Modelling the distributions of Australian shrublands and shrub species: the role of climate and soil properties

Thesis submitted by

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Contents

Abstract

Shrubs, short multi-stemmed species, are an important plant growth form that can play a key role in biogeochemical cycles, stability of soil and prevention of soil and water erosion, provision of forage for livestock, and are a source of wood and non-woody products and foodstuff for many populations. However, there is a lack of knowledge regarding the influence of environmental variables on shrub distributions, and shrubland remains undefined as a plant functional type in most global vegetation models.

Broadly, the goal of my thesis was to assess relationships between the distribution of Australian shrubland and shrub species and environmental properties, specifically climate and soil characteristics. The objectives of my thesis were three-fold. I initially assessed how the climate envelope of shrubland differed from other major vegetation types (forest, woodland, grassland) as well as differences between the six major shrubland classes (Acacia, Chenopod, Heathland, Mallee, Tall shrublands, “other” shrublands). Using generalized linear models I found that shrublands separate from other major vegetation types along a seasonal soil moisture gradient, with shrublands being the dominant vegetation type in areas with lower moisture.

I then used MaxEnt, a species distribution model, to assess drivers of the distributions of 29 shrub species that together represented dominant members of each of the six shrubland classes. In particular, I sought to determine whether the inclusion of soil characteristics, along with climate variables, improved models of species distributions. I found that whilst models calibrated with soil and climate were

not significantly more powerful than those calibrated with only climate variables, for some species projections of the distribution of suitable habitat differed substantially across these models. This led to regional differences in projected species richness, highlighting the value of exploring a broader range of predictor variables when developing models, rather than relying solely on climate.

Finally, I examined spatial changes to the distribution of suitable habitat for the 29 shrub species that may occur due to climate change. Given uncertainty in the direction of future precipitation changes, I compared distribution patterns that may result under a hot, dry future versus a warm, wet future. In general, the size of suitable habitat was projected to decline for most species, with greater contractions in central and western regions of Australia and some extensions in temperate regions. Importantly, for some species the direction and magnitude of projected changes varied between models calibrated with only climate variables versus those calibrated with climate and soil variables. The net impact of this meant that different regional patterns in species richness may be projected as a result of model calibration and future climate scenario.

This thesis has identified the climate envelopes of shrublands and dominant Australian shrub species; highlighted the importance of considering soil properties when modelling plant species distributions; demonstrated potential impacts of climate change and how patterns of species richness may vary depending on whether the future is warm and wet or hot and dry; and revealed uncertainty in projections of future suitable habitat that may occur due to selection of predictor variables.

Statement of Candidate

I certify that the work in this thesis entitled "*Modelling the distribution of Australian shrublands and shrub species: the role of climate and soil properties*" has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

Yasmin Hageer (42253837)

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Statement of Contribution of Others

Chapters 1 and 5 of this thesis were conceived and written by me (referred to as YH in this Statement), with editorial assistance from my supervisor, Dr Linda Beaumont (herein LB).

Chapter 2 of this thesis was conceived by myself and Professor Sandy Harrison (herein SH). LB and John Baumgartner (herein JB) provided technical assistance with analyses and interpretation of the results. I wrote the chapter with editorial assistance by LB, SH and JB. Professor Lesley Hughes, Associate Professors Belinda Medlyn (BM) and Ian Wright commented on an earlier draft of this chapter.

Chapter 3 of this thesis was conceived by myself and LB. I undertook all analyses and wrote the chapter with editorial assistance by LB.

Chapter 4 of this thesis was conceived by myself and LB. I undertook all analyses and wrote the chapter with editorial assistance by LB. Scenarios of future climate used in this chapter were provided by Associate Professor Jeremy VanDerWal of James Cook University. JB provided assistance with developing R script. BM and BA provided guidance with selecting environmental predictors. IW also provided comments on the results of this study.

Chapter 1

Introduction

Chapter 1: Introduction

What is a shrub? This is not a straight forward question to answer. The word 'shrub' does not have a strict botanical meaning: some studies do not distinguish between shrubs and trees, some consider shrubs to be the functional equivalent of trees, only smaller (Hickler *et al.,* 2006; Woodward *et al*., 1998). Others regard shrubs as a distinct growth form (Meng *et al.*, 2009). This confusion may partly stem from the fact that some plant species are able to grow as trees or shrubs, depending upon environmental circumstances. For example, *Ceanothus* and *Manzanita* genera have many species that can be either shrubs or small trees (Litman & Nakamura, 2007). Generally, however, shrubs are defined as perennial woody plants of relatively low height and with several base stems (e.g. Meng *et al*., 2009; Zeng, 2010).

