

Using LiDAR for landscape-scale mapping of potential habitat for the critically endangered Leadbeater's Possum

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Executive summary

Leadbeater's possum (LBP) (*Gymnobelideus leadbeateri*) is a critically endangered arboreal marsupial located in Victoria's Central Highlands in southeastern Australia. Populations of hollow-bearing trees, the key nesting habitat resource for Leadbeater's Possum, are rapidly declining. Disturbances such as bushfires and timber harvesting are believed to be the major causes in the reduction of hollow-bearing trees and thus the extent, quality, and connectivity of LBP habitat. LBP also requires a connected understorey or midstorey for foraging and movement within the forest. Changes in LBP habitat at the landscape-scale are interpolated from plot-level measures and assumed distribution of habitat resources based on forest type and disturbance history. Long-term monitoring at the plot-level has reduced uncertainty around habitat resources required by LBP within the montane ash (*Eucalyptus regnans*, *E. delegatensis*, *E. nitens*) forests of the region; however, it has not addressed uncertainty around the landscape distribution of nesting and foraging habitat resources. Developing effective conservation strategies for LBP requires an understanding of the distribution and quality of available habitat across its potential range. This currently does not exist. I used Light Detection and Ranging (LiDAR) data to develop empirical models that quantify the distribution, quality, and connectivity of LBP habitat in the montane ash forests within a multi-scale framework.

LiDAR-derived topographic and vegetation structural metrics were integrated with different habitat analysis approaches to model the distribution of critical LBP habitat features (hollow-bearing trees, foraging and midstorey stratum connectivity) at multiple scales across ~340,000 ha of forest in Victoria's Central Highlands. In **Chapter 2**, tree-level individual tree delineation (ITD) algorithms were developed to identify individual trees and analyse tree crown attributes. ITD algorithms for overstorey trees were applied to the whole study area to estimate the abundance and distributions of large live trees with big crowns that have high probability of containing hollows. Based on field surveys in 1939 regrowth mountain ash, the dominant overstorey crowns identified by the ITD algorithms had an 86% success rate in identifying mapped trees in mature forest plots. Our landscape analyses estimated 405,000 large live trees (crown width >15m) and 572,000 (95%CI: 318,000-808,000) potential large live tree with hollows (DBH>150cm), which equate to a mean density of one live large old tree per ha across the Central Highlands. ITD algorithms were also used to map canopies and to calculate the proportion of projection area of midstorey stratum, a surrogate for midstorey coverage, for use in assessments of foraging habitat.

Hollow-bearing trees are a key feature of mature forests around the world. They provide critical habitat resources for hollow-dependent animals, many of which are threatened, due to a range of natural and human disturbances. In **Chapter 3**, to develop more accurate inventories of hollow-bearing trees (both live and dead form classes) across a large landscape, I used LiDAR-based metrics of forest structure and topography, coupled with datasets on environmental conditions to develop statistical models of abundance of hollow-bearing trees using machine learning tools. These provided empirical estimates of HBT density for every hectare of the Central Highlands within the LiDAR footprint. I identified 1,519,000 (95%CI: 1,306,000 – 1,730,000) hollow-bearing trees may occur across the full extent of Victoria's Central Highlands. This included 833,000 (95%CI: 742,000-923,000) live HBTs and 686,000 (95%CI: 564,000-807,000) dead

HBTs. The predictive models provided rigorous, repeatable estimates of tree abundance across a wide range of vegetation classes and forest management zones (with appropriate estimates of uncertainty), as well as a new understanding of the complexity of the structural, topographic, and environmental features associated with abundance of hollow-bearing trees and their spatial variability over large areas.

In addition to HBTs for nesting, LBP require a well-connected midstorey stratum to facilitate movement amongst nesting trees and foraging. In **Chapter 4**, the association between field-assessed multi-storey vegetation connectivity and LiDAR structural metrics was evaluated to develop landscape-scale predictions of connectivity and foraging habitat (density of live wattle) for LBP. Forest structural types with high midstorey connectivity, which are a critical habitat feature for LBP, occupied 17.2% of the study landscape. The landscape-scale predictions of vegetation connectivity provided an understanding of the factors (e.g., topography, fire, logging and interactions among strata) that help shape connectivity and foraging habitat. This understanding is critical for improving the management of the region's forests and, in particular, ensuring that both key habitat elements, HBTs and dense midstorey vegetation, either co-occur in the same stand or are in close proximity to ensure sufficient high-quality habitat for LBP over space and time.

In **Chapter 5** I used the landscape-level mapping of habitat resources developed in Chapters 2-4 to predict landscape-scale LBP habitat suitability based on fields records of LBP occurrence. The validated habitat suitability model for LBP had an overall accuracy of 87.3% and an AUC of 0.889. The model predicted that 28,000 ha (95%CI: 17,000ha-40,000ha) of the study landscape (i.e., 9.6%) supported suitable habitat for LBP. Twelve variables were found to have the strongest influence on estimating habitat suitability for LBP. Of these, four related to foraging habitat, three to nesting habitat, three to climatic and topographic factors, and two to disturbance history. Our approach highlights the potential for using high-resolution, spatially explicit data on forest structure at a landscape-scale to map the distribution and abundance of suitable habitat for a critically endangered species.

Habitat suitability models generally account for the selection of suitable habitat and their appropriate geographical extents. However, they rarely account for the accessibility of this habitat and connectivity among habitat patches. Effective conservation of species requires that patches of their habitat are connected in space and time. In **Chapter 6**, graph-theoretic connectivity networks based on resistance surfaces were generated from the LiDAR mapped cover of vertical stratum. The least-cost links between patches from networks were integrated with a kernel density estimator to identify functionally connected regions. The mapping of landscape connectedness identified a potential landscape-scale metapopulation structure for LBP within the Central Highlands. This provides a tool that could be used to expand the existing protected area network to support the metapopulation processes of LBP. The identification of functionally connected regions could enhance the conservation planning for long-term population persistence.

The conservation and management of endangered species is major focus of forest and land managers around

the world. High-quality data on the distribution and quality of habitat is critical to the development of effective conservation and recovery strategies for species. This thesis developed a set of habitat analysis models for quantifying habitat resources, habitat suitability and connectedness for the critically endangered Leadbeater's Possum across a range of spatial scales. These analyses highlight the benefits of using high-resolution, spatially explicit LiDAR data from the whole landscape to identify and map (1) the distribution and abundance of hollow-bearing trees, (2) midstorey stratum connectivity, (3) the distribution and abundance of suitable habitat, and (4) metapopulation structures within functionally connected regions. Dynamic modelling, informed by these LiDAR-derived models, can be used to forecast the likely consequences of changing habitat abundance under different management scenarios and evaluate both the short-term and long-term effectiveness of different conservation strategies.

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.
- iii) The thesis is less than 100,000 words in length, exclusive of tables, illustrations, bibliography, and appendices.

Ruizhu JIANG

Preface

This PhD thesis consists of seven chapters, five of which (Chapters 2-6) are unpublished but are intended for publication. The data that underpin the analyses were collected by me or provided by collaborating institutions. Data from the field-based surveys of Leadbeater's Possum from 2014-2017 were provided by Arthur Rylah Institute for Environmental Research (ARI). The 5T raw LiDAR data for the Central Highlands landscape was provided by the Department of Environment, Land, Water & Planning (DELWP). Additional records of camera sites to detect Leadbeater's Possum were collected by VicForests. I developed new approaches to process LiDAR data and collected field-based stem mapping data for validation of my models. In addition, I developed statistical models for multi-scale habitat analysis and wrote the thesis and the draft manuscripts for publication. Each of the data/analysis chapters of this thesis (Chapters 2-6) are intended for publication in peer-reviewed journals. Some of the methods described, particularly with regards to the LiDAR data and processing and the ARI field survey data are repeated in several chapters where they were used for multiple, but distinct, analyses. The following list outlines the intended papers for submission, the proposed journal, and the full list of authors:

Chapter 2:

Jiang, R., R. Trouvé L. Lumsden, P. J. Baker, and C. R. Nitschke. 2019. Prediction of large old trees with large crowns using a novel individual tree crown delineation method and airborne LiDAR data in Victoria's Central Highlands. *Ecological Applications*.

Chapter 3:

Jiang, R., C. R. Nitschke, R. Trouvé L. Lumsden, and P. J. Baker. 2019. Predicting landscape-scale variability in hollow-bearing tree abundance in Victoria's Central Highlands. *Ecological Applications*.

Chapter 4:

Jiang, R., P. J. Baker, R. Trouvé L. Lumsden, and C. R. Nitschke. 2019. Predicting connectivity of midstorey stratum using airborne LiDAR data: implications for modelling Leadbeater's Possum habitat at the landscape-scale. *Ecological Applications*.

Chapter 5:

Jiang, R., C. R. Nitschke, R. Trouvé L. Lumsden, T. McBride, and P. J. Baker. 2019b. Landscape-scale habitat suitability analysis for Leadbeater's Possum using LiDAR data in Victoria's Central Highlands. *Ecological Applications*.

Chapter 6:

Jiang, R., P. J. Baker, R. Trouvé and C. R. Nitschke. 2019a. Modelling landscape-scale habitat network connectivity for Leadbeater's Possum using airborne LiDAR data. *Ecological Applications*.

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Chapter 1.

1 Introduction

Biodiversity loss is a global phenomenon (Lindenmayer 2015a, Lindenmayer 2015b). In Australia, a large number of land mammals have already become extinct and many others have suffered steep rates of decline (Woinarski et al. 2014b, Woinarski et al. 2015). To reduce the risk of further species losses, better biodiversity management and monitoring programs are essential to balance forest resource use and biodiversity conservation (Hawksworth and Bull 2007, Li et al. 2011, Lindenmayer 2015b). Measurable outcomes are essential for evaluating the effectiveness of threatened species conservation efforts (Scheele et al. 2018). Traditionally, monitoring programs have focused on fine-scale (i.e., plot-level) measures due to cost-effectiveness (Innes 1998) and then extrapolated the results to the landscape scale (e.g., Burns et al. 2015; Lindenmayer and Sato 2018). However, directly extrapolating fine-scale metrics to broader scales does not account for how the level of ecological organisation may change with scale. This can lead to erroneous conclusions about changes in a species' abundance or occurrence at the landscape scale (Peterson and Parker 1998). Nitschke et al. (2007) argued that fine-scale measures, typical of most monitoring programs, must be integrated with landscape-scale analyses of a species' response to broad-scale heterogeneity to reduce both statistical and structural uncertainty in effectiveness monitoring (Nitschke et al. 2007). Without explicit acknowledgement of the scaling issues associated with extrapolation, conservation efforts may have a lower likelihood of achieving the desired outcomes.

Recent advances in the development of geographical information systems (GIS), remote sensing (RS) techniques, and information technology (IT) provide new opportunities to address landscape-scale relationships and changes in forest ecosystems (Lee et al. 2010, Li et al. 2011). In particular, Light Detection and Ranging (LiDAR) technology that acquires three-dimensional geospatial data on forest structure at high spatial resolutions with high accuracy over large areas has the potential to directly bridge the gap between fine-scale surveys and landscape-scale monitoring (Lefsky et al. 2002, Lim et al. 2003, Martinuzzi et al. 2009, Fedrigo et al. 2018). LiDAR has been used to detect subtle differences and dynamics in vegetation structure between habitat types, particularly in sub-canopy forest structure (Bälsler et al. 2011, Fedrigo et al. 2018), the distribution of tree senescence classes and growth forms (Bater et al. 2007, Owers et al. 2014, Wing et al. 2015), and to improve the understanding of wildlife-habitat relationships (Jaime-González et al. 2017). LiDAR can acquire centimetre-scale measures of forest structure across hundreds of thousands of hectares, allowing for a simultaneous assessment of both statistical and structural uncertainty. This integration should improve the effectiveness of monitoring and aid managers in developing effective conservation strategies for forest-dependant biodiversity (Nitschke et al. 2007).

In my thesis, I utilised LiDAR data and landscape-scale surveys of occurrence and habitat structure to explore the distribution and quality of habitat for the critically endangered species, Leadbeater's Possum (LBP, *Gymnobelideus leadbeateri*), in the forested landscapes of Victoria's Central Highlands. The main objective of this thesis was to integrate fine-scale and broad-scale metrics of forest structure to map the potential habitat for LBP at the landscape-scale. Being able to map the key habitat features LBP across hundreds of thousands of hectares should provide direct empirical estimates of available habitat and potential population sizes without the uncertainties of extrapolating over 4-5 orders of spatial magnitude. This, in turn, should provide more robust data for conservation planning of this iconic species.

1.1 Leadbeater's Possum overview

1.1.1 General description of Leadbeater's Possum

Leadbeater's Possum (*Gymnobelideus leadbeateri*) is a small, nocturnal, arboreal mammal. It has a body length of 150 – 170 mm, tail length of 145 – 165 mm, and weighs 100 – 165 g (description from the Leadbeater's Possum Action Statement N0.62, 2014). Leadbeater's Possum (LBP) has been classified as a critically endangered species, currently listed under the Victorian *Flora and Fauna Guarantee Act 1988*, *Environment Protection and Biodiversity Conservation Act 1999*, *Advisory List of Threatened Vertebrate Fauna in Victoria*, and *IUCN Red List of Threatened Species*. The majority of LBP's diet is comprised of plant and insect exudates (gum, sap or nectar) and arboreal arthropods (including beetles, spiders and, particularly, large crickets) (Smith 1980, Smith 1984, Harley 2005). LBP is predominantly distributed in eucalypt forests and snow gum woodlands in the Central Highlands, roughly located from Toolangi in the west and Rubicon in the north to Mt Baw Baw in the east and Beenak in the south (Commonwealth of Australia 2016). Recently, new colonies have been discovered 15 km east of its known distribution (McBride et al. 2019).

1.1.2 Habitat attributes required by Leadbeater's possum

Leadbeater's Possum is predominately found in three vegetation types: montane ash forests, sub-alpine woodland and lowland floodplain forest. The main range of LBP is mountain ash forests. The montane ash forest is a globally iconic and unique ecosystem (Burns et al. 2015). The overstorey species of this forest type are mountain ash (*Eucalyptus regnans*), alpine ash (*E. delegatensis*) and shining gum (*E. nitens*). Mountain ash is the tallest flowering plant in the world. Individual trees may grow up to 90 m after several hundred years (Ashton 1976, Burns et al. 2015). LBP habitat is defined by the presence of two distinct structural features in montane forests: hollow-bearing trees that provide nesting habitat for LBP and a dense understorey of wattle species (Silver Wattle *Acacia dealbata*, Mountain Hickory Wattle *A. obliquinervia*, Forest Wattle *A. frigiscens*, Blackwood *A. melanoxylon*) that provide foraging habitat and arboreal paths for movement through the forest (Lindenmayer 1989b, Lindenmayer et al. 2000). Nearly all (96%) of the Leadbeater's Possum reserves (43,550ha) are located in

ash forest (Lumsden et al. 2013a, Nelson et al. 2015). The second commonly used habitat type is sub-alpine woodland dominated by snow gum (*E. pauciflora*). Approximately 4% of Leadbeater's Possum reserves are located in this vegetation type (Nelson et al. 2015). Finally, ~20 ha of lowland floodplain forest dominated by mountain swamp gum (*E. camphora*) near Yellingbo support an isolated population of LBP (Leadbeater's Possum Action Statement N0.62, 2014). McBride et al. (2019) recently found LBP in mixed eucalypt species forests containing *E. viminalis*, *E. radiata*, *E. dalrympleana*, *E. obliqua* and *E. cypellocarpa* within the Herb-Rich Foothill Forest ecological vegetation class.

Hollow-bearing trees (HBT) are important to arboreal fauna of conservation concern in montane ash forest, including LBP (Kramer et al. 2016, Lindenmayer et al. 2016b). Large trees play many ecological roles, including carbon storage (Thomas et al. 2013, Lindenmayer 2017) and provision of habitat for fauna (Kramer et al. 2016, Lindenmayer 2017). In addition, forests with old trees are important for hydrological and nutrient cycles (Manning et al., 2006; Lindenmayer et al., 2012b). HBTs vary considerably in structure. Form classes for HBTs are used to classify this variability based on the degree of senescence and collapse. Early studies of the LBP showed that they prefer the short, large, and dead trees with abundant hollows (Smith and Lindenmayer 1988). (Smith and Lindenmayer 1988) suggested that preferred HBT are large, with diameter at breast height (DBH) > 210 cm. Those trees are likely to be at least 190-220 years old, because mountain ash trees grow approximately 1cm in stem diameter per year (Ashton 1976). Montane ash trees normally do not start to form hollows until they are 120 years old (Ambrose 1982). However, there is little empirical data on tree age for these forests due to the lack of annual rings in these tree species (Simkin and Baker 2008). The abundance of live and dead HBT have been used to determine the spatial location of key habitat areas for LBP. The two LBP habitat protection zones in the Code of Forest Practices, Zone 1A and Zone 1B, are both defined by the presence of large HBTs. Zone 1A was initially defined as areas of ash forest with at least 12 live HBTs per three hectares or mature ash forest (>120 years old) or mixed aged Ash forest where the oldest age class is mature (>120 years old) (Macfarlane et al. 1991). This definition was recently changed to 8 live or dead trees per 3 ha area based on the recommendation of Leadbeater's Possum Advisory Group (2014). Zone 1B is defined as having 12 live or dead HBTs as well as a minimum of 5 m² of basal area of *Acacia* species (i.e., a dense, connected understorey).

Suitable foraging habitat for LBP is one of the most crucial forest structural requirements for LBP. Specifically, LBP requires foraging habitat with a high level of connectivity. As LBP does not have a gliding membranes, it needs near continuous foliage cover to facilitate movement through the forest (Macfarlane et al. 1997). Movement pathways can be formed by both tall understorey shrubs and regrowth Eucalypts. Lindenmayer et al. (1991b) found that the probability of LBP occurrence increased with an increase in the basal area of wattles (*Acacia* spp.) within a stand. Regenerating forests adjacent to nesting sites can also provide suitable foraging habitat provided they have a high biomass of wattles and high stem density (Smith et al. 1985, Nelson et al. 2015). In montane ash forests, the high-quality LBP habitat is comprised of a mixed-aged forest in which large HBTs (for nesting) co-occur with sufficient understorey wattles (for foraging and moving activities) or two sites in close proximity in which one provides nesting habitat and the other that contains suitable foraging resources and movement pathways (Lumsden et al. 2013a).

1.1.3 Major threats to Leadbeater's Possum

Disturbances such as bushfires and timber harvesting are believed to be the major causes in the reduction in the extent, quality, and connectivity of LBP habitat (Commonwealth of Australia 2016). Approximately one-third (~34%) of the area of the Central Highlands assumed to contain suitable LBP habitat was burnt in the 2009 Black Saturday bushfires (Leadbeater's Possum Advisory Group 2014). According to most recent LBP occupancy prediction models, only 2,225 ha of montane ash forests were suitable for LBP in 2015 (Lindenmayer 2015a, Lindenmayer et al. 2016a) and the population size of LBP has decreased to 1100 – 3125 individuals (Woinarski et al. 2014a). The predicted decline in the extent of suitable habitat is believed to have fragmented remaining populations, making LBP more vulnerable to future stochastic events (Lindenmayer and Possingham 1995b).

The number of large hollow-bearing trees appears to be declining rapidly in the Central Highlands (Lindenmayer et al. 1997, Lindenmayer et al. 2013). The rate of decline in the density of hollow-bearing trees in monitored sites within the Central Highlands is 4.4% annually (Lindenmayer et al. 1997, Lindenmayer et al. 2013). The 2009 bushfire killed large hollow-bearing trees, but also killed 1939 regrowth montane ash in areas impacted by high intensity fire. Trees in the 1939 age cohort would have replaced collapsing HBTs over the next 50-100 years. In addition, timber harvesting of 1939 regrowth has also reduce the supply of future HBTs across the Central Highlands (Myroniuk and Wilcken 1998).

A defining feature of LBP habitat dynamics is the different temporal scales at which HBTs recruit and persist (>100 years) and the wattle understorey recruits and persists (<100 years). The abundance and density of wattles declines in eucalypt stands as they mature due to density-dependant senescence (Trouv   et al. 2019). Most of the wattles that recruit after an intense bushfire will have died within 70-80 years (or less where the eucalypt overstorey is particularly dense). This senescence occurs decades before hollow-bearing trees begin to develop (Myroniuk and Wilcken 1998, Lindenmayer et al. 2012a). As a consequence, the highest densities of LBP are found in stands 15-50 years old where HBTs that have survived the fire or been created by the fire are intermixed with dense regenerating *Acacia* (Smith and Lindemayer 1992; Lindenmayer et al. 2017). It is the biggest challenge to ensure that both key habitat elements, HBTs and dense midstorey vegetation, either co-occur in the same stand or are in close proximity to ensure sufficient high-quality habitat for LBP over space and time.

1.1.4 Priority researches needed to enhance the conservation management

Current estimates of the extent and quality of LBP habitat and population size are based on extrapolations from plot-level metrics collected from a network of small, long-term monitoring plots in the Central Highlands (Lindenmayer et al. 2018). Three decades of monitoring in these plots has shown that LBP populations and HBTs are declining locally. However, a recent increase in survey activity across the Central Highlands LBP found over 200 new colonies since 2014. Recent findings by McBride et al. (2019) have also extended the known distribution of LBP. The conflicts between the increased detection of colonies, the expansion of the LBP home range extent and decline in occupancy in long-term monitoring plots indicates that there may be processes operating at

different spatial scales and highlight the possibility that structural uncertainty around LBP habitat at broader scales remains high. Quantifying the uncertainty regarding the distribution and patterns of nesting trees and understorey density at broad-scales is important for building robust conservation plans and improving existing models. Current landscape-level models of LBP occupancy are based on GIS-based variables that act as proxies for LBP habitat (Lumsden et al. 2013a; Victorian Environmental Assessment Council 2017). Existing models are based on poor correlations and lack most of the key habitat features, such as the presence of HBT and vegetation connectivity that may make predictions of LBP habitat far less accurate and have wide margins of error (Blair et al. 2017). Ambiguity around the amount of habitat that exists across the range of LBP has been acknowledged in the Commonwealth of Australia's National Recovery Plan for Leadbeater's Possum (*Gymnobelideus leadbeateri*) (2016). In the LBP Recovery Plan, the following knowledge gaps were listed as priority research needs to enhance the species' conservation status:

- finer-scale mapping of HBTs across the montane ash forests, to improve occupancy or other distributional modelling, and to develop more precise local and regional conservation plans;
- finer-scale mapping of understorey density or connectivity, to provide more complete spatial information to improve occupancy or distribution models, and to develop more precise local and regional conservation plans; and
- identifying the most important habitat attributes required by LBP to update or expand the extent of the current reserve network.

1.2 Habitat analysis model overview

Tools for quantifying habitat quality and predicting biodiversity change are essential for biodiversity conservation (Elith 2000, Cardinale et al. 2012, Vellend et al. 2013, Dornelas et al. 2014, Ewers et al. 2017, Leroux et al. 2017). A suite of models derived from different ecological theories have been used to predict the abundance, diversity and distributions of species based on environmental conditions and ecological processes (Thuiller et al. 2013, Leroux et al. 2017).

1.2.1 Species distribution models and habitat suitability index

During the last two decades, species distribution models (SDM) and habitat suitability index (HSI) models have become an increasingly important tool for identifying the habitat for species and supporting their conservation and management (Guisan and Thuiller 2005, Austin 2007, Rodríguez et al. 2007, Farrell et al. 2013, Guisan et al. 2013, Rechsteiner et al. 2017). Habitat suitability is determined by the response of species to a set of spatially environmental variables (Elith 2000). A definition of suitable habitat for a species requires an understanding of the way in which environmental variables affect the likelihood that a species will be found at a given location (Burgman 1989, Prober and Austin 1991, McIntyre and Lavorel 1994, Coates 1996, Elith 2000). SDMs based on empirical relationships between a species distribution data (e.g. occurrence, abundance) and environmental or spatial predictors are typically used to quantify species-habitat relationships (Elith and Leathwick 2009, Martinuzzi et al. 2009, Araújo and Peterson 2012, Tattoni et al. 2012, Leroux et al. 2017). Generalized linear models (GLM), general additive models (GAM), boosted regression trees (BRT), and random forests (RF) are the

most common statistical approaches used to develop for SDMs (Hastie et al. 2009, Martinuzzi et al. 2009, Maroco et al. 2011, Shoemaker et al. 2018). These methods estimate the probability of presence based on presence-absence data of the species. The predicted probability of presence may be used as an index of habitat quality (HSI) (Elith 2000). SDMs and HSIs have been used:

1. to identify species-specific habitat requirements (Vierling et al. 2011a, Farrell et al. 2013, Zellweger et al. 2013, Rechsteiner et al. 2017),
2. to map species distributions and understand the effects of environmental variables on species distribution (Zaniewski et al. 2002, Jeschke and Strayer 2008, Braunisch et al. 2014, Vogeler et al. 2014, Breiner et al. 2015, Rechsteiner et al. 2017, Shoemaker et al. 2018); and
3. to guide a variety conservation applications including spatial conservation prioritization and land-use management (e.g. protected areas design;) and restoration planning (Chetkiewicz and Boyce 2009, Bässler et al. 2011, Flaherty et al. 2014, Meller et al. 2014, Leroux et al. 2017, Rechsteiner et al. 2017).

1.2.2 Landscape connectivity network

SDMs and HSI generally account for the selection of suitable habitat and their appropriate geographical extents (Courbin et al. 2009, McLoughlin et al. 2010, Moreau et al. 2012, Courbin et al. 2014), but rarely for the accessibility of high quality habitat and connectivity among habitats (Courbin et al. 2014, Stevenson-Holt et al. 2014, Guo et al. 2018). Effective biodiversity conservation within dynamic landscapes requires a connectivity model to evaluate the impacts of changes in landscape structure on the movement of animals (Crooks and Sanjayan 2006, Galpern and Manseau 2013, Stevenson-Holt et al. 2014). Landscape connectivity is defined as the degree to which the landscape facilitates or impedes species movement amongst resource patches (Taylor et al. 1993, Crooks and Sanjayan 2006). Animal movement, habitat selection and their influence on behavioural and physiological responses strongly depend on the spatial arrangement of resource patches in the landscape (Stevenson-Holt et al. 2014). Habitat accessibility is not only related to the structural attributes of connectivity (i.e., spatial arrangement of patches), but also to its functional aspects (i.e., movement capacity) (Crooks and Sanjayan 2006, McIntire et al. 2007, Dancose et al. 2011). Assessing functional connectivity requires identifying the potential movement pathways of species across modified and fragmented landscapes (Stevenson-Holt et al. 2014). There are two distinct ways of producing functional connectivity maps, least-cost surfaces and graph theory (Galpern 2011).

- (1) Least-cost surfaces estimated the distance between any pixels of a raster layer and the locations of identified suitable habitat patches. The distance was weighted by resistance values (cost values) from a resistance surface using 'cost-distance' function (Stevenson-Holt et al. 2014).
- (2) Graph theory assumes the landscape to be composed of a set of nodes that are connected by links (Urban and Keitt 2001, Urban et al. 2009, Courbin et al. 2014). The network nodes represent high-quality patches, with the links reflecting the possibility for the focal species to move between two nodes (Theobald 2006, Dale and Fortin 2010, Galpern 2011, Courbin et al. 2014). Landscape graphs were developed to understand the connectivity relationships among resource patches (Cantwell and Forman 1993, Urban and Keitt 2001, Urban et al. 2009, Galpern 2011).

Using approaches for assessing connectivity can provide knowledge of how landscape structure may affect the movement of species. This is essential for addressing the impacts of habitat fragmentation (Fischer and Lindenmayer 2007), preventing the spread of pathogens and invasive species (Margosian et al. 2009), building protected area networks for conservation planning, maintenance of biodiversity values (Minor and Lookingbill 2010, Guo et al. 2018), and facilitating migratory responses to climate change (Heller and Zavaleta 2009).

1.3 LiDAR overview

Ecological research typically aims to estimate the effect of fine-scale predictors of vegetation structure and composition and land use data over broader spatial extents to determine habitat site selection (Misenhelter and Rotenberry 2000, Farrell et al. 2013). Traditional sources of fine-scale vegetation structure and land cover data are derived from two-dimensional (2D) satellite or aerial imagery such as MODIS and LANDSAT, and these have been widely used to model wildlife habitat across large spatial extents (Moen and Gutiérrez 1997, McDermid et al. 2005, Kramer et al. 2016, Milanesi et al. 2017a). While such data are informative, evidence suggests that three dimensional (3D) vegetation structure, such as vegetation height and shrub density, are often more related to species habitat use and thus may be better predictors of a species distribution (Johnson 2007, Farrell et al. 2013, Melin et al. 2016, Rechsteiner et al. 2017). To characterize the habitat features at fine-scales, in particular the understory structure condition, the ideal tool is one that can map the 3D architecture of forest in great spatial detail (Vierling et al. 2008).

Light detection and ranging (LiDAR) technology is one source of geospatial data which can record 3-D (x, y, z) information of the object at high spatial resolutions and vertical accuracies (Lefsky et al. 2002, Lim et al. 2003). The x, y records of an airborne-LiDAR are based on the GPS location of the flight carrying a sensor to emit and record the radiation signal of laser pulses (Devereux and Amable 2009). The returned signal of laser pulses can be stored as either discrete points or continuous waveform data (Lim et al. 2003). Waveform sensors provide an overwhelming quantity of data and so are less appropriate for high-resolution natural resource applications (Lefsky et al. 2002, Lim et al. 2003). Discrete return systems are capable to offer broader and high-resolution products of ground and canopy surfaces, making them advantageous for mapping (Evans et al. 2009). The z values of discrete points are calculated according to the travel time between the emitting of pulse, hitting of target and the signal returning back (Vierling et al. 2008). Ground points (the signal returns from ground surface) can be separated from the points of other objects to extract a high-resolution topographic surface model, digital elevation model (DEM) (Kilian et al. 1996), and then generate a wide range of topographic metrics, such as slope, aspect, gully and ridge (Lefsky et al. 2002). For most ecological applications, it is the LiDAR points of the vegetation canopy that are of primary interest (Lefsky et al. 2002). The raw LiDAR points of canopy are usually normalized to the ground surface so that the z values of LiDAR points are expressed in terms of canopy heights above the ground instead of elevation above sea level (Mitchell et al. 2012). Height-normalized LiDAR points are commonly used to evaluate the canopy height, cover, and other canopy structure variables. LiDAR has been successfully used:

- (1) to identify habitat features at tree-level, such as segmenting the LiDAR point cloud to detect individual trees which can be used to reconstruct the density of large-diameter trees per area (Kramer et al. 2016);
- (2) to directly quantify habitat structure, such as canopy height and strata density (Lefsky et al. 1999b, Zimble et al. 2003); and
- (3) to estimate species distribution by building statistical models between variables extracted from the LiDAR point cloud and field data (Popescu et al. 2011, Mitchell et al. 2012, Sheridan et al. 2015).

1.3.1 Individual tree measurement from LiDAR

LiDAR data can provide individual tree information by segmentation of the point cloud or delineation of an individual tree crown (Morsdorf et al. 2004, Li et al. 2012a, Jakubowski et al. 2013, Amiri 2014). Two major methods can be used to analyse individual trees.

- (1) Vector-based cluster analyses, such as k-means clustering and mean-shift (Morsdorf et al. 2004, Li et al. 2012a), can classify LiDAR points into groups (clusters) that are relatively close within themselves and far away between others on the basis of a distance metric calculated by the coordinate axes x, y, and z. It summarizes the distances between all pairs of points, which is not efficient for large-scale tree segmentation across the landscape (Morsdorf et al. 2004).
- (2) Raster-based morphological analyses can delineate individual crowns from a canopy height surface model (CHM). A commonly used raster-based individual tree delineation (ITD) algorithm is marker-controlled watershed segmentation (Madhuri Kalapala 2012, Amiri 2014). The watershed segmentation is targeted on the raster layer of canopy height surface (CHM) generated from the maximum height of height-normalized LiDAR points in 0.5 m or 1m cell size (Khosravipour et al. 2014, Saremi et al. 2014). The marker-controlled watershed segmentation algorithm includes three major steps: edge detection, tree-top detection, and crown delineation (Wulder et al. 2000, Wang et al. 2004).

1.3.2 Vertical forest structure and canopy penetration

The main advantage of LiDAR data is the height information, which directly reflects the vertical structure of the vegetation. Different forest stand development stages, growth forms, and plant species can have significant differences in the vertical organization of canopy elements. A foliage-height profile derived from the leaf area of distinct, non-overlapping layers (strata) can be used to discriminate distinct forest structures (Parker et al. 1995). Replacing the foliage cover with LiDAR point densities in different height layers can yield a canopy profile model (CPM) that can be used to categorize forest vertical structure (Parker et al. 2004). LiDAR can also classify forest structures by horizontal vegetation density, such as forest openness or the degree of crown closure in the forest canopy. The proportion of single returns from laser pulses reflects the permeability of object surface. Dense surfaces, such as buildings and the ground, have only a single return, while forest canopies generally produce multiple returns (Hu 2004). Holmgren et al. (2008) found that the proportion of single returns was related to the openness of forest canopy. They discovered that single returns for coniferous

trees were higher than for deciduous trees, because the latter typically have more open crowns. The penetration of LiDAR points into closed-canopy broadleaf forests can be used to distinguish growth stages of the forest, such as young, intermediate, mature, and old-growth stand conditions (Harding et al. 2001, Hudak et al. 2008). Previous studies have found that vegetation structural types, classified by canopy height and strata density, are important for habitat site selection and foraging activity of many bird species (Farrell et al. 2013)

1.3.3 Large area monitoring and mapping with less cost and integrated with other data sources

Conventional forest inventory metrics can be estimated by building regression models linking forest inventory data collected from field plots and LiDAR canopy metrics (Lefsky et al. 1999a, Mitchell et al. 2012). An accurate and efficient estimation method has been developed to estimate canopy features such as biomass, basal area, and stand density (Popescu et al. 2011, Mitchell et al. 2012, Sheridan et al. 2015). The common models used to address different forest inventory issues include:

- vegetation classification based on both vertical and horizontal structure patterns (Lee et al. 2004, Holmgren et al. 2008, Morsdorf et al. 2010, Calders et al. 2014)
- estimation of forest inventory parameters, such as biomass, canopy volume, and stand basal area based on LiDAR metrics (Lefsky et al. 2002, Drake et al. 2003, Mitchell et al. 2012)
- modelling the structural dynamics and site productivity with temporal data (Tompalski *et al.* 2015).

LiDAR-derived vegetation structural metrics and other ecologically relevant metrics have been found to significantly increase the performance and accuracy of species distribution models (SDMs) (Rechsteiner et al. 2017). LiDAR-based habitat suitability models reliably predict local-scale habitat structure and quality with high model performance scores (Rechsteiner et al. 2017). For instance, Martinuzzi et al. (2009) used LiDAR data to estimate the presence/absence of understory shrub species and different snag diameter classes important for birds at the stand level. Several different algorithms have been used to build occurrence models with LiDAR data. These include: classification regression trees (CRT) (Quinn and Keough 2002, Han et al. 2011, Han and Kamber 2012), linear discriminant analysis (LDA) (Scholkopf and Mullert 1999, McLachlan 2004), logistic regression (Shi et al. 2013, Latifi et al. 2015b), and random forests (RF) (Breiman 2001).

1.4 Research objectives

I identified the need for a set of analytical tools to quantify habitat quality and change within multi-scale frameworks. Airborne LiDAR is a promising approach to meet many of the requirements for multi-scale habitat analysis. However, LiDAR has not been used in Australia to assess habitat quality and connectivity of an endangered species. The primary research question of this thesis is:

How can airborne LiDAR be used to characterise the distribution, quality, and connectivity of habitat at landscape-scale for the critically endangered Leadbeater's Possum?

I integrated LiDAR-derived topographic and vegetation structural metrics with different habitat analysis approaches across multiple scales to map critical LBP habitat features (HBTs, foraging, and connectivity) across 342,960 ha of forest in Victoria's Central Highlands. I then used the landscape-level mapping of habitat resources to predict landscape-scale habitat suitability based on records of LBP occurrence. In these analyses, LiDAR-derived topographic and vegetation structural metrics were complemented by GIS-based environmental variables such as climatic variables, vegetation type, fire history, and logging history.

To address the research objectives, the thesis is structured around five core chapters. The landscape-level metrics of the density of HBTs and vegetation connectivity should be generated first, then the predicted the density of HBTs and vegetation connectivity can be used to build habitat suitability models for LBP. In Chapter 2, I develop individual tree delineation (ITD) algorithms to identify individual trees within the forest. ITD algorithms of overstorey were applied to the whole study area to estimate the abundance and distributions of large-crowned trees that have high probability of having hollows. The relationship between the abundance of large trees and environmental factors were also explored. In Chapters 3-5, I predicted the abundance and diversity of HBTs (Chapter 3), the connectivity of different vertical layers (Chapter 4), and the probability of occurrence of LBP (Chapter 5) based on LiDAR metrics and GIS-based environmental variables. In Chapter 6, I used plot-level connectivity surfaces of different vertical canopy layers (from Chapter 4) and LiDAR-derived midstorey coverage (from Chapter 2) to create different resistance surfaces and connectivity networks for LBP to identify functionally connected regions. These are critically important for identifying barriers to LBP movement and corridor networks for conservation planning. The application of LiDAR data to characterize habitat patches and habitat connectivity over large landscapes has not been well explored to date. The workflow of my thesis is shown in Figure 1-1.

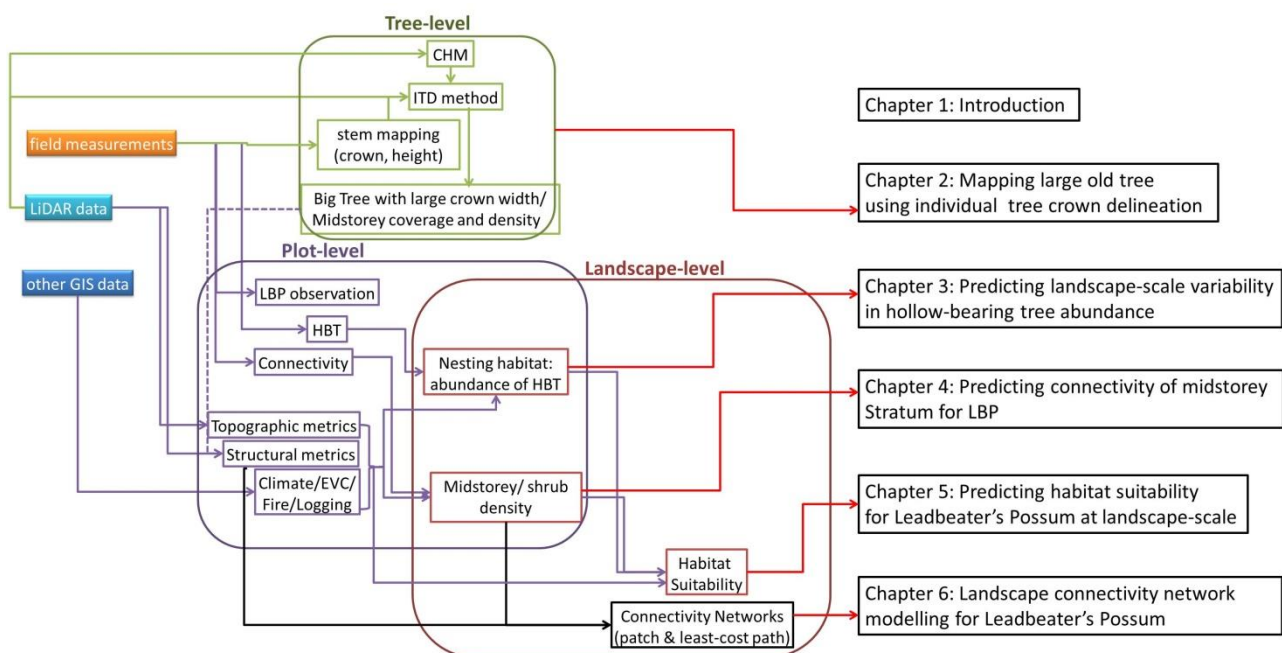


Figure 1-1 Workflow of my thesis study.

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Chapter 2.

2 Prediction of large old trees with large crowns using a novel individual tree crown delineation method and airborne LiDAR data in Victoria's Central Highlands

Abstract

Large trees are considered keystone structures in forests, woodlands, savannas, agricultural landscapes, and urban areas around the world. Individual large old trees and small stands of such trees can play numerous ecological roles in ecosystem processes such as hydrological regimes, carbon storage and nutrient cycling, and provision of wildlife habitat for a wide range of plant and animal species. Accurate assessment of the size, locations and populations of large old trees is critical for sustainable and precise conservation management. Airborne Light detection and ranging (LiDAR) technology is a remote-sensing technique that acquires three-dimensional geospatial data of ground objects from the top which provides essential geometric information on individual trees at high spatial resolutions and with high accuracy. LiDAR-derived individual tree segmentation delineation (ITD) methods can identify individual trees and then extract and measure specific size attributes such as crown diameter, crown projection area, and canopy height. Most of the previous research on high-resolution individual tree crown delineation has focused on coniferous forest. We used high-resolution, LiDAR-based remote-sensing data to develop a new individual tree delineation algorithm for irregular-shaped crowns in broadleaf mountain ash forest. We then aggregated individual crown attributes at plot- and landscape-level to estimate the abundance of large trees with large crowns across ~491,000 ha of Victoria's Central Highlands. We also coupled plot-level crown attribute metrics with datasets on environmental variables to quantify the association between environmental conditions and large tree abundance. We used the relationship between crown size, stem diameter, and tree age to predict the abundance of potential live old-growth trees with hollows (i.e. hollow-bearing trees). Our analyses estimated 405,000 trees with large crowns width ($CW > 15m$) and 572,000 (95%CI: 318,000-808,000) potential large old tree with hollows, which is a mean density of one large old trees per ha across the Central Highland. The abundance of large trees was strongly associated with gullies and flat area. Trees in rainforest and riparian areas had larger average size and higher density of large crowns than in other vegetation classes. Our analyses highlight the benefits of using high-resolution, spatially explicit data from the whole landscape to map the distribution and abundance of potential large old trees.

2.1 Introduction

2.1.1 The importance and assessment of large old trees

Large trees are considered keystone structures in forests, woodlands, savannas, agricultural landscapes, and urban areas, providing a key ecological role not provided by younger, smaller trees (Lindenmayer et al. 2012b, Stagoll et al. 2012, Kramer et al. 2016). Individual large old trees and small stands of such trees can contribute to numerous ecosystem processes such as hydrological regimes, carbon storage, nutrient cycling, and provision of habitat for a wide range of plant and animal species (Thomas et al. 2013, Lindenmayer and Laurance 2016, Lindenmayer 2017). Globally, 30% of all vertebrate species use large old trees and their associated hollows for nesting habitat (Lindenmayer et al. 2012b). In Australia, approximately 290 vertebrate species, including many rare and threatened species, utilize large old tree (Gibbons et al. 2000b). Populations of large old trees however are rapidly declining all over the world (Lindenmayer and Wood 2010, Lindenmayer et al. 2012b). Threats to large old trees include natural drivers like fire (Williams et al. 1999, Kolb et al. 2007), drought (Bennett et al. 2015) and overgrazing or browsing by native herbivores (Vanak et al. 2012, Lindenmayer 2017) but also human activities such as logging, land clearing, agricultural intensification, and fire and fuel management (Maron and Fitzsimons 2007, Gibbons et al. 2008, Lindenmayer et al. 2012b, Crowther et al. 2015, Lindenmayer 2017). Accurate assessment of the size, locations and populations of large old trees is critical for sustainable forest management and conservation planning (Chang et al. 2013, Lindenmayer and Laurance 2016, Mifsud and Harris 2016, Wu et al. 2016, Lindenmayer 2017).

Reliable mapping the aging of large individual trees is difficult. Typically the relative tree size, on a species- and ecosystem-specific basis, is used to identify large old trees (Lindenmayer and Laurance 2016). Mapping of large old trees at the landscape-scale requires the determination of individual tree locations using parameters such as tree height, tree density, crown diameter, and tree species; all of which can influence the identification of large old trees (Chen et al. 2006, Koch et al. 2006b, Kwak et al. 2007a, Wu et al. 2016). Airborne Light detection and ranging (LiDAR) technology is a remote-sensing technique that acquires three-dimensional geospatial data of ground objects providing essential information about forest structure, especially about the geometric information of individual trees at high spatial resolutions and with high accuracy (Lefsky et al. 2002, Lim et al. 2003, Chen et al. 2006, Martinuzzi et al. 2009, Wu et al. 2013, Wu et al. 2016, Fedrigo et al. 2018). Methods for estimating density and populations of large trees from LiDAR can be divided into two categories: (1) individual tree detection and (2) statistical modeling at stand-level that utilises at least one LiDAR-derived variable (Kramer et al. 2016, Wu et al. 2016). Compared with statistical models, individual tree detection and delineation (ITD) requires denser airborne LiDAR data; however, it has been shown to be more accurate for predicting individual tree parameters (Hyypä et al. 2001, González-Ferreiro et al. 2013, Kramer et al. 2016, Wu et al. 2016).

Most studies have focused on the capability of LiDAR to identify live trees with intact crowns, but linking

individual tree identification with ecological function (e.g., large trees with hollows) using LiDAR has not yet been widely used and has significant potential. Although the largest individuals of a tree species are not always the oldest (Lindenmayer and Laurance 2016), studies have found strong relationships between crown size and stem diameter (DBH) (Shimano 1997, Hemery et al. 2005) and between DBH and large old trees with the hollows (Gibbons et al. 2000a, Gibbons et al. 2002, Fox et al. 2008, Fox et al. 2009, Lindenmayer et al. 2013). In southeast Australia, live mountain ash (*Eucalyptus regnans*) trees with DBH > 150 cm have >50% probability of having a hollow (Fox et al. 2008). These relationships suggest significant potential to link LiDAR-derived estimates of individual crown size (from individual tree delineation) to density of potential large old trees (DBH > 150 cm). This methodology would allow for landscape-scale estimates of large tree abundance to be quantified and their locations to be mapped. The latter would allow for the monitoring of long-term changes in large tree abundance using repeated capture of airborne LiDAR data.

2.1.2 Individual tree delineation (ITD)

Individual tree segmentation or delineation (ITS or ITD) methods can identify individual trees and quantify specific size attributes such as crown diameter, crown projection area, and canopy height (Kato et al. 2009, Li et al. 2012b, Dalponte et al. 2014, Hamraz et al. 2016, Khosravipour et al. 2016). Vector-based cluster analyses, such as k-means clustering and mean-shift (Morsdorf et al. 2004, Li et al. 2012a), classify LiDAR points into groups (clusters) on the basis of proximal distance metrics calculated from the x, y, and z coordinates (Morsdorf et al. 2004). Three-dimensional vector-based cluster analysis has been proven to accurately segment both overstorey (Morsdorf et al. 2004) and understorey trees in multi-layered forests (Yao et al. 2013, Ferraz et al. 2016). This method however requires calculating the distances between all pairs of points which requires long computing times (Zhao et al. 2014, Wu et al. 2016), imposes significant computational demands (Sačkov et al. 2017) and is prohibitively slow for large-scale analyses (i.e., every tree within a landscape). To overcome these limitations LiDAR-derived raster-based approaches offer an approach with high accuracy coupled with a fast and efficient algorithm (Wu et al. 2016).

Our study focused on the ability and accuracy of detecting dominant overstorey trees with large crowns using raster-based morphological analysis. Raster-based graphical and morphological analyses allow delineating individual crowns from an overstorey canopy height model raster layer (CHM) (Wu et al. 2016). One of the most common ITD methods is marker-control watershed delineation, which yields favourable results for regular crown shapes (Kwak et al. 2007b, Madhuri Kalapala 2012, Soille 2013, Amiri 2014, Ayrey et al. 2017). CHM is typically generated from the maximum height of height-normalized LiDAR points in 1m or smaller cell sizes. The accuracy of this approach however is highly dependent on forest structure (Jaskierniak et al. 2015). Most of the previous research on high-resolution individual tree crown delineation has focused on coniferous forest, where crowns are conical and the top of the crown is located in the center of the (typically circular) crown (Ke and Quackenbush 2011). In forests dominated by angiosperms, such as deciduous forest (Koch et al. 2006a) and the eucalypt forests in this study, individual trees often have irregular-shaped crowns that make this geometric pattern of conical

crowns more difficult to recognize. To improve the accuracy and efficiency of watershed delineation of overstorey trees, there are three major aspects that need to be addressed: the targeted raster layer, tree-top detection, and crown edge detection.

Targeted raster layer

Changing the target raster layer from CHM to densities of high points model (DHP) has been demonstrated to produce more accurate results for deciduous trees (Rahman et al. 2009). The DHP method relies on the assumption that the LiDAR point density of an overstorey tree crown is high at the center of the crown and decreases towards the edge of the crown (Rahman and Gorte 2008, Rahman et al. 2009). However, Rahman et al. (2009) simply selected points above the reference height (i.e., the threshold height that distinguishes the overstorey tree crowns vs the understorey vegetation and ground surface) to represent the overstorey crown. This may cause an irregular distribution of DHP from the centre to the edge of the crown if an incorrect reference height is used to remove LiDAR points of very dense undergrowth vegetation (Rahman and Gorte 2009). Instead of using a fixed reference height below which LiDAR points are classified as belonging to the understorey, the height of the separation can be set to vary with overstorey height and forest type. One promising approach would be to use the height-to-live-crown base (HCB), defined as the height below which trees of a given height have no crown and above which they have a crown. We would classify LiDAR points below the HCB as belonging to the understorey and points above as belonging to the overstorey. Height-to-live-crown base (HCB) can be predicted from total tree height (HT) (Ritchie and Hann 1987, Nutto et al. 2006, Rijal et al. 2012, Sharma et al. 2017) because of the strong relationship between these features (e.g., R^2 of 0.79 in conifers and 0.80 in broadleaf trees; Rijal et al. 2012). In practice, we would use field data to calibrate a $HCB=f(HT)$ model; as CHM is available for the entire landscape it is logical to substitute HT for CHM for the predictions of canopy surface of HCB.

Tree-top detection

The success of watershed delineation of overstorey trees relies on accurate tree-top detection (Wang et al. 2004). When tree-top detection is poor, over-segmentation can occur (i.e., an individual tree will be mistakenly divided into multiple trees), an issue that can be particularly acute for trees with large crowns. Accurate tree-top marker control prevents severe over-segmentation problems in the traditional watershed algorithm (Wang *et al.* 2004). A common technique for identifying tree tops uses a local maximum filter to identify the peaks of tree crowns with a static-size, moving window (commonly 3×3 , 5×5 , or 7×7 pixels), depending also on the crown size (Wulder et al. 2000, Persson et al. 2002b, Popescu et al. 2002, Popescu and Wynne 2004). The local maximum method makes the assumption that the peak of the tree-crown reflectance is located at or very close to the treetop (Brandtberg and Walter 1998). An image-smoothing targeted raster layer can help to reduce the noise effect (Dralle and Rudemo 1996).

Crown-edge detection

Accurate edge detection of crowns reduces the identification of pseudo tree-tops (the local maximum occurs on

the crown edge or forest gaps) (Wang *et al.* 2004) and prevents multiple trees being merged together incorrectly (Brandtberg and Walter 1998). CHM and DEM both reflect variability in height across a surface. So topographic analysis tools, such as slope, aspect and slope of aspect (SOA) of CHM can be used to analyze CHM (Persson *et al.* 2002a, Wu *et al.* 2016). SOA of CHM represents the rate of change of aspect of a crown; therefore, the maximum value of SOA of CHM is located along the crown edge (“gully”) or tree top (“ridge”). Therefore, high values of SOA of CHM combined with the negative terrain surface of CHM indicate crown edges. Forest gaps can also be detected from the negative terrain surface using neighborhood analysis tools (such as focal statistic tool in ArcGIS) to identify surfaces that are relatively lower within a larger identified neighborhood.

Other raster-based ITD methods

Other than watershed delineation method, a few studies using raster-based ITD methods, such as layer stacking and localized contour, have showed a high level of accuracy in the delineation of individual trees. Layer stacking is a method which slices the entire forest point cloud at 1-m height intervals and isolates trees in each layer. Merging the results from all layers produces representative tree profiles (Ayrey *et al.* 2017). Layer stacking has high accuracy for detecting the location of individual trees. Ayrey *et al.* (2017) was able to identify 75% of trees correctly detected in pure deciduous stands, crown size however was underestimated. Localized contour seeks to capture the topological structure of the canopy and quantifies the topological relationships of tree crowns using a graph theory-based localized contour tree method which is used to segment individual tree crowns in a manner analogous for detecting hills on a topographic map (Wu *et al.* 2016). This approach essentially creates crown contours based on the CHM. The overall accuracy of individual tree crown delineation achieved 75- 94% in coniferous forests (Wu *et al.* 2016).

The overarching goal of this study was to develop a robust ITD method for mountain ash (*Eucalyptus regnans*) trees in southeast Australia, and to map the distribution and abundance of potential large trees with high likelihood of hollows (DBH>150cm) in Victoria’s Central Highlands using airborne LiDAR. The specific objectives of the study were to:

1. develop a robust ITD algorithm suitable for eucalypt trees, and compared with existing ITD methods (traditional watershed delineation, layer stacking and localized contour).
2. build a statistical model to predict DBH using crown diameter derived from LiDAR-based ITD algorithm;
3. map the distribution and population of potential large hollow bearing trees (DBH>150cm) at the landscape-scale; and,
4. understand relationships between environmental variability and the size and abundance of potential large trees (DBH>150cm) using LiDAR, topographic, climatic, and disturbance history data

2.2 Method

2.2.1 Study Area

The study area is located in the Victorian Central Highlands in southeastern Australia (Figure 2-1). Native vegetation in Victoria has been classified into Ecological Vegetation Classes (EVCs) that represent special characteristics of different vegetation types. Three major vegetation classes in this study are wet - damp forest, Riparian Forest and Cool Temperate Rainforest. The study area is primarily wet - damp forest (62.1%), Riparian Forest (5.1%), and Rainforest (2.5%) occupying smaller amounts and dry forests, grasslands and woodlands occupying the remaining 30% of the landscape. The dominant tree species in the wet - damp forest EVC are mountain ash (*Eucalyptus regnans*), alpine ash (*Eucalyptus delegatensis*), and shining gum (*Eucalyptus nitens*). The Central Highlands experience generally cool summers and mild, humid winters with frequent frosts and occasional periods of snow (Burns et al. 2015). Mean annual temperatures ranged from 6-15 °C and mean annual precipitation ranged from 690-2090 mm over the period 1981–2010 (Stewart and Nitschke 2017, Fedrigo et al. 2019).

2.2.2 Field data

Stem mapping individual tree in field to validate individual tree delineation algorithm

We established three approximately 1-ha plots in mountain ash forest to validate our ITD algorithm. The boundaries and canopy height of each plot are shown in Figure 2-1a. In each plot, all dominant overstorey trees were mapped, identified to species, and measured for DBH, total height (HT), height to the base of the live crown (HCB), and mean crown width (CW). The distances from tree bole to the northern, southern, western and eastern edge of the tree crown were measure, and the mean distance between northern to southern crown edge and western to eastern crown edge was estimated as the mean crown width (CW). Within each plot in an area of approximately 2000m² (20 × 100m), mid- and understorey trees with DBH>10cm were mapped and measured stem and crown attributes. These three ITD plots were located in different growth stages (see Table 2-1). In total, 873 trees were measured, including 309 dominant overstorey trees, 422 mid- and under-storey trees, and 142 suppressed canopy or dead trees (Table 2-1). The dominant overstorey species was *E. regnans* and the most common mid- and understorey species were *A. dealbata* and *A. frigescens*, respectively.

Table 2-1 Number of trees measured in each ITD method validation plot.

Plot	Growth stage and forest type	Total number of trees	Dominant overstorey live tree	Mid-/understorey live tree	Suppressed canopy or dead tree
1	1939 regrowth montain ash forest	245	65	141	39
2	1977 regrowth montain ash forest	456	207	150	99
3	Multi-cohort forest	172	37	131	4
Total		873	309	422	142

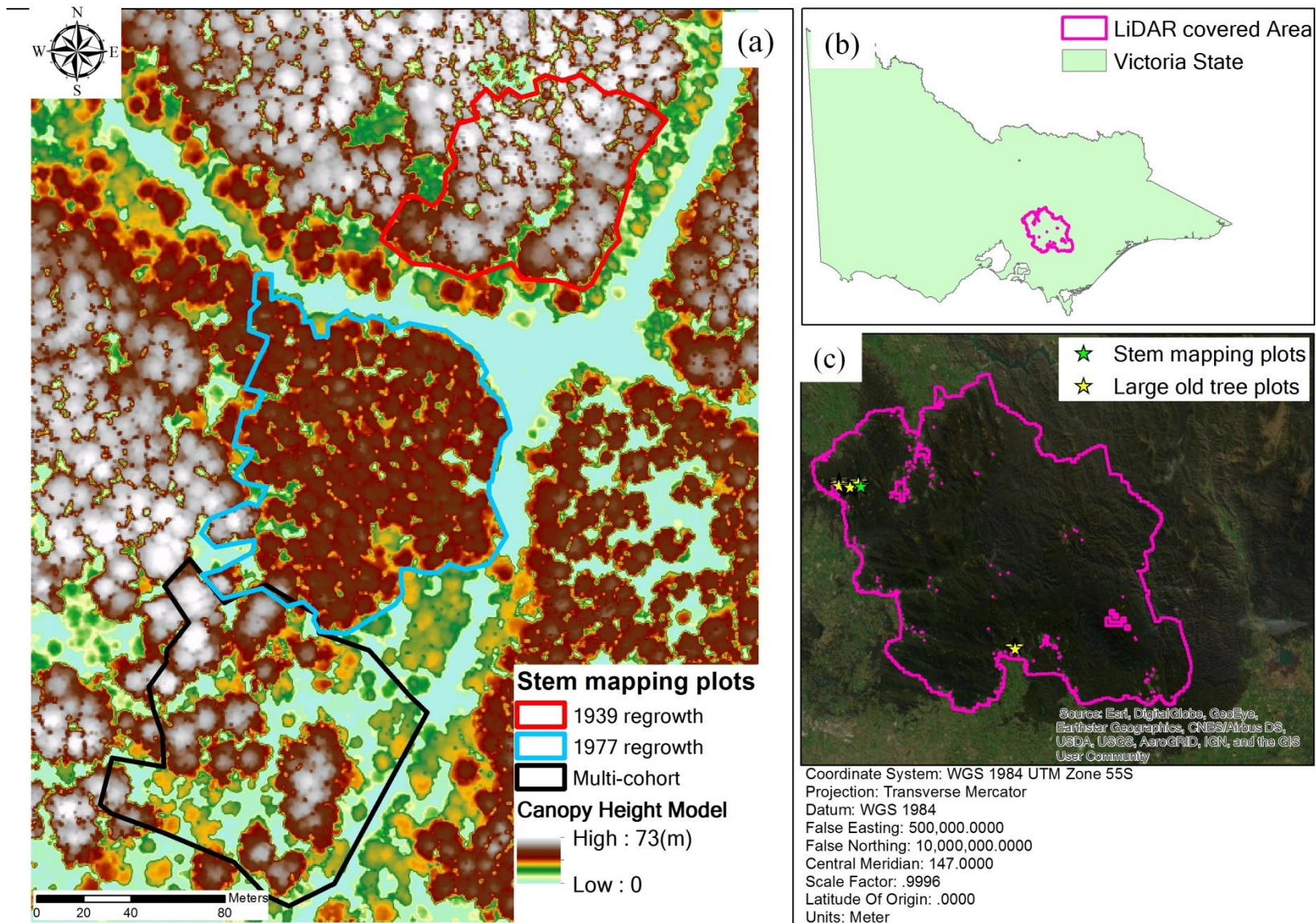


Figure 2-1 a) Locations and canopy height model (CHM) of three stem mapping plots for individual tree delineation (ITD) validation; b) The map shows the total LiDAR coverage (purple polygon) in Victorian Central Highland; c) locations of stem mapping plots (green stars) and large old tree plots (yellow stars) in study area

We used 101 records of total height (HT) and height to the base of the live crown (HCB) of *E. regnans* to develop a HCB-HT relationship (see Figure 2-2). The locations of live overstorey trees were used to test the capability and accuracy of the ITD method to detect and delineate the crowns of individual trees in the forest canopy. Field-measured mid- and understorey tree heights were used to validate a midstorey canopy height model (MsCHM) developed from the LiDAR ITD method.

Large old tree plots

The maximum DBH in the three 1-ha stem mapping plots was 178 cm and only six overstorey trees in them had observed hollows. To avoid over-fitting of our ITD algorithm in the plots where the algorithm were generated, and to test the capability of our ITD algorithm to delineate trees larger than 174 cm DBH that are typically found in multi-aged forests, we identified and selected 69 large old trees with hollows (i.e. hollow-bearing trees) in an additional 15 1-ha plots located in old-growth forest stand, mapped and measured DBH for each selected HBT tree. The locations of 15 large old tree plots in study area were shown in Figure 2-1c.

2.2.3 LiDAR data and GIS products

LiDAR raw data

Discrete return airborne LiDAR data were acquired by RPS Group Plc in late 2015 and early 2016 using Trimble AX60 laser sensor mounted on a fixed wing aircraft. The aircraft was flown at 800 m above ground with flying speed of 62m/s. Mean pulses per meter send to ground was 2-4 pts/m and average point spacing was about 0.46m. LiDAR data covered 513,322 ha of the Central Highlands of Victoria (coverage can be seen in purple polygon in Figure 2-1) and the LiDAR dataset was cut into 53311km² tiles. After electing relevant EVCs for the study area, the valid area to predict abundance of large old trees was 491,400 ha, including 305,200 ha of wet - damp forest, 24,900 ha of riparian forest, and 12,400 ha of rainforest.

GIS layer

Ecological Vegetation Classes (EVC) and Forest Management Zone (FMZ) used were sourced from the Victorian Department of Environment, Land, Water, and Planning (DELWP). Bioclimatic variables, such as annual mean temperature and annual precipitation, developed by Stewart and Nitschke (2017) were used. Precipitation based BIOCLIM variables were from Fedrigo et al. (2019). The resolution of bioclimate data was 250m. Kriging interpolation was used to change the resolution of bioclimate data into 100m.

LiDAR topographic metrics

A high-resolution digital elevation model (DEM) was derived from a LiDAR ground-based point cloud using FUSION/LDV Software (McGaughey 2009). From this DEM, the slope, aspect, and slope of aspect (SOA) of

DEM were generated using ArcGIS (v. 10.5). SOA of DEM represents the rate of change of the aspect in the horizontal direction (Zhou et al. 2018); therefore, the maximum value of SOA of DEM is located at the dividing line at ridge or gully. A gully index was calculated using SOA of DEM values and a negative terrain surface. The negative terrain surface was created using ArcGIS focal statistic tool (“moving window”) to identify relatively lower surfaces within a specific neighborhood. Map of slope and gully index in study area were shown in Figure A2 2 in Appendices 2. The resolution of all LiDAR topographic metrics was 1ha.

2.2.4 Individual tree delineation (ITD)

LiDAR Processing to delineate individual overstorey tree crowns

Our ITD algorithm was developed using a watershed segmentation method on raster layers representing integrated information of canopy height model (CHM) and densities of high points model (DHP) at very fine resolution (0.5m) (CHM×DHP). To create regular distribution of DHP, we first used the HCB-HT relationship to classify LiDAR points into dominant overstorey trees and under- /mid-storey trees, and then removed the LiDAR points under HCB belonging to undergrowth vegetation. Canopy gaps were detected by using focal statistic tool (“moving window”) in ArcGIS to identify CHM surfaces that are relatively lower within a larger identified neighborhood. The LiDAR points of vegetation located in canopy gaps were also removed. We then created DHP only based on LiDAR points of dominant overstorey canopies. Tree top detection with a local maximum filter was based on the developed raster layer CHM×DHP. Crown edge detection used the successive application of terrain surface analysis tools and neighborhood tools, including slope of CHM, aspect of CHM, SOA of CHM, and focal statistic tool (“moving window”) in ArcGIS. High values of SOA of CHM combined with the relatively lower canopy height surface within a specified neighborhood were used to identify crown edges. Window size of focal statistic tool to identify crown edges was 5m, and window size of focal statistic tool to identify canopy gaps was 20m. This produced a top-edge-enhanced raster layer of CHM×DHP for use in watershed segmentation. Based on the above approaches, the following workflow to delineate overstorey tree crowns in this study was applied:

1. Create a 50cm resolution canopy height model (CHM);
2. Create a height to crown base model (HCBM) based on HCB-HT relationship calibrated from field data (Figure 2-2);
3. Identify canopy gaps;
4. Filter LiDAR points below the HCBM as they likely belong to understorey crowns. This retains LiDAR points belonging to the overstorey;
5. Filter points located in canopy gaps;
6. Create a DHP model based on LiDAR points of overstorey crowns only;
7. Tree-top detection based on a targeted raster layer of CHM×DHP;
8. Crown edge detection based on a targeted raster layer of CHM; and
9. Marker-control watershed delineation on a top-edge-enhanced raster layer of CHM×DHP.

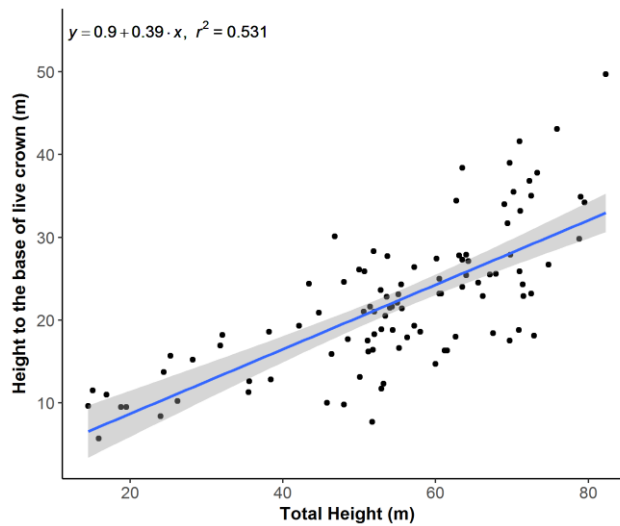


Figure 2-2 The linear model and R^2 of HCB-HT relationship calibrated from field data

LiDAR processing to detect midstorey tree tops

Watershed segmentation is not suitable for crown delineation of midstorey tree, because of continues connected canopies. As a result, we used a local maximum filter to detect midstorey tree tops. The six steps we used for detecting midstorey tree tops follow:

1. Remove the LiDAR points above the HCBM and keep the LiDAR points located in canopy gaps;
2. Create a raw midstorey CHM (MsCHM) based on the remaining LiDAR points;
3. Smooth the MsCHM raster to reduce the noise effect, including detection and removal of high pits from LiDAR points of overstorey stem;
4. Classify LiDAR points below the smoothed MsCHM and above 8 m as midstorey crowns (where 8m is the reference height threshold distinguishing midstorey and understorey in this study);
5. Create a final midstorey CHM (fMsCHM) based on LiDAR points of midstorey crown; and
6. Detect midstorey tree-tops based on a targeted raster layer of fMsCHM.

Accuracy of ITD method

The stem-mapped locations of live overstorey trees in the three 1-ha stem mapping plots were used to validate the accuracy of ITD method. Four validation indicators were calculated to evaluate the ITD method: overall accuracy (ACC), sensitivity (true positive rate, TPR), commission rate (CR) and omission rate (OR) (Sačkov et al. 2017). The calculation of each of these metrics was based on the following. Crowns were correctly detected by ITD method are considered True Positives (TP). Crowns that were missed by the ITD method compared to field data and crowns that where merged with their neighbours are considered false negatives (FN). Crowns that were over-segmented crowns by ITD and ITD crowns containing two or more true crowns are false positives (FP). The specific equations for each validation metric are shown in Table 2-2. For crowns that were correctly segmented (True positive), we also estimated the R^2 between LiDAR-derived crown width and the crown widths measured in the field to evaluate the capability of our ITD approach correctly delineate individual crowns. The LiDAR-derived crown width was estimated based on the projection area of each delineated polygon for each overstorey tree crown by ITD.

Table 2-2 The confusion matrix of ITD outputs and the equations of each validation measures. True condition is based on directly observed data from stem-mapped plots and predicted condition is from LiDAR-derived ITD analyses.

		True condition		Equations for individual metrics	
		Condition positive (CP)	Condition negative (CN)	ACC = (TP + TN)/(TP+FP+TN+FN)	
Predicted condition	Predicted condition positive (PP)	True positive (TP) = ITD correctly detected	False positive (FP) = ITD merged crown + ITD over-segmented	True positive rate (TPR), Sensitivity = TP/CP = TP/ (TP + FP)	Commission rate (CR) or false positive rate (FPR) = FP/PP = FP/(TP+FP)
	Predicted condition negative	False negative (FN) = missed field crown + merged field crown	True negative (TN)=0	Omission rate (OR) = FN/CP = FN/(TP + FN)	True negative rate (TPR) or Specificity = TN/CN=TN/(TN+FP)

Comparison with existing ITD methods

To test the performance of our approach we compared it to traditional watershed delineation (Madhuri Kalapala 2012, Amiri 2014), layer stacking (Ayrey et al. 2017) and localized contour (Wu et al. 2016) methods. We used these approaches to delineate the crowns in one hectare stem-mapped plot located in 1939 regrowth mountain ash stand. Four validation indicators (overall accuracy (ACC), sensitivity (true positive rate, TPR), commission rate (CR) and omission rate (OR)) were calculated and used to compare the model performance with our ITD approach. We also compared the crown shape delineated from these four methods.

2.2.5 Estimation the DBH of individual tree

DBH-CW_L allometry

We collected the DBH data from 158 individual trees (89 from stem mapping plots and 69 from large old tree plots) and matched the location of each tree within crowns delineated by our LiDAR-derived ITD algorithm. We used a Generalized Linear Model (GLM) with gamma distribution to characterize the relationship between LiDAR-derived crown attributes (crown width from LiDAR, CW_L) and logarithm of the field-measured stem diameter (DBH). The DBH-CW_L allometry follows:

$$DBH = \exp(a_0 + a_1 * CW_L) \quad (1)$$

where DBH is the tree diameter at breast height over bark, CW_L is the mean crown width derived by LiDAR ITD, and a_0 and a_1 are model parameters. Mean crown width was calculated from the delineated polygon area of each crown.

DBH Model validation and uncertainties

We used 5-fold cross validation to evaluate model performances. The 158 trees dataset was split into 5 proportional folds (~32 trees per fold). For each of 5 folds, 4/5 of the sample was used as a training set and 1/5 as a test set. Model performance indicators were gathered from test results for 5 runs, and the mean values of each indicator were considered for model validation and comparison (Maroco et al. 2011). We used R² between

observed DBH and predicted DBH, Root mean squared error (RMSE), Mean Absolute Error (MAE) and Residual Standard Error (RSE) of test set to evaluate model performance.

We used Monte Carlo methods and sampled from the variance-covariance matrix of parameter estimates (a_0 and a_1) to propagate the uncertainties into our total estimation of DBH (Trouv  t al. 2017).

Potential large old tree with hollows

Previous studies have shown that live mountain ash trees with DBH > 150 cm had >50% chances of having hollows, while trees with DBH < 100 cm were unlikely to have hollows (Fox et al. 2008). The relationship between live tree DBH and probability of hollow incidence based on Fox et al. (2008) were shown in Figure A2 1 in Appendices 2. In this study, we used the threshold value of 150cm of predicted DBH from DBH-CW_L allometry to separate large old trees from young or regrowth trees. We used Eq.1 to estimate the DBH of every individual crowns delineated by ITD method across the whole landscape in Victoria Central Highland.

2.2.6 Distribution and abundance of large trees and environmental impacts

Generating overstorey and midstorey metrics

We applied our ITD method on forests with canopy height > 20m across the whole study landscape in Victoria's Central Highlands. The locations of individual tree top, crown widths (CW), and crown heights (HT) of overstorey canopy were demarcated at the tree-level and then aggregated into plot-level metrics (20m×20m plot and 1ha plot), such as the number of trees per plot, average crown width per plot, and average crown height per plot. For our analyses, we only aggregated crowns that were >8 m in width. This rule was chosen because according to our DBH-CW_L allometry (result shown in 2.3.4 DBH estimation by LiDAR-based crown width), trees with a crown width < 8m are most likely have DBH < 100cm and therefore little chance of being a large trees with hollows. Overstorey crowns were classified into four categories (8-10m, 10-15m, 15-20m, and >20m) based on crown width to represent different growth stages of the canopy.

Where crowns had large perimeter:area ratios, this was used to indicate the presence of irregular crown forms. We refer to the perimeter:area ratio as the line density of the crown edge based on the method used to measure the crown perimeter. A live tree with a well-formed crown will have a relatively low line density for its crown edge, whereas a standing dead stag with many dead branches will have high line density for its crown edge. We used the line density of crown edges derived from the crown-edge detection step of ITD to compute a Stag Index describing the irregularity of the crown shape.

We used our ITD approach to classify LiDAR points belonging to midstorey canopies and detected tree tops. For midstorey metrics, within each plot, we used LiDAR points associated with the midstorey canopies to calculate the proportion of projection area of midstorey LiDAR points, a surrogate for midstorey density. The detection results for tree tops were used to aggregate the number of trees and mean midstorey height within each plot. We

used 1-ha as the plot size in this study, but 20×20m pixel size were also generated for use in other studies (see Chapter 6). 1-ha-metrics were used to build SDM and HSI in Chapter 3, Chapter 4 and Chapter 5, and 20m metrics of midstorey coverage were used to build landscape connectivity network in Chapter 6. A summary of the LiDAR metrics generated in this chapter are shown in Table 2-3.

