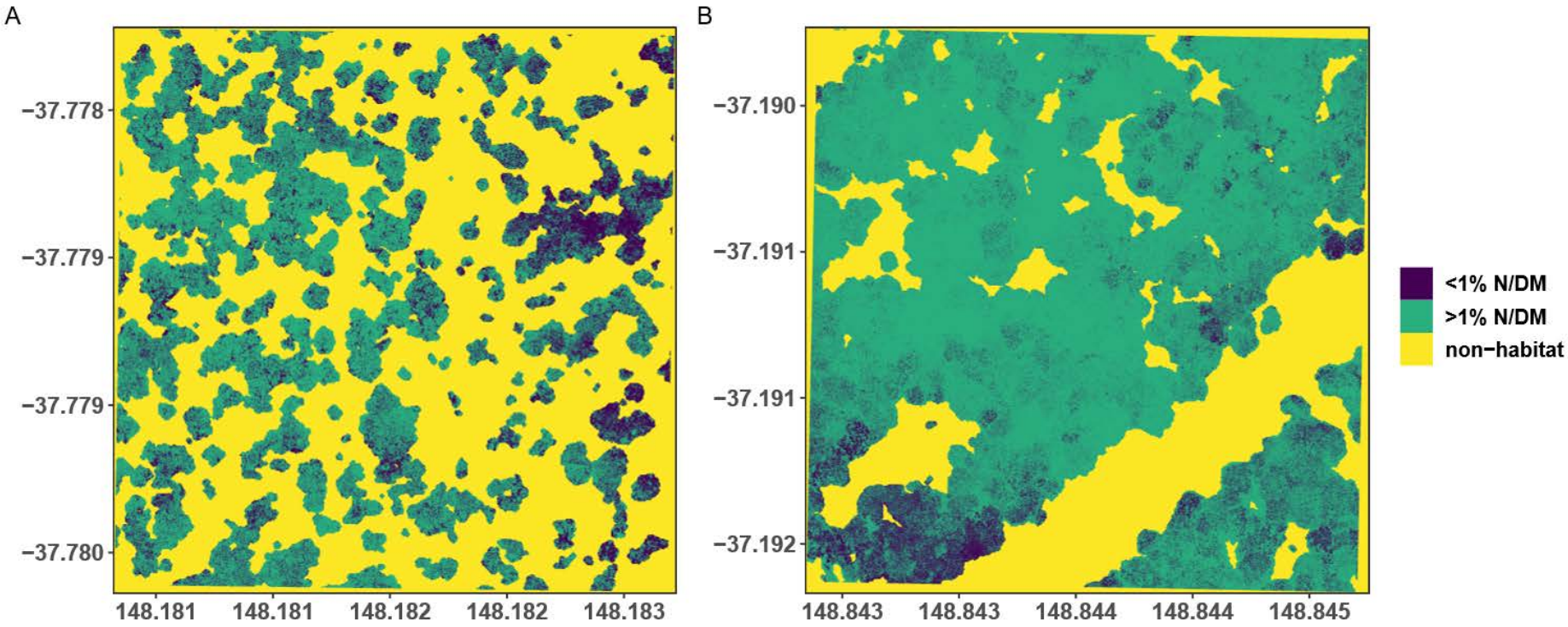

Figure 4.7. A lowland plot (Plot 10) where two greater glider detections where made outside the plot area (A) and a high elevation plot (Plot 6) with five observations within the plot and 14 total observations (B) along a 1km spotlighting transect. Both plots have a similar area of non-feeding habitat (dark blue, ~10% of the plot area) but opposite amounts of feeding habitat and non-habitat. The lowland plot (A) is predicted to have ~60% non-habitat (e.g. subcanopy crowns or forest gaps, yellow areas) and ~30% feeding habitat (areas classified as having ≥1N % DM, green areas), whereas the highland plot (B) has ~30% non-habitat and 60% feeding habitat. Assuming the spatial configuration of feeding habitat is constant beyond the plot boundaries, a glider would require twice as much area in the lowlands to access the same amount of feeding habitat. Assuming average home ranges for gliders are constant (e.g. 2.6 ha), a survey through the lowland plot (A) would only cover ~50% of the assumed home range of a potential greater glider occupying the site, while covering an entire home range in the highland plot (B), which has implications on the likelihood of detection.

Plant secondary chemistry may influence greater glider distribution and therefore detection as well. Tannins binding proteins to plant tissue can cause large differences in N and digN in some species, while herbivory defences from formylated phloroglucinol compounds (FPCs) may limit the quality of foliage high in digN (Lawler et al. 1998b, Lawler et al. 1998a, Marsh et al. 2003). The ability to similarly predict and spatially map digN (see Youngentob et al. 2012, Wu et al. 2019) and a method that can remotely sense FPC concentrations may therefore assist in distinguishing and classifying feeding habitat in more detail. The latter may be possible using hyperspectral leaf reflectance (Ebbers et al. 2002, Couture et al. 2016). Given FPCs only occur in one of the two *Eucalyptus* subgenera found in the study area (*Symphomyrtus*), there may also be potential to use multi- or hyperspectral canopy reflectance patterns for classification at the sub-generic level (Goodwin et al. 2005, Baldeck et al. 2015). This may further aid in characterizing the nutritional suitability at the home range scale. We accounted for many possible factors that may explain non-detection or lower population densities, such as fires, drought or timber harvesting and therefore lack of hollows for nesting during site selection. Nevertheless, another explanation may be owl predation (see e.g. Kavanagh 1988) or historical factors such as disease outbreaks.

Analytical and operational limitations

Both N and digN were significantly associated with the eight spectral predictor variables. Models predicted nitrogen at the canopy level, as well as feeding habitat at the home range scale (4 ha). However, our digN model was found to be explanatory only and lacked predictive power. Predictions exhibited poor performance in independent model validation (best R^2 = 0.12, average R^2 = 0.03, Appendix 3 Table S3). The reason for this might be that digN is influenced by many constituents, such as N, lignin, tannins and cellulose concentrations that modify digestibility (Degabriel et al. 2008) and might therefore not have distinct direct relationship to spectral reflectances covered by our sensor or indices. Wu et al. (2019) found that digN was best predicted with blue multispectral bands at lower wavelengths (400–450 nm), while Youngentob et al. (2012) reported the highest predictive performance when integrating at least four hyperspectral bands with wavelengths between ~1300–2174 nm. It may therefore be the case that our multispectral sensor, which is limited to wavelengths between 475–840 nm was unable to register these spectral components of the foliage. Nevertheless, we found that vegetation indices can be used to reduce the limitations small multispectral sensors using centre wavelengths may have. Therefore, there can be other indices not considered here, that may improve predictive performance of digN models, which should be further explored. Indices contributed more to overall model performance than averaged spectral reflectance and Youngentob et al. (2015) also found that spectral indices were useful

for predicting greater glider abundance. While hyperspectral sensors may have advantages in terms of spectral range, multispectral imagery is more accessible, has better cross-platform integration, and is easier to process.

When interpolating our canopy models to predict leaf nitrogen spatially at the home range scale, we encountered issues arising from non-linear averaging (i.e., Jensen's inequality, see Denny (2017)). Canopy models were based on reflectance averages of crown foliage, which had a lower variance than the variance in the predictors at the home range scale. The high variance of the home range scale predictors increased the effect of Jensen's inequality and therefore reduced the robustness of average-condition models for predicting across a wider range of conditions (Roussel and Auty 2019). We used supervised classification on a binomial response variable describing the presence or absence of feeding habitat to overcome this issue. Interpolation issues did not arise in similar studies. Youngentob et al. (2012) reported that the use of maximum spectra produced better models than averages, while Wu et al. (2019) used a pixel averaging approach much like ours. We did not find maximum spectra to improve models in our analyses. Our image ground resolution was much higher (~2.5 cm) than either of the other studies (1.24 – 7.5 m), due to our UAV imagery being collected from only ~120 m altitude. The orders-of-magnitude increase in spatial resolution produced, greatly improved tree delineation and the quality of our canopy height models (CHMs), which were crucial in classifying spatial predictions and identifying non-habitat. Nevertheless, it may have exacerbated the effects of Jensen's inequality through the larger number of pixels, which led to greater variance in the raw spectral reflectance than canopy averages of 1000s of pixels.

Using small and highly mobile UAVs with spectral sensors to map foliar nutrition quality over large areas has the potential to better integrate forest management and conservation planning. A pragmatic issue that will arise is the type of UAV and the scale of sampling. While our multirotor UAV can readily sample areas of up to 20 ha per flight and therefore cover multiple greater glider home ranges, fixed-wing (FW) UAVs may be better suited to capture imagery over larger areas (Anderson and Gaston 2013). This will allow for determination of canopy N and feeding habitat at the scale of several square kilometres (100s of hectares) in a few flights, potentially covering a population-range scale. However, these platforms require clearings for take-off and landing, which may not be readily available in heavily dissected or mountainous terrain where, in our case, greater gliders typically occur. In more recent years, FW UAVs have been successfully equipped with vertical take-off and landing (VTOL) abilities (Goodbody et al. 2017), which may be useful when capturing imagery of larger areas of tall forests in complex terrain.

Conclusion

We used UAV multispectral imagery, individual tree-sampling of foliar nutrition and forest structure and transect-based surveys for southern greater gliders to successfully characterise and map the nutritional quality in a landscape of a threatened arboreal folivore, the southern greater glider, in southeastern Australia. Our findings and models have important management implications for the detection and retention of high-quality feeding habitat at both the canopy level of individual trees and spatially at the home range scale, as well as for survey design. Although successfully modelling and mapping total nitrogen, digestible nitrogen models could not be extrapolated spatially using the spectral bands and vegetation indices available. The ability to map digestible nitrogen would enhance the classification of folivore habitat in more detail, considering the negative effects of plant secondary metabolites. Future research should focus on identifying additional spectral bands or indices to predict digestible nitrogen spatially. It is now important to integrate these methods into platforms that can capture larger areas, which will allow a swift and low-cost assessment of greater glider feeding habitat to aid in their management and conservation at the landscape scale.

5. The influence of spatial pattern in foraging habitat on the abundance and home range size of an arboreal marsupial in southeast Australia

Introduction

A species' habitat niche is comprised of favourable conditions and required resources, which allow the establishment of populations and their persistence in a landscape (Warren et al. 2008). Different combinations of these elements lead to some habitat being higher or lower quality, which is measured as habitat suitability (Hirzel and Le Lay 2008). Although it is possible to determine and monitor habitat requirements at the patch scale (e.g., through forest surveys), it remains difficult to extrapolate from field observations to scales relevant to entire populations (With and King 2001), because the factors determining habitat suitability may occur at different scales and vary in spatial arrangement (Huston 1999). For example, a species' tolerance of certain climatic conditions will be influenced by landscape-scale climate and weather patterns and variability (Briscoe et al. 2015, Wagner et al. 2020), whereas foraging or nesting resources are the result of stand-scale forest dynamics (Moore et al. 2010, McLean et al. 2015). Although species may be able to persist in a range of landscape configurations and resulting variations in habitat suitability, population density will vary as it is driven by resource availability (Wallis et al. 2012). Resources and conditions shaping habitat suitability may be spatially dispersed or aggregated and drive abundance and density of habitat (Nitschke et al. 2020) and therefore density of individuals in a given area (Fahrig 2001). Furthermore, disturbances to these resources may change the amount, distribution, and configuration of suitable habitat within forest stands and across landscapes (Devictor et al. 2008). A loss of habitat may reduce the ability of individuals or populations to persist (Fahrig 2001). The extent and intensity of a disturbance can lead to a spatially aggregated or dispersed habitat structure. Catastrophic, stand-replacing fires can cause an aggregated spatial effect (Walker et al. 2019), whereas certain forest management methods such as selective timber harvesting may lead to resources and habitat becoming more dispersed (Kavanagh and Webb 1998, McLean et al. 2018). To facilitate informed decisions in species management and conservation, it is important to quantify how both abundance and patterns of resource availability influence the persistence or loss of fauna populations (Lande 1987). Such knowledge is critical for understanding how populations may respond to disturbances of different spatial extents, patterns, and severity.

Species with distinct habitat requirements are well suited for testing the effects of habitat configuration and abundance on their occurrence (Mazerolle and Villard 1999). Examples exist from wetland bird and turtle species in Canada, where habitat amount was more important than spatial configuration (Quesnelle et al. 2013), and the northern spotted owl (*Strix occidentalis caurina*) in the Pacific Northwest, for which a mosaic of old-growth forests and other vegetation types improved population fitness and persistence (Franklin et al. 2000, Jones

et al. 2018). In southeastern Australia, the southern greater glider (*Petauroides volans*) is well known for its distinct habitat requirements, which are strongly influenced by three factors that operate over multiple spatial scales. At the landscape scale, climate shapes the distribution of the species due to a narrow thermotolerance, which restricts populations to cooler and wetter parts of the landscape (Rübsamen et al. 1984, Kearney et al. 2010, Wagner et al. 2020). Areas at high elevation, for example, are mostly climatically suitable. At low elevations, arid conditions make most of the area unsuitable, restricting the greater glider to landscape features such as gullies, that act as microclimatic refugia (Wagner et al. 2020). At the stand scale, a specialised diet consisting entirely of nutrient-rich *Eucalyptus* leaves and the need for multiple large tree hollows for denning, shapes the establishment and spatial configuration of individual home ranges (Kavanagh and Lambert 1990, Lindenmayer et al. 1990b, Smith et al. 2007). Suitable tree species with leaves rich in foliar nitrogen are typically dispersed at low elevation but highly aggregated at mid- and high elevation sites (Wagner et al. in review-a - Chapter 4). In tall, mature forests, hollow-bearing trees used for nesting can be abundant and typically do not limit habitat suitability where forest areas have not been disturbed by fires or timber harvesting (Wagner et al. in prep - Chapter 3). However, areas subjected to timber harvesting or forest fires may experience drastic reductions in nesting resources and therefore habitat suitability (McLean et al. 2015, Lindenmayer and Sato 2018, McLean et al. 2018). Across the greater glider's range in Victoria, factors such as feeding, and nesting resources occur in different abundances and spatial arrangements. This shapes habitat suitability and acts as a filter on occurrence and abundance of greater gliders. Individual greater gliders have been reported to increase their home range sizes where resource availability is limited (Kavanagh and Wheeler 2004, Smith et al. 2007). This suggests that occupancy and population density may be closely related to the spatial arrangement of favourable climatic conditions and habitat resources (Wallis et al. 2012), as well as the amount of habitat in an area (Youngentob et al. 2013).

Populations of greater gliders are in decline (Lindenmayer et al. 2011, Lindenmayer and Sato 2018, Smith and Smith 2020). Their conservation is of great concern; however, their capacity to persist in different parts of the landscape is still unclear (DELWP 2019). At the landscape scale, a changing climate has led to a contraction in the species' distribution to higher elevations (Smith and Smith 2020, Wagner et al. 2020). Stand-altering or -replacing disturbances as a result of forest fires and timber harvesting, have been found to influence persistence at finer scales (Possingham et al. 1994, Kavanagh 2000, Pope et al. 2004, Lindenmayer et al. 2013, Youngentob et al. 2013, McLean et al. 2018). With continued climatic change, it is important to understand the effects of decreasing climate suitability on populations but also the interacting impacts of disturbances, which are increasing in severity

(Ward et al. 2020). The severity and extent of disturbance influences the amount and arrangement of habitat, which can influence population persistence and abundance in disturbed areas (Kavanagh 2000, McLean et al. 2018). Understanding how changes in the amount and spatial arrangement of habitat influences populations of greater gliders at coarse and fine scales is critical for successful conservation planning.

Given the broad-scale influence of climate on greater gliders (Wagner et al. 2020), we previously hypothesized that a reduction in climatic suitability will reduce animal abundance and density, independent of the finer-scale spatial configuration and amount of feeding habitat. Climate should limit greater glider occurrence to areas with both suitable climate and available feeding and nesting resources. This has been observed in the mature forests of East Gippsland, Victoria, where areas that contain high-quality feeding habitat today, but are no longer climatically suitable, have seen a decline in greater gliders since the 1980s (Wagner et al. 2020, Wagner et al. in review-a - Chapter 4). Here we extend this to incorporate the spatial pattern of foraging resources. We hypothesize that both the spatial configuration of feeding habitat and disturbances will affect resource availability and therefore population density. Earlier studies have shown that greater gliders can persist in forests that retained ≥40% of their initial basal area after disturbance (Kavanagh 2000) and are better suited than other arboreal mammals to survive in aggregated strips of managed forest landscapes due to their diet (Lindenmayer et al. 1993a). While greater gliders can persist in areas of selective timber harvesting, population density decreases with logging intensity (McLean et al. 2018). Nevertheless, the exact role of spatial aggregation of either the feeding habitat itself or the disturbance affecting it, on greater glider abundance and density, is still poorly understood. Throughout its range and a variety of forest types, greater glider home range sizes can vary between one to 18 hectares, which may be a response to resource availability (Henry 1984, Kehl and Borsboom 1984, Comport et al. 1996, Kavanagh and Wheeler 2004, Pope et al. 2004, Smith et al. 2007). We expect that dispersed habitat or disturbances that create more dispersed feeding resources will lead to more drastic increases in home range sizes and reduce available or accessible feeding habitat in individual home ranges more rapidly, therefore reducing population density more drastically.

Our aim is to assess the relationship between spatial aggregation of habitat resources, different types of disturbances and greater glider population density and persistence. We further aim to identify greater glider population responses and thresholds of habitat suitability to aid in estimating the likelihood of population persistence under climate change and after disturbances from forest fires (Lindenmayer et al. 2013, Berry et al. 2015, Chia et al. 2016) and timber harvesting (Kavanagh 2000, McLean et al. 2018).

Methods

We developed a generalized modelling framework to test relationships between spatial patterns and species abundance, density, and persistence using neutral landscape models (With and King 2001). Neutral landscapes simulate landscape patterns based on theoretical spatial distributions or properties of real landscapes (Gardner et al. 1987, With 1997, Gardner and Urban 2006). To test our hypotheses, we used field observations as well as observations from published literature, to make assumptions about what makes home ranges for greater gliders functional and under which conditions functionality would be lost and reductions in animal abundance or density might be expected to occur. The key criteria we identified are:

1. A maximum home range size of six hectares. This is based on observations of maximum home range sizes for female greater gliders, which share home ranges less frequently and express only limited rates of home range extension with resource scarcity (Henry 1984, Kehl and Borsboom 1984, Comport et al. 1996, Kavanagh and Wheeler 2004, Pope et al. 2004, Smith et al. 2007).
2. Home ranges need to include at least 2.6 ha of foraging habitat. This is based on the average observed home range size in mature undisturbed forests dominated by preferred, nitrogen-rich *Eucalyptus* species (Henry 1984, Kehl and Borsboom 1984, Comport et al. 1996, Kavanagh and Wheeler 2004, Pope et al. 2004, Smith et al. 2007).
3. At least 25% of the total home range area needs to be feeding habitat (where foliage has ≥1% nitrogen per gram dry mass, Cork 1992). In a previous study, greater gliders were not detected in sites that were predicted to have <25% feeding habitat (Wagner et al. in review-a - Chapter 4).
4. As our models are based on observations made from undisturbed mature mixed-species forests with abundant nesting resources, we assume tree hollows are not limiting site occupancy (Wagner et al. in prep - Chapter 3).

All spatial and statistical analyses for this study have been carried out in R 4.0.3 (R Core Development Team 2020). Neutral landscapes were generated from random clustering according to Saura and Martínez-Millán (2000) using the package *NLMR* (Sciaini et al. 2018).

Step 1. Simulating landscape-scale effects of climate change on feeding landscapes

To test the effect of a gradual decrease in climatic suitability on a landscape containing high-quality feeding habitat, we generated neutral landscapes, based on the relative proportions

and spatial aggregation of predicted feeding habitat (canopy nitrogen is ≥1% N DM), non-feeding habitat (<1% N DM), and non-habitat (neither feeding or nesting trees or features such as canopy gaps) from 4-ha plots located in high-elevation, mixed-species *Eucalyptus* forests in East Gippsland, Victoria (n = 10, Appendix 4 Table S1, see Wagner et al., in review-a – Chapter 4). Per-class fraction was derived by dividing the area of the three classes by the total area and spatial aggregation was determined using the package *landscapemetrics* (Hesselbarth et al. 2019). As climatic suitability occurs at coarser resolution than feeding habitat and over large (landscape) scales (Wagner et al. 2020), we extrapolated predicted properties and aggregated the spatial resolution to simulate 1000 ha landscapes at 1 ha cell size from our fine-scale (4 ha at ~2.5 cm^2 resolution) spatial predictions of feeding habitat (Fig. 5.1A+B).

Next we generated nine neutral landscape climate masks, simulating climatic suitability extent between 10-90% of the total area over 1000 ha (Fig. 5.1C). As climatic suitability occurs clumped over large areas rather than dispersed (Wagner et al. 2020), we generated these masks at maximum class aggregation, using an 8-neighborhood rule (p = 0.58, Saura and Martínez-Millán 2000). Each climate mask was applied to the simulated feeding habitat landscapes using the package *raster* (Hijmans 2019). Masking any of the three existing classes with the climate layers added a new class to the feeding landscapes, describing areas that have become climatically unsuitable and therefore non-habitat (Fig. 5.1D). Along with the 10 initial neutral landscapes (i.e., 100% climatic suitability), these maps (n = 100, 10 initial neutral landscapes as control + (9 masks x 10 initial landscapes)) were analysed for changes in suitable and unsuitable habitat area caused by a simulated decrease in climatic suitability. We calculated area and aggregation metrics such as number of patches or edge density for (remaining) feeding habitat. Using the selected assumed minimum home-range size for greater gliders in mature forests as minimum area of feeding habitat required (2.6 ha, Smith et al. 2007), we calculated the potential number of animals per hectare based on remaining accessible feeding habitat (i.e., feeding habitat in climatically suitable areas) for each resultant neutral landscape.

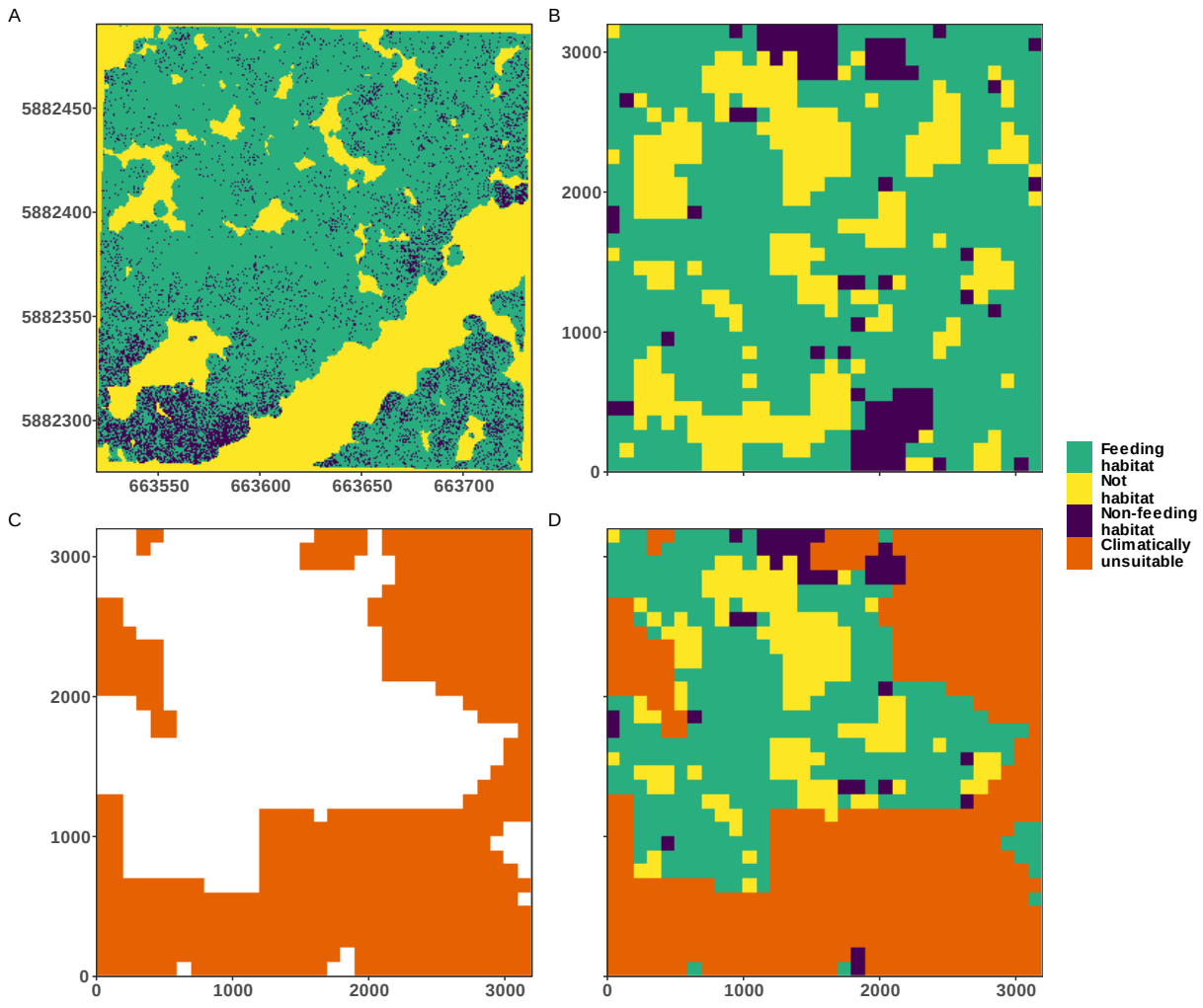

Figure 5.1. Analysis steps to simulate landscape-scale effects of climate change on feeding landscapes. A) a 4-ha spatial prediction of feeding (green), non-feeding (blue) and no habitat (yellow) to an actual high-elevation mixed-species stand (Wagner et al. in review-a - Chapter 4) and its 1000 ha neutral landscape equivalent (B). A climate mask (C) simulating ranges of climatic suitability (in this case 50% area becomes climatically unsuitable - orange) is applied to these neutral landscapes (B), resulting in a landscape with an additional class of climatically unsuitable habitat (D), rendering the other classes inaccessible.

Step 2. Simulating stand-scale clumped and dispersed feeding habitat

To test what influence spatial aggregation of feeding habitat has on home-range structure and density at a finer (stand) scale, we generated binary neutral landscapes that contained either feeding habitat or no feeding habitat (Fig. 5.2). Home range structure refers to the individual home range sizes and ratio of feeding habitat area to the total area within a home range (i.e., feed-area-ratio). Home range density (number of home ranges) was used as a proxy for animal abundance (i.e., number of animals per 100ha). Depending on elevation, topography, and resulting forest structure and composition, feeding habitat can be either clumped or dispersed (Wagner et al., in review-a – Chapter 4).

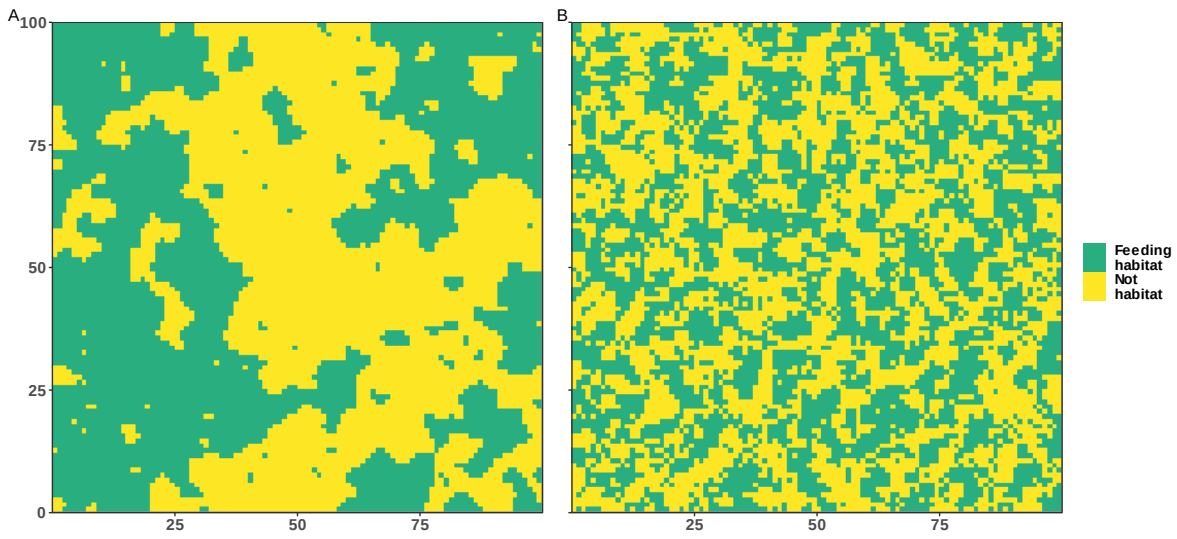

Figure 5.2. 50% feeding habitat generated with maximum (A) and minimum (B) aggegation, resulting in 100-ha neutral landscapes representing clumped (A) and dispersed (B) feeding resources.

To account for this variation we generated nine (10-90% area of feeding habitat) 100-ha random cluster landscapes at a 10 m^2 resolution both at maximum (p = 0.58), and minimum (p = 0.1, Saura and Martínez-Millán 2000) aggregation (n = 18). For each landscape, we calculated the potential maximum number of home ranges or animals based on the total area of available feeding habitat, divided by the hypothesized minimum area of feeding habitat required of a home range (2.6 ha). To determine the optimal spatial arrangement and size of home ranges that met this requirement within all generated neutral landscapes, we used *k*-means clustering (Hartigan and Wong 1979) on cells of feeding habitat only (Fig. 5.3A). *K* equalled the potential maximum number of home ranges in any generated feeding landscape (Eq. 1). Cells were assigned their cluster number and a convex hull was calculated for each cluster, outlining the home range boundaries (Fig. 5.3B).

$$k = \frac{Amount\ of\ total\ feeding\ habitat\ in\ ha}{Assumed\ minimum\ home{-}range\ size\ (2.6\ ha)} \quad \text{(Equation 1)}$$

For each feeding landscape we tallied the total number of home ranges and calculated the size and feed-area-ratio of all potential home ranges. Next we removed any home ranges from further analysis that were unlikely to be functional based on size (>6 ha, see Smith et al. 2007) and/or feed-area-ratio (<25% of total home range area, see Wagner et al. in review-a - Chapter 4). The resulting dataset was then used to compare differences in habitat potential between types of aggregation based on data distribution and to determine critical thresholds for the formation of suitable conditions across simulated sites.

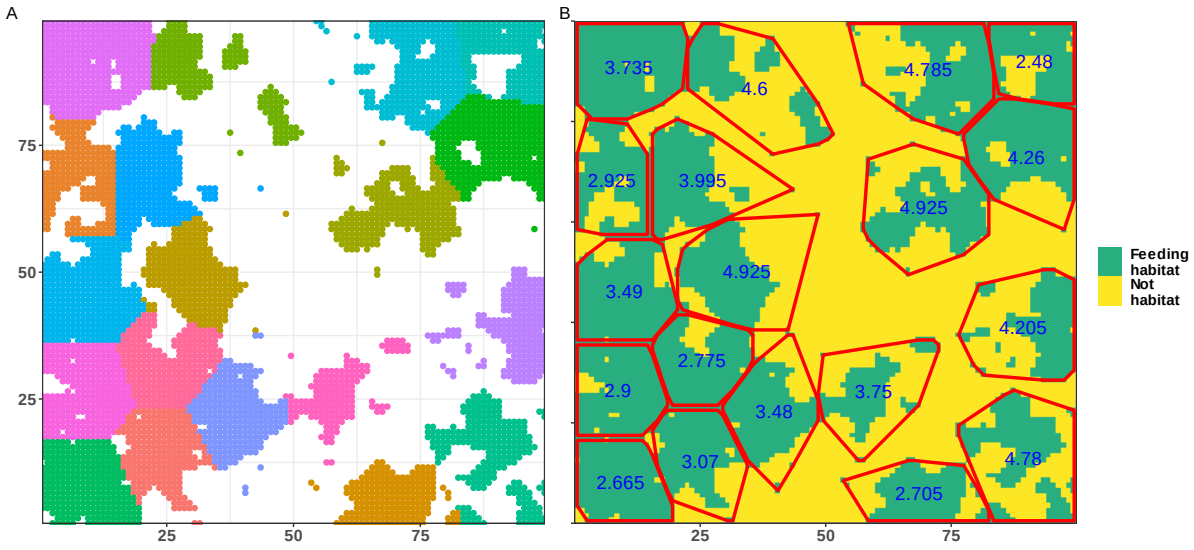

Figure 5.3. A: Spatial representation of cells with feeding habitat that have been clustered (colored points) using k-means clustering, based on the potential maximum number of home ranges in the respective stand. B: Convex hulls were created for each cluster to visualize the potential home ranges and calculate their properties such as size in ha (blue numbers) and amount of feeding habitat within each home range (green areas).

Step 3. Simulating stand-scale effects of disturbance

To test the influence of spatial aggregation and intensity of disturbances on home range-, and population potential based on the feeding properties of real landscapes, we generated 100 ha neutral landscapes (10 m^2 cell size) based on aggregation and class fraction of all study sites in East Gippsland, Victoria (n = 30, classes = feeding, non-feeding, and not habitat), according to methods outlined in Step 1 (Fig. 5.4A). Next, we generated aggregated and dispersed (maximum and minimum aggregation) disturbance masks for 10 – 90% area affected (n = 18) in a similar process to generating climate suitability masks before (Fig. 5.4B+D). These were used to change any covered area in the generated neutral landscapes to non-habitat (n = 570, i.e., 30 initial undisturbed landscapes as control and 540 (30 landscapes x 18 disturbance masks) landscapes resulting from disturbance at different aggregations and intensities, Fig. 5.4C+E). As in Step 2, we used *k*-means clustering and created convex hulls of potential home ranges for each of these feeding landscapes. We filtered for functional home ranges and analysed differences between, and effects of clumped and dispersed disturbances at different intensities (fraction of area disturbed) on home range potential and population structure.