Shrublands can be classified as regions where shrubs cover more than 30% of the ground (Shmida, 1985; DEWR, 2007), and are found within many of the world's climate zones. The most extensive shrublands occupy arid and semi-arid regions (Sala *et al*., 1989) in the southwest of North America, Middle East, Central Asia, southern South America, and South Africa and central of Australia. Temperate or Mediterranean shrublands include those in the Mediterranean Basin (Mooney, 1981), northern China (Zeng *et al*., 2008) and eastern Australia (ESCAVI, 2003). Boreal shrublands are located in northern Asia and North America, and high elevation areas such as the Tibetan Plateau (Zeng, 2010).

Shrubs and shrublands provide a number of key ecosystem functions and services. As one of the main isoprene emitters shrubs can alter air chemistry and influence ozone quantity (Pfister *et al*., 2008). Dust can be an aerosol precursor (Prentice *et al*., 2007) and dust swept from arid regions can be substantially reduced

by coverage of shrubs (Engelstaedter, 2003) which protect the soil surface from erosion to a greater extent than grasses do (Tegen *et al*., 2002; Urban *et al*., 2009). Shrubs can also sink substantially more atmospheric carbon, thereby reducing carbon pollution, compared to grasses (Burrows *et al*., 1998) - more practically, it has been suggested that roadside shrubs could be convenient urban sinks for carbon pollution (Lavelle, 2014) .

Other economic benefits of shrubs include their provision of forage for livestock during times when herbaceous fodder is not available (Dynes & Schlink, 2002), thereby benefiting rangeland grazing enterprises (Auken, 2000; Asner *et al*., 2004). Activity of soil micro-organisms and deposition of nutrients beneath shrubs leads to positive plant–soil feedbacks (Daryanto *et al*., 2013). For instance, shrub encroachment can result in greater soil carbon and nitrogen concentration (Brantley & Young, 2010; Eldridge *et al*., 2011) and a decline in soil pH (Eldridge *et al*., 2011): this may enhance ecological productivity and economic development potential in areas occupied by shrubs (Eldridge *et al*., 2011).

On a local scale, shrubs can also alter microclimate and influence the composition of communities. For instance, encroachment of the shrub *Leptospermum scoparium* in the herb-rich woodland in southern Australia has reduced understory species richness (Price & Morgan, 2008). Those authors found that shading caused by this species has resulted in higher soil moisture and lower light intensity beneath the shrub canopy, reducing germination of understory herbs. As such, shifts in the distributions of shrubs in response to climate or environmental changes may have major economic and environmental ramifications.

Drivers of the distribution of shrubs: climate and soil

Distribution of plant species including shrubs and shrubland ecosystems has strong ties to biology, ecology, climatology, and soil. As for other vegetation types, on large spatial scales the distribution of shrubs is primarily controlled by climate, and this control operates at different levels of biological organisation, ranging from species (Peterson, 2001) to biomes (Wang *et al*., 2013). Plants need water to grow and energy to use this water. Variation in shrub species assemblages along climatic gradients has been found to be associated with physiological processes affected by temperature and moisture (Stephenson 1990). Shrubs possess a number of mechanisms that enable them to dominate environments with low moisture by lowering their cost of growth and increasing water use efficiency (Smith *et al*., 1997; Wilson, 1998; Reynolds *et al*., 1999).

The root system of shrubs develops deeper than that of grasses (Burgess, 1995) and can extract soil water from a larger area than their crown size (Kummerow, 1981). Deeper roots enable shrubs to obtain most of their water from deep within the soil profile, while grasses are dependent on water from the upper soil layers (Sala *et al*., 1989). These mechanisms enable shrubs to survive harsh conditions such as drought, wind erosion, overgrazing and sand burial (Li *et al*., 2009).