The environmental impacts on large crowns density

To explore the association between environmental variables and the density of large crowns per ha, we explored the relationship between the number of large overstorey crowns per ha with bioclimatic variables (annual mean temperature, annual precipitation) and LiDAR-derived topographic variables (slope and gully). We considered all trees with crown width >15m to compute the density of large tree per ha, as according to our DBH-CW_L allometry (result shown in 2.3.4 DBH estimation by LiDAR-based crown width), trees with crown width >15m are typically larger than 150cm DBH and are thus likely to have hollows (Fox et al. 2008). We further summarized the abundance of overstorey crowns with CW>15m across different vegetation classes and forest management zones in study area.

Table 2-3 LiDAR overstorey and midstorey metrics Metrics

Category	Variables	ShortName
Overstorey	Average Overstorey tree crown width (CW) /plot	OvCWavg
	Total Overstorey tree CW/plot	OvCWsum
	Average large crowns height /plot	OvHtavg
	Number of level 1 CW /plot (8m < CW ≤ 10m)	OvN08t10
	Number of level 2 CW /plot (10m < CW ≤ 15m)	OvN10t15
	Number of level 3 CW /plot (15m < CW ≤ 20m)	OvN15t20
	Number of level 4 CW /plot (CW > 20m)	OvN20t30
	Number of Large Crowns /plot (CW > 8m)	OvNum
	Line density of edge of overstorey tree crown (Stag Index)	CLdens
Midstorey	MS Coverage (%)	MsCover
	Number of Midstorey trees /plot	MsNum
	Average Midstorey tree height /plot	MsHtavg

2.3 Result

2.3.1 Delineated overstorey crowns and method validation

The ITD approach that we developed for this study was able to correctly detect individual trees in different growth stages of the mountain ash forest (Table 2-4, Figure 2-4), although the accuracy varied among growth stages. Our algorithm was most accurate in the 1939 regrowth and multi-cohort stands that were dominated by 1939 regrowth mountain ash trees (ACC = 0.8 in both plots). The dominant overstorey crowns identified by ITD in these plots had an 86% chance of being the true crowns and an 8% chance to being over-segmented (i.e., a single tree crown

being classified as two or more individual crowns by ITD). The ITD algorithm had a 13% chance of missing a true crown. In 1977 regrowth forest (i.e. ~38 year old), the ITD algorithm was much less effective (ACC = 45%). Only 53% crowns were correctly detected and 47% of crowns were merged with their neighbours or being missed. Figure 2-4 showed the results of our ITD method in each stem mapping plots where the individual crowns been correct and incorrectly detected. Missed field crowns in the 1939 regrowth and multi-cohort stands were most likely suppressed overstorey trees, while missed field crowns in the 1977 regrowth forest were located in “canopy gaps” identified by our ITD method. We found a strong linear relationship between the LiDAR-derived crown width and the crown widths measured in the field ($R^2 = 0.84$; Figure 2-3). The strength of this relationship highlights the accuracy of the crown dimensions generated by the ITD algorithm, which is important for developing estimates of DBH for predicting probability of hollow occurrence.

Table 2-4 Accuracy of individual tree delineation results for each plot.

		Plot1	Plot2	Plot3
		1939 regrowth	1977 regrowth	mulit-cohort
Number of trees				
TRUE Positive (TP)	Field measurement	65	207	37
	ITD correctly detect	56	109	32
FALSE Negative (FN)	Missed field crown	3	7	5
	Merged field crown	6	91	0
FALSE Positive (FP)	ITD >2 crowns	3	33	0
	ITD over-segmented	2	0	3
Model Validation				
Accuracy (ACC)		0.800	0.454	0.800
Sensitivity (TPR)		0.862	0.527	0.865
Omission Rate (OR)		0.138	0.473	0.135
Commission Rate (CR)		0.082	0.232	0.086

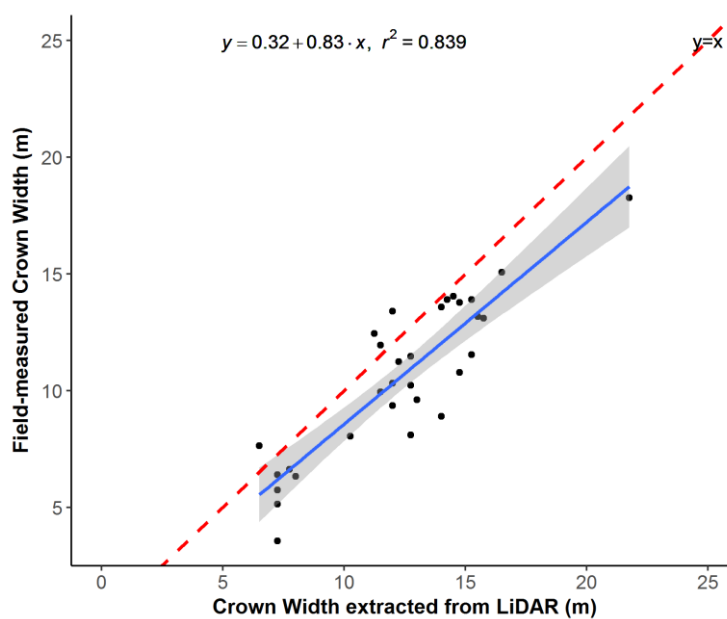


Figure 2-3 The relationship between field-measured crown with and crown width extracted from LiDAR

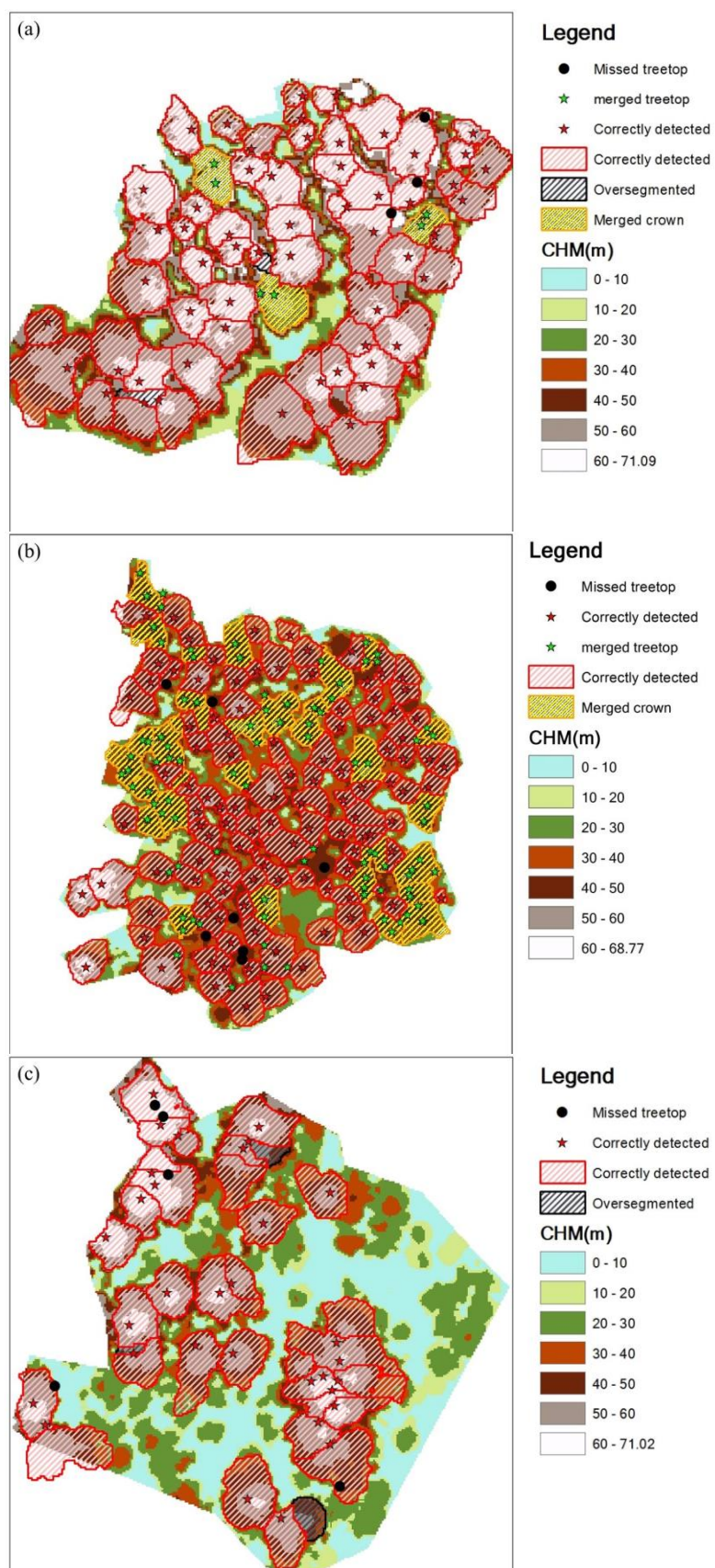


Figure 2-4 Stem-mapped plots for validation of individual tree delineation (ITD) of tree crowns in a) 1939 montain ash forest; b) 1977 regrowth montain ash forest; and c) mulit-cohort forest. Each panel shows individual trees that were correctly and incorrectly classified using our ITD algorithm.

2.3.2 Midstorey canopy height surface and height validation

When we applied the ITD algorithm to the midstorey, it generated a smooth midstorey CHM, reflecting the height variance of the midstorey canopy (Figure 2-5b). We measured midstorey canopy height of 40 trees located in Plot 1 (i.e., mature 1939 regrowth) and compared them to the canopy height estimated from the midstorey CHM. There was a strong positive, linear relationships ($R^2=0.66$, Figure 2-5a); however, it was difficult to directly match field-mapped individual midstorey trees with midstorey treetops detected by ITD. In part this may be due to a bias between field-recorded and LiDAR GPS coordinates.

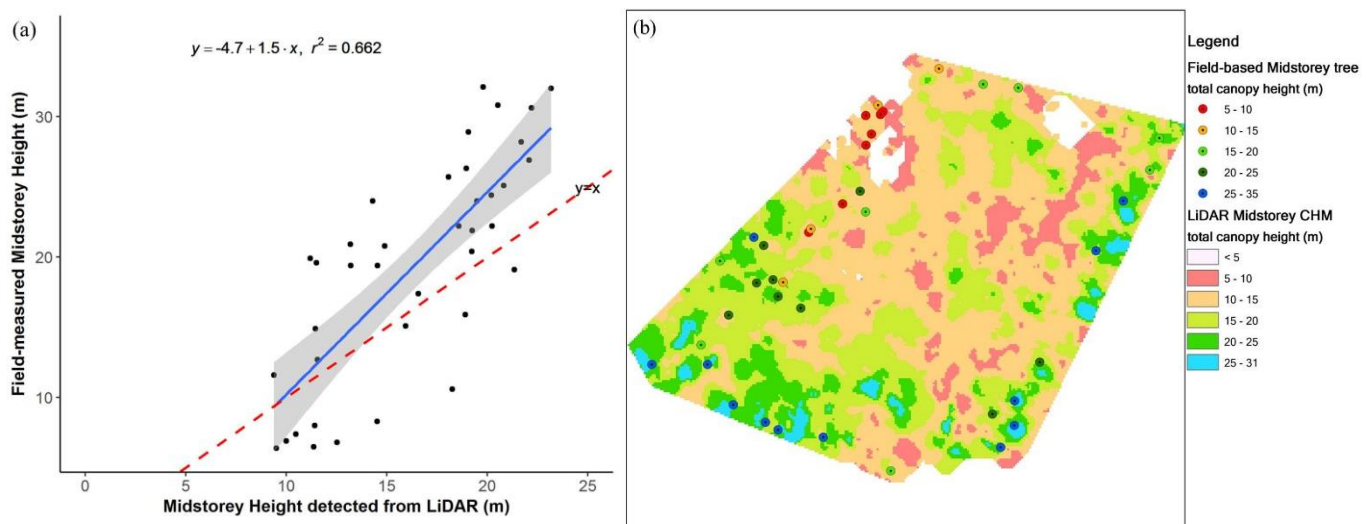


Figure 2-5 Validation for midstorey height detected from ITD: a) shows an observed and predicted midstorey canopy heights; panel b) shows a comparison of the field-based canopy height measurements and how they compared to the midstorey CHM.

2.3.3 Comparison with other algorithms

The comparison of the developed algorithms with layer-stacking, localized contour and marker-control watershed segmentation are summarized in Table 2-5 and Figure 2-6. The highest accuracy of tree top detection was layer-stacking method (ACC=90%). Trees detected by layer-stacking had a 92% chance of being the true crowns. No crown was over-segmented by layer-stacking. When compared to our ITD algorithm (top-edge enhanced watershed delineation), layer stacking correctly identified 9.6% more trees. Traditional marker-control watershed segmentation and localized contour method both performed badly in our stem mapping plots. Traditional marker-control watershed segmentation method trends to have highest rate to over-segment trees among four methods. The overall accuracy of localized contour was the lowest among all four methods (ACC=46%). 28% of crowns delineated by localized contour were merged with their neighbors.

In terms of characterizing crown shape, layer stacking tended to underestimate crown size, because it excluded layers that were farthest from the tree center. Crown shapes delineated by localized contour were also smaller than the actual tree crown shapes, due to the fact that only closed contour lines were considered

in this method. Traditional marker-control watershed segmentation algorithms often mistakenly merged smaller trees within or around the crowns of primary trees, and so it tended to overestimate crown size. Although the overall accuracy of our ITD algorithm was slightly less than for layer-stacking, it delineated tree crowns precisely along the crown edge, which provided more accurate information of the size off tree crowns.

Table 2-5 Accuracy of individual tree delineation results for each method

		Traditional Watershed	Layer-stacking	local Contour	ITD in this study
	Number of trees				
TRUE Positive (TP)	Field measurement	65	65	65	65
	ITD correctly detect	52	60	38	56
FALSE Negative (FN)	Missed field crown	0	1	9	3
	Merged field crown	13	4	18	6
FALSE Positive (FP)	ITD >2 crowns	6	2	9	3
	ITD over-segmented	25	0	9	2
	Model Validation				
	Accuracy (ACC)	0.54	0.90	0.46	0.80
	Sensitivity (TPR)	0.80	0.93	0.59	0.86
	Omission Rate (OR)	0.20	0.01	0.42	0.14
	Commission Rate (CR)	0.37	0.03	0.32	0.08
	Delineated Crown Size	Overestimate	Underestimate	Underestimate	Match

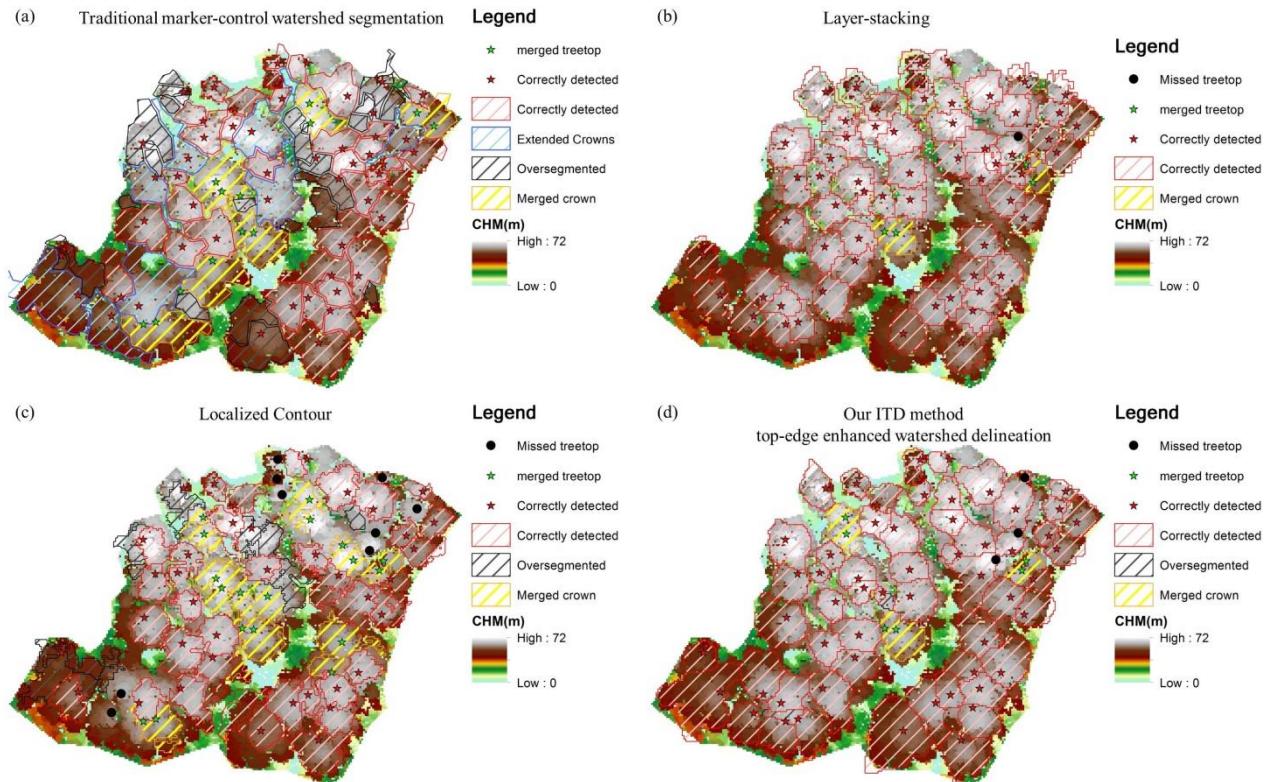


Figure 2-6 Stem-mapped plots for plot1-1939 regrowth forest of delineated tree crowns using: a) traditional marker-control watershed segmentation method; b) layer-stacking method; c) localized contour method; and d) our top-edge enhanced watershed delineation method. Each panel shows individual trees that were correctly and incorrectly classified using our ITD algorithm.

2.3.4 DBH estimation by LiDAR-based crown width

DBH-CW_L allometry allowed us to use LiDAR-derived mean crown width (CW) to estimate DBH. Mean crown width was calculated from polygon area of each crown delineated by our ITD method. As shown in Table 2-6, the collected field-assessed DBH data ranged from 51cm to 363cm, with the mean of 129cm. LiDAR-derived crown width ranged from 5.3m and 21m, with the mean of 12m. The mean R^2 between observed DBH and predicted DBH in test set was 0.331 (Table 2-7). Model summaries for the DBH-CW_L allometry were shown in Table 2-8 and Figure 2-7. There is a spread in residual variance after ~15m CW_L which reduces the accuracy of the model when used for predicting the DBH of large trees.

Table 2-6 Data summary of field-assessed DBH and LiDAR-derived crown attributes (mean crown width, crown area, perimeter and tree height). Minimum (min), maximum (max), mean, standard error (se) and standard deviation (sd) summarize observed values across all sampled trees.

	min	max	mean	se	sd
DBH	51.2	363.0	129.5	4.6	58.3
Crown width	5.3	21.0	12.3	0.3	3.3
Crown area	21.8	347.3	126.1	5.0	63.2
Perimeter	21.0	118.0	55.9	1.3	16.9
Height	33.8	71.4	57.2	0.7	8.6

Table 2-7 The mean and standard deviation (sd) of R^2 between observed DBH and predicted DBH, RMSE, MAE and RSE of test sets and all sampe data using 5-folds cross validation to predict DBH using generalized linear model (GLM) method.

Fold	Test set				All data
	R^2	RMSE	MAE	RSE	R^2
1	0.031	49.695	35.797	1.375	0.327
2	0.579	36.790	24.018	0.463	0.330
3	0.267	54.943	37.554	0.740	0.329
4	0.242	67.557	45.984	0.838	0.330
5	0.539	40.400	28.209	0.469	0.331
mean	0.331	49.877	34.312	0.777	0.329
std	0.227	12.241	8.547	0.373	0.002

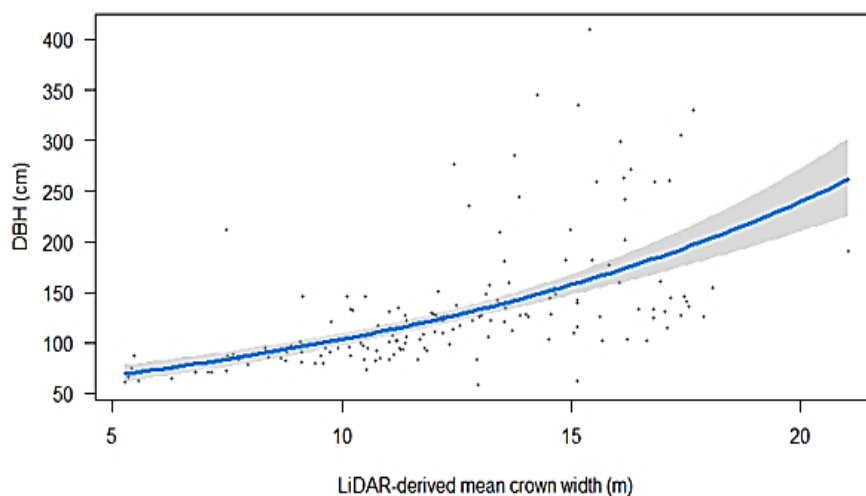


Figure 2-7 the results of a fitted model of CW_L:DBH, showing the expected value (blue line) and a confidence interval for the expected value (gray band) using “visreg” package in R

Table 2-8 CW_L :DBH GLM model result summary.

Generalized Linear Model (GLM) with gamma distribution (Eq.1) was used to characterize the relationship between LiDAR-derived crown attributes (crown width, CW_L) and logarithm of the field-measured stem diameter (DBH).

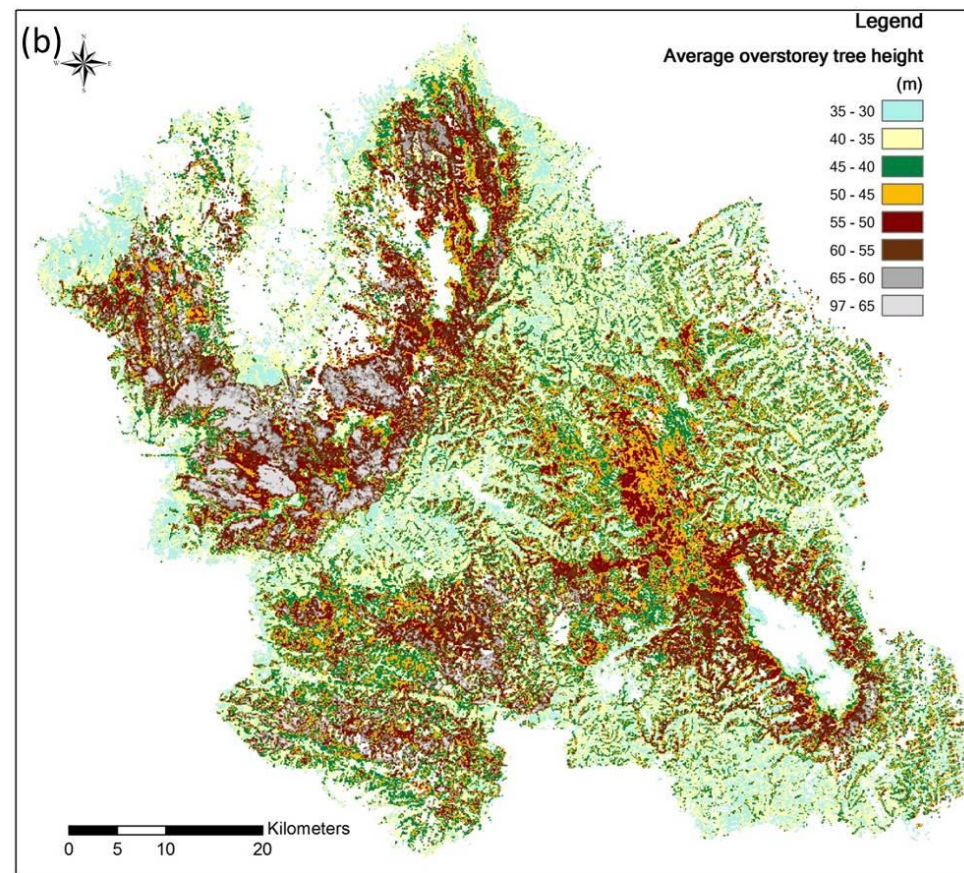
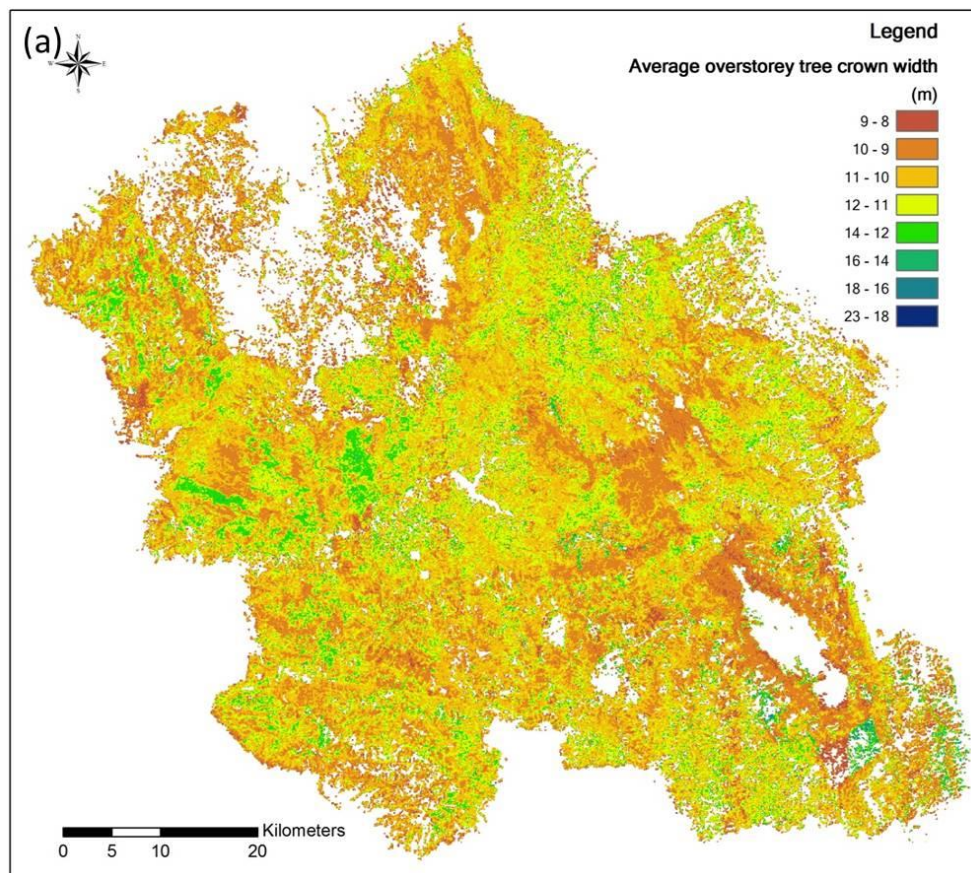
	Parameter	Estimate	Std.Error	t value	Pr(> t)		df.resid
(Intercept)	a_0	3.798	0.100	37.9	<2e-16 ***		156
CW_L	a_1	0.084	0.008	10.63	<2e-16 ***		

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

2.3.5 Distribution pattern of large trees across landscape

As shown in Table 2-9, 24,380,000 overstorey crowns were delineated by our ITD method across the study landscape. 405,000 trees had crown widths > 15m (~1.7% of total delineated crowns). The average crown width, crown area, and crown perimeter were 7.4m, 51m², and 33.7m, respectively. The average crown width in rainforest was about 1m larger than trees in wet - damp and riparian forests. The proportion of trees with large crowns ($CW > 15m$) in rainforest (3.3%) and riparian area (2.5%) was higher than in wet - damp forest. The management zone with the smallest mean crown width and lowest proportion of large trees in Victoria Central Highlands was the special management zone (SMZ). Areas that are protected from timber harvesting (e.g., National parks, NP and special protection zone, SPZ) had slightly larger crowns than State Forest General Management Zones (GMZ). The spatial distributions of overstorey crown attributes across the area of the Central Highlands included in this study are shown in Figure 2-8, including average overstorey tree crown width per ha (only trees with $CW > 8m$ were aggregated), average overstorey tree crowns height per ha (only trees with $CW > 8m$ were aggregated), the number of large trees with large crowns ($CW > 15m$) per ha; and Stag index.

Based on the DBH- CW_L allometry there are 572,000 (95%CI: 318,000 - 808,000) trees with DBH>150cm (that have >50% of having a hollow) across all form classes across the area of the Central Highlands included in this study. That is roughly equivalent to 1.2 trees per ha (Table 2-10). The proportion of potential large old trees among all delineated overstorey crowns is about 2.3%, which is 0.6% more than the proportion of trees with large crowns ($CW > 15m$). The distribution pattern of potential large old trees in vegetation classes and forest management zone was similar to large crowns. Highest abundance of potential large old tree located in rainforest, followed by riparian area. The abundance potential large old trees in NP and SPZ were higher than in GMZ and SMZ.



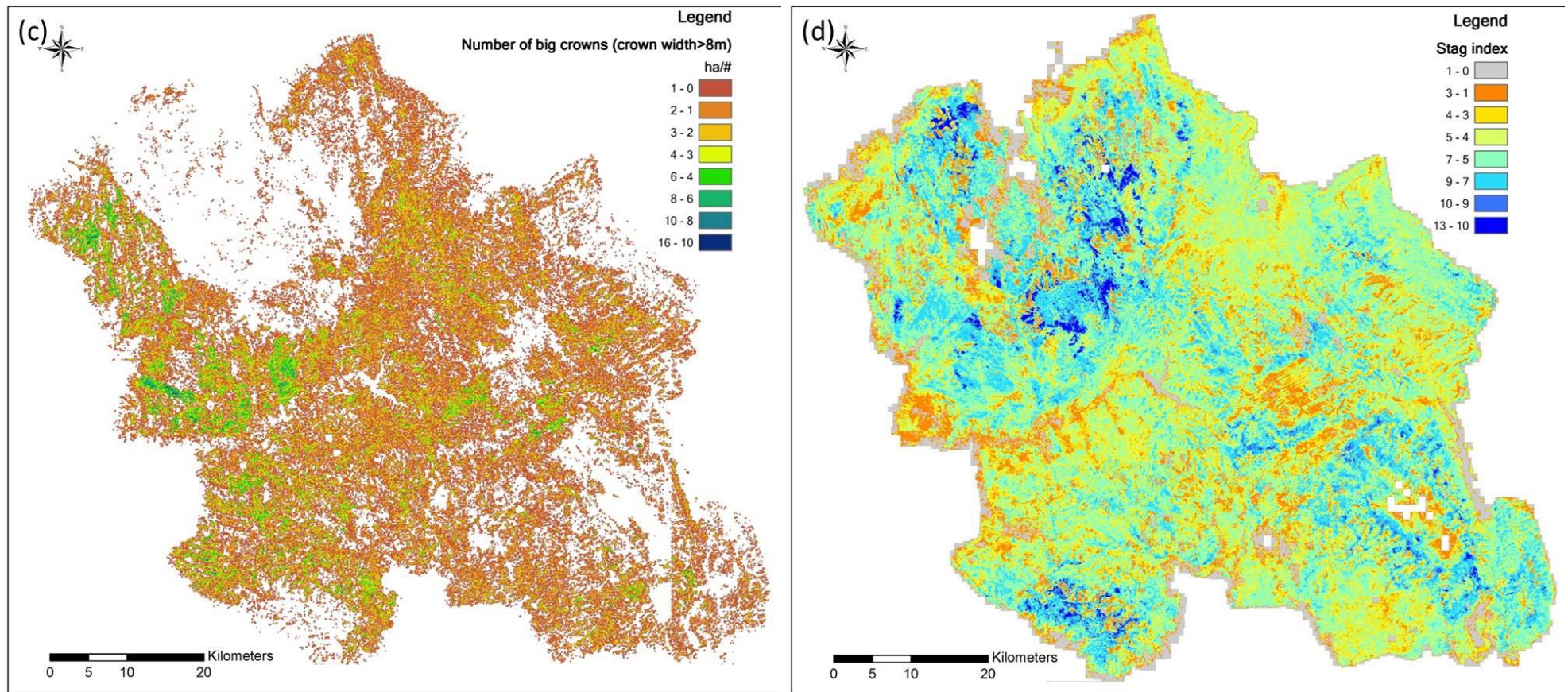


Figure 2-8 Distribution map of 1ha-metrics of overstorey crown attributes aggregated from individual crown data from our ITD method across Victoria's Central Highlands. The crown attributes are: a) average overstorey tree crown width per ha (only trees with CW>8m were aggregated); b) average overstorey tree crowns height per ha (only trees with CW>8m were aggregated); c) the number of large trees with large crowns (CW>15m) per ha; and d) line density of edge of overstorey tree crown (Stag Index).

Table 2-9 The mean crown width, crown area, and perimeter of all overstorey crowns, and the abundance of crowns larger than 15m by ITD algorithm across different vegetation classes and forest management zones in Victoria's Central Highland. GMZ, SMZ, and SPZ are different management zones within Victoria's State Forests (see text for details).

	Area	Total crowns	crown width (m)		crown area (m ²)		Perimeter(m)		crown width > 15m		
			mean	sd	mean	sd	mean	sd	crowns	% of all crowns	#/ha
Total study area	491,400	24,380,000	7.4	3.1	51.0	43.4	33.7	14.6	405,000	1.7%	0.8
Wet or Damp forests	305,200	18,995,000	7.5	3.1	51.6	42.6	33.9	14.4	303,000	1.6%	1.0
Riparian area	24,900	1,115,000	7.6	3.4	54.7	48.3	34.7	15.9	27,000	2.4%	1.1
Rainforests	12,500	606,000	8.3	3.4	63.6	49.5	37.4	15.7	20,000	3.3%	1.6
GMZ	162,400	10,833,000	7.4	3.1	50.8	42.3	33.7	14.3	162,000	1.5%	1.0
NP	81,500	6,274,000	7.5	3.2	52.0	44.1	33.9	14.8	113,000	1.8%	1.4
SMZ	15,200	882,000	7.3	3.0	48.8	41.3	33.1	14.3	12,000	1.4%	0.8
SPZ	45,800	3,216,000	7.6	3.2	53.1	45.4	34.1	15.1	66,000	2.1%	1.4

*GMZ: general management zone; NP: national parks; SMZ: special management zone; SPZ: special protection zone

Table 2-10 Estimated number (and 95% CIs) of potential large old trees (DBH>150cm) across different vegetation classes and forest management zones in Victoria's Central Highland. GMZ, SMZ, and SPZ are different management zones within Victoria's State Forests (see text for details).

	Area	Total trees	Total trees >150 cm DBH	% of all trees	trees per ha
Total	491,400	24,380,000	572,000 (318,000-808,000)	2.3% (1.3%-3.3%)	1.2 (0.6 - 1.6)
Wet or Damp forests	305,200	18,995,000	430,000 (237,000-611,000)	2.3% (1.2%-3.2%)	1.4 (0.8 - 2.0)
Riparian area	24,900	1,115,000	39,000 (22,000-54,000)	3.5% (2.0%-4.8%)	1.6 (0.9 - 2.2)
Rainforests	12,500	606,000	27,000 (16,000-37,000)	4.5% (2.6%-6.1%)	2.2 (1.3 - 3.0)
Parks	162,400	10,833,000	159,000 (89,000-224,000)	1.5% (0.8%-2.1%)	1.0 (0.5 - 1.4)
GMZ	81,500	6,274,000	231,000 (127,000-328,000)	3.7% (2.0%-5.2%)	2.8 (1.6 - 4.0)
SMZ	15,200	882,000	17,000 (9,000-24,000)	1.9% (1.0%-2.7%)	1.1 (0.6 - 1.6)
SPZ	45,800	3,216,000	92,000 (52,000-129,000)	2.9% (1.6%-4.0%)	2.0 (1.1 - 2.8)

*GMZ: general management zone; SMZ: special management zone; SPZ: special protection zone

2.3.6 Effect of environmental variables on the abundance of trees with large crowns

The relationships between the abundance of large tree with large crowns (CW>15m) and environmental variables are shown in Figure 2-9. The abundance of large crowns showed unimodal responses to both annual mean temperature and annual precipitation. With optima from 10-13°C of annual mean temperature and from 1200mm-1500mm of annual precipitation, the number of large crowns per ha in these optimal conditions was higher than one tree per ha. Trees with large crowns were also more abundant on flat areas where slope was < 30 degrees and in gullies (i.e., high gully index values).

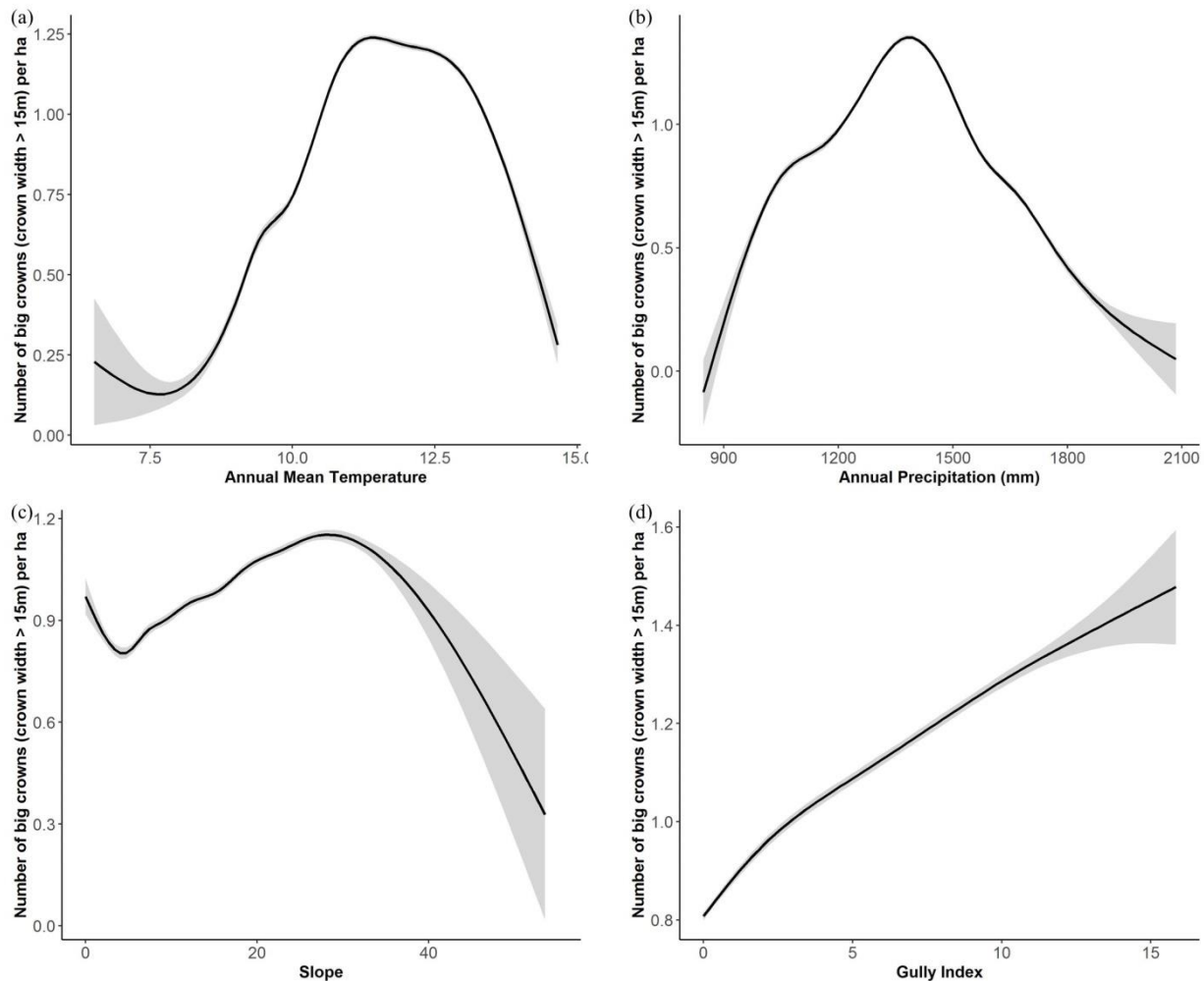


Figure 2-9 The number of large trees with big crowns (crown width > 15m, corresponding to a DBH > 150 cm) across the whole study area changed with: a) annual mean temperature (°C); b) annual precipitation (mm); c) slope (°); and gully index. The relationships were demonstrated using “gam” method for scatterplot smoothing in R “ggplot2” package.

2.4 Discussion

Large trees are considered keystone structures in forests, woodlands, savannas, agricultural landscapes, and urban areas around the world (Lindenmayer et al. 2012b, Stagoll et al. 2012, Kramer et al. 2016). They are typically associated with older forests due to the length of time required for trees to grow big. Due to a range of natural and human-induced disturbances, populations of large old trees are rapidly declining all over the world (Lindenmayer et al. 2012b, Lindenmayer 2017). Large old trees are now rare habitat features on forested landscapes (Lindenmayer et al. 2012b). Maps of the locations, the size, and abundance of large trees can help guide conservation management (Ellis et al. 2015, Lindenmayer and Laurance 2016, Mifsud and Harris 2016, Lindenmayer 2017). Most surveys of large old trees are ground-based, which limits their extent, repeatability, and extrapolability. Developing methods for efficiently estimating densities of large trees over large-spatial scales allows for a better understanding of the distribution of large trees and can provide for more effective long-term monitoring programs and be used to develop robust predictions (i.e. lower statistical and structural uncertainty, see Nitschke et al. (2007)) of habitat and habitat change fauna species dependent on large trees at broad-scales.

We used LiDAR-based remote-sensing data to develop a new algorithm for individual tree crown delineation in broadleaf forest canopies to estimate the number of large trees with large crowns and potential live old-growth trees in the Central Highlands of Victoria. We validated the result of our ITD plots in three ground-based plots that systematically sampled all location of individual trees. Our ITD method was most accurate in the 1939 regrowth and multi-cohort stands that were dominated by 1939 regrowth mountain ash trees (the overall accuracy was 80% in both plots). The dominant overstorey crowns identified by ITD in these plots had an 86% chance of being the true crowns. At a landscape level, our approach estimated about 24 million overstorey crowns in tall forest stand (stand height > 20m) across the whole landscape in Victoria Central Highland. 1.7% of them have crown width larger than 15m, which represents ~405,000 trees. We also integrated the crown attributes from ITD method with the DBH estimation model to evaluate the abundance of potential large old trees. We assumed that trees with a DBH>150cm have high probability to be a large old trees with hollows (Fox et al. 2008, Fox et al. 2009). At the landscape level, our approach estimated the presence of ~ 572,000 (95%CI: 318,000 - 808,000) potential large live trees with hollows (i.e. trees with DBH>150cm), with 1.2 trees ha⁻¹ on average. Lindenmayer and Wood (2010) identified that large live trees with hollows had ~ 30% chance of collapsing over a 25 year period at 29 sites. This rate of collapse could lead to the loss of these live large trees within the next 40-50 years (Lindenmayer and Sato, 2018). A key uncertainty around the observed collapse at these sites is if it is a fine-scale or broad-scale phenomena. The mapping of large – live trees with hollows will allow for landscape-level monitoring and modelling to test if the current decline in large trees is scale-dependent.

Our analyses of the environmental impacts on the abundances of large trees with large diameters were consistent with previous findings. For example, Lindenmayer et al. (2016) found that live hollow-bearing trees are more likely to be found on sites with a high Topographic Wetness Index, which is consistent with our finding of them in rainforest and riparian forests. We also found a non-linear relationship between large crowns abundance and slope, with greater abundance of large crowns on flat areas. These areas are typically excluded from timber harvesting

due to Code of Forest Practices restrictions on harvesting in riparian areas (The State of Victoria Department of Environment and Primary Industries 2014). These areas also occur in sheltered positions that may serve as areas of post-fire refuge due to the moderating effect of topography and mesic vegetation on fire severity (Berry et al. 2015). Our research also found that there was an optimal temperature and precipitation condition for trees with large crowns in the study area. This may reflect a productivity gradient where trees are able to attain larger sizes or a reduced fire frequency allowing trees to live longer.

Our ITD method showed promise as a novel method for delineation individual crowns in broadleaf forests with heterogeneous crowns. Our ITD method showed an improved tree top detection rate over the traditional watershed segmentation and localized contour methods. While both methods are known to perform well in conifer forests (Ke and Quackenbush 2011, Wu et al. 2016), they were not suitable for detecting tree tops in our dense *Eucalyptus* forests with heterogeneous crowns. The highest detection rate was by the layer stacking method (ACC=90%), but layer stacking method tended to underestimate crown size. This is because layer stacking method excluded layers that were farthest from the tree center (i.e. tree bole). The layer stacking method excluded layers with some abnormally large clusters of LiDAR points which may belong to neighboring trees or narrow crowns, however, this step might also excluded some valid layers (Ayrey et al. 2017). By mistakenly removed valid layers as abnormally clusters, the crown size delineated from layer stacking method was underestimated. Although the tree top detection rate of our ITD algorithm was less than layer-stacking, its ability to delineate tree crowns precisely along the crown edge provided more accurate mapping and measurement of crowns shape and size. The ability to accurately estimate tree crown size is of critical importance for estimating large trees and potential occurrence of hollows in the forests of the study area.

The development of the top-edge enhanced watershed delineation algorithm in this study required that several parameters had to be calibrated to the specific forest types. The parameters, such as the neighborhood area in focal statistic tool in ArcGIS, in this study were optimised to detect large dominant overstorey trees in multi-cohort forests. The tree crowns in the younger, homogenous stands with higher density (such as 1977 regrowth plot in this study) were much less well differentiated and thus more difficult to correctly delineate. The DBH-CW_L allometry is also species-specific which may need to be recalibrated for other tree species. The estimation of potential large live trees was based on empirical model between crown width and stem diameter. This means that our method is unable to delineate trees with large stem diameter if a significant portion of the tree top is dead or broken. Finally the abundance of dead old trees cannot be mapped using the ITD approach and requires an alternative method such as stand-level statistical models of relating forest structure to their occurrence (Kramer et al. 2016). Despite these limitations, this study has shown that it is possible to map large-live trees at the landscape-scale and in doing so providing a critical resource for forest and conservation managers concerned about hollow-dependent fauna.

2.5 Conclusion

We used high-resolution, LiDAR-based remote-sensing data to develop a new individual tree delineation algorithm for irregular-shaped crowns in broadleaf mountain ash forest. Our ITD method was most accurate in the 1939 regrowth and multi-cohort stands that were dominated by 1939 regrowth mountain ash trees (the overall accuracy was 80% in both plots). We used the relationship between crown size, stem diameter, and tree age to predict the abundance of potential live old-growth trees with hollows (i.e. hollow-bearing trees). Our analyses estimated 405,000 trees with large crowns width ($CW > 15\text{m}$) and 572,000 (95%CI: 318,000-808,000) potential large old tree with hollows ($DBH > 150\text{cm}$), which equate to a mean density of one live large old tree per ha across the Central Highlands. The abundance of large trees was strongly associated with gullies and flat area. Trees in rainforest and riparian areas had larger average size and higher density of large crowns than in other vegetation classes. Our analyses highlight the benefits of using high-resolution, spatially explicit data from the whole landscape to map the distribution and abundance of potential large old trees.

Appendices 2

Tree-level Live HBT occurrence model

In State Forest Resource Inventory (SFRI) plots (same dataset as the one analyzed by Fox, 2008), 185 out of 2,487 living trees had hollows. DBH ranged from 20.60cm to 387.80cm, with the mean of 77.99cm.

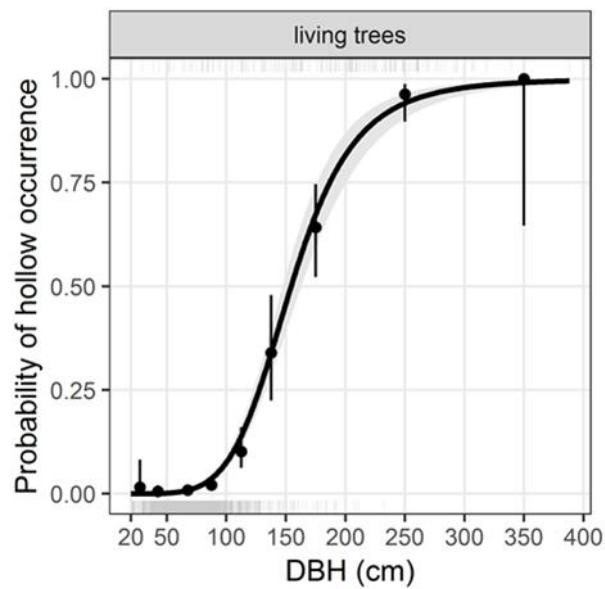


Figure A2 1 The relationship between DBH and probability of hollow occurrence
The black solid line and the shaded area show mean predicted probabilities and 95% credible intervals. Black dots are aggregated probability of hollow per DBH classes and error bars are 95% Wilson binomial CI. Grey rugged points are observed absences and presences (0 and 1, respectively).

Table A2 1 live HBT probability model result summary.

	Estimate	Std.Error	z value	Pr(> z)	
(Intercept)	-31.4929	2.0747	-15.18	<2e-16	***
log(DBH)	6.2342	0.4311	14.46	<2e-16	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

AUC	df.resid
0.94*	2484

Map of slope and gully index

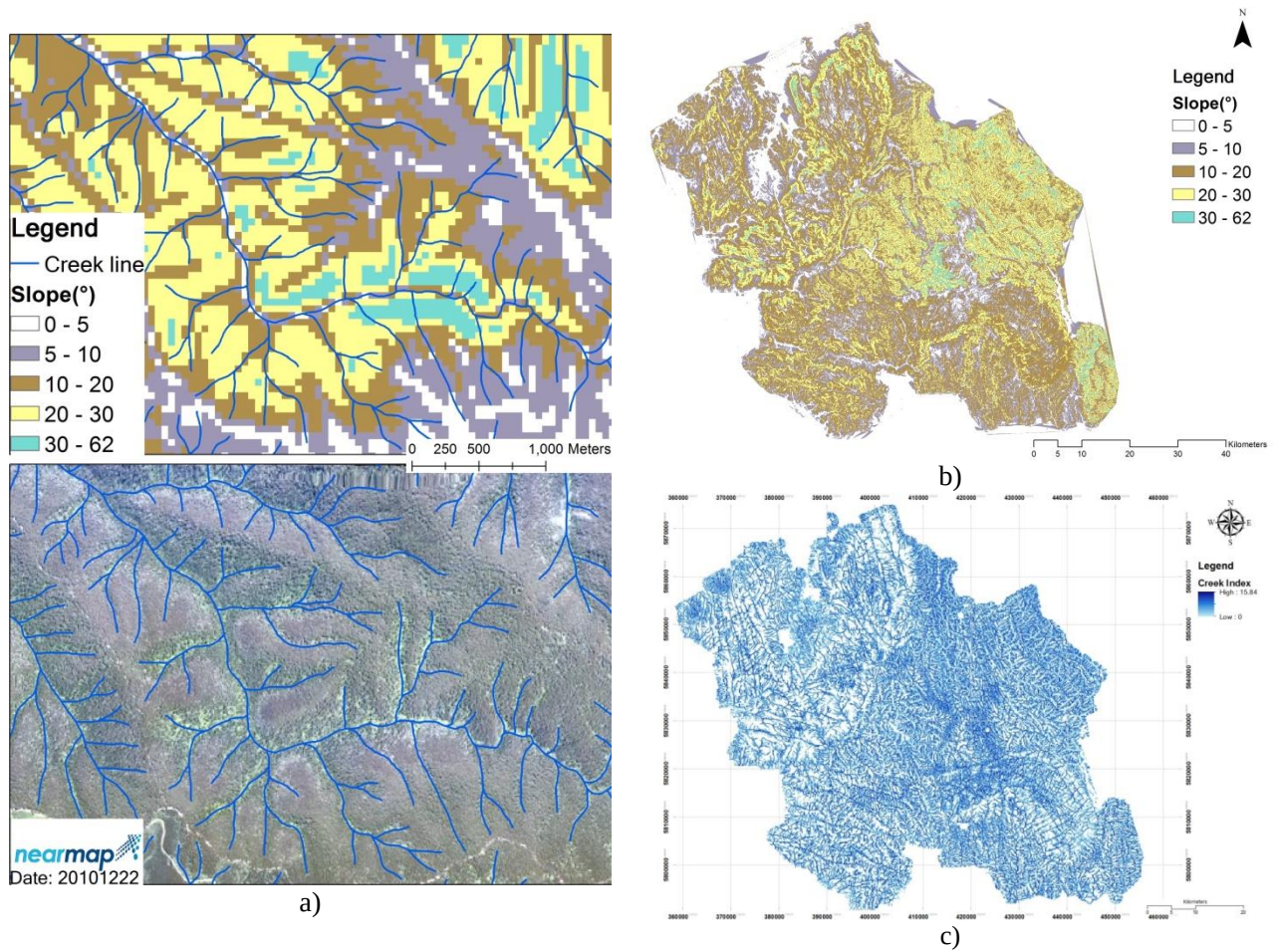


Figure A2 2 a) Map of example of slope within 1-ha plots;
 b) spatial distributions of slope in Victorian Central Highland
 c) spatial distributions of gully index in Victorian Central Highland

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Chapter 3.

3 Predicting landscape-scale variability in hollow-bearing tree abundance in Victoria's Central Highlands

Abstract

Hollow-bearing trees (HBTs) are a key feature of mature forests around the world. They provide a critical habitat resource for hollow-dependent animals, many of which are threatened due to a range of natural and human disturbances. Developing strategic conservation plans for arboreal species associated with HBTs requires an understanding of the spatial distribution and temporal dynamics of HBTs across scales. This requires accurate inventories of HBTs within stands and landscapes. Historically, HBT inventories have been ground-based, making them costly to implement and limited in spatial scale. The result is that estimates of HBT abundance at the landscape scale is based on extrapolations from much smaller areas that have been directly observed. Developing remote-sensing methods to estimate the landscape-scale abundance of HBTs has the potential to improve the quality and accuracy of data on HBT distributions across forested landscapes. In this study we used high-resolution, LiDAR-based metrics of forest structure and topography, coupled with datasets on environmental conditions, to develop predictive models of HBT abundance across ~340,000 ha of Victoria's Central Highlands. We developed statistical models of HBT abundance using machine-learning tools to identify key structural, topographic, and environmental predictors. Our analyses predicted a mean density of 4.4 HBT per ha across the Central Highlands. This is nearly five times greater than recent estimates of HBTs based on long-term plots in the Central Highlands. However, we found the patterns of density varied substantially by tenure and vegetation type for different HBT form classes. In addition, we identified complex relationships between key predictors and the abundance of HBTs, reflecting local-scale variability in environmental conditions, disturbance history, and forest management practices. Our analyses highlight the benefits of using high-resolution, spatially explicit data from the whole landscape to predict HBT abundance.

3.1 Introduction

Hollow-bearing trees (HBTs) are regarded as a keystone habitat structure in forest ecosystems around the world (Lindenmayer et al. 1991a). HBTs provide nesting, roosting, and shelter sites for many forest-dependent fauna (Lindenmayer and Wood 2010, Burns et al. 2015, Lindenmayer et al. 2017). Globally, 30% of all vertebrate species use HBTs for one or more of these activities (Lindenmayer et al. 2012b). In Australia, approximately 290 vertebrate species, including many rare and threatened species, utilise HBTs (Gibbons et al. 2000b). In the mountain ash (*Eucalyptus regnans*) forests of southeast Australia, ~40 vertebrate species rely on HBTs (Lindenmayer et al. 2012b). As a keystone habitat feature in these ecosystems, reductions in their abundance could place HBT-dependent fauna at risk due to habitat loss and facilitate a loss in ecosystem functioning (Lindenmayer et al. 2012b).

In many regions of the world, the large trees that provide hollows are declining (Lindenmayer and Wood 2010, Lindenmayer et al. 2012b). In the mountain ash forests of southeast Australia a decline in both live and dead HBTs has been observed in a network of long-term forest study plots, with dead HBTs collapsing two to six times faster than live HBTs (Lindenmayer and Wood 2010). The current decline in HBTs is predicted to accelerate over the next 10-20 years leaving few HBTs in these forests (Lindenmayer and Sato 2018). Lindenmayer and Sato (2018) have suggested that the observed decline in HBT has resulted in a hidden collapse of these ecosystems with the occurrence of cavity-dependent fauna declining significantly since 2004.

To date, much research has focused on predicting the availability and distribution of HBTs. Several studies have built predictive models using information on tree size, form, and species (Lindenmayer et al. 1991a, Gibbons et al. 2000b). Others have considered abiotic factors such as disturbance history, topography and climate as covariates with individual-tree attributes (Lindenmayer et al. 1993, Bennett et al. 1994a). Gibbons et al. (2000) and Fox et al. (2008) found that larger diameter trees are more likely to have hollows than smaller trees. At the site-level, the abundance of hollow-bearing trees is associated with topography, forest type, number of large stems, logging history, and climate (Lindenmayer et al. 1991a, Lindenmayer et al. 1993, Bennett et al. 1994a, Ball et al. 1999). These models have established simple rules for hollow development, but have limited ability for predicting landscape-scale distributions of HBTs because data on key predictors (e.g., stand density, number of large trees) is not available for most parts of these landscapes (Fox et al. 2009, Owers et al. 2014).

Increasing knowledge of the availability and distribution of HBTs throughout landscapes is crucial for the sustainable management and conservation of forests and forest biodiversity (Davis et al. 2014). For example, HBTs are more likely to persist in particular parts of landscapes (Lindenmayer et al. 2012b). Lindenmayer et al. (2016) found that live HBTs were more abundant on wet sites in reserved areas that were old and long unburnt (*i.e.*, old-growth) or mixed aged (*i.e.*, containing two or more cohorts). Collapsed HBTs were more likely to occur in young forests and areas impacted by moderate- to high-severity fire (Lindenmayer et al.

2016b). Understanding what factors shape the distribution and abundance of HBTs is critical for identifying areas within landscapes that are likely to provide the greatest habitat suitability for cavity-dependant fauna (Lindenmayer et al. 2016b). Most research has focused on the factors influencing HBT abundance at the site level. Predicting the distribution and population structure of HBTs at the landscape-level is essential for developing conservation plans that can foster a sustainable supply of HBTs for fauna that depend upon them (Lindenmayer et al. 2012b). Remote-sensing data, validated by ground-based measurements, provides a novel approach for quantifying the distribution of HBTs at broad spatial scales.

Light detection and ranging (LiDAR) is a remote-sensing technique that acquires three-dimensional geospatial data on forest structure at high spatial resolutions and with high accuracy (Lefsky et al. 2002, Lim et al. 2003, Martinuzzi et al. 2009, Fedrigo et al. 2018). LiDAR has also been used to locate and survey tree structure, growth form, and senescence class with a high level of accuracy at low cost over large areas of forest (Bater et al. 2007, Owers et al. 2014, Wing et al. 2015). For example, in southeastern Australia Fedrigo et al. (2018) used LiDAR data to identify different stand types where the ability to detect sub-canopy forest structure was critical for differentiating between different vegetation communities. The ability of LiDAR to measure both canopy and sub-canopy structure suggests that this approach might be effective for identifying both large overstory dominant live HBT and dead HBT, which are typically located in the forest understorey. Bater et al. (2007) were able to use LiDAR structural metrics of forest stands to estimate proportion of trees in different stages of decay in a conifer-dominated coastal forest of British Columbia, Canada. Martinuzzi et al. (2009) evaluated the use of LiDAR data and a machine-learning algorithm for mapping the presence/absence of different snag diameter classes important for birds in mixed-conifer forest in Northern Idaho (USA). Owers et al. (2014) used LiDAR and high-resolution multispectral aerial imagery to predict the occurrence of five forms of HBT in mixed forest in NSW, Australia.

A major challenge in identifying HBTs is the need to discriminate amongst various form classes—from live, mature trees with hollows to the decaying remnants of former trees. Arboreal species often have specific requirements for the type of tree that they will nest in (Smith et al. 1991). In the Central Highlands of Victoria HBTs are typically classified into one of nine forms based on observable characteristics, such as living or dead, tall or short, and percentage of broken tree top (Smith et al. 1991). These forms reflect stages of advancing senescence and collapse, with live HBT classified as forms 1 and 2 and dead HBT form classes 3-9. Using LiDAR to estimate HBT distribution and abundance by form class could provide estimates of the population structure of HBT that can then be used to assess the rates of HBT recruitment, loss, and transition amongst form classes at the landscape scale.

The Central Highlands of Victoria present a challenging, but important, case study for developing remote-sensing tools for estimating HBT abundance due to the ecological importance of HBTs in these ecosystems and the dependence of several threatened arboreal mammal species on HBTs. The overarching goal of this study was to map the population structure of different form classes of HBTs in Victoria's Central

Highlands using airborne LiDAR. The specific objectives of the study were to:

1. understand relationships between environmental variability and the occurrence and abundance of HBTs using LiDAR, topographic, climatic, and disturbance history data; and
2. predict the distribution and population structure of HBT of different form classes at the landscape-level.

3.2 Methods

3.2.1 Study Area

The study area is located in the Central Highland of Victoria in southeastern Australia (Figure 2-1a). The Central Highlands experience mild summers and cool, humid winters with frequent frosts and occasional periods of snow. Mean annual temperatures ranged from 6-15 °C and mean annual precipitation ranged from 690-2090 mm over the period 1981–2010 (Stewart and Nitschke 2017, Fedrigo et al. 2019). The three major ecological vegetation classes (EVCs) in this study area are wet or damp forest (89%), riparian forest (7%), and rainforest (4%). The dominant tree species in the wet or damp forest are mountain ash (*Eucalyptus regnans*), alpine ash (*Eucalyptus delegatensis*), and shining gum (*Eucalyptus nitens*) [collectively known as montane ash]. More than 40% of the montane ash forest in the Central Highlands of Victoria was burnt during the 2009 Black Saturday wildfires (Blair et al. 2018).

3.2.2 Field-based HBT assessment

Ground-based surveys of hollow-bearing trees (HBTs) were conducted by the Arthur Rylah Institute for Environmental Research (ARI). Between 2014 and 2017, ARI staff established and surveyed 438 1-ha sites within the Central Highlands (red dots in Figure 2-1). Of these, 422 plots were located in the three major EVCs for study area; this included 382 sites in wet or damp forest, 14 sites in riparian forest, and 26 sites in rainforest. Within these 422 plots, 1445 HBTs were identified, mapped, and measured for diameter at breast height (DBH; cm), height (m), HBT form class, and observed hollow attributes. HBTs were classified into one of nine form classes, defined by the degree of senescence and collapse (Figure 3-2). All HBTs were also classified as either survey standard HBTs or ecological HBTs. Survey standard HBTs can be mature, senescent, or dead trees, and contain at least one hollow, are >6m tall and >1.5m DBH, and are one of the three montane ash species. These trees meet the current criteria for HBTs in the published government survey standards (Nelson et al. 2017). Ecological HBTs may be living or dead trees of any species and must contain an observable hollow. Hollows include cavities, spouts, broken tops and/or cracks/fissures. Dead trees <50cm DBH were excluded, unless an obvious hollow of the type used by Leadbeater's Possum (*Gymnobelideus leadbeateri*) was present. The most obvious difference between survey standard and ecological HBTs was the inclusion of many understory species, including *Acacia dealbata*, *Acacia frutescens*, *Acacia melanoxylon*, and *Nothofagus cunninghamii*, in the latter.

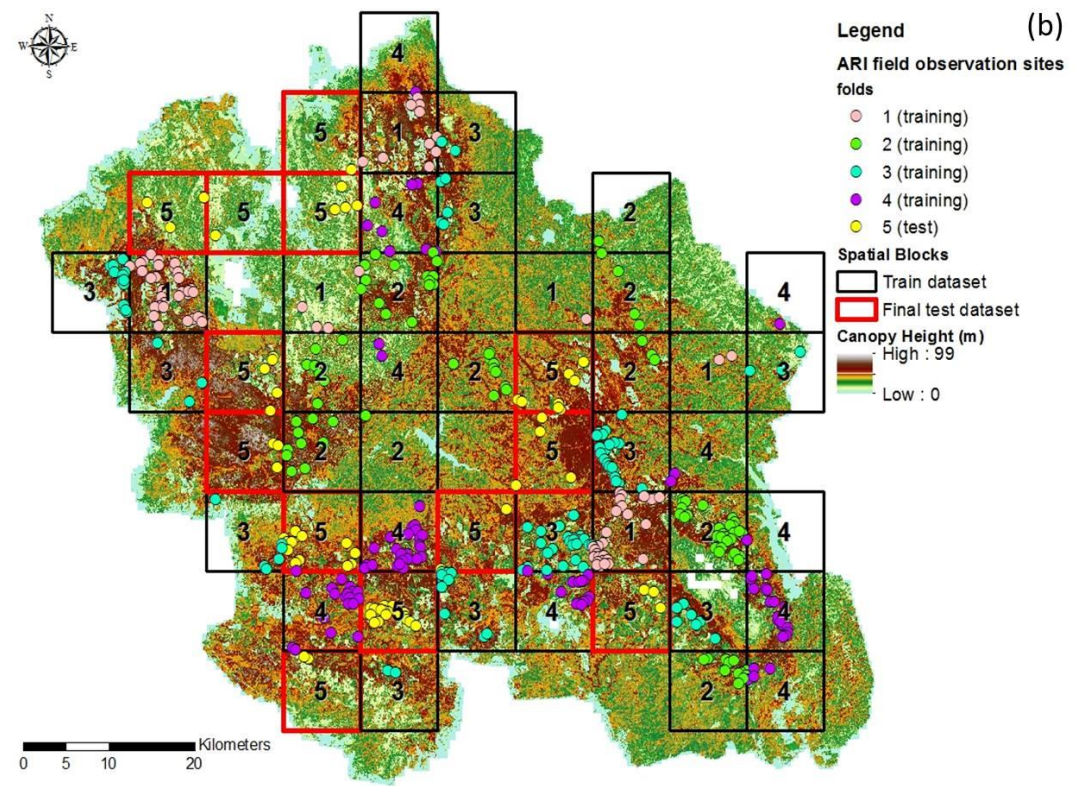
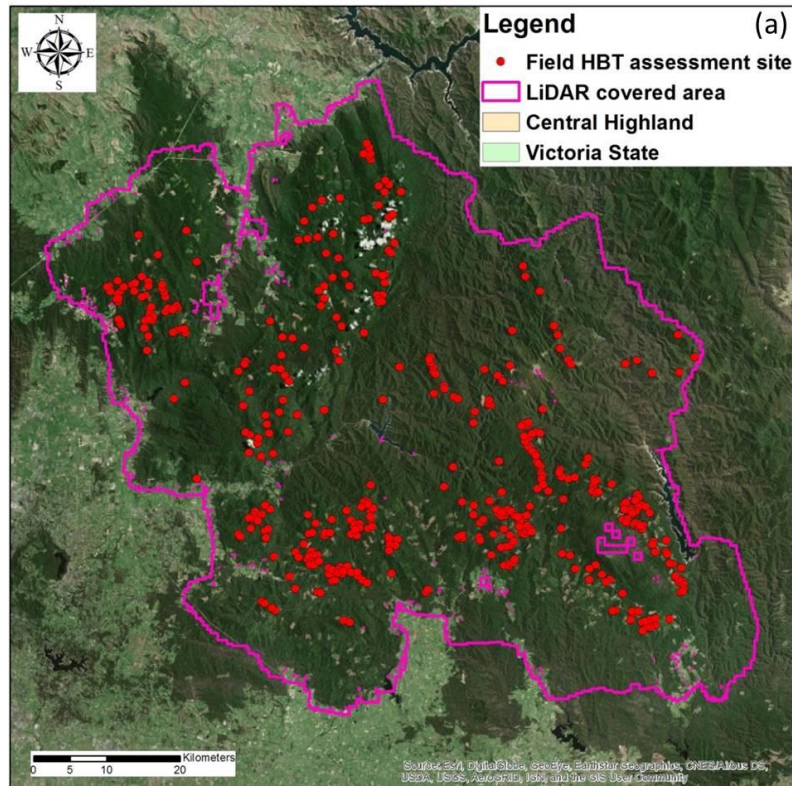


Figure 3-1 The study area in Victoria's Central Highlands. The map shows (a) the total LiDAR coverage and the locations of field HBT assessments, and (b) the location of each fold of 5-fold block-cross validation.

The ecological HBT definition was broader and more inclusive than the survey standard definition, but more accurately reflected the total number of hollows in the study sites. Due to the uneven number of HBTs across the nine form classes commonly used in these forests, we reclassified all trees into three form classes based on similar attributes. We defined them as (Figure 3-2):

1. HBT0t2, which includes form classes 0.5, 1, and 2 (i.e. live HBTs).
2. HBT3t4, which includes form classes 3 and 4 (i.e., tall, dead HBTs with branches).
3. HBT5t8, which includes form classes 5 and 8, (i.e., dead HBTs with no branches).

We used these data on HBT abundance within the ARI plots to develop and test HBT density prediction models based on LiDAR-derived metrics and other spatially explicit data for a range of environmental factors.

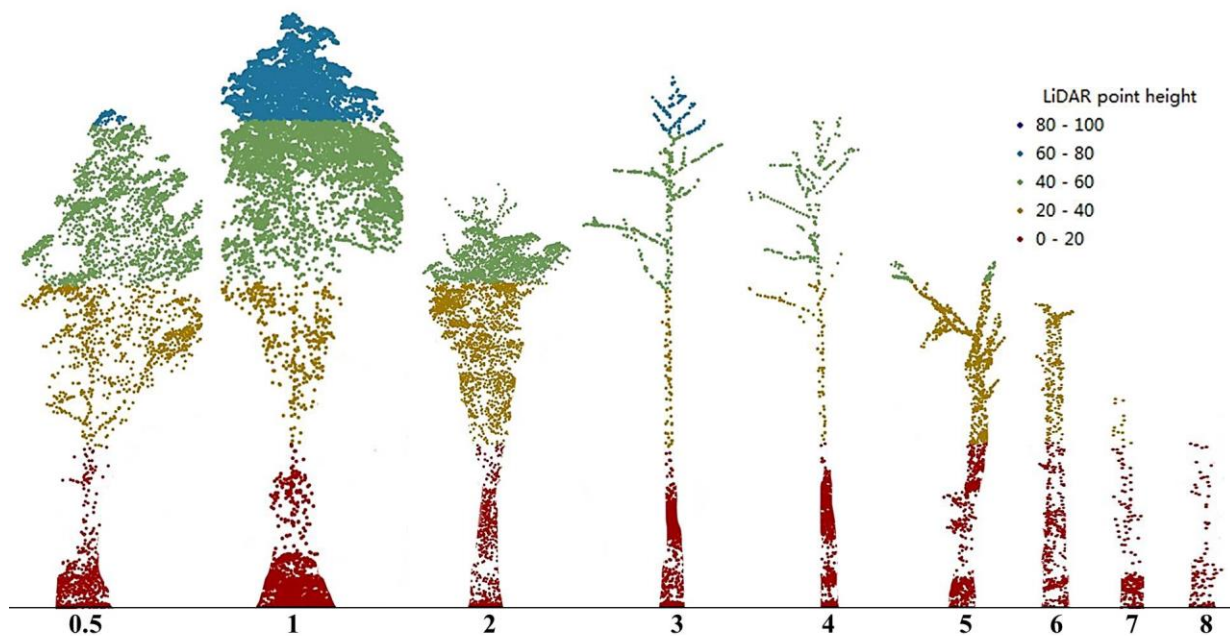


Figure 3-2 LiDAR point profiles of nine forms of potential hollow-bearing trees (modified from Smith and Lindenmayer 1988 and Smith et al. 1991):

0.5, Not yet mature; 1, Mature living tree; 2, Mature living tree, dead or broken top; 3, Dead tree most branches still intact; 4, Dead tree with 0-25% of top broken off, branches stubs only; 5, Dead tree top 25-50% broken off; 6, Dead tree top 50-75% broken off; 7, Solid dead tree >75% broken off; 8, Hollow stump

3.2.3 LiDAR data and GIS products

LiDAR raw data

Discrete return airborne LiDAR data were acquired by RPS Group Plc in late 2015 and early 2016 using a Trimble AX60 laser sensor mounted on a fixed-wing aircraft. The aircraft was flown at 800 m above ground with flying speed of 62 m/s. The mean number of pulses per meter sent to ground was 2-4 pts/m with an average point spacing of 0.46 m. LiDAR data covered 513,322 hectares (ha) of Victorian Central Highlands (coverage can be seen in purple polygon in Figure 2-1). After filtering the landscape for ecological vegetation classes (EVCs) relevant to our study objectives, the final study area was 342,960 ha. This included 305,200 ha of wet or damp forest, 24,900 ha of riparian forest and 12,400 ha of rainforest. Within this area, 112,205 ha (32.8% of the total area) were burnt in the 2009 Black Saturday bushfire.

Climate, Forest Type and Disturbance Data

Spatial layers for EVCs, logging history, and fire history were sourced from the Victorian Department of Environment, Land, Water, and Planning (DELWP). We also included 19 bioclimatic variables in the analyses (see Table 3-1 for a full list). Bioclimatic variables for temperature developed by Stewart and Nitschke (2017) were used. Precipitation based BIOCLIM variables used were from Fedrigo et al. (2019). The resolution of bioclimate data was 250m. Kriging interpolation was used to change the resolution of bioclimate data into 100m.

LiDAR topographic metrics

A high-resolution (1m) digital elevation model (DEM) was derived from a LiDAR ground-based point cloud using FUSION/LDV Software (McGaughey 2009). From this DEM the slope, aspect, and slope of aspect (SOA) were generated using ArcGIS (v. 10.5). SOA represents the rate of change of the aspect in the horizontal direction (Zhou et al. 2018); therefore, the maximum value of SOA is located at topographic dividing lines such as ridges or gullies. A gully index was calculated from a high value of SOA and negative terrain surface. The negative terrain surface was created using ArcGIS focal statistic tool (“moving window”) to identify relatively lower surfaces within a specific neighborhood. The resolution of all LiDAR topographic metrics was 1ha.

LiDAR metrics of forest structure

LiDAR-derived metrics of forest structure were derived from height or height-related variables. The percentiles of stand height and strata density (percentage of LiDAR points between two heights) are commonly used LiDAR metrics (Goodwin et al. 2006, Hudak et al. 2008, Martinuzzi et al. 2009, Mitchell et al. 2012). For example, the 99th percentile is often used to represent maximum stand height rather than the maximum z-value of LiDAR points, thereby eliminating the influence of extreme outliers (Jenkins 2012). Strata density is often used to represent foliage density or connectivity within a vertical layer (Parker et al.