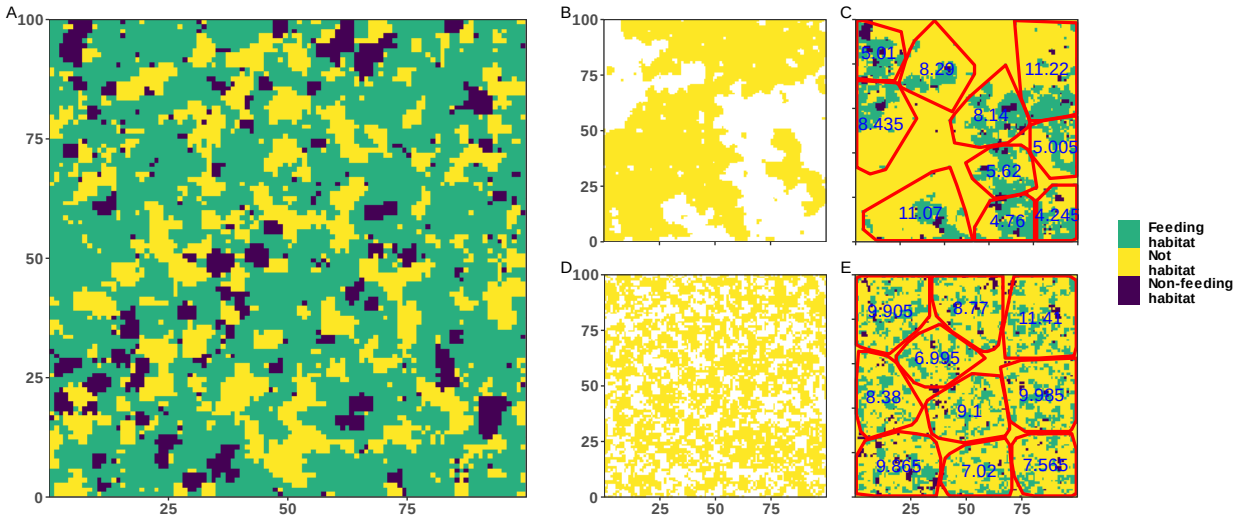

Figure 5.4. A: 100 ha neutral landscape based on properties from spatial predictions of feeding habitat (Fig. 5.1A, Wagner et al. in review-a - Chapter 4) were subjected to randomly generated clumped (B) and dispersed (D) disturbances affecting 10-90% of the total area (yellow). Disturbed areas were masked to become non-habitat (C+E, yellow) and remaining home ranges were analysed for size, amount of feeding habitat and feed-area-ratio. Any home range that did not match assumptions of functionality was removed from further analysis. In this case a disturbance, removing 60% of the initial basal area led, to either persistence of five functional home ranges (C) or a local extiction, where all remaining potential home ranges were too large to be functional (E).

Results

Effects of decreasing climatic suitability on feeding habitat

Simulated 1000-ha feeding landscapes ranged in total feeding habitat area from 427 to 715 ha, which equated to an average potential population density of 0.2 ($\pm$ 0.04) animals per hectare. By gradually reducing the climatic suitability within these landscapes from 100 to 10%, we observed a near-linear decrease in potential population density and decrease in deviation from the mean density (Fig. 5.5). As climatic suitability decreased, landscapes converged in area and arrangement of remaining suitable habitat. When only 10% of the total area was climatically suitable, accessible feeding habitat ranged from 33 to 81 ha (out of 1000 ha), equivalent to an average density of 0.02 ($\pm$ 0.005) animals per ha. On average, a 10% reduction in climatically suitable area led to a 10% reduction in potential population density, independent of the initial spatial arrangement of feeding habitat across these landscapes. The reduction in accessible feeding habitat was also associated with a decrease in edge density and increasing patch aggregation, indicating not only that accessible feeding habitat had decreased but that it also became spatially more clumped (Appendix 4 Fig. S1).

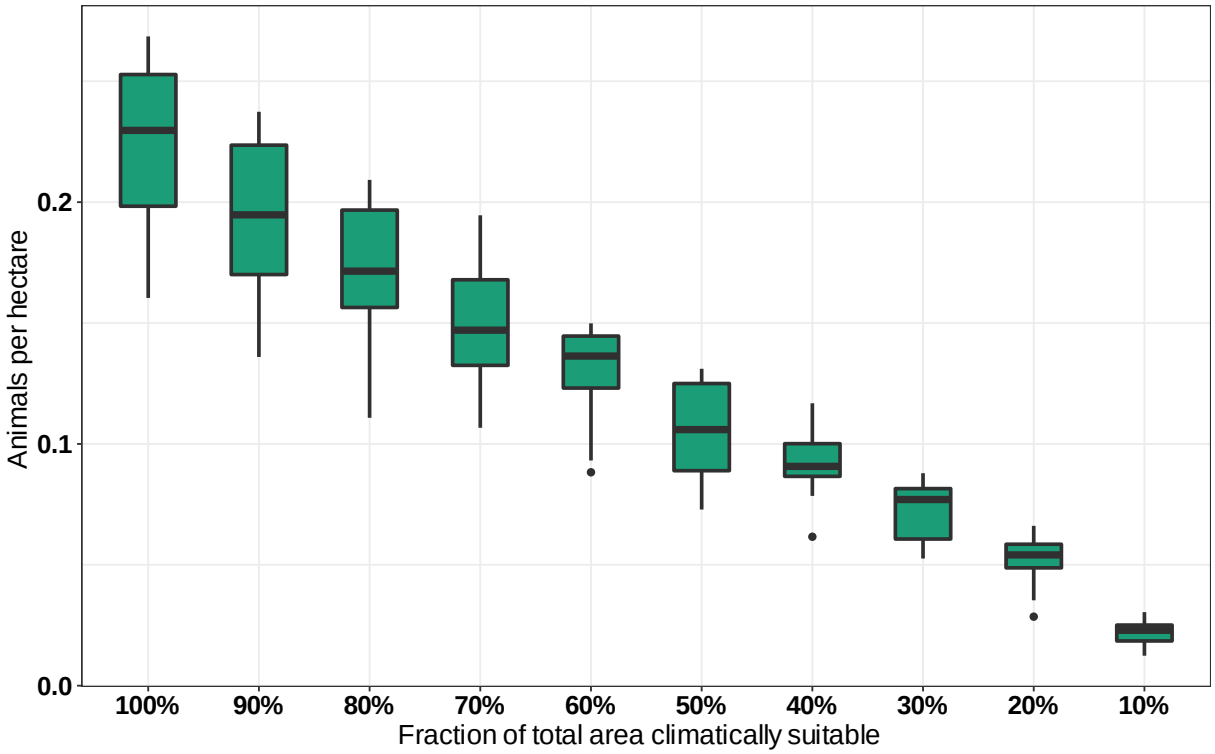

Figure 5.5. Observed declines in animal density (y-axis) with reductions of climatically suitable area across all 1000-ha neutral feeding landscapes.

Effects of spatial aggregation of feeding habitat on stand scale population potential

A linear decrease in population density was observed when simulating different rates of feeding habitat at the 100-ha (stand) scale. For both clumped and dispersed feeding habitat, a 10% decrease led to a ~10% reduction in the number of potential home ranges across the 18 simulated landscapes. We observed ~35 home ranges at 90% and ~4 at 10% feeding habitat for both aggregation types (Appendix 4 Fig. S2A). Differences between clumped and dispersed feeding habitat were found in home range (cluster) area and feed-area-ratio within the modelled home ranges (n = 343). Average home range area was significantly larger ($p < 0.01$) and feed-area-ratio per home range significantly lower ($p < 0.001$) for dispersed than clumped feeding habitat (Appendix 4 Fig. S2B+C). With decreasing feeding habitat, the coefficient of variation increased from 10% to 60% for home range area and from 12 to >95% for feed-area ratio, while remaining stable below 10% in dispersed habitat for both variables (Appendix 4 Fig. S3).

When filtering for functional home ranges (home range area ≤ 6 ha, feed-area-ratio ≥ 25%, n = 292), spatial distribution became more important. Landscapes with dispersed feeding habitat had lower home range potential than landscapes with clumped feeding habitat when total feeding habitat was below 50%. The potential for the landscape to contain functional home

ranges (i.e., where the number of home ranges dropped to 0) was lost at 30% dispersed feeding habitat. Landscapes with clumped feeding resources lost all home range potential when feeding habitat comprised only 10% of the landscape; however, only one home range remained at 20% feeding habitat (Fig. 5.6A). A similar coefficient of variation (Appendix 4 Fig. S4) in both home range area and feed-area-ratio was observed for landscapes with clumped feeding habitat after functional home range formation occurred at 30% total feeding habitat (Fig. 5.6B+C).

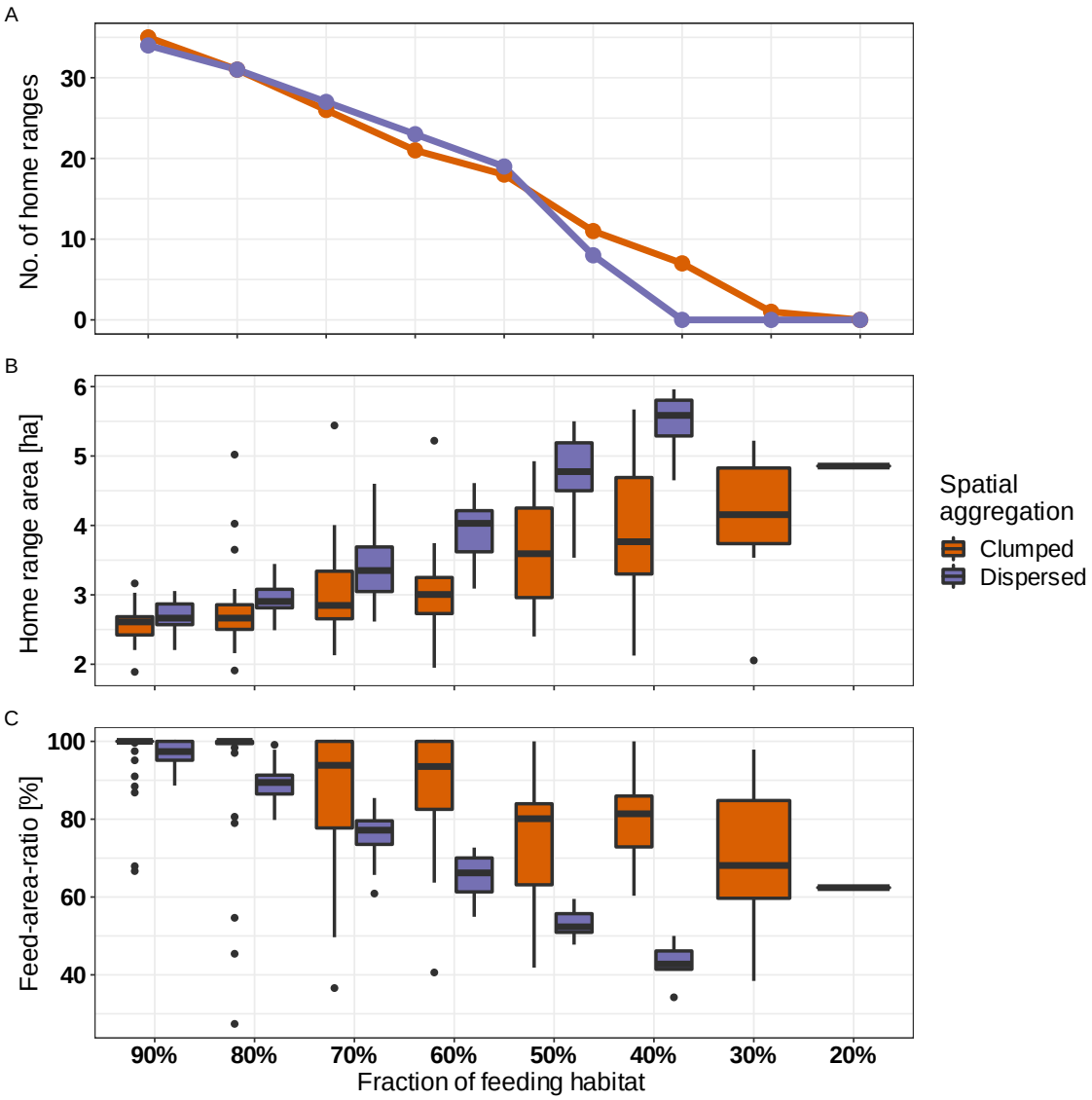

Figure 5.6. Reduction in number of home ranges (A), increases in home range area (B) and changes in feed-area ratio (C) for functional home ranges with decreases in feeding habitat area in 100 ha neutral landscape simuations of clumped (orange) or dispered (purple) feeding resources.

Here, even at a low total feeding habitat area, relatively small home ranges (minimum of 3.5 ha) with large amounts of feeding resources (maximum of 98% feed-area-ratio) could exist at

realistic numbers of individuals per 100 ha (n = 7 home ranges across 100 ha, Appendix 4 Fig. S5). In landscapes with dispersed feeding habitat, functional home range formation first occurred at 40% total feeding habitat. When feeding habitat was dispersed, similar home range areas and feed-area-ratios attained at 30% clumped feeding habitat were not reached unless ≥70% of area (70 out of 100 ha) was feeding habitat (Fig. 5.7).

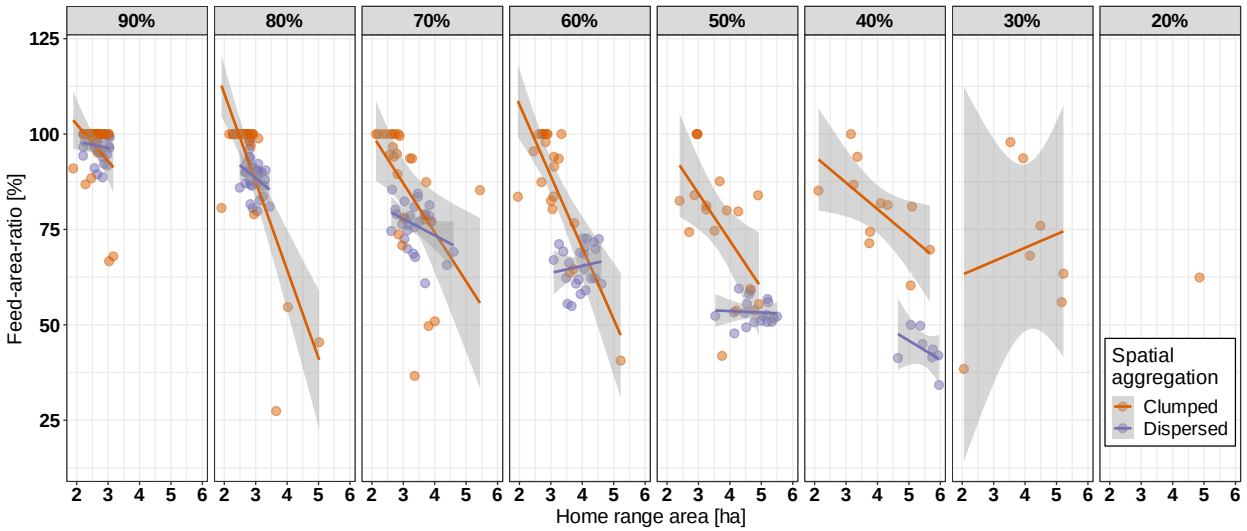

Figure 5.7. The relationship between home range area and feed area ratio of simulated home ranges for clumped (orange) or dispersed (purple) feeding resources at different rates of total feeding habitat (90%-10%, facets).

Effects of intensity and spatial aggregation of disturbance on feeding habitat and population persistence

For a hypothesized minimum required feeding habitat area of 2.6 ha per home range, our analyses resulted in a total of 5885 modelled home ranges across simulated sites and disturbance types (clumped or dispersed disturbances at different intensities). We observed a similar linear trend of decreasing number of home ranges with remaining undisturbed area and only slight differences between clumped or dispersed disturbance (Appendix 4 Fig. S6A). Differences were observed in home range area and feed-area-ratio resulting from different disturbance types, where dispersed disturbances lead to larger home ranges containing less feeding habitat at lower intensity. For the feed-area-ratio, the coefficient of variation, and therefore range of potential feeding habitat within a home range, was larger when the disturbance was aggregated. However, with increasing extent of disturbance, many modelled home ranges became either too large or too scarce in feeding habitat (or both) to be functional according to the assumptions on functionality that we specified. Modelled home ranges approached hypothesized loss of functionality earlier at low elevation sites and when landscapes were affected by dispersed disturbances (Appendix 4 Fig. S6B+C).

When considering only functional home ranges (n = 3414), the potential of a 100-ha feeding landscape to support a population size of >1 home range was lost sooner for landscapes affected by dispersed disturbances (<40% at mid- and <50% area undisturbed at high elevation). Landscapes generated using low-elevation site properties lost their potential to support home ranges at <80% remaining undisturbed area (Fig. 5.8). A large variation in both home range area and feed-area-ratio for landscapes affected by clumped disturbance allowed for home ranges to form at higher disturbance intensity (80% disturbed at mid-elevation and 70% at high elevation). Even when affected by severe clumped disturbances, some landscapes retained the potential for small home ranges, largely covered by feeding habitat. For example, at 30% remaining undisturbed area, the smallest home range was 1.3 ha and the largest feed-area-ratio was 94% (Appendix 4 Fig. S7).

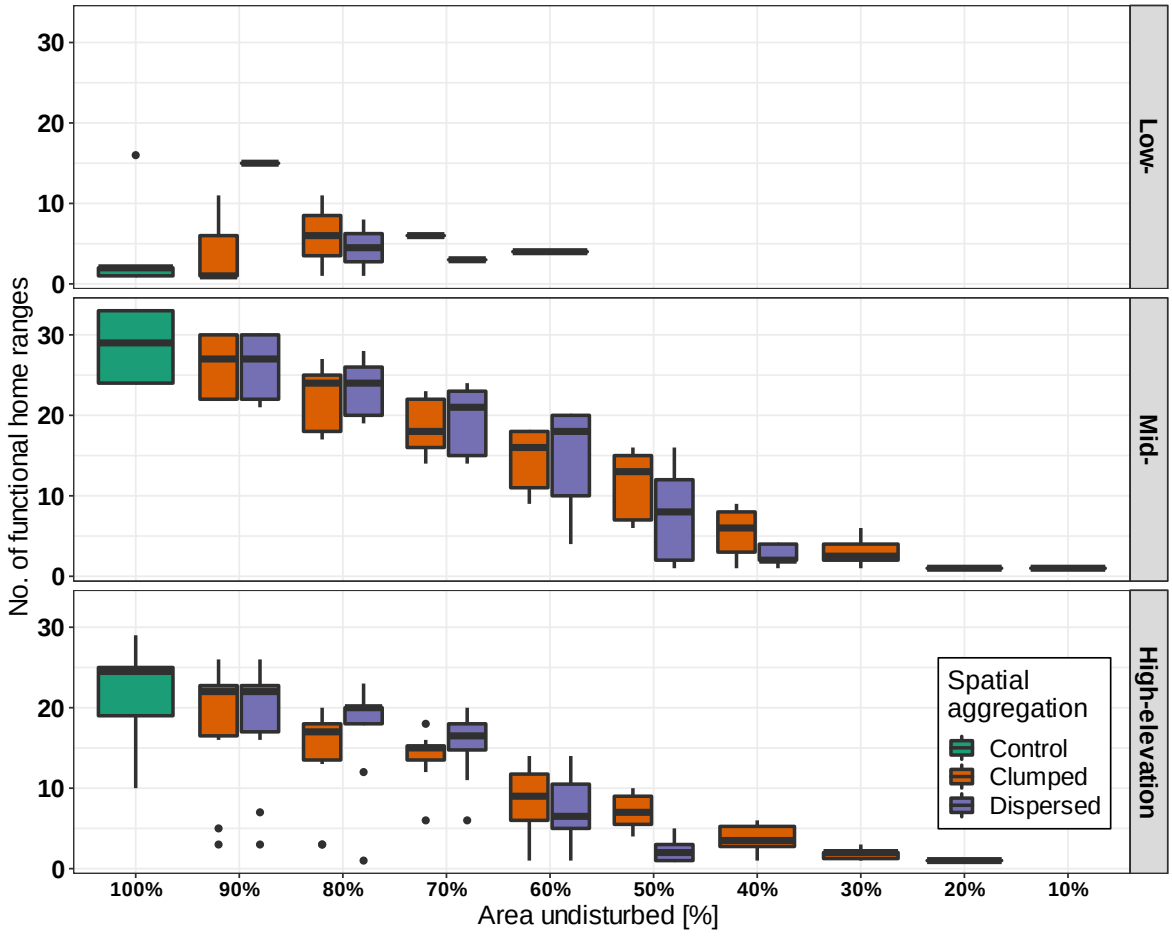

Figure 5.8. Observed declines in number of functional home ranges in neutral landcscapes based on the spatial configuration and properties of survey sites in East Gippsland (faceted by elevation band, see Wagner et al. in review-a - Chapter 4) with increasing disturbance intensity (remaining undisturbed area, x-axis).

Size, feed-area-ratio, and number of home ranges were dependent on the initial spatial aggregation of the feeding landscape and the intensity and aggregation of the disturbance

mask. Landscapes affected by dispersed disturbances exhibited less variation in home range size and feed-area ratio. Increasingly severe dispersed disturbances caused home range numbers to drop more rapidly, and individual remaining home ranges to become larger and contain less feeding habitat. Therefore, an exhaustion of habitat potential was reached at lower fractions of disturbed area. We observed a linear relationship between feed-area-ratio and home range area as an effect of dispersed disturbance. The relationship was nonlinear for high intensity clumped disturbances. Across all simulated landscapes, ranges of feed-area-ratio and home range size were comparable only up to 80% undisturbed area, after which effects on home ranges from both types of disturbance started diverging (Fig. 5.9). With increasing intensity of disturbance, the range and standard deviation (SD) for both home range area and feed-area-ratio remained stable in landscapes affected by clumped disturbance and decreased with dispersed disturbance (Table 5.1).

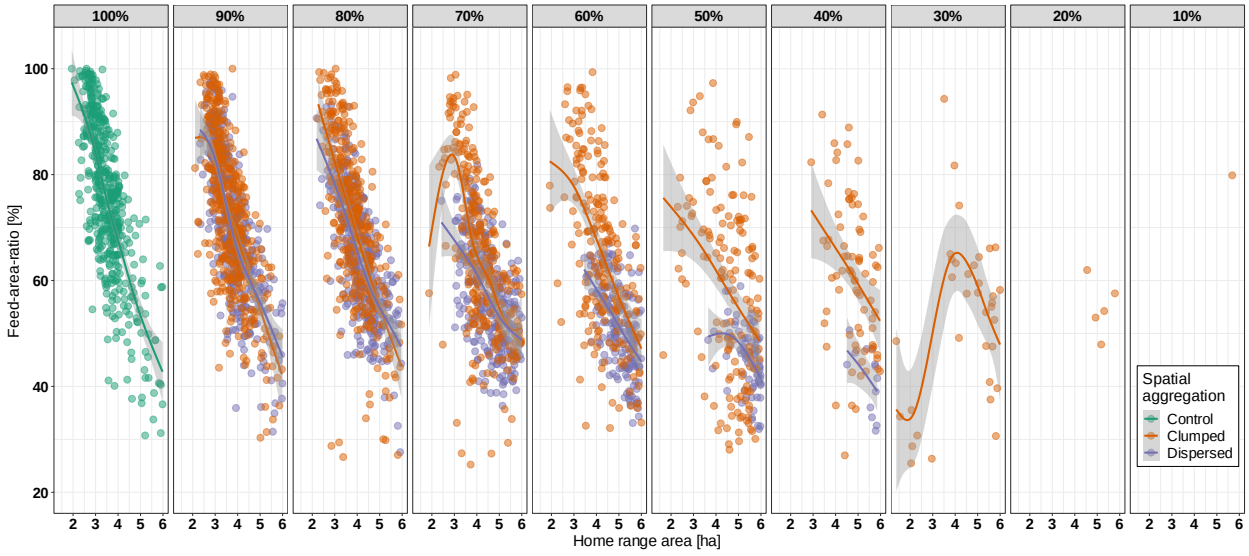

Figure 5.9. The relationship between home range area and feed area ratio of simulated home ranges for undisturbed areas (green) and under clumped (orange) or dispersed (purple) disturbances. Facets illustrate the conditions under different disturbance itensities (100-10% area undisturbed),

Table 5.1. Observed changes in home range area and feed-area-ratio of simulated home ranges under different rates and spatial aggregations of disturbance

Spatial aggregation	Home range area range (ha)	SD home range area	Feed-area-ratio range (%)	SD feed-area-ratio
100%				
Control	4.04	0.75	69.26	14.75
90%				
Clumped	3.86	0.74	69.69	14.24
Dispersed	3.66	0.75	66.31	13.22
80%				
Clumped	3.69	0.78	73.33	15.25
Dispersed	3.76	0.74	65.57	11.58
70%				
Clumped	4.12	0.84	73.62	14.98
Dispersed	3.58	0.76	45.49	9.67
60%				
Clumped	4.08	0.88	67.21	15.39
Dispersed	2.54	0.62	36.72	7.84
50%				
Clumped	4.28	0.97	69.24	16.89
Dispersed	2.35	0.54	26.99	5.95
40%				
Clumped	3.06	0.71	64.35	13.91
Dispersed	1.34	0.47	18.96	6.16
30%				

Clumped	4.62	1.40	68.81	15.86
20%				
Clumped	1.24	0.46	14.06	5.24
10%				
Clumped	0	-	0	-

Discussion

While regional and global drivers of habitat loss, such as climate- and land-use change, are altering ecosystems and threatening species at an increasing rate (Rosenzweig et al. 2008, Butchart et al. 2010, Lindenmayer et al. 2012b), the importance of drivers at finer spatial scales is often overlooked (Villard and Metzger 2014). While large scale drivers may cause complete losses of habitat suitability (Kearney et al. 2010, Adams-Hosking et al. 2011, Wagner et al. 2020), the spatial configuration of habitat may mitigate some of the effects of habitat loss from disturbances that occur at finer scales (Villard and Metzger 2014). Using a generalized simulation framework to develop neutral landscapes, we observed both coarse- and fine-scale effects on the suitability of southern greater glider habitat.

Climate

In our simulations we found that unfavourable climatic conditions overwhelmed the impacts of feeding resource availability. These findings further reinforce recent conclusions that coarse determinants of habitat suitability have a stronger effect on greater glider population persistence at a landscape scale (Kearney et al. 2010, Wagner et al. 2020). The average linear decrease in potential greater glider population density from decreasing climatic suitability was unrelated to the initial amount and spatial arrangement of the high-quality feeding landscapes we used to test these effects. The observed population decline related to climate and independent of habitat availability has been observed on biodiversity worldwide (Mantyka-Pringle et al. 2012) and was reported for greater gliders (Smith and Smith 2020, Wagner et al. 2020), butterflies (Parmesan et al. 1999), mountain pygmy possums (*Burramys parvus*, Hoffmann et al. 2019), koalas (*Phascolarctos cinereus*, Adams-Hosking et al. 2011), and moose (*Alces alces*, McCann et al. 2013). Continuous unsuitable climatic conditions in the form of high ambient temperatures and low water availability will negatively affect the greater glider's ability to forage, reproduce, and persist in these landscapes (Rübsamen et al. 1984, Foley et al. 1990, Kavanagh and Lambert 1990, Youngentob et al. 2021).

Our findings also align with recent observations of local extirpations of greater glider populations from otherwise suitable landscapes at mid-elevation forests in East Gippsland, Victoria (Wagner et al. 2020) and in areas in New South Wales such as Booderee National Park (Lindenmayer et al. 2011) and low-elevation forests of the Blue Mountains (Smith and Smith 2020). Our results highlight that greater gliders are vulnerable to climate-driven loss, even in areas with ample feeding and nesting resources. As such, climate change should be considered a key threatening process when assessing, managing, and conserving the species. Any area that is conserved or retained for greater glider populations but is unsuitable due to unfavourable climatic conditions will not contribute to population persistence. As the climatic conditions in the real landscapes that our simulations were based on are climatically suitable (and may be for the foreseeable future), their protection remains crucial for southern greater glider conservation (Wagner et al. 2020).

Spatial aggregation of feeding habitat

While climate change is the dominant driver of habitat suitability within these landscapes, in areas where the climatic conditions are suitable other factors may limit habitat suitability. The aggregation and amount of foliar feeding resources can vary throughout mature forest landscapes (Appendix 4 Table S1, Moore et al. 2010, Wagner et al. in review-a - Chapter 4). Based on our simulations, these conditions may lead to different abundances and densities in greater glider populations at the stand scale. The spatial aggregation of feeding habitat drove the configuration of potential functional home ranges in our simulations (i.e., amount of home ranges and size and feeding resources per home range). Simulated stands with dispersed feeding resources exhibited more stable and predictable patterns of home range density. But these conditions also led to an earlier loss of home range potential. When forage resources were scarcer, home range areas needed to increase to cover the required 2.6 ha of feeding habitat, while feed-area-ratios within simulated home ranges decreased. This resulted in a loss of functionality and reduction in number of home ranges at higher rates of total feeding area per stand. In forest stands populated by greater gliders that had trees selectively removed, population densities decreased dependant on the amount of harvesting (McLean et al. 2018). Based on our findings, this decrease in population density may therefore be explained by the reduction and increased dispersal of feeding resources that lead to larger individual home ranges. Greater gliders are known to extend home-range sizes when habitat resources are scarce or fragmented (Smith et al. 2007, Youngentob et al. 2013). Clumped feeding habitat allowed for more stable populations at lower rates of total feeding area, but this was dependent on spatial arrangement of the feeding habitat (Fig. 5.7). Even at low rates of total available feeding habitat, a population of greater gliders could theoretically reach higher densities when

feeding resources were clumped. Similar effects on home range sizes and population density have been observed in capybaras (*Hydrochoerus hydrochaeris*, Corriale et al. 2013), river otters (*Lutra canadensis,* Blundell et al. 2000) and Tengmalm's owls (*Aegolius funereus*, Santangeli et al. 2012).

If the initial amount and aggregation of feeding habitat drives greater glider population structure at the stand scale in mature forests, conservation and management should take these factors into account when carrying out fauna surveys, establishing reserves, or altering forest structure. Based on our simulations, only when a forest habitat is composed of ≥70% feeding habitat are potential population and home range structures comparable between forests with clumped and dispersed resources (Fig. 5.7). These conditions are rare in real landscapes (see Appendix 4 Table S1). Below this amount, anticipated conservation targets may only be met by increasing reserve areas or higher rates of habitat retention during timber harvesting. Similarly, the response of these different habitat configurations to disturbance will vary.

Disturbance

The primary disturbances impacting forest-dependent fauna in southeast Australia at the population scale are forest fires and timber harvesting operations (Lindenmayer et al. 2013, Nitschke et al. 2020). Both have been identified as major threats to forest-dependent species such as southern greater gliders, as they alter the structure of the forest by removing foraging and nesting resources (Franklin et al. 2000, Lindenmayer and Sato 2018, McLean et al. 2018). Greater glider populations have the ability to persist in forests that have experienced basal area losses of up to 60% (Kavanagh 2000), an effect that we observed in our simulations of different disturbance intensities (Fig. 5.8). The ability of populations to persist, however, was strongly dependent on the initial spatial configuration of the stand and the spatial aggregation of the disturbance itself. When disturbances were spatially clumped, greater glider habitat features persisted at higher densities, even when only small areas remained undisturbed (Fig. 5.9). Indeed, the level of spatial aggregation was the difference between a local population persisting or going locally extinct when subjected to disturbances of identical intensity (e.g., removing 60% of initial basal area, Fig. 5.4). Some habitat configurations were therefore able to mitigate negative effects of habitat loss (Villard and Metzger 2014). Disturbances leading to dispersal of resources, for example resulting from certain silvicultural techniques such as single-tree retention (Ashton and Kelty 2018), may lead to more severe stand-scale losses of feeding resources and reduce the ability of greater gliders to form or retain functional home ranges. In fact, different forms of tree retention following timber harvesting may lead to distinctly different configurations of habitat and could have the potential to influence population persistence (Lindenmayer 1994, DELWP 2019).

The ability to determine where critical feeding resources are and what their spatial configuration is, may allow retaining them fully under certain retention strategies. High-resolution data from multispectral remote sensing that allows assessing and mapping feeding resources at operational scales may therefore be an important tool in arboreal folivore conservation (Youngentob et al. 2012, Youngentob et al. 2015, Wu et al. 2019, Wagner et al. in review-a - Chapter 4). Our findings suggest that current (voluntary) prescriptions that retain a minimum of 40% basal area (DELWP and ARI staff, personal communication, April & May 2021 & DELWP 2019) or single-tree retention (DEPI 2014, Ashton and Kelty 2018) may not suffice for permanent greater glider persistence at a stand scale, if forage trees are poorly spatially distributed (Figs. 5.8 + 5.9). Similarly, determining habitat resources remotely after high intensity disturbances such as wildfires (Catling et al. 2001, Haslem et al. 2011, Ward et al. 2020) may allow mapping of functional fire refugia (Berry et al. 2015), which may still act as greater glider habitat, or estimate remaining suitable habitat. With this knowledge, managers can protect and support surviving populations by guiding silviculture or designing reserves at finer scales.