Soil provides physical support, water and essential nutrients for plants, as well as habitat for micro-organisms whose activity may enhance soil characteristics and, therefore, sustain plant growth. In temperate and arid regions, shrubs usually occupy shallow, coarse and infertile soils (Groves, 1994; Burke *et al*., 1998). It has been hypothesised that trees may be absent from areas with extremely infertile and sandy soils, as these soils may reduce the opportunities for inoculation of tree roots with mycorrhizal organisms (Burrell, 1969).

Shrubs and climate change

Globally, a broad range of taxa spanning terrestrial, marine and freshwater environments will need to respond to anthropogenic climate change (IPCC 2014). The primary responses of shrubs include a) declines in cover and mortality, b) range expansion or encroachment and c) woody thickening.

While some shrub species can tolerate severe and prolonged drought, as demonstrated in the Mediterranean (Ogaya *et al*., 2011), declining precipitation across the semi-arid savannah of Southern Africa has driven a decline in shrub cover (Tews *et al*., 2006). Conversely, higher temperatures have contributed to increased mortality of dominant woody species including shrubs and the establishment of annual grasses in deserts of North America (WDFW, 2011) and in southern Texas (Archer *et al*., 1988) to the benefit of grasses.

Shrub expansion or encroachment has been reported across different ecosystems and can result in enormous changes in ecosystem functioning, for example in African savanna (e.g. O'Connor & Crow, 1999; Roques *et al*., 2001), North American semi-arid grassland (Van Auken, 2014), and in woodlands in Australia's east (Eldridge *et al*., 2011) and south (Price & Morgan, 2008) as well as its semi-arid savanna (Fensham *et al*., 2005). It is in boreal zones however, where the climate fingerprint on shrubs is most evident, with a growing body of literature documenting range expansion of shrub species (e.g. Sturm *et al.,* 2001; Tape *et al*., 2006; Post *et al.,* 2009; Naito & Cairns, 2015)

While increases in the abundance of shrubs or range margin shifts have been related to direct climate impacts, such as warmer temperature and shifts in precipitation (e.g. Eamus & Palmer, 2007; Taylor & Kumar, 2013) indirect factors such as elevated CO_2 may play a role in increasing the distribution of evergreen

vegetation, including shrubs, across Australia (Macinnis-Ng *et al*., 2011), particularly those in semi-arid grasslands (Morgan *et al*., 2007) Other studies, however, have connected woody thickening to anthropogenic disturbances within the environment (Daryanto *et al*., 2013; Norman *et al*., 2014; Silva *et al*., 2014).

To date, few dynamic global vegetation models have included shrubs as a distinct plant functional type (although see models modified by Cox, 2001; Zeng *et al*., 2008; Dallmeyer *et al*., 2011). This is partly due to the lack of knowledge regarding the role of climate in defining shrubland distribution. Thus, if parameterisation of shrublands in a vegetation modelling context was explicitly defined, more confidence could be placed in projections of global vegetation types and the impacts of climate change and disturbances.

Australian shrubs and shrubland ecosystems

As on other continents, Australian shrub species are a key environmental and economic resource. For example, among the most widespread vegetation communities in Australia are Acacia shrublands dominated by Mulga (*Acacia aneura*) and Mallee shrublands dominated by *Eucalyptus* species. These play a valuable role in enhancing biodiversity, supporting remnant populations of a broad number of animal species, and are important for ecotourism and conservation (DEWR, 2007).

Consequently, the study of climate and soil dynamics is crucial to our ability to understand the distribution of shrubs and shrublands, and their potential responses to climate change. To date, the inclusion of soil variables in modelling studies and assessments of the relative importance of soil versus climate variables in driving species distributions has been limited. The objective of this thesis, therefore, was to explore relationships between climate, soil and the distribution of Australian

shrublands and shrub species (note that this thesis often refers to particular Australian states and territories, for which a map is provided in Appendix 1).

In the second chapter, I assessed the distribution of shrubland as a vegetation class. My key goals were to a) identify climate variables associated with the cover of shrubland as a major vegetation type, and of six classes of shrubland; b) identify the climate space occupied by shrubland, compared to other major vegetation types, and each shrubland class, and c) use Generalized Linear Models (GLMs) to predict the distribution of shrubland and shrubland classes across Australia.