1995, Parker et al. 2004). The LiDAR structural metrics used in this study are listed in Table 3-1. The resolution of all LiDAR structural metrics was 1ha.

LiDAR overstorey and midstorey metrics

LiDAR overstorey and midstorey metrics were derived from the results of individual tree detection and delineation. For overstorey, the locations of individual tree tops, crown widths (CW), and tree height (HTs) can be determined using individual tree delineation (ITD) algorithm. These can then be aggregated into plot-level variables (1ha plot), such as the number of trees per hectare, mean crown width, and mean crown height. Individual trees were classified into four size classes based on crown width (see more in Chapter 2) based on crown width to represent different growth stages of the forest. We also calculated perimeter-to-area ratios for all crowns >8m wide. Crowns with large perimeter-to-area ratios indicated irregular crown forms. A live tree with a well-formed crown will have a relatively low line density and therefore a small perimeter-to-area ratio, whereas a standing dead snag with lots of dead branches will have high line density values. We used the line density of crown edges derived from the crown-edge detection step of ITD to compute a Stag Index (CLdens in Table 3-1) describing the irregularity of the crown shape. For the midstorey within each plot, LiDAR points were used to calculate the proportion of projection area of midstorey LiDAR points, a surrogate for midstorey density. The detection results for tree tops in the midstorey were used to determine the number of trees and the mean midstorey height within each plot.

In total, we considered 62 environmental variables to build the HBT density model (see Table 3-1 for a complete list and the abbreviations for each variable). They include vegetation class, year of most recent fire, year of most recent logging, 19 climate variables, seven topographic variables, and 33 plot structure variables (including nine for overstorey and three for midstorey).

Table 3-1 LiDAR metrics used to build classification model

Category	Variables	Short Name
Vegetation type	Ecological Vegetation Classes	EVC
Disturbance	Year of most recent Fire	Fire
	Year of most recent Logging	logging
Topography	Aspect	Aspect
	Cos of Aspect	CosAsp
	Gully Index/Creek Index	GullyIndex/CreekIndex
	Elevation	DEM
	Sin of Aspect	SinAsp
	Slope	Slope
	Slope of Aspect	SoA
Bioclimatic	Annual Mean Temperature	BIO01
	Mean Diurnal Range	BIO02
	Isothermality	BIO03
	Temperature Seasonality	BIO04
	Max Temperature of Warmest Month	BIO05
	Min Temperature of Coldest Month	BIO06
	Temperature Annual Range	BIO07
	Mean Temperature of Wettest Quarter	BIO08
	Mean Temperature of Driest Quarter	BIO09
	Mean Temperature of Warmest Quarter	BIO10
	Mean Temperature of Coldest Quarter	BIO11
	Annual Precipitation	BIO12
	Precipitation of Wettest Month	BIO13
	Precipitation of Driest Month	BIO14
	Precipitation Seasonality	BIO15
	Precipitation of Wettest Quarter	BIO16
	Precipitation of Driest Quarter	BIO17
	Precipitation of Warmest Quarter	BIO18
	Precipitation of Coldest Quarter	BIO19

Category	Variables	ShortName
Plot height (Statistical summary for height of height-normalized Lidar points)	max plot height	max
	mean plot height	mean
	Standard deviation of plot height	std
	p10: 10th percentile of height	p10
	p25: 25th percentile of height	p25
	p50: 50th percentile of height	p50
	p75: 75th percentile of height	p75
	p90: 90th percentile of height	p90
Vertical Canopy strata density	% of all returns between height strata 0.5 - 5m	S00
	% of all returns between height strata 5-10m	S05
	% of all returns between height strata 10-15m	S10
	% of all returns between height strata 15-20m	S15
	% of all returns between height strata 20-25m	S20
	% of all returns between height strata 25-30m	S25
	% of all returns between height strata 30-35m	S30
	% of all returns between height strata 35-40m	S35
	% of all returns between height strata 40-45m	S40
	% of all returns between height strata 45-50m	S45
	% of all returns between height strata 50-55m	S50
	% of all returns between height strata 55-60m	S55
	% of all returns between height strata 60-65m	S60
Overstorey	Average Overstorey tree crown width (CW) /plot	OvCWavg
	Total Overstorey tree CW/plot	OvCWsum
	Average big crowns height /plot	OvHtavg
	Number of level 1 CW /plot (8m < CW <= 10m)	OvN08t10
	Number of level 2 CW /plot (10m < CW <= 15m)	OvN10t15
	Number of level 3 CW /plot (15m < CW <= 20m)	OvN15t20
	Number of level 4 CW /plot (CW > 20m)	OvN20t30
	Number of Big Crowns /plot (CW > 8m)	OvNum
	Line density of edge of overstorey tree crown (Stag Index)	CLdens
Midstorey	MS Coverage (%)	MsCover
	Number of Midstorey trees /plot	MsNum
	Average Midstorey tree height /plot	MsHtavg

3.2.4 HBT density model building, model validation and uncertainty analysis

Random forest model to predict HBT density and variable importance

To estimate the number of HBTs across all form classes in a site, we developed a machine-learning approach based on a large set of structural, topographic, and environmental predictors (Table 3-1). Specifically, we used random forests (RF; also known as random decision forests), a supervised machine-learning method for classification or regression. Random Forest algorithms operate by constructing a large number of decision trees (i.e., a forest) (Breiman 2001), each of which represents a predicted class and a vote for that class. After each iteration, individual decision trees are combined using the rule of majority votes. When used in regression, the forest takes the average of predictions. Random Forest models have advantages in detecting nonlinear relationship and complex interactions, and are less prone to over-fitting (Martinuzzi et al. 2009). We used the ‘randomForest’ package in R (Liaw and Wiener 2002).

The RF algorithm also provides the relative importance of each predictor variable, by quantifying changes in classification error when the “out of bag” (OOB) data for that variable is altered (Martinuzzi et al. 2009, Shoemaker et al. 2018). For regression/ density model, variable importance is calculated by increase in mean squared error (IncMSE) and increase in node purity (IncNodePurity). We used the ‘measure_importance’ function from ‘randomForestExplainer’ package in R to generate four importance indices, including increase in mean squared error (IncMSE), increase in node purity (IncNodePurity), mean minimal depth (MinDepth) and p-value (Paluszynska and Biecek 2017).

An RF model can also provide partial dependence plots (PDP) that demonstrate the dependency of the average effect on a chosen variable. In this study, PDPs can graphically characterize relationships between individual predictor variables and the density of HBTs in each form class. PDPs were also used to determine whether a variable, on an overall average, had a positive or negative effect on the model (Friedman 2001). Meanwhile, to understand heterogeneous patterns of specific observations, we also generated Individual Conditional Expectation (ICE) plots to demonstrate the dependence of the prediction on an individual variables for each observations separately, resulting in one line per observation, compared to one line overall in partial dependence plots (PDP) (Goldstein et al. 2015). The R package ‘ICEbox’ was used to create ICE plots (Goldstein et al. 2017).

Block cross-validation validation and significant variables selection

We used 5-fold block cross-validation to evaluate model performance and systematically compare models of varying complexity to choose the most robust model with the fewest variables (i.e., the most parsimonious model). Conventional (random) cross-validation approaches assume that observations are independent (Trachsel and Telford 2016). However, ecological data are often spatial autocorrelated (Legendre 1993). If training and testing datasets were not spatially separated for species distribution modelling (SDM), performance statistics might be over-optimistic (Roberts et al. 2017). The variogram range method has been

used to define the optimal separation distance between training and testing sets (Valavi et al. 2019). The range was estimated using the empirical semi-variograms, and the range over which residuals are approximately independent could be used as block size for block cross-validation (Valavi et al. 2019). The semivariance variograms of the density of each HBT classes were shown in Figure A3 1 in Appendices 3. The maximum spatial autocorrelation range of HBTs was 6km and maximum range of vegetation connectivity index was 8km (Figure A4 1 in chapter4). The block size was select to be 9km in this study.

The 9km×9km spatial blocks were split into five folds of equal size, while the field observation plots located in each block was also split into five groups. The spatial distribution of blocks for each fold was shown in Figure 2-1b. One group was withheld for final validation test, while the other four groups (training sets) were used to develop the model. The training sets were repeated four times with each of four folds being withheld once as test set for model selection. Model performance indicators were gathered from test results for the four runs, and the mean values of each indicator were considered for model validation and comparison (Maroco et al. 2011). Root mean squared error (RMSE), mean absolute error (MAE), and residual standard error (RSE) were calculated for each test set to evaluate model performance.

All 62 variables (Table 3-1) were considered for inclusion in the RF analyses to estimate HBT density. The first step of the analysis was variable selection, which involved grouping and reducing the number of potential predictors. We grouped predictor variables that had Pearson correlations >0.8. Only one variable was selected to represent each group based on lowest RMSE performed with that variable in the test set for block validation. For example, the 19 climate variables were reduced to three variables that broadly represented temperature, precipitation, and diurnal range of temperature. The variable reduction groupings are shown in Table A3 1 in the Appendices.

Variable grouping reduced the total number of variables to 40. The number of variables was further reduced based on the rank of importance of each predictor variable, starting with the least important. We used mixed variable importance index ($\text{MixedVI} = \text{IncMSE} \times \text{IncNodePurity} / \text{MinDepth} / \text{p-value}$) as the metric representing the importance of each variable. The combination of variables with the lowest RMSE for test sets was selected to be the final prediction model.

Model validation, calibration and model uncertainties

The machine-learning algorithm for estimating HBTs had some calibration issues because the predictions from the random forest algorithm are a weighted average of a subset of the data, and tend to be biased away from the extremes (Steele et al. 2018). Further analyses, such as regression models on the calibrated model (Boström 2008, Dankowski and Ziegler 2016) could improve the random forest estimates. The final HBT density model selected based on four training sets were applied to final validation test set to validate the model, and applied to the whole dataset to generate calibrated HBT density. We used generalized additive

model (GAM) to fit predicted outcomes with observations. The standard error estimates are returned for each prediction to estimate 95% confidence intervals.

3.3 Results

3.3.1 Characteristics of each HBT class based on field measurements

There were 1445 HBTs in the 422 ARI sites (mean = 3.4 trees per site). The histogram of the number of all HBT classes per ha is shown in (Figure 3-3). The number of HBTs per site varied from 0 to 31, but the data were heavily skewed because most sites had few HBTs—there were no HBTs on 113 sites and only 1 HBT on 78 sites. The numbers of survey standard and ecological HBTs in each form class are shown in Table 3-2. The number of ecological HBTs is larger than the number of survey standard HBTs. Notably, for form class 7 and 8 (HBT7-8) there are three times as many ecological HBTs as survey standard HBTs.

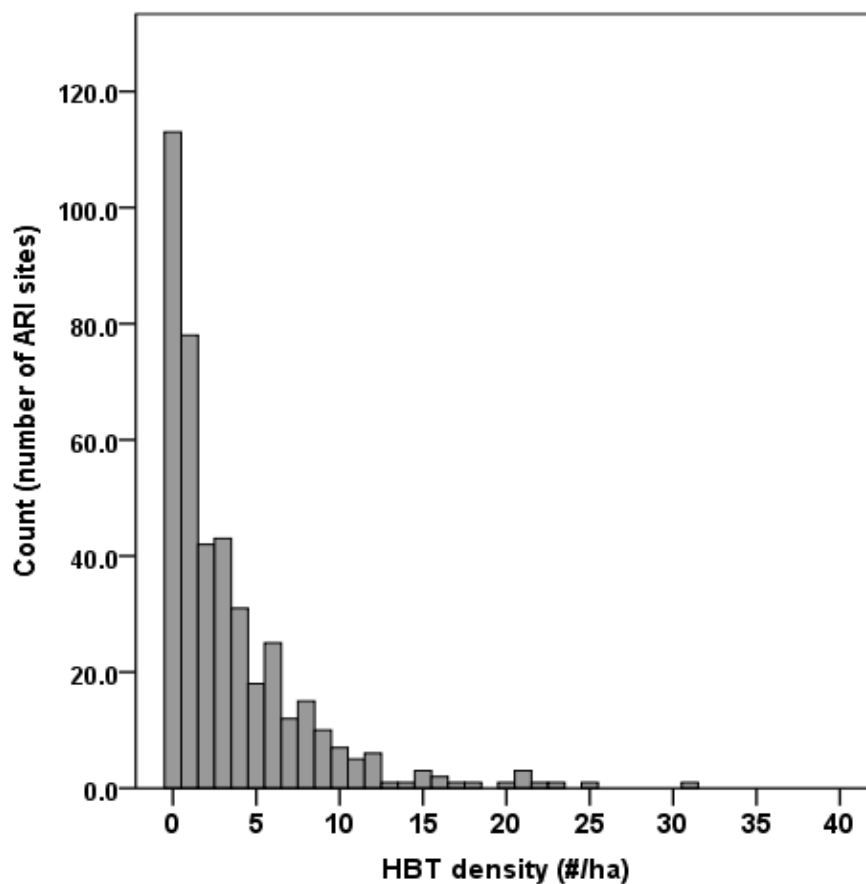


Figure 3-3 The number of all HBTs per ha distributed in 422 ARI sites

Table 3-2 The number of survey standard and ecological HBTs of each form in 422 ARI HBT assessment sites

Form	Ecological HBTs	Survey Standard HBTs	All HBTs
0.5	151	1	152
1	155	118	273
2	102	90	192
3	71	61	132
4	77	23	100
5	45	42	87
6	110	64	174
7	165	57	222
8	61	18	79
3-8	30	2	32
Uncertain	2	0	2
All	969	476	1445

3.3.2 HBT density model and validation

The random forest (RF) algorithm was used to estimate site level densities of HBTs for all form classes. The relationship between HBT density estimates based on the RF algorithm and field-based estimates of HBT density had RMSE ranging from 1.64 to 2.41 for different HBT form classes (Table 3-3). According to the relative squared error (RSE), the prediction model of live HBT (HBT0t2) was better than the prediction models of dead HBT (HBT3t4 and HBT5t8). Details of the model validation results for each HBT form class are shown in Figure 3-4. The RF algorithm predictions of HBT density tended to overestimate true HBT densities, when $\text{HBT} < 2 \text{ ha}^{-1}$, while underestimate true HBT when $\text{HBT} \geq 2 \text{ ha}^{-1}$. Thus, we calibrated the model predictions using GAM model to be the final estimates of HBT density.

Table 3-3 The validation results of the random forest model predictions for HBT density of each HBT classes, predictions of HBT density are the predictions in final validation test set

Form	RMSE	MAE	RSE
HBT0t2	2.413	1.597	0.877
HBT3t4	1.822	0.847	1.081
HBT5t8	1.641	1.266	1.225

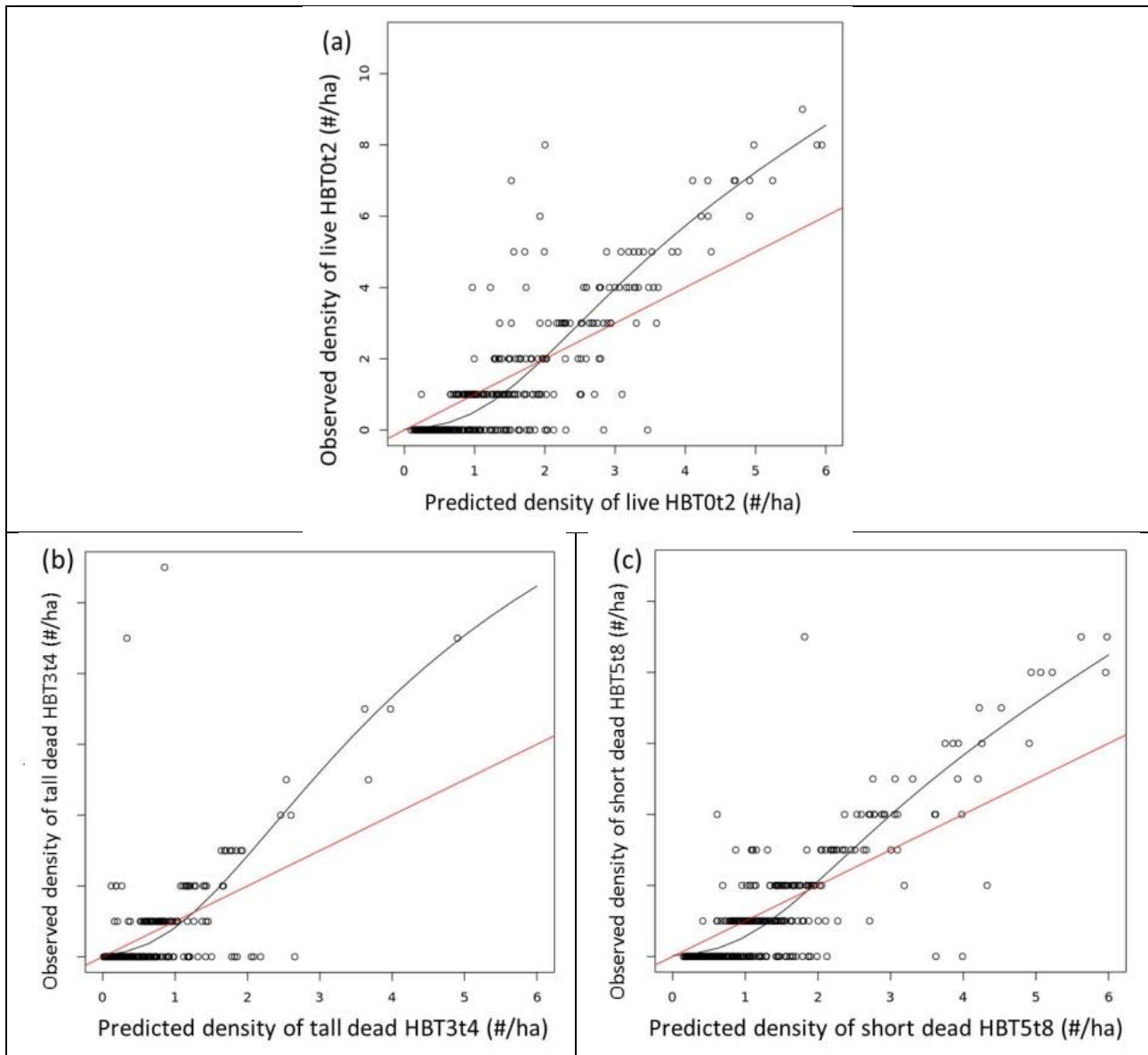


Figure 3-4 Calibrated results of each HBTs classes for all observations: (a) the density of live HBT0t2 (b) the density of tall dead HBT3t4 and (c) the density of short dead HBT5t8. The red line is the 1:1 line of estimates to observations. The black line is the model fit.

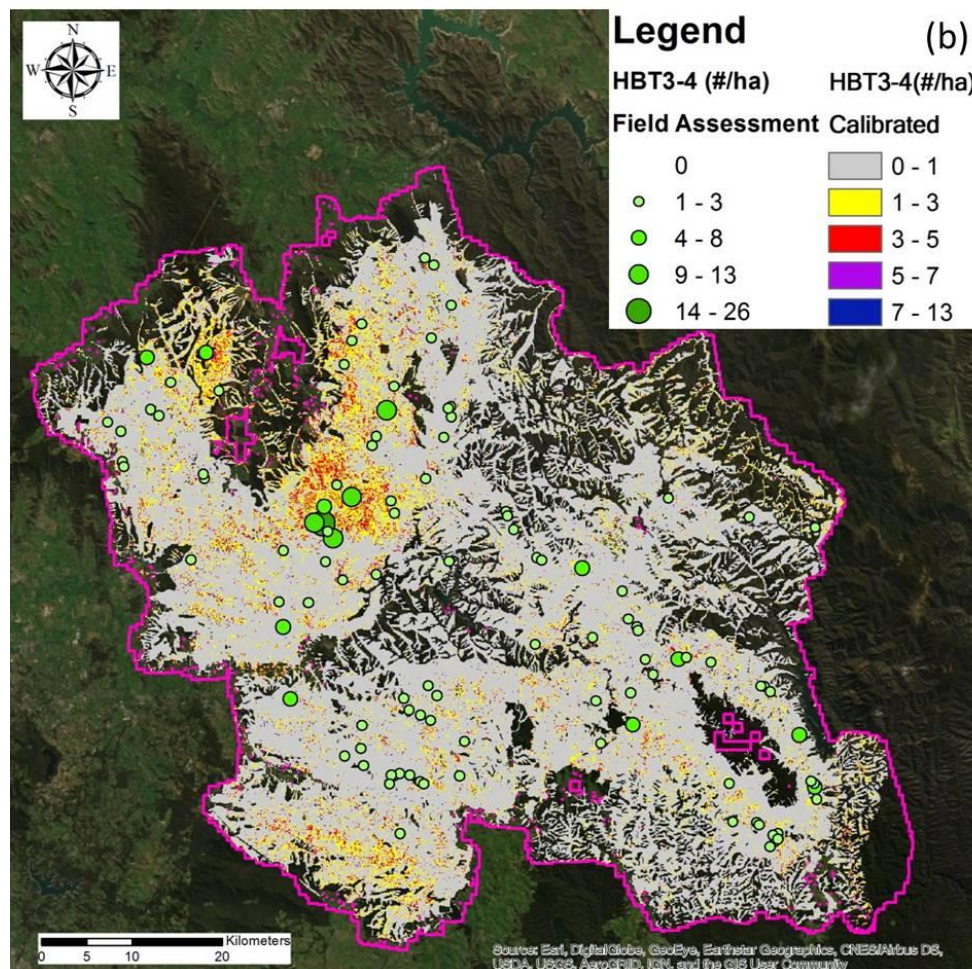
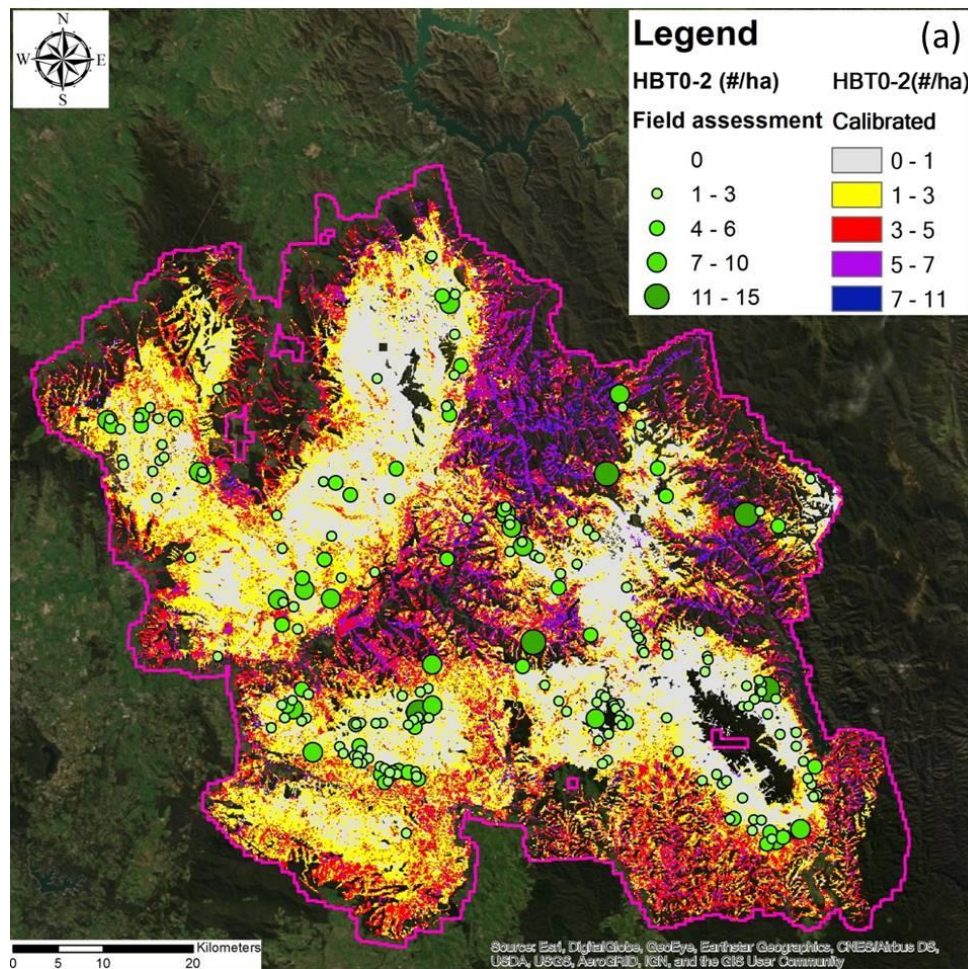
3.3.3 HBT density distribution pattern across landscape

Based on the RF prediction model there are 1,519,000 HBTs (95%CI: 1,306,000 –1,730,000) across all form classes across the 342,960 ha of the Central Highlands included in this study. That is roughly equivalent to 4.4 HBTs per ha (Table 3-4). The estimated number of HBTs (and 95% CI) for each HBT form class, by vegetation class and tenure is provided in Table A3 2 in the Appendices. Riparian areas have ~1 more HBT per ha than other vegetation classes, especially for the live HBTs (HBT0t2). When all HBT form classes are pooled, National Parks and Special Management Zone (SPZ) have higher densities of HBTs than State Forest General Management Zones (GMZ). The spatial distributions of HBT density across the area of the Central Highlands included in this study are shown in Figure 3-5.

Table 3-4 The total number and mean density of HBTs in each HBT class across different vegetation classes and forest management zones in Victoria's Central Highland. GMZ, SMZ, and SPZ are different management zones within Victoria's State Forests (see text for details). HBT refers to all hollow-bearing trees, SS refers to only survey standard HBTs, and Ecol refers to HBTs that do not meet the survey standard (see text for explanation).

Category	Area	HBT0t2	HBT3t4	HBT5t8	All HBT	HBT0t2	HBT3t4	HBT5t8	All HBT
	(ha)	sum	sum	sum	sum	mean (#/ha)	mean (#/ha)	mean (#/ha)	mean (#/ha)
Total	342,960	833,000	244,000	442,000	1,519,000	2.4	0.7	1.3	4.4
Wet or Damp forests	305,599	726,000	210,000	396,000	1,332,000	2.4	0.7	1.3	4.4
Riparian area	24,875	88,000	22,000	32,000	142,000	3.5	0.9	1.3	5.7
Rainforests	12,486	19,000	11,000	14,000	44,000	1.5	0.9	1.1	3.5
GMZ	162,461	376,000	112,000	198,000	686,000	2.3	0.7	1.2	4.2
Parks	81,625	181,000	63,000	119,000	363,000	2.2	0.8	1.5	4.4
SMZ	15,252	35,000	13,000	18,000	66,000	2.3	0.9	1.2	4.3
SPZ	45,926	111,000	30,000	60,000	201,000	2.4	0.7	1.3	4.4

*GMZ: general management zone; SMZ: special management zone; SPZ: special protection zone



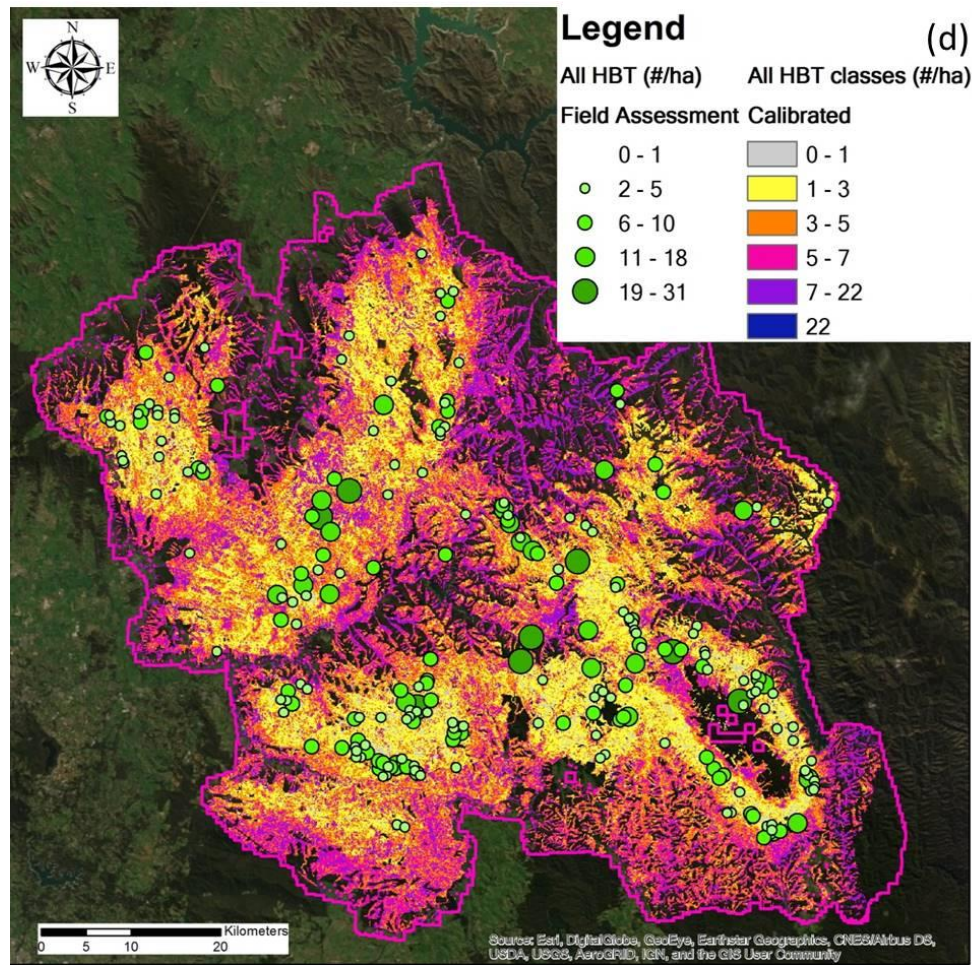
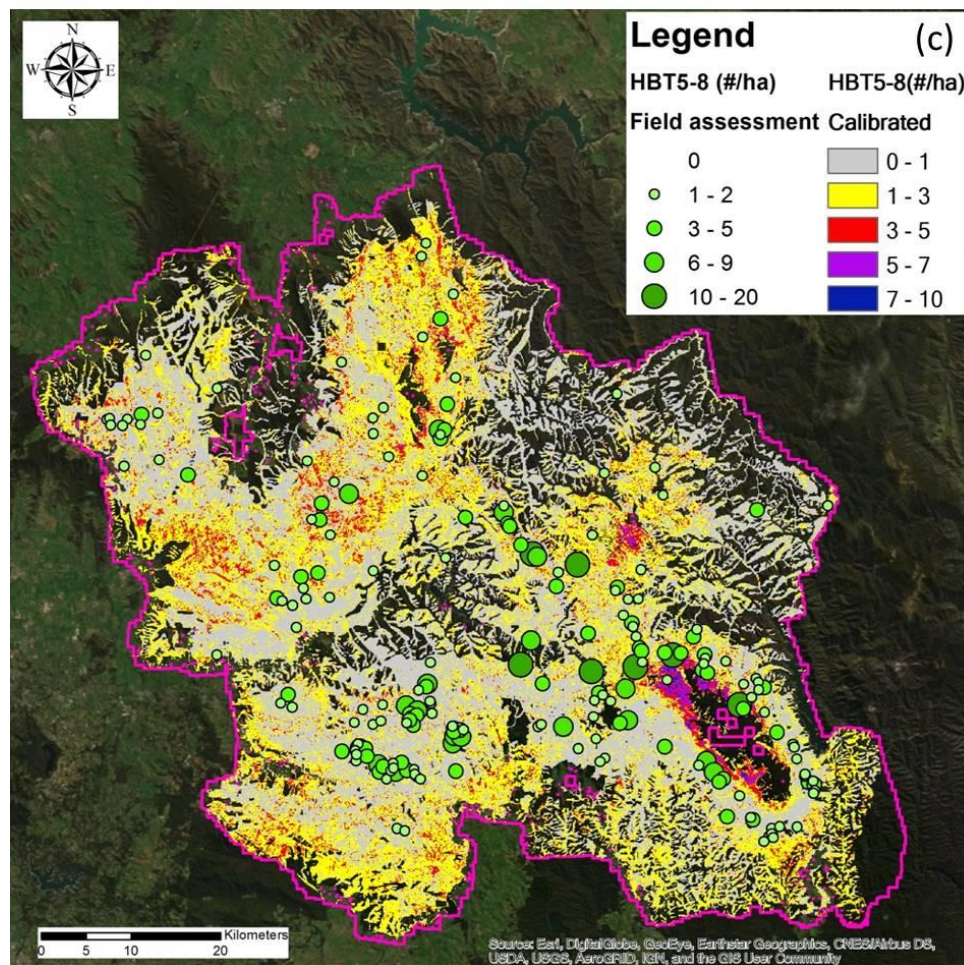


Figure 3-5 Distribution map of HBT density estimated from the plot-level RF-based model and assessed by field data across Victoria's Central Highlands of a) live HBT (HBT0t2); b) HBT3t4; c) HBT5-8; and d) all HBT classes

3.3.4 Predictor variables for each HBT class

The final RF models that we used to estimate HBT densities included 27 structural, topographic, or environmental variables from the original set of 62 variables. The final models for the various form classes used different combinations of these variables, which were 14 variables for live HBT (HBT0t2), 6 variables for tall dead HBT (HBT3t4) and 13 variables for short dead HBT (HBT5t8). The importance of each predictor variable across the HBT models is shown in Table 3-5 and Figure A3 3.

Table 3-5 Variable importance indices (mean minimal depth, increase in mean squared error and increase in node purity, p-value and mixed variable importance index) of significant predictor variables for different HBT classes.

HBT	Important Variables	Short Name	Mean min depth	MSE increase	Node purity increase	P-value	mixed VI*
HBT0t2	Average overstorey tree crown width (cw)	ovcwavg	2.57	0.06	179.9	0.00	5.84E+06
	Sin of Aspect	sinasp	3.72	0.13	107.7	0.00	2,319
	Slope	slope	3.40	0.11	134.3	0.01	547
	Precipitation of Driest Quarter	bio17	2.87	0.54	158.0	0.14	212
	Cos of Aspect	cosasp	4.23	0.07	87.2	0.02	65.0
	Isothermality	bio03	3.49	0.27	124.7	0.17	54.7
	Number of big crowns per ha (with crown width >15m and <= 20m)	ovn15t20	3.07	0.48	128.5	1.00	20.0
	Stag Index	cldens	3.61	0.06	126.6	0.24	9.63
	strata density between 15m-20m	s15	3.82	0.13	107.5	0.39	9.29
	Mean Temperature of Driest Quarter	bio09	4.12	0.25	88.9	1.00	5.49
	strata density between 20m-25m	s20	3.95	0.16	101.6	0.99	4.26
	Temperature Annual Range	bio07	3.53	0.09	130.3	0.83	4.20
	Aspect	aspect	4.30	0.08	86.7	0.97	1.59
	strata density between 30m-35m	s30	3.05	-0.06	161.9	0.80	-3.79
HBT3t4	Number of midstorey trees per ha	msnum	2.10	0.57	191.7	0.02	2,190
	slope of aspect	soa	1.93	0.28	193.0	0.03	1,100
	strata density between 5m-10m	s05	2.62	0.42	163.1	0.86	31.0
	Average overstorey tree height	ovhtavg	2.46	0.17	168.0	0.71	16.6
	Aspect	aspect	2.21	0.08	171.1	0.96	6.32
	25th percentile of plot height	p25	2.29	-0.10	197.0	0.73	-11.8
HBT5t8	Mean Temperature of Warmest Quarter	bio10	2.93	0.16	142.9	0.00	1,552
	strata density between 5m-10m	s05	3.66	0.10	96.3	0.01	297
	Aspect	aspect	3.06	0.08	106.3	0.02	128
	Stag Index	cldens	3.57	0.27	130.8	0.34	29.5
	strata density between 0m-5m	s00	3.51	0.30	124.9	0.39	28.1
	Average midstorey tree height	mshtavg	3.25	0.08	104.7	0.26	10.1
	Precipitation of Coldest Quarter	bio19	3.35	0.22	108.4	0.89	7.95
	strata density between 10m-15m	s10	3.92	0.11	100.0	0.40	7.25
	strata density between 40m-45m	s40	3.29	0.22	105.4	0.98	7.21
	midstorey coverage	mscover	3.28	0.16	112.6	0.88	6.16
	strata density between 35m-40m	s35	4.04	0.08	96.2	0.99	1.91
	slope of aspect	soa	3.85	0.00	99.4	0.66	0.02
	Cos of Aspect	cosasp	4.35	-0.01	80.5	0.95	-0.15

* The mixed variable importance index was calculated by $\text{IncMSE} \times \text{IncNodePurity} / \text{MinDepth} / \text{p-value}$

The most important variable to predict the density of live HBT (HBT0t2) was the average overstorey tree crown width, which was generated by individual tree delineation approaches in chapter 2. The density of midstorey trees was the most significant variable to identify tall dead HBT (HBT3t4). The density of short dead HBT (HBT5t8) was strongly associated with bioclimate data, especially correlated to mean temperature of warmest quarter. Midstorey structural metrics were not useful to estimate the density of live HBT, while overstorey metrics were not important variables to short dead HBT. Bioclimate data have less impact on the abundance of tall dead HBT.

Here we describe the association of different HBT form classes with specific predictor variables. The individual panels in Figure 3-6 to Figure 3-8 show the relationship between different predictor variables and various HBT form classes. The y-axes represent the number of HBTs per ha for each HBT class.

Climate

Different components of annual temperature were important predictors for various HBT form classes. For example, live HBT (HBT0t2) were associated with warm areas, whereas short dead HBT (HBT5t8) were more closely associated with cooler areas (Figure 3-6). The lowest densities of HBT5t8 occurred where the mean temperature of the warmest quarter was $>15^{\circ}\text{C}$. Temperature was not a significant predictor of HBT3t4 abundance. Precipitation was a significant predictor of HBT0t2 and HBT5t8 abundance (Figure 3-6). HBT0t2 were associated with sites that received relatively little precipitation during the driest quarter, whereas HBT5t8 were associated with higher precipitation sites. When the precipitation of the driest quarter was >220 mm, the number of HBT0t2 per ha was <1.5 .

Topography

Topographic features of the sites had some influence on HBT density in various form classes. Live HBTs (HBT0t2) were associated with steep slopes (particularly ~ 30 degrees) (Figure 3-7a). The spatial distribution of slope values is shown in Figure A3 2 in Appendices 3 for a single small area within the Central Highlands and for the whole Central Highlands. HBT3t4 and HBT5t8 densities were all positively associated with slope of aspect (i.e., higher density of HBT3t4 and HBT5t8 is located at ridges or gullies) (Figure 3-7b).

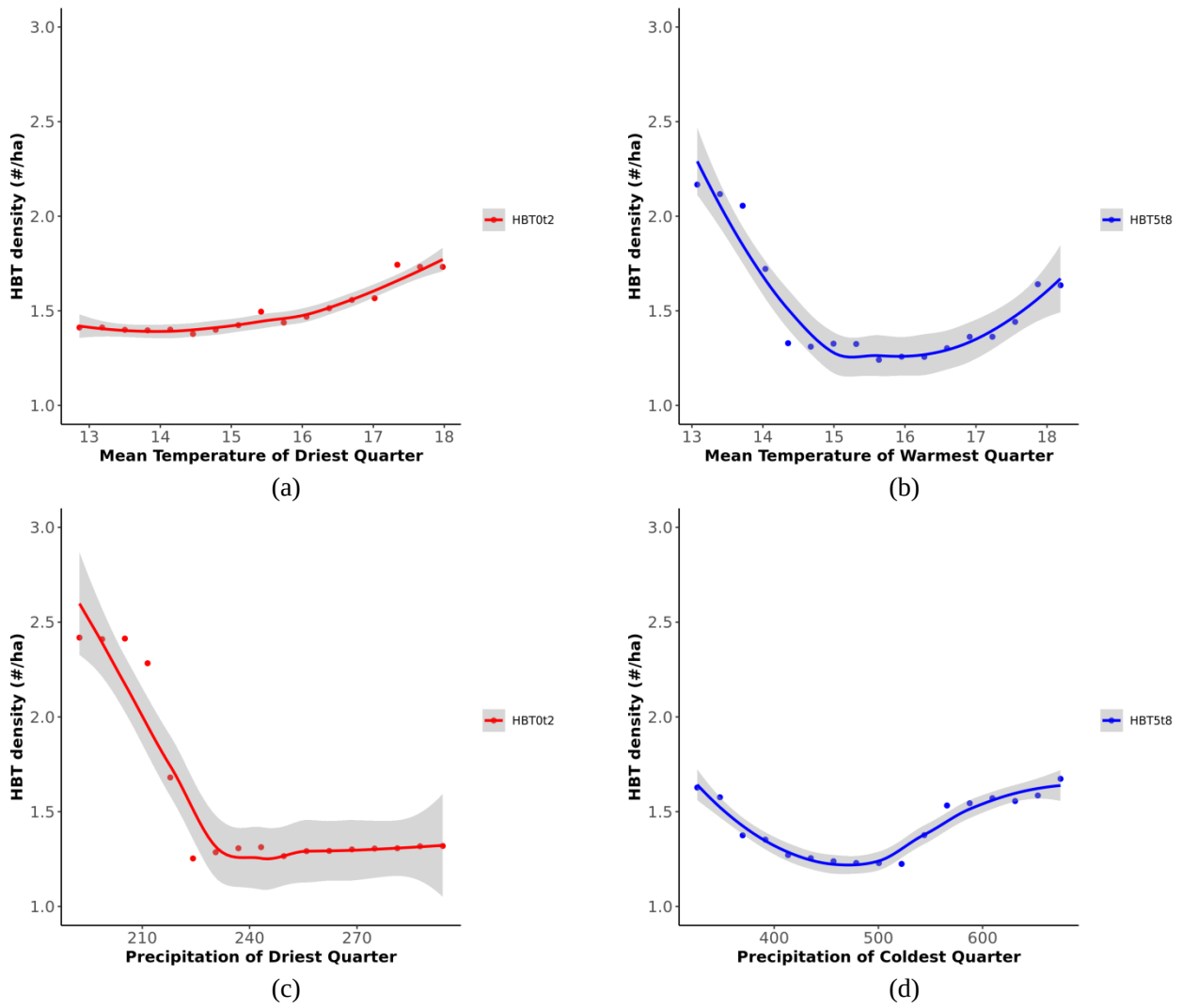


Figure 3-6 Partial dependence relationships between climatic variables and HBT density: (a) Mean temperature of driest quarter, (b) Mean temperature of warmest quarter, (c) Precipitation of driest quarter and (d) Precipitation of coldest quarter

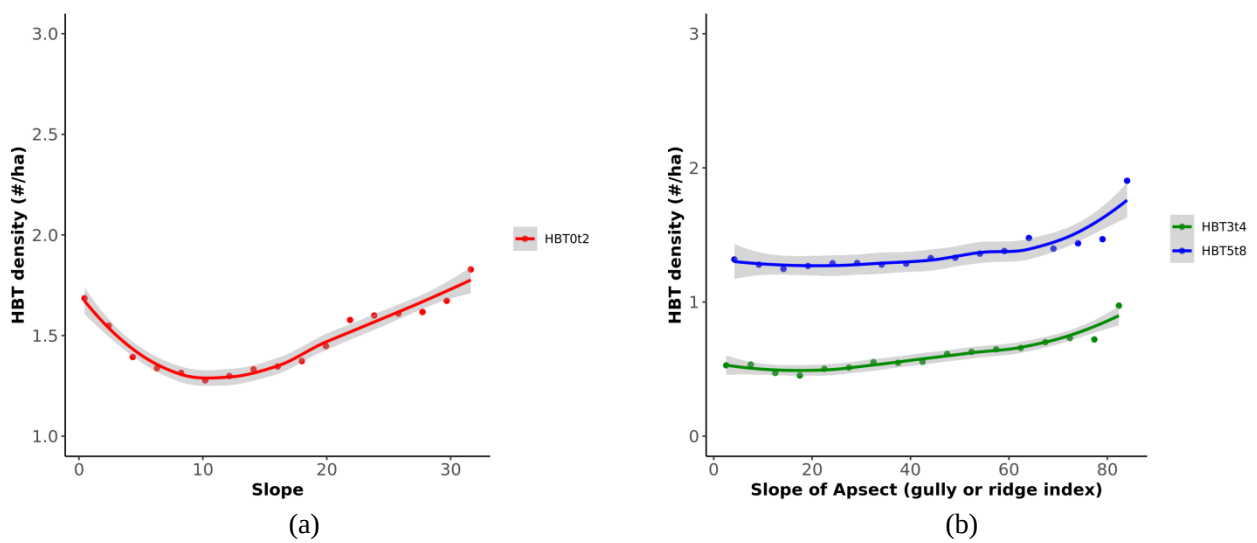


Figure 3-7 Partial dependence relationships between topographic variables and HBT density: (a) Slope, and (b) slope of aspect (soa, higher value of soa is located at topographic dividing lines such as ridges or gullies.)

Logging

Partial dependence relationships of random forest regression model, logging and fire effects did not have significant impact on the abundance of HBTs. However, when using spatial distance analysis at landscape-level, the predicted density of HBT0t2 increased notably when the study plots were >250 m from the edge the logging coupes (Figure 3-8).

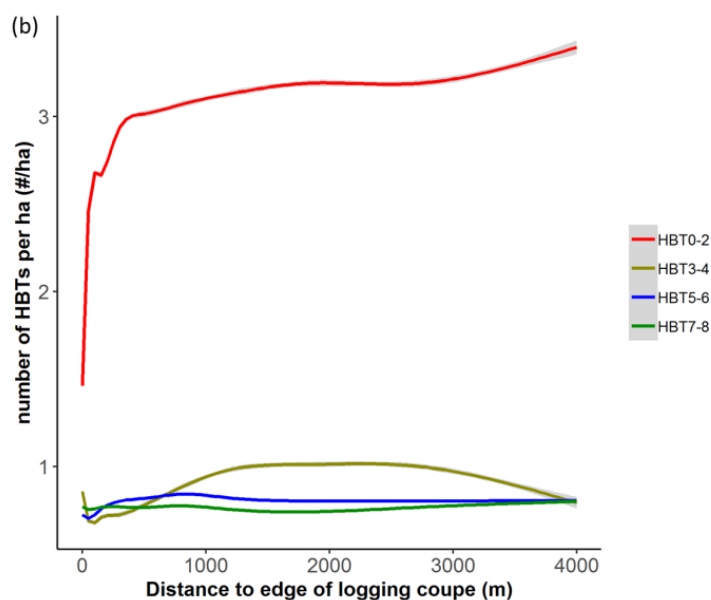


Figure 3-8 The number of each HBT classes per ha changes with distance to the edge of logging coupes, using spatial distance analysis at landscape-level

Forest Structure

Overstorey crown structure (generated in Chapter 2) was a more important predictor of live HBT (HBT0t2) density than dead HBT (HBT3t4 and HBT5t8) density (Figure 3-9a). Forest stands with large mean crown widths (i.e., >10m) and three or more very large crowns (i.e., >15m) were more likely to have high densities of live HBTs. Taller mean canopy height of dominant crowns and the less density of midstorey trees were important predictors of HBT3t4. High densities of HBT5t8 were associated with higher midstorey coverage and taller midstorey trees.

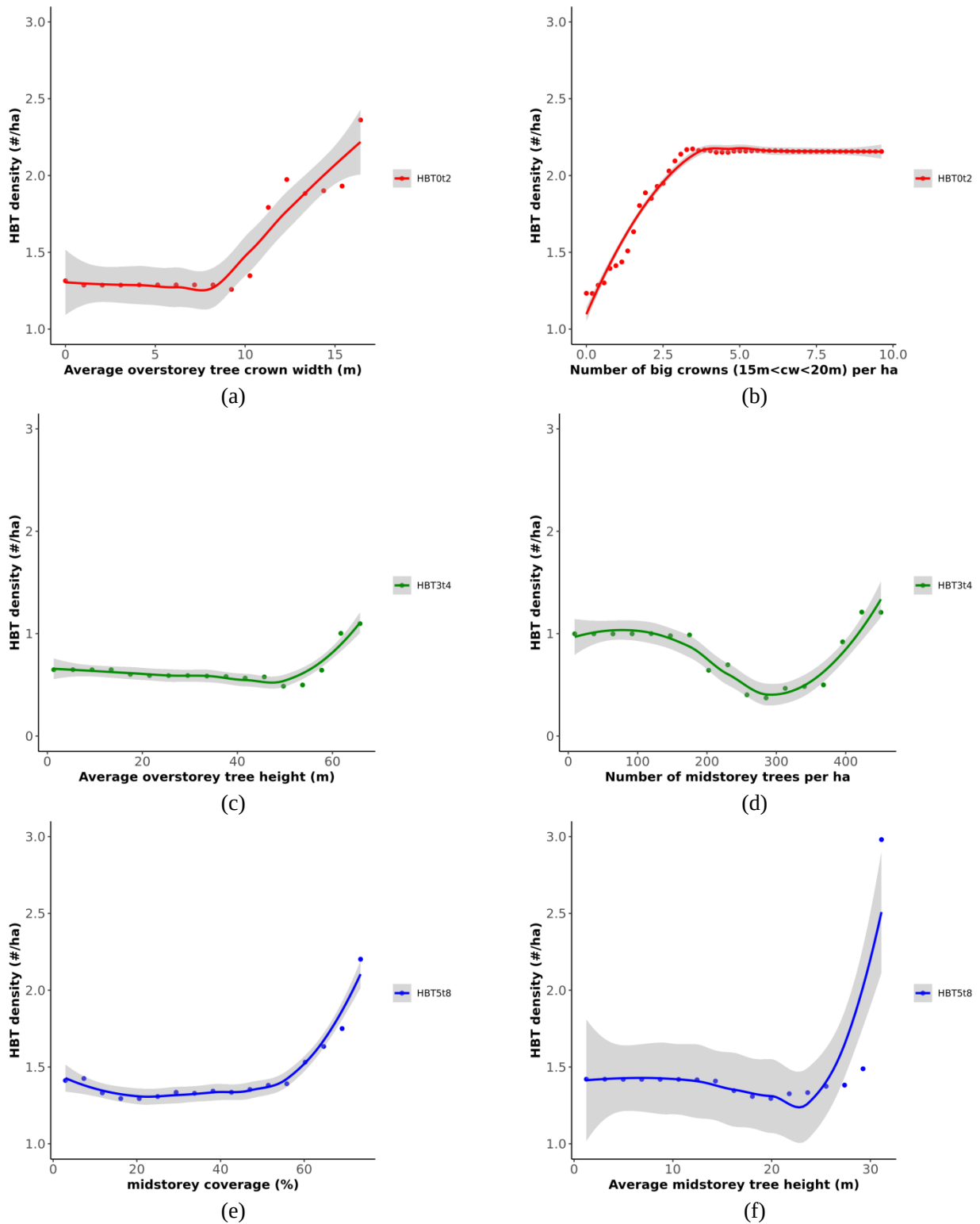


Figure 3-9 Partial dependence relationships between overstorey and midstorey crown attributes and HBT density: (a) Mean crown width of overstorey per ha, (b) Number of big crowns (15m<cw<20m) per ha, (c) Number of big crowns (8m<cw<10m) per ha, (d) Number of midstorey trees per ha, (e) The coverage (%) of midstorey, and (f) Mean total height of overstorey per ha

Vertical Canopy Structure

We calculated standardized z-scores for density in all 5-m vertical strata slices and the mean standardized density for each stratum (Figure 3-10). The mean standardized strata density reflects different vertical distribution patterns of foliage density and may differ between plots with and without HBTs. Each HBT form class was associated with a particular vertical canopy profile. For example, HBT3t4 was associated with a high density of ground-layer vegetation (stratum height <5m), whereas HBT0t2 and HBT7t8 were associated with little to no ground-layer vegetation. In contrast, HBT3t4 was associated with less dense midstories (stratum height 10-30m), while HBT0t2 and HBT7t8 were associated with high midstorey density. However, sites with abundant HBT0t2 had relatively high midstorey canopy heights (15-20m), while HBT7t8 was associated with relatively low midstorey canopy heights (10-15m). The earlier stages of HBTs (HBT0t2 and HBT3t4) were associated with taller mean overstorey canopy height (>60m), whereas the more senescent and degrading HBT classes (HBT5t8) were associated with lower mean overstorey canopy height (<55m).

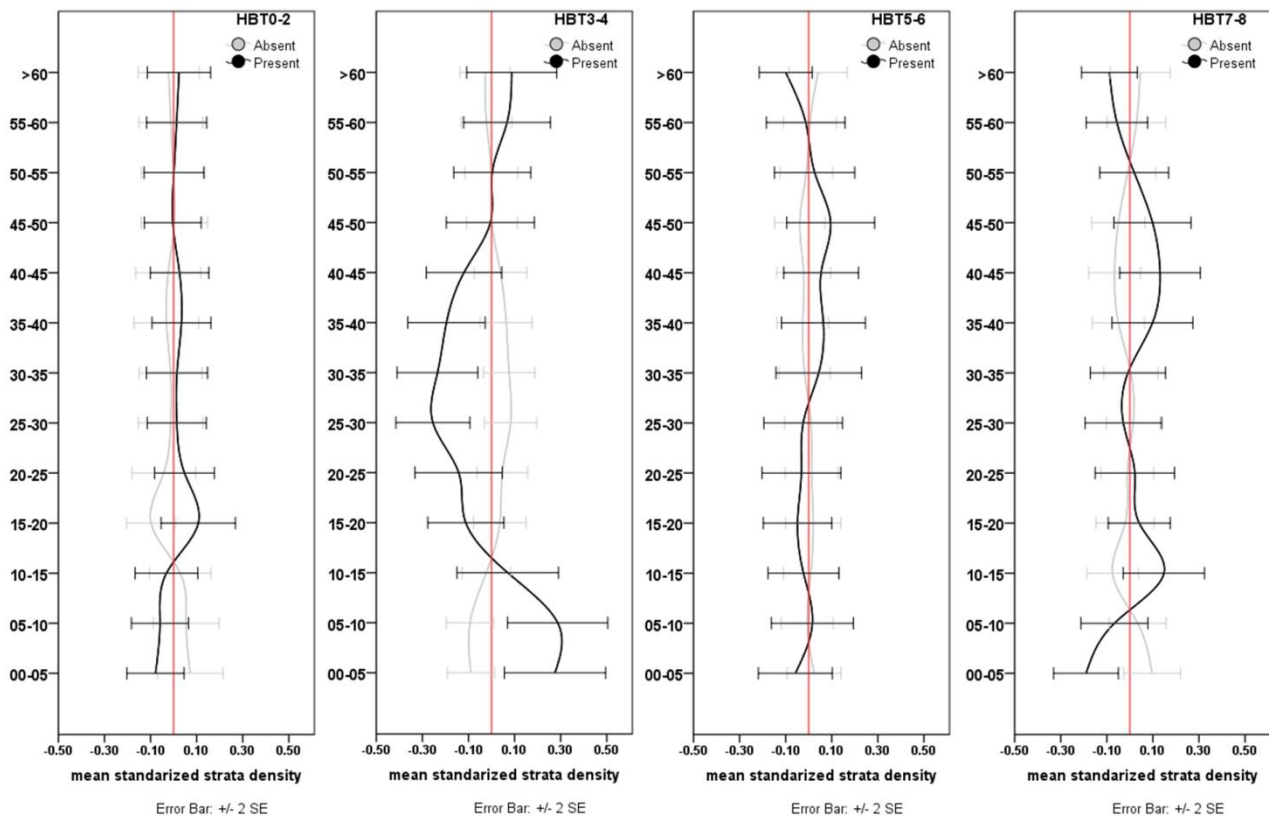


Figure 3-10 Standardized vertical strata densities for each HBT form class. This provides an indication of variation in forest structure associated with each HBT form class. The black line connects the mean standardized values in each height class for plots with HBTs present; the grey line connects these values for plots in which HBTs were absent.

When we consider all of the predictor variables and their relationships with HBT presence/absence, these results suggest that live HBTs (HBT0t2) were most likely to occur in unlogged forests with high densities of tall trees with large crowns and relatively low midstorey density. They also were associated with drier sites and steeper slopes. HBT3t4 were most likely to occur in taller forest stands with thick ground-layer vegetation and relatively little vegetation in the midstorey. They were not strongly associated with any climatic or topographic factors. HBT5t8 were associated with cool, flat areas, stands with relatively more

large-crowned overstorey trees, and more midstorey than ground-layer vegetation.

3.4 Discussion

Hollow-bearing trees (HBTs) are a key structural feature of many forested ecosystems around the world (Lindenmayer et al. 2016b). They are typically associated with older forests due to the length of time required for hollows to develop from branch abscission, internal decay, and stem growth. However, due to a range of threats, including various natural and human-induced disturbances, old forests are increasingly rare within forested landscapes and HBTs are increasingly rare within forest stands (Lindenmayer et al. 2012b). The abundance of HBTs has been reported to be declining rapidly in Victorian Central Highlands (Lindenmayer et al. 1997, Lindenmayer et al. 2013, Blair et al. 2018). Burns et al. (2015) predicted that by 2040, the populations of HBTs will be less than 10% of what they were in 1997. Bushfires are a major threat because they accelerate the loss of HBTs hollow-bearing trees and kill older regrowth forests, which support large trees that would replace collapsing HBTs over coming decades (Lindenmayer et al. 1997, Lindenmayer et al. 2013). The predicted loss of HBTs and lack of recruitment represent significant threats to fauna that depend on hollows for nesting and shelter (Lindenmayer and Wood 2010, Lindenmayer and Sato 2018). A major challenge for managers and agencies responsible for forested landscapes is the difficulty of determining how many HBTs actually occur within these landscapes and their spatial distribution. The lack of an inventory of HBTs over large spatial scales limits the ability of management agencies to prioritise areas for conservation, identify areas suitable for resource extraction, and develop long-term, strategic plans that balance social, economic, and biodiversity needs. Most surveys of HBTs are ground-based, which limits their extent, repeatability, and extrapolability. Developing methods for efficiently estimating HBT densities over large spatial scales would allow for a better understanding of the scale and distribution of HBTs. The estimation of HBT densities by form class at large spatial scales provides a snapshot of HBT population structure from which changes in HBT demography can be estimated over time and space. When combined these data can provide the foundations for more effective long-term monitoring programs and robust predictions of changes in habitat for hollow-dependent fauna.

We used LiDAR-based remote-sensing data to develop algorithms and workflows to estimate the number of HBTs in the Central Highlands of Victoria. This involved the development of structure metrics of midstorey and large overstorey using individual tree crown delineation in closed forest canopies (see Chapter 2) and the integration of existing machine-learning tools for complex datasets. We developed random forest models for estimating the abundance of HBTs and validated them against hundreds of ground-based plots that systematically sampled all HBTs in all form classes. This provided a unique and extensive empirical dataset for developing and testing our HBT prediction models. At a landscape level, our approach estimated between 1.3 and 1.7 million HBT with 4.4 HBT ha⁻¹ on average. The average of 4.4 HBT ha⁻¹ is substantially higher than those of Burns et al. (2015) who estimated 3.8 HBT ha⁻¹. Burns et al. (2015) and Lindenmayer and Sato (2018) predicted that the number of HBTs in the landscape will decline to between 0.29-0.82 ha⁻¹ by 2067

due to the ongoing collapse (and lack of recruitment) of HBTs. In particular, they expressed concern about the dead HBT (form classes 3-8), which are collapsing at a greater rate than live HBT (form classes 0-2) (Lindenmayer and Wood 2010). Live HBT were found to have collapsed by 9% over a 14-year period, less than 1% per annum (Lindenmayer and Wood 2010). Our estimates of live HBT were 2.4 (± 0.5) live HBT ha⁻¹. Given the collapse rate for live HBT calculated by Lindenmayer and Wood (2010), this would amount to 1.6 (± 0.3) live HBT ha⁻¹ by 2067. These estimates are 2 to 7 times higher than those estimated by Burns et al. (2015) and Lindenmayer and Sato (2018).

The discrepancies in these results likely arise from differences in methodological approaches. Specifically, our approach was based on predictive models driven by high-resolution, spatially explicit, empirical data across the entire Central Highlands landscape, whereas the estimates of Burns et al. (2015) and Lindenmayer and Sato (2018) are derived from extrapolations from a small, but putatively representative, set of study plots (see (Dietze 2017) for a discussion of prediction vs extrapolation). We used directly measured structural and environmental features of the forest and landscape across the whole landscape. Such a discrepancy in scales has the ability to modify any biases in the survey plot design. Our approach to quantifying landscape structure and topography provides a rich resource for making empirical predictions at the landscape scale. In contrast, the extrapolative approach depends on the assumption that the network of study plots upon which it is based is representative of the full range of variability within the landscape. While these plot-based studies have provided important insights into temporal dynamics of HBT dynamics at small spatial scales, they are limited in their ability to capture the spatial dynamics of a landscape. Extrapolating ecological dynamics from a study area of ~440 ha to a landscape of ~340,000 ha that is characterized by such complex topography, environmental conditions, and disturbance history without accounting for this complexity will underestimate the full range of variability within the landscape. The shortcomings of extrapolation are likely to be magnified by stratifying a landscape using predetermined predictor variables (see Burns et al. 2015; Lindenmayer et al. 2016) and is particularly problematic in complex forest landscapes. For example, Kasel et al. (2017) found that time since last fire based on three fire history classes explained only 2% of beta-diversity in the Central Highlands region while variability in climate, topography, and forest structure explained up to 50% species of turnover. Pulkkinen et al. (2018) found that post-stratification reduced the variance of estimators of forest inventory variables using remote sensing data by 30-80% compared to approaches that used pre-stratified classes across the entire national forest inventory network of Switzerland. Our approach of using Random Forest classification tree modelling for post-stratification of the forest landscape into sub-strata based on model data rather than pre-determined stratification of forest types is a more robust approach for reducing model variance and providing credible model predictions across large landscapes (Pulkkinen et al. 2018). Directly incorporating spatial variability in landscape-scale predictors of forest structure, climate, and topography through the use of high-resolution remotely sensed data and machine learning is therefore likely to provide more realistic and more nuanced estimates of HBT abundance and their variability across the landscape.

Our analyses of the factors influencing the distribution of HBTs were consistent with previous findings. For example, like Lindenmayer et al. (2016) we found that live HBT (HBT0t2) were more likely to be found in unlogged areas. We also found a non-linear association between HBT abundance and slope, with greater abundance of HBT on flat and steep sites depending on form class. Lindenmayer et al. (2016) found that live HBT and HBT suitable for Leadbeater's Possum are more likely to be found on sites with a high Topographic Wetness Index, which is consistent with our finding of increased HBT0t2 and HBT5t8 in riparian areas. These areas are typically excluded from timber harvesting due to Code of Forest Practices restrictions on harvesting in riparian areas (State of Victoria Department of Environment and Primary Industries 2014). These areas also occur in sheltered positions that may act as fire refugia due to the moderating effect of topography and mesic vegetation on fire severity (Berry et al. 2015). The greater abundance of live HBTs on steep slopes aligns with areas within the landscape that are excluded from timber harvesting due to Code of Forest Practices restrictions on harvesting on slopes that exceed 30° slope (Victorian Department of Environment and Primary Industries 2014). The increased likelihood of finding live HBT in drier areas is also consistent with the aspect and elevation responses identified by Lindenmayer et al. (2016). They found that more HBTs are found at lower elevations and on westerly aspects. These sites are typically drier because precipitation is positively and temperature negatively correlated with elevation, while east-west aspect is significantly correlated with heat load index in this region (Kasel et al. 2017).

Not all of our results were consistent with Lindenmayer et al. (2016). In particular, we found that the HBT form classes differed in their environmental associations, whereas Lindenmayer et al. (2016) did not. For example, our results showed that HBT3t4 had no relationship with topography or climate, HBT0t2 were associated with warm and dry sites that are steep, and HBT5t8 showed preferences for cool, moist sites that are near gullies. There are two potential explanations for the observed differences between live and dead HBTs and environmental predictors. First, if the short-dead HBT (HBT5t8) are older than current live HBT, then they may have been protected in cool, wet sites from historical fires or drought. The tree height of HBT7t8 was shorter than midstorey canopy height (maximum height is 22.5m). The shade under the midstorey canopy may decrease the decomposition rate. Second, if the dead HBT are the same age as the live HBT, then they may be in more advanced stages of collapse due to higher decay rates in cool, wet sites. However, more data on tree age are required to understand this relationship. The combination of large live trees, dead HBT (i.e., HBT5t8), and abundant midstorey are consistent with the definition of Zone 1B habitat required for the critically endangered Leadbeater's possum (Lumsden et al. 2013b).

Estimates of HBT abundance varied by tenure and vegetation type in complex ways. Total HBT abundance (i.e., all form classes) tended to be higher (~5%) in areas that are protected from timber harvesting (e.g., Parks, SPZ) or in which timber harvesting is limited by concerns for specific features of the forest (i.e., SMZ) than in the GMZ. However, the differences among specific HBT form classes were more varied. For example, Parks had 14% more HBT3t4 and 25% more HBT5t8 than State Forest GMZ. In contrast, densities of HBT0t2 were lower in Parks than in the State Forest GMZ. Dead HBT (HBT3t4 and HBTt8) densities

were broadly similar across the three vegetation types in the study area, although slightly higher in riparian forests. Riparian forests had twice more densities of HBT0t2 than rainforests. This variability in HBT density by form class and across forest management zones and vegetation types underscores the need for spatially explicit predictive models that account for the spatial variability inherent in such complex landscapes. These results also highlight the need to consider the spatial variability in the population demography of HBTs for making predictions of future HBT losses in landscapes. Spatial variability in the distribution of different HBT form classes across a landscape subject to varying forms of management and complex patterns of environmental heterogeneity suggests that the potential collapse of forest function (see Lindenmayer and Sato 2018) is unlikely to occur in a homogeneous pattern across the landscape. The greater density of live HBTs and similar densities of dead HBTs in riparian forest highlights the importance of these areas for hollow-dependent fauna and demonstrates why riparian networks have a significant and positive impact on the occurrence of arboreal marsupials (Lindenmayer et al. 1993). The higher abundance of live HBTs in riparian forests also suggests that the topography and mesic vegetation has had a historically moderating effect on fire severity, thereby promoting the persistence of HBTs under past and recent wildfires (Berry et al. 2015). The distributed network of riparian forests across the landscape and the high abundance of live and dead HBTs suggest that these areas are likely to provide a well-distributed network of HBT that are at a low risk of collapsing over the next 50 years. This highlights the need to conserve riparian forests from timber harvesting and consider them high-value assets to protect from future wildfires through strategic fuel management in the surrounding landscape.

3.5 Conclusion

LiDAR-derived structural and topographic data combined with high-resolution climate datasets provide for robust empirical predictions of HBT population structure at the landscape scale. Our HBT prediction models provided rigorous, repeatable estimates of HBT abundance across a wide range of vegetation classes and forest management zones. They provide new estimates of the total abundance of HBTs across the Central Highlands (with appropriate estimates of uncertainty) as well as a new understanding of the complexity of the structural, topographic, and environmental features associated with HBTs and their spatial variability over large areas. In particular, our analyses represent a significant advance over previous estimates (e.g., Burns et al. 2015) that are based on extrapolations from a small number of survey plots to the whole of the Central Highlands landscape. The spatial estimates of HBT demography provide a rich resource for undertaking future population viability analyses of HBT populations and model the spatial and temporal risk of HBT collapse and the impact this may have on hollow-dependent fauna at the landscape scale.

Appendices 3

The semivariance variograms of the density of each HBT classes

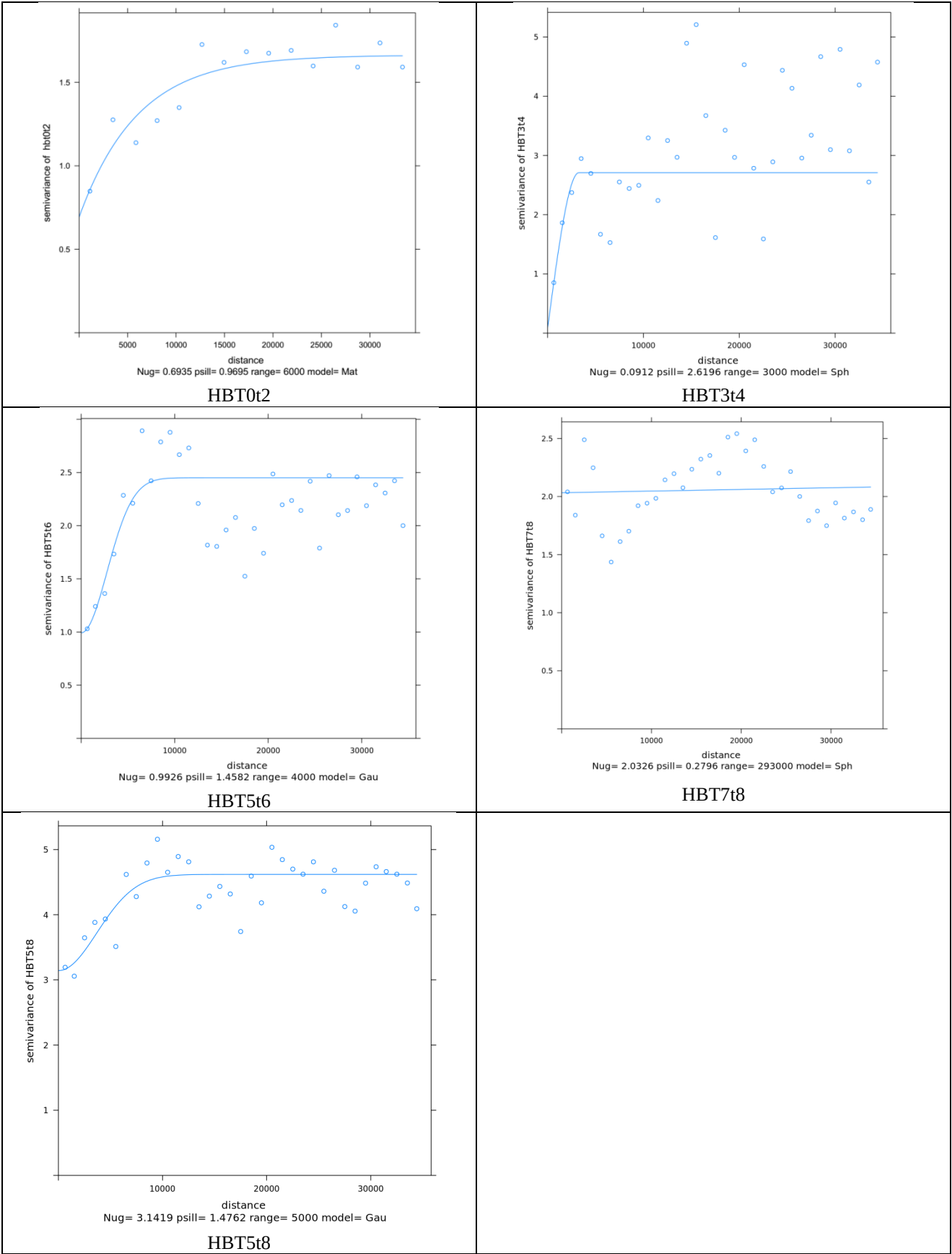


Figure A3 1 The semivariance variograms of the density of each HBT classes.

Variable selection results of HBT density model by Self-correlated grouping

Table A3 1 Self-correlated group of environmental variables, group member and variables selected to represent each group in prediction model of four HBT classes.

Group Name	Group Member	No.	HBT0t2	HBT3t4	HBT5-8
Precipitation	DEM, BIO04/12/13/14/15/16/17/18/19	10	BIO17	dem	BIO19
Temperature	BIO01/05/06/08/09/10/11	7	BIO09	BIO05	BIO10
Diurnal Range	BIO02/03	2	BIO03	BIO02	BIO02
Lidar Height	max/mean/std/p50/p75/p90	6	max	p90	p90
LiDAR top canopy strata density	S55/S60	2	s55	s60	s60
Overstorey Crown Counts	OvCWsum/OvN08to10/OvN10t15	4	ovnum	ovcwsum	ovn08t10

Mean density and 95% CI of the total HBTs for each HBT form class

Table A3 2 Estimated number of HBTs (and 95% CIs) for each HBT class across different vegetation classes and forest management zones. LCI is lower confidence interval (i.e., 2.5%ile); UCI is upper confidence interval (i.e., 97.5%ile).