Limitations and future research

In this study we used neutral landscape simulations as models of landscape structure to test theoretical effects of changing foraging resources on populations of southern greater gliders. We were able to quantify potential population responses to changes in climate or the quantity and configuration of forage habitat and identify critical thresholds for persistence. These are two of the major contributions neutral landscape models may provide in ecological research (With and King 1997). Our simulated landscapes were based on, and extrapolated from, real and modelled landscape features. In the absence of data, hypothesized effects were tested using generalized assumptions on greater glider population structure such as maximum home range sizes (Pope et al. 2004, Smith et al. 2007) and minimum amount of feeding habitat per home range (Wagner et al. in review-a - Chapter 4). Our results regarding species persistence and animal density matched field observations (Kavanagh 2000, McLean et al. 2015), which suggests our assumptions were robust and logical; however, it is important to test this theoretical knowledge gained with field experiments that control for the assumptions made when using simulated neutral landscapes (With 1997, With and King 1997). This will provide a means to validate the critical persistence thresholds that our neutral models identified. Radio- or GPS-tracking studies could help identify differences in minimum and maximum home range sizes (Harris et al. 1990, Girard et al. 2002) in different parts of the landscape with different configurations of habitat after recent disturbance events such as the Black Summer wildfires (Ward et al. 2020). Coupling this data with spatial predictions of feeding (Youngentob et al.

2012, Wu et al. 2019, Wagner et al. in review-a - Chapter 4) and nesting resources (Owers et al. 2015) will provide a better understanding of the species' perception of its habitat (Moore et al. 2010) and its ability to persist in different parts of the landscape before and after disturbances.

Conclusion

Using a generalized spatial simulation framework based on neutral landscape models, we demonstrated that the spatial configuration of feeding resources and disturbances affect population density and persistence of southern greater gliders in mature *Eucalyptus* forests. Unfavourable climatic conditions acting at larger spatial scales, unrelated to the spatial arrangement of feeding habitat, may create constraints to accessing feeding and nesting resources. At the stand scale greater glider density depended on the spatial arrangement of feeding resources, with clumped feeding habitat allowing earlier population formation and larger populations. Similar population structures in dispersed or clumped habitat were observed only when 70% or more of an observed area was feeding habitat. Disturbances to feeding resources could either retain a population or lead to extinction, depending on spatial aggregation and intensity. Compared to clumped disturbance events, increasingly severe dispersed disturbances caused potential home ranges to disappear more rapidly, and remaining home ranges to become larger and contain less feeding habitat. Our results have important implications for the conservation and retention of critical feeding habitat of southern greater gliders and provide insights into important factors to ensure that greater gliders persist in these landscapes.

Thesis conclusion and future research

The central aim of this thesis was to better understand the habitat and ecology of the greater glider (*Petauroides volans*), an iconic and widely distributed, long-considered common Australian arboreal marsupial, that is now of conservation concern (Lindenmayer et al. 2011, Lindenmayer and Sato 2018). I explored major factors of greater glider habitat selection and suitability across multiple spatial scales to better understand what is contributing to their observed decline. From my findings, I derived implications for management and conservation to support the protection of the species and its mature forest habitat. Habitat preferences of the greater glider are derived from its unique physiology (Rübsamen et al. 1984), diet (Kavanagh and Lambert 1990) and arboreal life-cycle (Gibbons and Lindenmayer 2002). Studies on these requirements have led to important conclusions about the negative impacts of disturbances on the species and about causes of population declines (Lindenmayer and Sato 2018). Greater gliders however, have also disappeared or suffered declines in population density where disturbances have not played a major role (Lindenmayer et al. 2011, Smith and Smith 2018), raising questions about other, more indirect factors, that could be affecting habitat selection and suitability. To better understand what causes these declines, the research I carried out was designed to explore the impacts of climate, foliar nitrogen and habitat configuration on the occurrence and habitat suitability of greater gliders in largely undisturbed mature forests in their southeastern distribution in the state of Victoria, Australia. The questions I aimed to answer revolved around how climate may shape habitat suitability at the landscape scale due to the greater gliders' narrow thermotolerance (Chapter 2); how both nesting and feeding resources are distributed in mature mixed-species *Eucalyptus* forests and relate to greater glider occurrence (Chapter 3); and if foliar nitrogen – an important measure of food quality for folivores – can be estimated at operational scales, using novel remote sensing methods (Chapter 4). Subsequently, and based on the findings from my research aiming to answer these questions, I explored how the amount and spatial configuration of habitat resources and favourable conditions may affect greater glider abundance and distribution (Chapter 5, Fig. 6.1). This conclusion chapter summarises the major findings of my thesis and discusses implications for management and conservation of both the greater glider and its mature forest habitat. I outline future research opportunities that will be worth pursuing, based on the findings in this thesis, to gain an even deeper understanding of how greater gliders use and perceive their habitat and what may cause population declines and persistence.

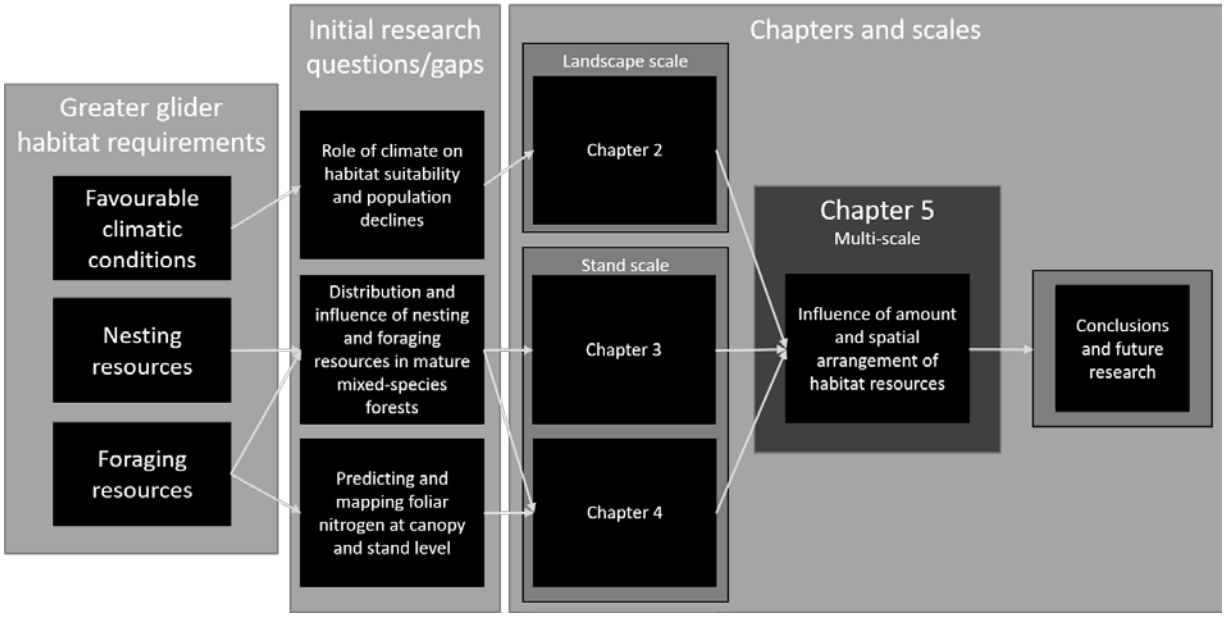

Figure 6.1. Revisiting the thesis and chapter structure.

Main thesis results and conclusions – a summary

Chapter 2: Using presence:absence data from recent greater glider surveys, detailed daily climatic data spanning 33 years (see Stewart and Nitschke 2017a), alongside topographic and disturbance variables, I tested if climate shapes occurrence and habitat suitability of the species in Victoria. Using machine learning models, I identified that, across the landscape, climatic conditions associated with low temperatures and high precipitation and condensation were shaping the occurrence of greater gliders, while disturbance variables played a minor role. Out of all variables selected for the final model of habitat suitability, 2/3 were climatic. Variables describing aridity or nights hotter than the thermoneutral point of the greater glider (20°C), were most important and driving model performance. Furthermore, I found that climatic conditions have changed over time, rendering many sites that were historically occupied by greater gliders, climatically unsuitable today. I identified important climatic refugia and areas that are currently suited to sustain greater glider populations in a warming and drying climate (see Wagner et al. 2020). The ability of these refugia to support greater gliders under future climate change requires further study.

Chapter 3: Collecting forest structural, leaf and soil chemistry, fauna survey and GIS data from mature mixed-species forests in East Gippsland, Victoria, I quantified the availability and distribution of hollow occurrence and foliar nitrogen across a topographic and elevation gradient. Greater gliders were predominantly found in highly productive, high elevation sites,

where tree species with high foliar nitrogen levels dominated the canopy. Hollow occurrence and abundance were high across study sites and did not differ significantly between elevations and forest types. Both these stand-scale determinants of greater glider habitat selection could be estimated from survey, chemistry and GIS data using generalized linear models and covariate relationships were explored with structural equation models. Hollows were best estimated from tree and forest structure and age, with large mature trees with poorer form most likely to contain hollows. Foliar nitrogen was driven by site productivity and climate, but tree and stand age had negative effects on nitrogen levels and digestibility. I concluded that hollows are not limiting, and foliar nitrogen is a major driver of habitat suitability in the mature forests of the study landscape at the stand scale. My results also highlight the need for a heterogenous forest structure to provide both foraging and nesting opportunities for greater gliders.

Chapter 4: For this chapter, I sought to determine if favourable habitat conditions could be assessed through remote sensing to reduce time-intensive laboratory determinations of foliar nitrogen. I used multispectral canopy reflectance, collected by an unoccupied aerial vehicle (UAV), leaf sampling and in-vitro digestions and machine learning models to estimate canopy nitrogen and spatially map favourable feeding habitat for the greater glider. I found correlations between canopy spectral reflectance, derived vegetation indices and canopy nitrogen. Using supervised classification, these models were also capable of spatially predicting feeding habitat that had $\geq$1% nitrogen per gram dry mass (see Cork 1992). These spatial predictions were further refined by using another data product from UAV imagery – canopy height models – to remove any subcanopy and gap non-habitat areas from the predictions and then assess the spatial configuration of feeding resources within the study sites at a scale relevant to the greater gliders' home range (4 ha).

Chapter 5: Finally, I explored how spatial configuration and aggregation of favourable habitat resources and conditions affect greater glider abundance and density. I developed a generalized spatial framework using neutral landscape models based on the properties of real landscapes, and both literature and field observations to hypothesize functional greater glider home ranges. At the landscape scale, I found that any decrease in climatic suitability also decreased potential population density, independent of the initial spatial configuration of the feeding landscape. At the stand scale however, the spatial configuration of feeding habitat was driving population density. Dispersed resources required increased home range sizes for individual greater gliders to obtain sufficient feeding resources and resulted in smaller local populations. Clumped resources were predicted to support larger populations of greater gliders, even when only small fractions of the simulated stand contained feeding habitat. Disturbances to these resources

could either retain a population or lead to extinction, depending on spatial aggregation and intensity. Increasingly severe dispersed disturbances caused potential home ranges to disappear more rapidly and remaining home ranges to become larger and contain less feeding habitat. The ability of greater gliders to establish populations and persist under disturbance was therefore highly dependent on the spatial aggregation of important habitat resources and the type and severity of disturbance. Changes in climate, however, will act at a different scale and may override favourable habitat conditions at the stand-level.

Important implications for management and conservation

A central aim of this thesis was to better understand causes for greater glider population declines, where threats from disturbances such as fire and timber harvesting may not be a factor. My findings have some important implications to improve or adapt future management of the greater gliders' arboreal habitat and some new factors to consider in their conservation. As these findings refer to different spatial scales – landscape scales of 1000 ha or more and stand scales spanning between 4 to 100 ha (Turner and Gardner 2015) – I will discuss the most important conservation and management implications based on scale.

Managing and conserving greater glider habitat across the landscape

Chapter 2 provides insight into the great importance of a climate regime favouring the greater gliders' narrow thermotolerance (Rübsamen et al. 1984) and links the species' unique physiology to climatic factors occurring across entire landscapes (Kearney et al. 2010, Wagner et al. 2020). I observed the high importance of a favourable climate across the greater gliders' main areas of distribution in Victoria and was able to link population declines and habitat contractions to changes in climate over time (Wagner et al. 2020 - Chapter 2). Climate was an important driver of habitat suitably across all studied regions and climate change contracted habitat across all three landscapes. My findings may help explain population declines in other regions where timber harvesting, fire or both were not a factor, such as Booderee National Park and the Blue Mountains in New South Wales (Lindenmayer et al. 2011, Smith and Smith 2018). Nevertheless, climate is not yet considered in management and conservation of greater glider habitat, although its importance in Victoria has been recognized in late 2019 (see DELWP 2019). While vast areas, especially in the Central Highlands of Victoria and East Gippsland, have become climatically unsuitable since the 1980s, I was able to identify climatic refugia and even some areas that developed more favourable conditions over time (Wagner et al. 2020 - Chapter 2). Based on my results, the Immediate Protection Areas (IPAs) established in late 2019 and aimed at conserving mature forests and forest-dependant fauna such as the

greater glider (see DELWP 2019), only covered small fractions of climatically suitable habitat. According to my models, there were around 300,000 ha of highly suitable habitat outside any current reserve or protected area, that may have greatly contributed to the greater gliders' conservation (Wagner et al. 2020 - Chapter 2). Large parts of this suitable habitat range burnt severely during the devastating 2019/20 'Black Summer' bushfires in the east of Victoria (Ward et al. 2020). Some areas of high greater glider abundance and stable climatic conditions such as the mature forests around Bendoc on the Errinundra Plateau (Fig. 6.2, Wagner et al. in prep, Wagner et al. in review-a - Chapters 3+4), which are managed for timber, were spared and could therefore be a logical target for protecting functional refugia for threatened species conservation under a future of climate change and increasingly frequent fires (Hoffmann et al. 2019, Geary et al. 2021). Based on results from Chapter 5 an important advice for future management decisions is also related to the relationship between climate occurring over large scales and other habitat resources at finer scales. In areas where greater gliders are disappearing even with an abundance of suitable feeding- and nesting habitat, climate change should be considered a threatening process when assessing, managing and conserving habitat. Any fraction of otherwise suitable area that is conserved, but inaccessible due to unfavourable climate, may not actually lead to population persistence (Wagner et al. in review-b - Chapter 5) – a process that may have contributed to the protection of climatically unsuitable areas when establishing IPAs in Victoria in 2019. My models also suggest climatically suitable habitat in areas not usually considered greater glider habitat. Some of these regions, such as high elevation snow gum (*Eucalyptus pauciflora*) forests in alpine regions, may not have preferred fine-scale habitat resources in the form of tree hollows or high quality foliage (Cunningham et al. 2004). Other areas however, may exhibit both suitable climate and mature forests composed of favourable tree species but have not been surveyed recently. They may thus be home to greater glider colonies outside the scope of current conservation discussions. Habitat suitability maps from Chapter 2 may therefore be a valuable tool to designing and implementing future survey programs.

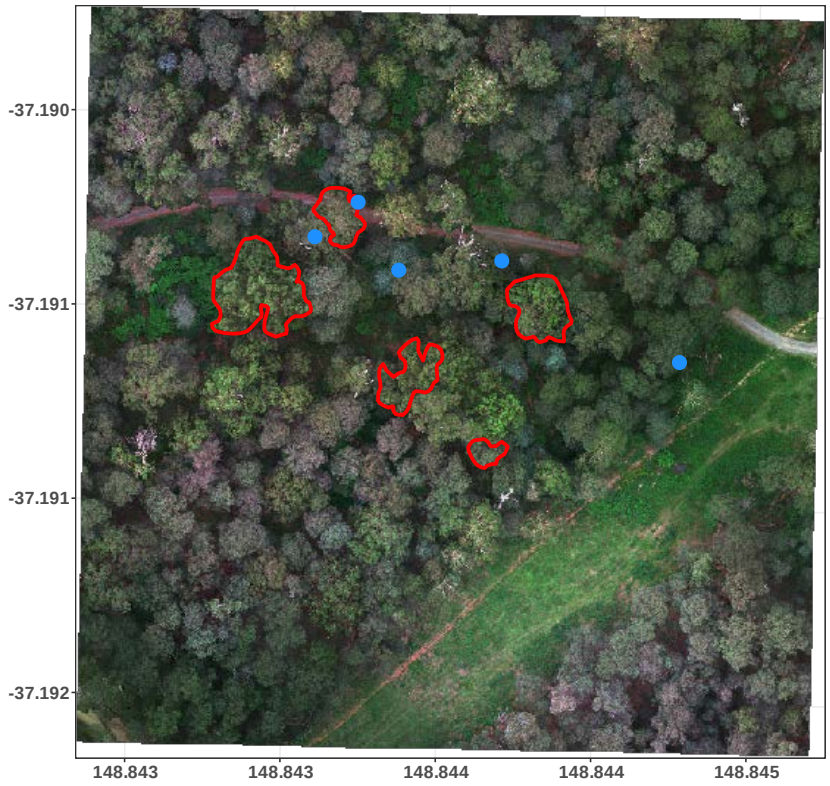

Figure 6.2. Aerial view of a survey plot in Bendoc State Forest (SF), adjacent to Mustards Road on the Errinundra Plateau, East Gippsland. This site is composed of mature *Eucalyptus obliqua* and *E. croajingolensis*, high in foliar nitrogen and abundant with tree hollows. During our fauna surveys for Chapters 3 and 4, we encountered a high abundance of greater gliders at this site. Five individuals were spotted within the 4-ha plot area (blue points), some of which were observed on or near our five sample trees (red outlines). Along the 1 km survey transect following the forest track, a total of 14 greater gliders were recorded. As this area was subject to future timber harvesting, our findings were reported to DELWP and greater glider numbers confirmed by government contractors carrying out pre-harvest surveys. The area is now a 100 ha greater glider reserve. At other sites in the area, we encountered similar abundances of greater gliders, but not reaching the threshold of 10 per transect kilometre that would warrant reporting survey results. Some forests in Bendoc SF have since been harvested at variable rates of tree retention. Locations of fauna observations from our surveys are available on the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/).

Implications for fine-scale detection and management of habitat resources

At finer scales, hollow occurrence and trees with high foliar nitrogen drive habitat suitability for greater gliders (Gibbons and Lindenmayer 2002, Youngentob et al. 2011). The ability to determine these resources is crucial to for example assess and conserve remaining undisturbed habitat in managed forest landscapes impacted by wildfires (Ward et al. 2020, Geary et al. 2021). Studying factors driving hollow occurrence and foliar nitrogen levels in Chapter 3, I identified maturing and ageing trees may increase habitat suitability through the formation of hollows, while also becoming less favourable to forage on, due to decreases in digestibility or nitrogen levels. Although mature forest ages are important for the formation of hollows and therefore form the basis of stand-scale habitat suitability for many arboreal species (Gibbons

and Lindenmayer 2002, Fox et al. 2009), my findings and those of others indicate that uniformly old forests may not express the most favourable feeding conditions for folivores (Moore and Foley 2005, Moore et al. 2005, DeGabriel et al. 2009b, DeGabriel et al. 2009a, Youngentob et al. 2011, Wagner et al. in prep - Chapter 3). Consequently, we observed few or no greater gliders when surveying in some tall but even-aged forests near the Arte River Flora Reserve, East Gippsland, composed of species that can contain high levels of foliar nitrogen (such as *Eucalyptus obliqua*). Therefore, a heterogenous forest structure that provides both foraging and nesting opportunities should improve habitat suitability, which could be an important consideration in silviculture and reserve design.

Although generalized linear models could determine both hollow occurrence and foliar nitrogen from forest inventory and GIS data in Chapter 3, remote sensing approaches to replace time- and labour-intensive surveys may improve and speed up habitat assessments to aid decision making. In Chapter 4, I developed a comprehensive method to remotely determine where critical feeding resources are, and how they are spatially configured. Methods of assessing and mapping feeding resources at operational scales can be an important tool in the conservation of arboreal species. It may be used for mapping functional fire refugia that act as crucial remaining habitat after severe fires (Berry et al. 2015), or improve tree retention strategies (Youngentob et al. 2012, Youngentob et al. 2015, Wu et al. 2019, Wagner et al. in review-a - Chapter 4). With information from my models and mapping, managers could protect habitat and support populations of greater gliders by guiding silviculture or designing reserves at finer scales. It may also shed light on the performance of current survey standards (see Nelson et al. 2018). As the configuration and abundance of feeding resources can vary greatly and affect population densities, spotlighting survey methods may need to be adapted for different forest types to ensure comparable detection rates across landscapes (Wintle et al. 2005, Wagner et al. in review-a - Chapter 4).

Using the resulting feeding habitat maps from Chapter 4 and extrapolating them using neutral landscape models, I was able to evaluate some current management strategies aimed at retaining greater glider populations in managed forests in Chapter 5. Some, especially clumped, habitat configurations were able to mitigate negative effects of habitat loss (see Villard and Metzger 2014). Dispersed disturbances that may result from certain silvicultural techniques, such as single-tree retention (Oliver and Larson 1996), can lead to more severe stand scale losses of feeding resources and therefore likely negatively affect greater glider population persistence (Wagner et al. in review-b - Chapter 5). Methods and voluntary prescriptions of retaining a minimum of 40% tree basal area in greater glider habitat managed for timber (DELWP and ARI staff, personal communication, April & May 2021 & DEPI 2014, DELWP

2019), may not suffice to retain functional greater glider populations at a stand scale, if forage resources are distributed in certain spatial configurations (Fig. 6.3). An assessment of the amount and spatial arrangement of feeding resources prior to management actions within a potentially occupied site could therefore support choosing the best retention strategy based on habitat distribution and abundance.

Figure 6.3. Left: A/Prof. Craig Nitschke inspecting a harvested forest coupe near Bendoc on the Errinundra Plateau, that was subject to seed-tree retention and subsequent burning. Right: Aerial view of a high rate of aggregated retention in managed *Eucalyptus regnans* forests in the Central Highlands of Victoria near the Acheron Way. Based on findings from Chapter 5, these distinctly different retention strategies can lead to unique spatial patterns of feeding habitat and may therefore either cause a local extirpation, by dispersing potential habitat or persistence of a greater glider population, by retaining sufficient aggregated resources. Picture Credits: Benjamin Wagner.

Opportunities for future research

From the findings and implications of my thesis outlined above, some interesting new research questions could be derived:

- *Can current climatic refugia provide suitable habitat under different climate change projections, and will new refugia develop?*

- *What is the response of important flora, associated with, and important for, arboreal folivore habitat to climate change?*

- *Can we develop or improve methods of remotely sensing hollow occurrence and abundance to comprehensively integrate both stand-scale determinants of habitat suitability?*

- *Can models using UAV multispectral imagery to estimate foliar nutrition be improved to map digestible nitrogen or leaf toxins?*

- *Can simulated patterns of greater glider habitat selection and population structure in response to habitat arrangement and disturbance be observed in nature?*

More questions come to mind, some of which are detailed in the research chapters of my thesis. As these questions and opportunities for subsequent research pertain to different factors of greater glider habitat suitability, it is best to discuss them separately.

Climate and physiology

An important research endeavour building on my findings around the importance of climate in shaping greater glider habitat, will be exploring how current climatic refugia develop under climate change projections in southeastern Australia. Using highly detailed climate data, I identified drastic changes and contractions between the 1980s and early 2010s in the favourable temperature-, precipitation- and condensation conditions greater gliders require (Wagner et al. 2020 - Chapter 2). It would therefore be important to estimate, whether these changes continue in the future and determine where the most stable habitat under different climate change projections can be found. While changes and range shifts have been predicted in literature under a 3°C warming scenario (Kearney et al. 2010), they were less pronounced in the southeast. This may be attributed to the coarse 9" resolution used to predict habitat across all of eastern Australia (Kearney et al. 2010). Fine-resolution data, such as developed by Stewart and Nitschke (2017a) and applied in Chapter 2, may be beneficial in studying a variety of climate change scenarios on greater glider habitat in their southeastern distribution. Recent genetic evidence supporting three greater glider species (McGregor et al. 2020) should also encourage research into adaptions to environmental conditions of these (new) species. As greater gliders occur in distinctly different climatic regions of Australia (Jackson 2012), their physiology should have evolved to different night-time temperatures and the southeastern greater gliders' 20°C thermoneutral point (Rübsamen et al. 1984) may not be a universal measure of habitat suitability. A better understanding of the effects of climate on greater

glider populations across their geographic range, as has been identified for other folivores (see e.g. Briscoe et al. 2015), will enable managers to identify and conserve climatic reserves throughout their geographic range.

While it has been shown that an increase in ambient temperatures will affect populations and distributions (Kearney et al. 2010, Smith and Smith 2020, Wagner et al. 2020), other effects of climatic change on forest habitat, such as increased ambient CO_2 levels, have not yet been investigated in relation to greater glider habitat suitability. Research on southeastern Australian eucalypt species shows species-specific responses to differences in temperature, soil moisture and humidity, as expressed by reduced growth, flowering phenology and range-shifts and thus negative effects on plant productivity (Rawal et al. 2014, Rawal et al. 2015a, Au et al. 2019a). This may link the spatial scales addressed in this thesis and climate change with negative effects on feeding resources. Observations on effects of elevated CO_2 levels on *Eucalyptus* foliage indicate a change in foliar C:N ratios in favour of carbon, indicating lower levels of nitrogen may be available to folivore species when feeding under such conditions (Lawler et al. 1997, Cotrufo et al. 1998, Kanowski 2001). Increased ambient carbon dioxide levels were found to lower leaf nitrogen and increase phenolics and condensed tannins, making the leaves not only poorer in nutrients, but also less digestible (Lawler et al. 1997). Similar results were reported for Australian mid-successional and pioneer species, which showed only 30% of ambient nitrogen levels in an increased CO_2 experimental environment (Kanowski 2001). Findings on important foraging species for folivores such as the greater glider are still rare, but experiments studying effects of elevated CO_2 levels on mature plants, such as EucFACE (see e.g. Hasegawa et al. 2016, Andresen et al. 2020), may enhance our knowledge on further potential threats of climate change to arboreal folivores and their habitat.

Hollow-bearing trees

Although I identified that hollow occurrence did not limit greater glider occupancy in the mature forests studied for this thesis, hollow bearing trees are amongst the most important factors of arboreal fauna habitat selection (Gibbons and Lindenmayer 2002). It would therefore be beneficial to develop methods to determine the occurrence and abundance of hollows remotely. When, for example, assessing feeding habitat using UAVs, one could integrate both measures driving occurrence and abundance at the stand level into a comprehensive habitat detection methodology. The strong importance of tree and forest structural metrics driving hollow occurrence identified in Chapter 3 and literature (see Lindenmayer et al. 1991b, Fox et al. 2008, Wagner et al. in prep - Chapter 3) should provide an opportunity to develop models to predict hollow occurrence based on forest structure from remote sensing (Popescu and Wynne 2004, Getzin et al. 2012). Tree heights, crown area and even diameters can be derived

from remote sensing data such as laser scanners (LiDAR) or photogrammetry and have been successfully applied in estimating hollow occurrence in Australia and elsewhere (see Koch et al. 2006, Koch and Baker 2011, Khosravipour et al. 2014, Ellis et al. 2015, Owers et al. 2015, Stone et al. 2016, Fedrigo et al. 2019). Tree height and diameter were most important in estimating hollow abundance and occurrence in the mixed-species forests I studied, but diameter is not as easily estimated from photogrammetry-derived UAV imagery as compared to LiDAR data (Khosravipour et al. 2014, Scher et al. 2019). Nevertheless, relationships between diameter, tree height and crown area may help estimating a tree's diameter from such data (Ashton 1976, Oliver and Larson 1996). In a trial with data from Chapter 3, the tree diameter from my 150 sample trees was positively related to both tree height and crown area. Subsequently, I extracted the maximum height and crown area from photogrammetry-derived canopy height models of my sites and used generalized linear models to predict each tree's diameter from remotely sensed data only (Fig. 6.4). Using the predicted diameters and extracted tree heights from UAV canopy height models, I tested whether I can estimate hollow occurrence from this data only and found similar patterns as observed in the models based on survey data presented in Chapter 3 (Fig. 6.5).

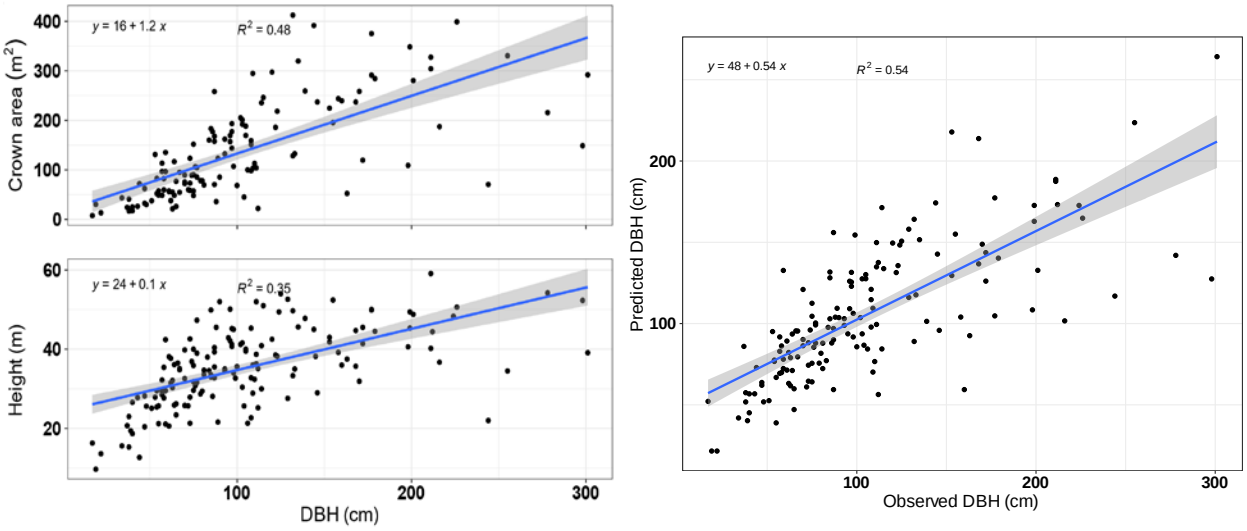

Figure 6.4. Preliminary results towards a method of remotely sensing tree diameter and hollow occurrence from photogrammetry. Left: The relationship between tree diameter and crown area or height in the mature *Eucalyptus* forests sampled in East Gippsland. Right: Linear regression between tree diameter measured in the field (x-axis) and as predicted from UAV-derived tree height and crown area (y-axis).

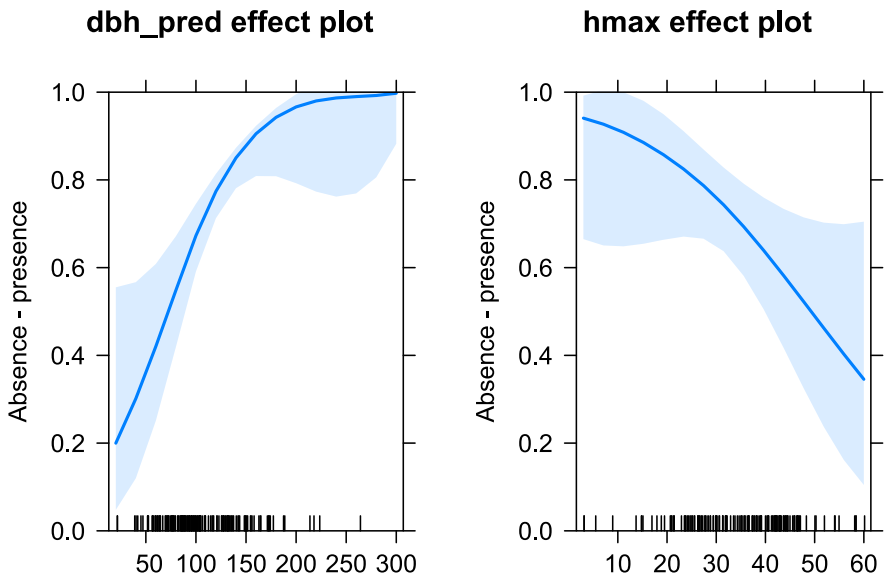

Figure 6.5. Partial dependence plots from a generalized linear model using predicted tree diameter (dbh_pred) and maximum tree height extracted from a UAV-derived canopy height model (hmax) to estimate tree hollow presence or absence. I observed similar responses from remotely sensed data as observed in Chapter 3. Both variables were significant in estimating hollow occurrence (both $p<0.01$).

This preliminary analysis did not fit the scope of Chapters 3 or 4 and was not included in the thesis. Nevertheless, it sheds light on the possibilities to further develop and improve methods of remotely sensing factors of habitat suitability for greater gliders and other arboreal species.

Foliar nitrogen

An attempt to map digestible nitrogen (digN) similar to total nitrogen (N) in Chapter 4, did not produce satisfying results. This may be due to missing lower multi- (see Wu et al. 2019) or hyperspectral reflectance bands (see Youngentob et al. 2012) in the sensor I used. Furthermore, I was not able to consider the effects of plant secondary chemistry on greater glider occurrence and abundance due to timely and budgetary restrictions. Tannins binding proteins to plant tissue cause large differences in N and digN and anti-herbivory defences may limit the quality of foliage high in digN (Lawler et al. 1998b, Lawler et al. 1998a, Marsh et al. 2003). The ability to similarly predict and spatially map digN (see Youngentob et al. 2012, Wu et al. 2019), and a method that can remotely sense FPC concentrations, could distinguish and enhance classifying feeding habitat in the study region in more detail. The latter may be possible using hyperspectral leaf reflectance (see Ebbers et al. 2002, Couture et al. 2016). Given FPCs only occur in one of the two *Eucalyptus* subgenera found in the study area (*Symphomyrtus*), there may also be potential using multi- or hyperspectral canopy reflectance patterns for classifications at the sub-generic level (Goodwin et al. 2005, Baldeck et al. 2015). This ability may further aid in characterizing feeding habitat abundance and configuration at

the home range and stand scale. I found that vegetation indices can be used to reduce the limitations small multispectral sensors with a limited wavelength range can have. Therefore, there may be other indices, not considered in my analysis (Xue and Su 2017), that may enable modelling and mapping digestible nitrogen and other chemicals.