In Chapter 3 I focused on dominant shrubland species rather than ecosystems. This chapter explored how climate and the physical and chemical properties of soil influence the distribution of species. Specifically, I assessed whether the inclusion of soil characteristics in conjunction with climate variables increased the predictive power of models of the distributions of 29 native Australian shrub species. I hypothesised that, given the importance of soil in controlling the distributions of plants, models calibrated with both soil and climate variables would have higher accuracy (from the perspective of predictive power and elological relevance of the predictions), compared to those calibrated with only climate variables or only soil variables.

The key focus on Chapter 4 was climate change and how the distributions of species targeted in Chapter 3 may be altered under contrasting future climate scenarios. To further explore uncertainty in the output of species distribution models, I assessed how projections of suitable habitat may diverge when two sets of models (one calibrated with climate and soil variables and the other with only climate variables) are projected onto scenarios of future climate change.

The final chapter provides the key findings of this thesis and discusses implications and directions for future research.

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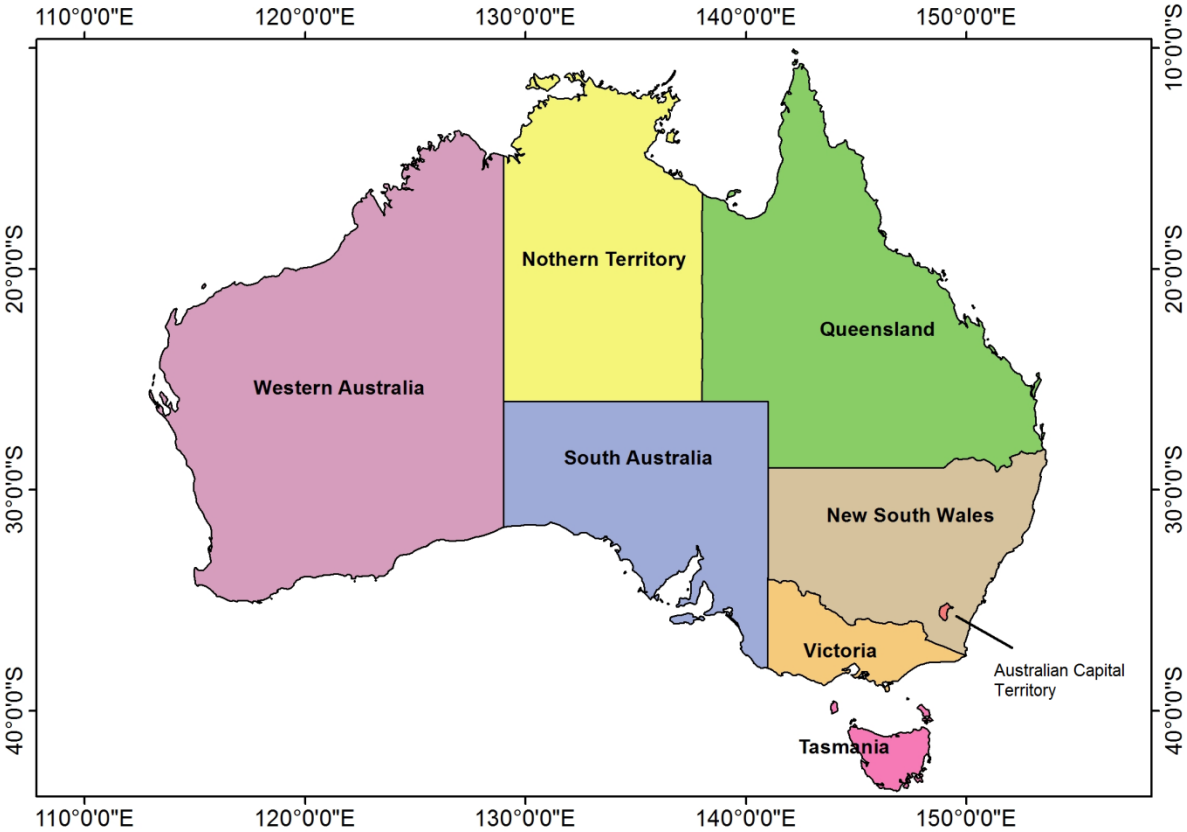
Appendix 1

Figure 1.1 A map of Australian states and territories.