	HBT0t2	HBT3t4	HBT5-8	All HBT
<i>Category</i>	<i>Total (LCI-UCI)</i>	<i>Total (LCI-UCI)</i>	<i>Total (LCI-UCI)</i>	<i>Total (LCI-UCI)</i>
All	833,000(742,000- 923,000)	244,000(177,000- 311,000)	442,000(387,000- 496,000)	1,519,000(1,306,000- 1,730,000)
Wet or Damp forests	726,000(647,000- 805,000)	210,000(153,000- 268,000)	396,000(347,000- 445,000)	1,332,000(1,147,000- 1,518,000)
Riparian area	88,000(79,000- 98,000)	22,000(16,000- 29,000)	32,000(28,000- 36,000)	142,000(123,000- 163,000)
Rainforests	19,000(16,000- 21,000)	11,000(8,000- 14,000)	14,000(12,000- 16,000)	44,000(36,000- 51,000)
Parks	181,000(161,000- 200,000)	63,000(46,000- 81,000)	119,000(104,000- 133,000)	363,000(311,000- 414,000)
GMZ	376,000(335,000- 417,000)	112,000(81,000- 142,000)	198,000(174,000- 223,000)	686,000(590,000- 782,000)
SMZ	35,000(31,000- 39,000)	13,000(10,000- 17,000)	18,000(16,000- 20,000)	66,000(57,000- 76,000)
SPZ	111,000(99,000- 123,000)	30,000(21,000- 38,000)	60,000(53,000- 68,000)	201,000(173,000- 229,000)

*GMZ: general management zone; SMZ: special management zone; SPZ: special protection zone

Example of spatial distributions of slope

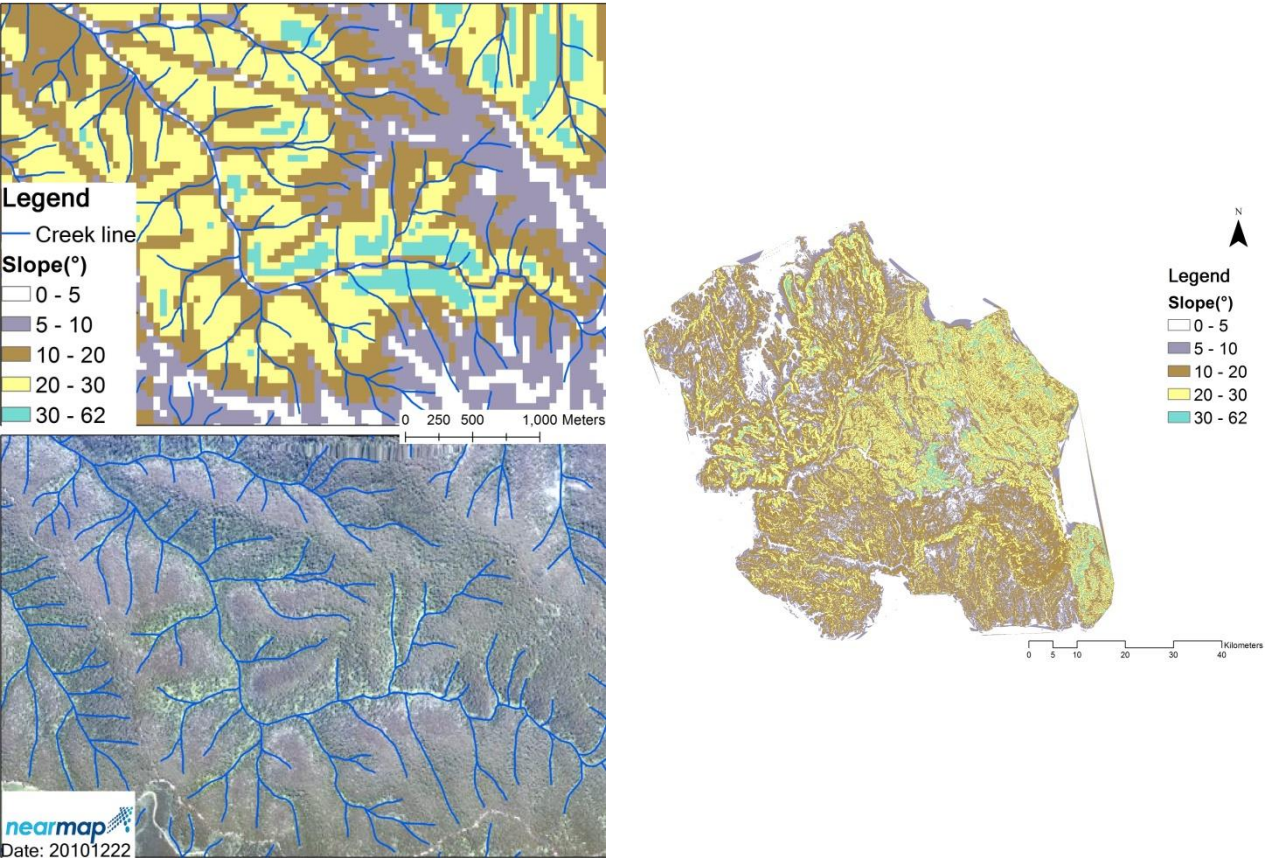


Figure A3 2 The spatial distributions of slope within a subsection of the Central Highlands (left panels) and across the whole Central Highlands landscape (right panel).

The multi-way importance plots of different predictor variables for each HBT class

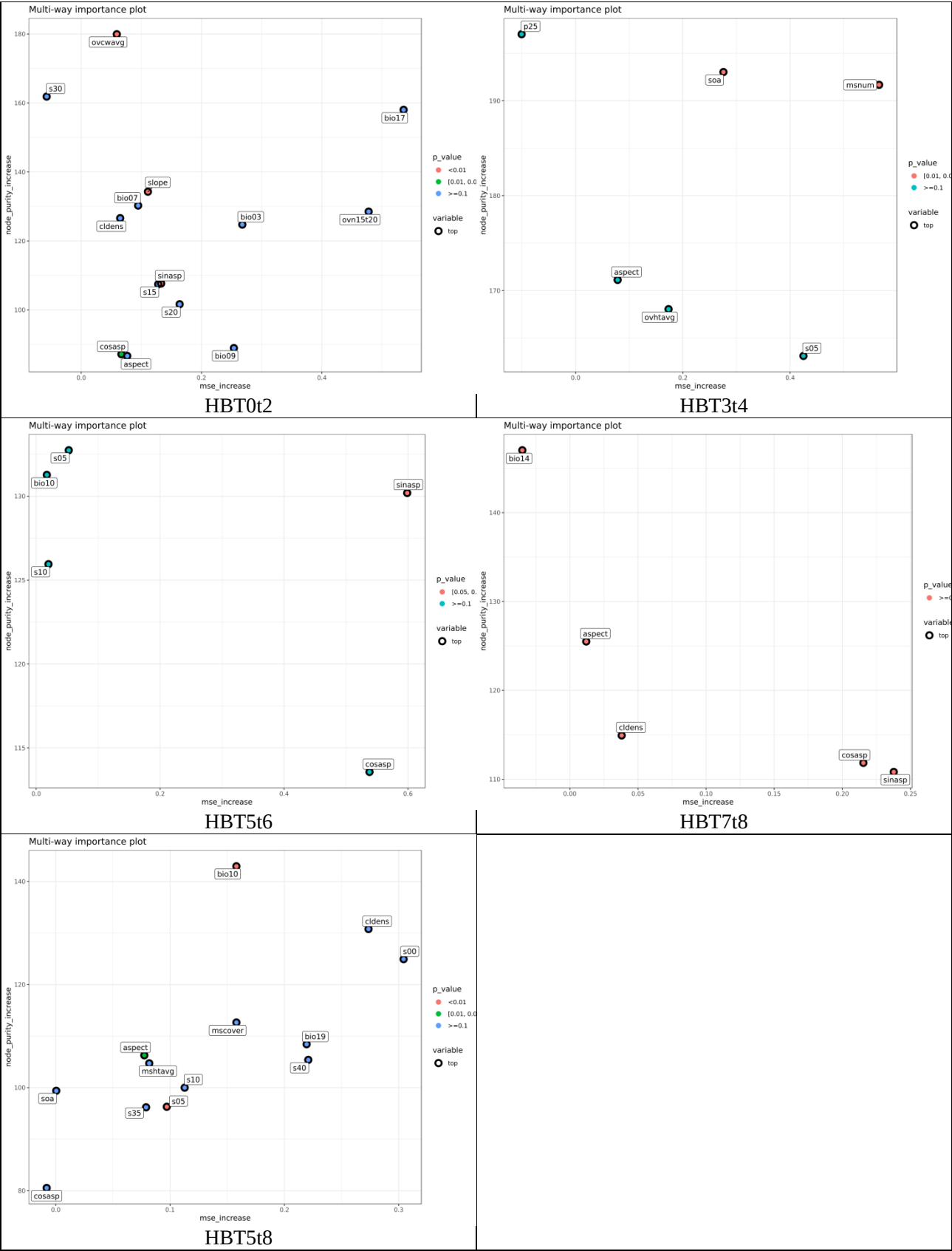
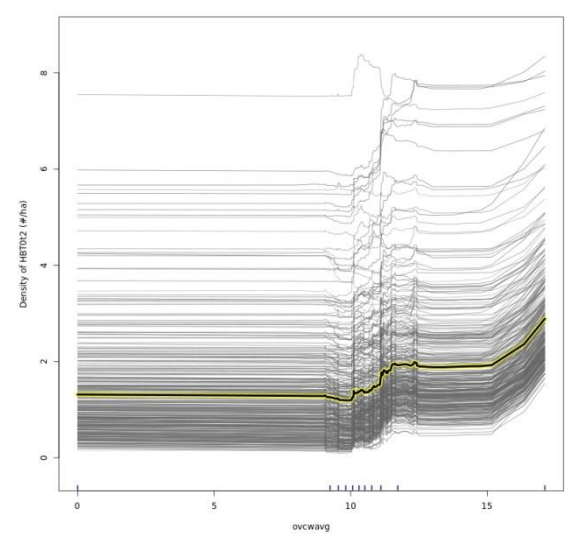
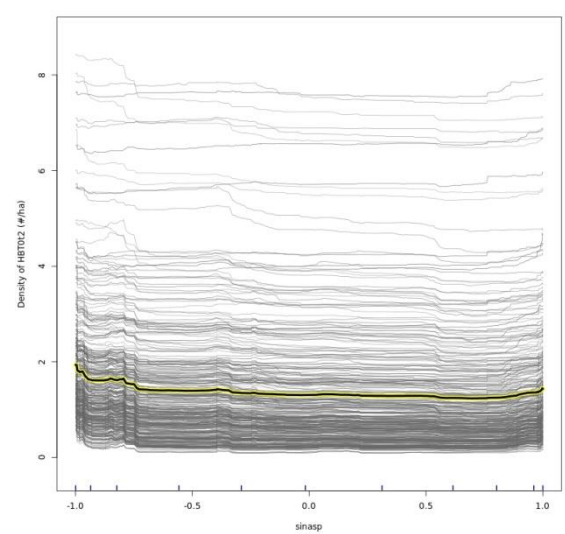


Figure A3 3 The multi-way importance plots: increase in mean squared error (mse_increase), increase in node purity (node_purity_increase) and p-value of different predictor variables for each HBT class.

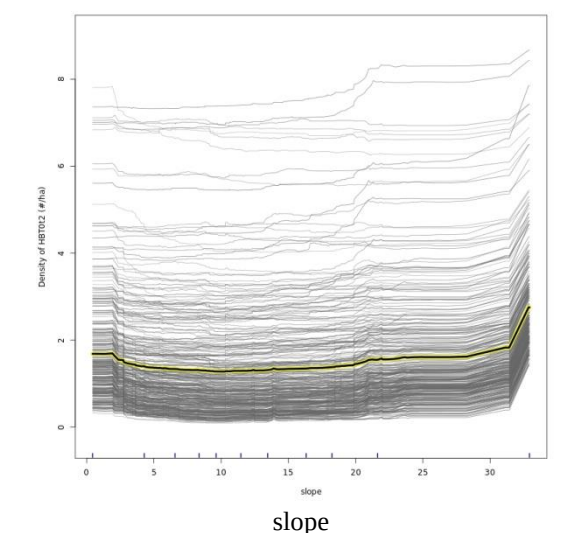
Individual Conditional Expectation (ICE) plots of important predictor variables for live HBT (HBT0t2)



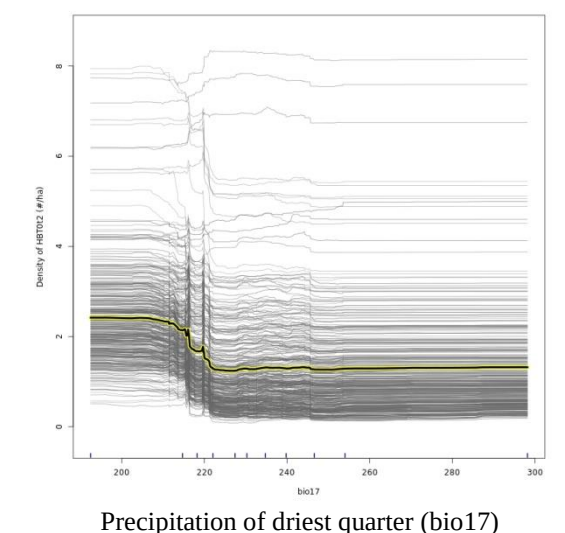
Average overstorey tree crown width (ovcwavg)



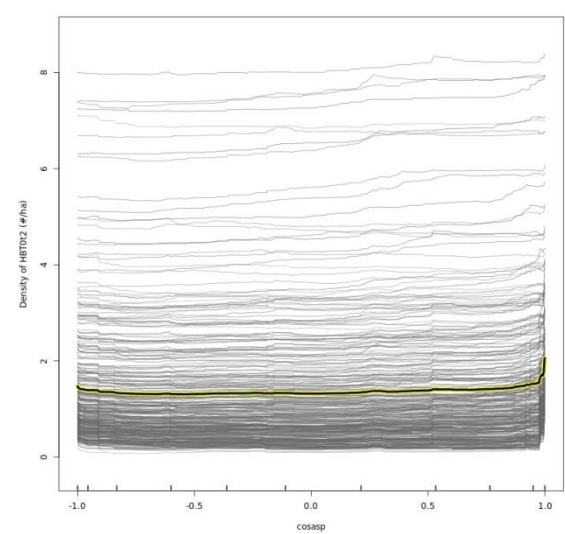
Sin of aspect (sinasp)



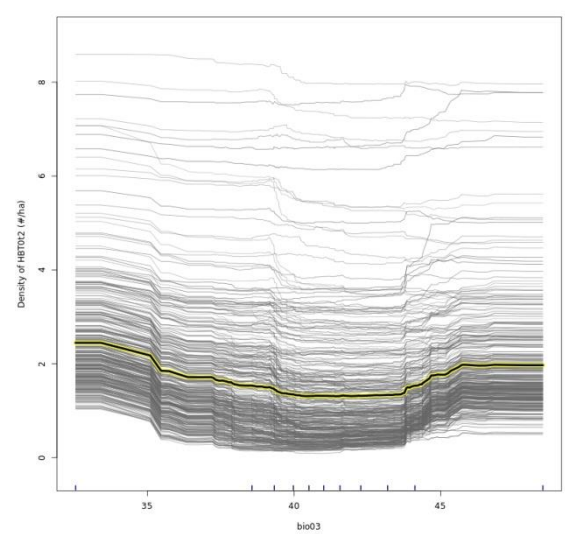
slope



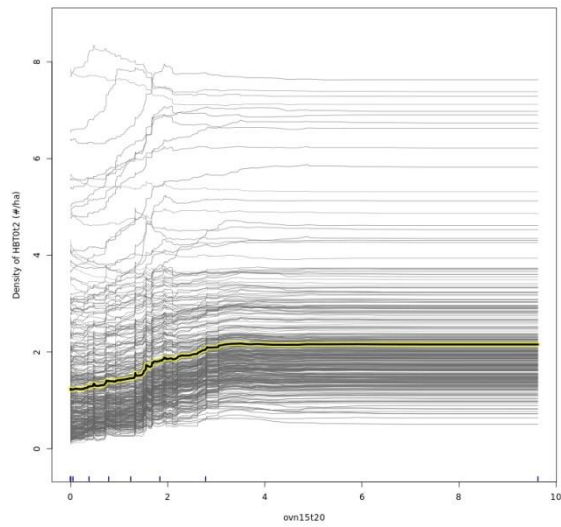
Precipitation of driest quarter (bio17)



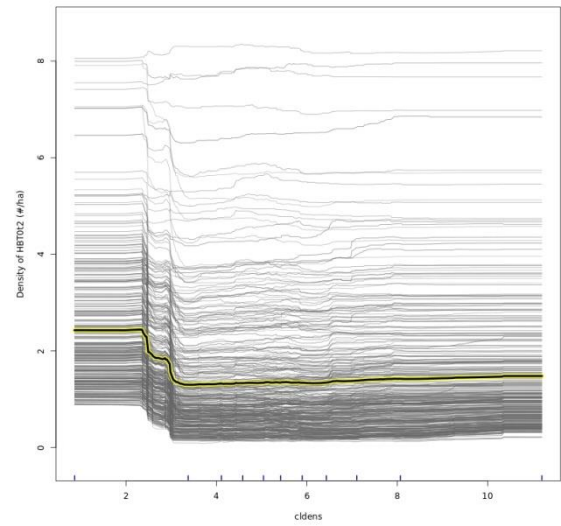
Cos of aspect (cosasp)



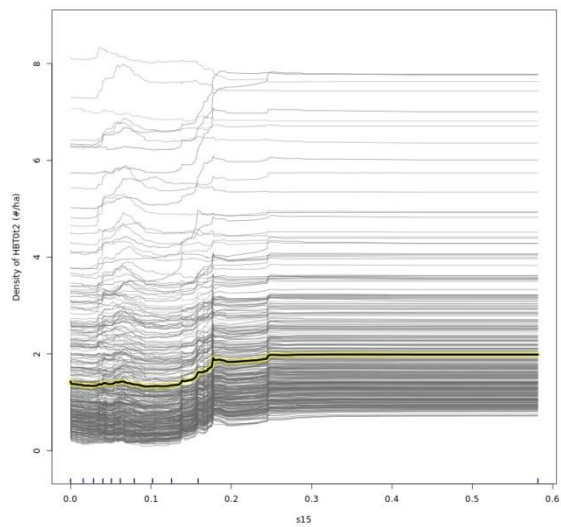
Isothermality (bio03)



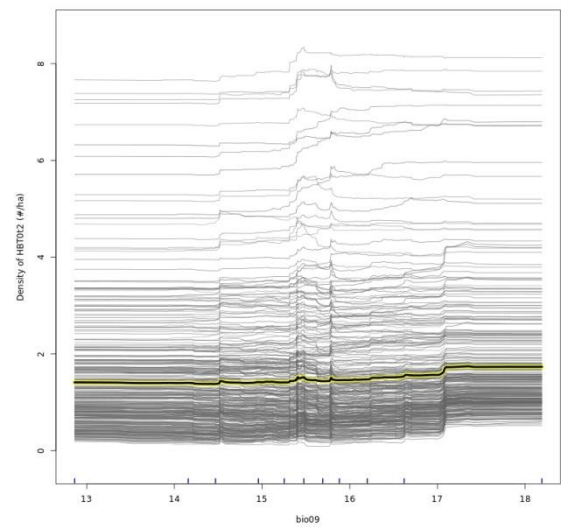
Number of big crowns per ha (with crown width >15m and ≤ 20m, ovn15t20)



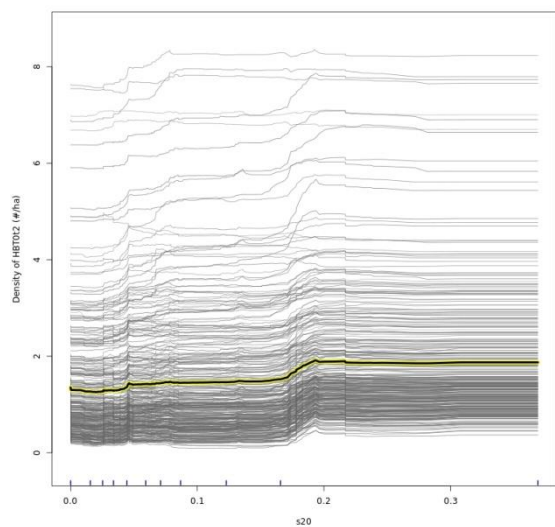
Stag Index (cldens)



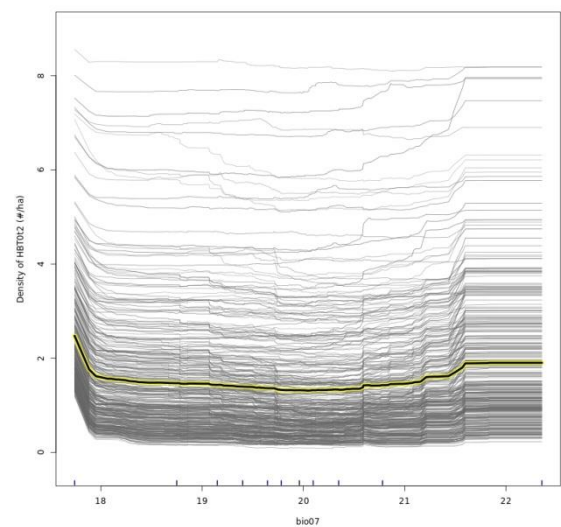
strata density between 15m-20m (s15)



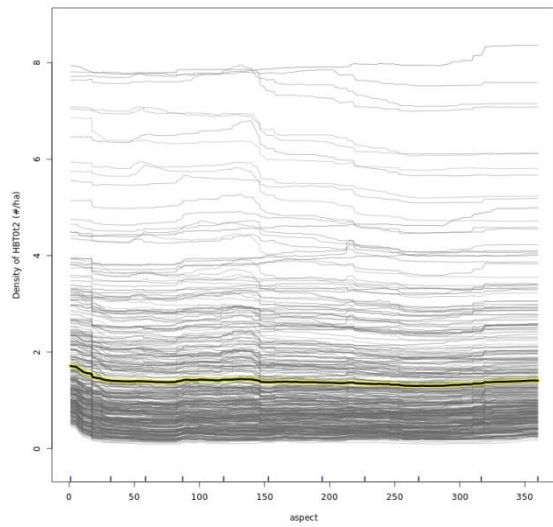
Mean temperature of driest quarter (bio09)



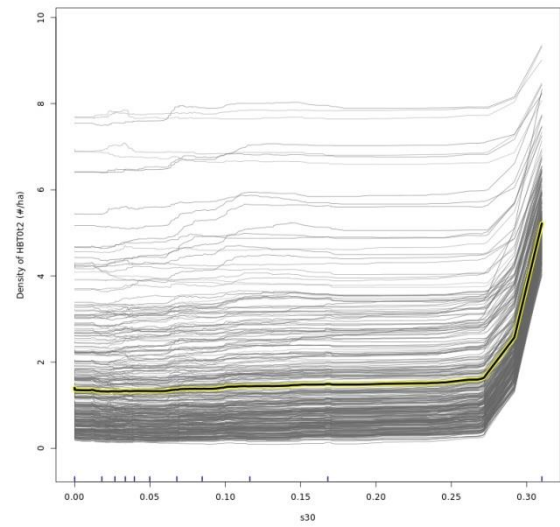
strata density between 20m-25m (s20)



Temperature annual range (bio07)



Aspect



strata density between 30m-35m (s30)

Figure A3 4 Individual Conditional Expectation (ICE) plots of important predictor variables for live HBT (HBT0t2). Variables sorted by variable importance, including 1 average overstorey tree crown width (ovcwavg), 2 sin of aspect (sinasp), 3 slope, 4 precipitation of driest quarter (bio17), 5 cos of aspect (cosasp), 6 Isothermality (bio03), 7 number of big crowns per ha (with crown width >15m and <= 20m, ovn15t20), 8 stag Index (cldens), 9 strata density between 15m-20m (s15), 10 mean temperature of driest quarter (bio09), 11 strata density between 20m-25m (s20), 12 temperature annual range (bio07), 13 aspect and 14 strata density between 30m-35m (s30)

Individual Conditional Expectation (ICE) plots of important predictor variables for tall and dead HBT (HBT3t4)

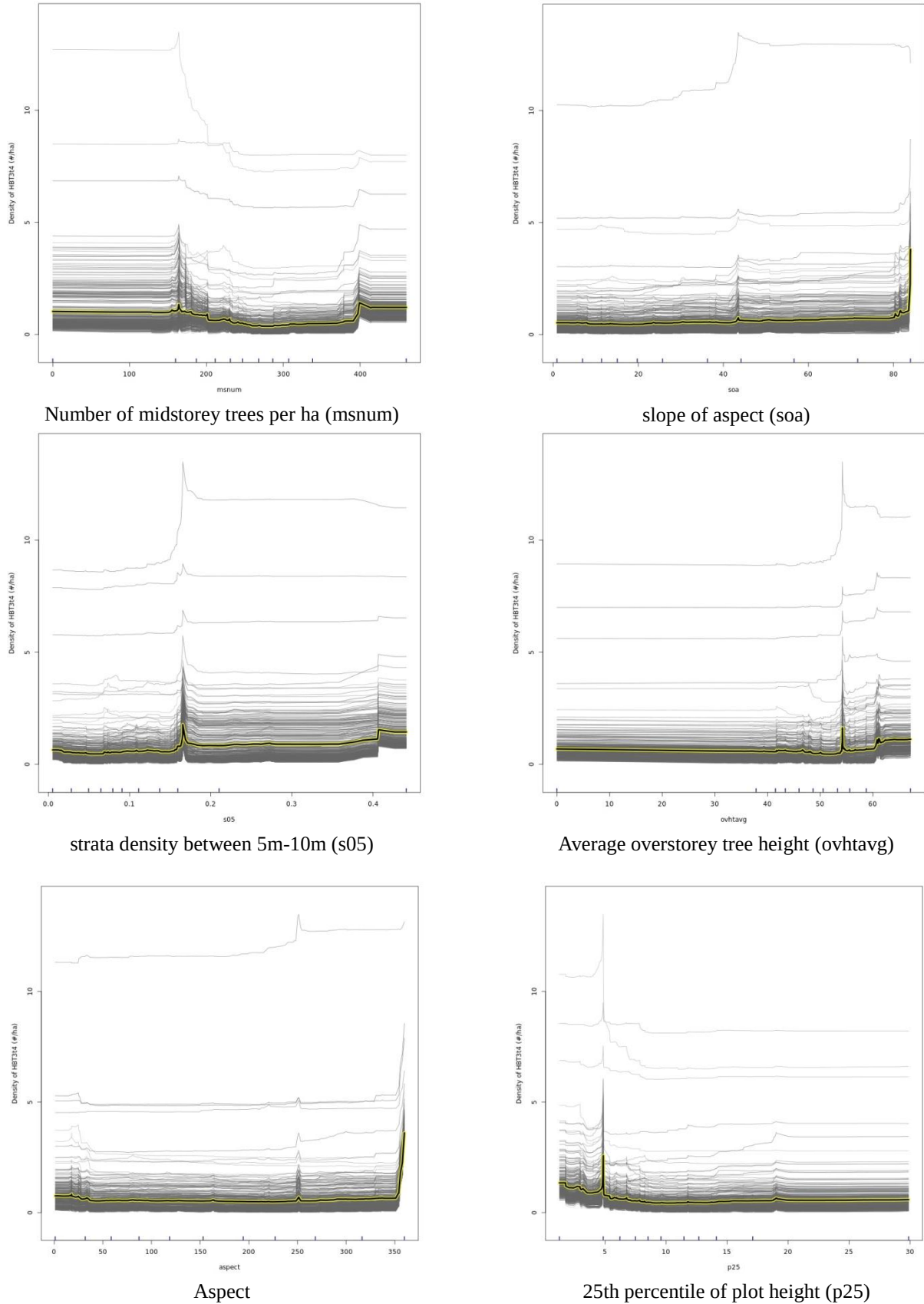
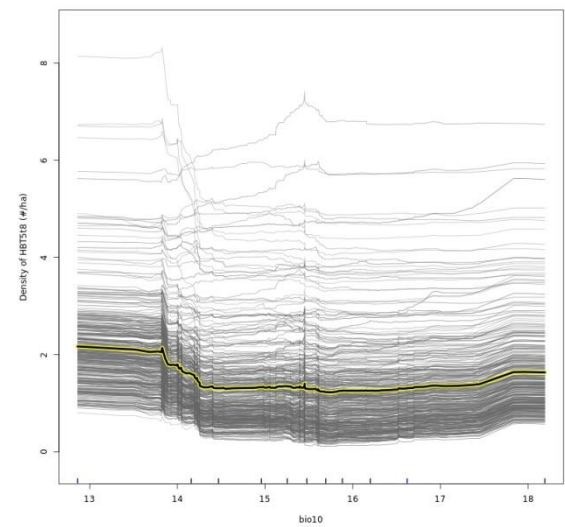
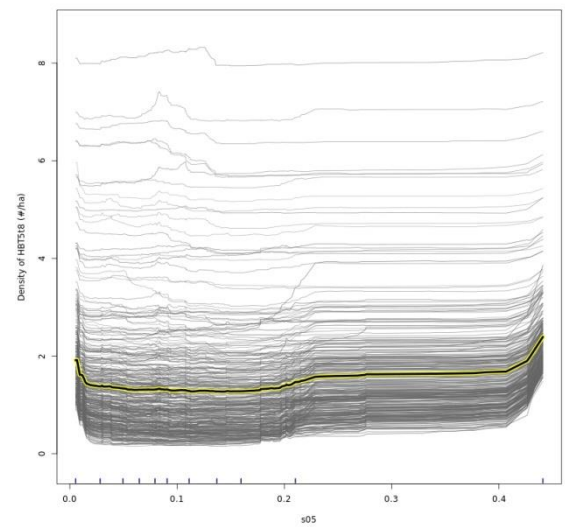


Figure A3 5 Individual Conditional Expectation (ICE) plots of important variables for HBT3t4. Variables sorted by variable importance, including 1 number of midstorey trees per ha (msnum), 2 slope of aspect (soa), 3 strata density between 5m-10m (s05), 4 average overstorey tree height (ovhtavg), 5 aspect and 6 25th percentile of plot height (p25)

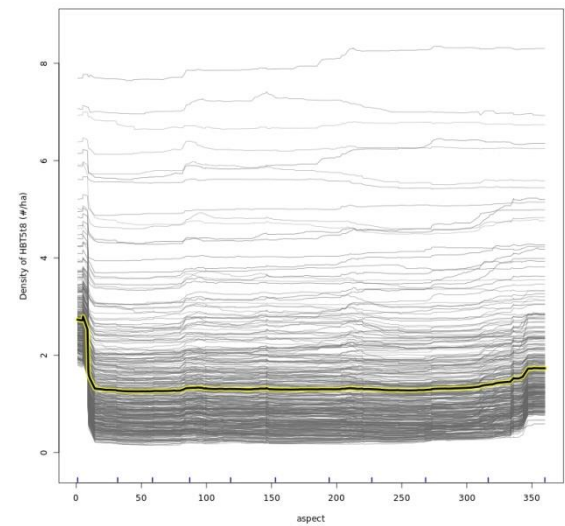
Individual Conditional Expectation (ICE) plots of important predictor variables for short and dead HBT (HBT5t8)



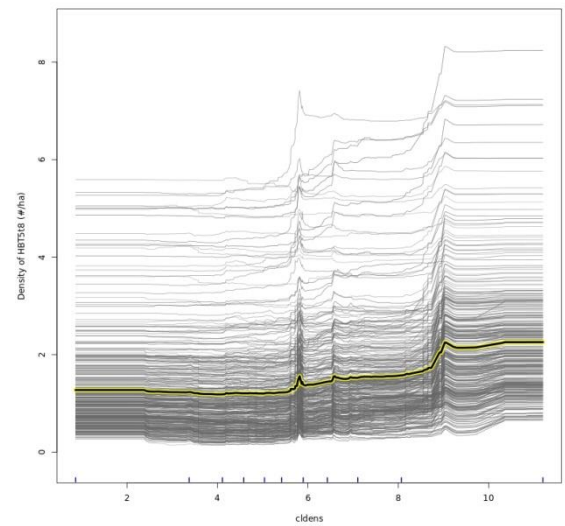
Mean Temperature of Warmest Quarter (bio10)



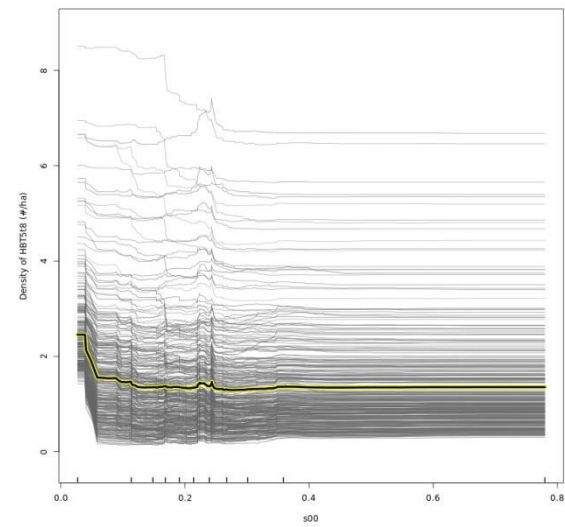
strata density between 5m-10m (s05)



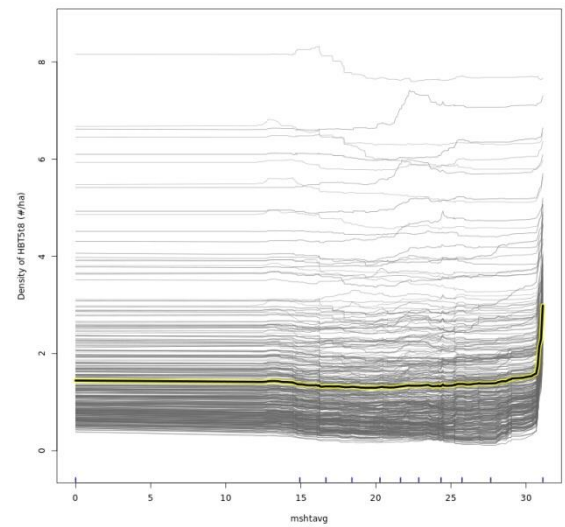
Aspect



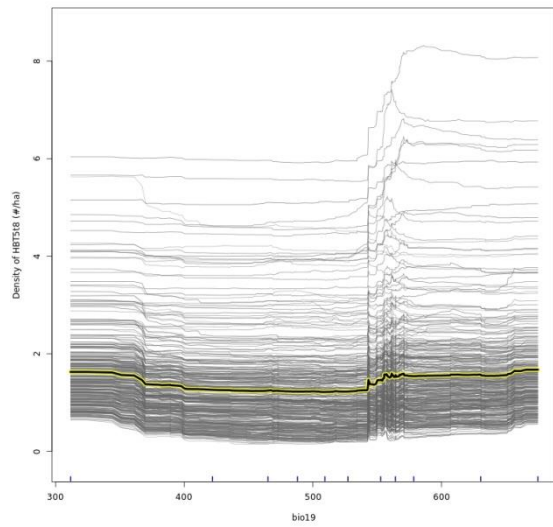
Stag Index (cldens)



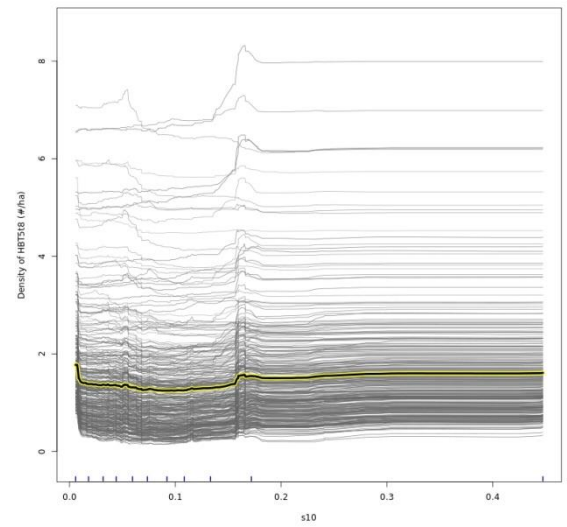
strata density between 0m-5m



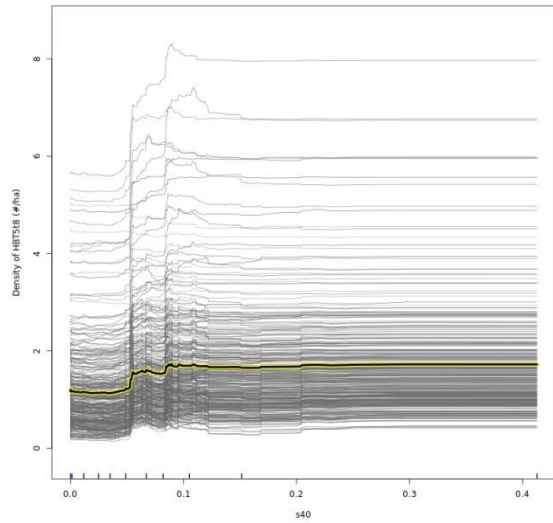
Average midstorey tree height (mshtavg)



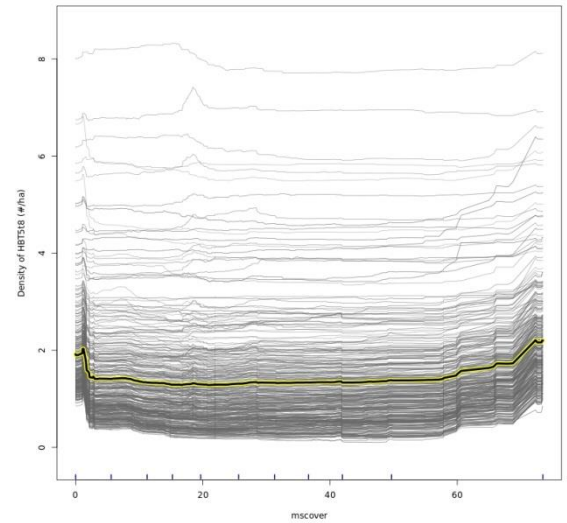
Precipitation of Coldest Quarter (bio19)



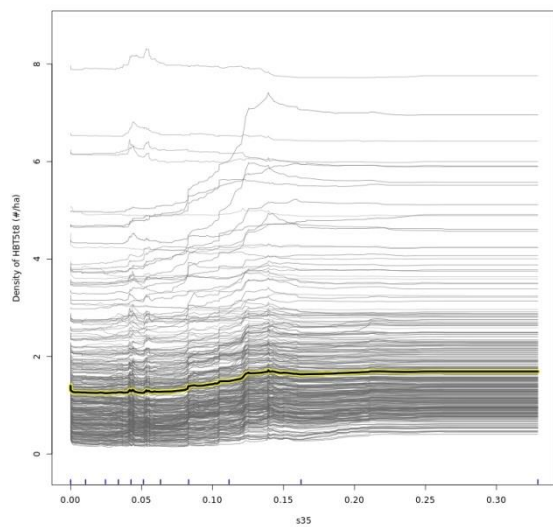
strata density between 10m-15m (s10)



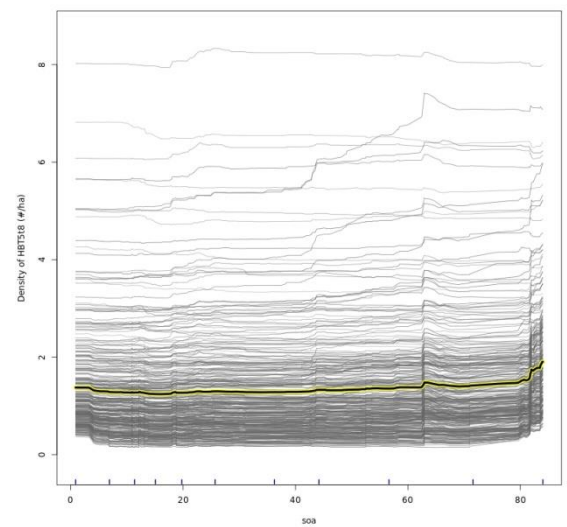
strata density between 40m-45m (s40)



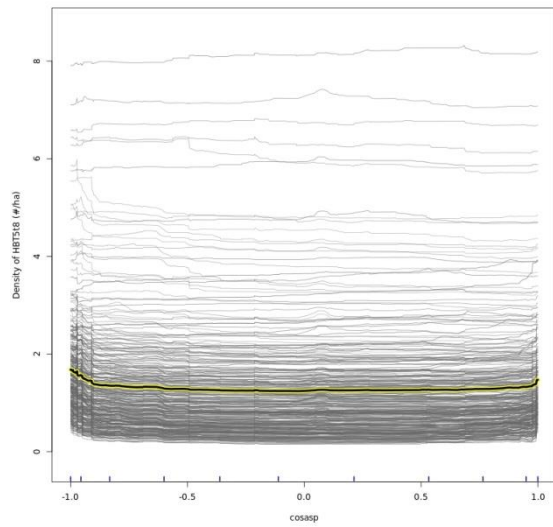
midstorey coverage (mscover)



strata density between 35m-40m (s35)



slope of aspect (soa)

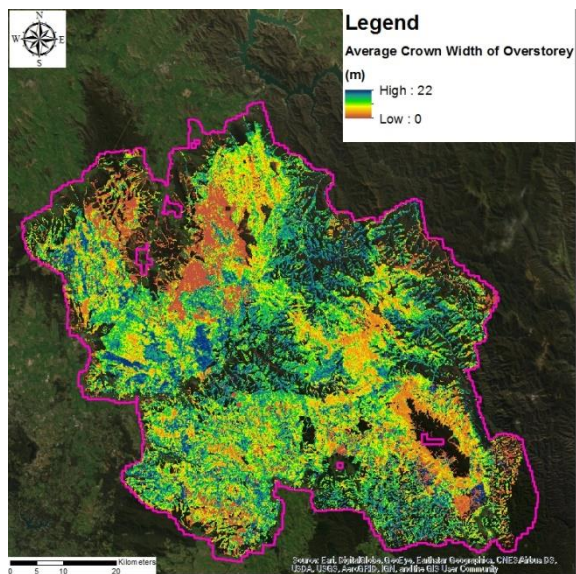


Cos of aspect (cosasp)

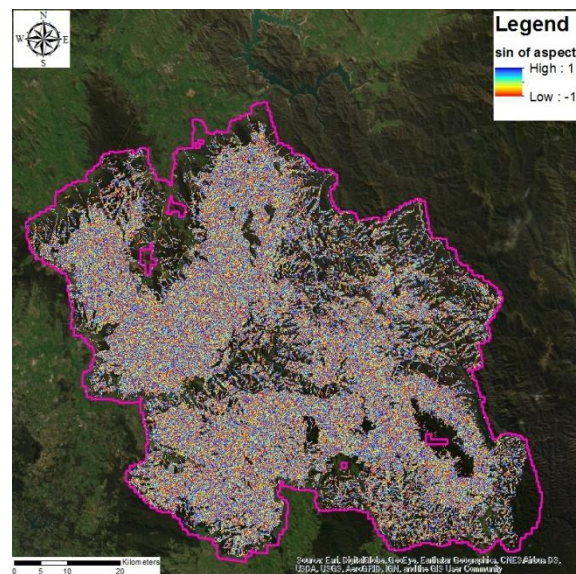
Figure A3 6 Individual Conditional Expectation (ICE) plots of important predictor variables for short and dead HBT (HBT5t8) .

Variables sorted by variable importance, including 1 mean temperature of warmest quarter (bio10), 2 strata density between 5m-10m (s05), 3 aspect, 4 stag index (cldens), 5 strata density between 0m-5m, 6 average midstorey tree height (mshtavg), 7 precipitation of coldest quarter (bio19), 8 strata density between 10m-15m (s10), 9 strata density between 40m-45m (s40), 10 midstorey coverage (mscover), 11 strata density between 35m-40m (s35), 12 slope of aspect (soa) and 13 cos of aspect (cosasp)

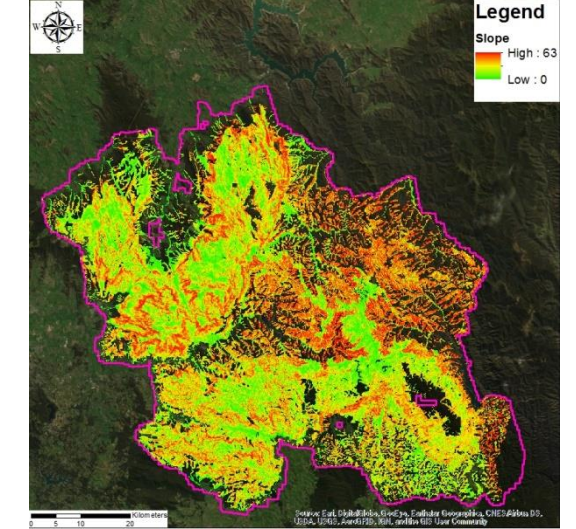
Maps of important predictor variables for live HBT (HBT0t2)



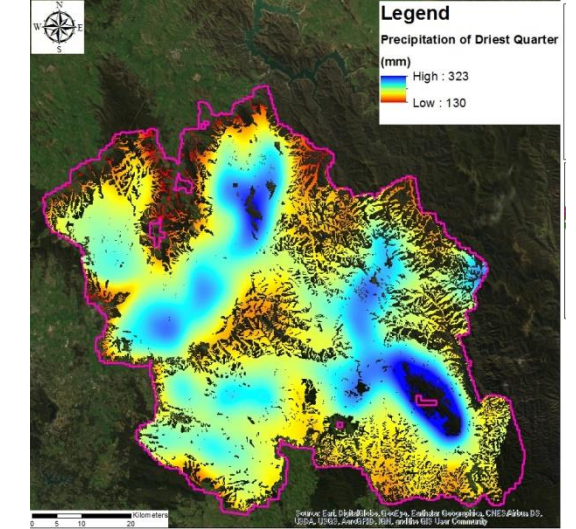
Average overstorey tree crown width (ovcwavg)



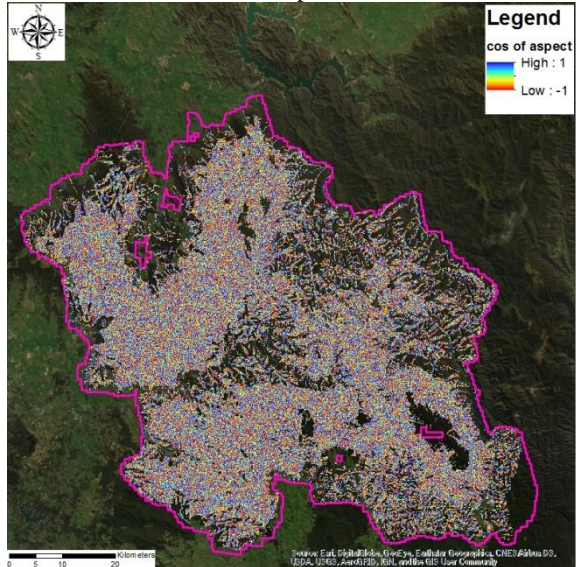
Sin of aspect (sinasp)



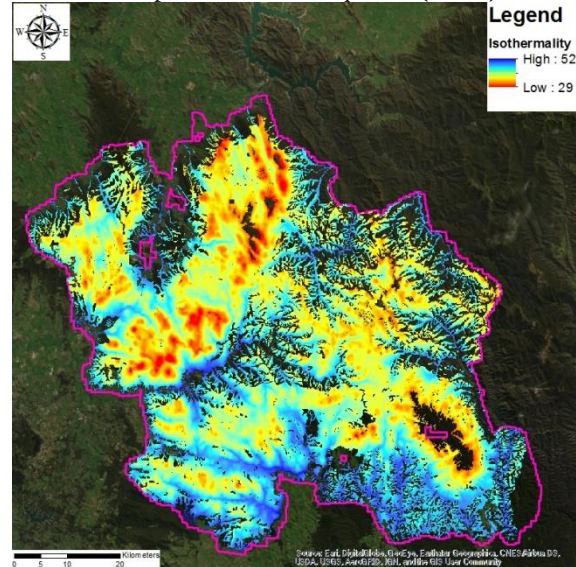
slope



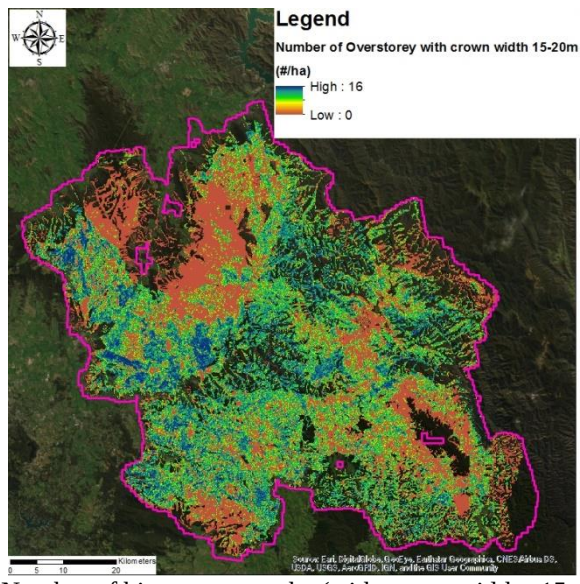
Precipitation of driest quarter (bio17)



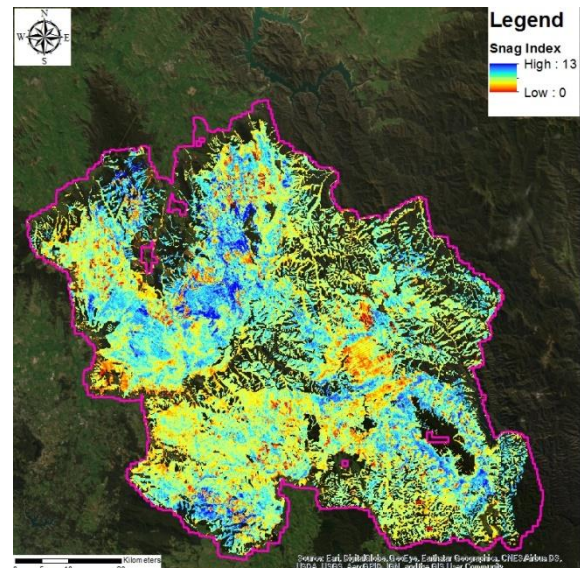
Cos of aspect (cosasp)



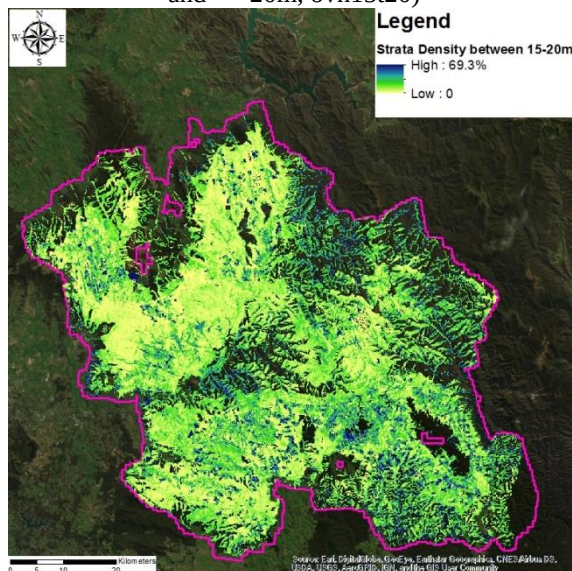
Isothermality (bio03)



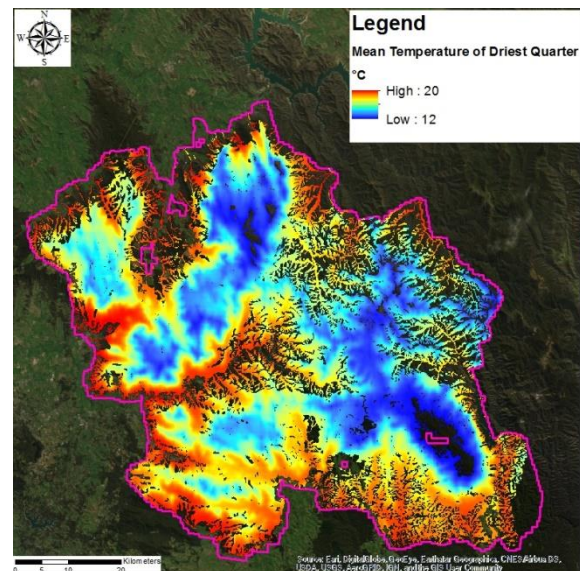
Number of big crowns per ha (with crown width >15m and <= 20m, ovrn15t20)



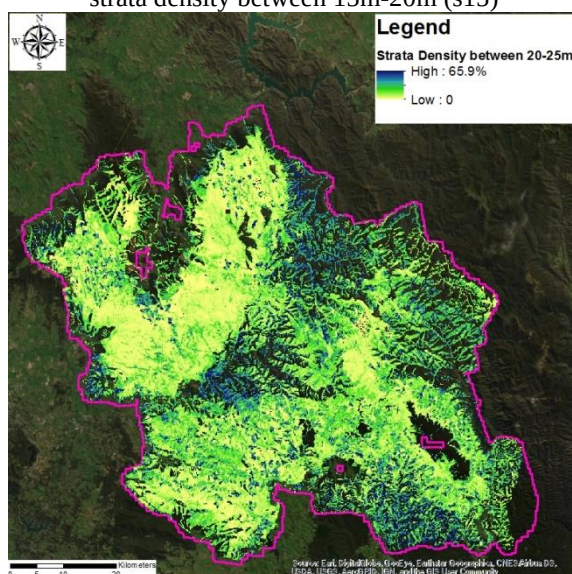
Snag Index (cldens)



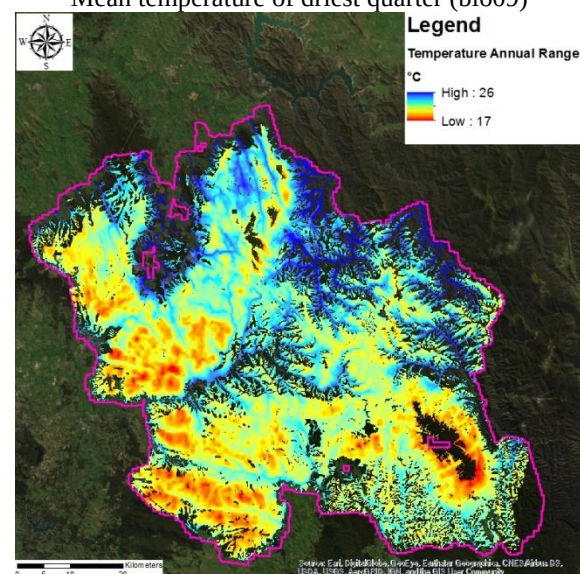
strata density between 15m-20m (s15)



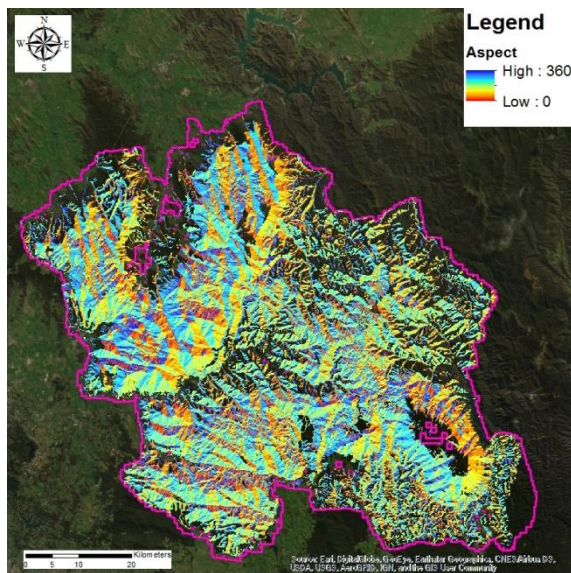
Mean temperature of driest quarter (bio09)



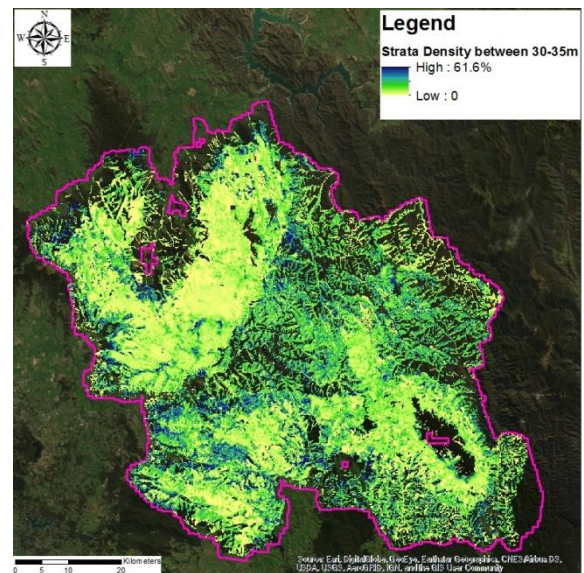
strata density between 20m-25m (s20)



Temperature annual range (bio07)



Aspect



strata density between 30m-35m (s30)

Figure A3 7 Distribution map of important predictor variables for live HBT (HBT0t2) across Victoria's Central Highlands.

Variables sorted by variable importance, including 1 average overstorey tree crown width (ovcwavg), 2 sin of aspect (sinasp), 3 slope, 4 precipitation of driest quarter (bio17), 5 cos of aspect (cosasp), 6 Isothermality (bio03), 7 number of big crowns per ha (with crown width >15m and <= 20m, ovn15t20), 8 stag Index (cldens), 9 strata density between 15m-20m (s15), 10 mean temperature of driest quarter (bio09), 11 strata density between 20m-25m (s20), 12 temperature annual range (bio07), 13 aspect and 14 strata density between 30m-35m (s30)

Maps of important predictor variables for tall and dead HBT (HBT3t4)

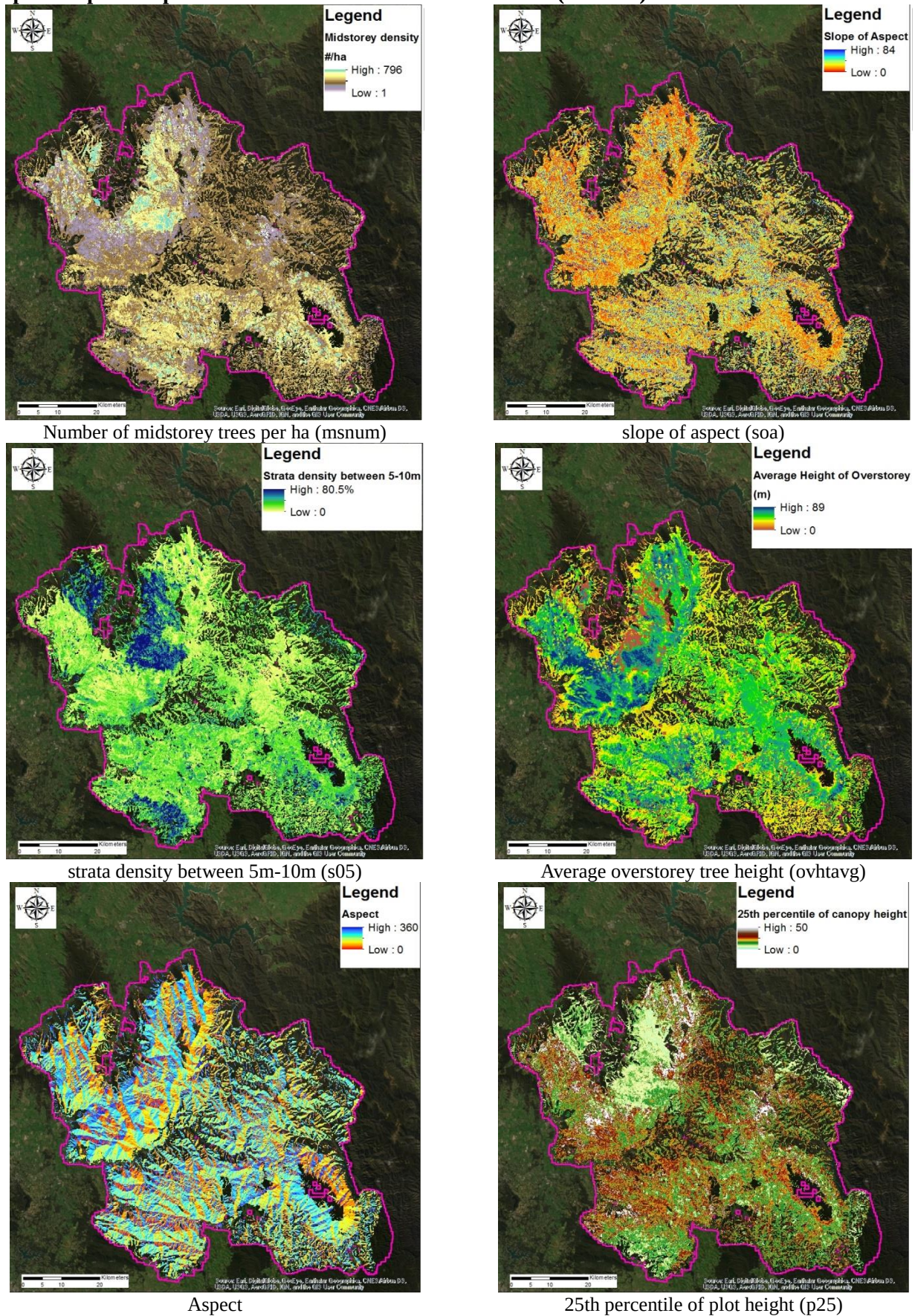
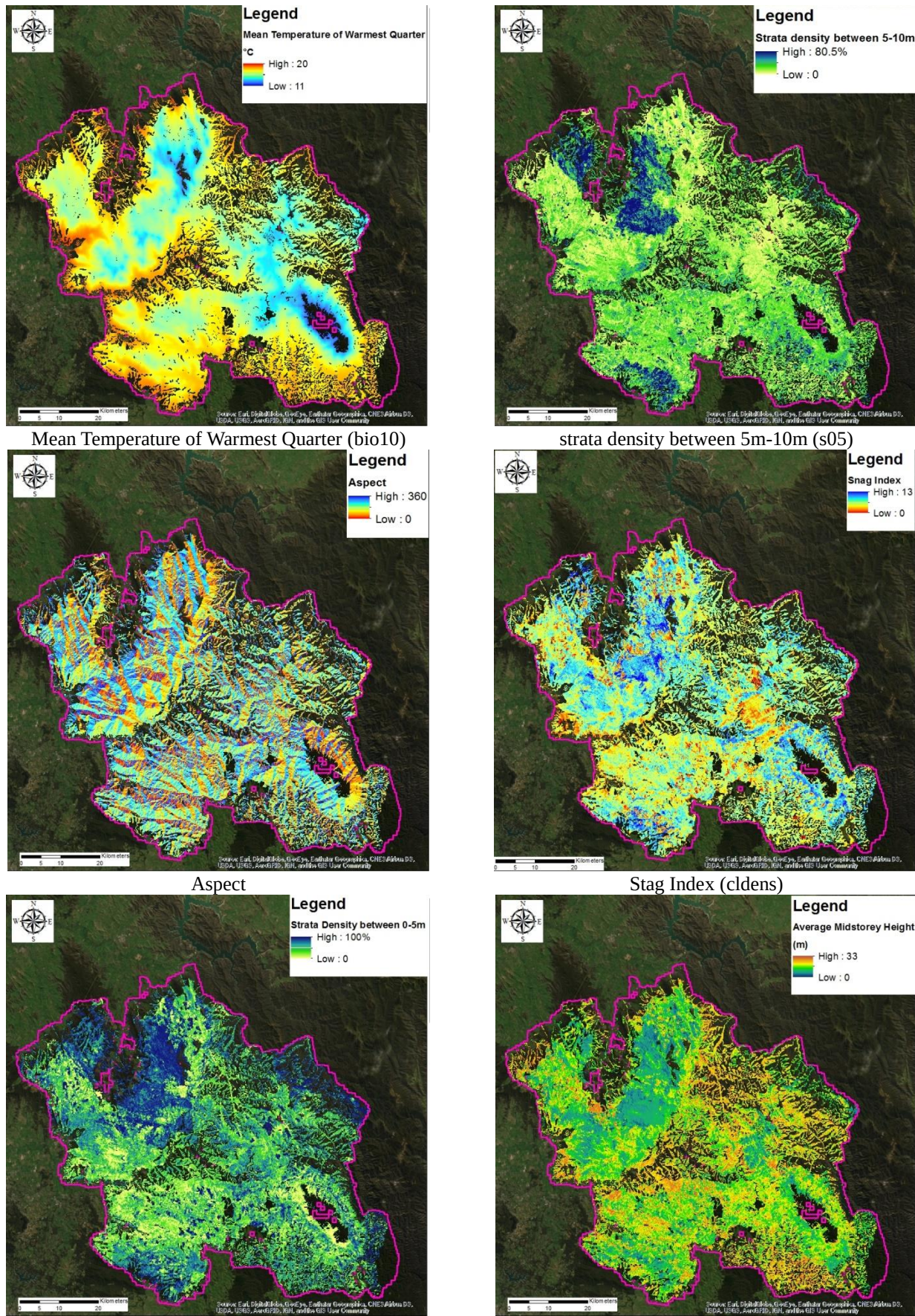


Figure A3 8 Distribution map of important predictor variables for tall and dead HBT (HBT3t4) across Victoria's Central Highlands.

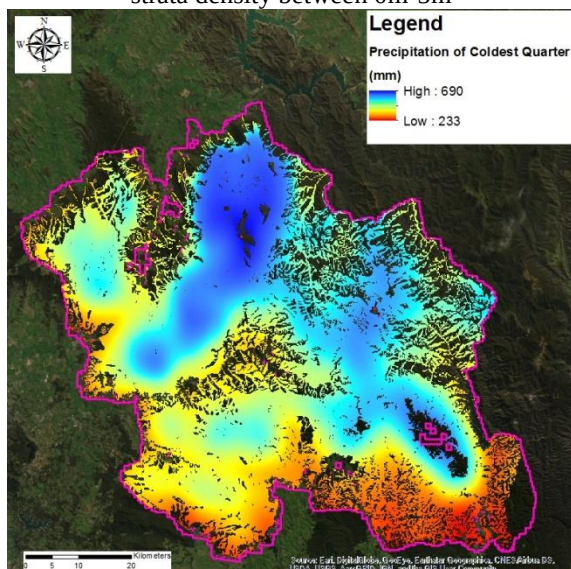
Variables sorted by variable importance, including 1 number of midstorey trees per ha (msnum), 2 slope of aspect (soa), 3 strata density between 5m-10m (s05), 4 average overstorey tree height (ovhtavg), 5 aspect and 6 25th percentile of plot

height (p25)

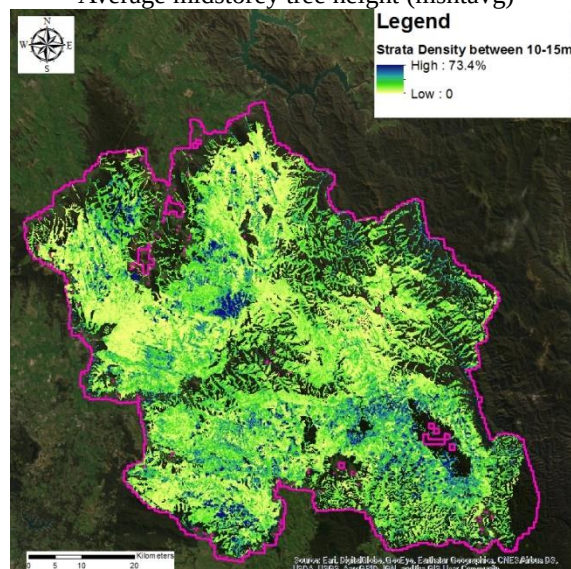
Maps of important predictor variables for short and dead HBT (HBT5t8)



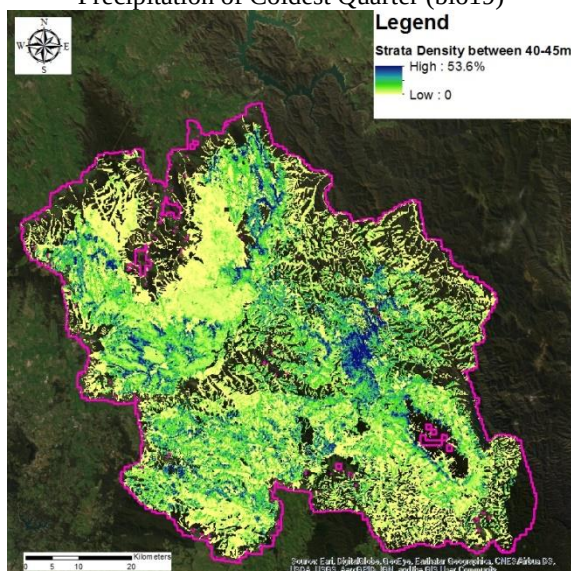
strata density between 0m-5m



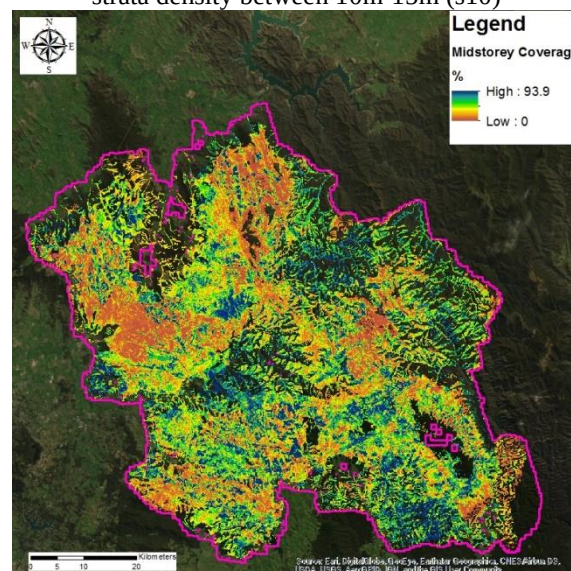
Average midstorey tree height (mshtavg)



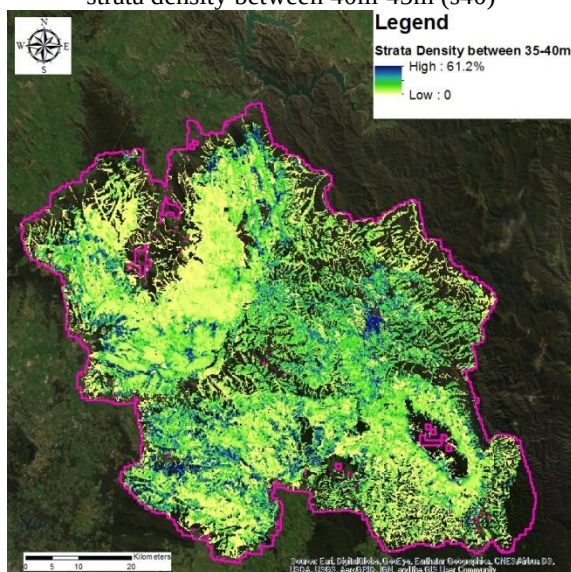
Precipitation of Coldest Quarter (bio19)



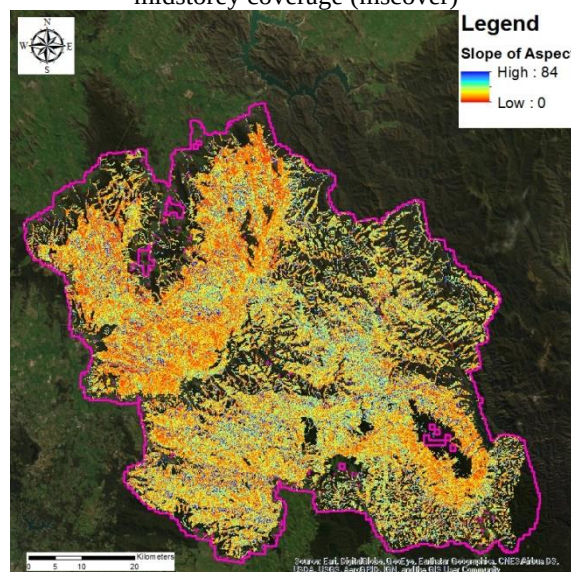
strata density between 10m-15m (s10)



strata density between 40m-45m (s40)

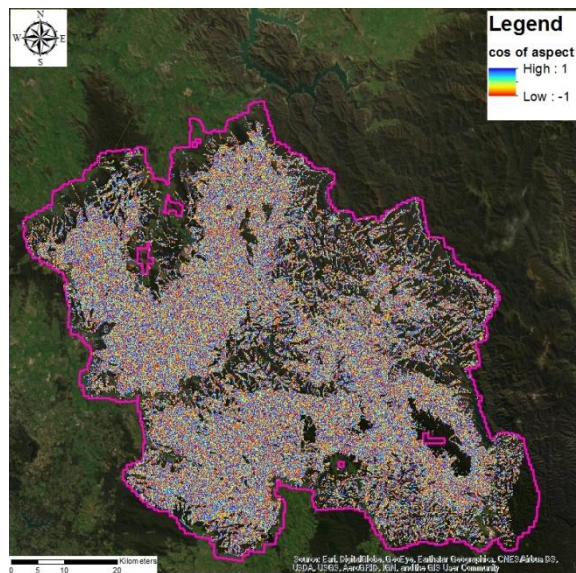


midstorey coverage (mscover)



strata density between 35m-40m (s35)

slope of aspect (soa)



Cos of aspect (cosasp)

Figure A3 9 Distribution map of important predictor variables for short and dead HBT (HBT5t8) across Victoria's Central Highlands.

Variables sorted by variable importance, including 1 mean temperature of warmest quarter (bio10), 2 strata density between 5m-10m (s05), 3 aspect, 4 stag index (cldens), 5 strata density between 0m-5m, 6 average midstorey tree height (mshtavg), 7 precipitation of coldest quarter (bio19), 8 strata density between 10m-15m (s10), 9 strata density between 40m-45m (s40), 10 midstorey coverage (mscover), 11 strata density between 35m-40m (s35), 12 slope of aspect (soa) and 13 cos of aspect (cosasp)

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Chapter 4.

4 Predicting connectivity of midstorey stratum using airborne LiDAR data: implications for modelling Leadbeater's Possum habitat at the landscape-scale

4.1 Introduction

Natural forests are highly complex ecosystems that provide wide range of ecological functions and services (Goodwin 2006, Hawksworth and Bull 2007, Li et al. 2011). Characterizing forest structure is an important part of any comprehensive biodiversity assessment (Miura and Jones 2010). Forest structure can be quantified by many features, such as overstorey canopy height and cover, understorey cover, tree diameters, and above-ground volume or biomass (Latifi et al. 2015a). Among these structural and functional features, indicators relating to the sub-canopy vegetation (including shrub, under-storey or mid-storey trees) are of particular interest for forest ecology and management (Goodwin 2006, Simonson et al. 2014, Latifi et al. 2015a). The understorey and midstorey strata has been shown to play an important role in forest ecosystems by affecting: (1) nutrient cycling and retention and (Yarie 1980, Ward 2000, Forrester et al. 2004, Goodwin 2006, Gilliam 2007), (2) forest dynamics and regeneration patterns (Connell and Slatyer 1977, Smidt and Puettmann 1998, Cater and Chapin 2000, Falkowski et al. 2009, Wing et al. 2012), (3) micro-climate and soil structure (Cater and Chapin 2000, Ramovs and Roberts 2003, Gómez - Aparicio et al. 2005), (4) fuel load and wildfire regimes (García et al. 2011, Soares-Filho et al. 2012, Gordon et al. 2017); and, (5) quality and accessibility of animal habitat (Lindenmayer et al. 1991b, Hinsley et al. 2006, Blair et al. 2017). The under-/ midstorey is crucial for the survival of a number of faunal species primarily because of the provision of foraging habitat (Smith 1984), shelter (protection from predators and climatic extremes) (Cox et al. 2000) and connectivity for the movement of fauna (Crooks and Sanjayan 2006). For example, researchers found the black rat (*Rattus rattus*) preferred habitats with dense understorey which provided enhanced protection from predators, and also increased food resources at ground level (Cox et al. 2000). The hazel grouse (*Bonasa bonasia* L.) strongly depends on multi-layered forests with shrub density and canopy height being important predictors of their habitat suitability (Rechsteiner et al. 2017). The diversity of understorey plants species affected the populations of understorey bird species in tropical forests (Stouffer and Bierregaard Jr 1995, Castellón and Sieving 2006).

The critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) found in south Australia, requires a dense midstorey stratum of Acacia (Silver Wattle *Acacia dealbata*, Mountain Hickory Wattle *A. obliquinervia*, Forest Wattle *A. frigiscens*, Blackwood *A. melanoxylon*) as foraging habitat (Lindenmayer 1989b, Lindenmayer et al. 1991b, Lindenmayer et al. 2000, Blair et al. 2017). LBP do not have a gliding membrane, as such, it needs a near continuous cover of foliage to move through the forest (Macfarlane et al. 1997). A high level of "connectivity" through the midstorey is therefore a significant predictor of Leadbeater's possum (LBP) habitat. Lindenmayer et al. (1991b) found that the probability of LBP occurrence increased with increasing stand basal area of *Acacia*

species. Finer-scale mapping of midstorey/ understorey density across the LBP home range is required however to improve the accuracy of current occupancy models and the more accurately map suitable habitat for LBP at the landscape-scale (Blair et al. 2017).

Accurate assessments of the properties and dynamics of forest multistorey structure at a broad spatial scales are vital for forests managers to understand forest ecosystem processes and develop management strategies (Goodwin 2006). Traditional field-based assessment on the vegetation structures have been limited to small geographical areas and are time-consuming (Olthof et al. 2003, Halpern et al. 2005, Goodwin 2006). Airborne light detection and ranging (LiDAR) is an effective and proven technology for high-resolution mapping of forest structures over large landscape extents (Lefsky et al. 2002, Lim et al. 2003, Hudak et al. 2008, Martinuzzi et al. 2009, Simonson et al. 2014, Fedrigo et al. 2018). The advantage of three-dimensional coverage of structural features using LiDAR is to capture subtle differences vegetation structure within and between forest types; in particular, and variations in sub-canopy structure (Hudak et al. 2006, B äsler et al. 2011, Latifi et al. 2015a, Fedrigo et al. 2018). For example, Hudak et al. (2006) integrated LiDAR data with regression models to predict total plot-level basal area and tree density and found that LiDAR-derived predictor variables explained 89% and 87% of the variation in total plot-level basal area and tree density, respectively. Martinuzzi et al. (2009) evaluated the use of LiDAR data and a machine-learning algorithm for mapping the presence/absence of understorey and habitat suitability for birds in mixed-conifer forest in Northern Idaho (USA). Latifi et al. (2015) suggested a significantly correlation between LiDAR metrics and the structural properties of lower forest layers. In southeastern Australia, Fedrigo et al. (2018) used LiDAR data to identify different vegetation types where the ability to detect sub-canopy forest structure was critical for differentiating between different vegetation communities.

In this study, we assessed the association between field-assessed vegetation connectivity and plot-level LiDAR metrics within multiple strata of the mountain ash (*Eucalyptus regnans*) forests of southeast Australia to develop landscape-scale predictions of connectivity and foraging habitat for the critically endangered LBP. The objectives of this study were:

- (1) to explore the ability of LiDAR metrics to model vegetation connectivity across multiple forest stratum at a landscape-scale; and,
- (2) to use landscape-scale models of stratum connectivity to explore relationships between environmental variability and vegetation connectivity;

4.2 Method

4.2.1 Study area

The study area is located in the Victorian Central Highland of southeastern Australia (Figure 4-1). Native vegetation in Victoria has been classified into Ecological Vegetation Classes (EVCs) to represent unique characteristics of different vegetation types. Three major vegetation classes in this study are EVC group 7 - wet - damp forest, EVC group 8 - riparian forest, and EVC group 9 – cool temperate rainforest. The study area is dominated by wet - damp forest (89%), with riparian forest (7%), and rainforest (4%) intermixed throughout. The dominant tree species in the wet - damp forest EVC are mountain ash (*Eucalyptus regnans*), alpine ash (*Eucalyptus delegatensis*), and shining gum (*E. nitens*). The Central Highland experiences cool summers and humid winters with frequent frosts and occasional periods of snow. Mean annual temperatures ranged from 6-15 °C and mean annual precipitation ranged from 690-2090 mm over the period 1981–2010 (Stewart and Nitschke 2017, Fedrigo et al. 2019). More than 40% of the mountain ash forest in the Central Highlands of Victoria was burnt during 2009 Black Saturday wildfires (Blair et al. 2018).

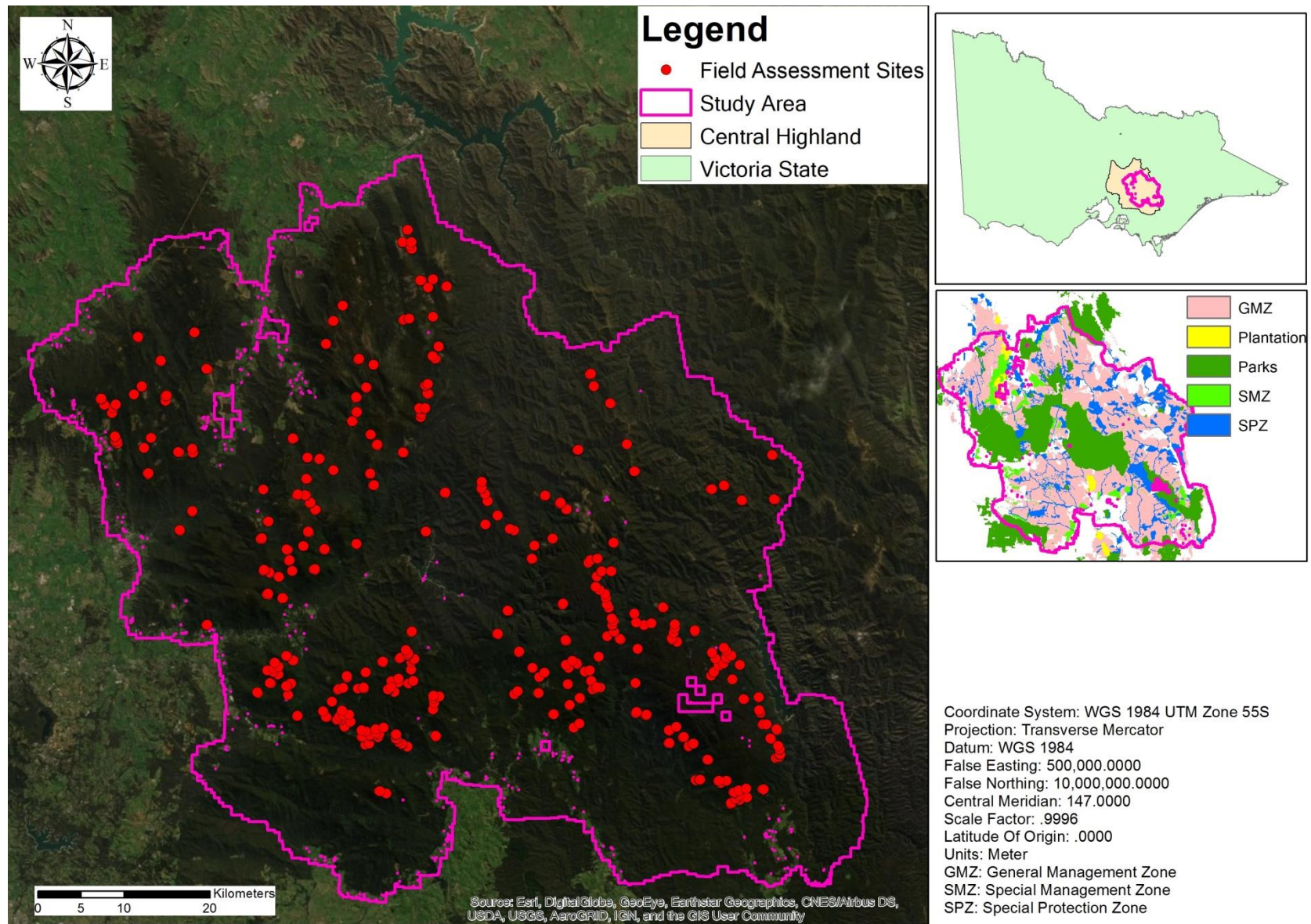


Figure 4-1 The study area in Victoria's Central Highlands. The map shows the total LiDAR coverage and the locations of field assessment sites, coverage of each forest management zone (FMZ)

4.2.2 Field-based habitat assessment for vegetation connectivity

Ground-based surveys of vegetation connectivity were conducted by field crews from the Arthur Rylah Institute for Environmental Research (ARI). Between 2014 and 2017, they established and surveyed 417 sites within the three major vegetation classes across the Victorian Central Highlands (see Fig 4-1). Plots were 1-ha in size, within which the connectivity at the shrub, mid-storey and canopy layers was measured in four 10m-radius plot located along north to south transects within the survey sites. The distribution of four 10m-radius plots (S1, S2, S3 and S4) located across the north to south transect within 1-ha survey sites are shown in 2. At these plots, the basal area of *Acacia* spp. was also measured (Table 4-1). The distribution of the mean connectivity index of the four 10m-plots within each 1-ha survey site for each vertical vegetation layers is shown in Figure 4-2 and summary statistics are provided in Table 4-1

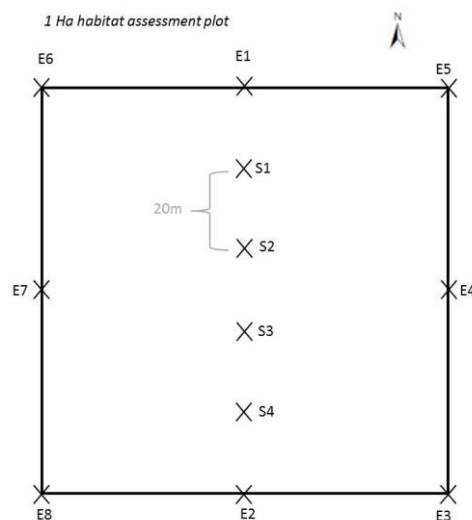


Figure 4-2 the distribution of four 10m-radius plots (S1, S2, S3 and S4) located across the north to south transect of 1-ha survey sites.

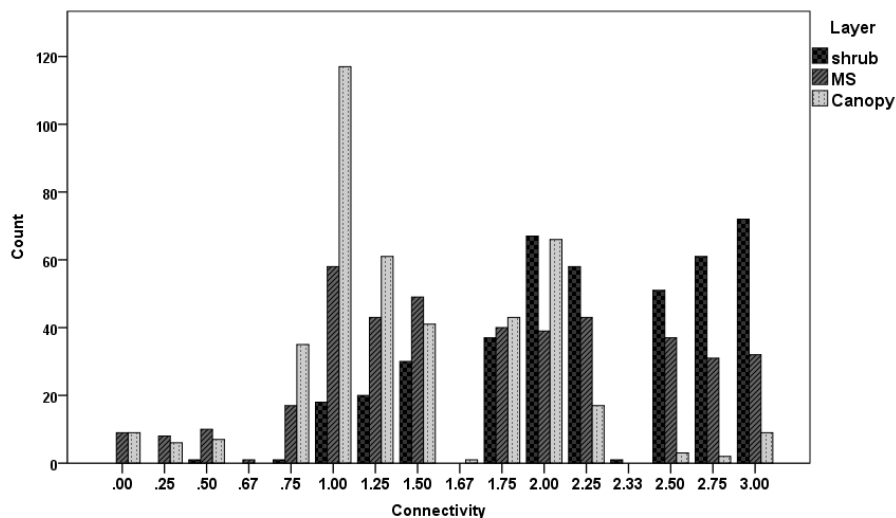


Figure 4-3 The mean connectivity index per ha of shrub layer, midstorey layer and top canopy layer distributed in 417 ARI sites

Table 4-1 Data summary of field-assessed live wattle density (m²/ha) and connectivity index of shrub layer, midstorey layer and top canopy layer. Minimum (min), maximum (max), mean, and standard deviation (sd) summarize observed values across all sampled trees and vegetation classes.

	All field data				wet - damp forest				riparian forest				rainforest			
	mean	sd	max	min	mean	sd	max	min	mean	sd	max	min	mean	sd	max	min
Shrub	2.2	0.6	3.0	0.5	2.3	0.6	3.0	0.5	1.9	0.6	2.8	1.0	2.2	0.6	3.0	1.0
Midstorey	1.7	0.8	3.0	0.0	1.7	0.8	3.0	0.0	2.2	0.7	3.0	1.0	1.7	0.7	3.0	0.5
Canopy	1.4	0.6	3.0	0.0	1.4	0.6	3.0	0.0	1.3	0.5	2.0	0.0	1.2	0.5	2.0	0.3
Live Wattle	4.3	5.1	33.5	0.0	4.5	5.2	33.5	0.0	2.8	4.3	15.6	0.0	3.1	3.8	13.3	0.0

The definition of vertical vegetation layers was dependent on vegetation type and canopy height. The height of shrub layer was defined as being above 0.5 but below 5m. The common species of were the tree ferns *Dicksonia antarctica* and *Cyathea australis* and the following shrubs: *Correa lawrenciana*, *Zieria arborescens*, and *Tasmania lanceolata*. The midstorey layer was comprised of taller shrubs (> 5m), such as *Bedfordia arborescens*, *Pomaderris aspera*, *Acacia dealbata*, *A. frigescens*, and *A. obliquinervia*. The canopy layer was defined as the uppermost-level dominated by Eucalyptus. In non-eucalypt stands, such as rainforest stands where the tree canopy layer is dominated by *Nothofagus cunninghamii* and *Atherosperma moschatum*, the upper most strata was considered as mid-storey. This classification was used to ensure connectivity metrics where comparable across all forest types. Connectivity was scored as categories based on the inter connectedness of vegetation cover within a stratum. Increased connectedness increases the ability of LBP to move through the forest while foraging. The connectivity index were:

- 0 = Connectivity absent, zero opportunity for LBPs to move around in that layer,.
- 1 = Connectivity present, but minimal,
- 2 = Connectivity present, LBPs can move around relatively easily but may need to move into another layer to access a different part of the layer in question within the 10 m radius plot; and,
- 3 = Connectivity continuous, LBPs can access every part of the 10 m radius plot within that layer.

4.2.3 Lidar metrics and GIS products

LiDAR raw data

Discrete return airborne LiDAR data were acquired by RPS Group Plc in late 2015 and early 2016 using Trimble AX60 laser sensor mounted on a fixed wing aircraft. The aircraft was flown at 800 m above ground level with flying speed of 62 m/s. Mean pulses per meter was 2-4 pts/m with an average point spacing of 0.46m. LiDAR data covered 513,322 hectares of Victorian Central Highlands (Figure 4-1). After selecting relevant EVCs for the study area, the final study area was 342,960 ha, which included 305,200 ha of wet - damp forest, 24,900 ha of riparian forest and 12,400 ha of rainforest. 112,205 ha of LiDAR covered study area were burnt in 2009, 32.8% of the total area.

Climate, Forest Type and Disturbance Data

Ecological Vegetation Classes (EVC), forest management zone (FMZ), logging history and fire history spatial data used were sourced from the Victorian Department of Environment, Land, Water, and Planning (DELWP). Nineteen bioclimatic variables were used in the analyses (Table 4-2). Bioclimatic variables for temperature developed by Stewart and Nitschke (2017) were used. Precipitation based BIOCLIM variables used were from Fedrigo et al. (2019). The resolution of bioclimate data was 250m. Kriging interpolation was used to change the resolution of bioclimate data into 100m.

LiDAR topographic metrics

A high-resolution digital elevation model (DEM) was derived from a LiDAR ground-based point cloud using FUSION/LDV Software (McGaughey 2009). From this DEM, slope, aspect, and slope of aspect (SOA) were generated using ArcGIS (v. 10.5). SOA represents the rate of change of the aspect in the horizontal direction (Zhou et al. 2018); therefore, the maximum value of SOA is located at the dividing line at ridge or gully. A gully index was calculated from a high value of SOA and negative terrain surface. The negative terrain surface was created using ArcGIS focal statistic tool (“moving window”) to identify relatively lower surfaces within a specific neighborhood. The resolution of all LiDAR topographic metrics was 1ha.

LiDAR structural metrics

LiDAR structural metrics used in the analyses were derived from height or height-related variables. The percentiles of stand height and strata density (percentage of LiDAR points between two heights) are commonly used LiDAR metrics (Goodwin et al. 2006, Hudak et al. 2008, Martinuzzi et al. 2009, Mitchell et al. 2012). For example, the 99th percentile is often used to represent maximum stand height rather than the maximum z-value of LiDAR points to eliminate the influence of extreme outliers (Jenkins 2012). Strata density is often used to represent foliage density or connectivity for each vertical layer (Parker et al. 1995, Parker et al. 2004). The LiDAR structural metrics used in this study are provided in Table 4-2. The resolution of all LiDAR structural metrics was 1ha.

A foliage-height profile derived from the leaf area of distinct, non-overlapping layer (strata) can be used to sort out distinct forest structures (Parker et al. 1995). Replacing the foliage cover with LiDAR points density from different height layers, a canopy profile model (CPM) built from LiDAR points can be used to categorize forest vertical structure (Parker et al. 2004). In this study, forest structure was classified by vertical layer connectivity, and then a CPM for each forest structure class was built to represent differences in vertical forest structure.

LiDAR overstorey and midstorey metrics

LiDAR overstorey and midstorey metrics were variables derived from the results of individual tree detection

and delineation (see Chapter 2). For overstorey, the locations of individual tree tops, crown widths (CW), and tree height (HTs) were determined using an individual tree delineation (ITD) algorithm. These were aggregated into plot-level variables (1ha plot), such as the number of trees per hectare, mean crown width, and mean crown height. Overstorey crowns were classified into four categories (8-10m, 10-15m, 15-20m, and >20m) based on crown width to represent different growth stages of the canopy. Crowns with large perimeter: area ratios indicated irregular crown forms. We used the line density of the crown edge based as a metric for the perimeter:area ratio. A live tree with a well-formed crown will have a relatively low line density and therefore a small perimeter:area ratio, whereas a standing dead stag with lots of dead branches will have high line density values. We used the line density of crown edges derived from the crown-edge detection step of ITD to compute a Stag Index (CLdens in Table 4-2) describing the irregularity of the crown shape. For the midstorey within each plot, LiDAR points were used to calculate the proportion of projection area of midstorey LiDAR points, a surrogate for midstorey density. The detection results for tree tops were used to determine the number of trees and the mean midstorey height within each plot.

In total, we considered 62 environmental variables when building the connectivity model. These variables are shown in Table 4-2. They include vegetation class, year of most recent fire, year of most recent logging, 19 climate variables, seven topographic variables, and 33 plot structure variables.

Table 4-2 LiDAR Metrics used to build classification model

Category	Variables	Short Name
Vegetation type	Ecological Vegetation Classes	EVC
Disturbance	Year of most recent Fire	Fire
	Year of most recent Logging	logging
Topography	Aspect	Aspect
	Cos of Aspect	CosAsp
	Gully Index/Creek Index	GullyIndex/CreekIndex
	Elevation	DEM
	Sin of Aspect	SinAsp
	Slope	Slope
	Slope of Aspect	SoA
Bioclimatic	Annual Mean Temperature	BIO01
	Mean Diurnal Range	BIO02
	Isothermality	BIO03
	Temperature Seasonality	BIO04
	Max Temperature of Warmest Month	BIO05
	Min Temperature of Coldest Month	BIO06
	Temperature Annual Range	BIO07
	Mean Temperature of Wettest Quarter	BIO08
	Mean Temperature of Driest Quarter	BIO09
	Mean Temperature of Warmest Quarter	BIO10
	Mean Temperature of Coldest Quarter	BIO11
	Annual Precipitation	BIO12
	Precipitation of Wettest Month	BIO13
	Precipitation of Driest Month	BIO14
	Precipitation Seasonality	BIO15
	Precipitation of Wettest Quarter	BIO16
	Precipitation of Driest Quarter	BIO17
	Precipitation of Warmest Quarter	BIO18
	Precipitation of Coldest Quarter	BIO19
Plot height (Statistical summary for height of height-normalized Lidar points)	max plot height	max
	mean plot height	mean
	Standard deviation of plot height	std
	p10: 10th percentile of height	p10
	p25: 25th percentile of height	p25
	p50: 50th percentile of height	p50
	p75: 75th percentile of height	p75
	p90: 90th percentile of height	p90

Category	Variables	Short Name
Vertical Canopy strata density	% of all returns between height strata 0.5 - 5m	S00
	% of all returns between height strata 5-10m	S05
	% of all returns between height strata 10-15m	S10
	% of all returns between height strata 15-20m	S15
	% of all returns between height strata 20-25m	S20
	% of all returns between height strata 25-30m	S25
	% of all returns between height strata 30-35m	S30
	% of all returns between height strata 35-40m	S35
	% of all returns between height strata 40-45m	S40
	% of all returns between height strata 45-50m	S45
	% of all returns between height strata 50-55m	S50
	% of all returns between height strata 55-60m	S55
	% of all returns between height strata 60-65m	S60
Overstorey	Average Overstorey tree crown width (CW) /plot	OvCWavg
	Total Overstorey tree CW/plot	OvCWsum
	Average big crowns height /plot	OvHtavg
	Number of level 1 CW /plot (8m < CW <= 10m)	OvN08t10
	Number of level 2 CW /plot (10m < CW <= 15m)	OvN10t15
	Number of level 3 CW /plot (15m < CW <= 20m)	OvN15t20
	Number of level 4 CW /plot (CW > 20m)	OvN20t30
	Number of Big Crowns /plot (CW > 8m)	OvNum
	Line density of edge of overstorey tree crown (Stag Index)	CLdens
Midstorey	MS Coverage (%)	MsCover
	Number of Midstorey trees /plot	MsNum
	Average Midstorey tree height /plot	MsHtavg

4.2.4 Connectivity index model building, model validation and uncertainty analysis

Random forest model to predict connectivity index and variable importance

To estimate the connectivity of each vertical vegetation layer in a site, we used a machine-learning approach based on a large set of structural, topographic, and environmental predictors (Table 4-2). Specifically, we used Random Forests (RF; also known as random decision forests), a supervised machine-learning method for classification or regression. RF operates by constructing a large number of decision trees (i.e., a forest) (Breiman 2001), each of which represents a predicted class and a vote for that class. After each iteration, individual decision trees are combined using the rule of majority votes. When used in regression, the forest takes the average of predictions. RF models have advantages in accounting for nonlinear relationships and complex interactions, and are less prone to over-fitting (Martinuzzi et al. 2009). We used the ‘randomForest’ package in R (Liaw and Wiener 2002).

The RF algorithm also provides the relative importance of each predictor variable, by quantifying changes in classification error when the “out of bag” (OOB) data for that variable is altered (Martinuzzi et al. 2009, Shoemaker et al. 2018). For regression/ density model, variable importance is calculated by increase in mean squared error (IncMSE) and increase in node purity (IncNodePurity). We used the ‘measure_importance’ function from ‘randomForestExplainer’ package in R to generate four importance indices, including increase in mean squared error (IncMSE), increase in node purity (IncNodePurity), mean minimal depth (MinDepth) and p-value (Paluszynska and Biecek 2017).

An RF model can also provide partial dependence plots (PDP) that demonstrate the dependency of the average effect on a chosen variable. In this study, PDPs can graphically characterize relationships between individual predictor variables and the connectivity index measured at field sites. PDPs were also used to determine whether a variable, on an overall average, had a positive or negative effect on the model (Friedman 2001). Meanwhile, to understand heterogeneous patterns of specific observations, we also generated Individual Conditional Expectation (ICE) plots to demonstrate the dependence of the prediction on an individual variables for each observations separately, resulting in one line per observation, compared to one line overall in partial dependence plots (PDP) (Goldstein et al. 2015). The R package ‘ICEbox’ was used to create ICE plots (Goldstein et al. 2017).

Block cross-validation validation and significant variables selection

We used 5-fold block cross-validation to evaluate model performance and systematically compare models of varying complexity to choose the most robust model with the fewest variables (i.e., the most parsimonious model). Conventional (random) cross-validation approaches assume that observations are independent (Trachsel and Telford 2016). However, ecological data are often spatial autocorrelated (Legendre 1993). If training and testing datasets were not spatially separated for species distribution modelling (SDM), performance statistics might be over-optimistic (Roberts et al. 2017). The variogram range method has been

used to define the optimal separation distance between training and testing sets (Valavi et al. 2019). The range was estimated using the empirical semi-variograms, and the range over which residuals are approximately independent could be used as block size for block cross-validation (Valavi et al. 2019). The semivariance variograms of the vegetation connectivity index of each vertical layer were shown in Figure A4 1 in Appendix 4. The maximum spatial autocorrelation range of vegetation connectivity index was 8km. The block size was select to be 9km in this study.

The 9km×9km spatial blocks were split into five folds of equal size, while the field observation plots located in each block was also split into five groups. The spatial distribution of blocks for each fold was shown in Figure 2-1b. One group was withheld for final validation test, while the other four groups (training sets) were used to develop the model. The training sets were repeated four times with each of four folds being withheld once as test set for model selection. Model performance indicators were gathered from test results for the four runs, and the mean values of each indicator were considered for model validation and comparison (Maroco et al. 2011). R^2 , root mean squared error (RMSE), mean absolute error (MAE), and residual standard error (RSE) were calculated for each test set to evaluate model performance.

All 62 metrics (see Table 4-2 for the complete list of predictors) were considered for inclusion in the RF analyses to estimate connectivity index. The first step of the analysis was variable selection, which involved grouping and reducing the number of potential predictors. We grouped predictor variables that had Pearson correlations >0.8. Only one variable was selected to represent each group based on lowest RMSE performed with that variable in the test set for cross validation. For example, the 19 climate variables were reduced to three variables that broadly represented temperature, precipitation, and diurnal range of temperature. The variable reduction groupings are shown in Table A4 1 in Appendices 4. After variable grouping, there were 37 variables left. We then proceeded to reduce the number of variables one by one based on the rank of importance of each predictor variable, starting with the least important. We used mixed variable importance index ($\text{MixedVI} = \text{IncMSE} \times \text{IncNodePurity} / \text{MinDepth} / \text{p-value}$) as the metric representing the importance of each variable. The combination of variables with the lowest RMSE for test sets was selected to be the final prediction model. The number of variables selected in the final model was shown in Table A4 2 in Appendices 4.

Model validation, calibration and model uncertainties

The final connectivity model selected based on four training sets were applied to final validation test set to validate the model, and applied to the whole dataset to generate calibrated connectivity index. We used generalized additive model (GAM) to fit predicted outcomes with observations. The standard error estimates are returned for each prediction to estimate 95% confidence intervals.

4.2.5 The environmental impacts on multi-storey connectivity

To understand the impacts of environmental factor on the dynamics of vegetation connectivity, we correlated the connectivity index of each vertical vegetation layer with environmental variables such as bioclimatic variables (annual mean temperature, annual precipitation) and LiDAR-derived topographic variables (slope and gully). Instead of using PDP to graphically characterize relationships between individual predictor variables and connectivity index, the relationships between environmental variable and predicted multi-storey connectivity across the whole landscape were demonstrated using “gam” method for scatterplot smoothing in R “ggplot2” package. We also summarized the connectivity index of each vertical layer across different vegetation classes and forest management zones in study area.

4.2.6 The interaction between top canopy layer and mid-/under-storey layer

We also demonstrated and compared the response of vegetation connectivity of mid-/under-storey after disturbance (either fire or logging) in the plot with Eucalypt dominated top canopy and the plot with less or no top canopy across the whole study area. The relationships were demonstrated using “gam” method for scatterplot smoothing in R “ggplot2” package.

4.3 Results

All Random Forest models of connectivity index showed reasonable goodness-of-fit statistics, with R^2 between predicted values and observed values ranging from 0.59-0.72 (Figure 4-5). The results revealed that the average multi-storey vegetation connectivity is correlated with selected LiDAR metrics. Correlations between the selected LiDAR metrics and the observed vegetation connectivity were stronger for midstorey ($R^2=0.72$) and lowest for Eucalypt dominated top canopy layer ($R^2=0.59$). The best variables for predicting connectivity index of different stratum were LiDAR derived structural variables. LiDAR-derived structural variables were found to be the most important variables as they had stronger relationships with vegetation connectivity and therefore selected in the final connectivity index prediction model (see Figure A4 2 in Appendix 4), while the majority of environmental variables were not selected to predict multi-storey connectivity. Predictive models of midstorey connectivity and wattle density only included structural variables (see Figure A4 2 in Appendices4). Midstorey connectivity was highly related to midstorey coverage (MsCover), number of midstorey trees per ha (MsNum), strata density between 10-15m (S10) and 10th percentile of 1ha-plot height (p10). The top three most important variables for predicting live wattle density were strata density between 10-25m (S15, S20) and the average canopy height of midstorey (MsHtavg). Connectivity of the shrub layer was highly correlated to strata density between 5-10m (S05) and 25th percentile of 1ha-plot height (p25). The 75th percentile of 1ha-plot height (p75) and strata density between 30-40m (S30 and S35) were significant predictors for canopy connectivity. The partial dependence plots (PDP) demonstrated illustrate the relationships between each structural variable and connectivity index of each layer and are shown in Figure A4 3-4 in Appendix 4. Different levels of connectivity for the midstorey layer resulted in different LiDAR point profiles as illustrated in Figure 4-4.

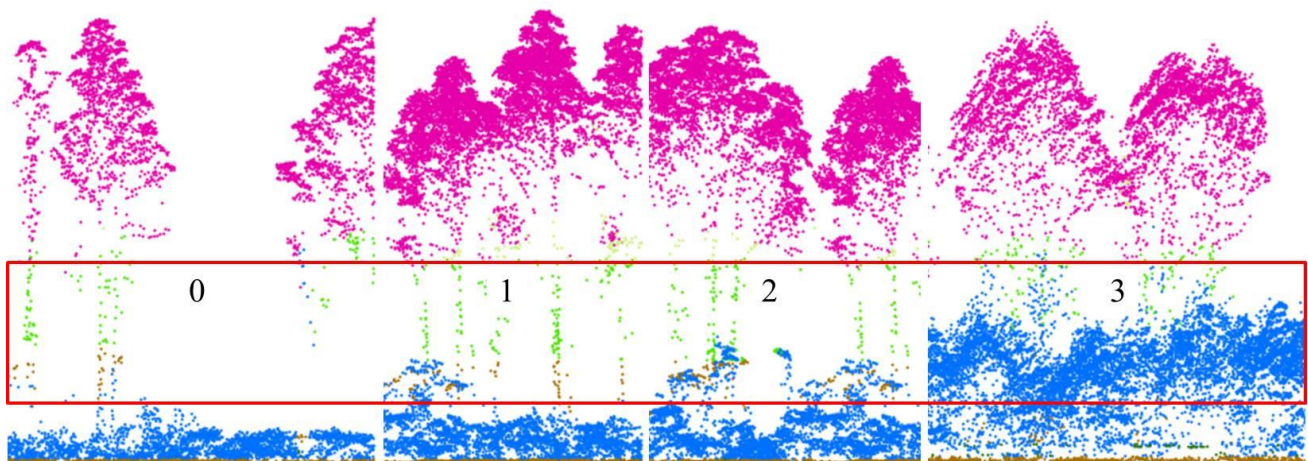


Figure 4-4 LiDAR point profiles showed different levels of connectivity index for midstorey layer (in red rectangle)

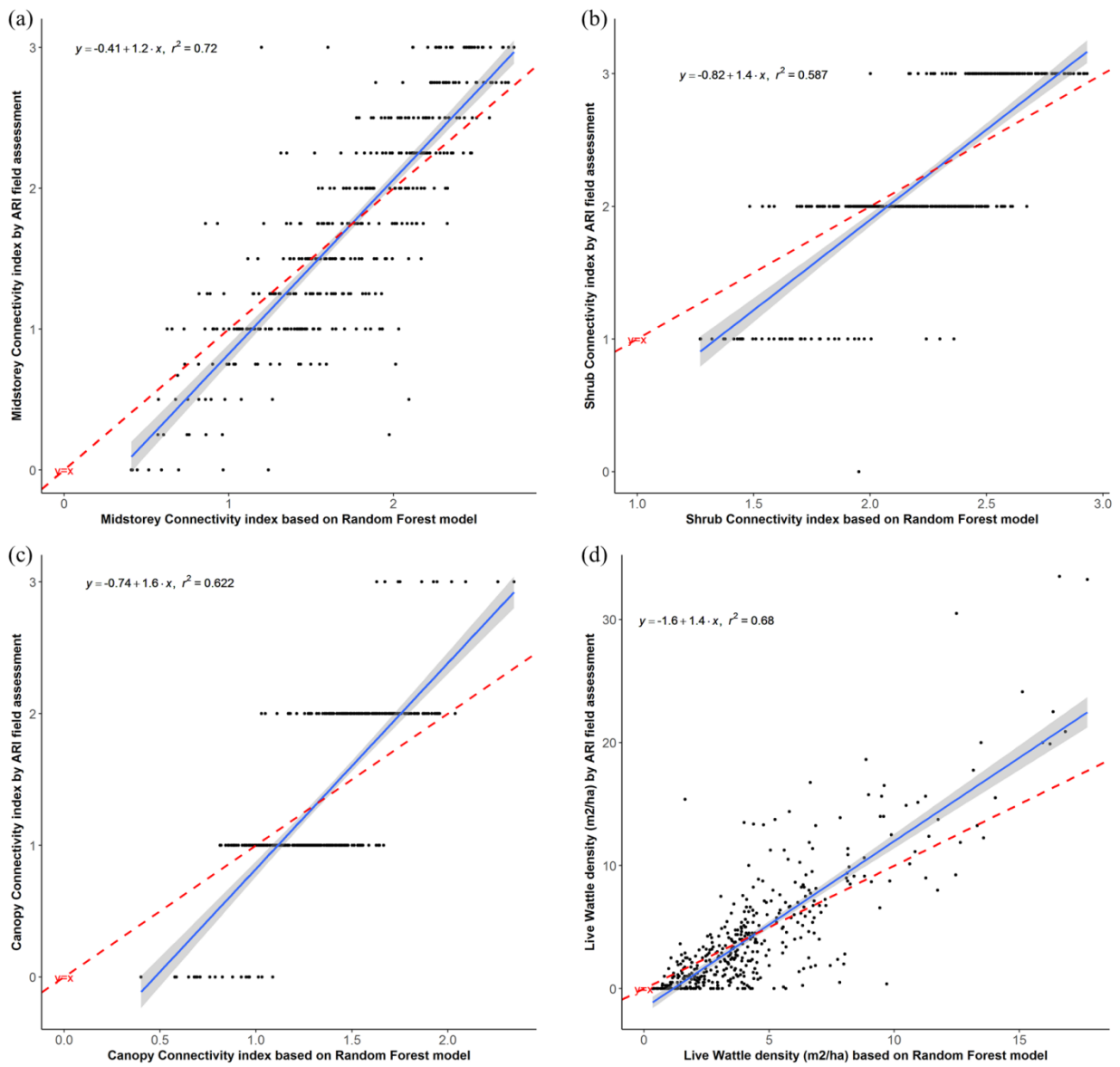


Figure 4-5 Validation results of connectivity index for a) midstorey layer; b) shrub layer; c) top canopy layer; and d) live wattle density. Red dash line ($y=x$) illustrated predicted connectivity index equal to observed connectivity index

4.3.1 Connectivity of vertical forest strata

In Victoria's Central Highland, the average shrub connectivity is higher than midstorey connectivity, and average midstorey connectivity is higher than canopy connectivity (see Table 4-3). Shrub connectivity index for the Central Highland landscape ranges from 0.79 to 3.00, with a mean value of 2.29. Midstorey connectivity index ranged from 0 to 3, with a mean value of 1.47. Canopy connectivity index ranged from 0.05 to 2.77, with a mean value of 1.32. Basal area of live wattle across the study area ranged from 0.11m²/ha to 28.45 m²/ha.

Top canopy connectivity levels were highest in wet - damp forests, while both shrub connectivity and midstorey connectivity was highest in rainforests. Mean midstorey connectivity index of rainforest was 20% higher than that of wet and damp forest; while average canopy connectivity index of rainforest was 20% lower than that of wet and damp forest. Mean live wattle density, which is the potential foraging habitat for LBP, in wet - damp forest and riparian forests was 52%-63% higher than that of rainforest. Connectivity of shrub and midstorey layers had less variance in riparian forests than other vegetation types; while canopy connectivity and live wattle density had lower variance in rainforests.

Connectivity levels varied across different forest management zones (see Table 4-3). Special management zones (SMZ) had on average higher connectivity of both midstorey and shrub layers. General management zone (GMZ) had higher density of live wattle, and higher canopy connectivity was in National Parks (Parks). Management zones where timber harvesting is not permitted (e.g., National Parks and special protection zones, SPZ) had the lower connectivity scores for sub-canopy layers. The spatial distribution of connectivity for each vertical vegetation stratum across the Central Highlands study area are shown in Figure 4-6.

Table 4-3 Data summary of predicted connectivity index of each vertical layers and live wattle density using random forest model. Mean, standard deviation (sd), minimum (min) and maximum (max), summarize predicted values across different vegetation classes and forest management zones in Victoria's Central Highland. GMZ, SMZ, and SPZ are different management zones within Victoria's State Forests (see text for details).

		All CH	Wet - Damp forests	Riparian	Rainforests	GMZ	Parks	SMZ	SPZ
Shrub Connectivity Index	mean	2.29	2.29	2.25	2.33	2.29	2.28	2.45	2.25
	SD	0.38	0.39	0.22	0.39	0.39	0.40	0.38	0.35
	Max	3.00	3.00	2.89	3.00	3.00	3.00	3.00	3.00
	Min	0.79	0.79	1.03	1.07	0.83	0.89	0.98	0.79
Midstorey Connectivity Index	mean	1.47	1.45	1.53	1.75	1.50	1.36	1.61	1.54
	SD	0.58	0.59	0.45	0.62	0.61	0.59	0.56	0.55
	Max	3.00	3.00	2.94	2.96	3.00	2.94	3.00	2.96
	Min	0.00	0.00	0.14	0.06	0.00	0.00	0.05	0.01
Top canopy Connectivity Index	mean	1.32	1.35	1.12	1.09	1.33	1.35	1.26	1.28
	SD	0.40	0.40	0.38	0.33	0.41	0.38	0.45	0.36
	Max	2.77	2.77	2.28	2.30	2.77	2.46	2.51	2.44
	Min	0.05	0.05	0.20	0.29	0.05	0.25	0.32	0.20
Live Wattle Density (m2/ha)	mean	4.44	4.47	4.82	2.95	4.99	3.14	4.65	4.00
	SD	3.94	4.02	3.41	2.27	4.30	3.07	3.94	3.27
	Max	28.45	28.45	23.80	20.42	28.45	24.40	24.78	25.68
	Min	0.11	0.11	0.19	0.16	0.12	0.11	0.13	0.14

*GMZ: general management zone; NP: national parks; SMZ: special management zone; SPZ: special protection zone

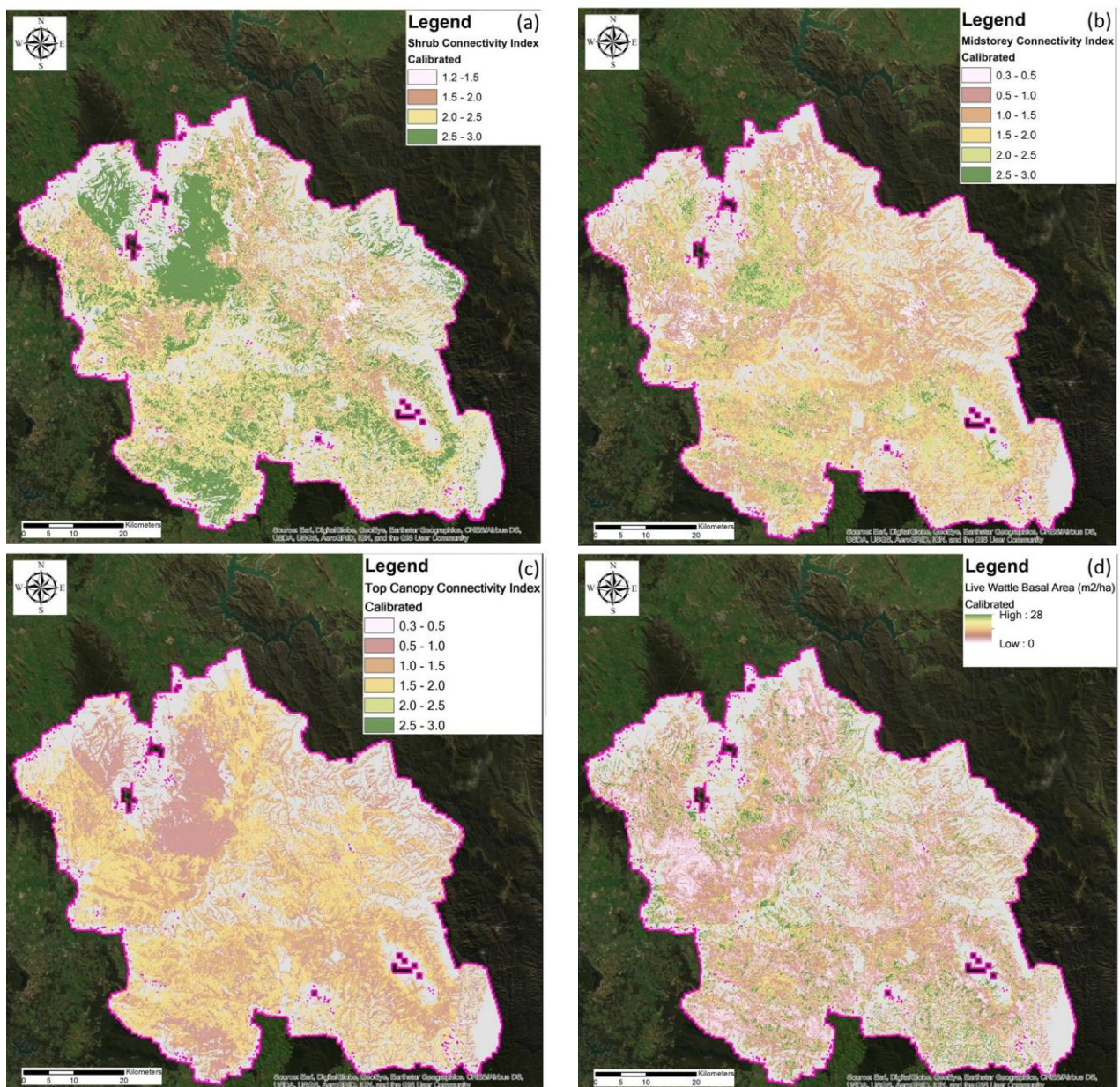


Figure 4-6 Distribution map of connectivity across Victoria's Central Highlands of a) shrub layer; b) midstorey layer; c) top canopy layer; d) Distribution map of live wattle density (potential foraging resources)

4.3.2 Forest Structure classified by vertical layer density

The study landscape was classified into 18 structure types based on multi-stratum connectivity levels (Table 4-4). The major forest structure types identified had low canopy and midstorey connectivity but high shrub connectivity (LC-LM-HS), which occupied 47.7% of entire landscape. The second most common structural type had low canopy, midstorey and shrub connectivity (LC-LM-LS, 11.2%). Third was no canopy, low midstorey connectivity and high shrub connectivity (NC-LM-HS, 10.7%) and fourth was low canopy, and high connectivity of midstorey and shrub layers (LC-HM-HS, 9.9%). The canopy profile models (CPM) of these four commonly distributed structure types are illustrated in Figure 4-7. Structure types with high midstorey connectivity, which are a critical habitat feature for LBP (Blair et al. 2017), occupied 17.2% of the study landscape.

Table 4-4 The area occupied by the 18 forest structure types classified based on connectivity profiles of vertical strata.

	Shrub	Midstorey	Canopy		
			No	Low	High
Area (ha)	Low	No	3	11,045	7
		Low	66	38,477	329
		High	687	11,688	366
	High	No	7,635	25,570	3
		Low	36,817	163,400	158
		High	12,064	33,996	215
% of total study area	Low	No	0.0%	3.2%	0.0%
		Low	0.0%	11.2%	0.1%
		High	0.2%	3.4%	0.1%
	High	No	2.2%	7.5%	0.0%
		Low	10.7%	47.7%	0.0%
		High	3.5%	9.9%	0.1%

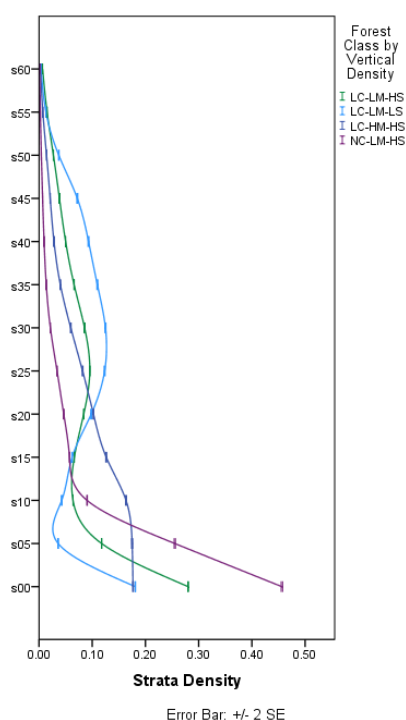


Figure 4-7 Canopy profile models (CPM) of four commonly distributed structure types in Victoria's Central Highlands

4.3.3 The impacts of environmental variables on connectivity index for each vertical layers

The relationships between connectivity index of each stratum and environmental variables across the whole study area are shown in Figure 4-8. Connectivity for all strata had non-linear relationships with annual precipitation and annual mean temperature. Canopy connectivity was highest where annual mean temperatures were between 9-13°C and annual precipitation between 1100-1800mm. Shrub stratum connectivity showed no clear trend in response to was found annual mean temperature and precipitation. Mean annual temperature did have a stronger had negative effect on midstorey connectivity. Connectivity of the midstorey stratum was 50% higher in cool areas (<7.5 °C) w than in warmer areas (>15 °C).

Slope had a stronger impact on connectivity of the shrub and canopy strata, but the response was opposite. Plots located in steeper area (slope $\geq 60^\circ$) had about 30% more shrub connectivity than flat areas (slope < 30°). In contrast, areas with the highest canopy connectivity are typically located in flat areas (slope < 35°). Connectivity of shrub and midstorey strata were not responsive to gully index, however canopy connectivity was 50% lower in gullies and increased with distance from gullies reflecting the transition from rainforest to eucalypt forest.

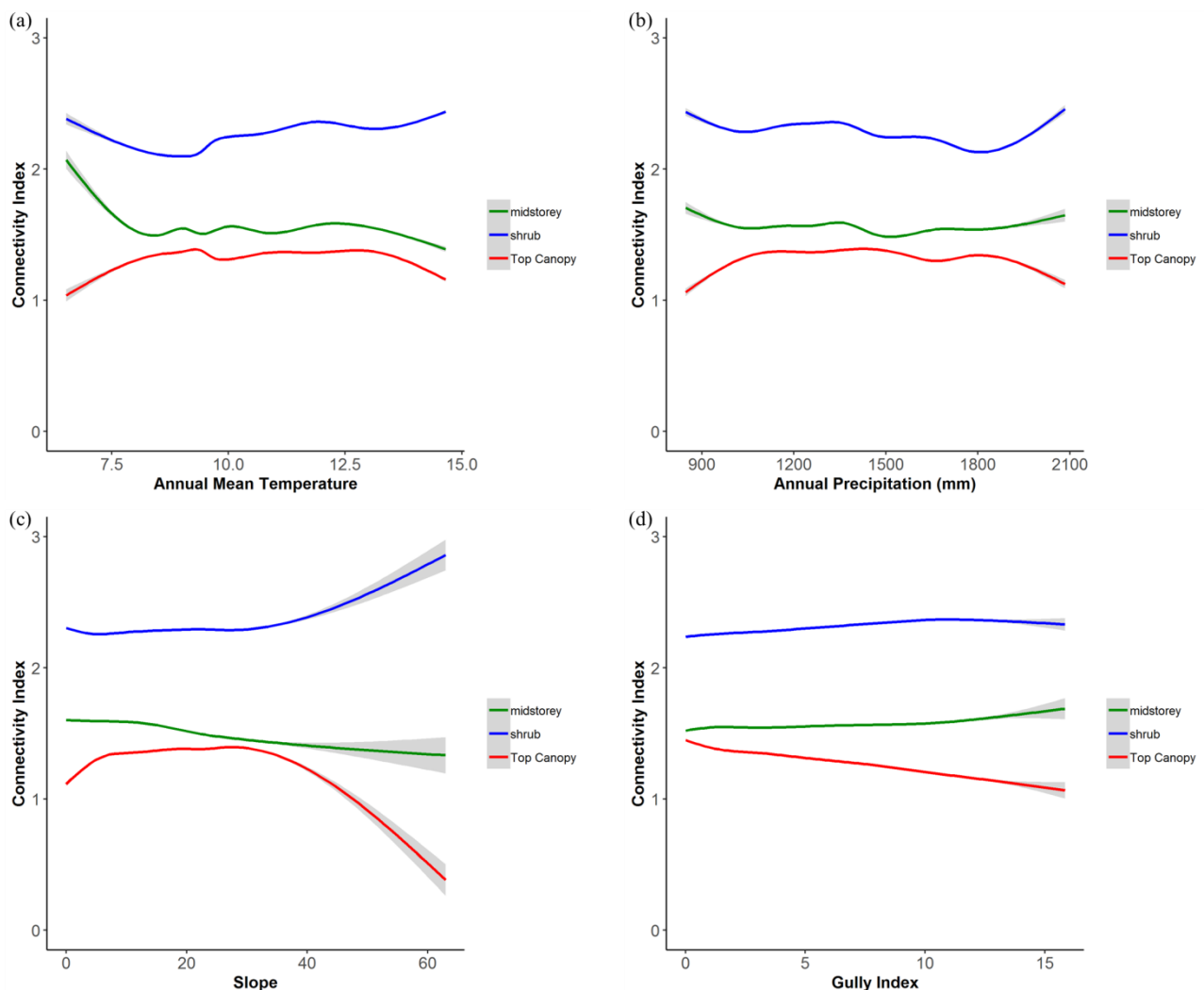


Figure 4-8 Change in connectivity for each vertical stratum in response to: a) annual mean temperature (°C); b) annual precipitation (mm); c) slope (°); and gully index. The relationships were demonstrated using “gam” method for scatterplot smoothing in R “ggplot2” package.

4.3.4 The impacts of fire and logging on connectivity

There are 219,347 ha in study area protected from timber harvesting. 48,576ha of plots had logging activities and also not visited by fire after logging. The relationship between stand age (year since last disturbance) and connectivity varied in response to fire and logging for all strata (Figure 4-9). The effect of logging on midstorey connectivity was more pronounced than for the other two strata. As shown in Figure 4-9b the highest connectivity was reached 20yrs after logging and then declined. In fire origin stands, midstorey connectivity reached peak connectivity after 40 years and then declined but not to same extent as in logged areas. Canopy connectivity in logged areas reached optimum 18-20yrs after logging, and subsequently remained stable; in contrast, in fire origin stands, canopy connectivity is variable exhibiting no clear response. Shrub connectivity peaks around 10yrs after logging and then gradually decreased. A similar pattern was found in fire origin stands; however, shrub connectivity was higher than in logged areas.

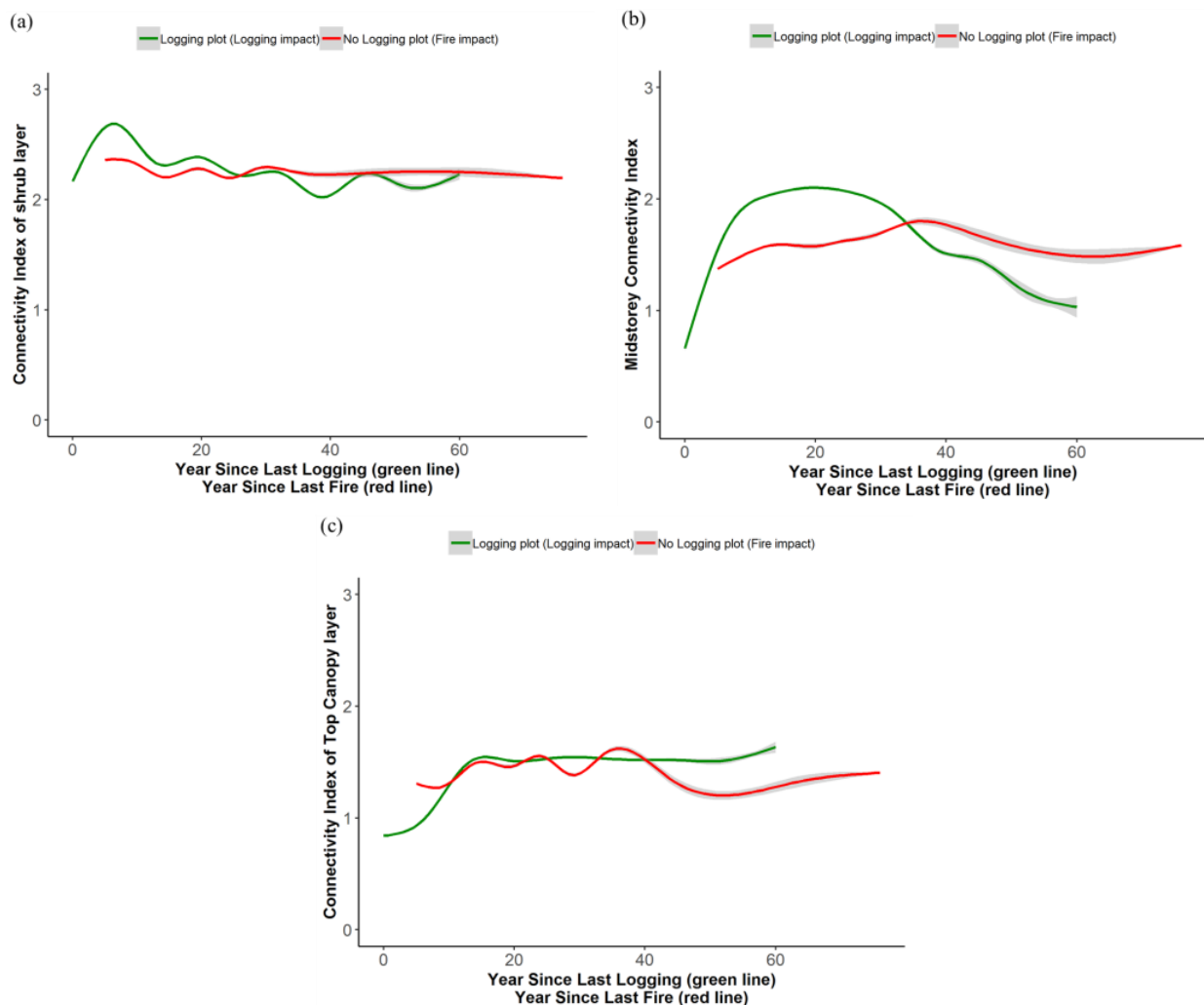


Figure 4-9 The relationship between fire (red line) or logging (green line) disturbance and connectivity index across the whole study area of a) shrub layer; b) midstorey layer; and c) canopy layer. The most recent fire occurred in 2009, and LiDAR data was captured in 2015 and 2016, so the minimal stand age of no logging plots was 6-7 yrs. Nearly all plots in study area visited by 1939 fire, so the maximum stand age of fire origin stands was -77 yrs.

4.3.5 Interactions between layers

As shown in Table 4-4, there was lack of plots with high connectivity of the canopy layer across the landscape. Based on connectivity score for the canopy, we classified the landscape into two categories: areas with Eucalypt dominated canopy layer (present-top plots), and areas with little or no Eucalypt canopy layer (absent-top plots). 83.3% of study area was occupied by plots with a eucalypt dominated canopy (~285,254ha), while 16.7% of the landscape contains forest not dominated by eucalypt cover. The connectivity of the canopy had stronger impact on the midstorey layer than the shrub layer (Figure 4-10). Higher canopy connectivity of canopy had a consistent and negative effect on the connectivity of the shrub layer. Shrub connectivity in non-eucalypt plots was always higher than in eucalypt dominated plots. Midstorey connectivity was higher in younger stands with eucalypt canopy cover but after 40 years it was higher in non-eucalypt dominated stands. In stands with eucalypt dominated canopy, midstorey connectivity peaked between 10 and 30 years before declining (see Fig 4-10).

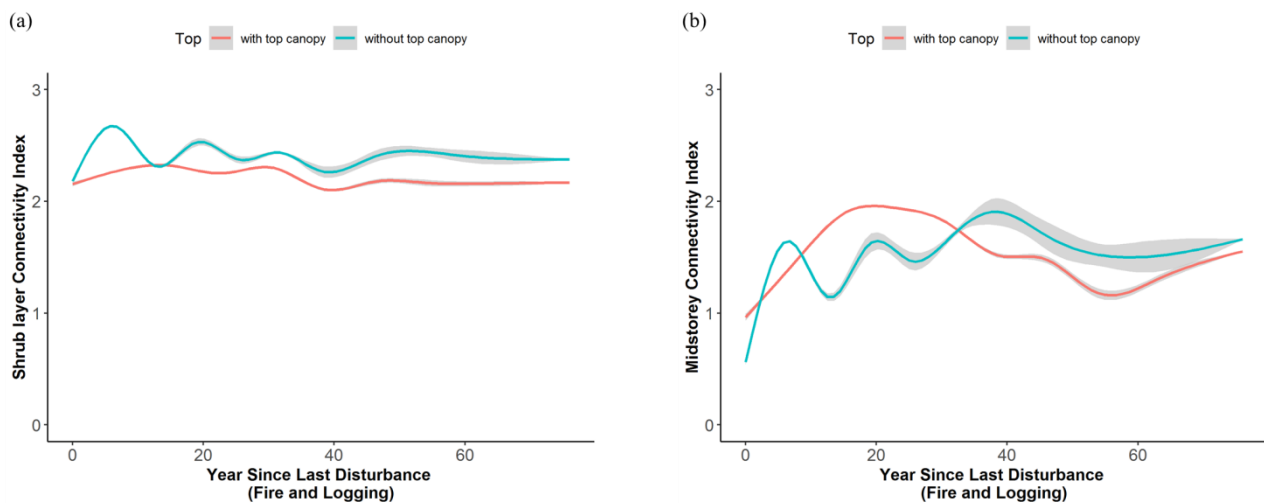


Figure 4-10 The response of vegetation connectivity after disturbance in the plot with Eucalypt dominated top canopy (red line) and the plot with less or without top canopy (green line) across the whole study area for a) shrub layer; and b) midstorey layer. The relationships were demonstrated using “gam” method for scatterplot smoothing in R “ggplot2” package.

4.4 Discussion

Fine-scale mapping of forest structure, particularly of midstorey and understorey stratum are essential for informing the management of forests for habitat conservation and fuel hazard reduction (Latifi et al. 2015a, Blair et al. 2017, Gordon et al. 2017). LiDAR-derived variables were found to be significant predictors of connectivity across forest stratum. Previous studies have found that regression models built on LiDAR metrics are worse at predicting midstorey density than overstorey density at the plot level (Coops et al. 2007, Latifi et al. 2015a). However, our prediction models found that correlations between the selected LiDAR metrics and the observed plot-level vegetation connectivity were stronger for midstorey ($R^2=0.72$) than upper canopy layer ($R^2=0.59$). The higher accuracy of predicting midstorey connectivity found in this study was due to the use of individual tree detection (ITD) method (see Chapter 2) to derive midstorey metrics instead of using a

threshold approach to demarcate canopy and midstorey stratum (Goodwin 2006). The approaches used in this study were (1) based on a function of canopy height (HCB-HT relationship in Chapter 2) and (2) identified midstorey stratum located in canopy gaps with canopy gaps detection methods. These approaches increased the detection of midstorey-only LiDAR points. The midstorey metrics generated from this filtered approach provided for more robust representation of midstorey structure which yielded stronger models of midstorey connectivity and density of live midstorey wattle.

Estimates of vegetation connectivity and live wattle density varied vegetation type in complex ways. As shown in Table 4-3, rainforest has 20% higher midstorey connectivity than that of wet and damp forest, on the contrary, rainforest has the lowest live wattle density, which is 52%-63% lower than that of wet - damp forest and riparian forests. Wattle species was major components of midstorey species in study area. This opposite distribution pattern of the predictions between live wattle density and midstorey connectivity among vegetation classes indicate that, although LiDAR data is not helpful to distinguish vegetation species at tree-level, it can be used to classify different vegetation types at plot-level, because different vegetation species often associated with different vegetation structures.

In the study area, the major forest structure type in Victoria's Central Highlands is characterized by low canopy and midstorey connectivity but high shrub connectivity (LC-LM-HS), this type occupied 47.7% of the study landscape. Areas with low canopy and shrub connectivity were found to be very rare. Lower connectivity of canopy layer likely results in higher light transmission which facilitates the development of more diverse and/ or abundant shrub layer with greater cover (Gracia et al. 2007, Coll et al. 2011). This supported by our findings on the interactions between canopy and shrub layer connectivity (see Figure 4-10). The interactions between forest stratum highlight the potential filtering of light resources that influence sub-canopy species dynamics (Simonson et al. 2014, Trouv   et al. 2019). Trouv   et al. (2019) found that midstorey *Acacia dealbata* grew more slowly, at lower abundance, and senesced earlier, when occurring in the stand overtopped by a eucalypt dominated canopy. Trouv   et al. (2019) found that the higher eucalypt basal area the greater the competitive effect on *Acacia dealbata*. We found that midstorey connectivity was lower in stands with a eucalypt dominated canopy compared to a non-eucalypt dominated canopy after 30 years after disturbance, which is congruent with the canopy-midstorey dynamics found by Trouv   et al. (2019). On the other hand, midstorey connectivity peaked 10 and 30yrs after disturbance when associated with a eucalypt dominated canopy. This may be explained by stratification theory proposed by Kohyama and Takada (2009). Kohyama and Takada (2009) showed that tree species can coexist through vertical stratification into multiple stratum if they have different maximum height traits and the sub-canopy species can tolerate growing in lower light conditions resultant from light interception in the canopy layer. In the forests of the study landscape the eucalypt canopy in mature forests can reach heights of 80 m while non-eucalypt species that comprise the midstorey layer rarely exceed 30 m in height (Costermans 2009). These differences in maximum height traits would promote one-sided competition and coexistence whereas in non-eucalypt dominated stands two-sided competition is more likely which reduces vertical stratification of the forest (Kohyama and Takada 2009).

LiDAR-based studies from other regions of the world have underlined the importance of topography on canopy characteristics (B. Jenkins and Coops 2011, Kane et al. 2015). In this study slope had a stronger influence of vegetation connectivity than other environmental variables. Midstorey was more connected near gullies and in flat riparian areas in the cooler and wetter parts of the landscape. This may be due to an increasing availability of soil nutrients and moisture in gullies. Previous studies have demonstrated that a hillslope gradient of less acidic, nutrient-rich soils of gully-bottoms to more acidic and nutrient-poor soils on ridge-tops occurs (García et al. 2006, Gomez-Aparicio et al. 2008, Aponte et al. 2011, Fedrigo et al. 2014). Another explanation is the higher probability of fire refuge and lower severity fires occurring in gullies and riparian areas (Collins et al. 2019) which could facilitate the persistence of multi-layered and connected stands.

Understating the distribution and dynamics of vegetation connectivity is critical for guiding the sustainable management of the region's forests and for conserving the critically endangered LBP (Blair et al. 2017, Trouvée et al. 2019). Management zones which are protected from timber harvesting (e.g., National Parks and SPZ) had the lowest connectivity stratum and wattle density. This suggests that LBP habitat in these zones may be more limited by connectivity and foraging habitat than by nesting resources which are more abundant in these zones (see Chapter 3). In our result, logging activities had stronger effect on vegetation connectivity than fire disturbance (Figure 4-9). Connectivity in areas subjected to timber harvesting reached its highest level at around 20 years post-harvest; this was about twice as fast as in fire-effect areas (35 years, Trouvée et al. 2019). Connectivity of midstorey however declined after 40 years to a level lower, on average, than in fire affected stands. This may reflect the greater influence of eucalypt canopy competition on increasing senescent rates of midstorey species such as *Acacia dealbata* in regenerated harvested areas compared to fire affected stands as artificial sowing of seeds in the former tends to lead to higher densities of eucalypts distributed uniformly across the harvested areas (Trouvée et al. 2019). Recruitment following wildfire tends to have a patchier distribution which promotes greater heterogeneity in canopy connectivity which can facilitate the maintenance of higher abundance of midstorey species such as *Acacia* that are critical to habitat of LBP (Trouvée et al. 2019). Studies on post-fire *Acacia* dynamics have however identified a decline in abundance after 40 years (Gordon et al. 2017) and in the Central Highlands between 60 and 100 years (Trouvée et al. 2019).

4.5 Conclusion

The results of this study highlight the utility of using LiDAR to derive landscape-scale predictions of forest structure and connectivity. For species dependent on connected canopy, midstorey, and shrub stratum, the landscape-scale, spatially-explicit predictions derived from LiDAR should provide conservation managers with the necessary datasets to develop robust models to inform conservation planning. For the critically endangered LBP, reliant on well-connected midstorey stratum, this research provides such predictions but also an understanding of the factors that help shape connectivity and foraging habitat across its home range.

This understanding is critical for improving the management of the region's forests so that habitat for LBP can be protected and created through the use of silvicultural prescriptions that balance connectivity, foraging and nesting resources over space and time.

Appendices 4

The semivariance variograms of connectivity index models of each vertical vegetation layer

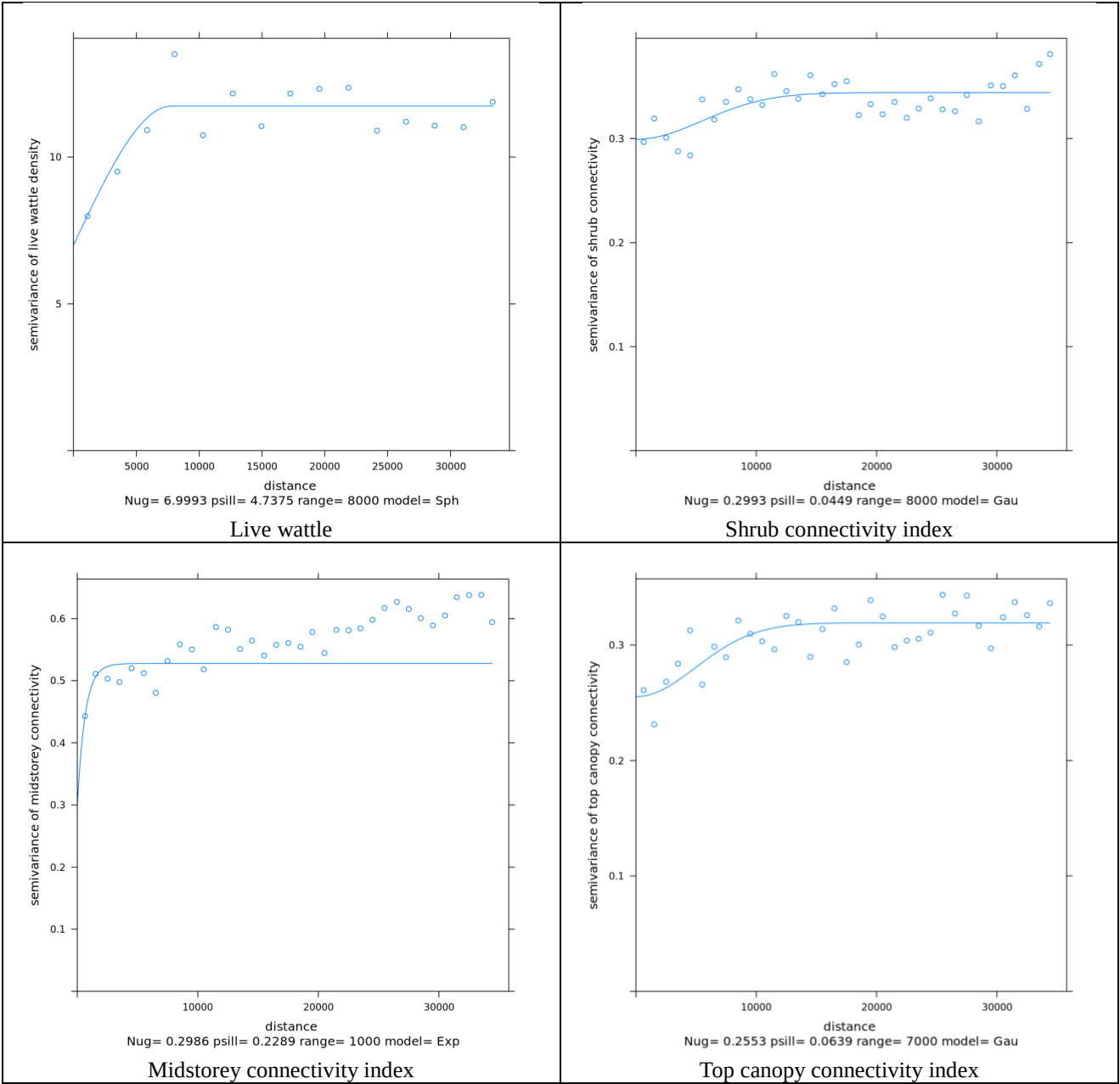


Figure A4 1 The semivariance variograms of connectivity index models of each vertical vegetation layer.

Variable selection results of habitat suitability model by Self-correlated grouping

Table A4 1 Self-correlated group of environmental variables, group member and variables selected to represent each group in prediction model of vegetation connectivity.

Group Name	Group Member	No.	Midstorey	Canopy	Shrub	Wattle
Precipitation	DEM,BIO04/12/13/14/15/16/17/18/19	10	bio17	dem	bio15	bio12
Temperature	BIO01/05/06/08/09/10/11	7	bio06	bio06	bio08	bio01
Diurnal Range	BIO02/03	2	bio03	bio02	bio03	bio02
Lidar Height	max/mean/std/p50/p75/p90	6	p90	p75	std	mean
LiDAR top canopy strata density	S55/S60	2	s55	s55	s60	s55
Overstorey Crown Counts	OvCWsum/OvN08to10/OvN10t15	4	ovn08t10	ovnum	ovnum	ovn08t10

Number of variables selected in final connectivity index models of each vertical vegetation layer

Table A4 2 The mean values of model performance indicators of final RF model of connectivity index for each layers or live wattle density using 5-fold cross validation and the number of variables selected in final model

Connectivity Index	Number of Variables	Test Set				All data
		R ²	RMSE	MAE	RSE	R ²
Midstorey	9	0.411	0.582	0.468	0.607	0.798
Live Wattle	12	0.379	4.151	2.970	0.653	0.774
Shrub	33	0.328	0.489	0.408	0.684	0.790
Canopy	32	0.276	0.494	0.379	0.750	0.780

The relative importance (increase in node purity; IncNodePurity) of different predictor variables for connectivity index models of each vertical layers

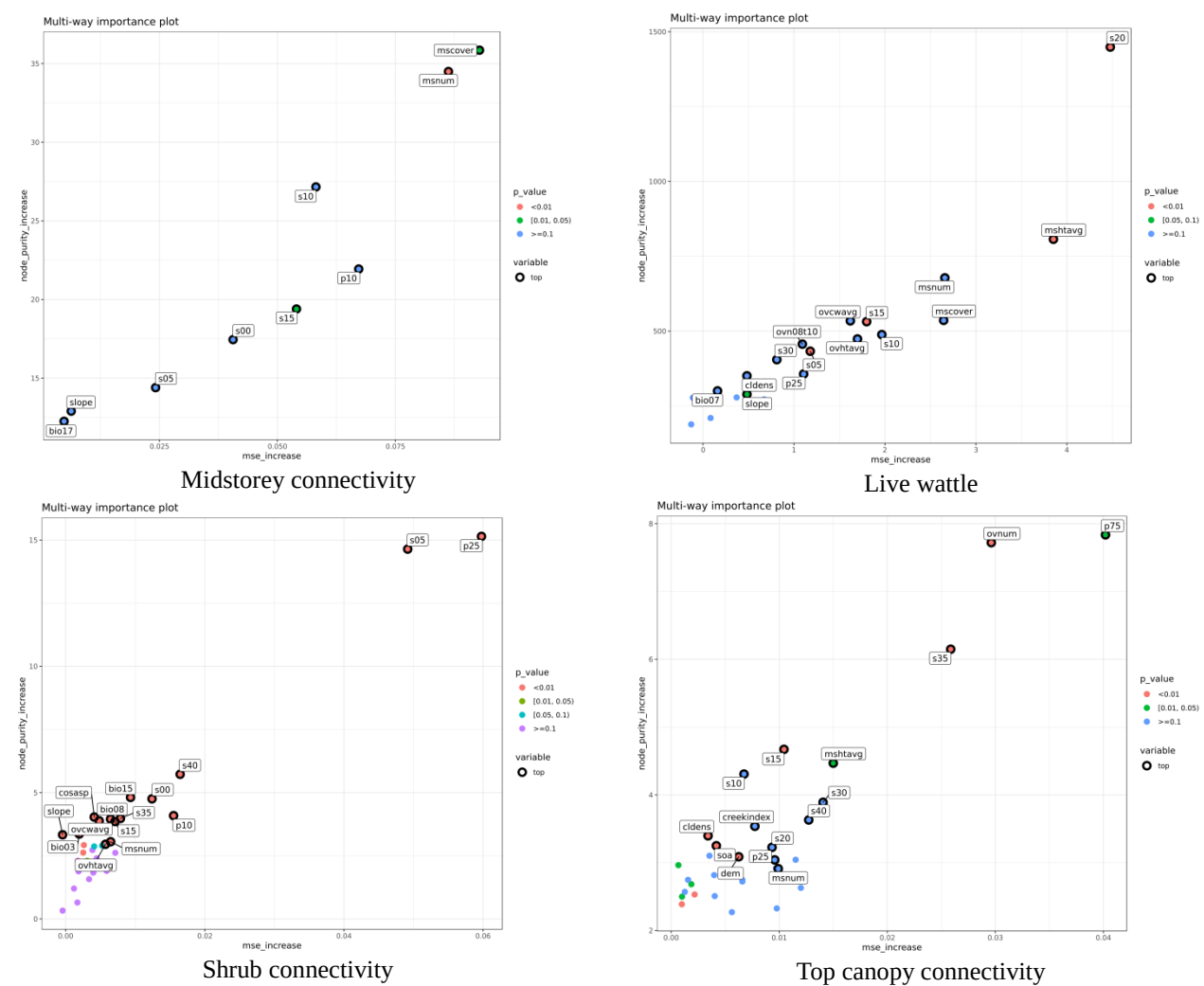


Figure A4 2 The relative importance (increase in node purity; IncNodePurity) of different predictor variables for each connectivity index of each vertical layers or live wattle density model using Random Forest algorithm.