Recent megafires severely burnt vast areas of both climatically and nutritionally suitable habitat in southeastern Australia (Ward et al. 2020, Geary et al. 2021). Greater gliders that survive fires in insulated hollows may face starvation due to limited migration capability or not being able to reach unburnt foraging habitat (Pope et al. 2004, Smith et al. 2007, McLean et al. 2018). As many of the greater gliders' favoured tree species are epicormic resprouters (Ashton 1976, Kavanagh and Lambert 1990, Cunningham et al. 2004) that may survive a fire event, interesting questions arise for population persistence in patchily burnt habitat. Koalas (*Phascolarctos cinereus*), in a study of their behaviour in burned and patchy habitat, recolonised and used previously burnt trees within a month after the fires, foraging on their young foliage (Matthews et al. 2016). Not much is known about whether greater gliders use epicormic leaves as a foraging resource, and their nutritional quality and chemical properties. Mature leaves can contain more nitrogen but are also more fibrous, and therefore major parts of their nutritional value can be indigestible, which is why many arboreal folivores favour young foliage (Kavanagh and Lambert 1990, Hume 1999, Moore et al. 2004b). This may have important implications for the recolonization of burnt habitat within a patchy burnt and unburnt habitat matrix: If greater gliders feed on epicormic leaves, burnt but regenerating forests may be more suitable habitat than previously thought and managed with caution. Since fires can remove large numbers of hollow-bearing trees and therefore nesting resources (McLean et al. 2015, Lindenmayer et al. 2019, Lindenmayer et al. 2020), investigations into the usefulness of nest boxes to improve habitat quality in such potential habitats (Lindenmayer et al. 2009, Goldingay et al. 2020) would further improve our understanding of what drives greater glider population decline or persistence after fires.

Greater glider habitat selection and population structure

Simulated landscapes in Chapter 5 were based on, and extrapolated from, real landscape features, quantified in Chapters 2 and 4. In the absence of data, greater glider population and home range structure in the study landscape were hypothesized from literature and my own observations and model findings (see e.g. Pope et al. 2004, Smith et al. 2007, Wagner et al. in review-a - Chapter 4). Species persistence thresholds and effects on animal density matched observations from other parts of the greater gliders' distribution (Kavanagh 2000, McLean et al. 2015), however, it is important to test the theoretical knowledge gained from simulation studies with field experiments that control for the assumptions made in generalized null models

(With 1997, With and King 1997). This would allow confirming or adapting critical persistence thresholds identified. Greater glider home ranges sizes can vary greatly in different parts of their distribution and in response to habitat fragmentation (see e.g. Pope et al. 2004, Smith et al. 2007). Therefore, a crucial starting point for such studies would be determining the rate of home range expansion when feeding and nesting resources become increasingly dispersed, and an assessment of average required rates of feeding habitat per home range in different forests types across the landscape. Radio- or GPS-tracking studies could help identify differences in minimum and maximum home range sizes in the mixed-species forests studied (Harris et al. 1990, Girard et al. 2002) and after recent disturbance events such as the Black Summer wildfires (Ward et al. 2020). Coupling this crucial data with spatial predictions of feeding (Youngentob et al. 2012, Wu et al. 2019, Wagner et al. in review-a - Chapter 4) and assessments of nesting resources (Owers et al. 2015, Wagner et al. in prep - Chapter 3), will provide a better understanding of the species' perception of its habitat and use of the resources available (see e.g. Moore et al. 2010). A field study examining the findings of Chapter 5 would therefore benefit our understanding of the ability of greater gliders to persist in different parts of the landscape before and after disturbance.

Closing remarks

Although for this thesis I set out to better understand habitat requirements to inform our understanding of the recent declines in greater glider populations, their mature arboreal habitat in southeastern Australia is home to a wide range of fauna and flora species. Due to its strict habitat requirements and distinct niche, species such as greater gliders present unique opportunities to study the complex and variable effects leading to fauna habitat formation, suitability and configuration across spatial scales (Mazerolle and Villard 1999). Because of the knowledge and understanding gained from studying such species, we can adapt and improve management and conservation. Therefore, the greater glider has become a flagship species for the conservation of old-growth forest ecosystems, with benefits to a range of associated species sharing its habitat (Fig. 6.6). Results presented here may therefore benefit the conservation of many of species relying on similar habitat and sharing their forest home with the greater glider.

Figure 6.6. Some species frequently observed during spotlighting surveys for greater gliders: Common ringtail possums (*Pseudocheirus peregrinus*, A – Picture Credits: Christoph Parsch), mountain brushtail possums (*Trichosurus cunninghami*, B), powerful owls (*Ninox strenua*, C - observed here with greater glider prey, Picture Credits: Mike Ryan), sugar gliders (*Petaurus breviceps*, D) and the critically endangered Leadbeater's possum (*Gymnobelideus* leadbeateri, E) are only a few of the many species sharing their arboreal habitat in mature and old-growth forests with the greater glider. Unless otherwise indicated, Picture Credits: Benjamin Wagner.

My research was inspired and based on important findings about the greater gliders' physiology, resource requirements and forest habitat, produced by determined and outstanding ecologists and researchers (e.g. Rübsamen et al. 1984, Foley and Hume 1987, Kavanagh and Lambert 1990, Cork 1992, Hume 1999, Moore et al. 2004b, Smith et al. 2007, DeGabriel et al. 2009a, Kearney et al. 2010, Youngentob et al. 2011, Briscoe et al. 2015, McLean et al. 2015, Lindenmayer and Sato 2018, McGregor et al. 2020, Smith and Smith 2020 and many more). I hope that my findings presented here, may aid in furthering our understanding of this unique species and help protecting it into an uncertain future. I further aspire that this work may motivate and drive others to explore and study forest fauna and flora to contribute to the conservation of Australia's unique arboreal wildlife and their precious forest habitat.

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Appendix 1

Chapter 2 - Supplementary figures and tables

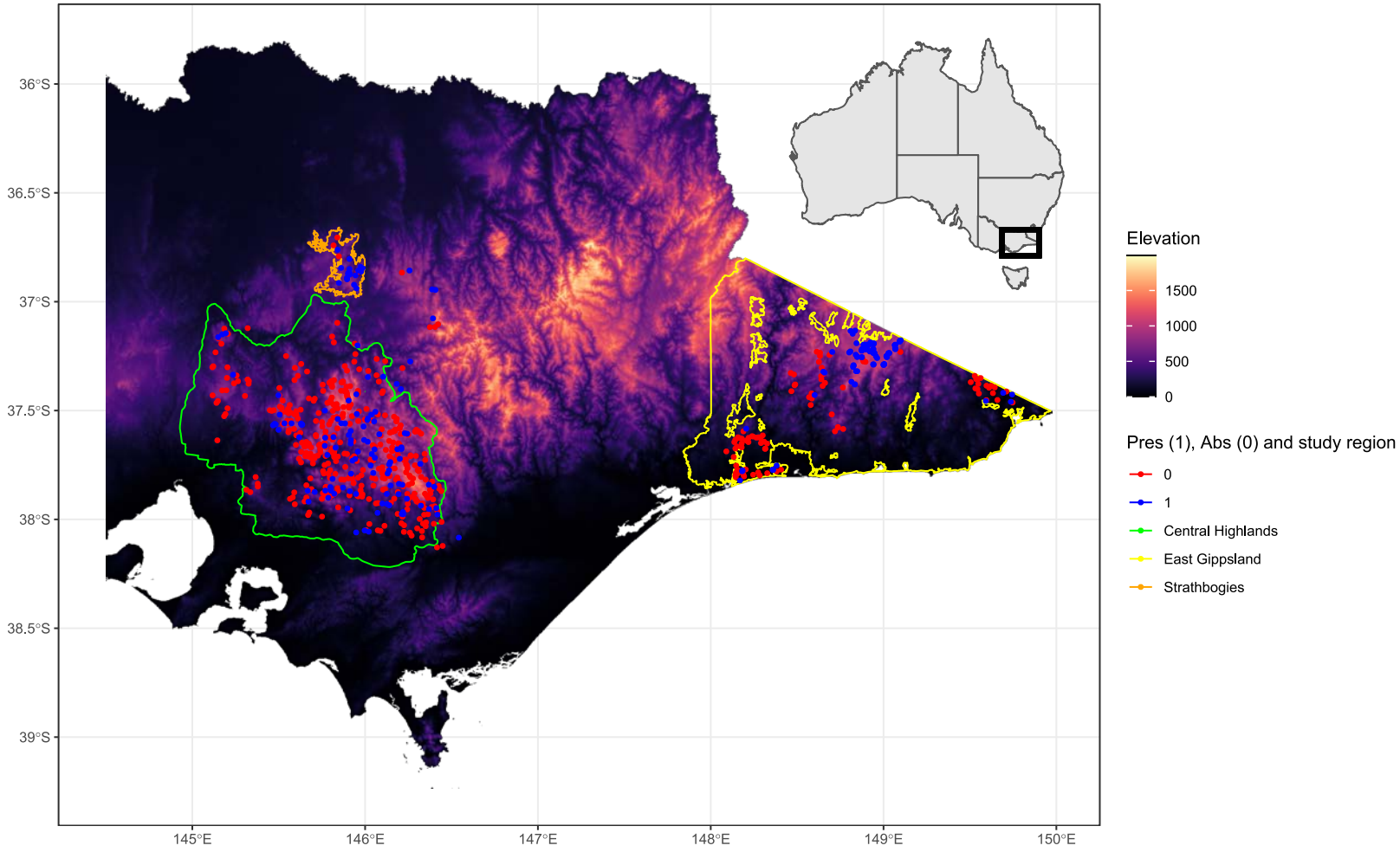


Figure S1. Map of study regions in eastern Victoria with focus landscapes (lines), total presence and absence observations (points) and elevation (colour gradient)

Table S1. Initial modelling variables before variable selection, their unit and description. Only variables related to the total 33-year timeframe were used in the modelling process.

Variable	Unit	Description
site	text	Site Name
GG	integer	Greater Glider presence (1) or absence (0)
Zone	integer	Site Zone (0 = Central Highlands, 1 = East Gippsland Highlands, 2 = Strathbogie Ranges)
FT	code	EVC Forest Type
Ele	numeric	Elevation of the Site
hn	integer	Number of Nights above 20*C from 1981 - 2014
NDVI	numeric	Landsat 8 NDVI value at survey date
slope	degree	Slope of Site
aspect	degree	Aspect of Site
parentmat	text	Parent Material of Site
soiltype	text	ASC soil type code (see http://www.clw.csiro.au/aclep/asc_re_on_line_V2/append2.htm)
soilsubtype	text	ASC soil sub type code (see http://www.clw.csiro.au/aclep/asc_re_on_line_V2/append2.htm)
pH	numeric	Soil pH of Site
ESPP1	code	Primary (most abundant) eucalypt species recorded in SFRI code
ESPP2	code	2nd most abundant eucalypt species recorded in SFRI code
SPP1COVER	percent	The percent of the ground area covered by the crowns of SPP1 (SFRI)
SPP2COVER	percent	The percent of the ground area covered by the crowns of SPP2 (SFRI)
EUCPREDOM	text	The relative abundance of SPP1, compared with SPP2, SPP3 and SPP4 (SFRI)
EUCGROUP	text	Species grouping based on species associations and wood characteristics (SFRI)
STANDHT	m	The midpoint of height class assigned to the dominant crown component recorded in SFRI code
EUCCOVPC	percent	The midpoint of the eucalypt crown cover class recorded in SFRI code
TREAT_YEAR	year	The year of TREATCAUSE. The 2nd calendar year of the financial year is recorded (SFRI)
TREATCAUSE	code	Most recent event (harvest or fire) that caused a moderate modification to the stand structure (SFRI)
CONDN	code	Summarizes past disturbance events and the effect on the stand structure (SFRI)
ORIGIN	year	The financial year that the stand originated. These include recorded (in logging history or fire severity mapping) or modelled value (SFRI)
fires	numeric	Number of fires (bushfires and planned burns) in site from 1980 - 2017

log	numeric	Number of timber harvesting operations carried out in site from 1980 - 2015
age	numeric	age of the stand according to SFRI (2017-tminsitesCHyy$TREAT_YEAR)
northness	angle	northness of site
eastness	angle	eastness of site
81to14MAP	mm	Mean annual precipitation from 1981 - 2014
81to14MAXP	mm	Maximum annual precipitation from 1981 - 2014
81to14MINP	mm	Minimum annual precipitation from 1981 - 2014
80sMAP	mm	Mean annual precipitation from 1981 - 1990
80sMAXP	mm	Maximum annual precipitation from 1981 - 1990
80sMINP	mm	Minimum annual precipitation from 1981 - 1990
90sMAP	mm	Mean annual precipitation from 1990 - 2000
90sMAXP	mm	Maximum annual precipitation from 1990 - 2000
90sMINP	mm	Minimum annual precipitation from 1990 - 2000
00sMAP	mm	Mean annual precipitation from 2000 - 2010
00sMAXP	mm	Maximum annual precipitation from 2000 - 2010
00sMINP	mm	Minimum annual precipitation from 2000 - 2010
10sMAP	mm	Mean annual precipitation from 2010 - 2014
10sMAXP	mm	Maximum annual precipitation from 2010 - 2014
00sMINP	mm	Minimum annual precipitation from 2010 - 2014
81to14MAT	°C	Mean annual temperature from 1981 - 2014
81to14MAXT	°C	Mean maximum temperature from 1981 - 2014
81to14MINT	°C	Mean minimum temperature from 1981 - 2014
80sMAT	°C	Mean annual temperature from 1981 - 1990
80sMAXT	°C	Mean maximum temperature from 1981 - 1990
80sMINT	°C	Mean minimum temperature from 1981 - 1990
90sMAT	°C	Mean annual temperature from 1990 - 2000
90sMAXT	°C	Mean maximum temperature from 1990 - 2000
90sMINT	°C	Mean minimum temperature from 1990 - 2000
00sMAT	°C	Mean annual temperature from 2000 - 2010
00sMAXT	°C	Mean maximum temperature from 2000 - 2010
00sMINT	°C	Mean minimum temperature from 2000 - 2010
10sMAT	°C	Mean annual temperature from 2010 - 2014
10sMAXT	°C	Mean maximum temperature from 2010 - 2014
10sMINT	°C	Mean minimum temperature from 2010 - 2014
81to14mdv	°C	Mean diurnal variation from 1981 - 2014
80smdv	°C	Mean diurnal variation from 1981 - 1990
90smdv	°C	Mean diurnal variation from 1990 - 2000
00smdv	°C	Mean diurnal variation from 2000 - 2010
10smdv	°C	Mean diurnal variation from 2010 - 2014
90to14et0mean	mm	Mean annual evapotranspiration from 1990 - 2014
90to14et0max	mm	Mean maximum evapotranspiration from 1990 - 2014

90to14et0min	mm	Mean minimum evapotranspiration from 1990 - 2014
90set0mean	mm	Mean annual evapotranspiration from 1990 - 2000
90set0max	mm	Mean maximum evapotranspiration from 1990 - 2000
90set0min	mm	Mean minimum evapotranspiration from 1990 - 2000
00set0mean	mm	Mean annual evapotranspiration from 2000 - 2010
00set0max	mm	Mean maximum evapotranspiration from 2000 - 2010
00set0min	mm	Mean minimum evapotranspiration from 2000 - 2010
10set0mean	mm	Mean annual evapotranspiration from 2010 - 2014
10set0max	mm	Mean maximum evapotranspiration from 2010 - 2014
10set0min	mm	Mean minimum evapotranspiration from 2010 - 2014
81to14EGmvpd	hPa	Mean annual vapor pressure deficit from 1981 - 2014
81to14EGmaxvpd	hPa	Mean maximum vapor pressure deficit from 1981 - 2014
81to14EGminvpd	hPa	Mean minimum vapor pressure deficit from 1981 - 2014
80smvpd	hPa	Mean annual vapor pressure deficit from 1981 - 1990
80sEGmaxvpd	hPa	Mean maximum vapor pressure deficit from 1981 - 1990
80sEGminvpd	hPa	Mean minimum vapor pressure deficit from 1981 - 1990
90smvpd	hPa	Mean annual vapor pressure deficit from 1990 - 2000
90sEGmaxvpd	hPa	Mean maximum vapor pressure deficit from 1990 - 2000
90sEGminvpd	hPa	Mean minimum vapor pressure deficit from 1990 - 2000
00smvpd	hPa	Mean annual vapor pressure deficit from 2000 - 2010
00sEGmaxvpd	hPa	Mean maximum vapor pressure deficit from 2000 - 2010
00sEGminvpd	hPa	Mean minimum vapor pressure deficit from 2000 - 2010
10smvpd	hPa	Mean annual vapor pressure deficit from 2010 - 2014
10sEGmaxvpd	hPa	Mean maximum vapor pressure deficit from 2010 - 2014
10sEGminvpd	hPa	Mean minimum vapor pressure deficit from2010 - 2014
81to14AHMImean	numeric	Mean annual heat moisture index from 1981 - 2014
81to14AHMImax	numeric	Mean maximum annual heat moisture index from 1981 - 2014
81to14AHMImin	numeric	Mean minimum annual heat moisture index from 1981 - 2014
80sAHMImean	numeric	Mean annual heat moisture index from 1981 - 1990
80sAHMImax	numeric	Mean maximum annual heat moisture index from 1981 - 1990
80sAHMImix	numeric	Mean minimum annual heat moisture index from 1981 - 1990
90sAHMImean	numeric	Mean annual heat moisture index from 1990 - 2000
90sAHMImax	numeric	Mean maximum annual heat moisture index from 1990 - 2000
90sAHMImix	numeric	Mean minimum annual heat moisture index from 1990 - 2000
00sAHMImean	numeric	Mean annual heat moisture index from 2000 - 2010
00sAHMImax	numeric	Mean maximum annual heat moisture index from 2000 - 2010
00sAHMImix	numeric	Mean minimum annual heat moisture index from 2000 - 2010
10sAHMImean	numeric	Mean annual heat moisture index from 2010 - 2014
10sAHMImax	numeric	Mean maximum annual heat moisture index from 2010 - 2014
10sAHMImix	numeric	Mean minimum annual heat moisture index from 2010 - 2014
X	integer	Latitude
Y	integer	Longitude
wetdaystotal	numeric	no of days with P ≥25mm 1981 - 2014

lastlog	date	year of last logging activity
timesincelog	numeric	years since last logging activity
lastfire	date	year of last fire
timesincefire	numeric	years since last fire
drydays	numeric	total number of days with precipitation <0.1mm since 1981
condtotaldays	numeric	no. of days with CI<01981
meancond	hPa	mean condensation of site 1981 - 2014
X80scondmean	hPa	mean condensation of site 1981 - 1990
X80scondmax	hPa	max condensation of site 1981 - 1990
X80scondmin	hPa	min condensation of site 1981 - 1990
X90scondmean	hPa	mean condensation of site 1990-2000
X90scondmax	hPa	max condensation of site 1990-2000
X90scondmin	hPa	min condensation of site 1990-2000
X00scondmean	hPa	mean condensation of site 2000 - 2010
X00scondmax	hPa	max condensation of site 2000 - 2010
X00scondmin	hPa	min condensation of site 2000 - 2010
X10scondmean	hPa	mean condensation of site 2010 - 2014
X10scondmax	hPa	max condensation of site 2010 - 2014
X10scondmin	hPa	min condensation of site 2010 - 2014
summermeanT	°C	mean summer temperature 1981 - 2014
summermaxT	°C	max summer temperature 1981 - 2014
summerminT	°C	min summer temperature 1981 - 2014
summerP	mm	mean summer precipitation 1981 - 2014
summercond	hPa	mean summer condensation 1981 - 2014
wintermeanT	°C	mean winter temperature 1981 - 2014
wintermaxT	°C	max winter temperature 1981 - 2014
winterminT	°C	min winter temperature 1981 - 2014
winterP	mm	mean winter precipitation 1981 - 2014
wintercond	hPa	mean winter condensation 1981 - 2014
springmeanT	°C	mean spring temperature 1981 - 2014
springmaxT	°C	max spring temperature 1981 - 2014
springminT	°C	min spring temperature 1981 - 2014
springP	mm	mean spring precipitation 1981 - 2014
springcond	hPa	mean spring condensation 1981 - 2014
autumnmeanT	°C	mean autumn temperature 1981 - 2014
autumnmaxT	°C	max autumn temperature 1981 - 2014
autumnminT	°C	min autumn temperature 1981 - 2014
autumnP	mm	mean autumn precipitation 1981 - 2014
autumncond	hPa	mean autumn condensation 1981 - 2014
TWI	numeric	Terrain Wetness Index of the site
meanT5year	°C	mean temperature of the last 5 years
maxT5year	°C	max temperature of the last 5 years
minT5year	°C	min temperature of the last 5 years

P5year	mm	mean annual precipitation of the last 5 years
cond5year	hPa	mean condensation of the last 5 years
meanT10year	°C	mean temperature of the last 10 years
maxT10year	°C	max temperature of the last 10 years
minT10year	°C	min temperature of the last 10 years
P10year	mm	mean annual precipitation of the last 10 years
cond10year	hPa	mean condensation of the last 10 years
meanT15year	°C	mean temperature of the last 15 years
maxT15year	°C	max temperature of the last 15 years
minT15year	°C	min temperature of the last 15 years
P15year	mm	mean annual precipitation of the last 15 years
cond15year	hPa	mean condensation of the last 15 years
meanT20year	°C	mean temperature of the last 20 years
maxT20year	°C	max temperature of the last 20 years
minT20year	°C	min temperature of the last 20 years
P20year	mm	mean annual precipitation of the last 20 years
cond20year	hPa	mean condensation of the last 20 years
meanT30year	°C	mean temperature of the last 30 years
maxT30year	°C	max temperature of the last 30 years
minT30year	°C	min temperature of the last 30 years
P30year	mm	mean annual precipitation of the last 30 years
cond30year	hPa	mean condensation of the last 30 years
conddays5year	numeric	total number of days with condensation during the past 5 years
conddays10year	numeric	total number of days with condensation during the past 10 years
conddays15year	numeric	total number of days with condensation during the past 15 years
conddays20year	numeric	total number of days with condensation during the past 20 years
conddays30year	numeric	total number of days with condensation during the past 30 years
drydays5	numeric	total number of days with <0.1mm rain during the past 5 years
drydays10	numeric	total number of days with <0.1mm rain during the past 10 years
drydays15	numeric	total number of days with <0.1mm rain during the past 15 years
drydays20	numeric	total number of days with <0.1mm rain during the past 20 years
drydays30	numeric	total number of days with <0.1mm rain during the past 30 years
raindays5	numeric	total number of days with ≥25mm rain during the past 5 years
raindays10	numeric	total number of days with ≥25mm rain during the past 10 years
raindays15	numeric	total number of days with ≥25mm rain during the past 15 years
raindays20	numeric	total number of days with ≥25mm rain during the past 20 years
raindays30	numeric	total number of days with ≥25mm rain during the past 30 years
hotnights5	numeric	total number of nights ≥20°C in the past 5 years
hotnights10	numeric	total number of nights ≥20°C in the past 10 years
hotnights15	numeric	total number of nights ≥20°C n the past 15 years
hotnights20	numeric	total number of nights ≥20°C in the past 20 years
hotnights30	numeric	total number of nights ≥20°C in the past 30 years
meanAHMI5year	numeric	mean Annual Heat Moisture Index of the past 5 years

meanAHMI10year	numeric	mean Annual Heat Moisture Index of the past 10 years
meanAHMI15year	numeric	mean Annual Heat Moisture Index of the past 15 years
meanAHMI20year	numeric	mean Annual Heat Moisture Index of the past 20 years
meanAHMI30year	numeric	mean Annual Heat Moisture Index of the past 30 years
meanFDSI5year	numeric	mean Forest Drought Severity Index of the past 5 years
meanFDSI10year	numeric	mean Forest Drought Severity Index of the past 10 years
meanFDSI15year	numeric	mean Forest Drought Severity Index of the past 15 years
meanFDSI20year	numeric	mean Forest Drought Severity Index of the past 20 years
meanFDSI30year	numeric	mean Forest Drought Severity Index of the past 30 years
parentmatnum	numeric	numeric code for parent material
soiltypenum	numeric	numeric code for soil type
soilsubtypenum	numeric	numeric code for soil sub type
ESPP1num	numeric	SFRI species 1 coded numeric
ESPP2num	numeric	SFRI species 2 coded numeric
EUCPREDOMnum	numeric	SFRI predominant species coded numeric
EUCGROUPnum	numeric	SFRI eucalypt group coded numeric
TREATCAUSEnum	numeric	SFRI treatment coded numeric
CONDNnum	numeric	SFRI stand condition coded numeric
firecat	numeric	time since fire in categories (timesincefire = 0, 1, timesincefire<10,5, timesincefire between 10 and 20, 4, timesincefire 20-30,5, older = 6)
logcat	numeric	time since log in categories (timesincelog = 0, 1, timesincelog<10,5, timesincelog between 10 and 20, 4, timesincelog 20-30,5, older = 6

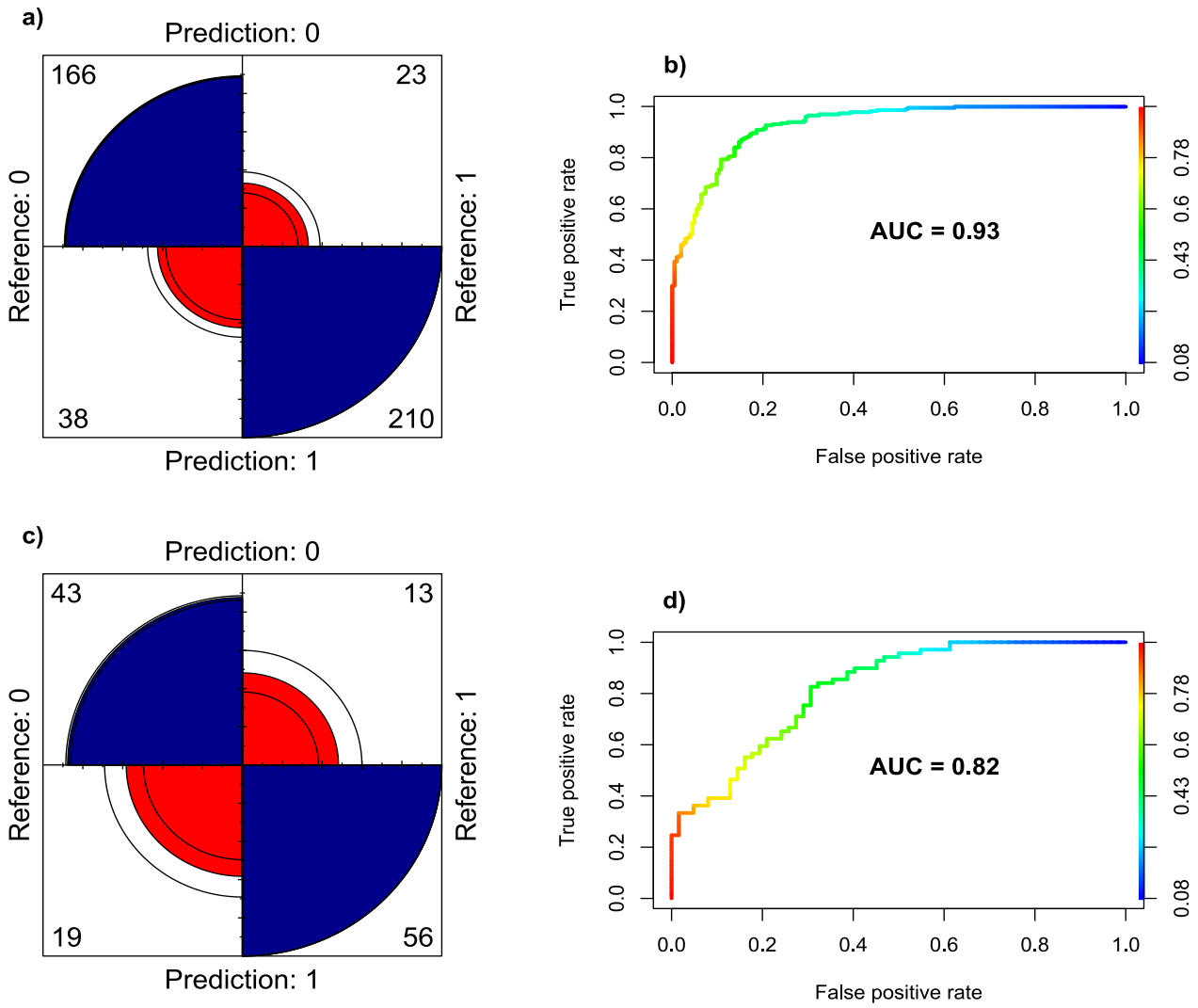


Figure S2. Confusion matrices and receiver operating characteristics curves (ROC) for cross-validation (a & b) and independent validation (c & d) of the final model. Dark blue charts indicate true, red charts false predictions. The size of each chart represents its fraction of the total number of observations.

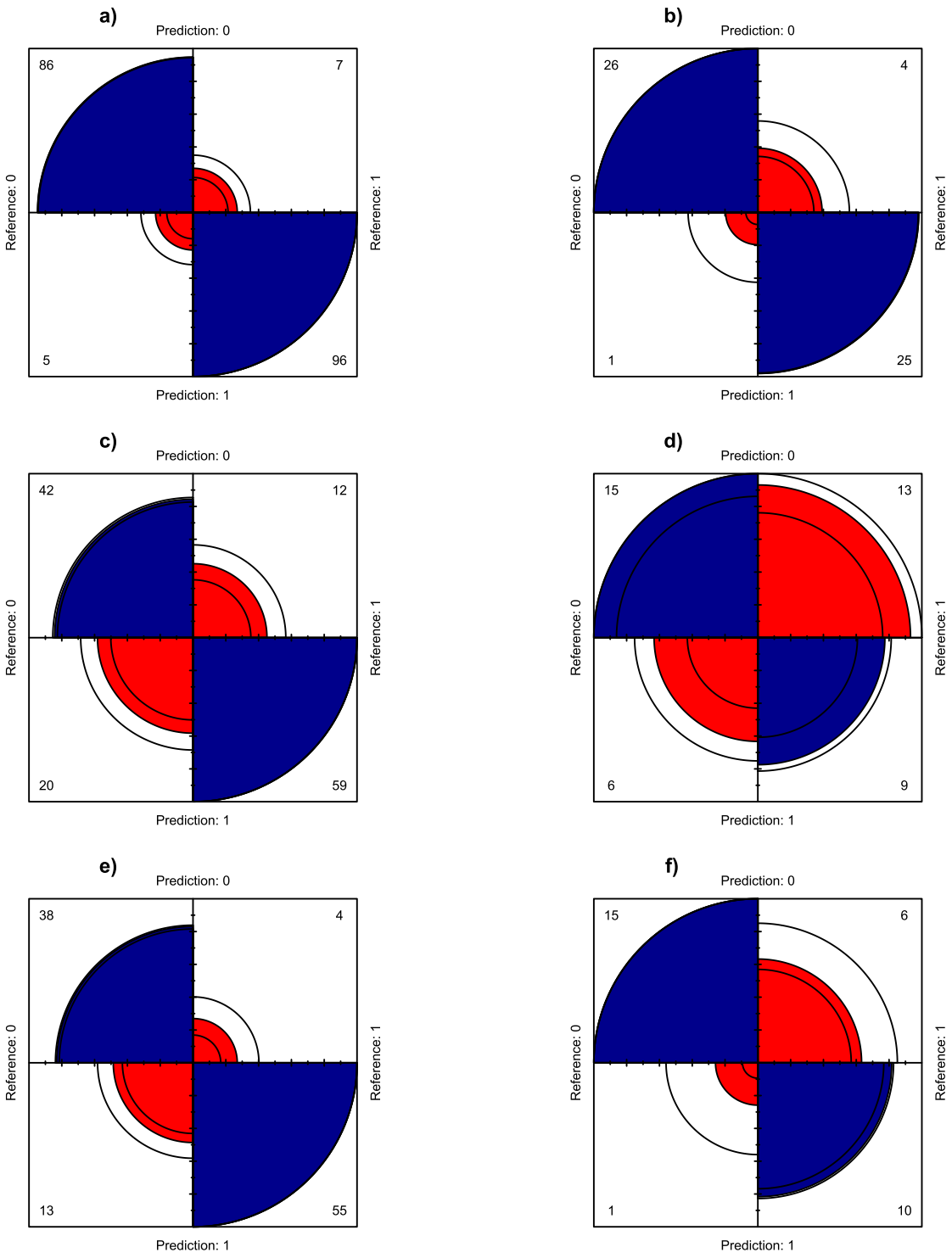


Figure S3. Separate landscape confusion matrices of cross-validation (left) and independent validation (right) for East Gippsland (a + b), Central Highlands (c + d) and the Strathbogie Ranges (e + f). Blue charts indicate true, red charts false predictions. The size of each chart represents its fraction of the total number of observations.