Chapter 2

Defining the climate envelopes of Australian shrublands

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Introduction

Shrublands are one of the most common vegetation types in Australia, occupying ~ two and a half million square kilometres—almost a third of the land area of the continent (DEWR, 2007). Shrublands are mostly distributed across the southern-central to western regions of Australia, as well as parts of the south-east. The National Vegetation Information System, which defines vegetation type based on growth form, height and cover of dominant vegetation within strata, regards "shrubs" (multi-stemmed species) as the dominant growth form in Shrublands (ESCAVI, 2003). Five major classes of shrubland are recognised within Australia, with a sixth class comprising mixed communities not aligned to the other five (ESCAVI, 2003).

Both in Australia and globally, climate determines the distribution of shrubland at broad spatial scales. In particular, gradients of temperature and moisture separate shrubland from other major vegetation types (i.e. forests, woodlands, grasslands) (Box, 1995). For instance, while forests and woodlands inhabit regions of high water availability in Australia, most shrubland communities occupy arid and semi-arid regions generally characterised by mean annual precipitation < 250 mm and 250 – 800 mm, respectively, although some shrubland classes (such as Heathland and Tall Closed Shrubland) occur in wetter, temperate regions of the country (Stern *et al*., 1999; Butt, 2004).

Grasslands dominated by perennial grasses also occur in Australia's arid and semi-arid regions (DEWR, 2007), though shrubs are able to compete with grass

species in these ecosystems due to their efficient use of low or irregular moisture (Mooney, 1981; Burgess, 1995; Sandra & Marcelo, 1997; Smith *et al*., 1997; Reynolds *et al*., 1999). Shrubs have deeper roots than grasses, enabling them to extract water from deeper soil layers, and therefore access moisture during periods of low rainfall (Burgess, 1995). In contrast, the shallow roots of many grass species prevents access to moisture held in deeper soil layers (Burgess, 1995), thereby limiting their growth in summer. Furthermore, relative to grasses, shrubs display higher rates of photosynthesis and respiration during the growing season (the period of maximal physiological activity and growth) (Reynolds *et al*., 1999). Shrubs also minimise energetic costs by reducing productivity outside their growing season, such as during drought (Oleson *et al*., 2004); lowering photosynthetic activity; and producing relatively small leaves (Smith *et al*., 1997).

While several studies have addressed general responses of shrub species or shrubland, in Australia and overseas, to climate and climate change (Sandra & Marcelo, 1997; Fitzpatrick *et al*., 2008; Altamirano *et al*., 2010; Zeng, 2010; Munson *et al*., 2011; Sardans *et al*., 2013), there remains a general lack of understanding of the climatic factors that characterise Australian shrubland as a major vegetation type, and the six classes of shrubland.

The aims of this Chapter, therefore, were to a) identify climate variables associated with the cover of shrubland as a major vegetation type, and of each class of shrubland; b) identify the climate space occupied by shrubland, compared to other major vegetation types, and each shrubland class, and c) use Generalized Linear Models (GLMs) to predict the distribution of shrubland and shrubland classes across Australia.

Methods

Vegetation Data

The distribution of vegetation types was obtained from the National Vegetation Information System, NVIS (ESCAVI, 2003). This database contains information on the floristic, structural and growth form characteristics of Australian extant native vegetation, collected at field survey sites and from remote sensing across all states and territories. Its foundation is an information hierarchy in which the dominance of a specific taxon/species is indicated by its relative biomass in each stratum or sub-stratum of a vegetation type. Thousands of distinct vegetation types have been identified and collated in the NVIS database. To develop continental scale gridded datasets NVIS aggregated the extant vegetation types into 23 major native vegetation groups (MVGs) (DEWR, 2007), which can broadly be defined as shrubland, forest, woodland or grassland, along with other land cover types (e.g. non-vegetation and non-native vegetation) (version 4.1; DSEWPaC, 2012). Shrubland is divided into six classes: Acacia shrublands; Chenopod shrublands, samphire shrublands and forblands; Heathlands; Mallee woodlands and shrublands; Low closed forests and tall closed shrublands; and Other shrublands. These will hereafter be referred to as “Acacia”, “Chenopods”, “Heathlands”, “Mallee”, “Tall shrubland”, and “Other”. A more detailed classification consisting of 83 major vegetation subgroups (MVS) has also been developed; of which 25 are shrubland or a combination of open woodland and sparse shrubland (Table 2.1).