Predictor structural variables for forest stratum

Strata density

Stratum density of the ground layer (height between 0-5m, S00) had a positive effect on shrub connectivity and negative effect on top canopy and live wattle density. S05 (height between 5-10m) is the most influential stratum density for predicting shrub connectivity. S05 was positively related to shrub connectivity but negatively related to canopy connectivity.

S10 was positively related to midstorey connectivity, midstorey was only related to S10. S10 was negatively related to shrub and canopy connectivity. Live wattle density was found to be at its lowest when S10 was around 10%-20%.

S15 and S20 are more important for predicting live wattle density than density of other stratum. S15 and S20 were positively related to live wattle density negatively related to shrub connectivity, and of little influence on canopy connectivity.

S30 and S35 were more important to canopy connectivity than other stratum density. S30 and S35 were positively related to canopy connectivity but negatively related to shrub connectivity.

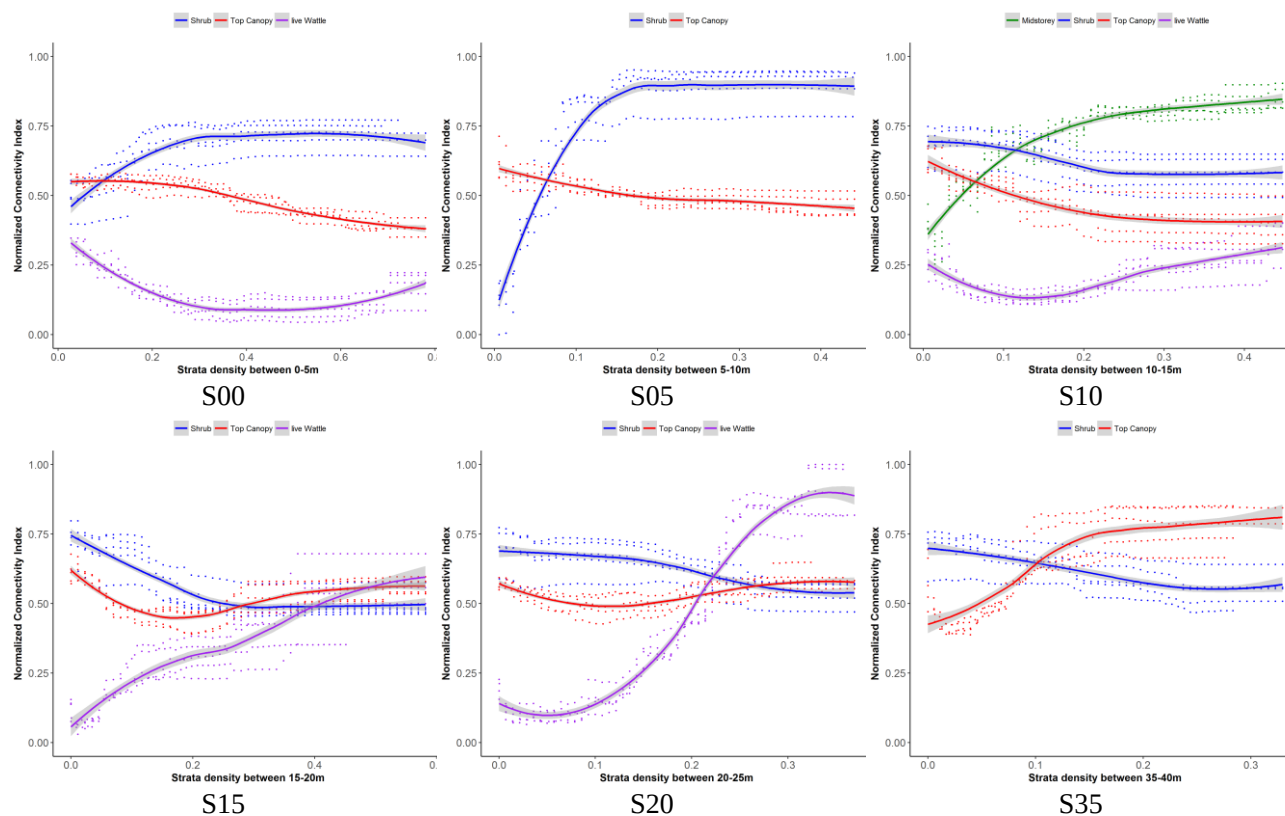


Figure A4 3 Partial dependence plot (PDP) of random forest model showing relationship between strata density and connectivity of each vertical layers

MsCover, MsNum an MsHtavg

Midstorey connectivity and live wattle density are all positively related to MsCover and MsNum. MsCover and MsNum are of lesser importance to shrub and canopy connectivity. The positive effect of average midstorey height on live wattle density is stronger than that of MsCover and MsNum on live wattle density.

Average dominant overstorey canopy height (OvHtavg) is negatively related to live wattle density and canopy connectivity suggesting that the shorter the overstorey canopy is the denser the wattle and canopy layer are. So young dense forests have more wattle and tall older forests have less. When average dominant overstorey crown width (OvCWavg) is $> 10\text{m}$, live wattle density was positive related to overstorey crown width. Canopy connectivity was positively related to number of dominant overstorey trees with crown width between 8-10m (OvN08t10)

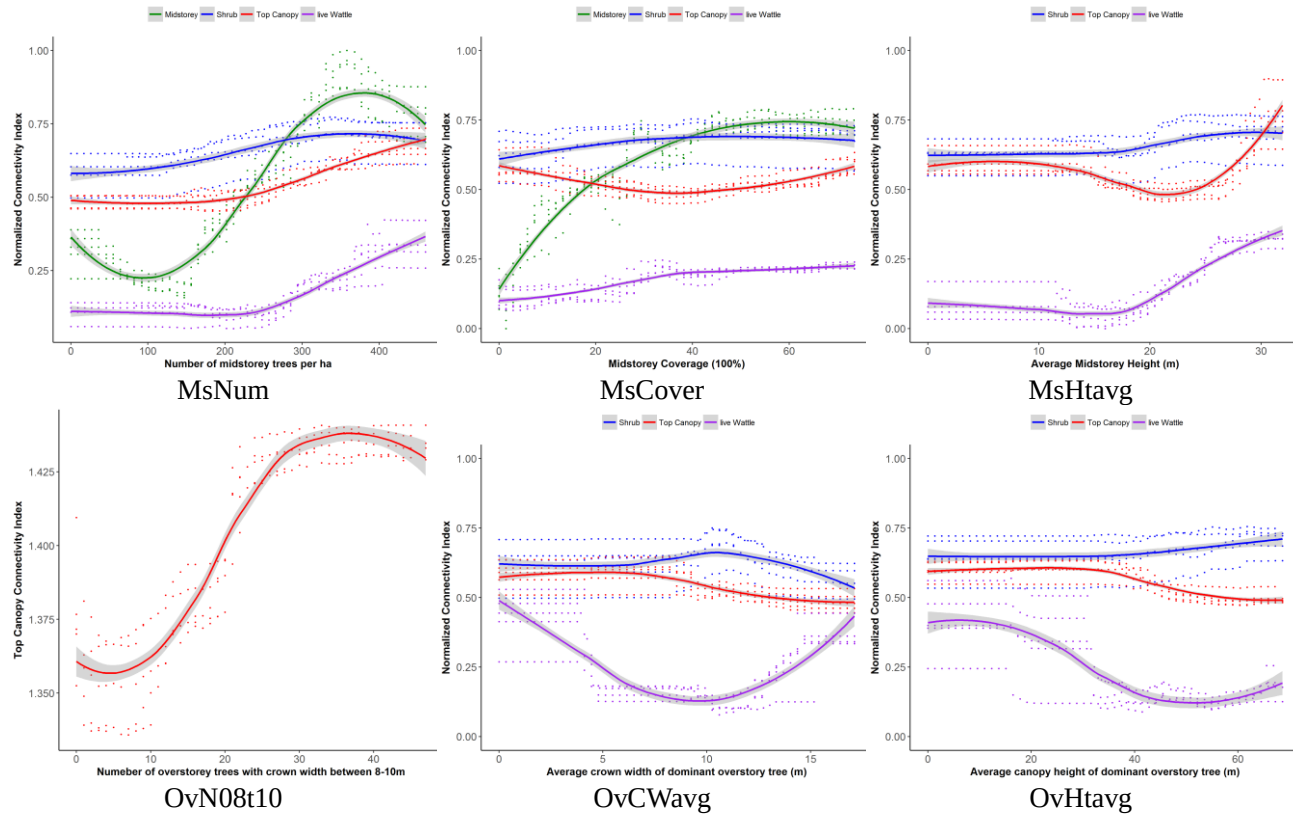


Figure A4 Partial dependence plot (PDP) of random forest model showing relationship between over-/ mid-storey metrics and connectivity of each vertical layers

Percentile of 1ha-plot height

Increased midstorey connectivity was found where the 10th percentile 1ha-plot height (p10) was > 5m. P10, p25 and p75 all had a negative effect on shrub connectivity. P75 was the most important variable influencing canopy connectivity. The highest canopy connectivity occurred when p75 was >40m.

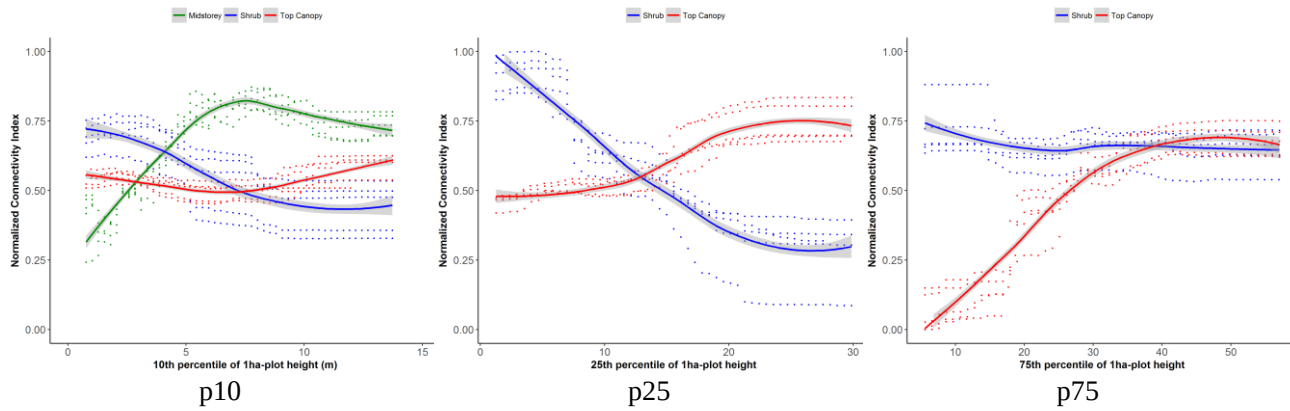


Figure A4 5 Partial dependence plot (PDP) of random forest model showing relationship between percentiles of 1ha-plot height and connectivity of each vertical layers

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Chapter 5.

5 Landscape-scale habitat suitability analysis for Leadbeater's Possum using LiDAR data in Victoria's Central Highlands

Abstract

Biodiversity loss is a global phenomenon. To prevent more species from extinction, improved management of biodiversity is essential; however, this requires measurable outcomes that can guide conservation efforts. Habitat suitability models are a widely used tool for setting conservation objectives and evaluating outcomes. Models that provide information on the potential distribution and abundance of a given species or its habitat are critical for informing conservation decisions. Most landscape-scale habitat suitability models use data on land use, vegetation type, climate, and soils, but rarely include data on key ecological structures that can have a significant influence on the occurrence and abundance of a species. LiDAR (Light Detection And Ranging) data into habitat models can bridge this gap by providing high-resolution descriptions of vegetation structure at fine spatial grains over large areas. In this study, we develop a landscape-scale habitat suitability model for the critically endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*, LBP). We used forest structure and topographic metrics generated from a high-resolution LiDAR dataset coupled with climate and management history data for a ~340,000 ha landscape in Victorian Central Highlands of southeastern Australia. We calibrated and validated the model using a network of 422 1-ha plots that surveyed for LBP and included detailed descriptions of vegetation structure. The validated habitat suitability model had an overall accuracy of 87.3% and an AUC of 0.889 in test dataset. The model predicted that 33,000 ha (95%CI: 25,000ha-43,000ha) of the study landscape (i.e., 9.57%) supported suitable habitat for LBP. We identified 17 significant variables that had the strongest influence on habitat suitability for LBP, including four related to foraging habitat, three to nesting habitat, three to climatic and topographic factors, and two to disturbance history. Our approach highlights the potential of using high-resolution, spatially explicit data on forest structure at a landscape-scale to map the distribution and abundance of suitable habitat for a critically endangered species.

5.1 Introduction

Biodiversity loss is a global phenomenon (Lindenmayer 2015b). Australia has the highest rate of mammal extinction in contemporary times and has an increasing number of threatened species that are on the verge of extinction (Woinarski et al. 2014b, Woinarski et al. 2015). To prevent future species loss, improvements in biodiversity management and monitoring programs are essential for balancing resource use and biodiversity conservation (Hawthornthwaite and Bull 2007, Li et al. 2011, Lindenmayer 2015b). At present, large-scale evaluation of conservation efforts in Australia are lacking (Cresswell and Murphy 2017, Scheele et al. 2018) despite spatial conservation prioritization, restoration planning and land-use management often operating at landscape scales (Ricklefs 2004, Bässler et al. 2011). Tools for quantifying habitat quality and predicting biodiversity changes at multiple spatial scales are required for biodiversity conservation (Elith 2000, Farrell et al. 2013, Leroux et al. 2017).

Habitat suitability models or indices (HSI) are a widely used tool for evaluating conservation outcomes, with the objective of quantifying the potential distribution and/or abundance of a species by estimating the amount and quality of habitat within a landscape (Turner et al. 2001, Edenius and Mikusiński 2006, Martinuzzi et al. 2009). They are a fundamental tool that researchers and managers use to make management decisions over large areas (Guisan and Zimmermann 2000, Pearson 2007, Tattoni et al. 2012). Habitat suitability models quantify species-habitat relationships based on presence/absence or presence-only data and their relationships with environmental variables (Martinuzzi et al. 2009, Tattoni et al. 2012). A reliable and accurate prediction of habitat suitability depends on the quality of data used to build the model (Martinuzzi et al. 2009, Tattoni et al. 2012). Traditional sources of environmental data at landscape scales typically include land use, soils or geology, and climate; however, information on important ecological features that species may utilize are typically excluded as they are rarely available in spatial datasets. The lack of spatially explicit metrics of key ecological features is a major limitation for modelling the habitat of species across broad scales. (Martinuzzi et al. 2009, Blair et al. 2017). LiDAR (Light Detection And Ranging) is remotely sensed data that could fill these data gaps as it provides fine-grained, three-dimensional information on both horizontal and vertical vegetation structure (Lefsky et al. 2002, Zimble et al. 2003, Miura and Jones 2010, Bässler et al. 2011), and the spatial distribution of key habitat structures (Vierling et al. 2008, Falkowski et al. 2009, Korpela et al. 2009, Vehmas et al. 2009, Collin et al. 2010, Bässler et al. 2011). A key strength of LiDAR is its ability to capture subtle differences in vegetation structure within and between forest types, as well as variations in sub-canopy structure (Bässler et al. 2011, Fedrigo et al. 2018). LiDAR has also been used to quantify the distribution of tree senescence classes and growth forms (Bater et al. 2007, Owers et al. 2014, Wing et al. 2015). This level of information on forest structure can improve the knowledge of species-habitat relationships for a range of forest-dependent species (Jaime-González et al. 2017). For example, LiDAR has been successfully applied to the prediction of species occupancy and species diversity in woodlands and forests (Hinsley et al. 2006, Vierling et al. 2008, Müller and Brandl 2009, Müller et al. 2009, Bässler et al. 2011, Vierling et al. 2011b, Jaime-González et al. 2017). The accuracy of LiDAR-derived habitat suitability models from previous studies has ranged from 79-92% (Martinuzzi et al.

2009, Goetz et al. 2010, Garabedian et al. 2014). In northeastern Italy, Tattoni et al. (2012) demonstrated that LiDAR-derived habitat variables (tree height, tree density, and length of ecotone) statistically improved the predictive power of habitat models for four species of birds. The improved models resulted in improved mapping of the spatial patterns of each species' habitat. Jaime-González et al. (2017) found that LiDAR-derived variables performed better than field-based variables for modelling habitat preferences of the wood mouse (*Apodemus sylvaticus*). A key strength of using LiDAR for habitat modelling is the objective measure of fine-scale data, which are typically restricted to observations from plot-data, across broad spatial scales (Jaime-González et al. 2017).

In this study, we use LiDAR data to model a habitat suitability index for the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*), across the wet eucalypt forests of the Victorian Central Highland in southeastern Australia. Leadbeater's possum (LBP) is a small, nocturnal and arboreal mammal, with a body length of 150 – 170 mm and tail length of 145 – 180 mm (Macfarlane et al. 1997). LBP has been classified as a critically endangered species, currently listed under the Victorian Flora and Fauna Guarantee Act 1988, Environment Protection and Biodiversity Conservation Act 1999, and is on the IUCN Red List of Threatened Species. The majority of the LBP's diet is exudates, including plant exudates (gum, sap, or nectar), and insects exudates (Smith 1980, Harley 2005). LBP also feeds on arboreal arthropods (including beetles, spiders and, particularly, large crickets) for protein intake (Smith 1980, Smith 1984, Harley 2005). LBP is predominantly distributed in the wet and montane wet eucalypt forests and subalpine woodlands of the Central Highlands (Commonwealth of Australia 2016). The main occurrence of LBP is in the region's montane ash forests (Blair et al. 2017). The dominant canopy tree species in these forests are mountain ash (*Eucalyptus regnans*), alpine ash (*E. delegatensis*), and shining gum (*E. nitens*). LBP habitat is defined by two specific features of these forests: a well-connected understorey for movement and foraging and hollow-bearing trees (HBTs) for nesting (Smith and Lindenmayer 1988). Areas of these forests that contain a well-connected understorey, predominately comprising wattle (*Acacia* spp.) species (silver wattle (*Acacia dealbata*), mountain hickory wattle (*A. obliquinervia*), and forest wattle (*A. frigiscens*) provide foraging habitat and movement corridors for LBP to move through (Lindenmayer 1989b, Lindenmayer et al. 2000). Large, old trees and stags that contain hollows provide critical nesting habitat for LBP. The occurrence of HBTs, either living or dead, and high density of *Acacia* are of equivalent importance for determining the occupancy of a site by LBP (Lindenmayer 1989a, Lindenmayer et al. 1991b). Importantly, these two resources must either co-occur within a site or be within close proximity for habitat to be considered high quality. How far LBP will move between these two resources is unclear. However, based on short-term radio-tracking data, LBP can move 100 m (and sometimes up to 600 m) between den sites in hollow-bearing trees (Lindenmayer et al. 2018).

It has been suggested that LBP populations are declining due to a loss of HBTs resulting from the cumulative effects of wildfire and timber harvesting (Blair et al. 2017, Blair et al. 2018). The observed decline in LBP site occupancy is based on long-term data from a network of monitoring sites in HBTs have declined over

time (Lindenmayer and Sato 2018). Changes in wattle abundance in these forests and the impact this may have on LBP site occupancy have not been reported; however, recent analyses suggest that this dynamic may contribute to site-level declines (Trouv  t al. 2019). A major issue with extrapolating fine-scale measures of these critical habitat elements to the landscape is the lack of spatially explicit data on their occurrence and abundance. Taylor et al. (2017) classified areas within the known LBP range as having no HBTs, dead HBTs, or living and dead HBTs based on assumptions related to forest age and disturbance history; however, their approach was subjective and lacked any metric of HBT abundance. While future LBP habitat is predicted to decline at known monitoring sites (Lindenmayer and Sato 2018), the absence of spatially explicit, landscape-scale data on the key habitat features limits empirical estimates of broader decline to extrapolation from the small number of existing study plots. A more effective approach to estimating LBP habitat trajectories would be to develop habitat models that are based on objective, high-resolution measurements of forest structure across the entire forested landscape.

Current models of LBP habitat distribution have been based on presence-only models (Taylor et al. 2017), which provide a measure of habitat suitability (but not occupancy (Gormley et al. 2011)) and habitat occupancy using presence/absence data (Lumsden et al. 2013b). Current LBP habitat models are primarily based on bioclimatic and GIS-based variables of forest structure. These data make assumptions about the occurrence of HBTs, *Acacia* density, and vegetation connectivity that are approximate at best and likely have wide margins of error (Blair et al. 2017). To address this issue we used a set of LiDAR-derived environment and habitat variables, including landscape-scale data on HBT density and vegetation connectivity, to map the extent of LBP habitat in Victoria's Central Highlands. The specific objectives of the study were to:

1. develop an objective model to predict the distribution of LBP habitat at the landscape-level using fine-scale data; and,
2. determine the influence of structural, climatic, topographic and disturbance variables on the occurrence of LBP habitat.

5.2 Method

5.2.1 Study area

The study area is located in Victoria's Central Highlands in southeastern Australia (Figure 4-1a). The Central Highlands experience cool summers and humid winters with frequent frosts and occasional periods of snow (Burns et al. 2015). Over the period 1981-2010 mean annual temperatures ranged from 615 °C and mean annual precipitation ranged from 690-2090 mm (Stewart and Nitschke 2017). The three major vegetation classes in this study are wet or damp forest, riparian forest, and rainforest. The composition of the study area is dominated by wet or damp forest (89%), followed by riparian forest (7%), and rainforest (4%). The dominant tree species in the wet or damp forest are mountain ash (*Eucalyptus regnans*), alpine ash (*Eucalyptus delegatensis*), and shining gum (*Eucalyptus nitens*). The 2009 Black Saturday bushfire burned 30-35% of the mountain ash forest (Leadbeater's Possum Advisory Group 2014).

5.2.2 Field-based habitat assessment for LBP

Ground-based surveys of hollow-bearing trees (HBTs) and vegetation connectivity were conducted by staff from the Arthur Rylah Institute for Environmental Research (ARI). Between 2014 and 2017 they established and surveyed 438 sites within the Central Highlands. Within each site they established a 1-ha plot and made a detailed description of forest structure and a complete inventory of HBTs. In total, 1653 HBTs were located, mapped, and measured for diameter and height, form class, and observed hollow attributes. Connectivity at the shrub, midstorey, and canopy layers within a subplot of 10 m radius were scored across the north to south transect at each site. The basal area of *Acacia* spp. was measured in each subplot.

LBP occurrence data (presence/absence) was collected by ARI and Vicforests in 576 plots across the three major EVCs. This included 518 sites in wet or damp forest, 17 sites in riparian forest, and 41 sites in rainforest. Among those 576 observation plots, 135 of them were located in forest burnt in 2009, and 12 of them recorded LBP presence, 8.9% of the plots. Two to three baited remote cameras were set at nest trees or in foraging habitat at each site and left in place for a minimum of 3-4 weeks to capture photos of LBP (Nelson et al. 2015). Of the 1107 cameras, 227 recorded the presence of LBP at the site. In all, LBP were found in 160 (28%) of the plots (green dots in Figure 4-1a).

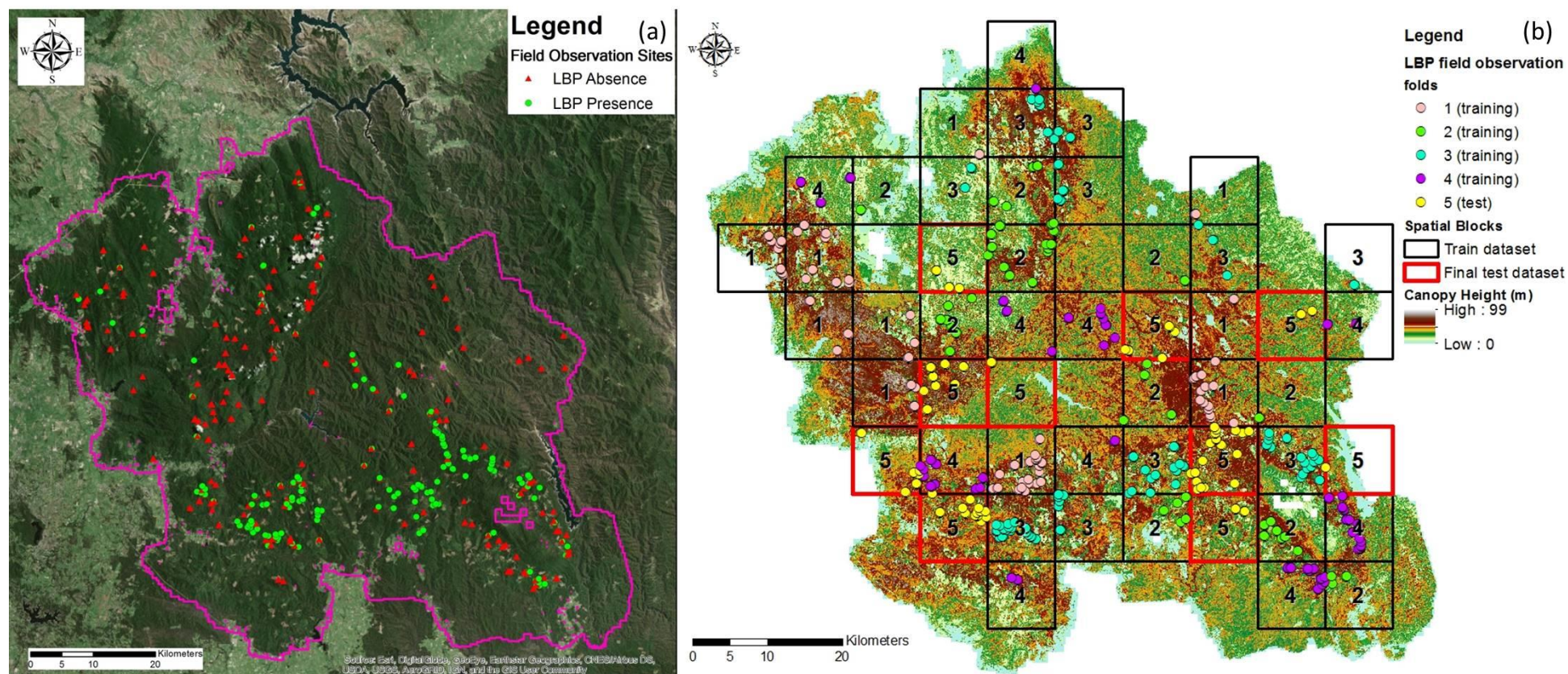


Figure 5-1 The study area in Victoria's Central Highlands. The map shows (a) the total LiDAR coverage and the locations of field LBP observation sites, and (b) the location of each fold of 5-fold block-cross validation.

All HBTs were classified into one of nine forms, defined by the degree of senescence and collapse (Figure 5-2). The HBTs were also classified as either survey standard HBTs or ecological HBTs. Survey standard HBTs can be mature, senescent, or dead trees, which contain at least one hollow, are >6m tall and >1.5m DBH, and are either mountain ash, alpine ash, or shining gum. These trees meet current criteria for potential HBTs in the published government survey standards (Nelson et al. 2017). Ecological HBTs may be living or dead trees of any species and must contain an observable hollow. Hollows include cavities, spouts, broken tops and/or cracks/fissures. Dead trees <50cm DBH were excluded, unless an obvious LBP-type hollow was present. A notable difference between the survey standard and ecological HBTs was the inclusion of hollows in many understory species, including *Acacia dealbata*, *A. frigescens*, *A. melanoxylon*, and *Nothofagus cunninghamii*.

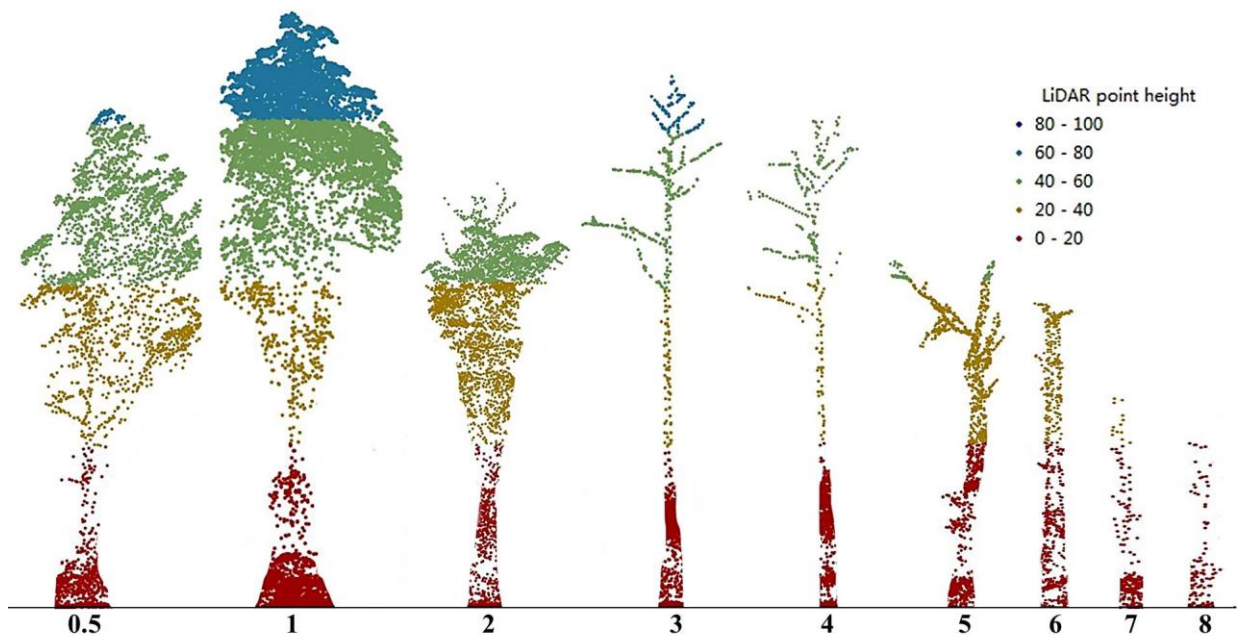


Figure 5-2 LiDAR point profiles of nine forms of potential hollow-bearing trees (modified from Smith and Lindenmayer 1988 and Smith et al. 1991):

0.5, Not yet mature; 1, Mature living tree; 2, Mature living tree, dead or broken top; 3, Dead tree most branches still intact; 4, Dead tree with 0-25% of top broken off, branches stubs only; 5, Dead tree top 25-50% broken off; 6, Dead tree top 50-75% broken off; 7, Solid dead tree >75% broken off; 8, Hollow stump

The definition of vertical vegetation layers was dependent on vegetation type and canopy height. The height of shrub layer is >0.5 and <5m. The common species in the understorey were tree ferns (*Dicksonia antarctica*, *Cyathea australis*) and woody shrubs, in particular *Correa* spp., *Zieria arborescens*, *Tasmannia lanceolata*. The midstorey layer is the upper foliage of taller shrubs (above 5m) and was dominated by *Bedfordia*

arborescens, *Pomaderris aspera*, and *Acacia* species. The canopy layer was dominated by eucalypts. Non-eucalypts were not found in the canopy layer. In rainforest dominated plots, *Nothofagus cunninghamii* and *Atherosperma moschatum* were considered as occurring in the midstorey. Connectivity at the shrub, midstorey, and canopy layers was scored based on the presence of vegetation at each layer and the ability of LBP to move through it. The connectivity index was based on the following classes:

- 0 = Connectivity absent, zero opportunity for LBPs to move around in that layer;
- 1 = Connectivity present, but minimal;
- 2 = Connectivity present, LBPs can move around relatively easily but may need to move into another layer to access a different part of the layer in question within the 10 m radius plot; and,
- 3 = Connectivity continuous, LBPs can access every part of the 10 m radius plot within that layer

5.2.3 Lidar metrics and GIS products

LiDAR raw data

Discrete return airborne LiDAR data were acquired by RPS Group Plc in late 2015 and early 2016 using a Trimble AX60 laser sensor mounted on a fixed-wing aircraft. The aircraft was flown at 800 m above ground with flying speed of 62 m/s. The mean number of pulses per meter sent to ground was 2-4 pts/m with an average point spacing of 0.46 m. LiDAR data covered 513,322 hectares (ha) of Victorian Central Highlands (coverage can be seen in purple polygon in Figure 4-1). After filtering the landscape for ecological vegetation classes (EVCs) relevant to our study objectives, the final study area was ~343,000 ha. This included 305,600 ha of wet or damp forest, 24,900 ha of riparian forest, and 12,500 ha of rainforest. Within this area, 112,205 ha (32.8% of the total area) were burnt in the 2009 Black Saturday bushfire.

Climate, Forest Type and Disturbance Data

Ecological Vegetation Classes (EVC), Forest Management Zone (FMZ), logging history and fire history spatial data used were sourced from the Victorian Department of Environment, Land, Water, and Planning (DELWP). Nineteen bioclimatic variables used in these analyses (Table 3-1). Bioclimatic variables for temperature developed by Stewart and Nitschke (2017) were used. Precipitation based BIOCLIM variables used were from Fedrigo et al. (2019). The resolution of bioclimate data was 250m. Kriging interpolation was used to change the resolution of bioclimate data into 100m.

LiDAR topographic metrics

A high-resolution digital elevation model (DEM) was derived from a LiDAR ground-based point cloud using FUSION/LDV Software (McGaughey 2009). From this DEM the slope, aspect, and slope of aspect (SOA) were generated using ArcGIS (v. 10.5). SOA represents the rate of change of the aspect in the horizontal direction (Zhou et al. 2018); therefore, the maximum value of SOA is located at topographic dividing lines such as ridges or gullies. A gully index was calculated from a high value of SOA and negative terrain surface. The negative terrain surface was created using ArcGIS focal statistic tool (“moving window”) to identify relatively lower surfaces within a specific neighborhood. The resolution of all LiDAR topographic metrics was 1ha.

LiDAR structural metrics

LiDAR-derived metrics of forest structure were derived from height or height-related variables. The percentiles of stand height and strata density (percentage of LiDAR points between two heights) are commonly used LiDAR metrics (Goodwin et al. 2006, Hudak et al. 2008, Martinuzzi et al. 2009, Mitchell et al. 2012). For example, the 99th percentile is often used to represent maximum stand height rather than the maximum z-value of LiDAR points, thereby eliminating the influence of extreme outliers (Jenkins 2012). Strata density is often used to represent foliage density or connectivity within a vertical layer (Parker et al. 1995, Parker et al. 2004). The LiDAR structural metrics used in this study are listed in Table 3-1. The resolution of all LiDAR structural metrics was 1ha.

LiDAR overstorey and midstorey metrics

LiDAR overstorey and midstorey metrics were derived from the results of individual tree detection and delineation (see Chapter 2). For overstorey, the locations of individual tree tops, crown widths (CW), and tree height (HTs) can be determined using individual tree delineation (ITD) algorithm. These can then be aggregated into plot-level variables (1ha plot), such as the number of trees per hectare, mean crown width, and mean crown height. Individual trees were classified into four size classes based on crown width (see more in Chapter 2) based on crown width to represent different growth stages of the forest. We also calculated perimeter-to-area ratios for all crowns >8m wide. Crowns with large perimeter-to-area ratios indicated

irregular crown forms. A live tree with a well-formed crown will have a relatively low line density and therefore a small perimeter-to-area ratio, whereas a standing dead snag with lots of dead branches will have high line density values. We used the line density of crown edges derived from the crown-edge detection step of ITD to compute a Stag Index (CLdens in Table 3-1) describing the irregularity of the crown shape. For the midstorey within each plot, LiDAR points were used to calculate the proportion of projection area of midstorey LiDAR points, a surrogate for midstorey density. The detection results for tree tops in the midstorey were used to determine the number of trees and the mean midstorey height within each plot.

Habitat feature metrics

The density of HBTs in each form class (Chapter 3), *Acacia* basal area, and the connectivity score of each vegetation layer at each site (Chapter 4) were used as predictors in our models of LBP habitat suitability.

In total, we considered 70 habitat-related variables to build the habitat suitability model. These variables are shown in Table 3-1. They include vegetation class, year of most recent fire, year of most recent logging, 19 climate variables, seven topographic variables, 33 plot structure variables (including 9 for overstorey and 3 for midstorey), and 7 habitat feature variables (including 3 for HBTs and 4 for connectivity).

Table 5-1 LiDAR Metrics used to build classification model

Category	Variables	Short Name
Vegetation type	Ecological Vegetation Classes	EVC
Disturbance	Year of most recent Fire	Fire
	Year of most recent Logging	logging
Topography	Aspect	Aspect
	Cosine of Aspect	CosAsp
	Gully Index/Creek Index	GullyIndex/CreekIndex
	Elevation	DEM
	Sine of Aspect	SinAsp
	Slope	Slope
	Slope of Aspect	SoA
Bioclimatic	Annual Mean Temperature	BIO01
	Mean Diurnal Range	BIO02
	Isothermality	BIO03
	Temperature Seasonality	BIO04
	Max Temperature of Warmest Month	BIO05
	Min Temperature of Coldest Month	BIO06
	Temperature Annual Range	BIO07
	Mean Temperature of Wettest Quarter	BIO08
	Mean Temperature of Driest Quarter	BIO09
	Mean Temperature of Warmest Quarter	BIO10
	Mean Temperature of Coldest Quarter	BIO11
	Annual Precipitation	BIO12
	Precipitation of Wettest Month	BIO13
	Precipitation of Driest Month	BIO14
	Precipitation Seasonality	BIO15
	Precipitation of Wettest Quarter	BIO16
	Precipitation of Driest Quarter	BIO17
	Precipitation of Warmest Quarter	BIO18
	Precipitation of Coldest Quarter	BIO19
Plot height (Statistical summary for height of height-normalized Lidar points)	Max plot height	max
	Mean plot height	mean
	Standard deviation of plot height	std
	p10: 10th percentile of height	p10
	p25: 25th percentile of height	p25
	p50: 50th percentile of height	p50
	p75: 75th percentile of height	p75
	p90: 90th percentile of height	p90

Category	Variables	Short Name
Vertical Canopy strata density	% of all returns between height strata 0.5 - 5m	S00
	% of all returns between height strata 5-10m	S05
	% of all returns between height strata 10-15m	S10
	% of all returns between height strata 15-20m	S15
	% of all returns between height strata 20-25m	S20
	% of all returns between height strata 25-30m	S25
	% of all returns between height strata 30-35m	S30
	% of all returns between height strata 35-40m	S35
	% of all returns between height strata 40-45m	S40
	% of all returns between height strata 45-50m	S45
	% of all returns between height strata 50-55m	S50
	% of all returns between height strata 55-60m	S55
	% of all returns between height strata 60-65m	S60
Overstorey	Average Overstorey tree crown width (CW) /plot	OvCWavg
	Total Overstorey tree CW/plot	OvCWsum
	Average big crowns height /plot	OvHtavg
	Number of level 1 CW /plot (8m < CW <= 10m)	OvN08t10
	Number of level 2 CW /plot (10m < CW <= 15m)	OvN10t15
	Number of level 3 CW /plot (15m < CW <= 20m)	OvN15t20
	Number of level 4 CW /plot (CW > 20m)	OvN20t30
	Number of Big Crowns /plot (CW > 8m)	OvNum
	Line density of edge of overstorey tree crown (Stag Index)	CLdens
Midstorey	MS Coverage (%)	MsCover
	Number of Midstorey trees /plot	MsNum
	Average Midstorey tree height /plot	MsHtavg
Connectivity	Connectivity Index of Midstorey layer	MScnt
	Connectivity Index of Shrub layer	Shrubcnt
	Connectivity Index of Top Canopy layer	Canopycn
	Density of live wattle (m2/ha)	WattleL
HBT	Density of all hollow-bearing tree form0-2 (#/ha)	hbt0t2
	Density of all hollow-bearing tree form3-4 (#/ha)	hbt3t4
	Density of all hollow-bearing tree form5-8 (#/ha)	hbt5t8

5.2.4 Habitat suitability model, model validation and uncertainty analysis

Random forest model to predict habitat suitability and variable importance

We used a machine-learning approach to estimate the probability of LBP presence based on a large set of structural, topographic, and habitat predictors (Table 3-1). The probability of LBP presence was considered as a habitat suitability index (HSI) in this study. Specifically, we used random forests (RF; also known as random decision forests), a supervised machine-learning method for classification or regression. RF operates by constructing a large number of decision trees (i.e., a forest) (Breiman 2001), each of which represents a predicted class and a vote for that class. After each iteration, individual decision trees are combined using the rule of majority votes. RF models have advantages in detecting nonlinear relationships and complex interactions, and are less prone to over-fitting (Martinuzzi et al. 2009). We used the Random Forest package in R (Liaw and Wiener 2002).

In addition, the RF algorithm provides the relative importance of each predictor variable, by quantifying changes in classification error (such as mean decrease in Gini impurity and mean decrease in accuracy) when the “out of bag” (OOB) data for that variable is altered (Martinuzzi et al. 2009, Shoemaker et al. 2018). We used the ‘measure_importance’ function from ‘randomForestExplainer’ package in R to generate four importance indices, including mean decrease in accuracy (accuracy_decrease), mean decrease in Gini impurity (Gini_decrease), mean minimal depth (MinDepth) and p-value (Paluszynska and Biecek 2017).

RF models can also provide partial dependence plots (PDP) to characterize relationships between individual predictor variables and the probability of observed LBP presence. PDPs were used to interpret complex machine learning models to express whether a variable is positively or negatively associated with the response variable (ie, the probability of LBP presence) (Friedman 2001). Meanwhile, to understand heterogeneous patterns of specific observations, we also generated Individual Conditional Expectation (ICE) plots to demonstrate the dependence of the prediction on an individual variables for each observations separately, resulting in one line per observation, compared to one line overall in partial dependence plots (PDP) (Goldstein et al. 2015). The R package ‘ICEbox’ was used to create ICE plots (Goldstein et al. 2017).

Block cross-validation validation and significant variables selection

We used 5-fold block cross-validation to evaluate model performance and systematically compare models of

varying complexity to choose the most robust model with the fewest variables (i.e., the most parsimonious model). Conventional (random) cross-validation approaches assume that observations are independent (Trachsel and Telford 2016). However, ecological data are often spatial autocorrelated (Legendre 1993). If training and testing datasets were not spatially separated for species distribution modelling (SDM), performance statistics might be over-optimistic (Roberts et al. 2017). The variogram range method has been used to define the optimal separation distance between training and testing sets (Valavi et al. 2019). The range was estimated using the empirical semi-variograms, and the range over which residuals are approximately independent could be used as block size for block cross-validation (Valavi et al. 2019). The semivariance variograms of probability of LBP presence were shown in Figure A5 1 in Appendix 5. The maximum spatial autocorrelation range of vegetation connectivity index was 8km. The block size was select to be 9km in this study.

The 9km×9km spatial blocks were split into five folds of equal size, while the field observation plots located in each block was also split into five groups. The spatial distribution of blocks for each fold was shown in Figure 4-1b. One group was withheld for final validation test, while the other four groups (training sets) were used to develop the model. The training sets were repeated four times with each of four folds being withheld once as test set for model selection. Model performance indicators were averaged across the five model runs, and the mean values were used as the basis for model validation and comparison (Maroco et al. 2011). The overall accuracy (ACC), sensitivity (true positive rate, TPR), specificity (true negative rate, TNR), and area under the receiver operating characteristic curve (AUC) were calculated for each test set as model performance indicators. The receiver operating characteristic curve (ROC curve) was used to evaluate the sensitivity against the specificity at various threshold values (Altman and Bland 1994). The AUC represents the probability that the classification will correctly rank a randomly chosen positive instance higher than a randomly chosen negative instance (Fawcett 2006). AUC is a widely used indicator of model performance in species distribution modelling (Lobo et al. 2008, Jiménez-Valverde et al. 2011, Jiménez-Valverde 2012, Tattoni et al. 2012). The equations for sensitivity and specificity are shown in Table 5-2. Sensitivity in this study represents the proportion of plots with LBP observations that are correctly identified as such, while specificity represents the proportion of plots without LBP that are correctly identified. The ACC, sensitivity, and specificity of LBP occurrence vary with threshold values for the probability of LBP presence.

Table 5-2 The confusion matrix of LBP occurrence and the equations of each validation measures. True condition is

based on directly observed data from ARI LBP observation plots and predicted condition is from LiDAR-derived random forest model of LBP occurrence.

		True condition		Equations for individual metrics	
		Condition positive (CP)	Condition negative (CN)	ACC = (TP + TN)/(TP+FP+TN+FN)	
Predicted condition	Predicted condition positive (PP)	True positive (TP) = LBP presence correctly detected	False positive (FP) = detected wrong LBP presence	True positive rate (TPR), Sensitivity = TP/CP = TP/(TP + FN)	Commission rate (CR) or false positive rate (FPR) = FP/PP = FP/(TP+FP)
	Predicted condition negative	False negative (FN) = missed observed LBP presence	True negative (TN)= LBP absence correctly detected	Omission rate (OR) = FN/CP = FN/(TP + FN)	True negative rate (TPR) or Specificity = TN/CN"

All 70 predictors were considered for inclusion in the RF analyses to estimate habitat suitability. The first step of the analysis was variable selection, which involved grouping and reducing the number of potential predictors. We grouped predictor variables that had Pearson correlations >0.8. Only one variable was selected to represent each group based on highest AUC performed with that variable in the test sets for cross validation. For example, the 19 climate variables were reduced to three variables that broadly represented temperature, precipitation, and diurnal range of temperature. The variable reduction groupings are shown in Table A5 1 in the Appendices.

After variable grouping 45 variables were retained. We then proceeded to reduce the number of variables one by one based on the rank importance of each predictor, starting with the least important. We used mixed variable importance index (MixedVI = accuracy_decrease × Gini_decrease / MinDepth / p-value) as a proxy for the importance of each variable. The combination of variables with the highest AUC for the withheld validation sets was selected as the final model. Selected variables and their importance values in the final model are shown in Figure 5-3.

Model validation, calibration and model uncertainties

To validate the model performance of habitat suitability index for LBP, we used the binomial proportion confidence interval in final validation test set. A binomial proportion confidence interval is a confidence interval for the probability of presence calculated from the outcome of a series of presence–absence incidents (Wallis 2013). In other words, it is an interval estimate of the probability that an individual is present when only the number of total incidents and the number of observed presence are known. There are several formulas

for binomial confidence intervals, we used the Wilson score interval, which is an improvement over the normal approximation interval in that the actual coverage probability is closer to the nominal value (Wilson 1927). The Wilson score interval was estimated by the “binom.wilson” function in the “binom” package in R (Dorai-Raj 2014). We divided the predicted probability of LBP presence into 10 levels, from 0 to 1 with intervals of 0.1, where 0 represents undesirable habitat and 1 represents optimal habitat. For each level of habitat suitability in final validation test set, the number of observed presence plots and the number of total plots was summarized and the Wilson score interval was estimated.

The final habitat suitability model selected based on four training sets were applied to the whole dataset to generate calibrated habitat suitability index. We used generalized additive model (GAM) to fit predicted outcomes with observations. The standard error estimates are returned for each prediction to estimate 95% confidence intervals.

5.3 Results

The final habitat suitability included 17 variables (Figure 5-3) from the 70 habitat-related variables that were available for inclusion. The most important three predictors were temperature seasonality (bio04); midstorey connectivity index (ms_cnt) and year of last logging (logging). And the least significant predictors were aspect and sin of aspect. Among the 17 variables included in the final model, four were related to foraging habitat (i.e., vegetation connectivity or densities) and five were associated with nesting habitat attributes. The remaining seven were climatic (3), topographic (3), or historical (1) factors.

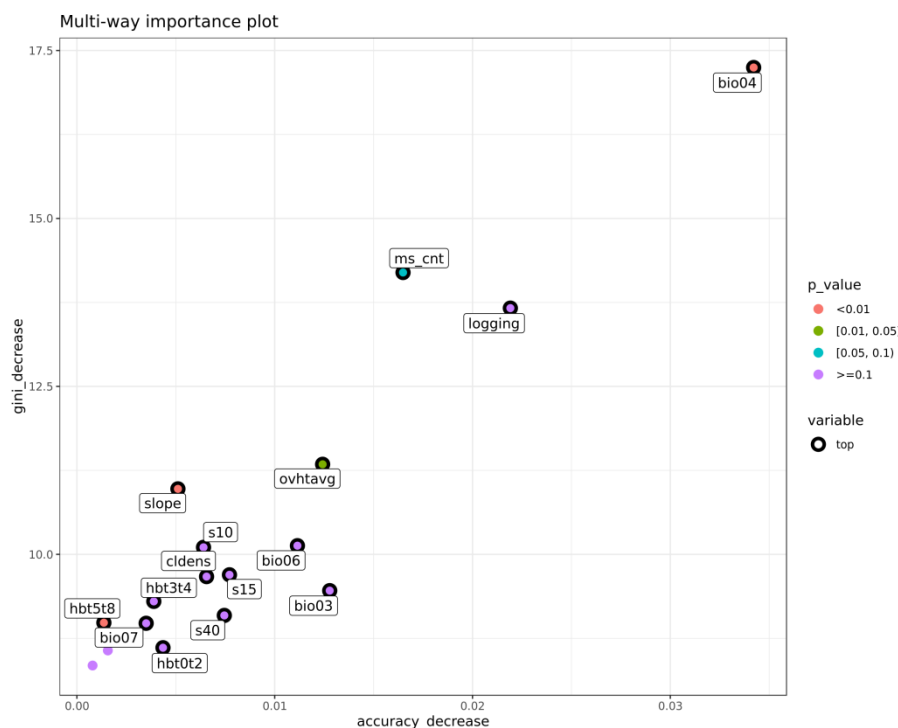


Figure 5-3 The significant variables and multi-way variable importance plot for the final habitat suitability model.

5.3.1 Model validation

The random forest algorithm was used to estimate the probability of LBP presence based on a large network of 1-ha plots established across Victoria's Central Highlands. As shown in Table 5-3, the AUC of the final validation test set was 0.889. The ACC, sensitivity, and specificity of LBP occurrence vary with threshold values for the probability of LBP presence (i.e. habitat suitability index for LBP). When predicted HSI ≥ 0.49 , the model would have the highest overall model accuracy (ACC) in the validation datasets, which is 87.3%, with 71.8% correctly detecting LBP presence and 95.8% correctly detecting LBP absences.

Binomial confidence intervals of the probability of observed LBP presence for different levels of predicted habitat suitability in the final validation test set are shown in Figure 5-4. When predicted HSI >0.5, the mean observed probability of LBP presence was higher than 0.75. When predicted HSI <0.5, the mean observed probability of LBP presence was lower than 0.35. The habitat suitability model has performed very well to detect LBP absence and presence.

Table 5-3 The model accuracy (ACC), sensitivity, specificity and AUC vary with threshold values for the probability of LBP presence (i.e. habitat suitability index for LBP) in final validation test set

Threshold value	ACC	sensitivity	specificity	AUC
0.45	84.50%	74.40%	90.10%	0.889
0.46	84.50%	74.40%	90.10%	0.889
0.47	85.50%	71.80%	93.00%	0.889
0.48	86.40%	71.80%	94.40%	0.889
0.49	87.30%	71.80%	95.80%	0.889
0.5	86.40%	69.20%	95.80%	0.889
0.51	85.50%	66.70%	95.80%	0.889
0.52	85.50%	66.70%	95.80%	0.889
0.53	84.50%	61.50%	97.20%	0.889
0.54	83.60%	59.00%	97.20%	0.889
0.55	82.70%	56.40%	97.20%	0.889

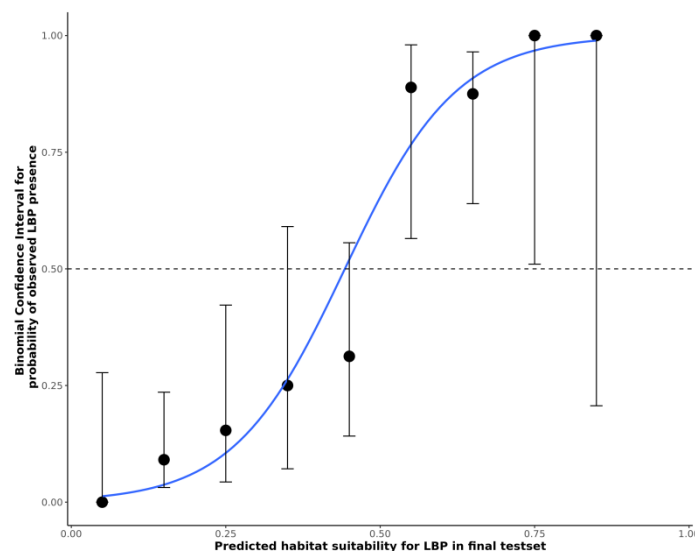


Figure 5-4 Binomial confidence interval of probability of observed LBP presence for different levels of predicted habitat suitability in final validation test dataset. The blue line is the model fit..

5.3.2 HBTs and Habitat Suitability

The density of both live and dead HBTs had significant effects on habitat suitability for LBP. The probability of LBP occurring at a site increased as the number of short and dead HBTs (hbt5t8) increased until a threshold was reached at five dead HBT per hectare (Figure 5-5). The probability of LBP occurring at a site decreased as the number of tall and dead HBT (hbt3t4) increased (Figure 5-5).

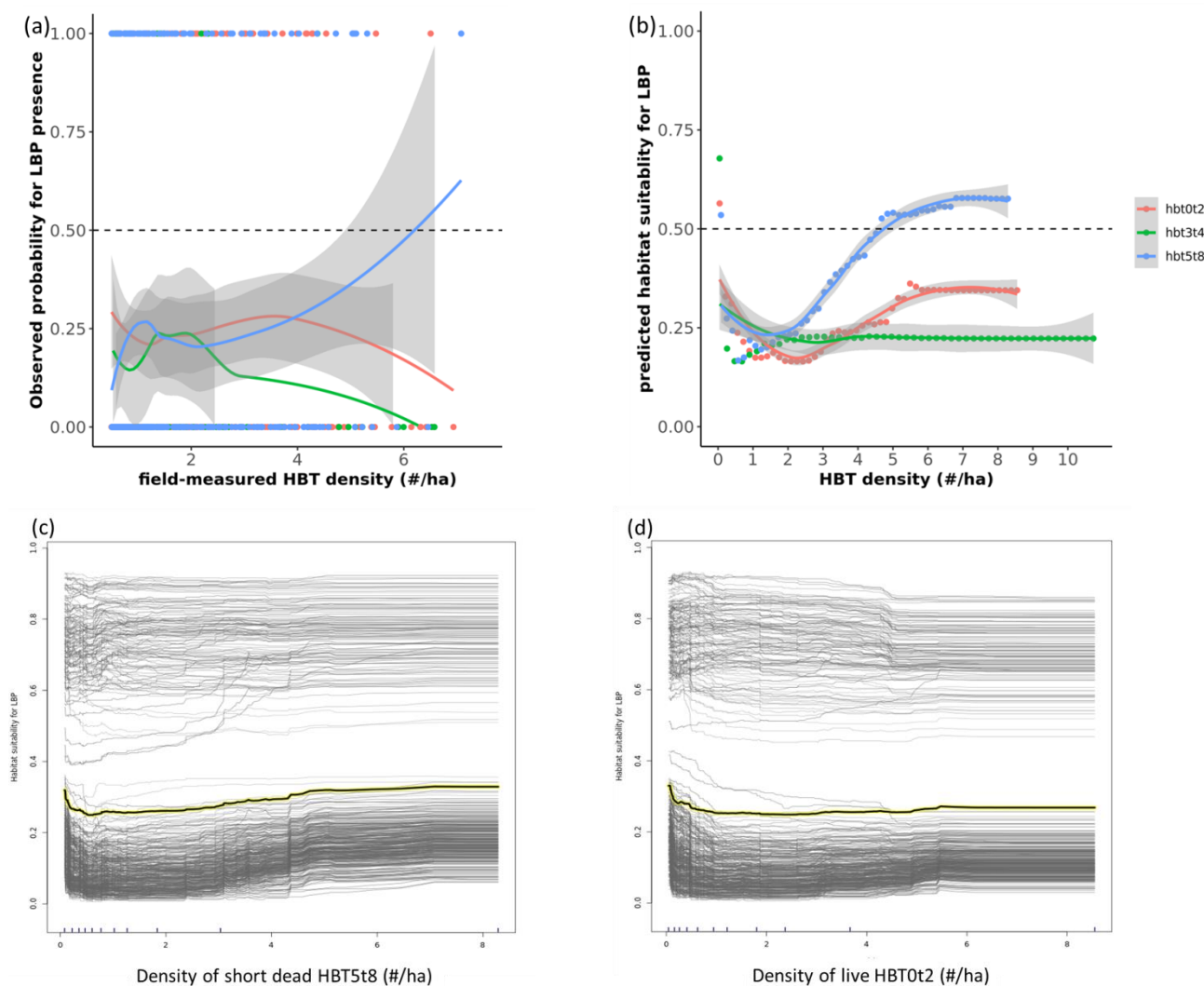


Figure 5-5 The relationship between HBT density of live HBT (hbt0t2), tall, dead HBT (hbt3t4) and short, dead HBT (hbt7t8) and probability of LBP presence: a) observed LBP occupancy versus HBT density based on ARI field data, and b) Partial dependence plot from random forest model showing relationship between LBP habitat suitability and HBT density. The solid lines in both figures are 'loess' smooths applied to the data. c) Individual Conditional Expectation plot showing the relationship between LBP habitat suitability and the density of short dead HBT (hbt5t8). Each line represents one site. d) Individual Conditional Expectation plot showing the relationship between LBP habitat suitability and the density of live HBT (hbt0t2). Each line represents one site.

Interestingly, the field-observed probability of LBP presence first increased slightly as the field-measured

number of live HBT (hbt0t2) increased until a threshold of four live HBTs per ha, then the probability of LBP presence at a site decreased as the number of live HBT increased (Figure 5-5a). On an overall average, the partial dependence plot indicated that predicted LBP habitat suitability increased with the density of live HBT (Figure 5-5b) when the number of live HBT was larger than two live HBTs per ha. But for specific sites with higher habitat suitability (i.e. HSI>0.4 in Figure 5-5d), the relationship between LBP habitat suitability and the density of live HBT was different. The predicted LBP habitat suitability was decreased as the number of live HBTs increased.

We quantified the mean and standard deviation of the distance between each LBP site and nearest location of a measured HBT, and the mean and maximum distance from the center of each 1-ha LBP plot with predicted occurrences of HBT form types across the study landscape (Table 5-4). Based on both field observations and model predictions the mean distance from HBT7-8 to study sites, those sites with LBP present were closer to HBT7-8 than those in which LBP was absent. However, sites with LBP were farther from other forms of HBTs (HBT0-6) than sites without LBP. The maximum distance between plots predicted to have LBP present and a plot with the predicted presence of any type of HBT was ~300m, whereas for the field sites that distance was about 100m. Based on the predicted habitat suitability for LBP, there are 27,665- 48,905 ha of suitable habitat (HSI >0.5) in which the nearest HBT less than 100m away.

Table 5-4 The mean and standard deviation (sd) of distance between each field LBP presence-absence site and nearest location of each measured HBT, and the mean and maximum distance from the center of each 1-ha plot with LBP presence-absence predictions to nearest plot with presence of each HBT form type across whole landscape. All distances are in meters.

Distance to HBT	Field Observation site						Predicted presence across whole landscape					
	All		Absence		Presence		All		Absence		Presence	
	mean	sd	mean	sd	mean	sd	mean	max	mean	max	mean	max
HBT0t2	180	314	177	319	190	303	42	1720	38	1720	83	1315
HBT3t4	368	437	297	410	521	456	234	3106	231	3106	267	2476
HBT5-6	328	435	298	440	389	419	163	1709	163	1709	174	1300
HBT7-8	356	441	380	469	311	383	186	3900	194	3900	87	1100
All HBT	41	23	41	23	42	24	9	447	7	447	24	316

5.3.3 The effect of vegetation connectivity on habitat suitability for LBP

LBP was found to prefer sites with a high level of connectivity in the midstorey layer. Sites modelled high probability of LBP occurring had a midstorey connectivity index > 2 (Figure 5-6a). The strata density in

midstorey between 10-15m (s10), 15-20 m (s15) and 40-45m (s40) were important predictors of suitable LBP habitat (Figure 5-6b). This was supported by the variable importance indices in which midstorey connectivity was more important than basal area of live *Acacia* in the habitat suitability model (Table A5 2 in the appendices 5). And the connectivity of shrub layer and top canopy layer (shrub_cnt and top_cnt) was not important to habitat suitability of LBP (Table A5 2 in the appendices 5).

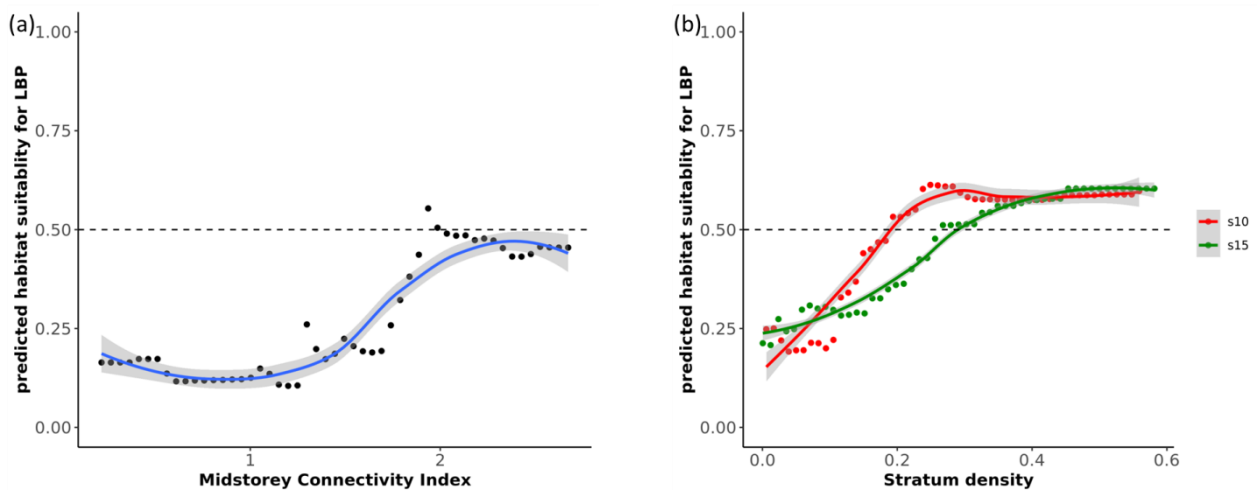


Figure 5-6 Partial dependence plot (PDP) of random forest model showing relationship between probability of LBP presence and a) midstorey connectivity and b) strata density between 10-15m (red line), 15-20m (green line) and 40-45m (blue line).

5.3.4 The impact of disturbances (fire/logging) on habitat suitability for LBP

Fire has a negative impact on habitat suitability for LBP, while logging increases habitat suitability for LBP (Figure 5-7a). The suitability of habitat is highest in areas logged from 1975 to 2000, which is where midstorey connectivity is at its highest level (Figure 5-7b). In areas affected by fire, there is a peak in connectivity that aligns with the 1983 fire in the parts of the Central Highlands, while connectivity is lower in stands impacted by fires before and after this fire (Figure 5-7b). Notably, the proportion of sites in which LBP was predicted to occur suggests that the suitability of habitat for LBP decreases with increasing distance from the edge of logged areas (Figure 5-8).

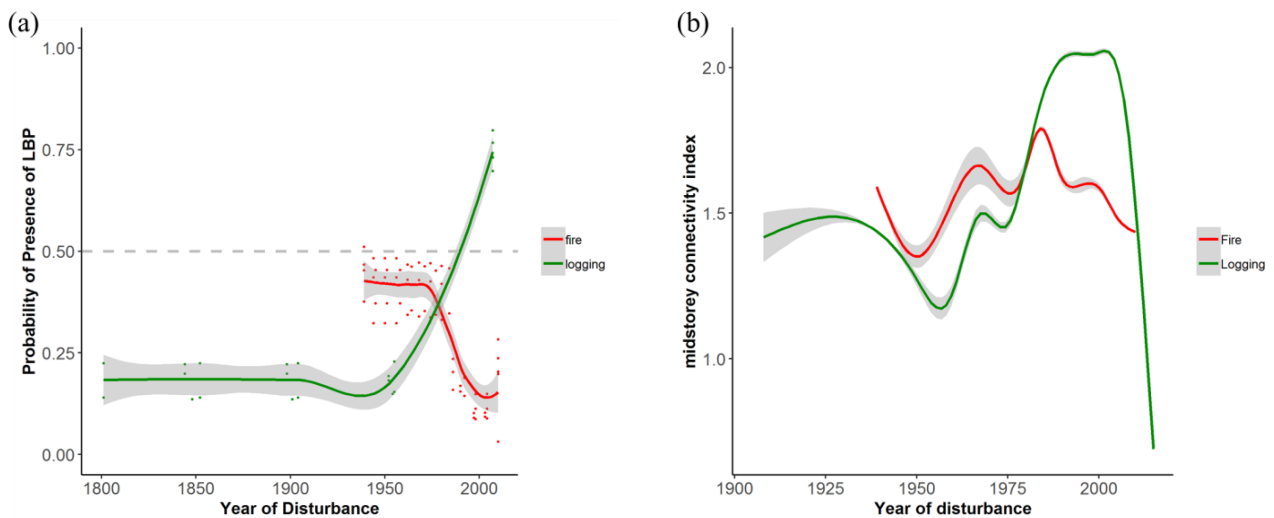


Figure 5-7 a) Partial dependence plot (PDP) of random forest model showing relationship between probability of LBP presence and year of last fire (red line) and year of last logging (green line); and b) landscape-level relationship between midstorey connectivity and year of last fire (red line) and year of last logging (green line), data from 342,960 1-ha plots across the whole study area, using the “gam” method for scatterplot smoothing.

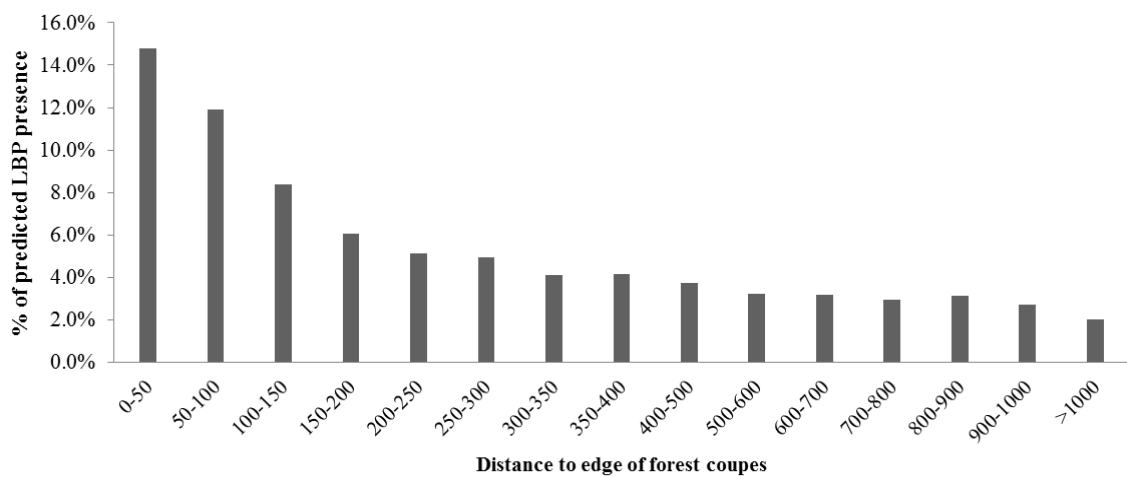


Figure 5-8 The percent of predicted LBP present plots changed with distance to edge of forest logging coupes across the whole study area.

5.3.5 The impact of climatic and topographic variables on habitat suitability for LBP

Climate and topography were important factors associated with LBP habitat. Areas with flat topography and areas with a cooler and wetter climate had higher habitat suitability (Figure 5-9). Areas with a mean temperature of coldest month below 0.5 °C were also more likely to have LBP present; whereas areas above 3 °C in coldest month were the least likely to have LBP. Sites with slope between 10 and 20 degrees had the lowest probability of LBP occurring.

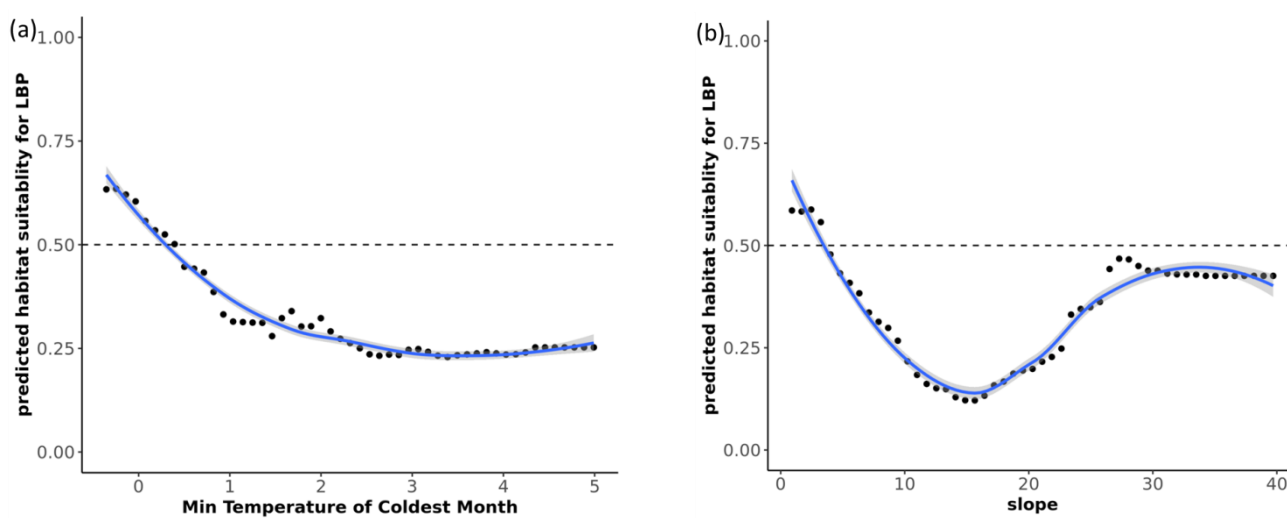


Figure 5-9 Partial dependence plot (PDP) of random forest model showing relationship between probability of LBP presence and a) mean temperature of coldest month; and b) slope at 1-ha scale.

5.3.6 The interactions among HBT, connectivity, climate and LBP occurrence

The relationship between density of HBT and midstorey connectivity is shown in Figure 5-10a. Figure 5-10b shows the interactions among HBT, temperature, and predicted habitat suitability for LBP across the whole study area. High densities of live HBTs (HBT0t2) was associated with lower densities of midstorey connectivity, while the density of the short dead HBTs (HBT5t8) increased with increasing midstorey connectivity. Plots with high density of short dead HBTs (HBT5t8) were typically found in cooler, moister areas, while areas with high densities of live HBTs (HBT0t2), and associated with lower connectivity, tended to have higher mean temperatures.

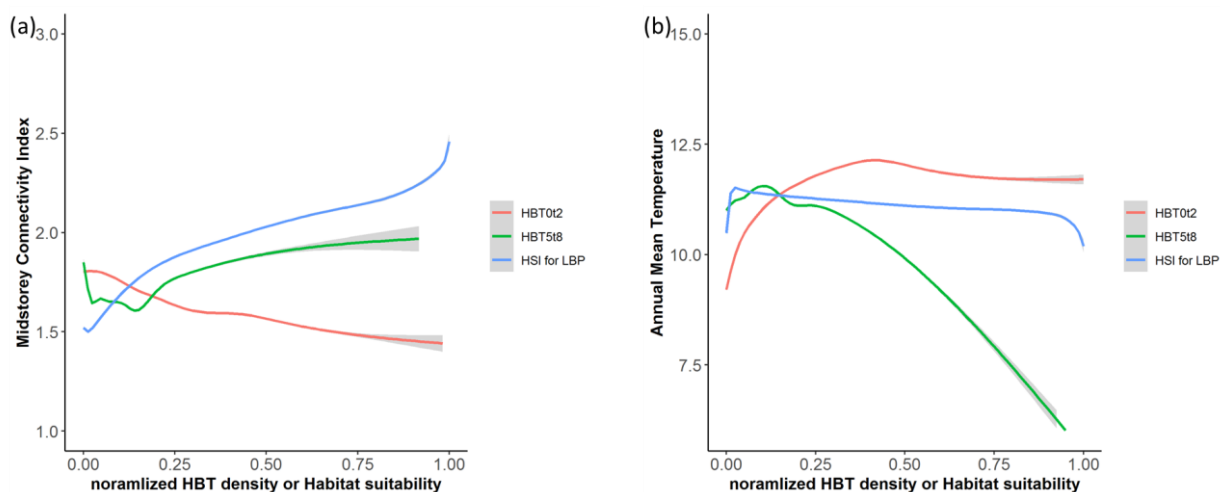


Figure 5-10 a) Midstorey connectivity level changed with predicted tree density of HBT0t2 (red line) and HBT5t8 (green line) across the whole study area, using “gam” method for scatterplot smoothing; b) Normalized tree density of HBT0t2 (red line) and HBT5t8 (green line) and habitat suitability index for LBP (blue line) changed with annual temperature across the whole study area, using “gam” method for scatterplot smoothing.