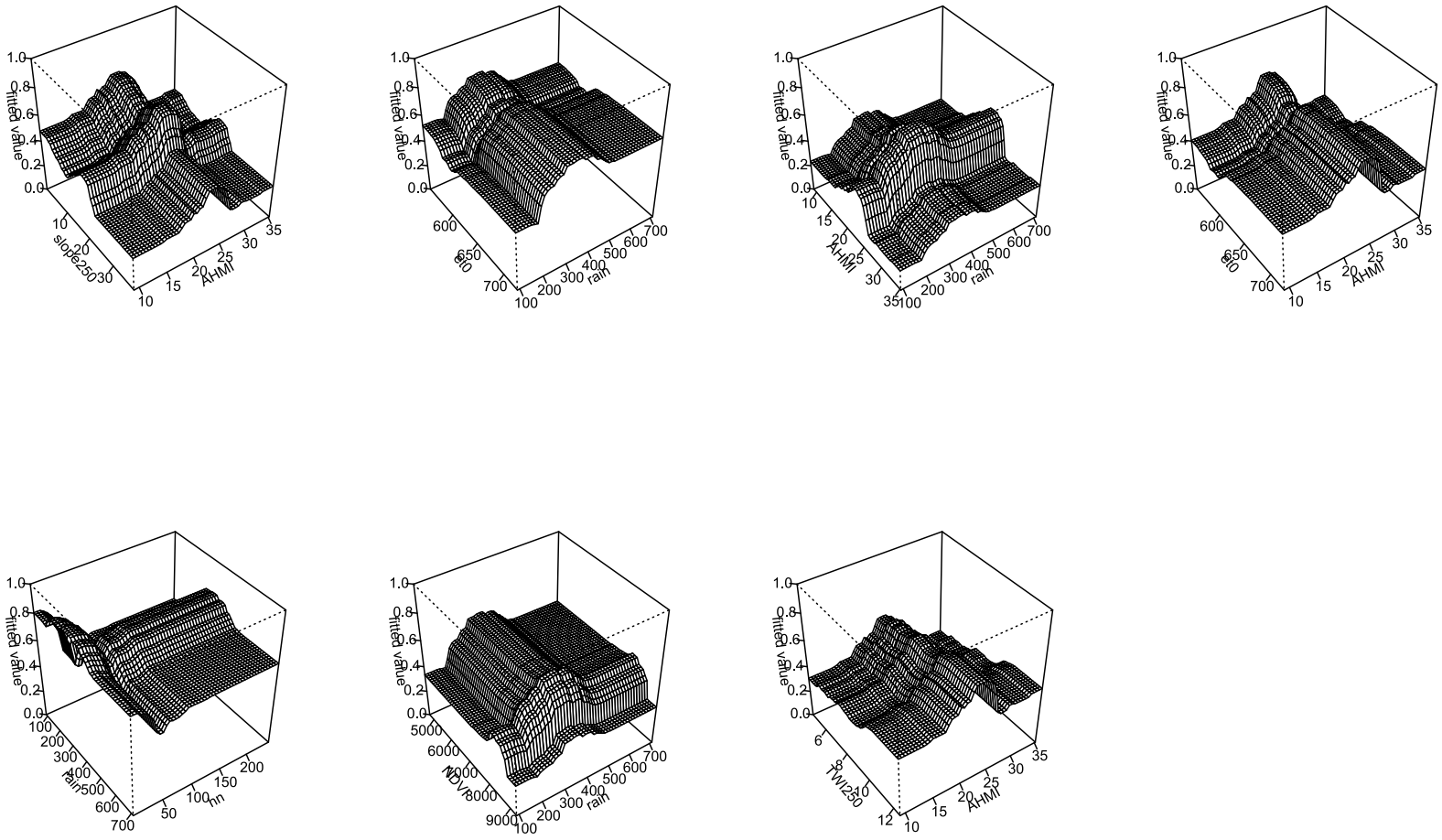


Figure S4. 3D joint partial dependence plots to illustrate the seven interactions derived by the BRT model, as suggested by Elith et al. (2008).

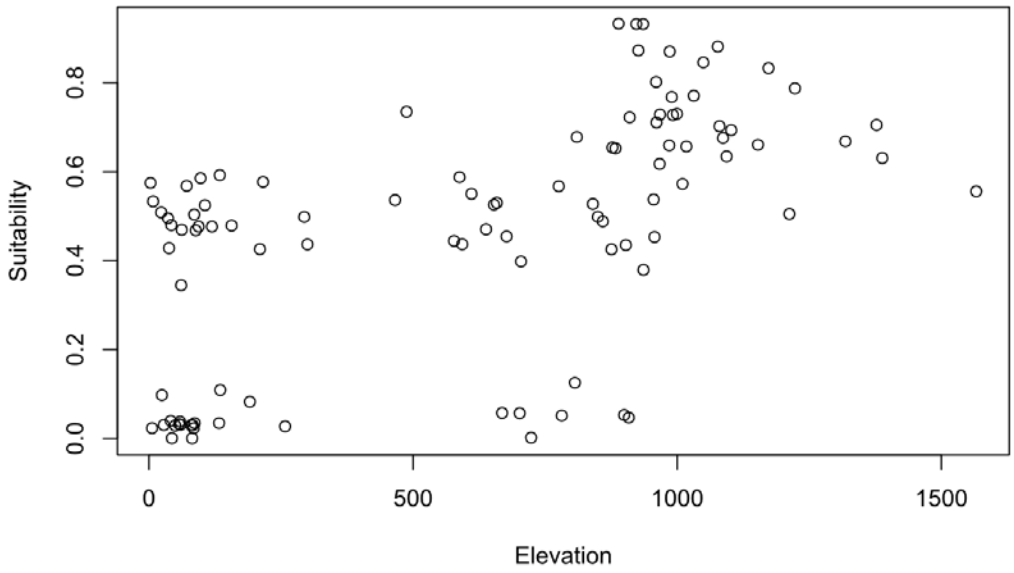


Figure S5. Scatterplot of 100 random pixels extracted from habitat suitability maps of all landscapes and a rescaled 30x30 m digital elevation model in meters.

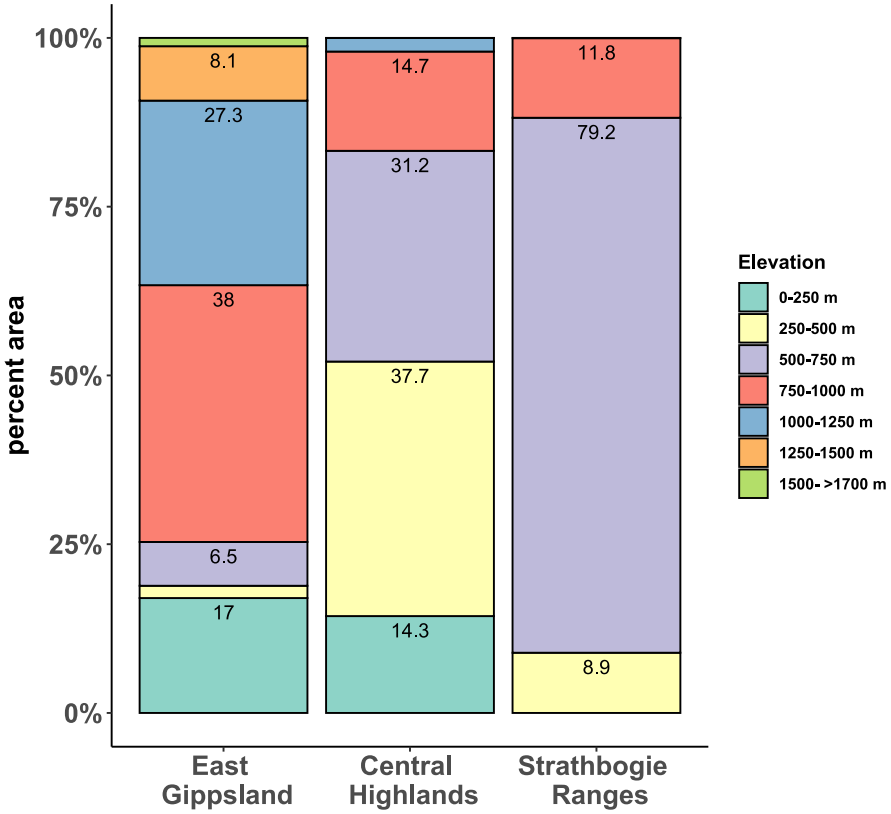


Figure S6. Elevational distribution of suitable habitat area within the three study regions.

Table S2. Landscape metrics of patch number and size for the East Gippsland study area

Landscape metric	Class	Metric-value
Mean patch area	not suitable, <500 m	3795 ha
	not suitable, >500 m	1008 ha
	suitable, <500 m	68 ha
	suitable, >500 m	502 ha
Total class area	not suitable, <500 m	702059 ha
	not suitable, >500 m	245946 ha
	suitable, <500 m	56203 ha
	suitable, >500 m	130611 ha
Number of patches	not suitable, <500 m	185
	not suitable, >500 m	244
	suitable, <500 m	826
	suitable, >500 m	260
Clumpiness	not suitable, <500 m	0.90
	not suitable, >500 m	0.89
	suitable, <500 m	0.66
	suitable, >500 m	0.91

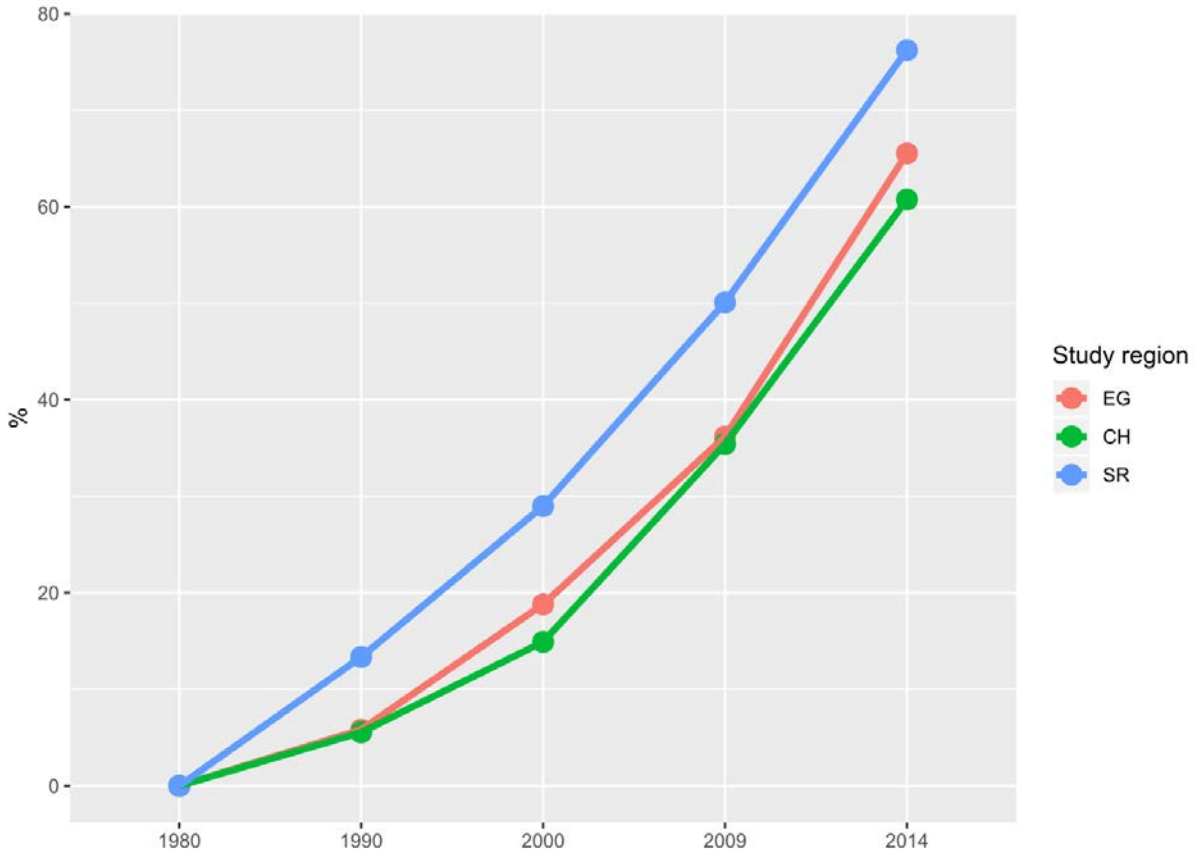


Figure S7. Percentage increase in hot nights in all study sites in East Gippsland (EG), the Central Highlands (CH) and Strathbogie Ranges (SR) study regions for three decades between 1980 and 2009 and the last 5 years (2009-2004) of available climate data.

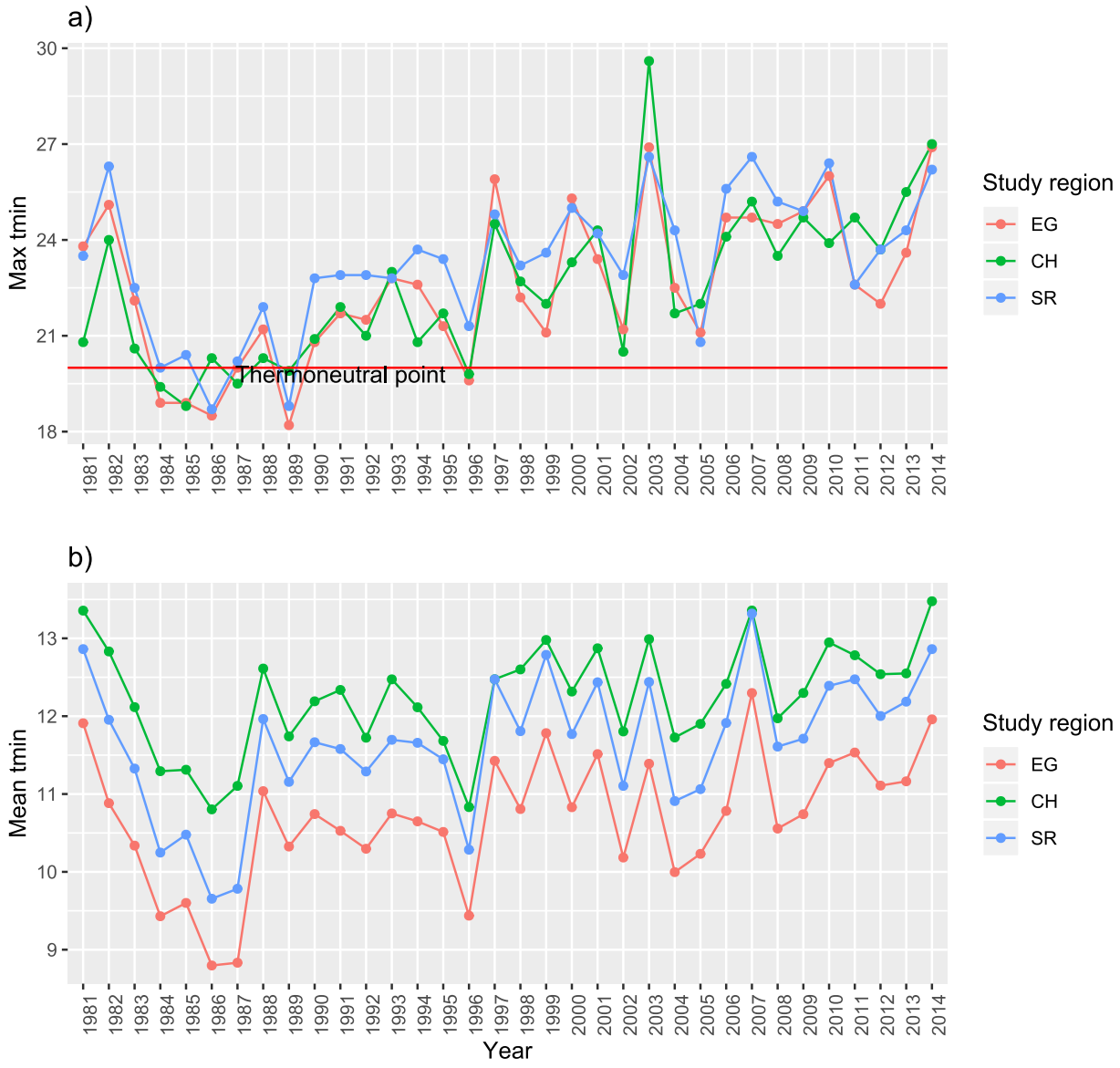


Figure S8. Annual maximum a) and mean b) summer nighttime temperatures (tmin in °C) for all study sites, grouped by region. The red line in a) illustrates the 20°C thermoneutral point of the greater glider

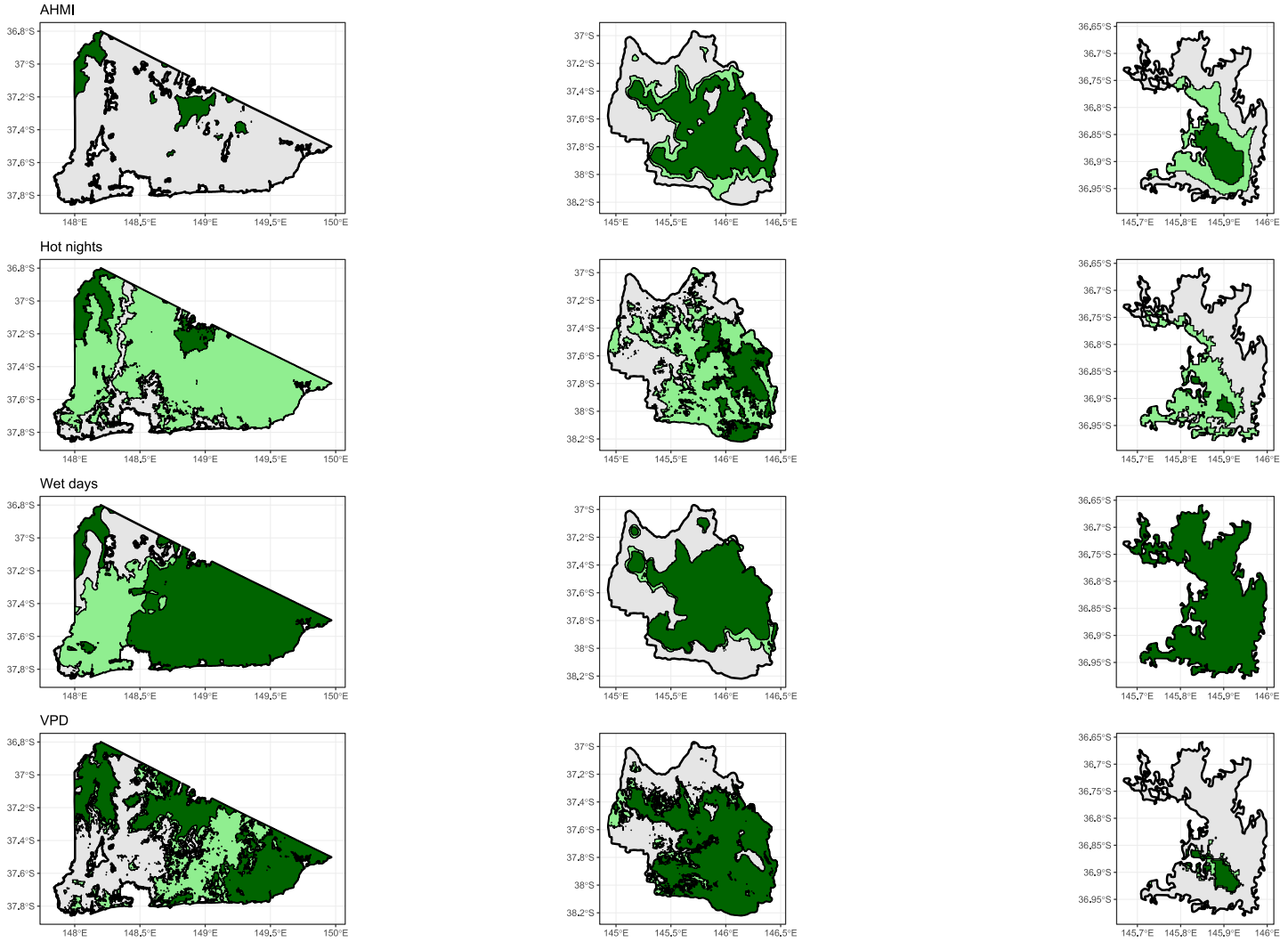


Figure S9. Suitable habitat extent for the four most important climatic variables (AHMI, hot nights, wet days and vpd) at two points in time in the three study regions (left to right: East Gippsland, Central Highlands and Strathbogie Ranges). Dark green areas indicate suitable habitat area extent according to variable threshold for 2003 - 2014, light green areas indicate extent for 1981 – 1992, based on daily climate data. If a graph shows no light green areas, an increase in suitable habitat occurred.

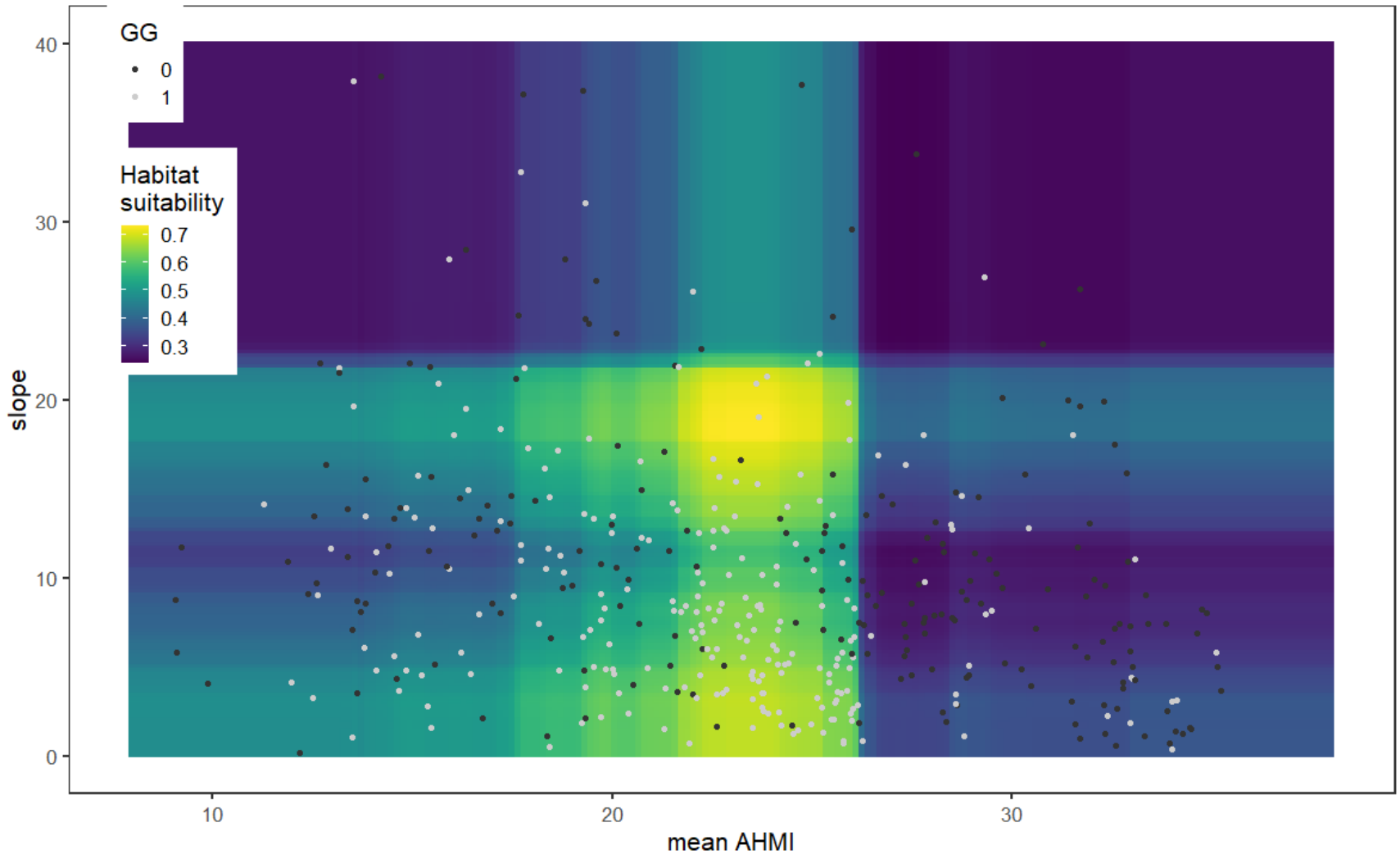


Figure S10. Heatmap of habitat suitability based on mean AHMI and slope, illustrating the strongest interaction in the final BRT model. The full range of slope and AHMI were used to predict habitat suitability, while all other variables were held at their means. Points are presences (1) and absences (0) from all surveys used to train the model (n = 437).

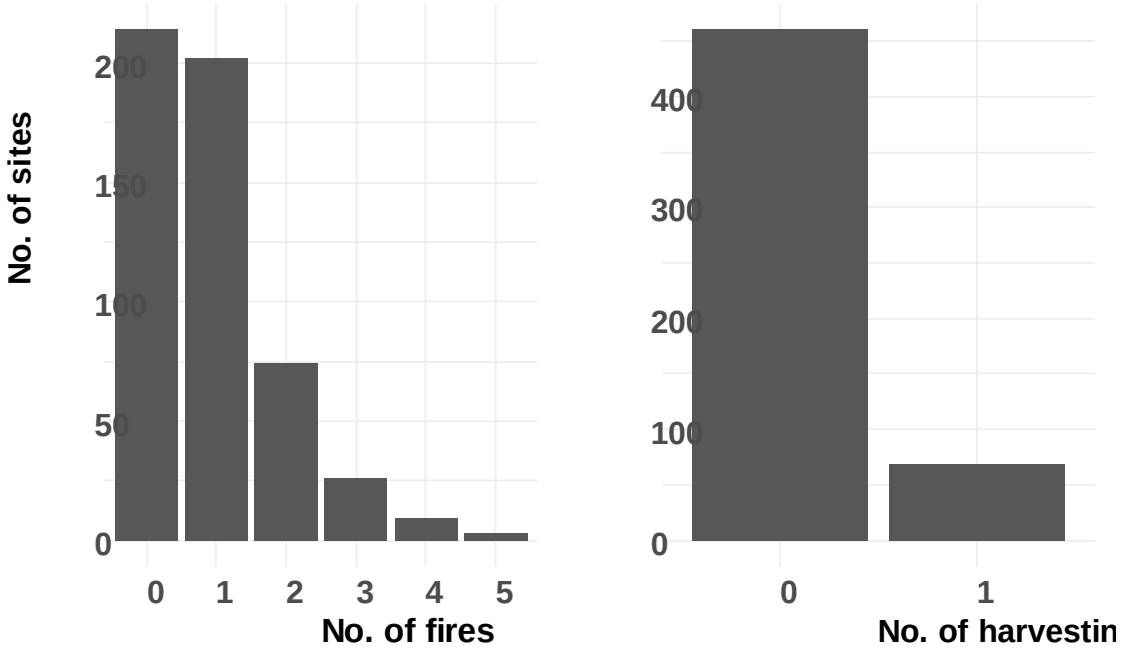


Figure S11. Frequency diagrams of disturbance history from 1980 - 2014 in all sites from the 2012 and 2015 surveys (n=528).

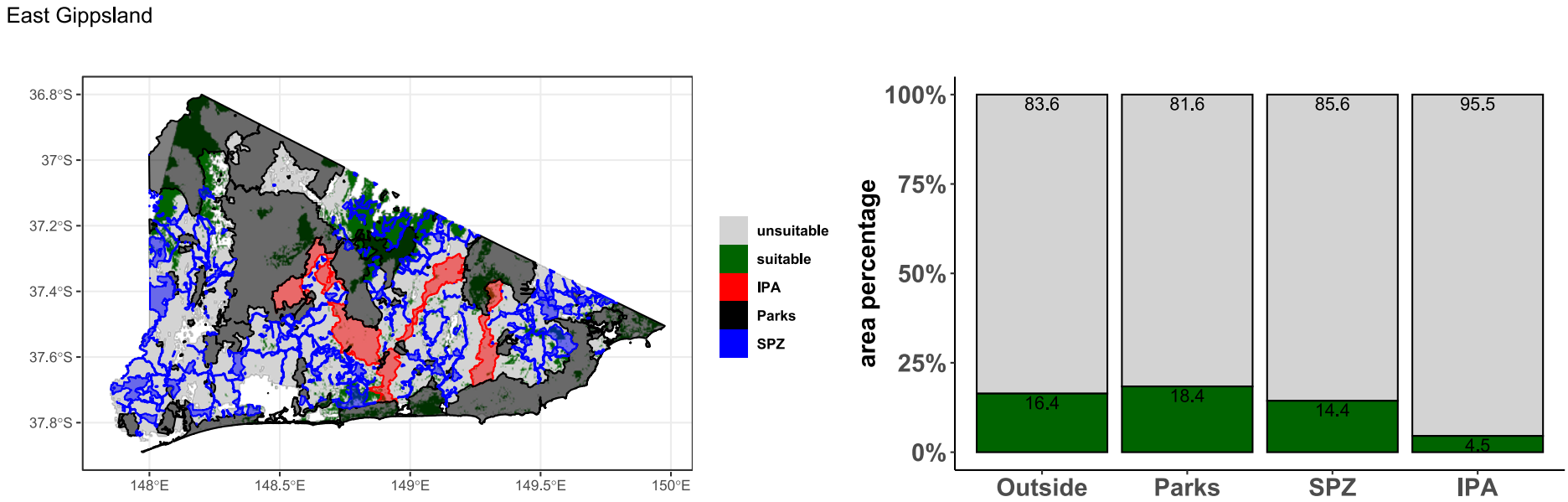


Figure S12. Areas and percentage of total area of suitable (dark green in underlying raster layer, modeled suitability score >0.47) and unsuitable (grey) areas in East Gippsland with protected area overlay. IPA = 2019 Immediate Protection Areas, Parks = National Parks and reserves, SPZ = Special Protection Zones.

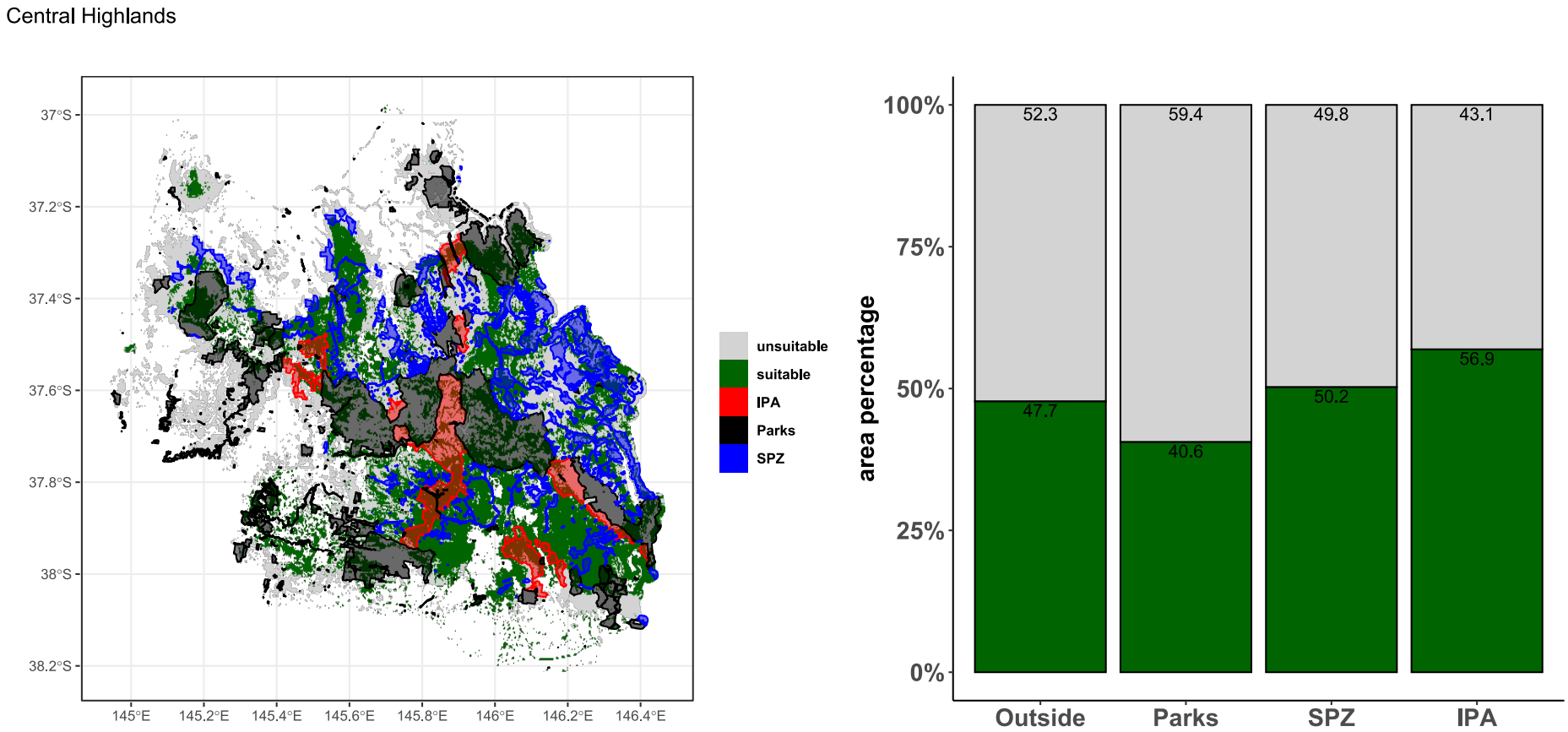


Figure S13. Areas and percentage of total area of suitable (dark green in underlying raster layer, modelled suitability score >0.47) and unsuitable (grey) areas in the Central Highlands with protected area overlay. IPA = 2019 Immediate Protection Areas, Parks = National Parks and reserves, SPZ = Special Protection Zones.