Aggregation of MVGs

I downloaded extant MVG and MVS gridded NVIS data at a spatial resolution of ~ 1 km (version 4.1). These data were converted to polygon layers using ArcGIS v10.1 (ESRI Inc., 2010) in order to reduce errors resulting from the way in which NVIS

aggregated MVS's into MVGs. Under this aggregation approach a MVG polygon may have consisted of more than one MVS, and the composition of these may not be immediately obvious from the title of the MVG. For instance, within Acacia shrubland, there are pockets of other MVSs that are actually classified as subtypes of forests, woodlands or grasslands. Therefore, to obtain more accurate representations of climate envelopes, I reclassified MVS polygons and recreated MVG classes, as described in Table 2.1. This process resulted in slight spatial differences between my classification of the six shrubland classes and the original shrubland MVGs (see Appendix 2.1 Figure A2.1). Finally, I placed each MVS into one of four broad vegetation groups: shrubland, forest, woodland, and grassland (Table 2.1).

Table 2.1 Major Vegetation Subgroups (MVS) as defined by the National Vegetation Information System (DEWR, 2007) were aggregated into four broad vegetation types or a 'mask' layer. Within Shrubland, associated MVSs were further classified into six classes.

Broad vegetation type	Vegetation major subgroup (MVS)
Shrubland	
Mallee woodland & shrubland	Mallee with either a) open shrubby, b) dense shrubby or c) tussock grass understorey, or d) hummock grass Open mallee woodlands & sparse mallee shrubland with either a) open shrubby, b) dense shrubby or c) tussock grass understorey, or d) hummock grass
Acacia woodland & shrubland	Acacia (+/- low) open woodlands & sparse shrubland and either a) +/- tussock grass, b) with shrubby understorey, c) chenopods or d) hummock grass Mulga (*Acacia aneura*) open woodlands & sparse shrubland and either a) +/- tussock grass or b) with hummock grass Mulga (*A. aneura*) woodlands and either a) +/- tussock grass and +/- forbs or b) shrubland with hummock grass Other Acacia tall open shrubland & shrubland
Low closed forests or tall closed shrubland	Low closed forest or tall closed shrubland (including Acacia, Melaleuca & Banksia)
Heathland	Heath or other sparse shrublands & sparse heathlands
Chenopods & samphire shrubland	Saltbush and/or Bluebush shrubland Mixed chenopod, samphire +/- forbs

Other shrubland	Lignum shrubland & wetlands Melaleuca shrubland & open shrubland Other shrubland Regrowth or modified shrubland
Forest	Brigalow (*Acacia harpophylla*) forests and woodlands *Callitris* forests and woodlands *Casuarina* and *Allocasuarina* forests and woodlands Cool temperate rainforest Dry rainforest or vine thickets Warm temperate rainforest Eucalyptus (+/- tall) open forest with dense broad-leaved &/or tree-fern understorey (wet sclerophyll) Eucalyptus open forests with a) grassy or b) shrubby understorey Eucalyptus tall open forests & open forests with ferns, herbs, sedges, rushes or wet tussock grasses Eucalyptus tall open forest with a fine-leaved shrubby understorey Forests & woodlands that are a) Leptospermum, b) Melaleuca open, c) Other Acacia, or d) Other Regrowth or modified forests & woodlands Tropical *Eucalyptus* forest & woodlands with either a) tall annual grassy understorey Tropical mixed species forests and woodlands Tropical or sub-tropical rainforest Unclassified forest
Woodland	Banksia woodlands; *Callitris* open woodlands *Casuarina*/*Allocasuarina* open woodlands with a) hummock grass, b) tussock grass, c) chenopod shrub or d) shrubby understorey Eucalyptus low open woodlands with a) hummock or b) tussock grass, or c) shrubby understorey Eucalyptus open woodlands with either a) grassy or b) shrubby understorey Eucalyptus woodlands with either a) hummock grass or b) tussock grass understorey, or c) ferns, herbs, sedges, rushes or wet tussock grassland; or with understorey that is a) chenopod or samphire or b) shrubby Eucalyptus (+/- low) open woodlands with a chenopod or samphire understorey Melaleuca open woodlands
Grassland	Blue grass (*Dicanthium*) & tall bunch grass (*Chrysopogon*) tussock grasslands; Hummock grasslands; Mitchell grass (*Astrebla*) tussock grasslands Other grasslands; Temperate tussock grasslands; Wet tussock grassland with herbs, sedges or rushes, herblands or ferns; Other tussock grasslands Regrowth or modified graminoids Saline or brackish sedgelands or grasslands; sedgelands, rushes or reeds
Mask	Boulders/rock with algae, lichen or scattered plants, or alpine feldmarks; Naturally bare, sand, rock, claypan, mudflat Freshwater, dams, lakes, lagoons or aquatic plants Salt lakes & lagoons; Sea, estuaries (includes seagrass); Mangroves Cleared, non-native vegetation, buildings; Unclassified native vegetation; Unknown/No data