5.3.7 Spatial distribution of suitable habitat for LBP

Within the study area, 32,830 ha (95%CI: 24,637 – 43,424) are predicted to be suitable habitat for LBP, about 9.57% of whole study area (Table 5-5). The distribution of predicted suitable LBP habitat varied by forest type and forest management zones (Table 5-5). There was little variance in the proportion of habitat occurring across the three forest types included in the study but there were notable differences associated with tenure. General Management and Special Protection Zones contained more suitable LBP habitat than other management zones. The spatial distribution of habitat for LBP across the montane ash forests of the Central Highland is shown in Figure 5-11.

Table 5-5 Area (and %) of predicted LBP presence-absence in different vegetation classes and forest management zone in the Central Highlands of Victoria.

	Area	Absence	Presence	%Presence
		Area	Area	%
All	342,960	310,130 (318,323 – 299,536)	32,830 (24,637 – 43,424)	9.57% (7.18% - 12.66%)
Wet/Damp forests	305,599	275,499 (282,785 – 266,242)	30,100 (22,814 – 39,357)	9.85% (7.47% - 12.88%)
Riparian Forests	24,875	23,031 (23,681 – 22,012)	1,844 (1,194 – 2,863)	7.41% (4.8% - 11.51%)
Rainforests	12,486	11,600 (11,857 – 11,282)	886 (629 – 1,204)	7.1% (5.04% - 9.64%)
GMZ	162,461	139,605 (144,412 – 133,703)	22,856 (18049 – 28,758)	14.07% (11.11% - 17.7%)
Parks	81,625	78,736 (79,833 – 77,004)	2,889 (1,792 – 4,621)	3.54% (2.2% - 5.66%)
SMZ	15,252	13,930 (14,295 – 13,509)	1,322 (957 – 1,743)	8.67% (6.27% - 11.43%)
SPZ	45,926	41,549 (42,846 – 39,963)	4,377 (3,080 – 5,963)	9.53% (6.71% - 12.98%)

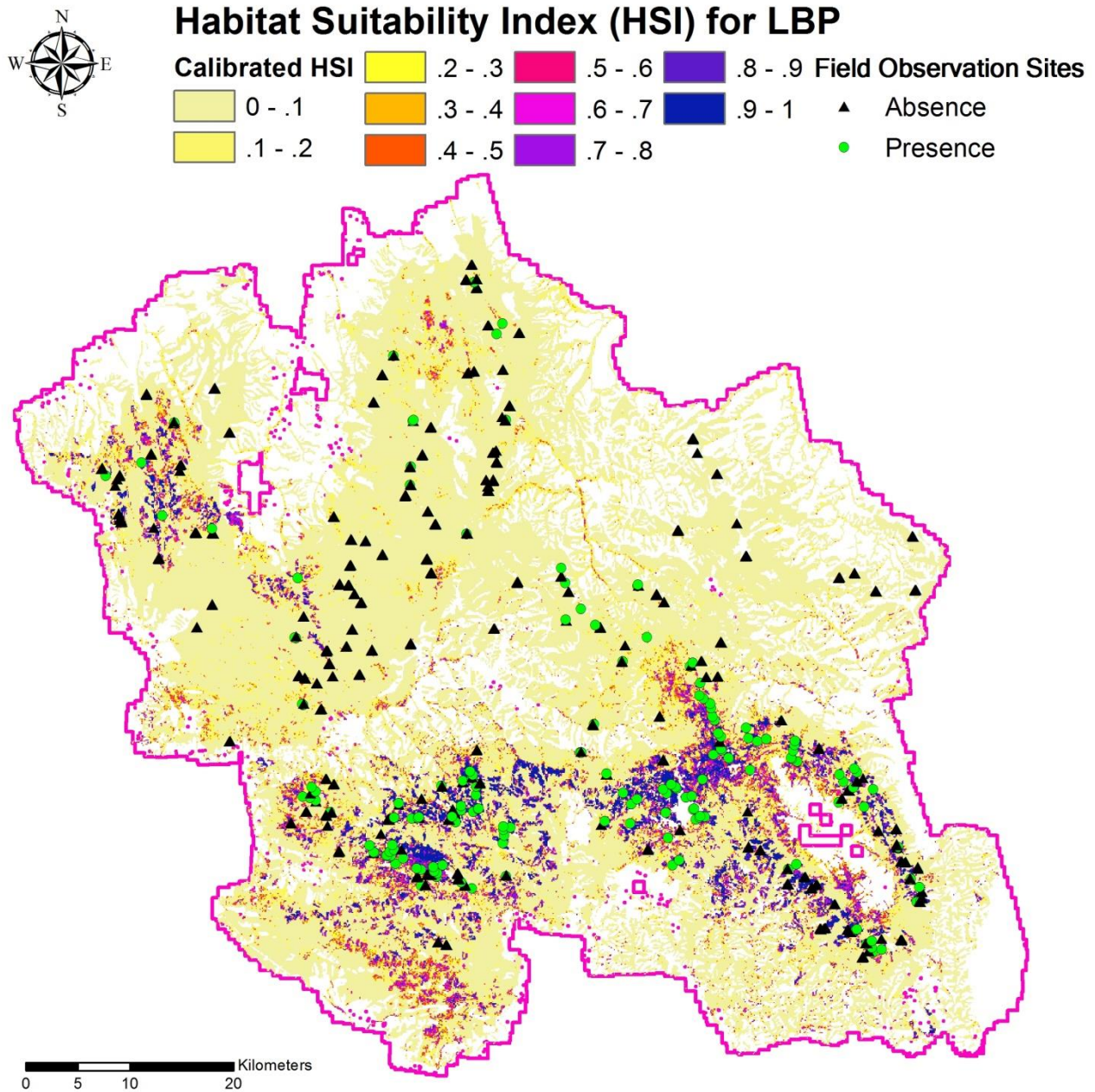


Figure 5-11 Distribution map of habitat suitability index (HSI) for LBP estimated from the random forest model and assessed by ARI field data across Victoria's Central Highlands (0 = unsuitable habitat, yellow; 1= optimum habitat, purple) .

5.4 Discussion

The extent and quality of habitat for the critically endangered Leadbeater's possum is widely believed to be rapidly declining due to bushfires and timber harvesting (Lindenmayer et al. 2015, Commonwealth of Australia 2016, Lindenmayer et al. 2016a). In part, concerns arose following the 2009 bushfire in which 34% of the estimated area of habitat was burned (Leadbeater's Possum Advisory Group 2014). A major challenge for determining the impact of fire and timber harvesting on the LBP is the lack of spatial data describing fine-scale habitat metrics that the species is associated with (Blair et al. 2017). Spatial layers of the location and abundance of hollow-bearing trees and a dense and connected *Acacia* midstorey have not been available. We used LiDAR data to develop a large number of habitat-related variables and compared them to hundreds of ground-based observation sites to develop models that quantified the suitability of LBP habitat in the montane forests of the Central Highlands region of Victoria.

At a landscape level, our approach suggests that there are ~33,000 ha (95%CI: 25,000ha-43,000ha) of suitable habitat in the Central Highlands. The proportion of the landscape that is suitable ranges from 7.2% - 12.7% of the total area, which is higher than previous estimates (6.7%, Lindenmayer (1989); <1.3%, Lindenmayer et al. (2015)). The differences between their results and ours most likely arise from differences in the data used to build the habitat model. Those studies extrapolated potentially suitable habitat over the Central Highlands landscape from site-level abundance of HTBs and the basal area of midstorey *Acacia* spp. from a network of study plots. Their approach assumed certain relationships between forest age and disturbance history, as well as the representativeness of their plots to the broader landscape. In contrast, our approach used objective and empirical measures of forest structure captured at each location in the landscape to estimate the fine-scale metrics associated with LBP habitat and then predict LBP habitat suitability. Landscape-scale remotely sensed data that relates forest structure to habitat attributes are less sensitive to scale-dependent uncertainties that result from extrapolating field-based plot surveys to broader scales (Estes et al. 2008, Jaime-González et al. 2017).

Of the 70 potential variables considered in our analyses, the final model retained a mix of structural, climatic, topographic and disturbance variables. We found that LBP preferred flat, wet and cold areas. These are consistent with previously published reports on habitat features of LBP (e.g., Lindenmayer et al. 1991, a,b). However, we also found that the relationship between habitat suitability and topography was non-linear

response, which much higher levels of occurrence on slopes $>30^\circ$. This may be associated with requirements under the Code of Forest Practices that prohibit logging operations on slopes $>30^\circ$. Lindenmayer et al. (2017) found that the most likely place to find LBP were in areas of regrowth forest disturbed between the 1960s and 1990s that supported HBTs. Our findings that areas logged between 1950 and 2000 were more suitable for LBP is consistent with these findings. Lindenmayer et al. (2017) also found that the old-growth forests are the least likely to support LBP, which is also consistent with our finding that the probability of occurrence declines with an increase in live HBTs. As the strata density in midstorey between 10-15m (s10), 15-20 m (s15) are the most important variables to LBP, LBP requires the continuous cover of foliage at 10–20m. This height is the mean height of the nest entrances of LBP (Smith and Lindenmayer 1988). We found that increasing density of live HBTs was associated with a decline in midstorey connectivity, while increasing density of dead HBTs was associated with increasing midstorey cover. This highlights the critical role that *both* nesting and foraging/connectivity resources play in determining habitat suitability for LBP at a given site (Lindenmayer *et al.* 1991a, 2017, Smith and Lindenmayer 1994). The requirement for at least three HBT per ha proposed by Lindenmayer et al. (1991a) was also supported by our analyses as we found the highest habitat suitability in sites with at least three dead HBT per ha. The close alignment of the parameters in our LiDAR-based habitat suitability and earlier field studies of LBP habitat identified by Lindenmayer (2000) suggests that our model captures the key features of LBP habitat. Our model has the advantage of being directly scalable to the whole landscape, given the availability of LiDAR-derived data metrics for the entire Central Highlands landscape.

A major challenge in conservation management for endangered species is estimating population sizes. For LBP in the Central Highlands populations sizes have been extrapolated from survey data collected in 29 field sightings at 180 field sites (Leadbeater's Possum Advisory Group 2014). With underlying assumptions about detection radius (150-250 m for LBP) and number of associated individuals per sighting (typically there are 2.5 individual LBP per colony), LPAG estimated the number of colonies to be between 1,578 and 4,384 and the number of individuals to be between 3,945 and 10,960 (Leadbeater's Possum Advisory Group 2014, Blair et al. 2017). This number of colonies equates to $\sim 31,000$ ha of forest in the Central Highlands. Applying the same assumptions to the results of our habitat suitability model, we estimated the number of colonies to be between 1,675 to 4,624, and the number of individuals to range from 4,188 to 11,560 individuals.

Table 5-6 Variability of population estimates with effective survey area (detection radius).

Radius (m)	Area (ha)	Blair et al. (2017)		This study	
		No. of colonies	No. of individuals	No. of colonies	No. of individuals
100	3.1	9,907	24,766	10,590(7,947-14,008)	26,476(19,869-35,019)
150	7.1	4,384	10,960	4,624(3,470-6,116)	11,560(8,675-15,290)
200	12.6	2,466	6,165	2,606(1,955-3,446)	6,514(4,888-8,616)
250	19.6	1,578	3,945	1,675(1,257-2,216)	4,188(3,142-5,539)
300	28.3	1,094	2,734	1,160(871-1,534)	2,900(2,176-3,836)
350	38.5	804	2,009	853(640-1,128)	2,132(1,600-2,820)
400	50.3	615	1,538	653(490-863)	1,632(1,225-2,158)
450	63.6	486	1,215	516(387-683)	1,290(968-1,707)
500	78.6	394	984	418(313-552)	1,044(784-1,381)

In our analysis, the most suitable habitat for LBP occurred in patches with low density of live HBT, but high midstorey connectivity. This is consistent with the findings of Lindenmayer et al. (2017) that regrowth forests with fewer HBTs were the most likely forest type in which LBP would emerge from HBTs. However, it may also be an artefact of the survey approach used. The majority of remote cameras used to capture LBP were placed in the forest stratum with dense understorey or midstorey, where the animals were most likely to be moving and foraging (Fleming et al. 2014, Nelson et al. 2015). Our model may therefore be predicting the connectivity of foraging habitat of LBP. The consistency of the HBT responses with the other published studies, however, suggests that this is not likely. To further test if the model is biased towards foraging habitat, we analyzed the distance between predicted areas of foraging suitability and HBT occurrence. We found that the mean distance between the nearest HBT and foraging habitat was 24 m and the maximum distance was 316 m. The latter is well within the movement range of 60-600m found by Lindenmayer et al. (2018). The distance is also within the movement ranges of the lowland LBP population at the Yellingbo Nature Conservation Reserve, which has been intensively studied. Harley (2005) found that females can move 125-1080 m and males 105-1460 m. These suggest that our model is likely capturing both the foraging and nesting requirements of LBP. However, we also suggested that in the future data collections of LBP, it is necessary to add more information about where the cameras were placed.

Previous studies of LBP nesting habitat (Smith and Lindenmayer 1988, Lindenmayer et al. 1990a, Lindenmayer et al. 1990b, Lindenmayer et al. 1991b) found that LBP preferred HBTs of Form Classes 7 and 8 (Smith et al. 1991). Our model suggests that LBP can be found in sites with live HBT0t2 or short dead

HBt5t8; however, stands with live HBt0t2 tend to be less suitable due to less abundant foraging and movement resources. Hollows typically occur in large trees, so stands with live HBts are likely to have substantial overstorey basal area. This has a suppressing effect on *Acacia* in the understorey and midstorey (Trouwée et al. 2019) and therefore may reduce the suitability of the stand for LBP.

It is also possible that some patches that have a high density of live HBts occur in areas that may be environmentally unsuitable for the occurrence of suitable nesting and connectivity resources. Patches with high density of dead HBt were typically found in cooler and wetter areas, whereas areas with a high density of live HBts and lower connectivity were found in warmer areas. Lindenmayer et al. (1991a) found that LBP were not typically found on steep slopes as the sites rarely support a well-connected understorey due to the lower soil moisture. It is possible that the warmer sites with live HBts are unable to support a highly connected understorey due to microclimatic conditions or that the warmer conditions promote greater tree productivity (Lindenmayer et al. 1991c) which in turn has facilitated the competitive exclusion of the midstorey (Trouwée et al. 2019).

Estimates of the total amount of suitable LBP habitat varied by tenure class in complex ways. The amount of suitable LBP habitat tended to be higher in the General Management Zone (GMZ) where timber harvesting occurs and in adjacent Special Protection Zones (SPZ) that are protected from timber harvesting and lower in National Parks and special management zones (SMZ) where timber harvesting is limited to address other values such as aesthetics. Connectivity of the midstorey vegetation was lowest in National Parks and generally higher in the SMZ, SPZ, and GMZ (see Chapter 4); however, the differences among specific HBt form classes were reversed. For example, National Parks had 25% more short dead HBts (HBt5t8) per ha than the GMZ (see Chapter 3). The density of HBts in SPZ was 8% more than in SMZ. Limited availability of either HBt or connected midstorey vegetation (or both) can reduce habitat suitability for LBP. Therefore, even though SMZ have the highest level of midstorey connectivity, the lower density of dead HBts reduced habitat suitability. Similarly, even though Parks have more available HBts, they lack midstorey connectivity, which also reduces the amount of suitable habitat for LBP. The relatively higher proportion of suitable LBP habitat in the SPZ is due to high levels of both HBts and connectivity. Although the increased level of midstorey connectivity in the GMZ due to historic logging activities has likely increased the habitat suitability for LBP, timber harvesting has also had a negative effect on the density of live HBts. This has likely led to a separation in time and space of foraging and nesting resources. In this zone increasing the availability of nesting trees for

LBP through the use of artificial nest boxes, protecting existing HBTs, promoting the recruitment of new HBTs, and while maintaining midstorey connectivity may all contribute to improving the habitat suitability for LBP (Harley 2006).

5.5 Conclusion

We used LiDAR-derived habitat metrics and hundreds of ground-based observation sites to develop models that captured the fine-scale metrics associated with LBP habitat in the montane forests of the Central Highlands region of Victoria. At a landscape level, our approach suggests that there are between 25,000 and 43,000 ha of suitable habitat in the Central Highlands. The proportion of the landscape that is suitable ranges from 7.2% - 12.7% of the total area by tenure. In our analysis, the most suitable habitat for LBP was modelled to occur in patches with high midstorey connectivity, high densities of short and dead HBTs, and low densities of live HBTs. Our approach highlights the potential for using high-resolution, spatially explicit data on forest structure integrated with habitat suitability models at a landscape-scale to map the extent of suitable habitat for a critically endangered species. This may have a range of important applications for conservation managers, such as identifying and prioritising areas of high habitat suitability for conservation and potential relocation.

Appendices 5

The semivariance variograms of probability of LBP presence

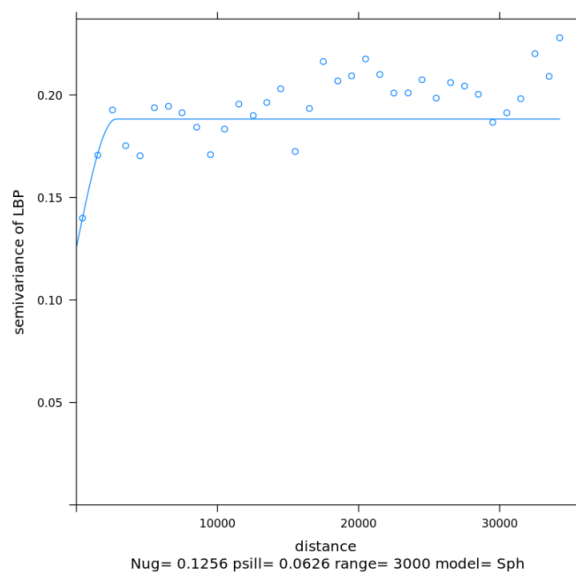


Figure A5 1 The semivariance variograms of the probability of LBP presence

Variable selection results of habitat suitability model by Self-correlated grouping

Table A5 1 Self-correlated group of environmental variables, group member and variables selected to represent each group in prediction model of LBP occurrence.

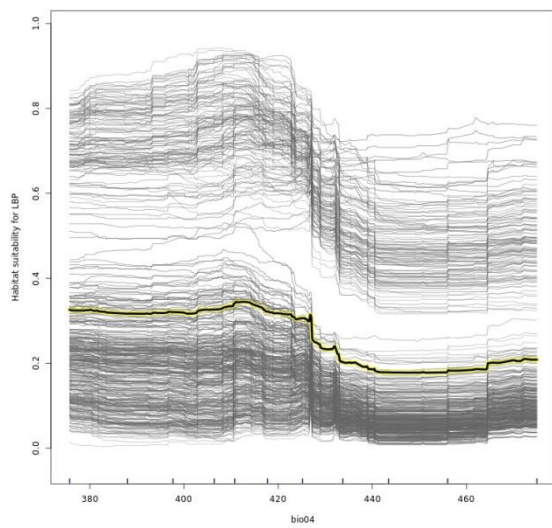
Group Name	Group Member	No.	Selected variable	AUC
Precipitation	DEM,BIO04/12/13/14/15/16/17/18/19	7	bio04	0.657
Temperature	BIO01/05/06/08/09/10/11	10	bio06	0.655
Diurnal Range	BIO02/03	2	bio03	0.653
Lidar Height	max/mean/std/p50/p75/p90	6	p90	0.651
Overstorey Crown Counts	OvCWsum/OvN08to10/OvN10t15	4	s55	0.649

Variable importance indices of all predictor variables for habitat suitability of LBP

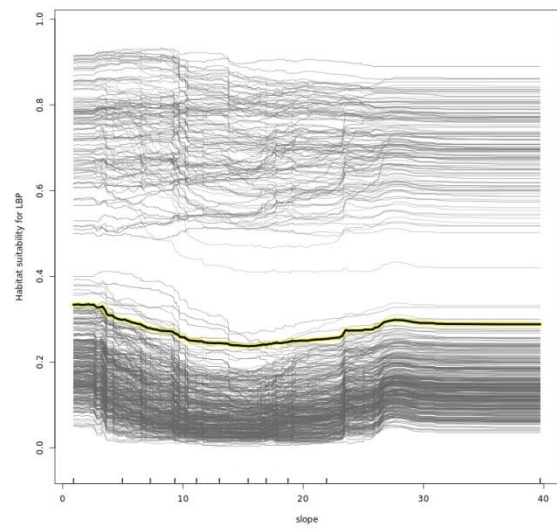
Table A5 2 Variable importance indices of all predictor variables for habitat suitability of LBP.

variable	mean_min_depth	accuracy_decrease	gini_decrease	p_value	mixedVI
bio04	3.60	1.25%	6.03	0.000	5.60E+20
slope	4.37	0.18%	4.04	0.000	1.15E+18
ms_cnt	4.05	1.15%	5.48	0.000	4.83E+11
s10	4.75	0.55%	4.01	0.097	9.14E+09
cldens	4.83	0.33%	3.65	0.002	6.85E+09
ovhtavg	4.71	0.86%	3.98	0.001	9.81E+05
bio06	4.99	0.40%	3.48	0.001	1.28E+04
hbt3t4	4.84	0.29%	3.86	0.003	5.17E+03
hbt5t8	5.17	0.14%	3.06	0.012	3.79E+03
hbt0t2	5.09	0.16%	3.39	0.001	1.73E+03
aspect	5.30	0.05%	3.01	0.042	1.10E+03
bio03	5.34	0.42%	3.48	0.014	1.18E+01
bio07	5.38	0.13%	2.95	0.236	1.05E+01
logging	4.26	1.14%	5.48	0.455	6.24E-01
s40	6.00	0.24%	2.70	0.457	4.15E-02
sinasp	6.01	-0.03%	2.50	0.367	3.02E-02
s15	5.44	0.46%	3.16	0.234	2.78E-02
mshtavg	5.54	0.36%	3.05	0.624	2.53E-02
s00	5.44	0.32%	3.01	0.311	1.73E-02
mscover	5.52	0.30%	3.16	0.355	9.50E-03
p25	5.69	0.30%	2.88	0.396	8.72E-03
creekindex	5.90	0.16%	2.63	0.658	8.53E-03
ovcwavg	5.74	0.20%	2.69	0.186	8.45E-03
msnum	5.53	0.33%	3.17	0.360	7.58E-03
p10	5.73	0.31%	2.71	0.373	7.02E-03
livewattle	5.79	0.36%	2.85	0.450	6.13E-03
s30	5.72	0.36%	2.85	0.604	6.11E-03
s50	6.06	0.59%	2.70	0.822	6.04E-03
s05	6.31	0.22%	2.41	0.761	5.24E-03
p90	5.83	0.28%	2.57	0.599	3.34E-03
s55	6.06	0.47%	2.61	0.867	3.16E-03
fire	6.75	0.65%	2.46	1.000	2.80E-03
soa	5.89	0.02%	2.43	0.543	1.79E-03
s45	6.00	0.33%	2.45	0.948	1.45E-03
top_cnt	6.20	0.21%	2.46	0.832	1.09E-03
liveeucal	5.92	0.13%	2.39	0.640	1.07E-03
s25	6.29	0.22%	2.25	0.924	9.30E-04
s20	6.41	0.25%	2.29	0.992	8.92E-04
ovnum	6.29	0.21%	2.28	0.970	7.97E-04
shrub_cnt	6.42	0.16%	2.28	0.910	7.37E-04
s35	6.41	0.20%	2.15	0.995	7.02E-04
ovn15t20	6.42	0.13%	2.18	0.945	5.47E-04
ovn20t30	8.61	0.01%	0.79	1.000	7.12E-06
evc	9.54	-0.01%	0.36	1.000	-1.70E-06
cosasp	5.05	0.02%	3.34	0.000	-1.15E+14

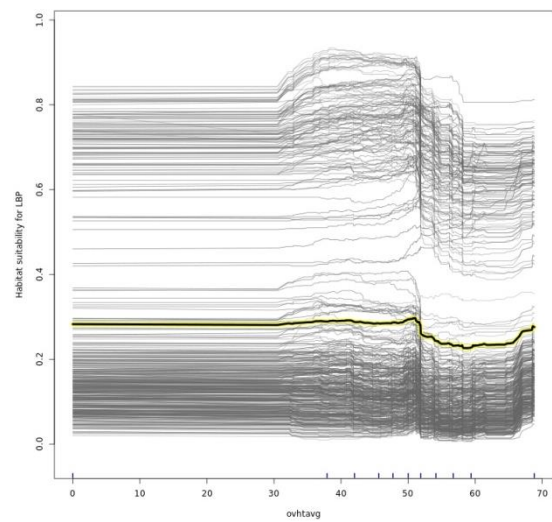
Individual Conditional Expectation (ICE) plots of important predictor variables for LBP



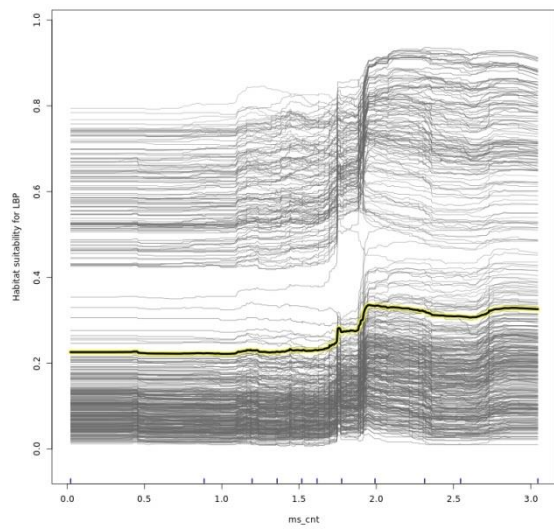
Temperature Seasonality (bio04)



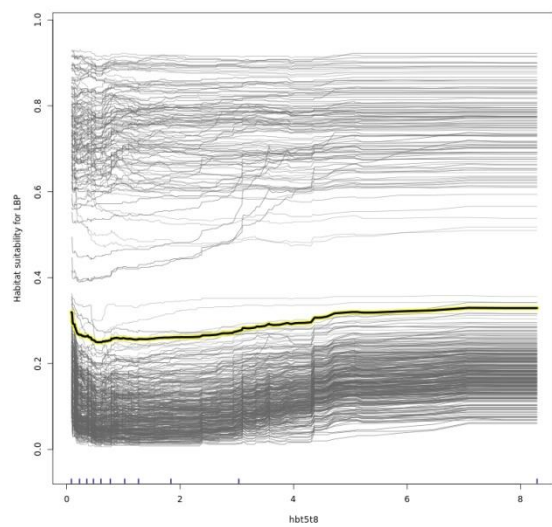
slope



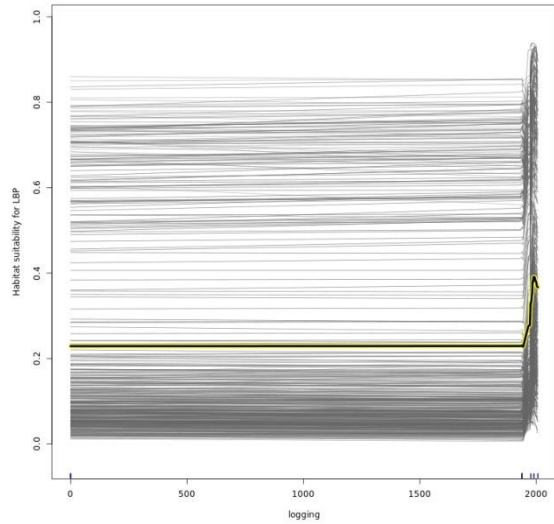
Average overstorey tree height (ovhtavg)



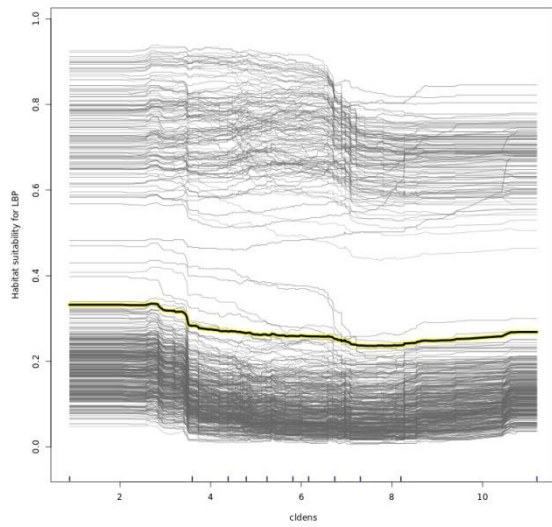
Midstorey connectivity index (ms_cnt)



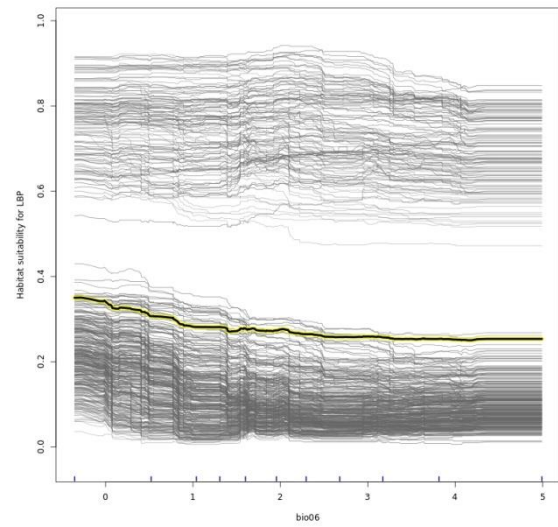
Density of all hollow-bearing tree form5-8 (hbt5t8)



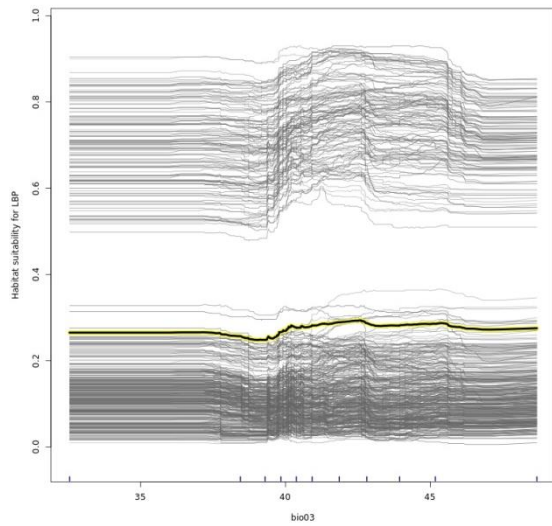
Year of logging (logging)



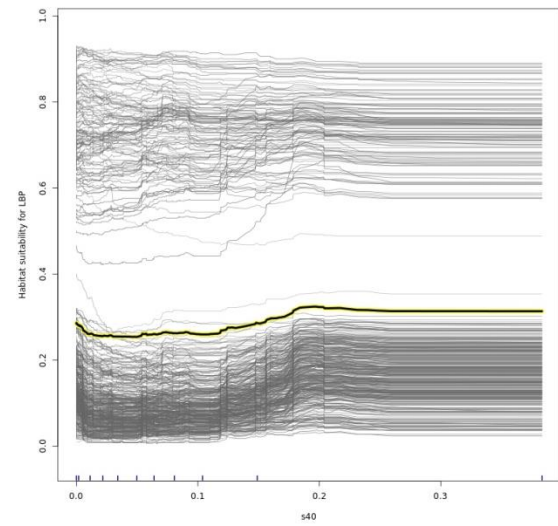
Stag Index (cldens)



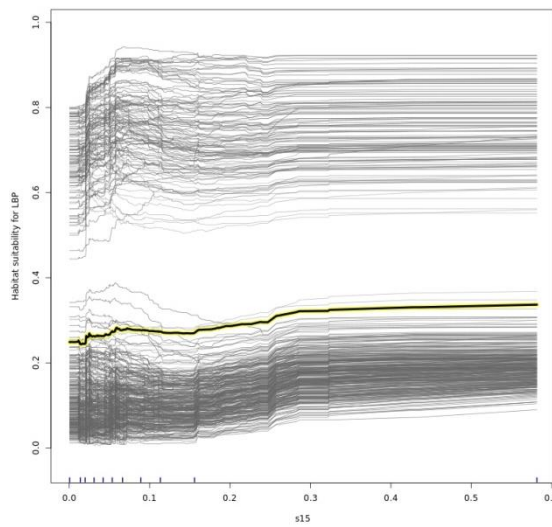
Min Temperature of Coldest Month (bio06)



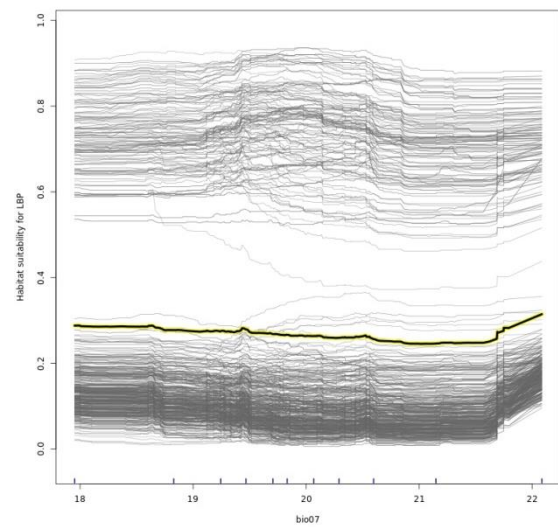
Isothermality (bio03)



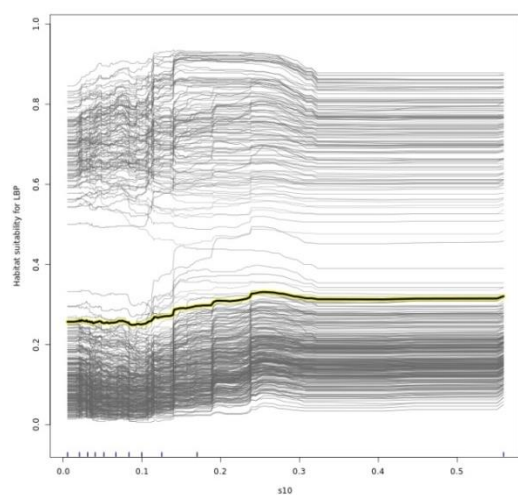
strata density between 40m-45m (s40)



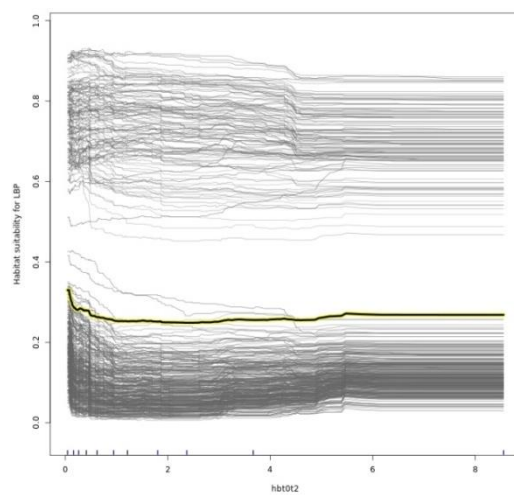
strata density between 15m-20m (s15)



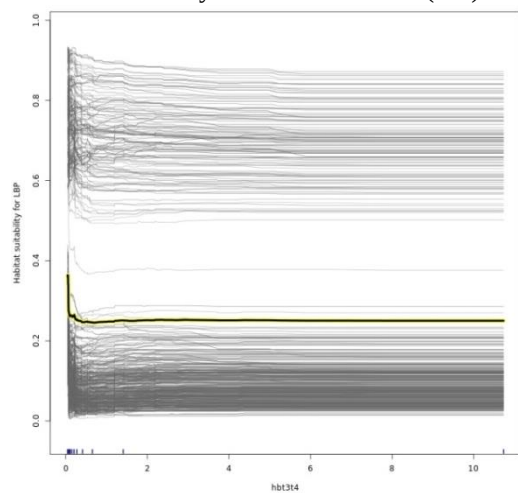
Temperature annual range (bio07)



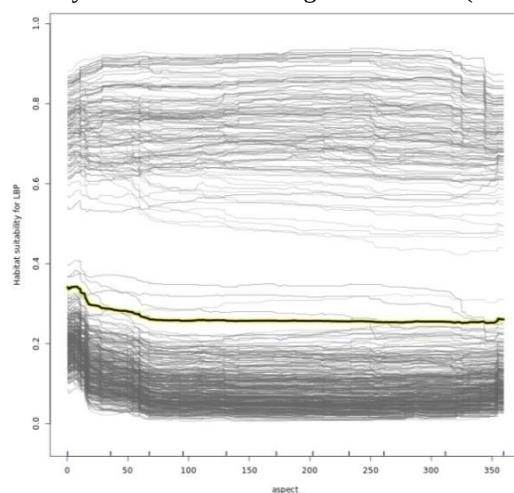
strata density between 10m-15m (s10)



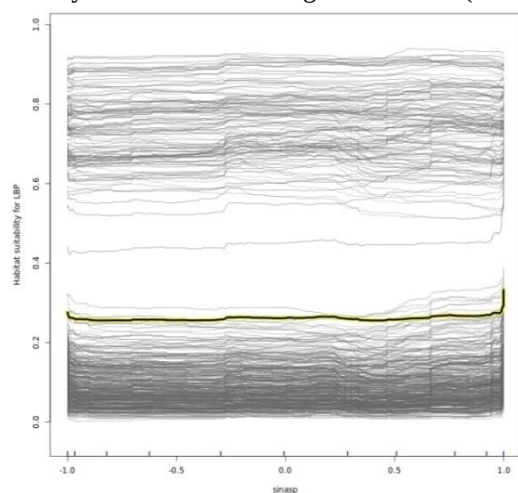
Density of all hollow-bearing tree form0-2 (hbt0t2)



Density of all hollow-bearing tree form3-4 (hbt3t4)



Aspect



Sin of aspect (sinasp)

Figure A5-2 Individual Conditional Expectation (ICE) plots of important predictor variables for LBP, sorted by variable importance.

Variables including 1 temperature seasonality (bio04), 2 slope, 3 average overstorey tree height (ovhtavg), 4 midstorey connectivity index (ms_cnt), 5 density of all hollow-bearing tree form5-8 (hbt5t8), 6 year of logging (logging), 7 stag index (cldens), 8 min temperature of coldest month (bio06), 9 isothermality (bio03), 10 strata density between 40m-45m (s40), 11 strata density between 15m-20m (s15), 12 temperature annual range (bio07), 13 strata density between 10m-15m (s10), 14 density of all hollow-bearing tree form0-2 (hbt0t2), 15 density of all hollow-bearing tree form3-4 (hbt3t4), 16 aspect, and 17 sin of aspect (sinasp)

LiDAR profile of plots with high density of live HBT and short dead HBT

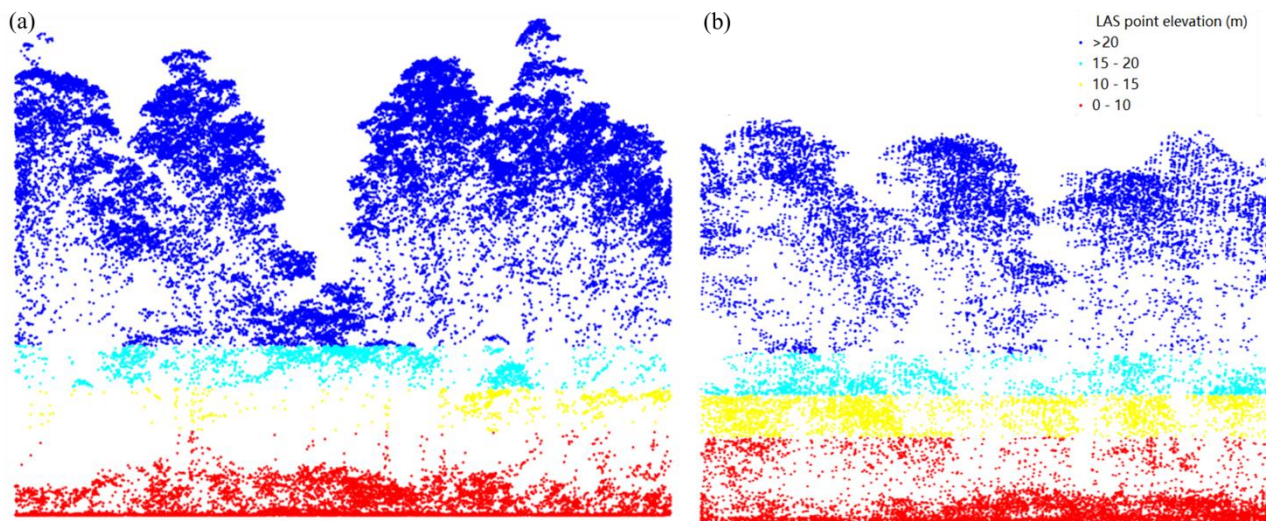
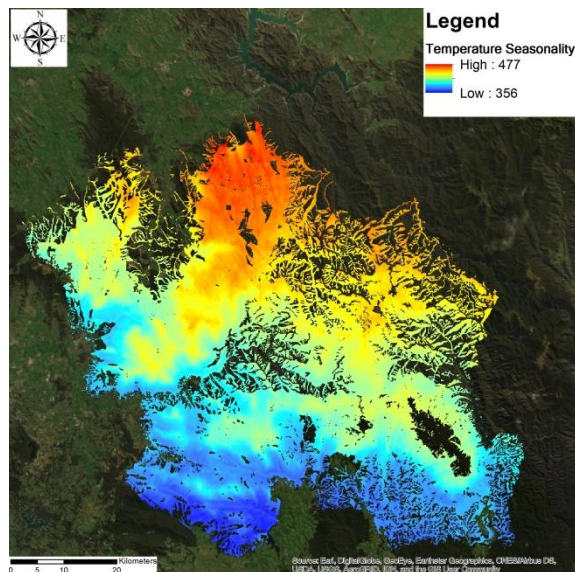
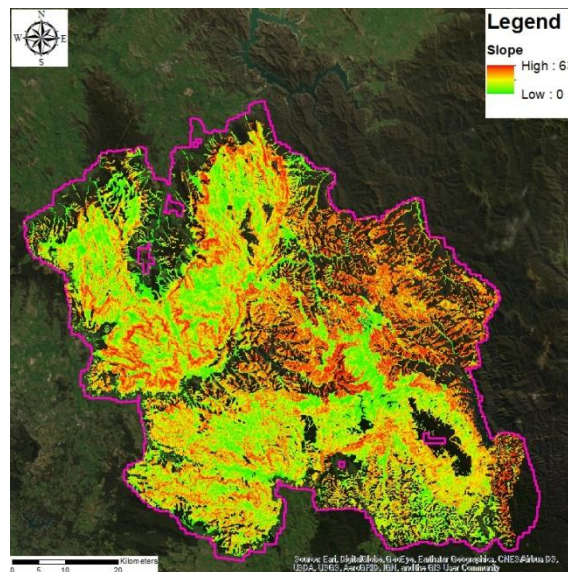


Figure A5 3 a) LiDAR profile of plots with high density of live HBT (HBT0t2); b) LiDAR profile of plots with high density of short, dead HBT (HBT7-8)

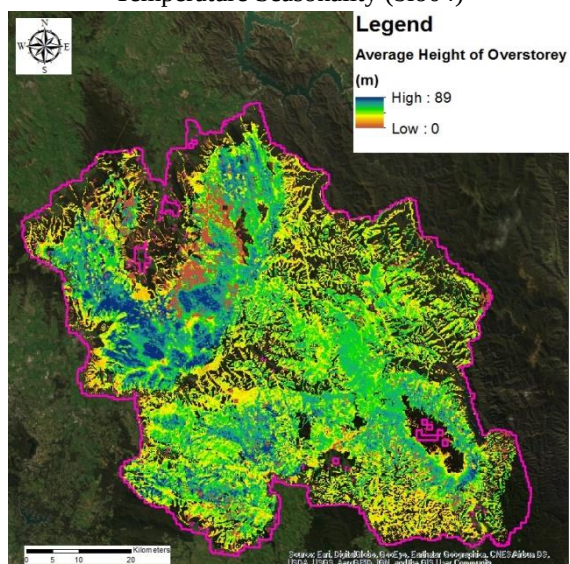
Maps of important predictor variables for LBP



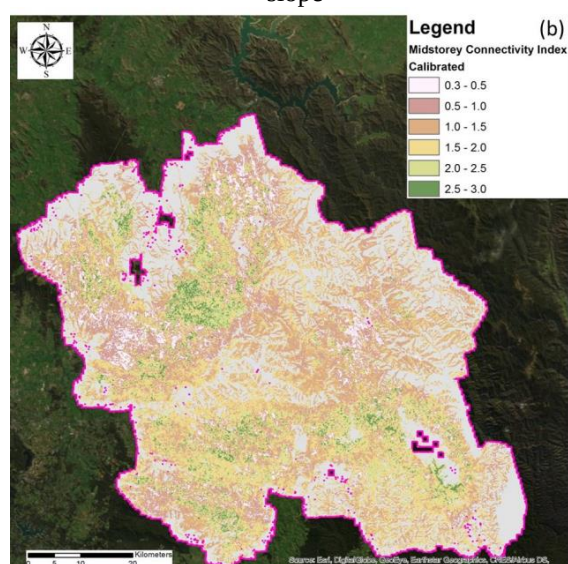
Temperature Seasonality (bio04)



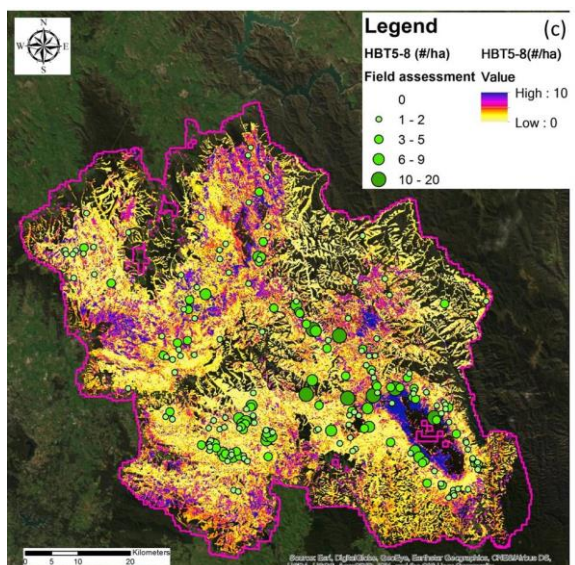
slope



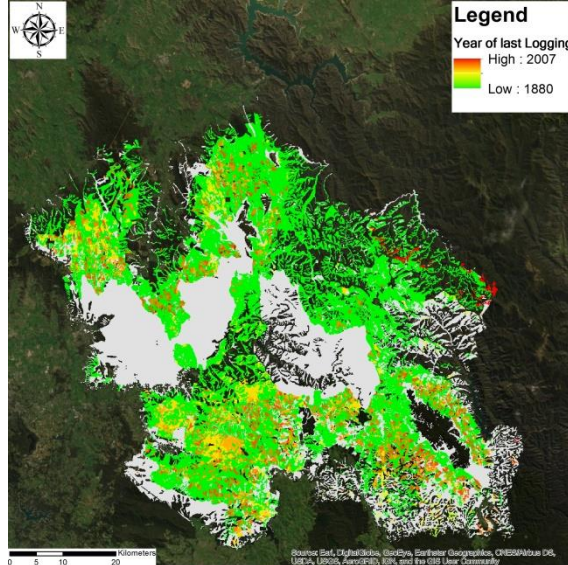
Average overstorey tree height (ovhtavg)



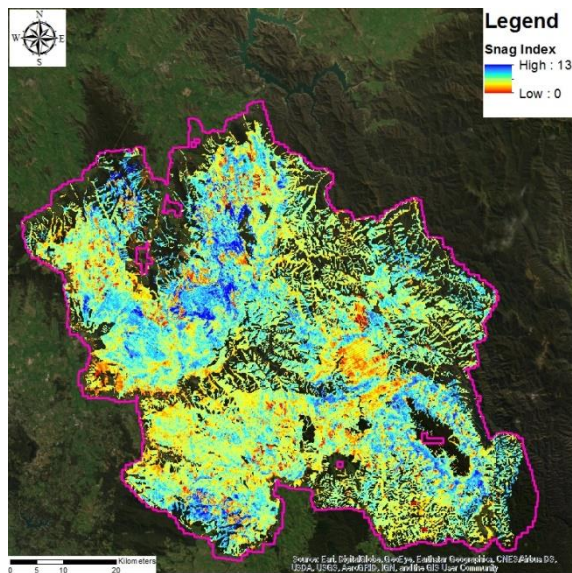
Midstorey connectivity index (ms_cnt)



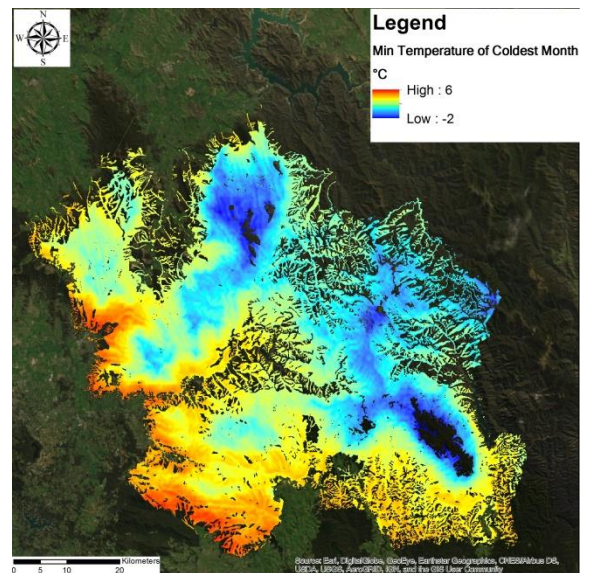
Density of all hollow-bearing tree form5-8 (hbt5t8)



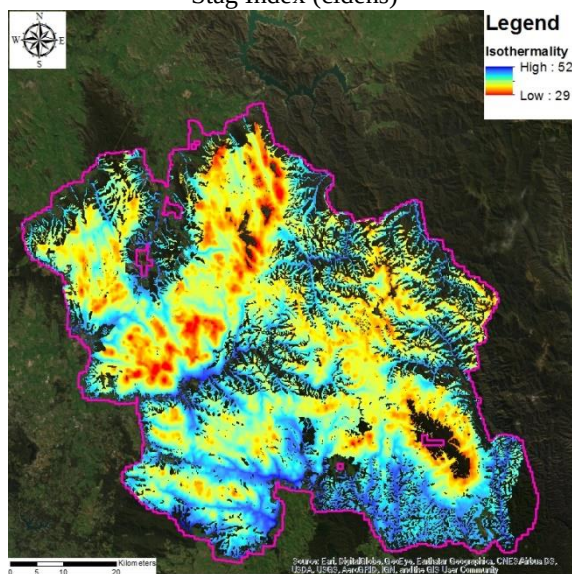
Year of logging (logging)



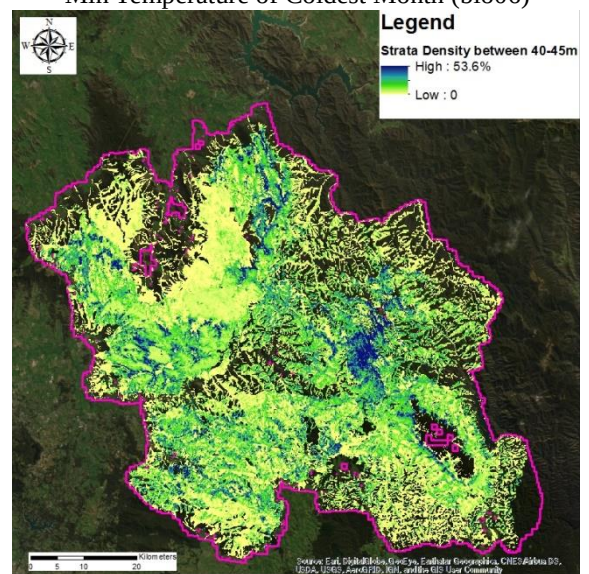
Stag Index (cldens)



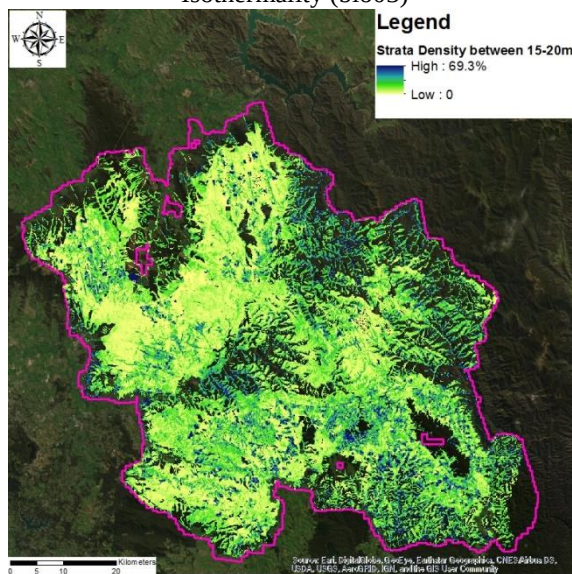
Min Temperature of Coldest Month (bio06)



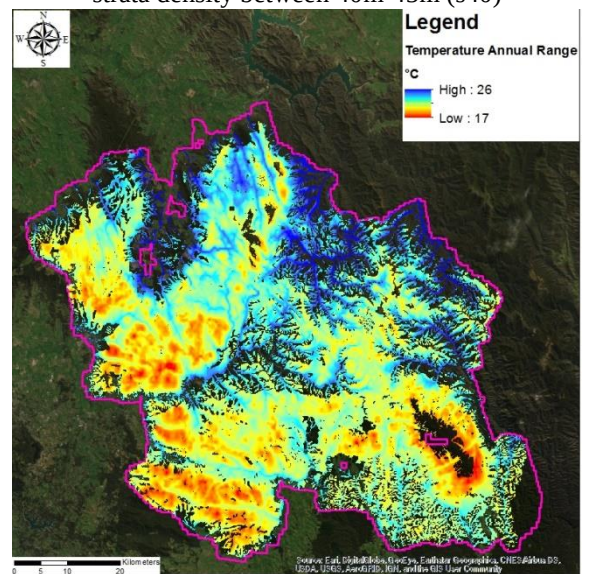
Isothermality (bio03)



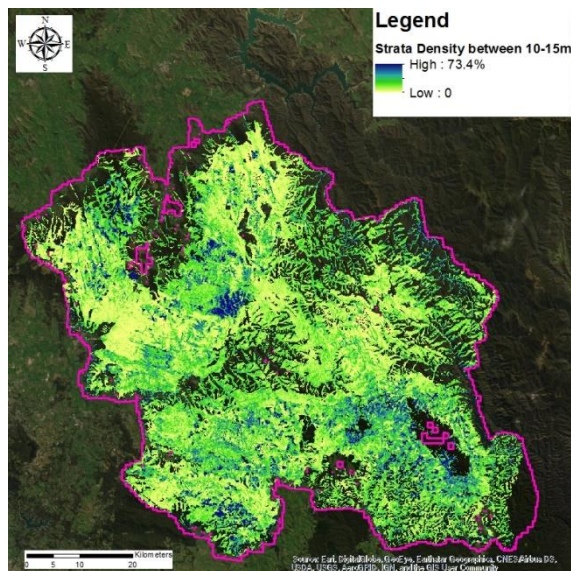
strata density between 40m-45m (s40)



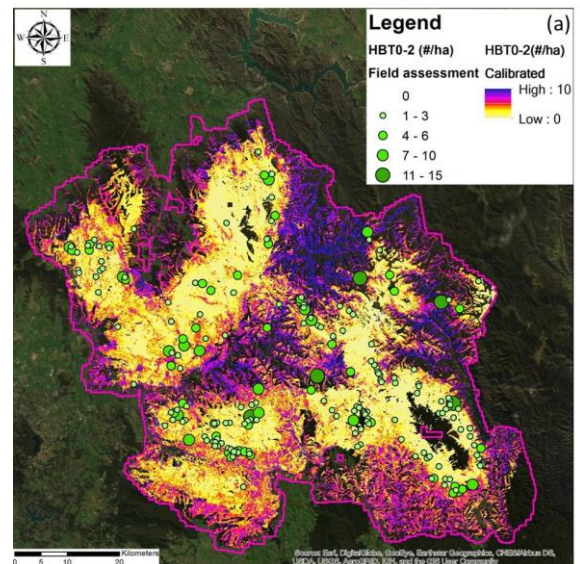
strata density between 15m-20m (s15)



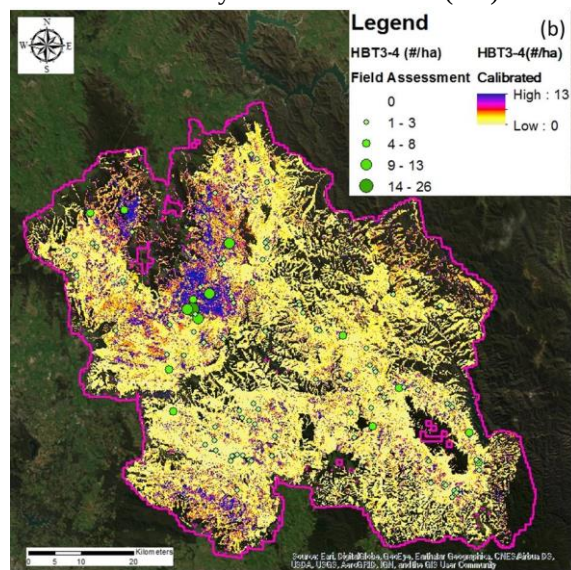
Temperature annual range (bio07)



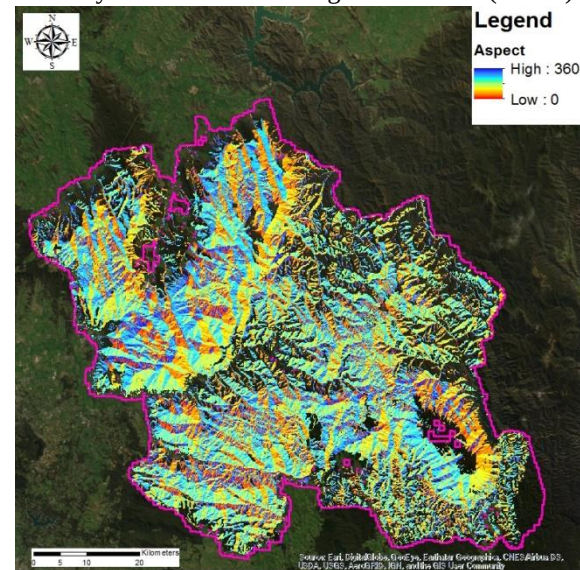
strata density between 10m-15m (s10)



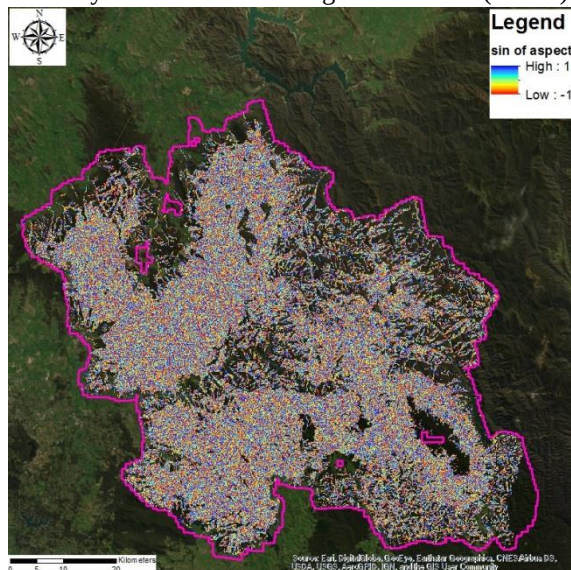
Density of all hollow-bearing tree form0-2 (hbt0t2)



Density of all hollow-bearing tree form3-4 (hbt3t4)



Aspect



Sin of aspect (sinasp)

Figure A5-4 Distribution map of important predictor variables for habitat suitability for LBP across Victoria's Central Highlands.

Variables sorted by variable importance, including 1 temperature seasonality (bio04), 2 slope, 3 average overstorey tree

height (ovhtavg), 4 midstorey connectivity index (ms_cnt), 5 density of all hollow-bearing tree form5-8 (hbt5t8), 6 year of logging (logging), 7 stag index (cldens), 8 min temperature of coldest month (bio06), 9 isothermality (bio03), 10 strata density between 40m-45m (s40), 11 strata density between 15m-20m (s15), 12 temperature annual range (bio07), 13 strata density between 10m-15m (s10), 14 density of all hollow-bearing tree form0-2 (hbt0t2), 15 density of all hollow-bearing tree form3-4 (hbt3t4), 16 aspect, and 17 sin of aspect (sinasp)

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Chapter 6.

6 Modelling landscape-scale habitat network connectivity for Leadbeater's Possum using airborne LiDAR data.

6.1 Introduction

Fragmentation of forest habitat is a major problem world-wide that is contributing to global biodiversity loss (Lindenmayer and Possingham 1996, Lindenmayer 2015b). To conserve forest-dependent species, effective and accurate tools are required for quantifying habitat amount and quality (Elith 2000, Cardinale et al. 2012, Vellend et al. 2013, Dornelas et al. 2014, Ewers et al. 2017, Leroux et al. 2017). During the last two decades, species distribution models (SDM) or habitat suitability index (HSI) models have become an increasingly important tool for identifying species habitat and quantifying the relationships between species abundance and environmental resources (Guisan and Thuiller 2005, Austin 2007, Rodríguez et al. 2007, Farrell et al. 2013, Guisan et al. 2013, Rechsteiner et al. 2017). SDMs and HSI generally account for the selection of suitable habitat and their appropriate geographical extents (Courbin et al. 2009, McLoughlin et al. 2010, Moreau et al. 2012, Courbin et al. 2014); however they rarely consider connectivity amongst predicted habitat areas (Courbin et al. 2014, Stevenson-Holt et al. 2014, Guo et al. 2018). For conservation to be effective the connectedness of habitat patches and how this changes over time and space need to be considered (Crooks and Sanjayan 2006, Galpern and Manseau 2013, Stevenson-Holt et al. 2014).

Landscape connectivity is defined as the degree to which the landscape facilitates or impedes species movement amongst resource patches (Taylor et al. 1993, Crooks and Sanjayan 2006). Animal movement, habitat selection and their influence on behavioural and physiological responses strongly depend on the spatial arrangement of resource patches in the landscape (Stevenson-Holt et al. 2014). Habitat accessibility is not only related to the structural attributes of connectivity (i.e., spatial arrangement of patches), but also to its functional aspects (i.e., movement capacity) (Crooks and Sanjayan 2006, McIntire et al. 2007, Dancose et al. 2011). Functional connectivity refers to the potential movement pathways of a species across modified and/or fragmented landscapes (Stevenson-Holt et al. 2014). Assessing connectivity can provide knowledge of how landscape structure may be influencing the movement of species which essential for addressing the impacts of

habitat fragmentation (Fischer and Lindenmayer 2007). Connectivity between habitat patches at finer-scales influences the local movement of individuals which directly affects colonisation but also influences other demographic processes such as survival (by determining access to foraging and nesting resources) and reproduction (Turner and Gardner 2015). At broader-scales, landscape connectivity can promote or hinder the movement of individuals between populations which can affect gene flow and thereby population fitness, adaptability and extinction risk (Turner and Gardner 2015). Populations that are connected within a landscape are considered metapopulations (Ryberg and Fitzgerald 2016). Meta-populations are characterised by landscape structure and composition in interaction with species habitat preferences and dispersal ability at multiple-scales (Ryberg and Fitzgerald 2016). Understanding the metapopulation structure of species is important for conservation planning (Minor and Lookingbill 2010, Guo et al. 2018) and determining the ability of species to be able to respond to climate change through migration (Heller and Zavaleta 2009). Landscape connectivity is an important component in defining metapopulations (Turner and Gardner, 2017). Simple landscape metrics of focal habitat connectivity may not be sufficient for characterising them however; spatially explicit consideration of the influence of landscape structure and composition on species habitat suitability and dispersal ability are necessary (Ryberg and Fitzgerald, 2016).

There are two distinct ways of producing functional connectivity networks: least-cost surfaces and graph theory (Galpern 2011). Least-cost surfaces estimated the distance between any pixels of a raster layer and the locations of identified suitable habitat patches. The distance was weighted by resistance values (cost values) from a resistance surface using ‘cost-distance’ function (Stevenson-Holt et al. 2014). Resistance surfaces contain a set of resistance values which represent a gradient of permeability across a landscape (Galpern 2011, Sawyer et al. 2011, Zeller et al. 2012) modelling the cost associated with animals movement and dispersal through a specific type of land cover (Compton et al. 2007, Beier et al. 2008). Graph theory assumes the landscape to be composed of a set of nodes that are connected by links, the output of which is a geospatial vector data (Urban and Keitt 2001, Urban et al. 2009, Courbin et al. 2014). The nodes of network represent potential high-quality patches with minimal cost values, and links reflect the least-cost paths for animals to move between two nodes (Theobald 2006, Dale and Fortin 2010, Galpern 2011, Courbin et al. 2014). Landscape graphs were developed to understand the structural connectivity of habitat configuration (Cantwell and Forman 1993, Urban and Keitt 2001, Urban et al. 2009, Galpern 2011).

Landscape graphs integrated with a thresholding (or scalar) approach was used to detect a series of functionally connected regions for identifying potential metapopulation structure, called “grains of

connectivity” approach (Bunn et al. 2000, Brooks 2003, Galpern and Manseau 2013). Another approach to assess functionally connected regions at the neighborhood or regional scale is based on a hybrid method which integrates the kernel density estimator (KDE) with least-cost paths (Compton et al. 2007, Li et al. 2016). The kernel estimator is a density estimator commonly used for home range analysis or scalar analysis (Worton 1989, Compton et al. 2007, Silverman 2018). Recently, KDE has been used in landscape ecological network analyses to provide relevant suggestions for the protection and planning of ecological networks at multiple scales (Compton et al. 2007, Bryan et al. 2011, Biondi et al. 2012, Vizzari and Sigura 2015, Li et al. 2016).

Both least-cost surfaces and graph theory use resistance surfaces that must reflect the habitat elements and movement barriers of a species. To avoid relying on plot-level data and/or subjective assessments to determine landscape resistance values, it is possible to use more data-driven and less biased approaches such as SDMs or HSI predictions (Wang et al. 2008, Spear et al. 2010, Stevenson-Holt et al. 2014, Milanesi et al. 2016, Milanesi et al. 2017a, Milanesi et al. 2017b), or vegetation structural attributes identified by airborne LiDAR (Light Detection And Ranging) (Guo et al. 2018). Airborne light detection and ranging (LiDAR) is an effective and proven technology for high-resolution mapping of forest structures over large landscape extents (Lefsky et al. 2002, Lim et al. 2003, Hudak et al. 2008, Martinuzzi et al. 2009, Simonson et al. 2014, Fedrigo et al. 2018). Assessment of forest structural features and vegetation types using LiDAR is a relatively mature application and has been used world-wide (Reutebuch et al. 2005, Morsdorf et al. 2010, Zald et al. 2014, Nijland et al. 2015, Guo et al. 2018). For example, Fedrigo et al. (2018) used LiDAR data to identify different vegetation types where the ability to detect sub-canopy forest structure was critical for differentiating between different vegetation communities in southeastern Australia. With LiDAR-derived forest inventory data of forest structural attributes across a large landscape scale (Hudak et al. 2006, Bässler et al. 2011, Latifi et al. 2015a, Fedrigo et al. 2018), it is possible to identify spatially-explicit habitat patches using LiDAR and to generate resistance surfaces to assess landscape connectivity networks. The application of LiDAR data to characterize habitat patches and their connectivity over large landscapes has not been well explored (Guo et al. 2018).

In this study, we focus on the application of LiDAR data to generate landscape habitat connectivity networks for the critically endangered Leadbeater’s possum (*Gymnobelideus leadbeateri*), across the montane ash (*Eucalyptus regnans*, *E. delegatensis*, and *E. nitens*) forests of the Victorian Central Highland in southeast Australia. Besides requiring ~3-4 hollow-bearing trees per hectare for nesting, a typical Leadbeater’s possum (LBP) habitat also requires a well-connected mid-storey for foraging (Lindenmayer 1989b, Lindenmayer et al.

1991b, Lindenmayer et al. 2000, Blair et al. 2017). The “connectivity” of the midstorey and understorey stratum is one of the most crucial attributes of LBP’s habitat (Blair et al. 2017). Since LBP doesn’t have gliding membranes, it needs a near continuous cover of foliage to move through the forest (Macfarlane *et al.* 1997). In this study, we used LiDAR-derived multi-storey connectivity index metrics (in Chapter 4) and midstorey coverage metrics (in Chapter 2) to generate resistance surfaces, and then used graph theory to create different landscape connectivity networks based on different vertical stratum. Finally, we integrated least-cost links from graph theory with KDE to identify functionally connected regions at multiple neighborhood scales. The objectives of this study were

- (1) to test the capability of using LiDAR-derive multi-scale vegetation connectivity metrics to characterize habitat patches and model habitat connectivity over large landscapes;
- (2) to understand which vertical canopy layer is the most important layer for LBP to create movement pathway by evaluating the response of LBP to these different landscape connectivity networks;
- (3) to identify functionally connected regions at large landscape scales, providing insights to improve spatial forest management and conservation planning; and,
- (4) to integrate the spatial patterns of functionally connected regions with areas of mapped habitat suitability (see Chapter 5) for LBP

6.2 Method

6.2.1 Study area

The study area is located in the Victorian Central Highlands of southeastern Australia (Figure 6-1). Native vegetation in Victoria has been classified into Ecological Vegetation Classes (EVCs) to represent unique characteristics of different vegetation types. Three major vegetation classes in this study are EVC 7 - wet - damp forest, EVC 8 - riparian forest, and EVC 9 – cool temperate rainforest. The study area is dominated by wet - damp forest (89%), with riparian forest (7%), and rainforest (4%) intermixed throughout. The dominant tree species in the wet - damp forest EVC are mountain ash (*Eucalyptus regnans*), alpine ash (*E. delegatensis*), and shining gum (*E. nitens*). The Central Highlands experience cool summers and humid winters with frequent frosts and occasional periods of snow (Burns et al. 2015). Mean annual temperatures ranged from 6-15 °C and mean annual precipitation ranged from 690-2090 mm over the period 1981–2010 (Stewart and Nitschke 2017, Fedrigo et al. 2019). More than 40% of the mountain ash forest in the Central Highlands of Victoria was impacted to some extent during the 2009 Black Saturday wildfires (Blair et al. 2018).

6.2.2 Field-based observation of LBP occurrence

LBP occurrence data (presence/absence) was collected by ARI (Arthur Rylah Institute for Environmental Research) and VicForests. Between 2014 and 2017, 576 LBP survey plots were established across the three major EVCs of the study area. In each survey plot, two to three baited remote cameras were set at nest trees or in foraging habitat and left in place for a minimum of 3-4 weeks to attempt to capture photos of LBP (Nelson et al. 2015). The majority of remote cameras used to capture LBP were placed in the forest stratum with dense understorey or midstorey, where the animals were likely to be moving and foraging (Fleming et al. 2014, Nelson et al. 2015). LBP was recorded as present on 160 out of 576 survey plots (~27%, see green dots in Figure 6-1). The plot network included 518 sites in wet - damp forest, 17 sites in riparian forest, and 41 sites in rainforest. Among the 576 survey plots, 135 were located in forest burnt in 2009, in 12 of which LBP was recorded as present (~9% of the 2009 burnt plots).