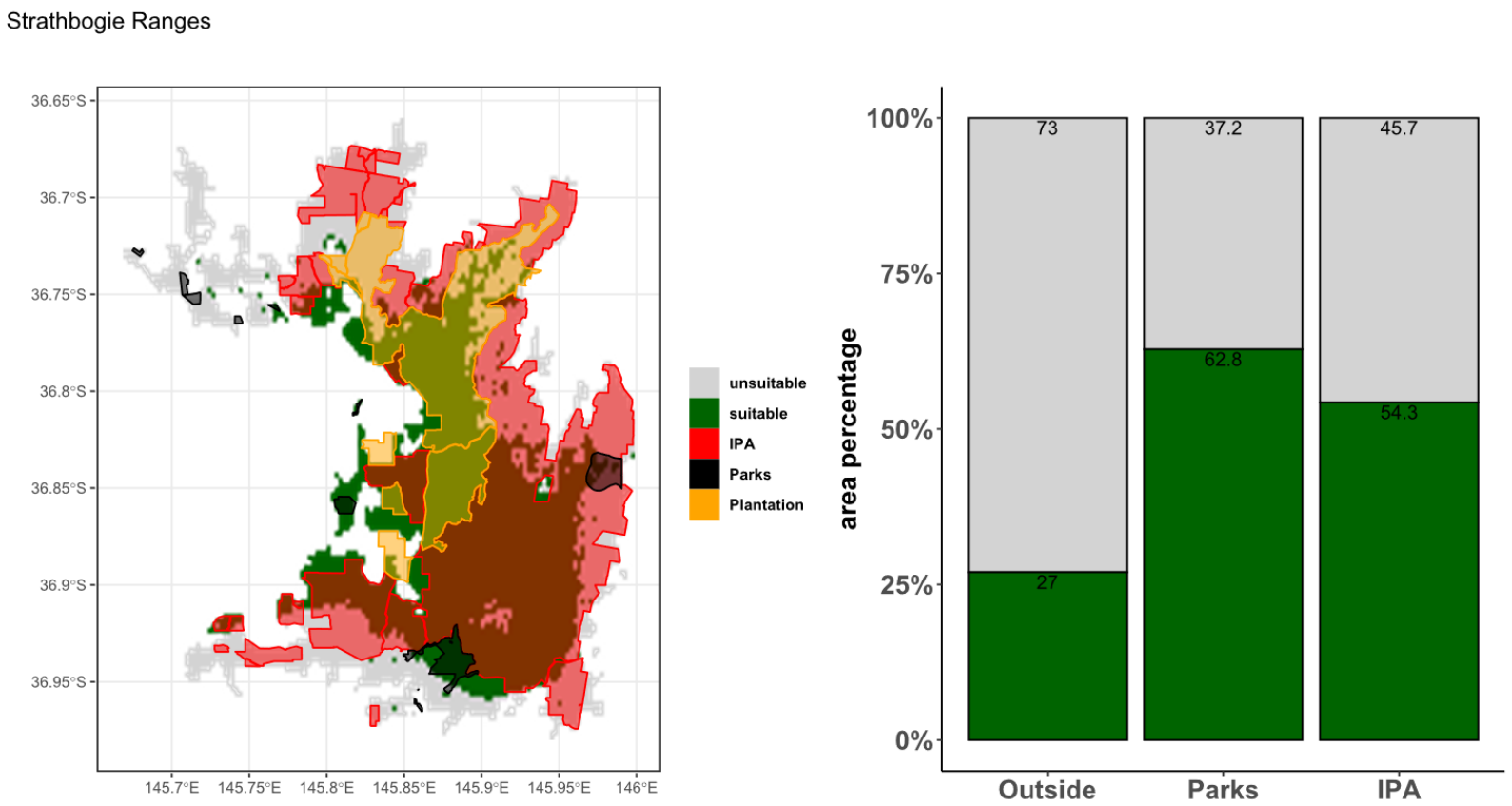


Figure S14. Areas of suitable and percentage of total area of suitable (dark green in underlying raster layer, modeled suitability score >0.47) and unsuitable (grey) areas in the Strathbogie Ranges with protected area overlay. IPA = 2019 Immediate Protection Areas, Parks = National Parks and reserves. SPZs and IPAs have been combined due to overlap and are displayed as IPAs only. Plantation areas (in orange) were not considered in the area calculation. Even though these areas were predicted to be suitable based on modeling variables, the respective vegetation in the plantations do not support greater glider populations.

Table S3. Area statistics for suitable (modeled suitability score >0.47) and unsuitable habitat in protected and unprotected areas of each study region. EG = East Gippsland, CH = Central Highlands, SR = Strathbogie Ranges.

Study Region	Type	Suitability	Area percentage of type	Area (in ha)	Area percentage of total suitable area
EG	IPA	unsuitable	95.45	67472.46	5.50
		suitable	4.55	3213.54	0.26
	Parks	unsuitable	81.61	347002.92	28.30
		suitable	18.39	78182.28	6.38
	SPZ	unsuitable	85.62	107894.16	8.80
		suitable	14.38	18117.00	1.48
	Outside	unsuitable	83.61	505250.46	41.21
		suitable	16.39	99043.56	8.08
CH	IPA	unsuitable	43.10	22215.60	2.59
		suitable	56.90	29325.78	3.42
	Parks	unsuitable	59.43	108719.82	12.68
		suitable	40.57	74202.48	8.65
	SPZ	unsuitable	49.76	48803.04	5.69
		suitable	50.24	49278.24	5.75
	Outside	unsuitable	52.27	274499.28	32.00
		suitable	47.73	250656.12	29.22
SR	IPA	unsuitable	45.73	10305.90	28.95
		suitable	54.27	12230.46	34.35
	Parks	unsuitable	37.20	362.34	1.02
		suitable	62.80	611.82	1.72
	Outside	unsuitable	73.04	8832.78	24.81
		suitable	26.96	3261.06	9.16

Citations – Appendix 1

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802-813.

Appendix 2

Chapter 3 - Supplementary figures

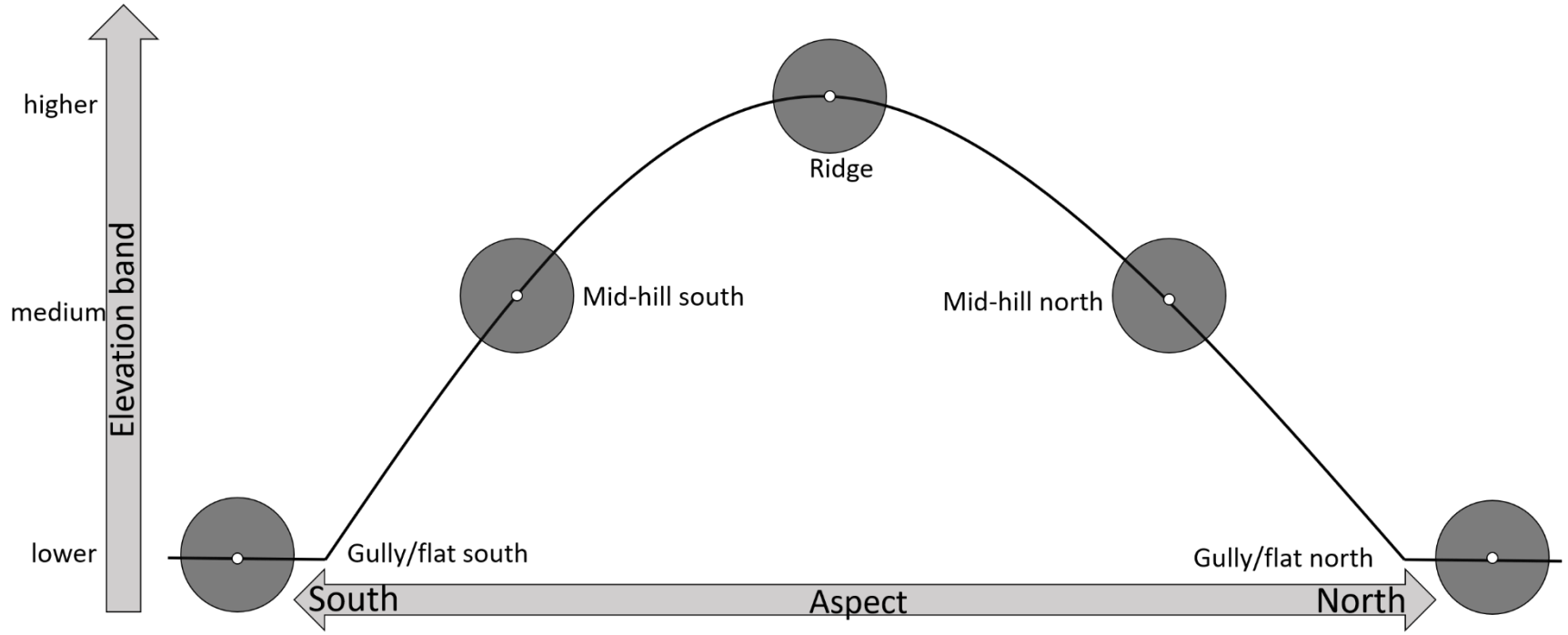
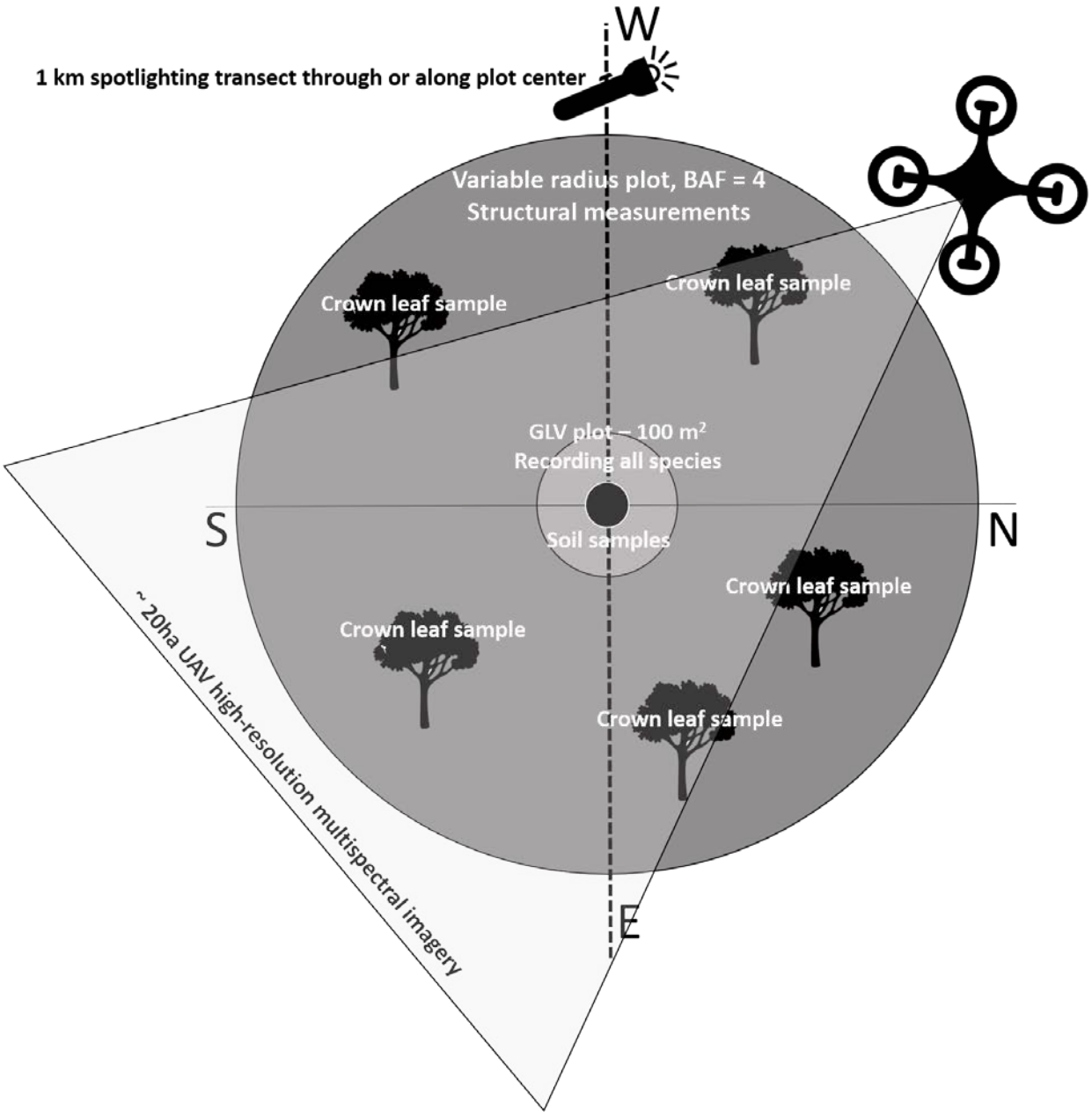


Figure S1. Transect design: Six of these transect were established within three elevation bands (two transects per band) between sea level and ~1200 m.a.s.l. Transects were laid out to ensure capturing the topographic variability of the landscape as expressed by elevation, slope and aspect and through that a variety of dominant *Eucalyptus* species forming the canopy.



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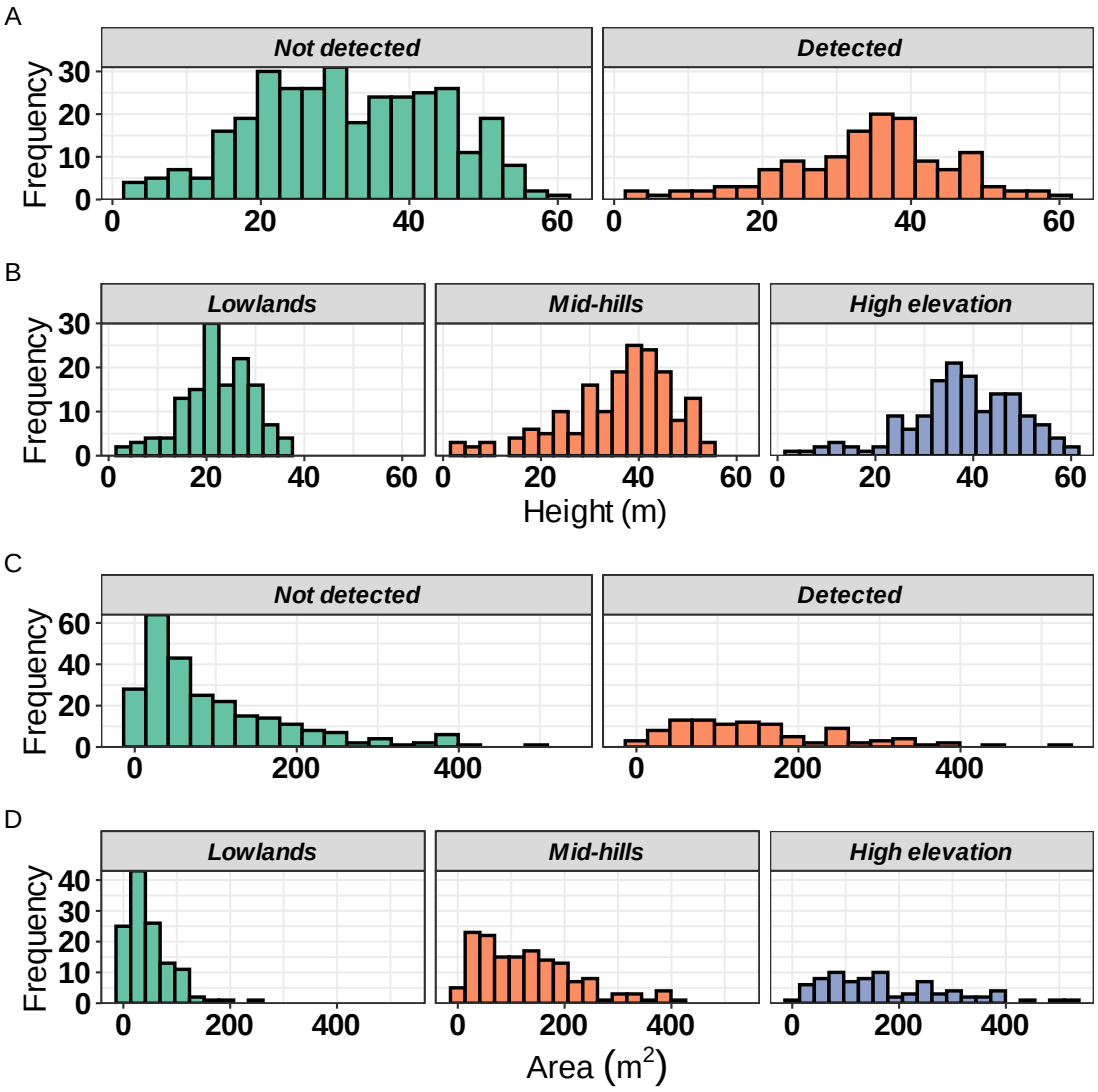


Figure S3. Observed distribution of tree heights (A+B) and crown areas (C+D) in plots with and without greater glider detections and by elevational band.

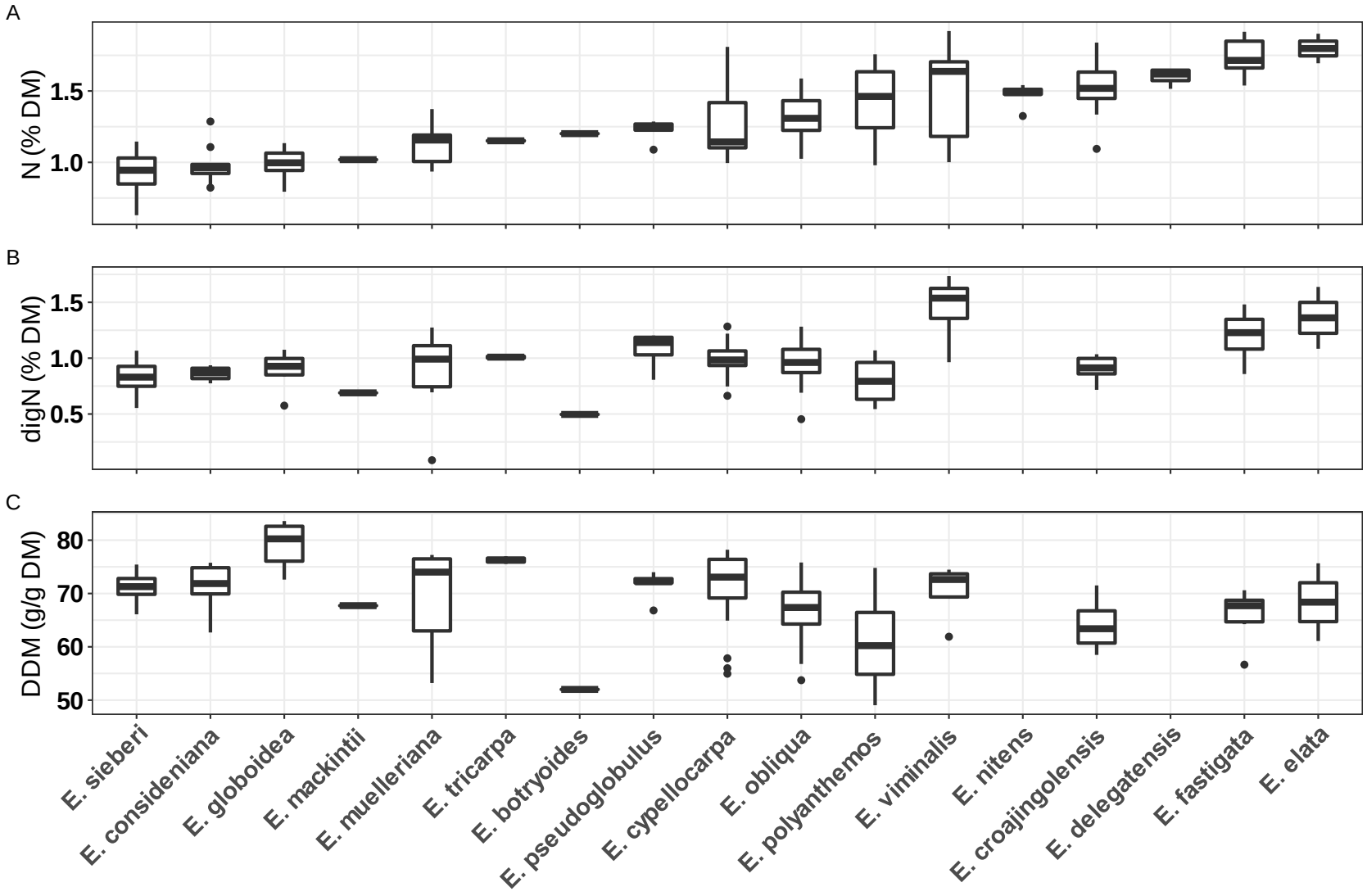


Figure S4. Chemically determined total (A), digestible nitrogen (B) and digestible dry matter (C) for the 17 *Eucalyptus* species sampled through our plot network. Note that due to sample loss, we could not analyse samples of *E. nitens* and *E. delegatensis* for digN and DDM.

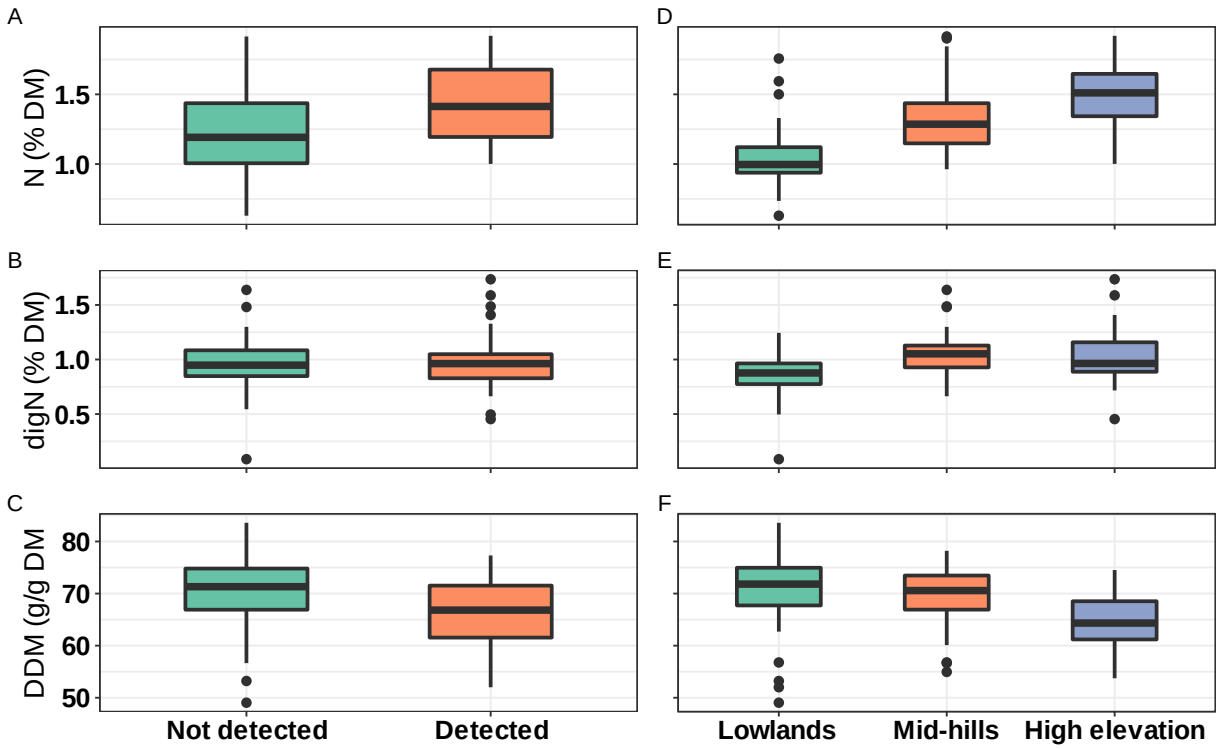


Figure S5. Differences in total, digestible nitrogen and digestible dry matter between greater glider presence and absence sites (A-C) and elevational bands (D-F).

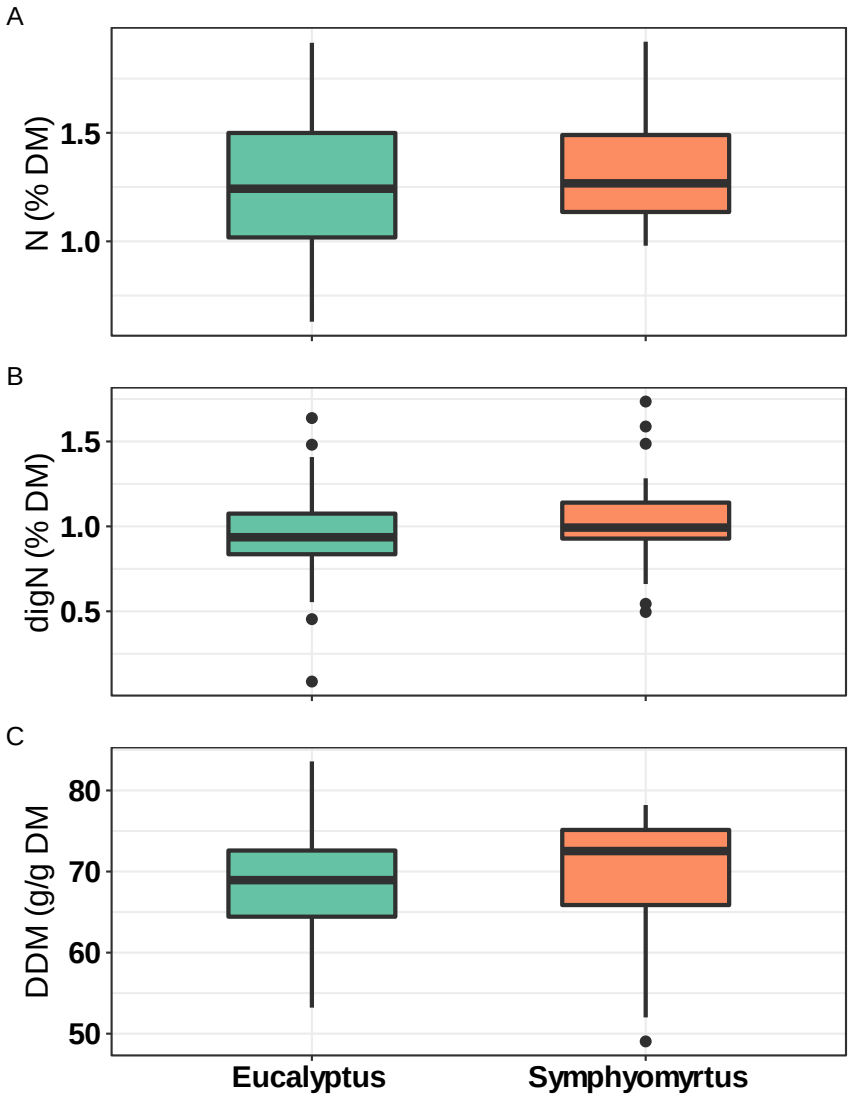


Figure S6. Differences in total (A), digestible nitrogen (B) and digestible dry matter (C) between *Eucalyptus* (*Monocalyptus*) and *Symphomyrtus* subgenera.

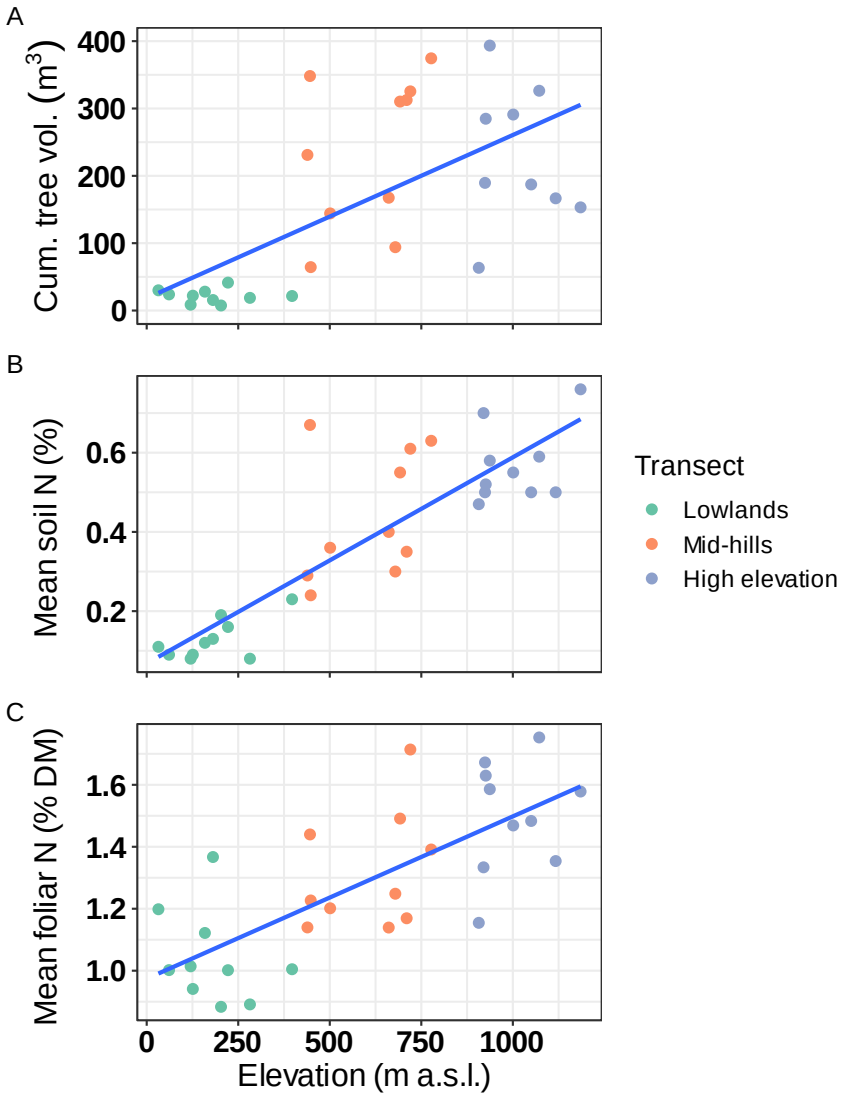


Figure S7. Changes in tree volume (A), mean soil (B) and foliar nutrition (C) per plot with elevation. The regression lines were fitted using univariate GLMs.

Chapter 3 - Supplementary tables

Table S1. Variable collected on the plot for trees within basal area factor (BAF) = 4.

Variable	Details
Species	Scientific name of tree species encountered in the plot
Diameter at breast height (DBH)	Tree diameter in cm measured at 1.3 m above the ground
Height	Tree height in meters, determined using a Vertex clinometer
Crown width	Length of crown in meters as projected on the ground from North to South and East to West. Used to determine crown area
Tree vigour	Tree vigour in three health categories (alive, senescing and dead)
Age class	Estimate of tree age based on structure in five categories (regrowth, mature, over-mature, late-mature, stag)
Structural layer	Description of structural layer a tree belonged to based on dominance and height in four categories (understorey, midstorey, subcanopy, canopy)
Presence and number of hollows	Trees were scanned for hollows using binoculars. When hollows were present, their numbers were counted
Type of hollows	Hollow type in different categories (e.g. fissure, trunk, chimney or slit)
Foliage cover	Estimated percentage of foliage cover projected on ground level

Table S2. Model results for separate model groups for hollow occurrence (top) and abundance (bottom).

Variable	Hollow occurrence: structure group			Hollow occurrence: site group			Hollow occurrence: nutrients group		
	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value
(Intercept)	-1.9	-2.7, -1.2	<0.001	1.8	0.31, 3.4	0.020	1.2	-0.13, 2.5	0.079
Age class	0.86	0.59, 1.2	<0.001						
Structural layer	-0.38	-0.85, 0.06	0.10						
Tree volume	0.07	0.04, 0.10	<0.001						
AHMI				-0.06	-0.12, -0.01	0.025			
Foliar nitrogen							-1.7	-3.1, -0.37	0.013
Soil nitrogen							2.9	1.2, 4.7	<0.001

Variable	Hollow abundance: structure group			Hollow abundance: site group			Hollow abundance: nutrients group		
	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value
(Intercept)	-0.22	-0.68, 0.24	0.4	-13	-21, -5.0	0.002	2.6	1.0, 4.2	0.002
Age class	0.67	0.40, 0.95	<0.001						
No. of fires	0.12	-0.03, 0.27	0.12						

Health category	-0.38	-0.83, 0.08	0.11						
Tree volume	0.06	0.05, 0.07	<0.001						
AHMI				0.09	0, 0.18	0.042			
Soil-type				1.1	0.31, 1.8	0.006			
Soil-subtype				2.8	0.82, 4.8	0.006			
Aspect				0	0, 0	0.062			
Condensation days				0	0, 0	0.003			
NDVI				0	0, 0	0.002			
Foliar nitrogen							-1.3	-2.8, 0.27	0.11
Soil P							-0.04	-0.08, 0.00	0.074
Soil nitrogen							3.2	1.3, 5.1	<0.001

[1]CI = Confidence Interval

Table S3. Model results for remaining foliar nitrogen model groups.

Variable	Foliar nitrogen: site group			Foliar nitrogen: structure group		
	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value
(Intercept)	0.26	-0.56, 1.1	0.5	1.6	1.5, 1.8	<0.001
AHMI	-0.01	-0.02, 0.00	0.019			
Aspect	0.001	0.00, 0.00	<0.001			
Condensation days	0.001	0.00, 0.00	<0.001			
NDVI	0.001	0.00, 0.00	<0.001			
Soil subtype	-0.14	-0.21, -0.08	<0.001			
TWI250	-0.09	-0.14, -0.03	0.001			
Age class				-0.16	-0.24, -0.07	<0.001
Trees per ha				0.001	-0.01, 0.00	<0.001
Hollows per ha				0.001	-0.01, 0.00	0.047
Tree volume				0.001	0.00, 0.01	0.007

[1]CI = Confidence Interval

Table S4. Model results for final combined models of digestible nitrogen and digestible dry matter (DDM).