Climate data

I generated average monthly values of precipitation, maximum and minimum temperature, solar radiation and evaporation (averaged over the period 1970 – 1999)

from ANUCLIM (version 6.1, Xu & Hutchinson, 2011, 2013) at a spatial resolution of 5 km. Using this dataset, I calculated a number of variables that have a physiological impact on plants, and which may influence the distribution of shrubland (Table 2.2):

- Temperature: mean annual temperature (MAT); mean temperature of the coldest (MTCO) and warmest month (MTWA); degree days above 0°C (GDD_0) and 5°C (GDD_5); photosynthetically active radiation during the period with temperatures above 0°C (PAR_0) (following Klassen & Bugbee, 2005; Gallego-Sala *et al*., 2010).
- Precipitation: mean annual precipitation (MAP); mean winter (Austral winter = June, July, August; P_w) and summer (Austral summer = December, January, February; P_S) precipitation; concentration of seasonal precipitation ($P_{(conc)}$) whereby higher values indicate that precipitation is restricted to part of the year while lower values indicate it is scattered throughout the year (Kelley *et al*., 2013);
- Moisture: Moisture Index (MI), calculated as the ratio of MAP to total annual equilibrium evapotranspiration (EET), where EET is calculated following Wang *et al*., (2013); the Cramer-Prentice α index of plant-available moisture (α = AET/EET, where AET is actual evapotranspiration) (Prentice *et al*., 1993); mean winter (α_w) and summer alpha (α_s); summer precipitation index (SPI) which was calculated as:

$$SPI = \frac{\sum_i^n P_i \cos\theta_i}{\sum_i^n P_i},$$

where P_i is the fraction of annual precipitation falling in month i, θ_i is the angle of month i (defined as January = 0˚, February = 30˚, ..., December = 330˚), and summation is over n = 12 months. In the Southern Hemisphere, SPI will be positive when precipitation is concentrated in summer and negative when it is concentrated in winter. This variable is similar to the ‘standardised precipitation index’

published by WMO (2012). The latter, however, can be applied to different sets of months whereas SPI is calculated for summer months only.

Other variables that may be important in delimiting the distribution of shrubland include soil depth and water holding capacity. I obtained soil moisture data from the Australian Water Availability Project (AWAP: Raupach *et al*., 2009, 2012). AWAP combines measurements and models to produce water fluxes and soil moisture variables across Australia, at ~ 5 km resolution, for two soil depths (layer 1 = 0 - 0.5 m; layer 2 = 0.5 - 1.5 m depth). I used AWAP data to calculate an additional nine soil moisture variables for the period 1970 - 1999. These were: mean annual soil moisture of layer 1 (SM_1) and layer 2 (SM_2); mean annual difference between these layers (SM_{1-2}); mean winter and summer soil moisture for layer 1 ($SM_{1(w)}$ and $SM_{1(s)}$, respectively) and layer 2 ($SM_{2(w)}$; $SM_{2(s)}$); and mean difference between soil layers 1 and 2 in winter ($SM_{1-2(w)}$) and summer ($SM_{1-2(s)}$). Values of these two variables will be positive when moisture availability is higher in layer 1 than layer 2, and negative when it is higher in layer 2 than layer 1 (Table 2.2).