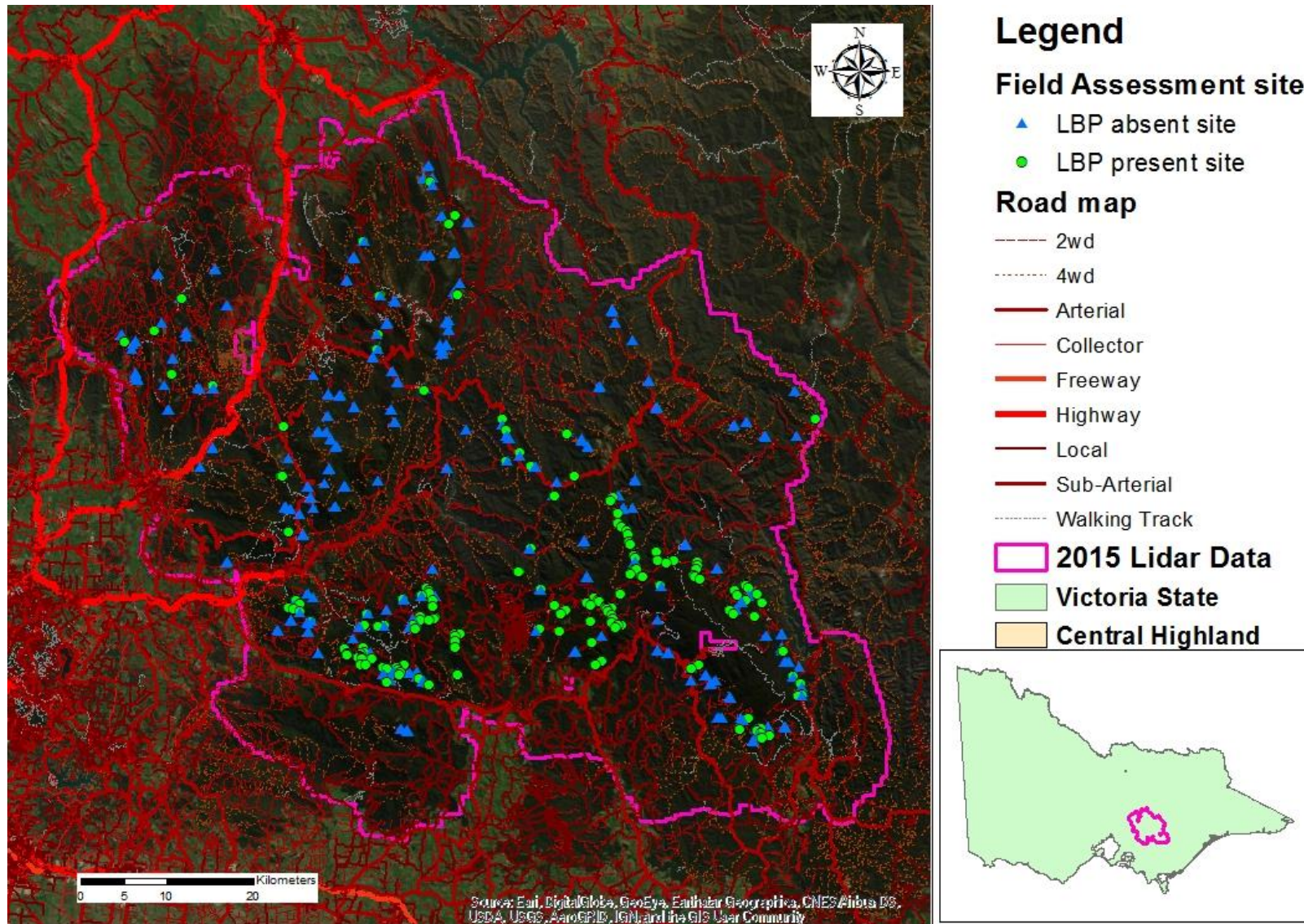


Figure 6-1 The study area in Victoria's Central Highlands. The map shows the total LiDAR coverage, the locations of field LBP observation sites and the road network

6.2.3 GIS products and Lidar-derived connectivity metrics

LiDAR raw data

Discrete return airborne LiDAR data were acquired by RPS Group Plc in late 2015 and early 2016 using Trimble AX60 laser sensor mounted on a fixed wing aircraft. The aircraft was flown at 800 m above ground with flying speed of 62 m/s. Mean pulses per meter sent to ground was 2-4 pts/m with an average point spacing of 0.46m. LiDAR data covered 513,322 hectares of Victorian Central Highlands (Figure 6-1). After electing relevant EVCs for the study area, the final study area was 342,960 ha, which included 305,200 ha of wet or damp forest, 24,900 ha of riparian forest and 12,400 ha of rainforest. 112,205 ha of LiDAR covered study area were burnt in 2009, 32.8% of the total area.

Road Network

Spatial data of road network were sourced from the Victorian Department of Environment, Land, Water, and Planning (DELWP). The map of road network was shown in Figure 6-1. The road type, road class code and resistance value assigned to each road class was shown in Table 6-1.

Table 6-1 Road type and their resistance value based Vicmap Transport (land.vic.gov.au)

Road Class Code	Road type	Resistance value
0	Freeway	13
1	Highway	12
2	Arterial	11
3	Sub-Arterial	10
4	Collector	9
5	Local	8
6	2wd	7
7	4wd	6
11	Walking Track	2
	No road	1

Midstorey coverage metrics using LiDAR-derived individual tree detection algorithm (chapter2)

LiDAR midstorey coverage metrics were variables derived from the results of individual tree detection (see Chapter 2). For the midstorey within each plot, LiDAR points were used to calculate the proportion of projection area of midstorey LiDAR points, a surrogate for midstorey density. The plot size selected in this study was 20m. The 20m-plot-size midstorey coverage metrics was used to test the capability of using LiDAR data to create high resolution connectivity networks over large landscapes.

Multi-storey connectivity metrics predicted from random forest model (chapter 4)

Connectivity score of each vertical vegetation layer at each site were used predictions of LiDAR structural metrics from random forest models developed in Chapter 4. We used the connectivity metrics of shrub layer (1haSh) and midstorey layer (1haMs) at a 1ha resolution to create resistance surface and landscape connectivity networks. Connectivity scores ranges from 1 to 3, where 1 represents no connectivity and 3 represent the maximum connectivity. We defined resistance as the inverse of connectivity (Galpern 2011).

Habitat suitability index predicted using random forest model (chapter 5)

The map of habitat suitability index for LBP was built using the 17 environmental variables that had the strongest influence on habitat suitability for LBP using random forest model in Chapter 5. The map was used to compare with the distribution pattern of high functionally connected regions from landscape connectivity networks.

6.2.4 Resistance surfaces from different vertical vegetation layers

First, we created a road resistance surface by assigning a relative cost or resistance value (see Table 6-1) to each road. Second, we created three 1ha multi-storey resistance surfaces by taking the inverse of the modelled connectivity scores of shrub (1haSh) and midstorey (1haMs) layers. We also created a 1ha understorey-midstorey resistance surface which estimated maximum connectivity scores per ha of two layers and used the inverse of this to determine the resistance value. The 1ha understorey-midstorey resistance surface (1haUM) is based on the assumption that LBP could use both vegetation layers to move through while foraging. The resistance values were:

- resistance 1 = No resistance, a continuous vegetation layer, LBPs can access every part of that layer within a plot;
- resistance 2 = Low resistance, LBPs can move around relatively easily but may need to move into another layer to access a different part of the layer; and,
- resistance 3 = High resistance, zero opportunity for LBPs to move around in that layer.

The 20m-plot-size midstorey coverage metrics were also reclassified to create a resistance layer comprised of three resistance levels t (20mMc):

- resistance 1 = midstorey coverage > 66%
- resistance 2 = 33% < midstorey coverage ≤ 66%
- resistance 3 = midstorey coverage ≤ 33%

Different levels of resistance for the midstorey layer in different LiDAR point profiles are illustrated in Figure 4-4.

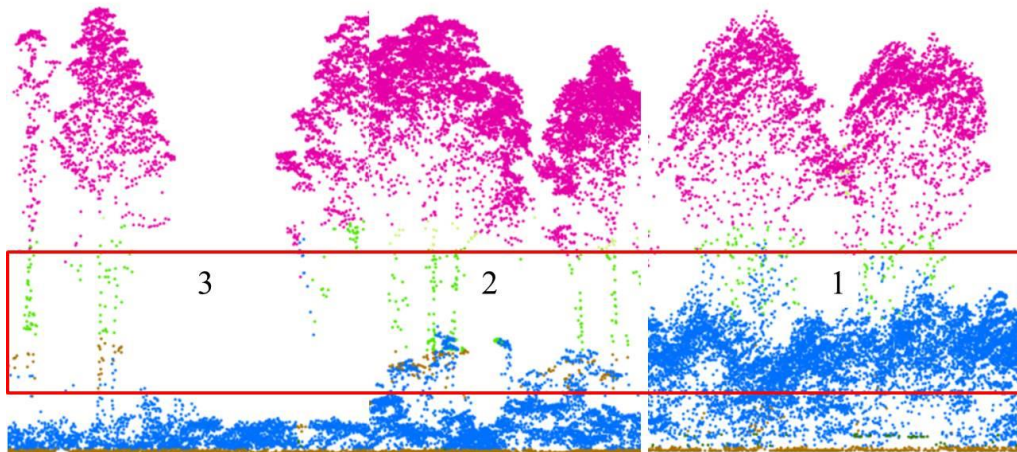


Figure 6-2 LiDAR point profiles showed different levels of resistance for midstorey layer (in red rectangle)

Finally, we included roads as a resistance surface as roads may restrict the movement of LBP (Blair et al. 2017). The four final resistance surfaces used to build landscape connectivity networks were road $\times$ 1haSh (1haShRd), road $\times$ 1haMs (1haMsRd), road $\times$ 1haUM (1haUMRd) and road $\times$ 20mMc (20mMcRd). The resistance value in other irrelevant vegetation classes or water body was assign with 255 (a value high enough that makes it impossible for LBP to move through).

6.2.5 Landscape connectivity networks using minimum planar graph theory (MPG)

We used minimum planar graph theory (MPG) to create spatial networks as this provides an efficient approximation of all possible pairwise links between graph nodes (Fall et al. 2007, Galpern 2011, Courbin et al. 2014). The MPG was built on resistance surfaces that were specific to each vegetation stratum. The construction of a landscape connectivity network for each stratum required two preliminary steps (O’Brien et al. 2006, Theobald 2006, Urban et al. 2009, Galpern 2011):

- (1) the identification of suitable habitat patches for LBP, which are considered as the nodes of the spatial network where the cost of moving within is minimal; and,
- (2) the determination of the relative cost of moving between patches to identify the links between nodes using least-cost path approach. A least-cost path represents the most likely movement or dispersal path for LBP traveling between two habitat patches.

In the MPG method, all nodes are connected by the reduced set of shortest and least-cost links without creating any cross of links (Theobald 2006, Fall et al. 2007). We used the “gsMPG” function of “grainscape” package in R to create the MPG (Galpern et al. 2012). We assumed that all pixels in a resistance surfaces with the resistance value equal to 1 were habitat patches for LBP. We extracted the polygons of patches and the polylines of links of networks from different resistance surfaces, and then compared the patch size and link cost / link length from different resistance surfaces.

6.2.6 Kernel density estimator (KDE) of least-cost paths to create functionally connected regions

This least-cost paths (links) can be integrated with a kernel density estimator (KDE) that measures the functional connectivity (or low cost distance) from a focal cell to all other neighborhood cells in the range of a specified radius (usually equal to the bandwidth) (Compton et al. 2007, Li et al. 2016). A least-cost “kernel” is a functionally connected region of the landscape and represents the interaction between a spatial region and the animals response to structure in that region (Galpern and Manseau 2013). In this study, we assumed the functionally connected regions to be determined by the spatial configuration of resistance represented by vegetation density (i.e. cost values of links), not the spatial configuration of resource patches. The boundaries of functional regions were associated with landscape structures that are assumed to have higher perceived movement costs for the animal, while the center of each region has lower movement costs and more links. We used “kernel density” tools in ArcGIS v10.5 to estimate kernel link density of links from different resistance surface and weighted by “least-cost” value. The “least-cost” value was the inversed cost value of each link. The functionally connected regions were scale-dependent. By changing the bandwidth of KDE, we generated different spatial configuration of functional regions with a 1km, 3km, and 5km-radius to represent the functional neighborhood scale for functionally connected regions. The workflow of generating landscape connectivity networks and functionally connected regions is shown in Figure 6-3.

6.2.7 Evaluating the response of LBP to connectivity networks from different resistance surfaces

To quantify how our different connectivity metrics relate to the probability of LBP occurrence, we used a generalized linear model (GLM) with a binomial distribution and a logit link.

$$p = 1/(1 + \exp(-(a_0 + a_1 * \log(x + 1)))) \quad (2)$$

where p is the probability of observed LBP occurrence, a_0 and a_1 are model parameters, and x is a set of spatial attributes of connectivity networks from different resistance surfaces. The x included:

- 1) the distance of each LBP observation site to nearest patch of networks for each resistance surface;
- 2) the distance to nearest least-cost path (link) of each LBP observation site which not located in patches;
- 3) the cost value of nearest least-cost path of each LBP observation site which not located in patches; and,
- 4) the kernel density of least-cost path for each resistance surface within different neighborhood scale.

For distance to nearest patch and link, to avoid invalid value as $\log(0)$, we used $(x + 1)$ to be predictors in GLM.

Area under the Receiver Operating Characteristic curve (AUC) was calculated for each GLM to estimate the model performance, and to select relative significant resistance surface and functionally connected regions at certain neighborhood scale for LBP. The Receiver Operating Characteristic curve (ROC curve) was used to evaluate the sensitivity against the specificity at various threshold values (Altman and Bland 1994). AUC is the probability that the classification will correctly rank a randomly chosen positive instance higher than a

randomly chosen negative instance (Fawcett 2006). AUC is a widely used indicator of model performance in resource selection modelling (Lobo et al. 2008, Jiménez-Valverde et al. 2011, Jiménez-Valverde 2012, Tattoni et al. 2012). The GLM models in this Chapter were not used to predict the probability of LBP presence. The model accuracy is not important, so it is not necessary to have high AUCs. The values of AUC of each model were only used as an indicator to compare relative significant resistance surface and functionally connected regions to LBP.

6.2.8 Suitable habitat in each functional-connected regions

After selected relative significant resistance surface and functionally connected regions at certain neighborhood scale for LBP, we summarized the total area and patch size of suitable habitat (i.e. plots with $HSI \geq 0.5$) in each functional regions. We also summarized the number of LBP presence site and probability of presence site located in each functionally connected region.

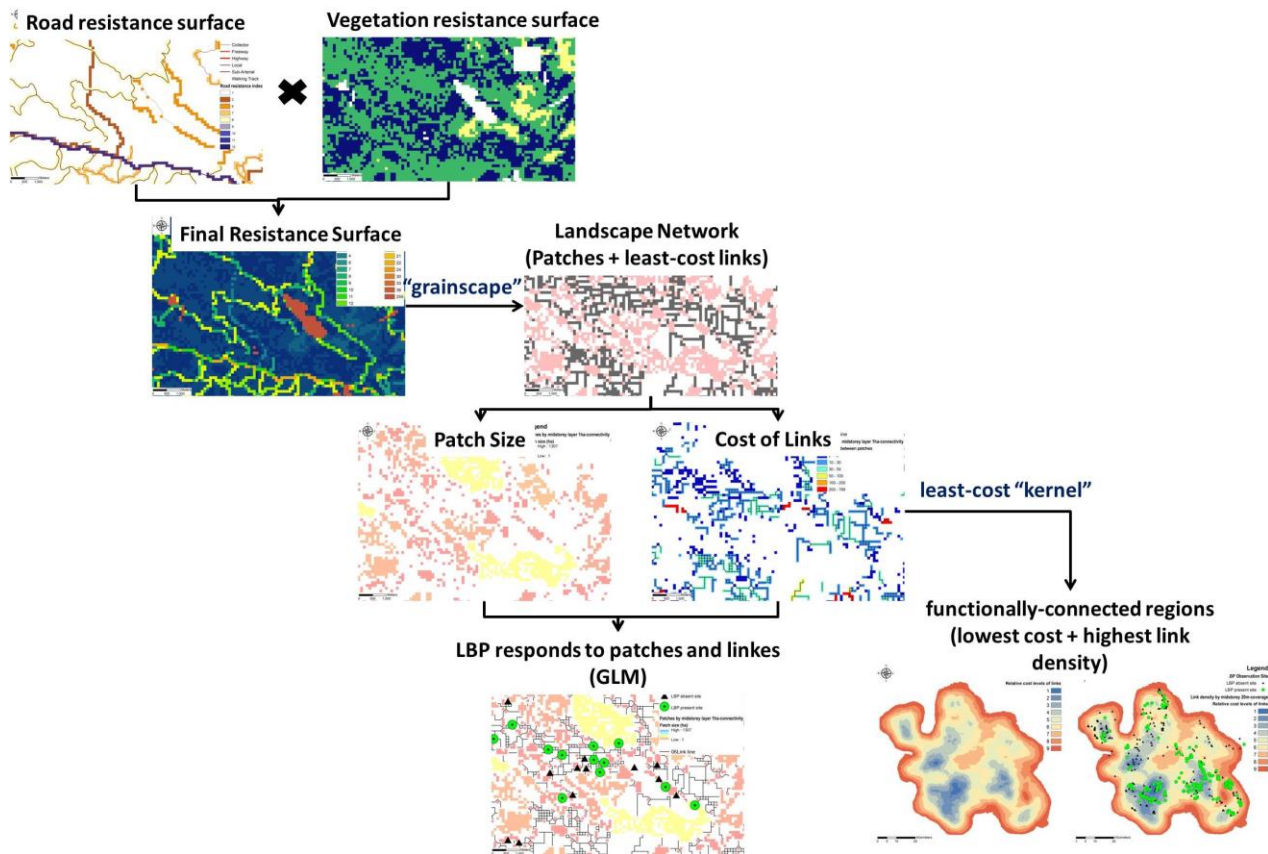


Figure 6-3 The workflow of generating landscape connectivity networks and functional-connected regions

6.3 Result

6.3.1 Distribution and spatial configurations of patches and links of connectivity networks

The four connectivity networks generated from four resistance surfaces resulted in very different spatial distributions of patches and links (Table 6-2, Table 6-3 and Figure 6-4). The network based on both shrub and midstorey surface (1haUMRd) had the lowest number of patches, largest patch size, the smallest number of inter-patch links, and the highest average cost of links compared to other vegetation layer. Whereas, the highest number of patches, smallest patch size, highest abundance of links and lowest average link cost was the network created from 20m midstorey coverage surface (20mMcRd). Patches of networks created from shrub-included surfaces (both 1haUMRd and 1haShRd) covered more of the study area (about 73% and 70%, respectively) than midstorey-only surfaces (both 1haMsRd and 20mMcRd). Patches from 20mMcRd covered only 4% of the whole study area, with the smallest average patch size of 0.3ha. The proportion of minimal patch size in all patches was 1.6-1.8 times higher in networks from midstorey-only surfaces (both 1haMsRd and 20mMcRd) than from shrub-included surfaces (both 1haUMRd and 1haShRd). The number of links of networks from 20mMcRd was 1.4-3 times higher than the number of links from other vegetation layer, but the average link cost of 20mMcRd was only 53%-95% of other vegetation surface. The proportion of minimal cost of links in all inter-patch links was smallest in mid-storey networks only.

Table 6-2 Summary of patches of four connectivity networks generated from four resistance surfaces of 1ha shrub layer, 1ha midstorey layer, 1ha under-/mid-storey layer and 20m midstorey layer. Number of patches, total patch area (ha), % of study area, mean, standard deviation (sd) and maximum (max) of patch size, number of minimal patch size, and the proportion of minimal patch in all patches were summarized across all study area for networks of different resistance surface.

Resistance Surface	No. of Patches	Patch Area (ha)	% of study area	mean	sd	maximum	Minimal Size*	
							No. of Patches	% in all patches
1haShRd	4,640	238,653	70%	51.43	177.33	2,696	1,418	31%
1haMsRd	7,814	49,843	15%	6.38	26.79	1,307	3,832	49%
1haUMRd	4,272	248,694	73%	58.21	197.76	3,285	1,263	30%
20mMcRd	41,142	12,310	4%	0.30	1.72	91.72	22,140	54%

*1ha minima size for surface 1haShRd, 1haMsRd, and 1haUMRd; and 0.04ha (20m×20m) minima size for surface 20mMcRd

Table 6-3 Summary of links between patches of four connectivity networks generated from four resistance surfaces of 1ha shrub layer, 1ha midstorey layer, 1ha under-/mid-storey layer and 20m midstorey layer. Number of links, mean and standard deviation (sd) of link cost, number of minimal cost links, and the proportion of minimal cost links in all links were summarized across all study area for networks of different resistance surface.

Resistance surface	No. of links	mean	sd	Cost of links = min cost	
				No. of links	% in all links
1haShRd	10,207	143.91	237.7	694	6.80%
1haMsRd	19,678	95.27	185.67	1,434	7.30%
1haUMRd	9,228	155.22	244.51	552	6.00%
20mMcRd	27,894	89.10	91.54	177	0.63%

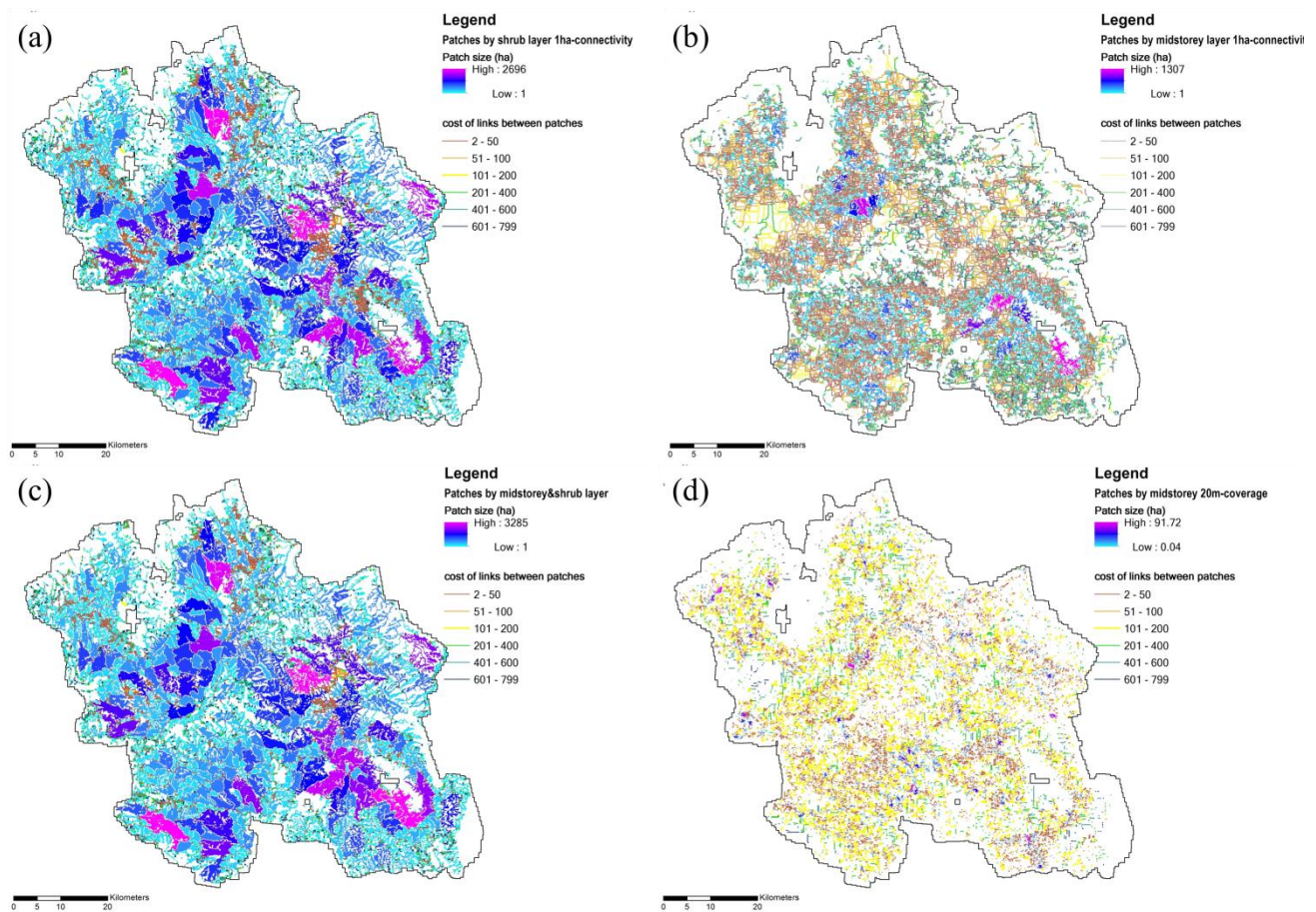


Figure 6-4 Four connectivity networks colored by patch size and cost value of links between patches for resistance surface of (a) road × 1ha shrub layer (1haShRd), (b) road × 1ha midstorey layer (1haMsRd), (c) road × 1ha under-/mid-storey layer (1haUMRd) and (d) road × 20m midstorey layer (20mMcRd)

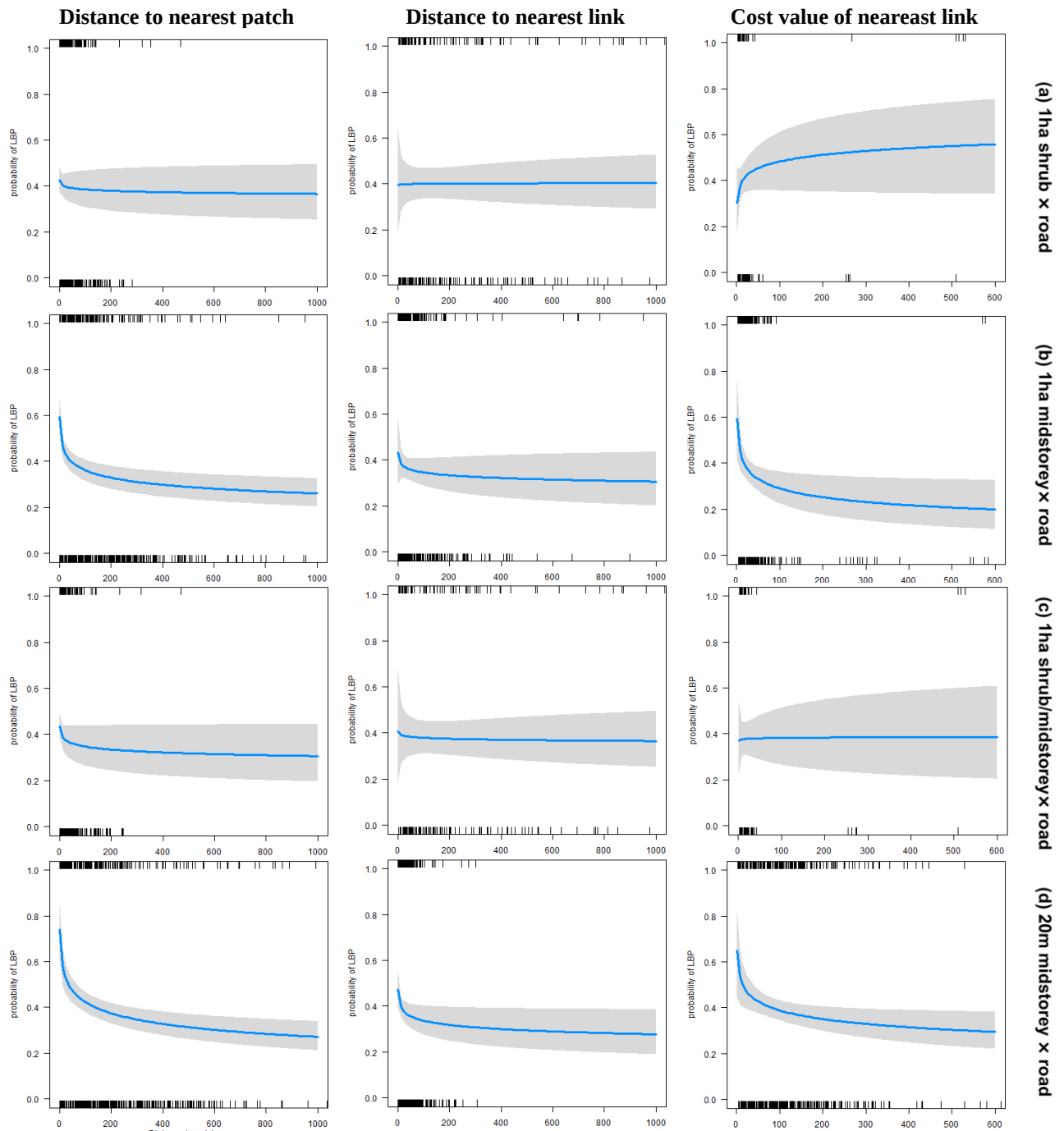
6.3.2 Response of LBP to the connectivity networks of different resistant surface

The generalized linear models (GLM) of the probability of LBP occurrence only showed better goodness-of-fit statistics in the models related to spatial attributes of networks from midstorey-only surfaces (1haMsRd and 20mMcRd) than other resistance surfaces (Table 6-4 and Figure 6-5). For midstorey-only surfaces, the GLM based on the distances to nearest patches (AUC=0.64, 0.60; p-values < 0.001) performed slightly better than cost value of nearest inter-patch links (AUC=0.63, 0.56; p-values < 0.005). The distance to nearest links only created from 20mMcRd had a significant relationship with LBP occurrence (AUC=0.58; p-values < 0.05). The highest AUC of GLM was estimated the probability of LBP occurrence based on the distances to nearest patches in networks from 1haMsRd resistance surfaces. In networks from midstorey-only surfaces, the probability of LBP occurring on a site decreased with the distance to nearest patches ($a_1=-0.20, -0.30$), the distance to nearest links ($a_1=-0.08, -0.12$) and cost value of nearest links ($a_1=-0.53, -0.30$). Cost value of nearest links had slightly higher negative effect on LBP occurrence than distance to nearest patches and links.

Table 6-4 Model summary. The AUC for generalized linear models (GLM) to quantify the probability of LBP occurrence related to spatial attributes (distance to nearest patch, distance to nearest links and cost value of nearest link) of connectivity networks from four resistance surface

spatial attributes	resistance surface	coefficients	estimate	95%CI		p-value	signif. codes	AUC
				min	max			
Distance to nearest patch	1haShRd	a0	-0.298	-0.521	-0.077	0.008	**	
		a1	-0.037	-0.129	0.055	0.433		0.516
	1haMsRd	a0	0.383	0.056	0.715	0.022	*	
		a1	-0.206	-0.285	-0.129	0.000	***	0.638
	1haUMRd	a0	-0.254	-0.466	-0.043	0.019	*	
		a1	-0.082	-0.183	0.017	0.107		0.532
	20mMcRd	a0	1.053	0.443	1.697	0.001	***	
		a1	-0.295	-0.425	-0.173	0.000	***	0.596
Distance to nearest link (least-cost path)	1haShRd	a0	-0.429	-1.428	0.548	0.393		
		a1	0.006	-0.191	0.205	0.955		0.504
	1haMsRd	a0	-0.272	-0.882	0.332	0.378		
		a1	-0.079	-0.237	0.078	0.325		0.537
	1haUMRd	a0	-0.373	-1.479	0.708	0.501		
		a1	-0.026	-0.241	0.190	0.814		0.504
	20mMcRd	a0	-0.110	-0.441	0.220	0.514		
		a1	-0.123	-0.230	-0.017	0.024	*	0.575
Cost value of nearest link (least-cost path)	1haShRd	a0	-0.554	-1.333	0.225	0.160		
		a1	0.012	-0.287	0.302	0.936		0.472
	1haMsRd	a0	1.098	0.265	1.964	0.011	*	
		a1	-0.528	-0.790	-0.280	0.000	***	0.625
	1haUMRd	a0	0.087	-0.760	0.990	0.844		
		a1	-0.311	-0.679	0.011	0.074	•	0.604
	20mMcRd	a0	0.859	-0.007	1.745	0.054	•	
		a1	-0.297	-0.491	-0.109	0.002	**	0.561

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1



6.3.3 Response of LBP to kernel density estimator (KDE) of least-cost paths at different neighborhood scale

The bandwidth of KDE selected for functional neighborhood scale to create functionally connected regions ranged from 1 to 5 km in networks of two midstorey-only resistance surfaces. Examples of KDE of least-cost paths weighted by “least-cost” values in a landscape at three neighborhood scales were shown in Figure 6-6. The GLM based on KDE of least-cost paths in networks from 20mMcRd (AUC=0.6, p-values < 0.001) preferred better than networks from 1haMsRd (AUC=0.5, p-values < 0.1) (Table 6-5). The probability of LBP occurring on a site increased with the kernel link density of least-cost paths weighted by “least-cost” values ($a_1 > 0$). The LBP present probability increased more strongly with kernel link density at broader neighborhood scale ($a_1 = 0.3$ in 1km and $a_1 = 1.2$ in 5km). The GLM of 20mMcRd surface started to show a reasonable goodness-of-fit statistics at a functional neighborhood scale of 3km, so we selected KDE of least-cost paths of 20mMcRd surface within 3km to create functionally connected regions. The maps of functional connectivity at three neighborhood scales were shown in Figure 6-7.

Table 6-5 Model summary. The AUC for generalized linear models (GLM) to quantify the probability of LBP occurrence related to kernel link density of least-cost paths (links) in connectivity networks from two midstorey-only resistance surfaces at different neighborhood scale (1km, 3km and 5km)

resistance surface	neighborhood scale	estimate	95% CI		p.value	signif. codes	AUC
			min	max			
20mMcRd	(Intercept)	-0.915	-1.103	-0.733	0.000	***	
	1km	0.255	0.039	0.493	0.028	*	0.582
	(Intercept)	-0.959	-1.148	-0.776	0.000	***	
	3km	0.827	0.388	1.303	0.000	***	0.611
	(Intercept)	-0.836	-1.026	-0.649	0.000	***	
	5km	1.226	0.681	1.802	0.000	***	0.622
1haMsRd	(Intercept)	-0.962	-1.173	-0.761	0.000	***	
	1km	0.012	-0.160	0.211	0.897		0.521
	(Intercept)	-1.127	-1.508	-0.776	0.000	***	
	3km	0.276	-0.211	0.796	0.280		0.498
	(Intercept)	-1.380	-1.837	-0.973	0.000	***	
	5km	0.734	0.111	1.423	0.028	*	0.522

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

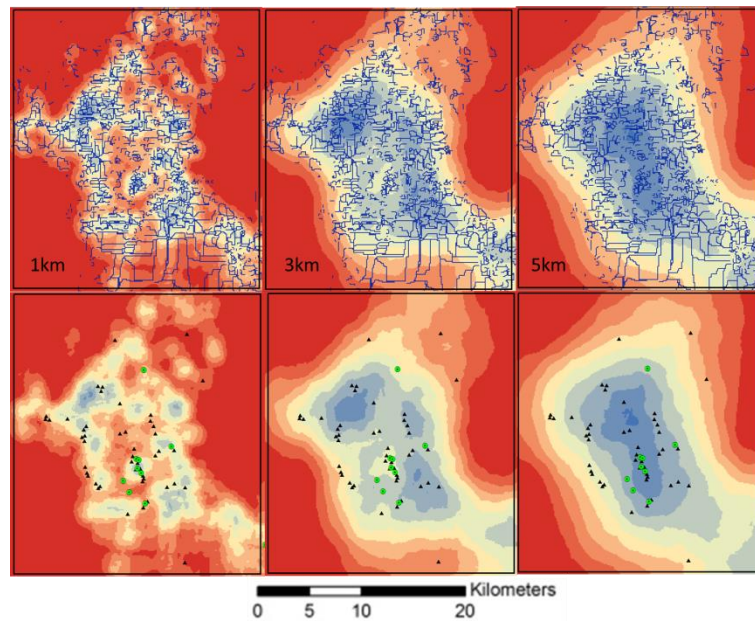


Figure 6-6 Examples of the kernel density estimator (KDE) of least-cost paths (blue line) in a landscape at three neighborhood scales: (a) 1km; (b) 3km; and (c) 5km. Darker blue shading indicates higher functional connectivity (lower movement cost and more links) at each scale.

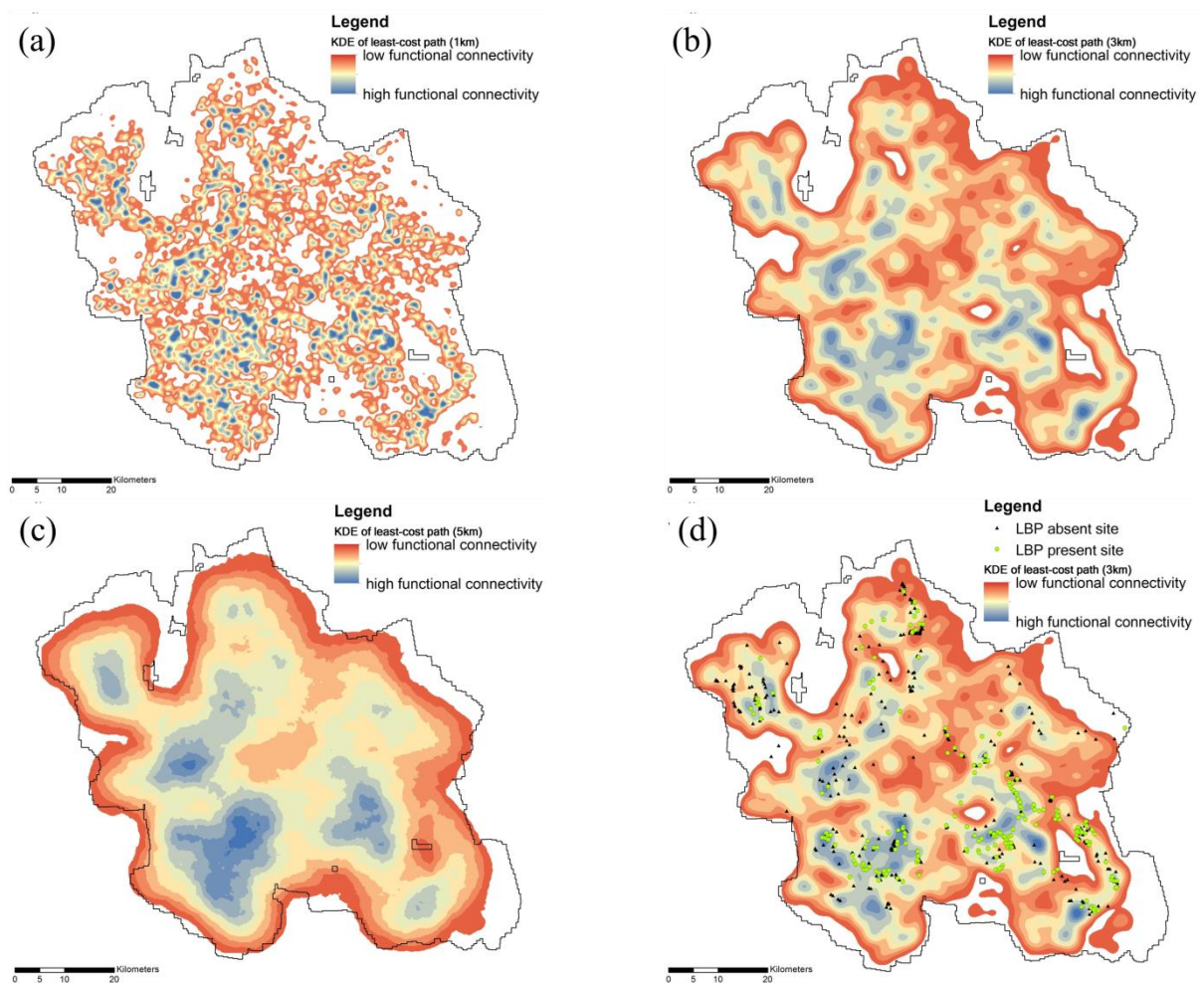


Figure 6-7 Maps of the kernel density estimator (KDE) of least-cost paths in the study area at three neighborhood scales: (a) 1km; (b) 3km; and (c) 5km. Darker blue shading indicates higher functional connectivity (lower movement cost and more links) at each scale. Figure (d) also showed the locations of field LBP observation sites overlaid above the KDE map of least-cost paths with a 3km neighborhood scale.

6.3.4 Suitable habitat patches for LBP in each functionally connected regions

We classified the landscape into high functionally connected regions and areas with low connectivity based on the value of kernel link density of least-cost paths for the 20mMcRd surface and using the 3 km neighborhood. We identified 28 high functionally connected regions, the size ranged from 47 ha to 36,382 ha (Table 6-6 and Figure 6-8). In total, there were 15,983 ha of high-quality habitat located in functional regions (Figure 6-9), which is approximately 60% total suitable habitat across the whole study area predicted in Chapter 5. Of the field-assessed LBP present sites 66% (n = 105) were located in the functionally connected regions. Functional regions with a smaller patch size (< 250ha) were less likely to have suitable habitat. For the five largest regions, there was no significant relationship between the region size and probability of LBP presence or percentage of suitable habitat. The highest probability of LBP presence and highest percentage of suitable habitat was in Region 2 (See Figure 6-8), which was the second largest. The largest region (Region 1) had the second highest probability of LBP presence and suitable habitat.

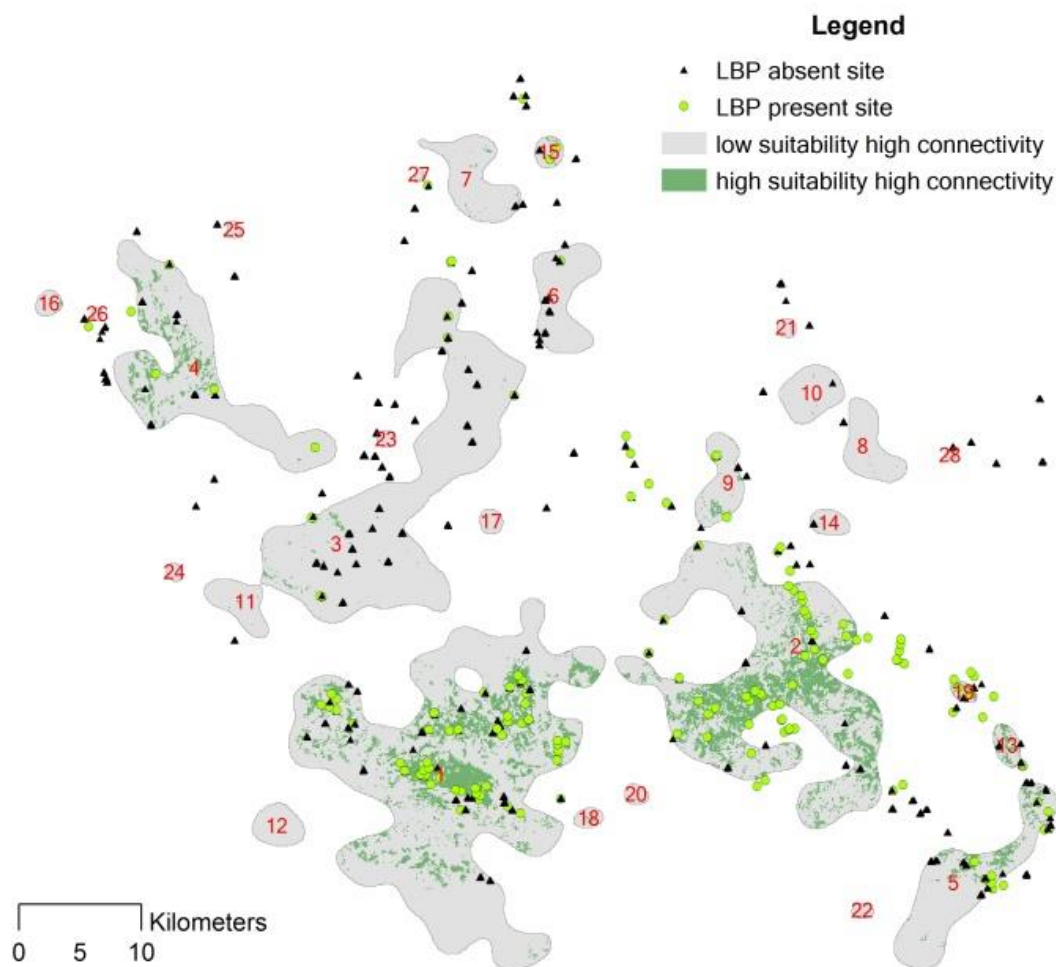


Figure 6-8 Map of functionally connected regions showed region ID (red letter), suitable habitat patches (green polygon) and locations of field LBP observation sites

Table 6-6 Summary of suitable habitat patches (HSI>0.5) and observation sites of LBP occurrence in each functionally connected region. The size, number of suitable habitat patches (N), total area (ha) of suitable patches, percentage (%) of suitable patch areas in each region, mean, standard deviation (sd), maximum (max) of patch size; number of LBP present and absent sites, the probability of LBP presence in each region and the proportion (%) of present sites of each region in all LBP present site were summarized for all functionally connected regions across the whole study area.

Region ID	Regional size (ha)	Suitable habitat patches						LBP occurrence			
		N	total area	% of each region	mean	sd	max	presence	absence	Prob. in each region	% all presence
1	36,382	744	6,890	19%	9.3	71.1	1,741	53	73	42%	33.1%
2	21,747	632	6,575	30%	10.4	159.2	3,993	30	15	67%	18.8%
3	20,549	65	162	1%	2.5	4.7	24	4	47	8%	2.5%
4	10,598	160	1,159	11%	7.2	16.7	127	4	16	20%	2.5%
5	6,134	93	637	10%	6.8	23	217	7	25	22%	4.4%
6	3,146	4	5	0%	1.3	0.5	2	1	15	6%	0.6%
7	2,904	22	39	1%	1.8	2	10	0	2	0%	0.0%
8	1,943	6	6	0%	1	0	1				
9	1,871	36	131	7%	3.6	12.3	74	2	1	67%	1.3%
10	1,741	7	8	0%	1.1	0.5	2	0	1	0%	0.0%
11	1,409	5	10	1%	2	1.4	4				
12	1,099	1	1	0%	0.5		1				
13	568	18	186	33%	10.3	20.3	82	0	2	0%	0.0%
14	532	1	1	0%	1		1	0	3	0%	0.0%
15	470	15	43	9%	2.8	2.4	9	2	2	50%	1.3%
16	340	1	7	2%	7		7				
17	298										
18	294	10	14	5%	1.4	1.1	4				
19	269	15	105	39%	7	10.2	32	2	2	50%	1.3%
20	243										
21	193										
22	163										
23	157										
24	140										
25	107										
26	78	2	4	4%	1.8	1.8	3				
27	55										
28	47										

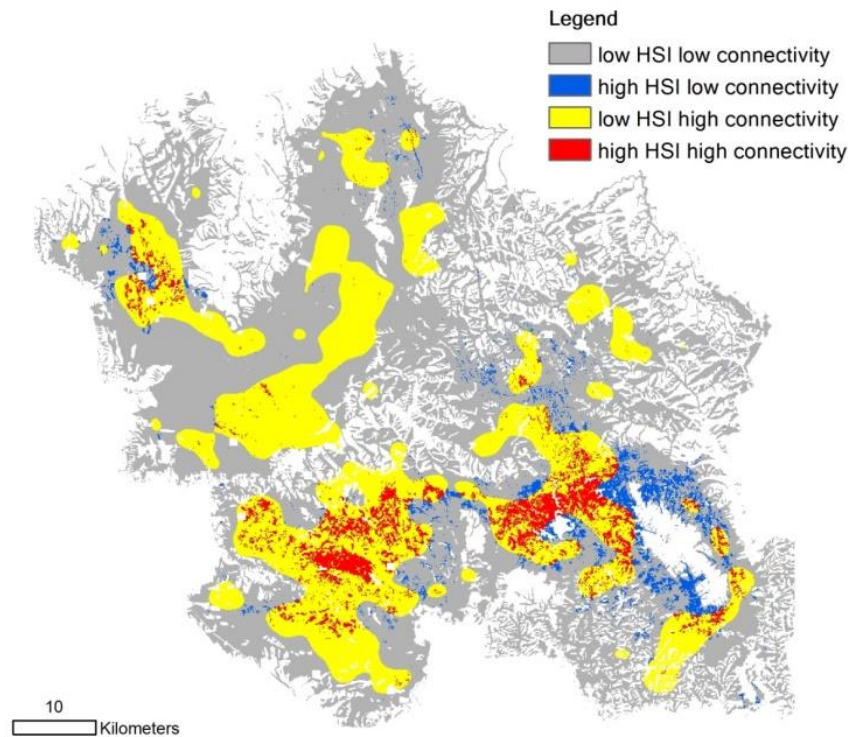


Figure 6-9 Map of the landscape of study area classified by functional connectivity level and habitat suitability level

6.4 Discussion

Landscape connectivity is vital for biodiversity conservation (Crooks and Sanjayan 2006). Knowledge about how structural attributes impact the movement and dispersal of fauna across large heterogeneous landscapes is often limited (Shirk et al. 2010, Zeller et al. 2012, Milanesi et al. 2017a). Evaluating connectivity networks in order to identify and protect functionally connected area is difficult to assess in the field and as a result presents a key challenge to applied ecology and conservation. (Galpern and Manseau 2013, Milanesi et al. 2017a, Pinaud et al. 2018). Our study is the first to evaluate the importance of landscape connectivity to LBP at the landscape-scale. Our findings highlighted the importance of considering the dynamics of the midstorey stratum at broad-scales for conserving LBP (Trouv   et al. 2019). To date the concern of habitat loss for LBP is centered on the decline of hollow bearing trees in the landscape (Lindemaner and Sato 2018) not the landscape dynamics of the midstorey. This work highlights the need to consider both.

The application of LiDAR-derived vegetation structure data to characterize model landscape functional connectivity over large landscapes has not been well explored (Guo et al. 2018). LiDAR-derived 3D vegetation structure data has been shown to improve estimates of functional landscape connectivity for animals compared to conventional 2D land cover data (Milanesi et al. 2017a). LiDAR derived data also allows for subjective assessments of resistance surfaces to be avoided, instead replaced with empirically derived resistance surfaces based on mapped vegetation structure that influences habitat use. We found that functionally connected regions can be generated from LiDAR data highlighting the potential for using this approach for determining potential metapopulation structures at the landscape-scale for forest dependent

species.

The mapping of landscape connectedness identified a landscape-scale metapopulation structure for LBP in the region. Previous research has assessed the population viability of LBP within a patch-based metapopulation structure with smaller areas within the landscape (Lindenmayer and Lacy 1995, Lindenmayer and Possingham 1995a, 1996). These studies did not address the entire landscape or consider the functionality of connectivity between habitat patches. Functional connectivity between habitat patches are required to reduce the risk of local extinction (Henderson et al. 1985, Lovejoy et al. 1986, Lindenmayer and Possingham 1996) and larger connected metapopulations offer the greatest probability of persistence (Forney and Gilpin 1989, Bennett 1990, Merriam and Lanoue 1990, Bennett et al. 1994b, Lindenmayer and Possingham 1996). For long-term population persistence, maintaining and improving functional connectivity within metapopulations is important for conserving species (Compton et al. 2007, Cushman et al. 2013, Milanesi et al. 2017a).

Functionally connected regions can be successfully applied to identify dispersal corridors that can facilitate movement and dispersal within the metapopulation and thereby increase population sizes (Galpern 2011, Milanesi et al. 2017a, Guo et al. 2018, Pinaud et al. 2018). If connectivity within and between functional regions is interrupted, natural dispersal that facilitates gene flow, recolonization, and rescue effects may be reduced which in turn disrupts metapopulation processes (Compton et al. 2007). Metapopulations in broader connected regions may be more likely to persist than those in smaller regions (Compton et al. 2007). The two largest regions identified in this study (Region 1 and Region 2) therefore are likely the most robust for LBP metapopulations, as high connectivity will allow for patches of habitat to be recolonized if local extinction occurs due to predation or disturbance. On the other hand, smaller metapopulations may be a greater risk to loss in habitat and off losses in fitness due to reduced gene flow. Of interest is Region 3 which was impacted by the 2009 Black Saturday fire (Figure A6 2 in Appendices 6). Currently habitat suitability is modelled as low but connectivity is high. The high functional connectivity will facilitate the recolonization of LBP in this region. Recent surveys (2019) by ARI has found LBP in 50% of plots within the fire affected area highlighting that recolonization is well underway through this highly-connected region. The identification of functionally connected regions provides a tool that could be used to expand the existing protected area network to support the metapopulation processes of LBP. By doing so, conservation planning will be enhanced for long-term population persistence (Guo et al. 2018).

Landscape dynamics can change connectivity and impact the movement of fauna (Galpern and Manseau 2013). LiDAR can aid in the evaluation of landscape change through the parameterization of models to explore land cover change (see Guo et al. 2018) or through monitoring of changes in connectivity over time. The dynamic modelling of changes in landscape connectivity might be able to help managers to forecast the likely consequences of habitat fragmentation under different management scenarios and evaluate both the short-term and long-term effectiveness of different conservation strategies (Bergsten et al. 2013, Rubio et al.

2015).

In this study, we assumed animals used the same desirable vegetation structures in all vegetation classes and so we found vegetation connectivity of midstorey was the most important vegetation layer for LBP to move through. In reality, LBP likely travel and forage across many forest types with various habitat structures. For example, LBP distributed in sub-alpine woodland (snow gum) used different structure of dense under-/mid-storey species (Mountain Tea Tree , *Leptospermum grandifolium*) to move around (Committee 2015). Excluding this species from midstorey layer to build connectivity networks may underestimate the functionally connected regions (blue polygons in Figure 6-9 near Region2 and Region5). Therefore, to provide the optimal conservation strategies, it was required to build specific vegetation connectivity networks of specific vegetation classes in regards to habitat requirements of LBP varied in different vegetation classes.

6.5 Conclusion

Landscape dynamics (i.e. disturbances, ecological succession) can change connectivity and impact the movement of fauna (Galpern and Manseau 2013). LiDAR can aid in the evaluation of landscape change through the parameterization of models to explore land cover change (see Guo et al. 2018) or through the monitoring of changes in connectivity over time through repeat data captures. Dynamic modelling, informed by these LiDAR derived models, can be used to forecast the likely consequences of habitat fragmentation and loss on landscape connectivity under different management scenarios and evaluate both the short-term and long-term effectiveness of different conservation strategies (Bergsten et al. 2013, Rubio et al. 2015). Combined these approaches provide a holistic approach that combines top-down and bottom-up synthesis that should reduce both structural and statistical uncertainty (see Nitschke et al. 2007) and facilitate the conservation of LBP and other fauna in these dynamic landscapes.

Appendices 6

Maps of the kernel density estimator (KDE) of least-cost paths within 5km of four networks

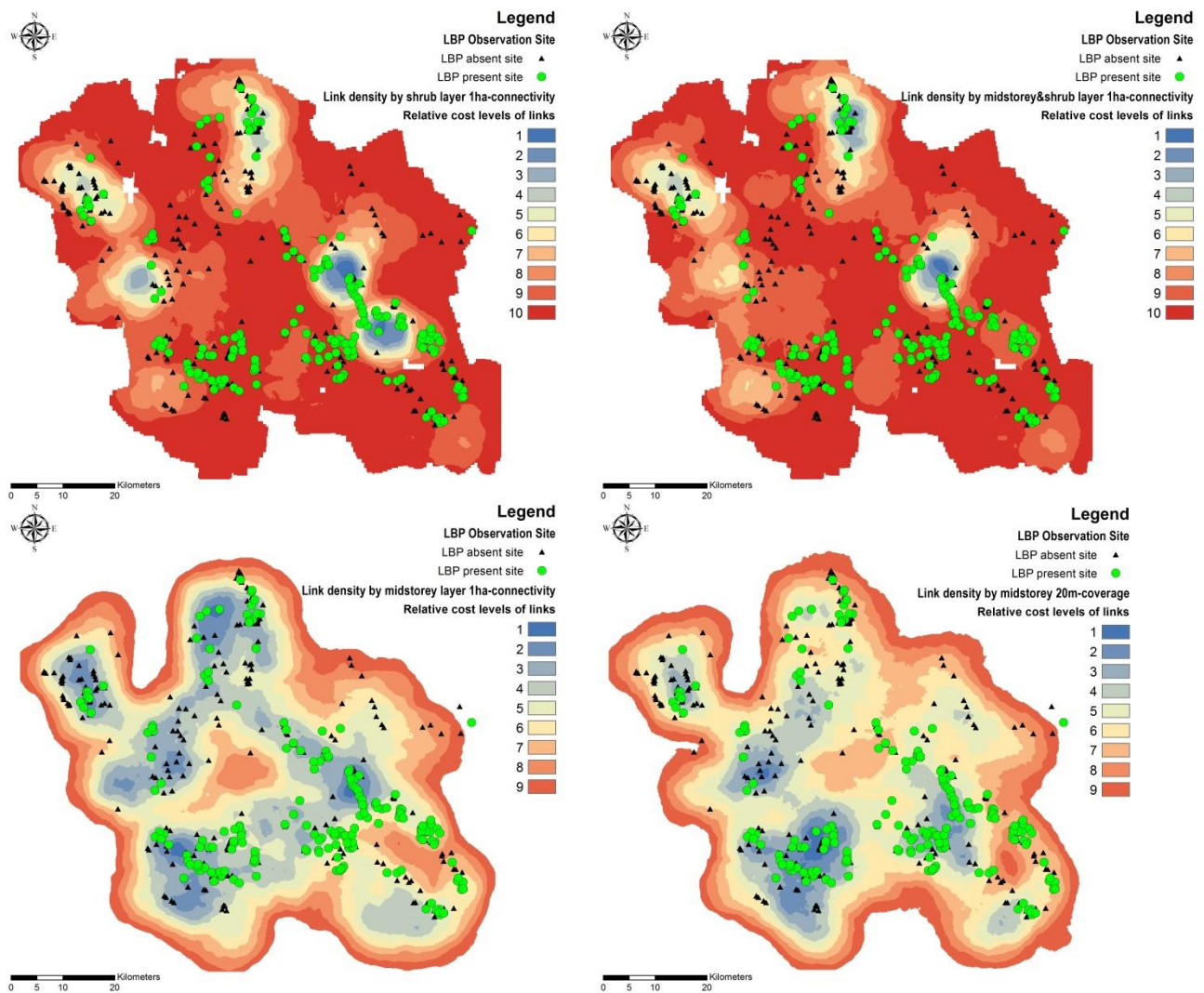


Figure A6 1 Maps of the location of LBP observation sites and the kernel density estimator (KDE) of least-cost paths within 5km of networks from resistance surface of: (a) 1haShRd; (b) 1haMsRd and (c) 1haUMRd; and (d) 2McRd. Darker blue shading indicates higher functional connectivity (lower movement cost and more links) at each scale.

Map of 2009 wildfire covered area and functionally connected regions

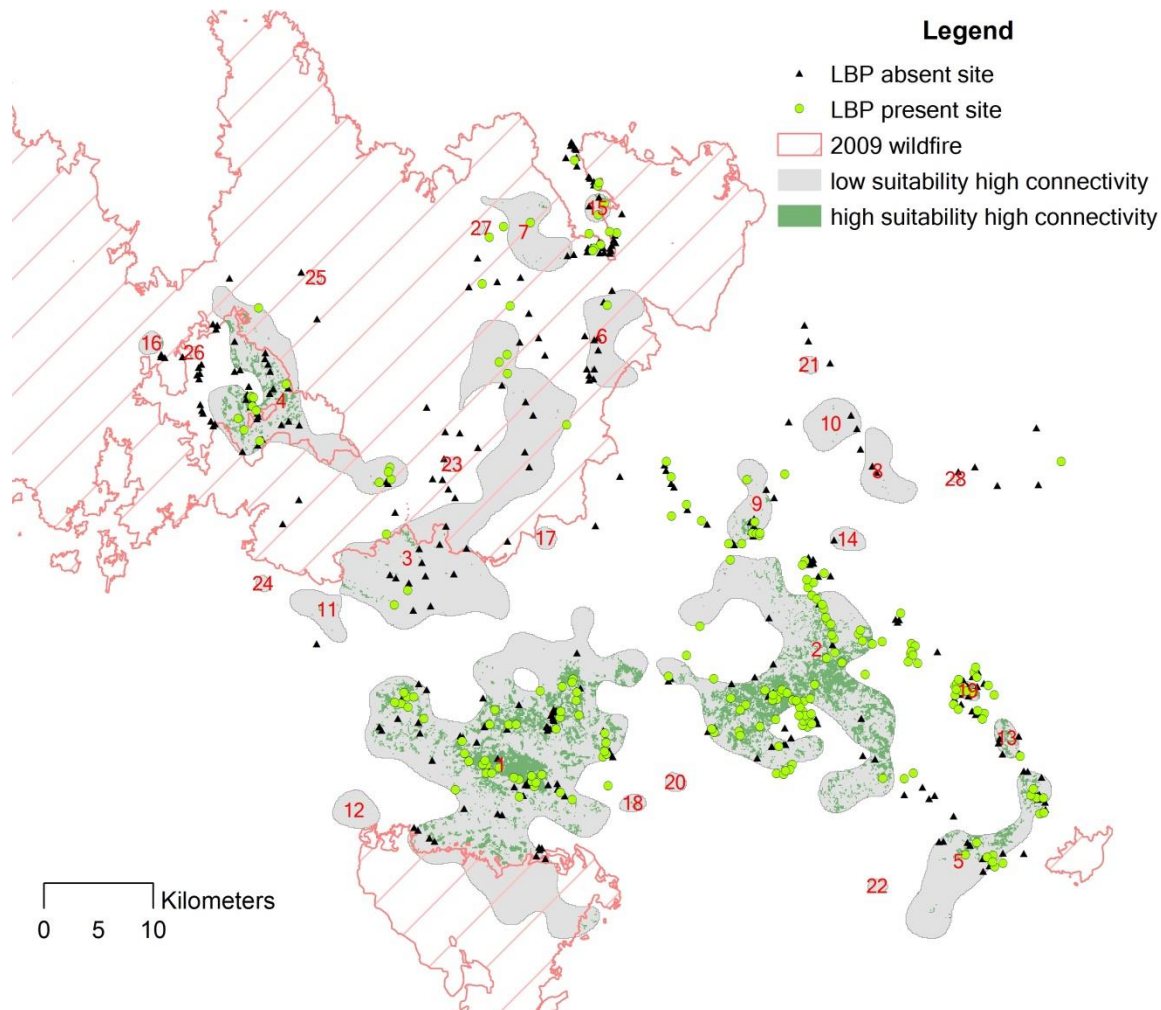


Figure A6 2 Map of 2009 wildfire covered area (pink polygon) and functionally connected regions showed region ID (red letter), suitable habitat patches (green polygon) and locations of field LBP observation sites

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Chapter 7.

7 General discussion and conclusion

Leadbeater's possum (LBP) is a critically endangered species located in Victoria's Central Highlands. To develop better conservation strategies for LBP, I utilised LiDAR data to explore the spatial distribution and quality of LBP habitat. I integrated LiDAR-derived metrics with different habitat analyses that incorporate multiple scales to map critical LBP habitat features (i.e., hollow-bearing trees and midstorey vegetation) across 342,960 ha of forest (Chapters 2-4). I then used the distribution of these habitat resources to map landscape-scale habitat suitability (Chapter 5) and functionally connected regions (Chapter 6) to inform the conservation of this endangered species.

Hollow-bearing tree

Large trees with hollows or hollow-bearing trees (HBTs) are an important resource for many species globally, including those of conservation concern (Kramer et al. 2016, Lindenmayer et al. 2016b). As a keystone habitat feature of many forested ecosystems, reductions in the abundance of HBTs could place hollow-dependent fauna at risk due to habitat decline and loss, which may impact ecosystem functioning (Lindenmayer et al. 2012b). Better knowledge of the availability and distribution of HBTs throughout landscapes is crucial for the sustainable management and conservation of forests and forest biodiversity (Davis et al. 2014). I developed two approaches to estimate the occurrence and the abundance of HBTs across large areas. The first involved the development of new algorithms for delineating individual tree crowns and estimating their size, which was used to predict the abundance of potential live old-growth trees with hollows (Chapter 2). The second approach involved developing statistical models using structural, topographic, and environmental predictors within a machine-learning context to estimate HBT abundance (Chapter 3). The estimates of live HBTs for these two approaches overlapped, but the individual tree delineation approach was lower with 572,000 (95%CI: 318,000-808,000) than the machine-learning approach with 833,000 (95%CI: 742,000-923,000) live hollow-bearing trees. Because the senescent trees lack full crowns that cannot be identified with the individual tree delineation method, I used the machine-learning approach to estimate the total number of HBTs (i.e., dead and alive) in the Central Highlands (Chapter 3). I estimated that in total there were 1,519,000 (95%CI: 1,306,000 – 1,730,000) HBTs pooled across all form classes (including live and dead HBTs). This included 833,000 (95%CI: 742,000-923,000) live HBTs and 686,000 (95%CI: 564,000-807,000) dead HBTs. This is equivalent to approximately 4.4 HBTs per ha (2.4 live HBT ha⁻¹ and 2.0 dead HBT ha⁻¹) across this landscape.

The differences in the number of live HBTs per ha predicted by the ITD approach (Chapter 2) than the machine-learning approach (Chapter 3) arise because the former tended to underestimate live HBT density, whereas the latter tended to overestimated live HBT density. The ITD method was based on an empirical relationship between crown width and stem diameter for mountain ash species only (*E. regnans*). If a significant proportion of the tree top is dead or broken, it will underestimate the stem diameter and, therefore, the probability of hollow occurrence. In addition, our field surveys suggested that smaller, suppressed live trees also have the potential to form hollows (e.g. Form Class 1 Ecological HBTs in Chapter 3). These would not be included in the ITD approach. Although our ITD algorithm was only validated in mountain ash (*E. regnans*) forest, forests with similar crown structure (shape) can also be accurately identified by this ITD algorithm, such as alpine ash (*E. delegatensis*), and shining gum (*E. nitens*). The limitation of the ITD method in this study was that the parameters were optimised to detect large dominant overstorey trees in mature or multi-cohort forests. For younger, homogenous stands with higher density (such as 1977 regrowth plot in this study), the accurate detection rate was very low. However, the key objective in this chapter is to locate where the trees with big crown size which have higher potential to be a hollow-bearing tree. Despite the limitations of this approach, the strong correlation between average crown width of overstorey and the density of live HBT in chapter 3 indicated that the big crown metrics generated by this ITD approach in chapter 2 is useful to address the research objective. However, in future researches, more stem mapping plots were required to collect in the field to validate this ITD method in other vegetation types.

The analyses of HBT densities presented in chapter 3 have shown the potential for mapping the abundance of large live trees and all form classes of HBTs at the landscape scale. I was able to identify complex relationships between predictor variables and the abundance of HBTs that reflect local-scale variability in environmental conditions, disturbance history, and forest management practices. The complex distribution patterns of different HBT form classes across different tenure and vegetation types provides new insights and a critical resource for forest and conservation managers concerned with hollow-dependent fauna. For example, the higher abundance of HBTs in riparian forests reinforces the need to protect riparian forests from timber harvesting and future wildfires.

Midstorey stratum and connectivity

Characterising forest structure is critical for any comprehensive assessment of diversity of forest ecosystems (Miura and Jones 2010). The understorey and midstorey strata also play an important role in forests (Goodwin 2006, Simonson et al. 2014, Latifi et al. 2015a). Since LBP do not have a gliding membrane (Macfarlane et al. 1997), the continuous cover of foliage in the lower strata are a crucial structural requirement for suitable habitat (Lindenmayer 1989b, Lindenmayer et al. 1991b, Lindenmayer et al. 2000, Blair et al. 2017). This thesis demonstrated the potential to utilise high-resolution remote-sensing data to characterise sub-canopy forest structure across multiple scales, ranging from individual trees (Chapter 2) and plot/stand-level predictions (Chapter 3) to whole landscapes (Chapter 4). In Chapter 2, our ITD approach

classified LiDAR points belonging to midstorey canopies and detected tree tops for midstorey stratum. Instead of using a threshold approach to demarcate canopy and midstorey stratum (Goodwin 2006), the approaches used in this study were based on (1) identification of sub-canopies below the upper canopy layer (e.g., HCB-HT relationship, Figure 2-2 in Chapter 2) and (2) identification of midstorey strata located in canopy gaps with no canopy layer above. These two approaches increased the detection of midstorey-only LiDAR points. The midstorey tree height estimated from this approach was showed a strong linear positive relationships with field-assess midstorey tree height ($R^2=0.66$, Figure 2-5a). I then used classified midstorey LiDAR points and detected midstorey treetops to generate midstorey metrics of coverage and stem density for broader-scale analysis. The 1-ha metrics were used to build plot-level species distribution models (SDMs) of habitat resources (Chapters 3 & 4) and habitat suitability (Chapter 5), and 20-m metrics of midstorey coverage were used to build the landscape connectivity network and identify the metapopulation structure for LBP (Chapter 6).

Improvements in measuring midstorey structure at fine scales (Chapter 2) could benefit the broader-scale midstorey structure analysis (Chapters 4 & 6). Previous studies have found that regression models built on LiDAR metrics are worse at predicting midstorey density than overstorey density at the plot level (Coops et al. 2007, Latifi et al. 2015a). However, our prediction models in Chapter 4 found that correlations between the selected LiDAR metrics and the observed plot-level vegetation connectivity were stronger for midstorey ($R^2=0.72$) than the upper canopy layer ($R^2=0.59$) (Figure 4-5). The midstorey metrics generated from the ITD approach provided a more robust representation of midstorey structure, which yields stronger plot-level models of midstorey connectivity. In Chapter 6, I compared the differences in functional connectivity networks generated from the two different midstorey metrics: (1) midstorey coverage directly generated from LiDAR data (20 m metrics of midstorey coverage Chapter 2) and (2) predicted midstorey connectivity integrated field-assessed data with LiDAR-derived structural variables (1 ha metrics of midstorey connectivity in Chapter 4). I found that the midstorey coverage directly generated from LiDAR data performed better than prediction metrics of the midstorey for identifying potential metapopulation structures for LBP habitat.

Vegetation density or connectivity assessed in Chapters 2 and 4 focused on the structural attributes of connectivity, while landscape connectedness analysed in Chapter 6 paid more attention to functional aspects of connectivity (Crooks and Sanjayan 2006, McIntire et al. 2007, Dancose et al. 2011). Assessing landscape-level functional connectedness can provide knowledge of how local-scale forest structure attributes may be influencing the movement of species. This is essential for addressing the impacts of habitat fragmentation (Fischer and Lindenmayer 2007), as well as metapopulation persistence (Compton et al. 2007, Cushman et al. 2013, Milanesi et al. 2017a). On the other hand, a reliable impact analysis of functional connectivity depends on the accuracy of structural assessment and the broader-scale structural predictions were strongly associated with improvements in fine-scale individual tree detection and analysis. Together these multi-scale analyses combine top-down and bottom-up approaches that should reduce both structural

and statistical uncertainty and facilitate the better forest management and conservation planning (Nitschke et al. 2007).

Landscape dynamics can change connectivity and impact the movement of fauna (Galpern and Manseau 2013). With more time series of LiDAR data acquired in the future for the same study area, I could use this multi-scale forest structure analysis framework to evaluate and monitor the forest dynamics, to forecast the likely consequences of habitat fragmentation and loss under different climate change scenarios, and to anticipate both the short- and long-term effectiveness of different conservation strategies (Bergsten et al. 2013, Rubio et al. 2015).

Previous studies suggested that wattle species provide foraging habitat for LBP (Lindenmayer 1989b, Lindenmayer et al. 2000). Based on variable important indices in Chapter 5, we noticed that midstorey connectivity was more important to LBP habitat suitability than the density of live wattle and connectivity of other vegetation layers. We would suspect that there are other food sources for LBP located in the sites with lower live wattle density but high level of midstorey connectivity and some future researches are needed to focus on other food source for LBP in those field sites.

Habitat analysis models

Tools for quantifying habitat quality and predicting biodiversity change are essential for biodiversity conservation (Elith 2000, Cardinale et al. 2012, Vellend et al. 2013, Dornelas et al. 2014, Ewers et al. 2017, Leroux et al. 2017). A suite of models derived from different ecological theories have been used to predict the abundance, diversity and distributions of species based on environmental conditions and ecological processes (Thuiller et al. 2013, Leroux et al. 2017). It is not surprising that general investigations of habitat usually apply a single habitat model to address a particular conservation problem (Leroux et al. 2017). The most important reason for the lack of multi-model habitat analyses is that we do not have a framework for combining and/or comparing models that are based on different assumptions and parameterized with different types of data (e.g. abundance or presence/absence) that provide disparate predictions (Leroux et al. 2017). In this thesis, I developed a framework for multi-model integration and comparison for real-world biodiversity conservation and planning of endangered species (LBP). The habitat analysis approaches used in this thesis included:

- (1) species distribution models (SDM) to map the abundance of key habitat resources (Chapters 3 & 4);
- (2) habitat suitability index (HSI) models to estimate habitat suitability for (Chapter 5); and
- (3) graph-theoretic connectivity networks which modelled potential metapopulation structure (Chapter 6).

Habitat suitability models generally account for the selection of suitable habitat and their appropriate geographical extents (Courbin et al. 2009, McLoughlin et al. 2010, Moreau et al. 2012, Courbin et al. 2014), but rarely for the accessibility of high-quality habitat and connectivity among habitats (Courbin et al. 2014,

Stevenson-Holt et al. 2014, Guo et al. 2018). Effective conservation of species requires that patches of their habitat are connected in space and time (Crooks and Sanjayan 2006, Galpern and Manseau 2013, Stevenson-Holt et al. 2014). In Chapter 6, graph-theoretic connectivity networks based on resistance surfaces were generated from the LiDAR mapped coverage of vertical strata. The least-cost links from networks were integrated with a kernel density estimator to identify functionally connected regions. The mapping of forest structural connectedness identified a potential landscape-scale metapopulation structure for LBP in the region.

In Chapter 5, the validated habitat suitability model for LBP had an overall accuracy of 87.3% and an AUC of 0.889 (Table 2-1). The model predicted that 33,000ha (95%CI: 25,000ha-43,000ha) of the study landscape supports suitable habitat for LBP. This is approximately 9.6% of the total study area (Table 5-6). Nearly 16,000 ha of these suitable habitat was located in functionally connected regions (Figure 6-9), which is approximately 60% of the total suitable habitat across the whole study area. Functional landscape connectivity can facilitate movement between habitat patches, and then improve the dispersal within the metapopulation, leading to increased population sizes (Galpern 2011, Milanesi et al. 2017a, Guo et al. 2018, Pinaud et al. 2018). Meta-population persistence can improve with larger functionally connected regions (Compton et al. 2007) containing high quality habitat. The two largest regions identified in this study (Region 1 and Region 2 in Figure 6-8) are likely the most promising for LBP metapopulation persistence as high connectivity will allow for habitat patches to be recolonized if local extinction occurs due to predation or disturbance. For functionally connected regions with low habitat suitability such as Region 3, which was impacted by the 2009 Black Saturday fire (Figure A6 2 in Appendices 6), the high functional connectivity may facilitate the recolonization of LBP in this region as habitat suitability changes over time. Recent surveys (2019) by ARI have found LBP in 50% of plots within the fire-affected area, highlighting that recolonization is well underway through this highly connected part of the Central Highlands landscape.

The conservation and management of endangered species is major focus of forest and land managers around the world. High-quality data on the distribution and quality of habitat is critical to the development of effective conservation and recovery strategies for species. By developing a statistical framework for multi-model integration and comparison of habitat analysis models, I identified high-quality habitat for the critically endangered Leadbeater's Possum that was associated with functionally connected regions. These can be used as the basis for conservation and relocation programs at the landscape scale in the coming years and decades.

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