Variable	Digestible nitrogen: final model			DDM: final model		
	Estimate	95% CI[1]	p-value	Estimate	95% CI[1]	p-value
(Intercept)	1.0	0.94, 1.0	<0.001	69	68, 70	<0.001
Age class	-0.05	-0.08, -0.01	0.014	-1.3	-2.4, -0.34	0.010
Foliage cover	0.04	0.00, 0.08	0.070			
Structural layer	0.04	0.00, 0.08	0.080			
Soil nitrogen	0.06	0.02, 0.10	0.006			
Aspect				1.3	0.31, 2.4	0.012

Condensation days	-2.3	-3.5, -1.1	<0.001
Soil K	-1.4	-2.5, -0.28	0.015
Slope	-2.0	-3.1, -0.94	<0.001
Soil-type	-1.7	-2.8, -0.54	0.005

[1]CI = Confidence Interval

Table S5. No. of observations of arboreal marsupials throughout all study sites. Greater glider observations are highlighted in bold font.

Transect	Plot	Species	Total no. of observations
Lowlands	T1.5P1	Ringtail possum	4
	T1.5P2	Sugar glider	1
	T1.5P3	Ringtail possum	1
	T1.5P4	Mt brushtail possum	1
		Sugar glider	4
		Yellow-bellied glider	1
	T1.5P5	Common brushtail possum	3
		Greater Glider	2
		Ringtail possum	3
		Sugar glider	1
		Yellow-bellied glider	1
	T1P1	Sugar glider	1
	T1P2	Sugar glider	4
	T1P3	Common brushtail possum	4
		Sugar glider	1
		Yellow-bellied glider	1
	T1P4	Mt brushtail possum	1
		Sugar glider	1
Mid-hills	T2.5P1	Mt brushtail possum	1
		Sugar glider	1
		Yellow-bellied glider	2
	T2.5P2	**Greater Glider**	1
	T2.5P3	Ringtail possum	1
	T2P3	Common brushtail possum	1
		Greater Glider	1
		Sugar glider	2

	T2P4	Mt brushtail possum	2
High elevation	T3.5P1	**Greater Glider**	22
		Mt brushtail possum	2
		Sugar glider	2
	T3.5P2	**Greater Glider**	3
		Mt brushtail possum	2
		Yellow-bellied glider	1
	T3.5P3	Mt brushtail possum	3
		Ringtail possum	2
		Yellow-bellied glider	1
	T3.5P4	**Greater Glider**	3
		Mt brushtail possum	2
		Ringtail possum	1
		Sugar glider	1
	T3.5P5	**Greater Glider**	5
		Mt brushtail possum	2
	T3P1	**Greater Glider**	5
		Mt brushtail possum	16
		Yellow-bellied glider	2
	T3P2	Mt brushtail possum	3
	T3P3	Mt brushtail possum	19
		Yellow-bellied glider	3
	T3P4	Mt brushtail possum	5
		Sugar glider	2
	T3P5	**Greater Glider**	2
		Mt brushtail possum	3
		Yellow-bellied glider	1

Appendix 3

Chapter 4 - Supplementary figures

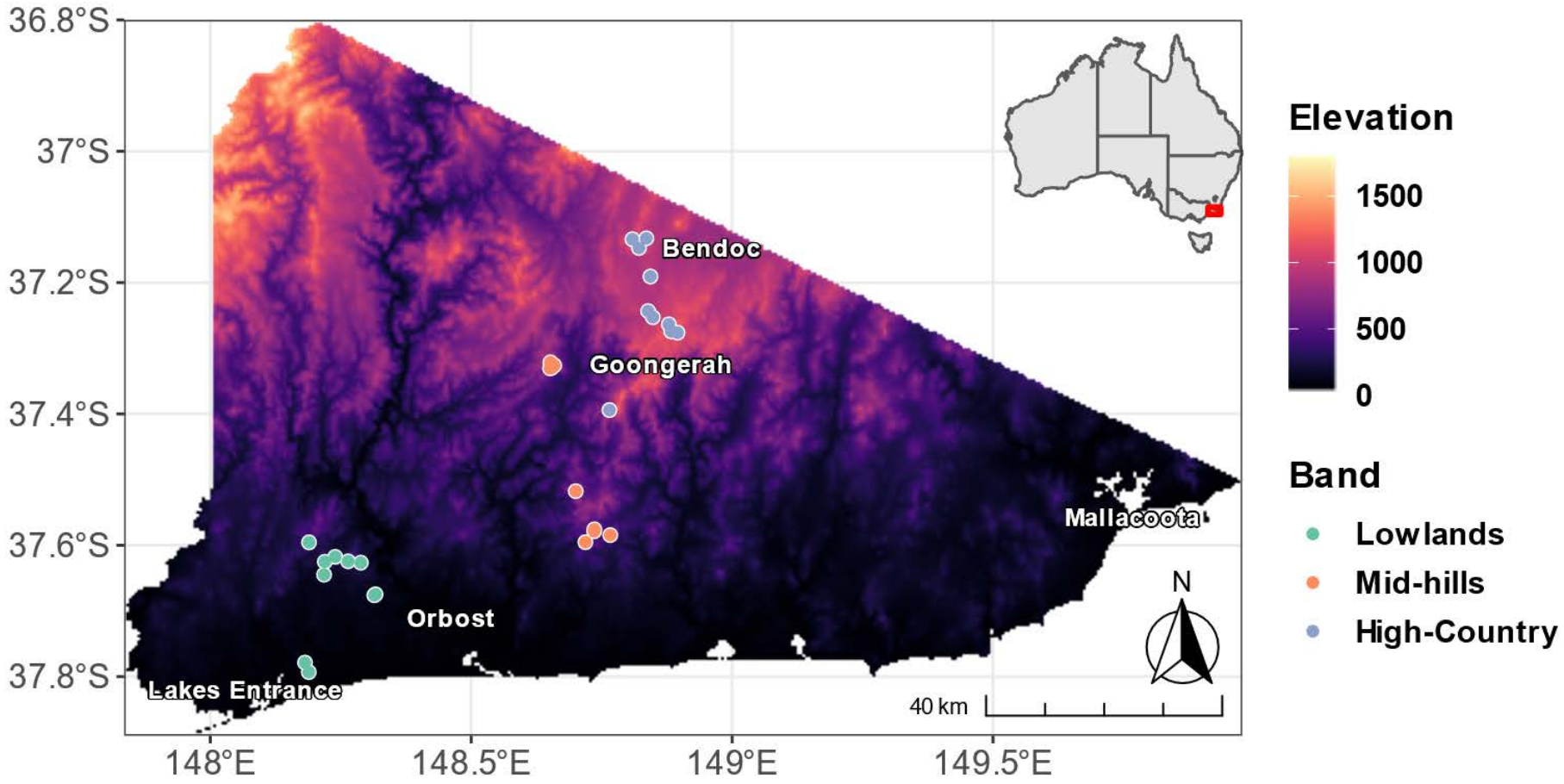
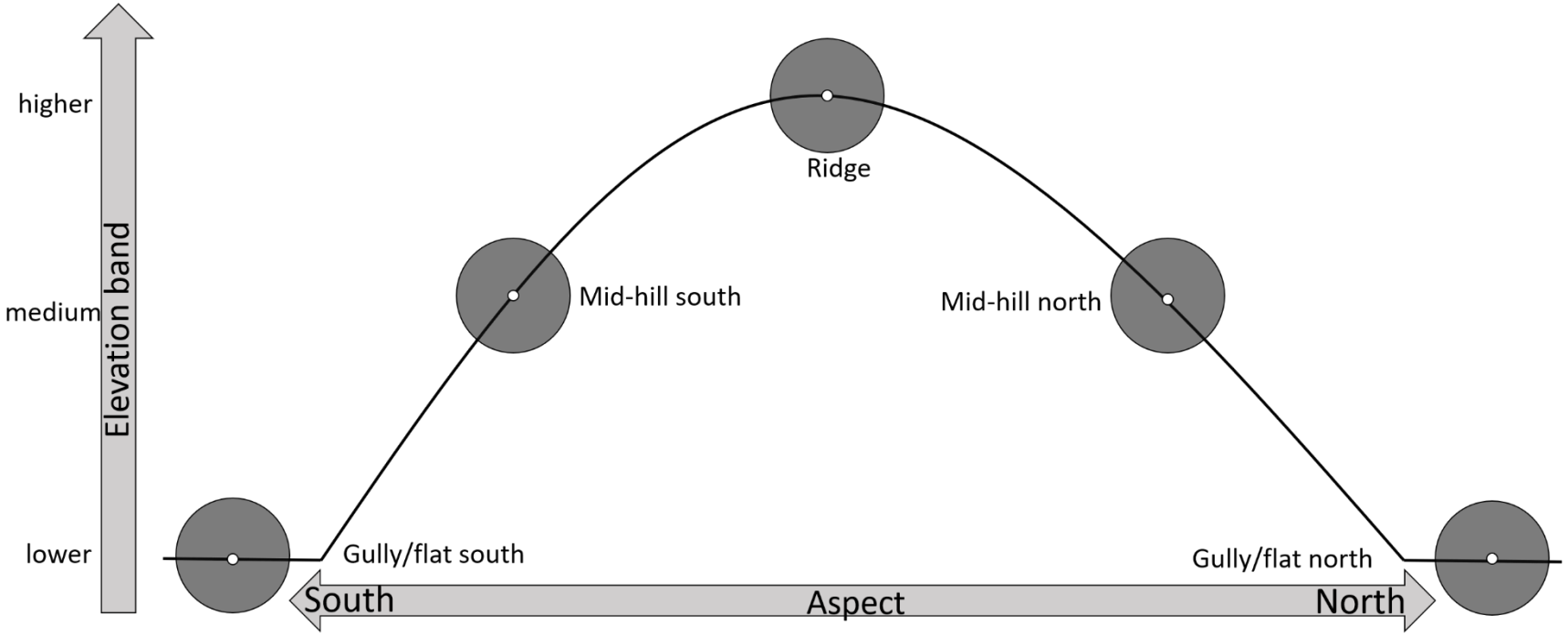


Figure S1. Study area map of East Gippsland, Victoria with major settlements and location of 30 study sites. Color gradient describes elevation in meters.



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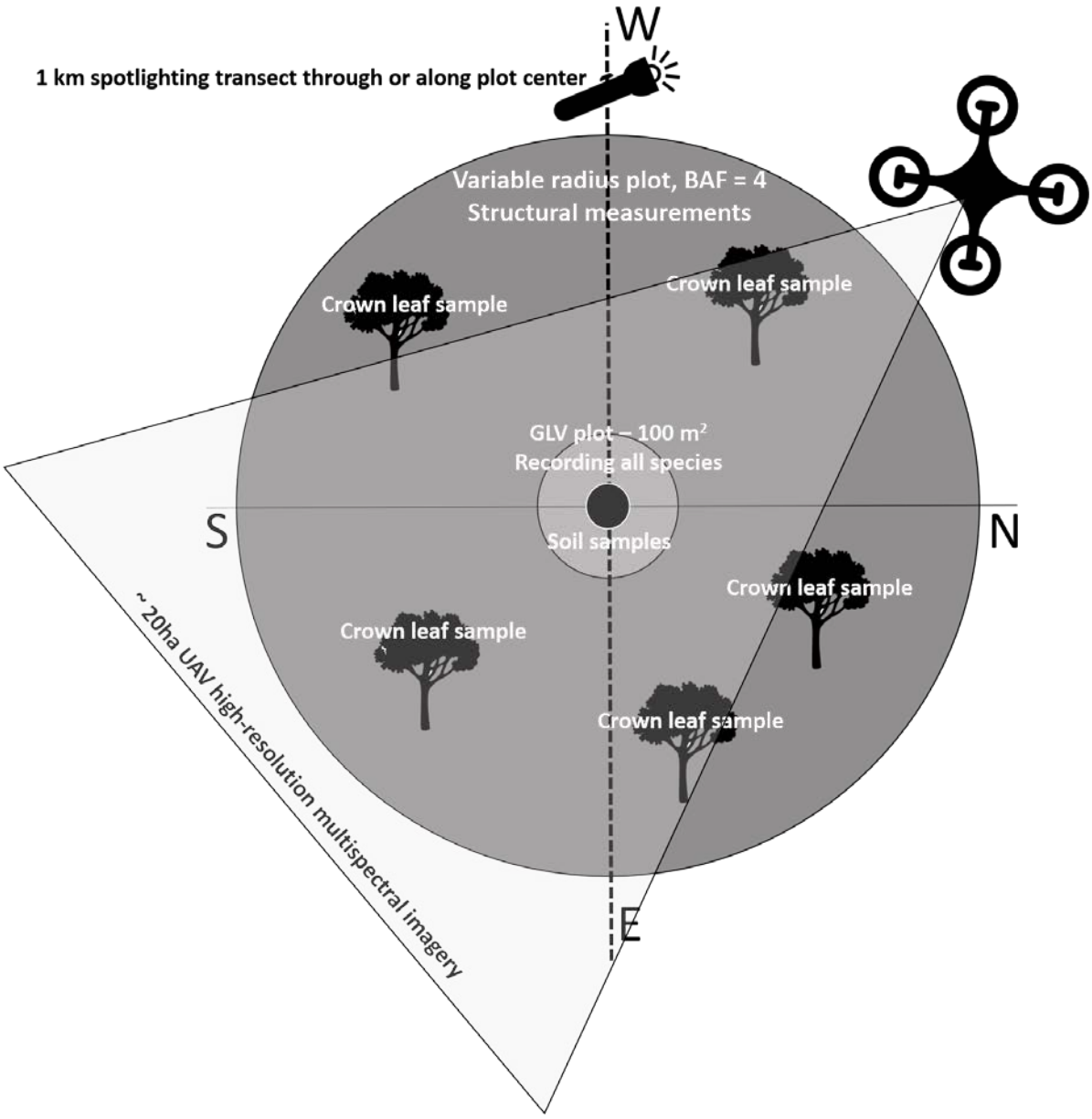

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Figure S4. DJI Phantom 4 UAV modified to carry a Micasense RedEdge M multispectral sensor. A 3D printed mount allows to attach the sensor between the landing skids of the UAV. The rod on the left carries the batteries to operate the camera and lifts the radiation sensor and GPS over the propellers for safe operation. This setup allows to capture both multispectral and RGB imagery simultaneously as it leaves the drone's sensor operational. The drone sensor can e.g. be used during operation to check for obstacles or ensure the programmed flight-lines are followed correctly.

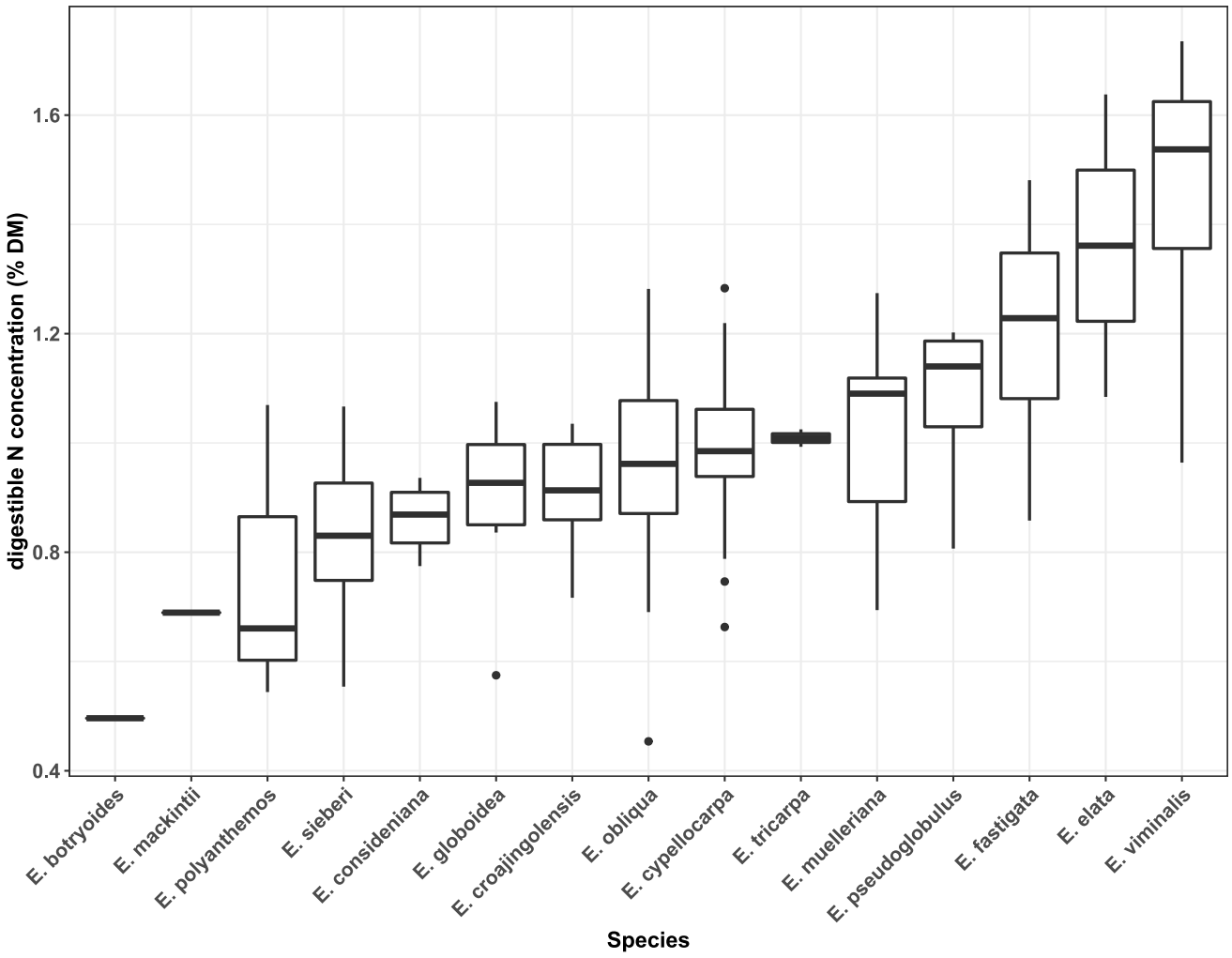

Figure S5. Observed ranges of digestible nitrogen (digN) concentration of 15 *Eucalyptus* species sampled

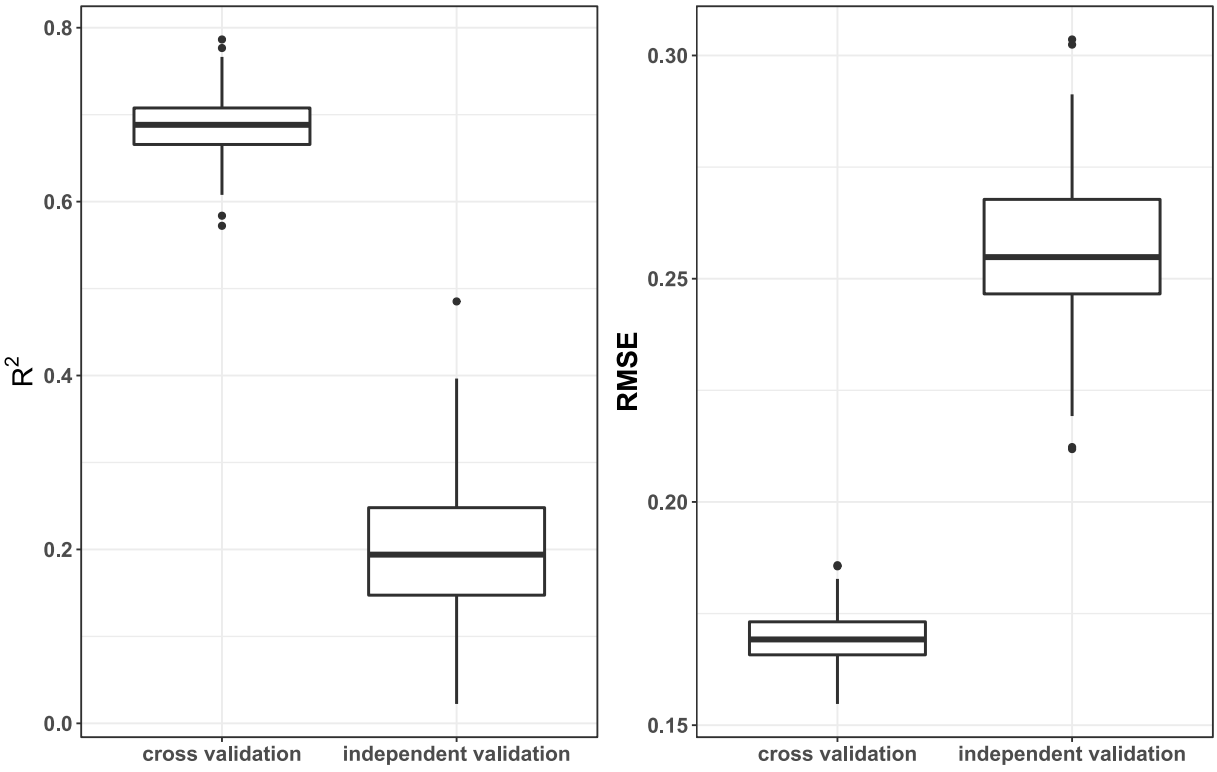

Figure S6. Model performance evaluation of independent 100 models of total nitrogen based on 100 random data splits based on R-squared (left) and root mean square error (right).

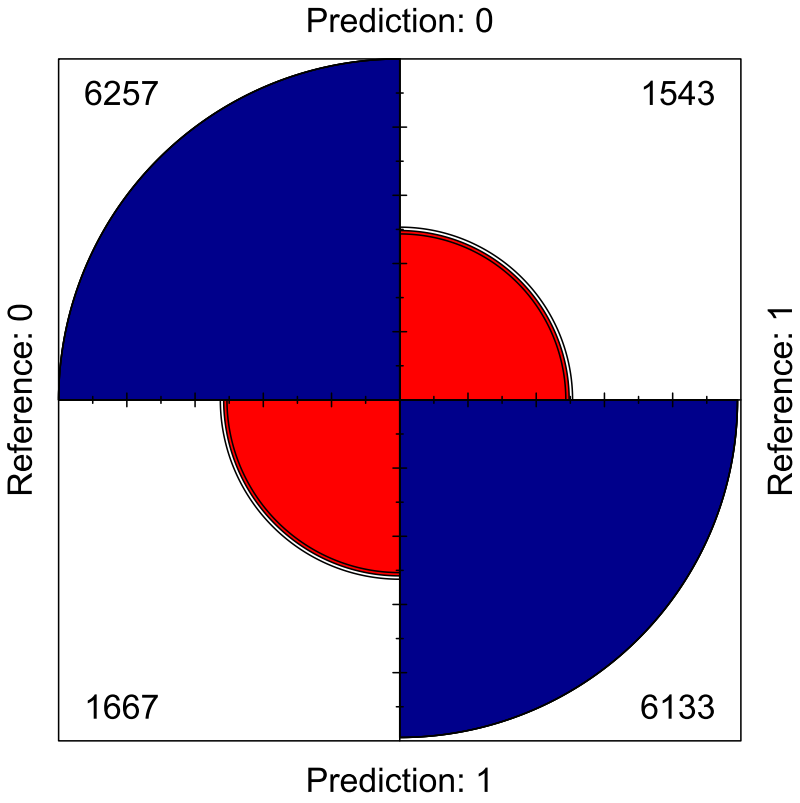

Figure S7. Fourfold plot illustrating independent supervised model prediction accuracy based on the confusion matrix of this model evaluation. ~80% of absence (top-left) and ~78% of presence (bottom-right) pixels were predicted correctly (blue charts).

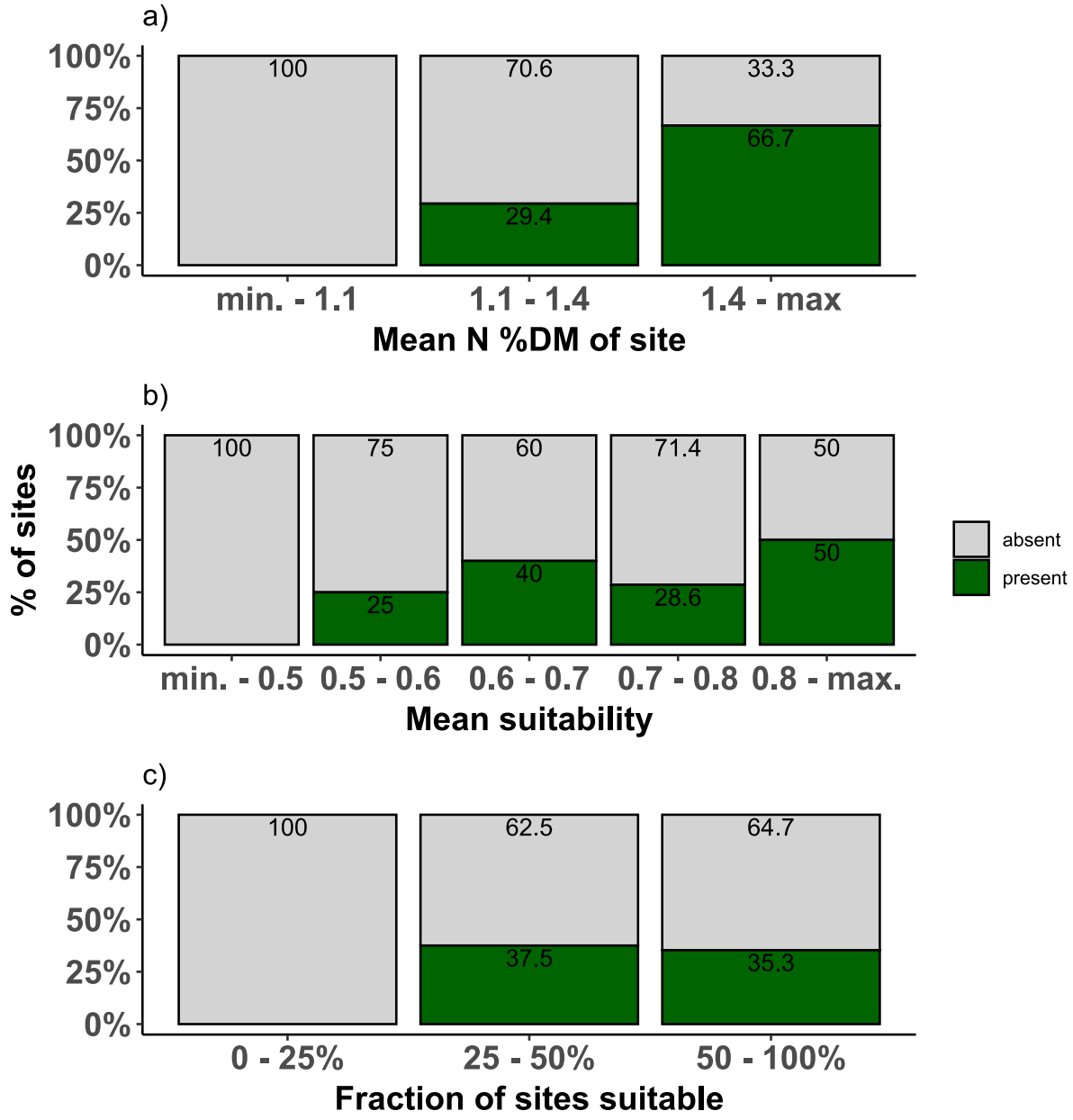

Figure S9. Fraction of occupied sites for the three detection thresholds identified: a) average plot level nitrogen (N) based on chemically determined N measures of five trees per plot, b) mean nutritional suitability from the supervised classification model for feeding habitat and c) proportion of feeding habitat, i.e. fraction of the site that was classified as ≥1% N DM.

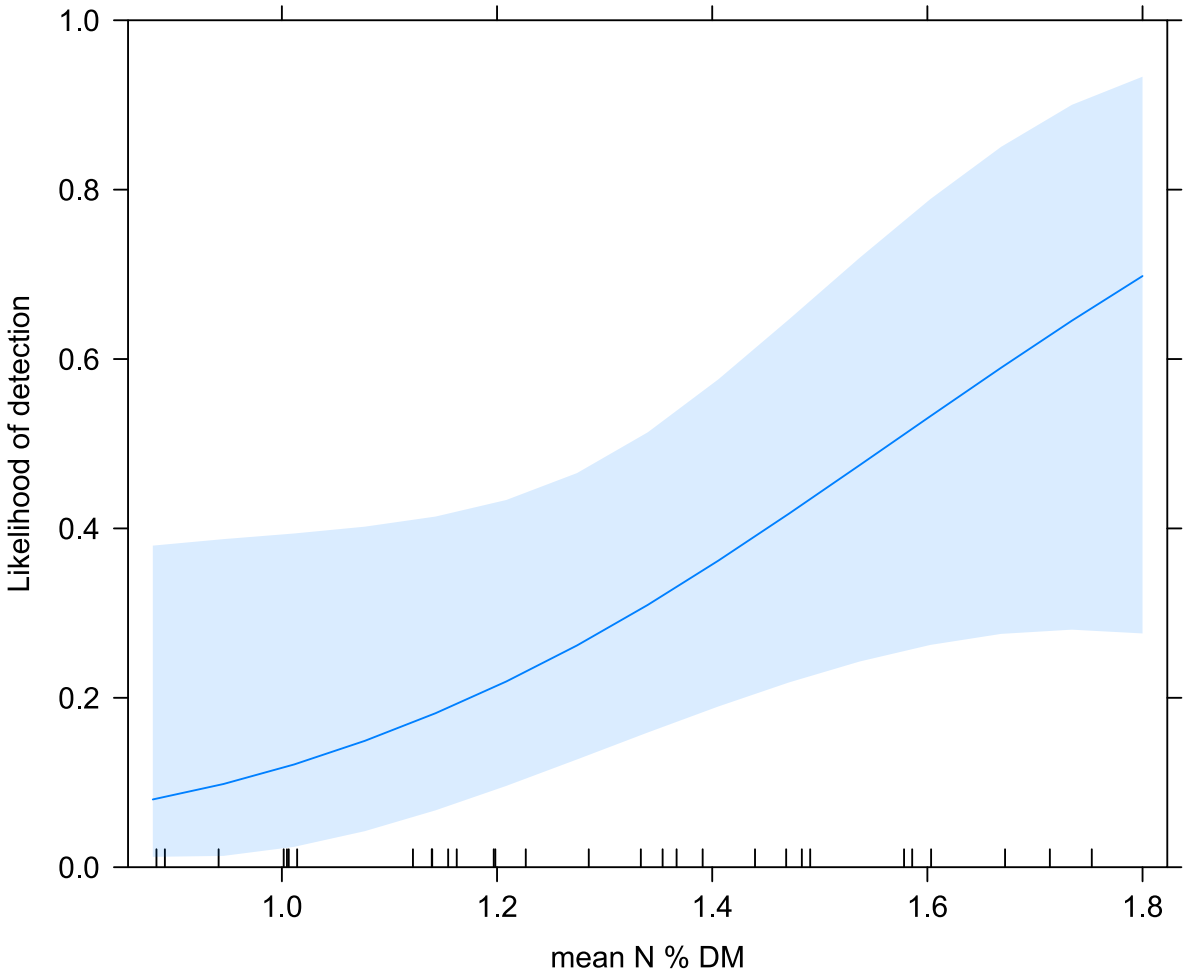

Figure S9. Partial dependence plot for binomial GLM model testing the relationship between mean plot level N and greater glider detection. Increasing levels of N had a positive effect the likelihood of greater glider detection.

Chapter 4 - Supplementary tables

Table S1. Site description of the 30 plots assessed for this study

Ground survey date	Transect	Plot	Latitude	Longitude	Elevation (m.a.s.l)	Slope (%)	Aspect (degrees)	Dominant canopy species	Dominant mid/understory species	Mean NDVI	Min. subcanopy height (m)
25/09/2018 9:00	T1	1	-37.6747	148.3167	120	3	350	*E. sieberi*	*Acacia mearnsii*	0.74	12.7
15/06/2018 10:30	T1	2	-37.6265	148.2884	181	35	180	*E. condensiana*	*E. condensiana*	0.74	18.8
14/06/2018 10:45	T1	3	-37.6244	148.2641	397	5	220	*E. sieberi*	*E. sieberi*	0.71	8.9
27/09/2018 13:54	T1	4	-37.6176	148.2393	222	23	340	*E. polyanthemos*	*Cassinia longifolia*	0.7	13.6
25/09/2018 13:43	T1	5	-37.6761	148.3144	126	2	145	*E. globoidea*	*Acacia longifolia*	0.79	13.7
29/09/2018 9:13	T1.5	1	-37.7932	148.1887	61	1	120	*E. globoidea*	*Allocasuarina verticillata*	0.73	16.3
26/09/2018 14:55	T1.5	2	-37.6448	148.218	159	8	130	*E. consideniana*	*Cassinia longifolia*	0.69	14.8
26/09/2018 10:25	T1.5	3	-37.5955	148.1892	203	1	85	*E. consideniana*	-	0.63	15.2
27/09/2018 15:51	T1.5	4	-37.6252	148.2194	282	20	355	*E. consideniana*	*Persoonia silvatica*	0.72	15.6
29/09/2018 14:10	T1.5	5	-37.7787	148.1815	32	3	60	*E. globoidea*	*Acacia vernicifolia*	0.74	20.4
3/10/2018 9:50	T2	1	-37.5953	148.7188	439	10	123	*E. obliqua*	*Cyathea australis*	0.87	14
1/11/2018 11:23	T2	2	-37.3261	148.659	661	20	299	*E. fastigata*	*Smilax spp.*	0.77	6.5
31/10/2018 11:49	T2	3	-37.3214	148.6518	777	12	93	*E. cypellocarpa*	*Carcinia and Polycyas*	0.81	15
30/10/2018 9:14	T2	4	-37.5176	148.7003	679	55	259	*E. sieberi*	*E. sieberi*	0.76	4
2/10/2018 9:53	T2	5	-37.5788	148.7356	501	5	300	*E. muellerinia*	*Eleaocarpus reticulatus*	0.82	13.7
4/10/2018 9:11	T2.5	1	-37.5845	148.7665	448	3	250	*E. pseudoglobulus*	*Acacia melanoxylon*	0.85	23.7
3/11/2018 12:13	T2.5	2	-37.3307	148.6512	692	8	340	*E. cypellocarpa*	*Acacia dealbata*	0.78	18

31/10/2018 15:26	T2.5	3	-37.3296	148.6541	710	6	305	*E. sieberi*	*Cassinia longifolia*	0.77	16.8
2/11/2018 11:20	T2.5	4	-37.3244	148.655	720	26	50	*E. fastigata*	*Cassinia trinerva*	0.79	25
1/10/2018 9:20	T2.5	5	-37.5758	148.7361	446	5	315	*E. obliqua*	*Acacia dealbata*	0.77	31.5
11/05/2018 10:47	T3	1	-37.2527	148.848	926	6	26	*E. croagingalensis*	*Persoonia silvatica*	0.82	18
9/05/2018 10:03	T3	2	-37.2635	148.8788	1001	14	325	*E. croajingalensis*	*Tasmannia lanceolata*	0.83	31
7/05/2018 15:43	T3	3	-37.2743	148.8832	1185	5	345	*E. delegatensis*	*Tasmannia lanceolata*	0.78	22.6
8/05/2018 9:26	T3	4	-37.2763	148.8954	1050	10	130	*E. nitens*	*Atherosperma moschatum*	0.8	16
10/05/2018 13:39	T3	5	-37.2434	148.8391	907	4	182	*E. viminalis*	*Tasmannia lanceolata*	0.76	23.3
6/11/2018 10:20	T3.5	1	-37.1907	148.8435	937	4	330	*E. croagingalensis*	*Caprosma quadrifida*	0.75	30
7/11/2018 13:17	T3.5	2	-37.1473	148.8215	1072	20	140	*E. cypellocarpa*	*Acacia dealbata*	0.76	12.5
5/11/2018 16:23	T3.5	3	-37.3941	148.7649	920	16	246	*E. obliqua*	*Cyathea australis*	0.77	3.5
8/11/2018 11:56	T3.5	4	-37.1339	148.809	1117	17	333	*E. obliqua*	*Leucopogon maccraei*	0.8	34.6
6/11/2018 15:18	T3.5	5	-37.1326	148.8356	924	8	49	*E. viminalis*	*Persoonia silvatica*	0.76	12.5

Table S2. All spectral indices considered as possible variable candidates in this study

Index	Full name	Formula	Reference
GDVI	Generalized Difference Vegetation Index	$NIR - Green$	Wu (2014)
GRVI	Green Red Vegetation Index	$\frac{NIR}{Green}$	Motohka et al. (2010)
NDGI	Normalized differential greenness index	$\frac{(Green - Red)}{(Green + Red)}$	Nedkov (2017)
NDI B/NIR	Normalized Difference Index - Blue/Near Infrared	$\frac{(Blue - NIR)}{(Blue + NIR)}$	Wu et al. (2019)
NDI RE/NIR	Normalized Difference Index Red Edge/Near Infrared	$\frac{(Red\ Edge - NIR)}{(Red\ Edge + NIR)}$	Wu et al. (2019)
NDRE	Normalized Difference Red Edge Index	$\frac{(NIR - Red\ Edge)}{(NIR + Red\ Edge)}$	Barnes et al. (2000)
NDVI	Normalized Difference Vegetation Index	$\frac{(NIR - Red)}{(NIR + Red)}$	Rouse Jr et al. (1974)
NDVIG	Normalized Difference Vegetation Index - Green	$\frac{(NIR - Green)}{(NIR + Green)}$	Jiang et al. (2013)
NDWI	Normalized Difference Water Index	$\frac{(Green - NIR)}{(Green + NIR)}$	Gao (1996)
NGRDI	Normalized Difference Green/Red Index	$\frac{(Green - Red)}{(Green + Red)}$	Gitelson et al. (2002)
RI	Redness Index	$\frac{(Red - Green)}{(Red + Green)}$	Escadafal and Huete (1991)
RVI	Ratio Vegetation Index	$\frac{R}{NIR}$	Pearson and Miller (1972)
SR	Simple Ratio	$\frac{NIR}{Red}$	Jordan (1969)

VARI	Visual Atmospheric Resistance Index	$\frac{(Green - Red)}{(Green + Red - Blue)}$	Gitelson et al. (2002)

Table S3. Average and median value of model evaluation metrics (mean absolute error (MAE), root mean squared error (RMSE) and r-squared) from 100 independent models of digestible nitrogen

Metric	Test	Mean	Median	Standard deviation	Standard error
MAE	Cross-validation	0.103	0.103	0.0025	0.0002
MAE	Independent validation	0.168	0.166	0.0175	0.0018
RMSE	Cross-validation	0.103	0.148	0.0090	0.0009
RMSE	Independent validation	0.223	0.223	0.0283	0.0028
R^2	Cross-validation	0.103	0.610	0.0752	0.0075
R^2	Independent validation	0.036	0.019	0.0429	0.0043

Citations – Appendix 3

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Appendix 4

Chapter 5 – Supplementary figures

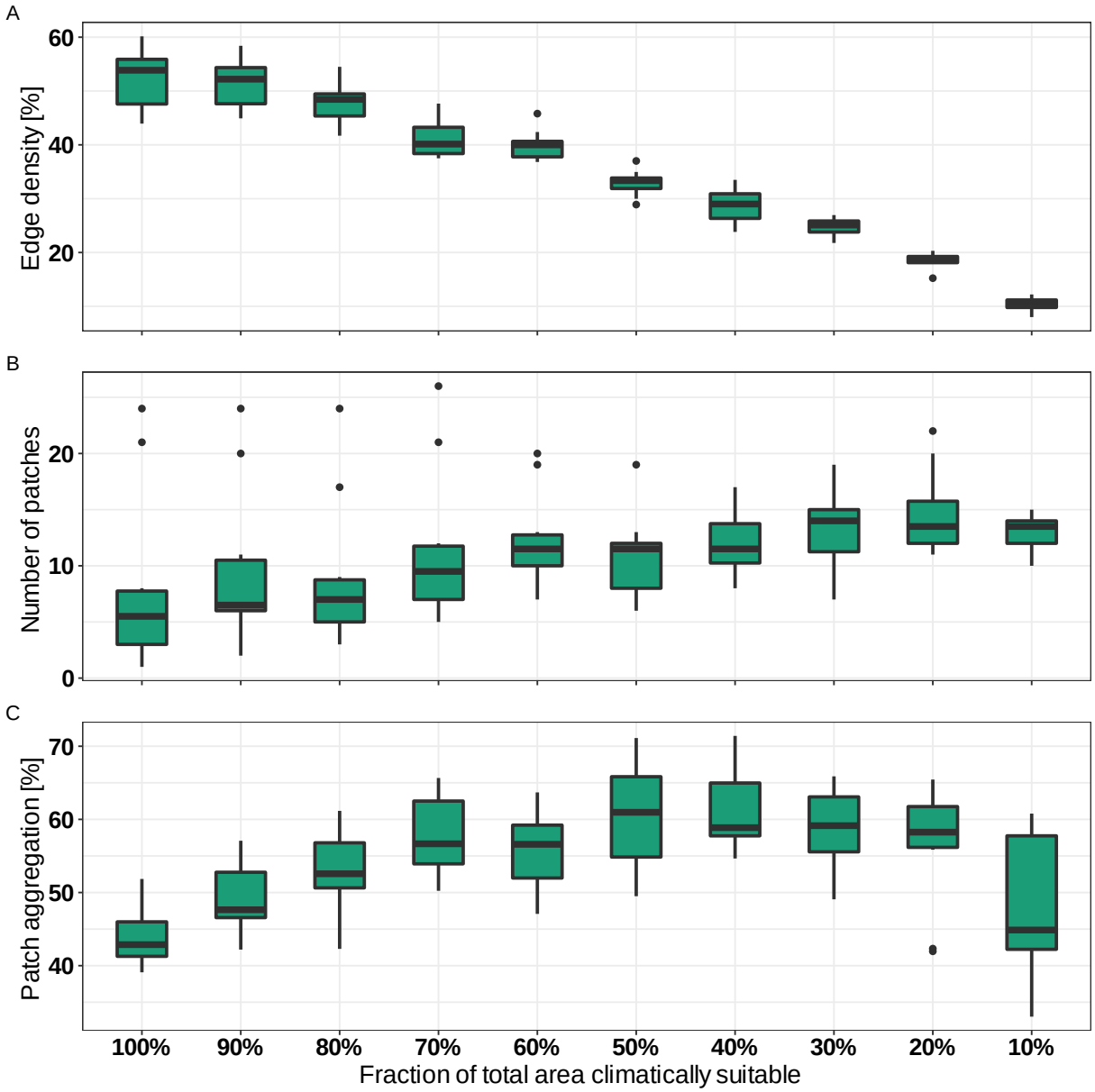

Figure 1. Spatial aggregation metrics of 1000-ha feeding landscape simulations under a modeled reduction in climatically suitable area

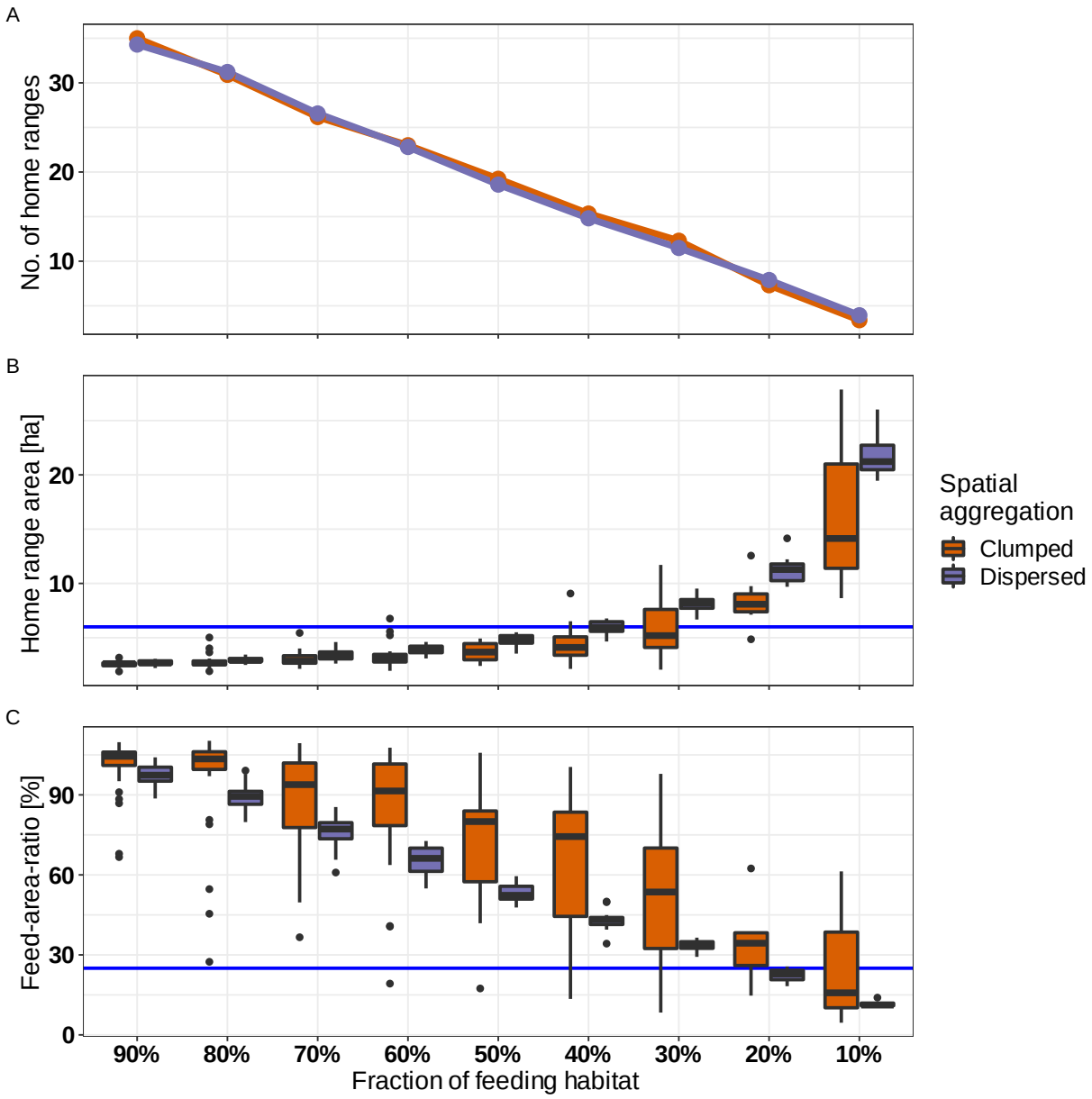

Figure S2. Reduction in number of home ranges (A), increases in home range area (B) and changes in feed-area ratio (C) before filtering for functional home ranges with decreases in feeding habitat area in 100 ha neutral landscape simuations of clumped (orange) or dispered (purple) feeding resources. Blue lines in (B) and (C) illustrate the functioal thresholds for home range area (max. 6 ha) and feed-area-ratio (min. 25%).

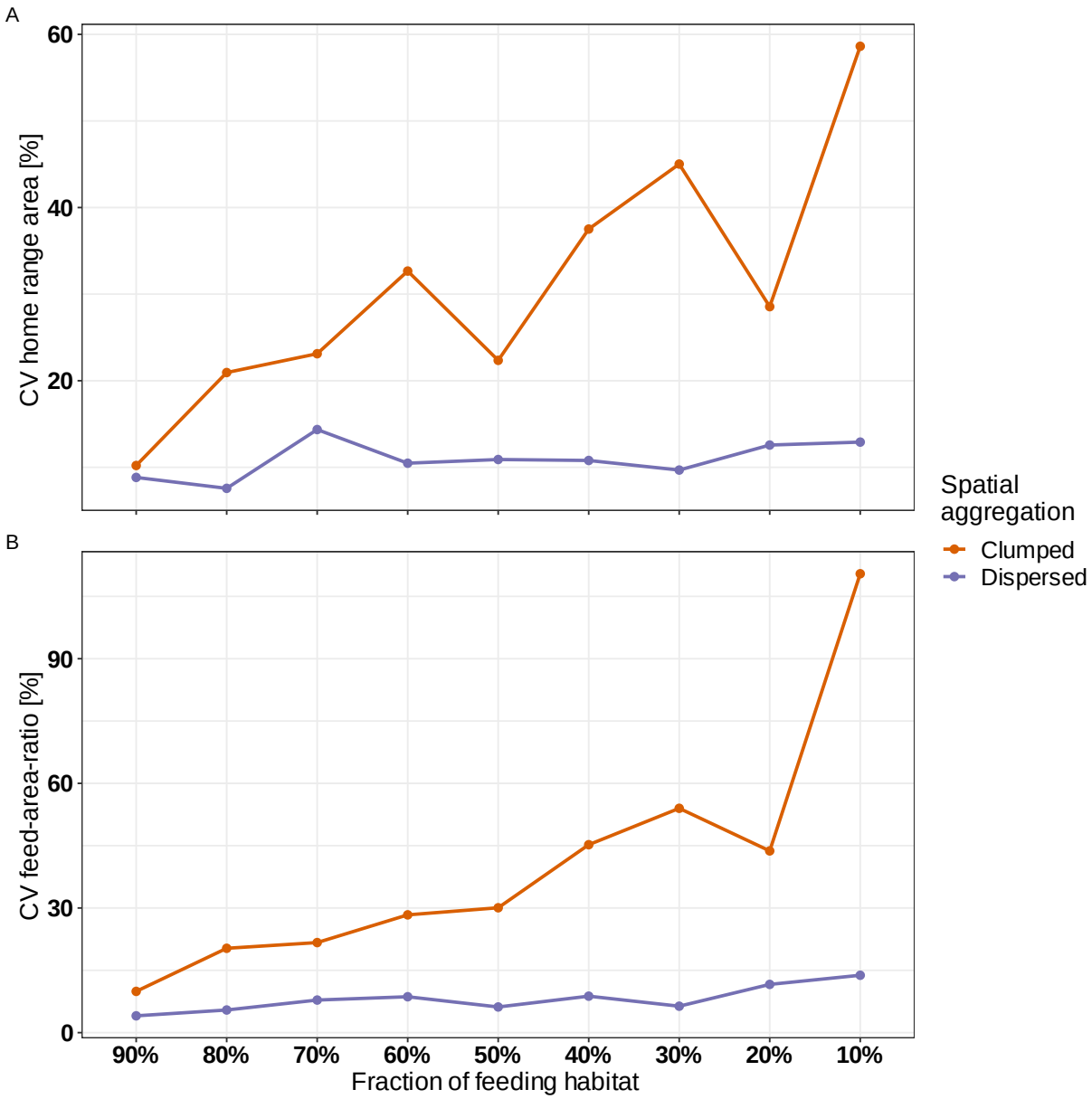

Figure S3. Changes in coefficient of variation (CV) of home range area and feed-area-ratio for all simulated home ranges under decreases in feeding habitat area in 100 ha neutral landscape simuations of clumped (orange) or dispered (purple) feeding resources.

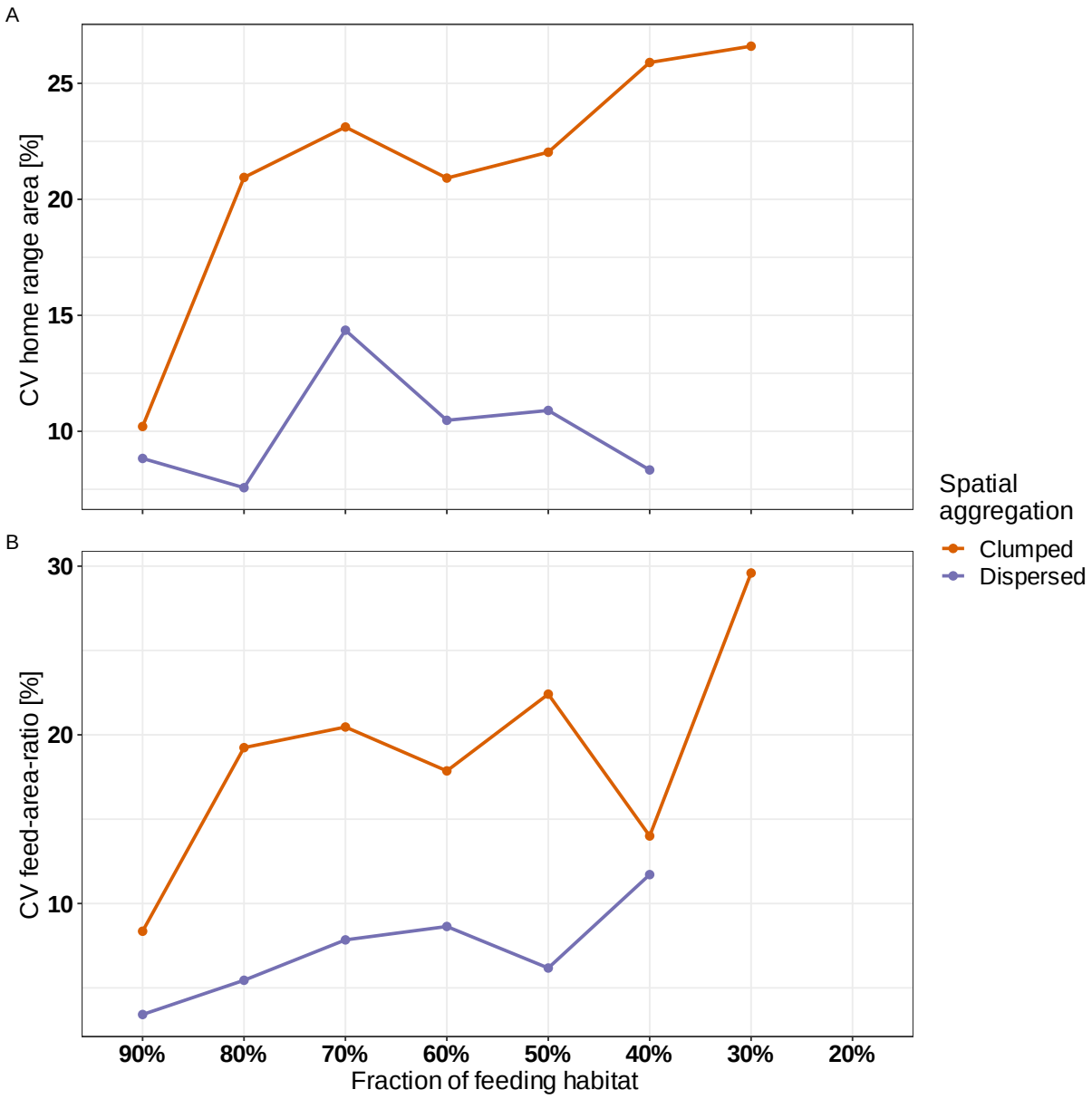

Figure S4. Changes in coefficient of variation (CV) of home range area and feed-area-ratio for functional home ranges only under decreases in feeding habitat area in 100 ha neutral landscape simuations of clumped (orange) or dispered (purple) feeding resources.

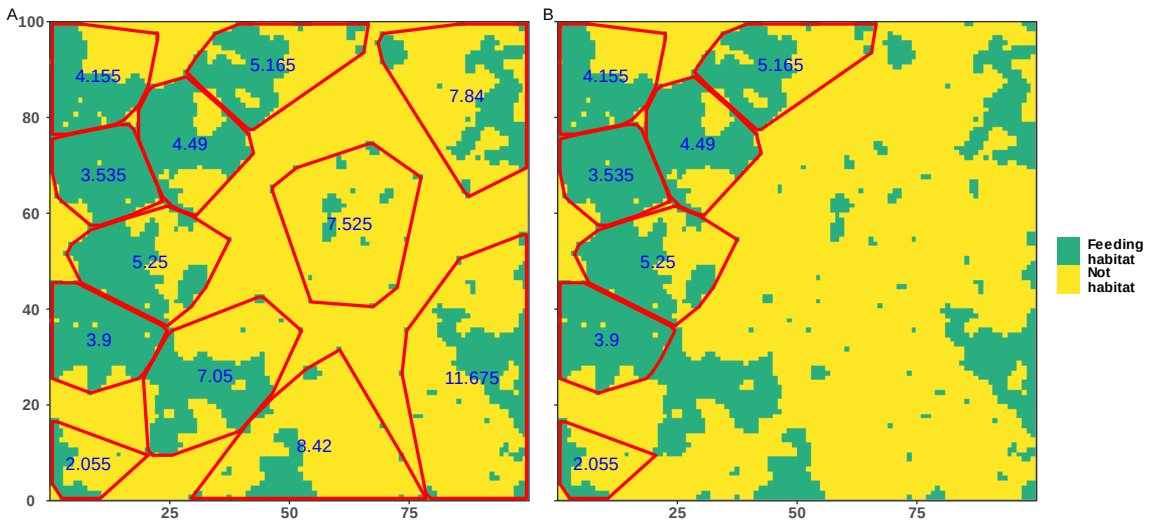

Figure S5. An example of a clustered 100-ha feeding habitat simulation filtered for functionality in home ragnes based on home range area, amount of feeding habitat per home range and feed-area ratio. A is the raw simulation of all home ranges based on *k*-means clustering, resulting in a total of 12 potential home ranges. After filtering for functionality based on the criteria outlined in the methods section, only 7 home ranges remain (B). Blue letters within individual clusters indicate cluster size in hectare.

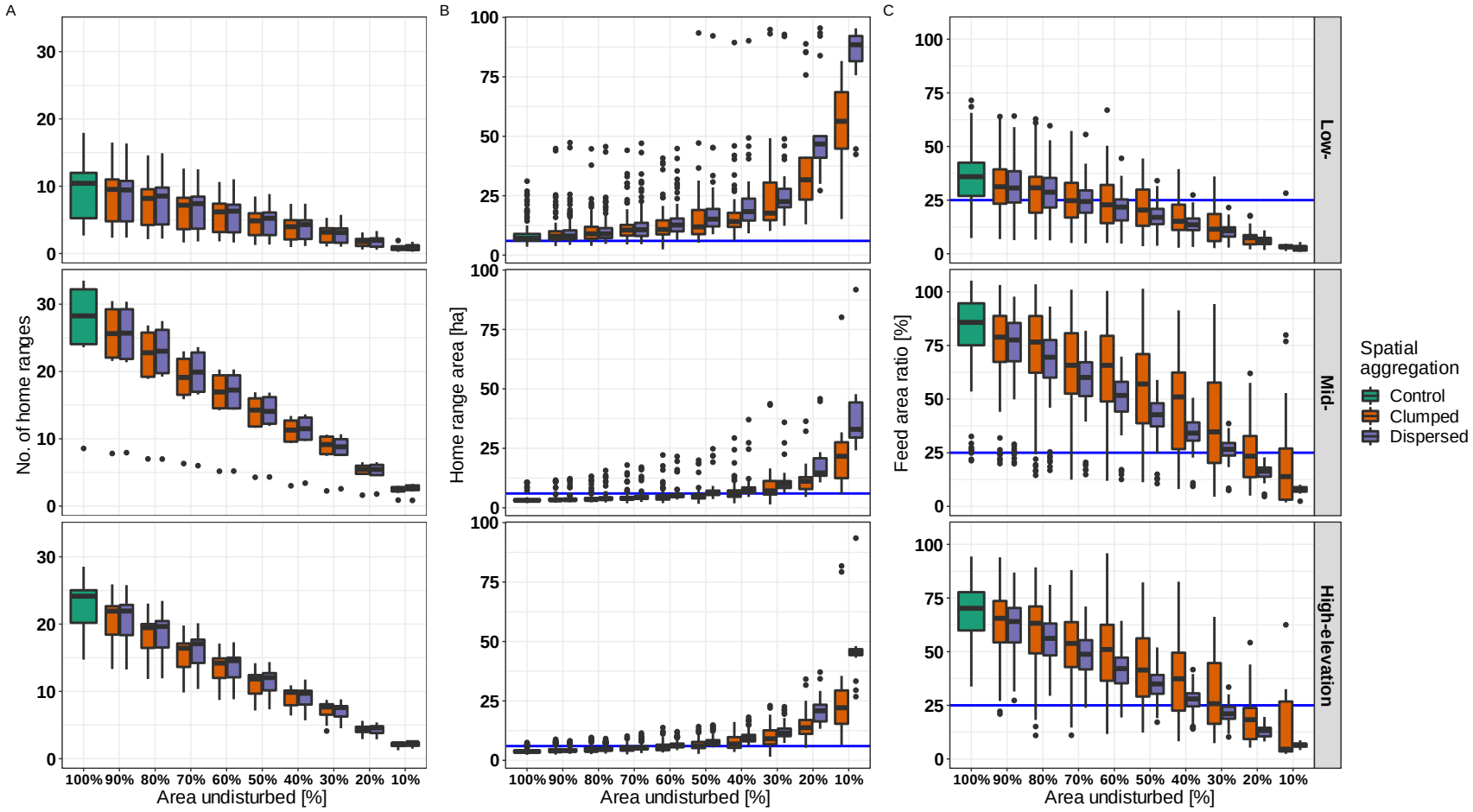

Figure S6. Development of number of home ranges (A), home range area (B) and feed-area-ratio (C) in neutral landscapes based on the properties of spatial predicitons of feeding habitat in different elevation bands of East Gippsland (facets) under increasing disturbance intensity (x-axis). These boxplot graphs are based on the raw data (n = 5885 home ranges), before filtering for functional home ranges only. Blue lines in (B) and (C) illustrate the functioal thresholds for home range area (max. 6 ha) and feed-area-ratio (min. 25%).

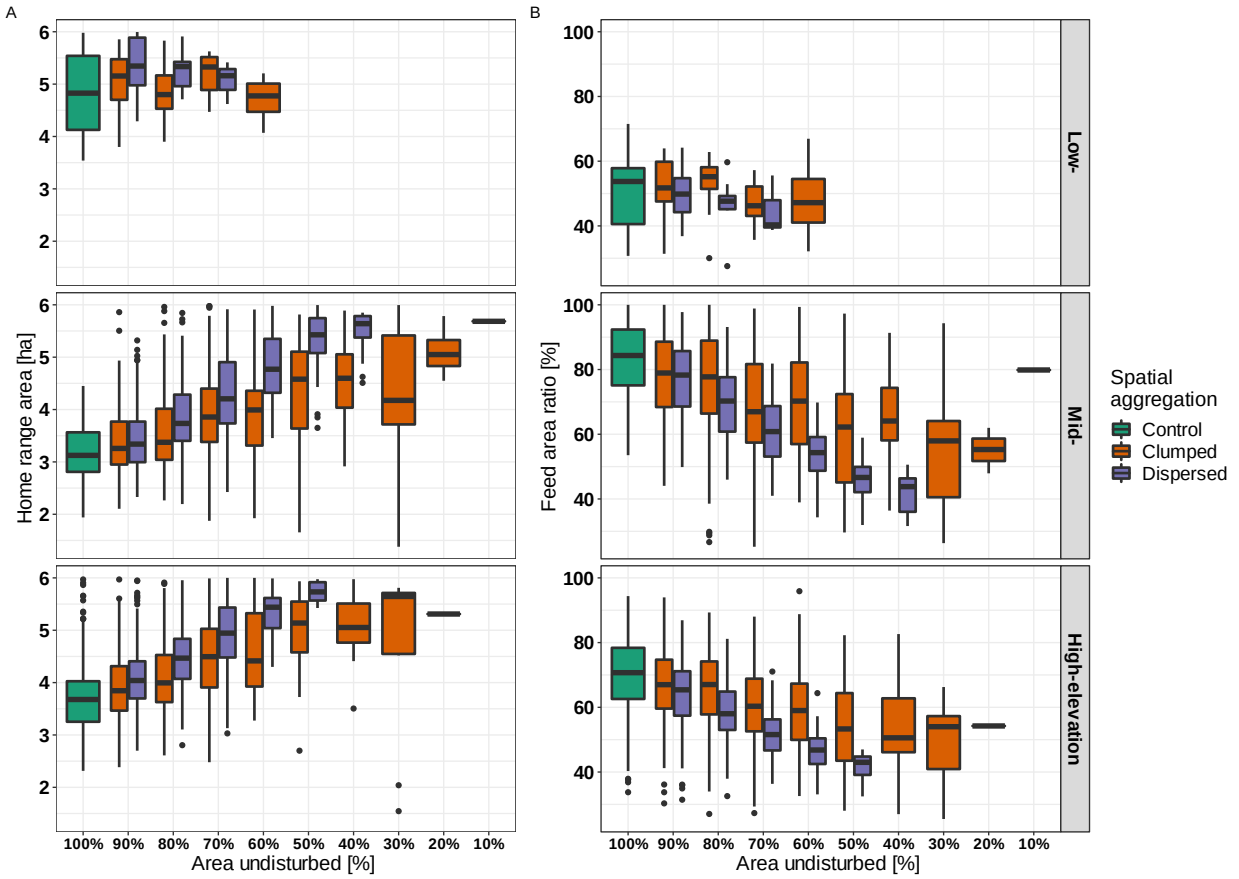

Figure S7. Observed changes in functional home range area (A) and feed-area-ratio (B) in neutral landscapes based on the spatial configuration and properties of survey sites in East Gippsland (faceted by elevation) with increasing disturbance intensity (remaining undisturbed area, x-axis).

Chapter 5 – Supplementary tables

Table S1. Spatial configuration of the feeding, non-feeding and non habitat and spatial aggregation of 30 spatial predictions to 4-ha survey plots in East Gippsland, Victoria (see Chapter 3).

Elevation band	Site	% Feeding habitat	% Not habitat	% Non-feeding habitat	Aggregation (%)
Low elevation	T15P1	23.73	61.02	15.26	90.00
	T15P2	29.13	53.07	17.80	88.37
	T15P3	13.43	54.32	32.26	81.38
	T15P4	14.86	54.54	30.60	81.29
	T15P5	29.65	58.80	11.55	88.86
	T1P1	30.28	58.77	10.95	90.20
	T1P2	46.01	38.98	15.01	83.47
	T1P3	33.97	34.66	31.37	79.99
	T1P4	7.25	84.65	8.10	94.92
	T1P5	14.21	66.00	19.80	91.70
Mid-elevation	T25P1	60.43	25.58	13.99	89.21
	T25P2	70.78	18.18	11.04	89.16
	T25P3	87.74	8.44	3.82	94.50
	T25P4	79.57	10.45	9.98	86.91
	T25P5	84.22	12.53	3.25	94.59
	T2P1	61.40	21.37	17.23	83.27
	T2P2	88.09	10.12	1.79	96.80
	T2P3	25.11	65.97	8.92	91.60
	T2P4	59.72	15.14	25.13	82.65
	T2P5	73.71	11.14	15.16	81.36
High elevation	T35P1	64.42	26.67	8.91	88.96
	T35P2	65.53	17.74	16.73	85.29
	T35P3	73.74	19.11	7.15	88.97
	T35P4	37.64	27.45	34.91	79.97

T35P5	57.33	22.71	19.96	80.58
T3P1	61.61	19.93	18.45	79.00
T3P2	63.51	21.68	14.80	83.15
T3P3	51.49	19.39	29.12	82.94
T3P4	39.20	56.68	4.13	93.61
T3P5	64.77	34.09	1.13	97.35