Identifying climate variables and fitting models

My first goal was to identify the climate variables controlling the distribution of shrubland relative to other major vegetation types and of each shrubland class. I used ArcGIS (ESRI Inc., 2010) to overlay the reclassified MVG polygon layer to a 5 km grid matching the resolution of the climate data. I then calculated the proportional cover of each of the four major vegetation types (shrubland, grassland, forest, woodland), for each 5 km cell. Grid cells that did not contain native vegetation, or consisted of water bodies (see Table 2.1), were masked and removed, leaving 295,210 cells containing data on native vegetation. Values for each climate variable were extracted at each of these cells.

Table 2.2 Climate variables derived from ANUCLIM (Hutchinson & Xu, 2010), indicated with an asterisk, and AWAP (Raupach *et al*., 2012), as well as method of calculation.

Variable	Abbreviation	Method or reference
Mean annual temperature (°C) *	MAT	
Mean temperature of the coldest month (°C) *	MTCO	Gallego-Sala *et al*., (2010)
Mean temperature of the warmest month (°C) *	MTWA	Gallego-Sala *et al.* (2010)
Total photosynthetically active radiation during the growing season, for days with temperature above 0°C (mol photon m^{-2}) *	PAR_0	Klassen & Bugbee, (2005); Gallego-Sala *et al.* (2010)
Accumulated growing degree days above 0°C *	GDD_0	Gallego-Sala *et al.* (2010)
Accumulated growing degree days above 5°C *	GDD_5	Gallego-Sala *et al.* (2010)
Mean annual precipitation (mm) *	MAP	
Mean summer precipitation (mm) *	P_s	Austral summer = December, January, February
Mean winter precipitation (mm) *	P_w	Austral winter = June, July, August
Summer precipitation index *	SPI	I.C. Prentice, pers. comm
Concentration of seasonal precipitation *	$P_{(conc)}$	Kelley *et al.*, (2013)
Moisture Index (dimensionless) *	MI	Prentice *et al.*, (1993)
Cramer-Prentice α index (dimensionless) *	α	Prentice *et al*. (1993)
Mean summer alpha (dimensionless) *	α_s	Austral Summer
Mean winter alpha (dimensionless) *	α_w	Austral Winter
Mean annual soil moisture of layer 1 (mm)	SM_1	
Mean annual soil moisture of layer 2 (mm)	SM_2	
Mean annual difference between two soil layers	SM_{1-2}	$SM_1 – SM_2$
Mean soil moisture in summer (layer 1) (mm)	$SM_{1(s)}$	Austral Summer
Mean soil moisture in winter (layer 1) (mm)	$SM_{1(w)}$	Austral Winter
Mean soil moisture in summer (layer 2) (mm)	$SM_{2(s)}$	Austral Summer
Mean soil moisture in winter (layer 2) (mm)	$SM_{2(w)}$	Austral Winter
Mean difference between soil layers 1 and 2 in summer	$SM_{1-2(s)}$	$SM1_{(s)} – SM_{2(s)}$
Mean difference between soil layers 1 and 2 in winter	$SM_{1-2(w)}$	$SM_{1(w)} – SM_{2(w)}$

Canonical Correspondence Analysis was used to explore relationships between bioclimatic variables and vegetation type (CCA, Ter Braak & Prentice, 1998), with the Akaike Information Criterion (AIC, Akaike, 1974) using a forward stepwise model selection algorithm to select the most important bioclimatic variables.

Next, I extracted percent grid cover for the six shrubland classes from each grid cell predicted by a GLM ensemble (described below) to contain shrubland as a major vegetation type. This resulted in 85,834 grid cells used in the analysis. Again, CCA was used to identify which of 24 bioclimatic variables were associated with each shrubland class, and separate GLMs for each class were developed to predict their potential distributions.

Following the methodology of Wang *et al*., (2013), GLMs (Müller, 2004) were constructed for each of the four vegetation categories and six shrubland classes separately, with the dependent variable being the proportion of each grid cell covered by a given vegetation type or Shrubland class ("proportional grid cover"). Univariate models with linear and quadratic terms were initially fitted using the bioclimatic variables identified through CCA as the most important. I assumed a binomial distribution to errors of the model, and used the logit link function. I then excluded any terms with coefficients that were not significant at $P < 0.05$, and quadratic terms with response curves lacking realism (i.e., U-shaped curves rather than Gaussian-shaped unimodal curves (Wang *et al.*, 2013) which represent more realistic (sigmoid) responses to climate predictors). Unrealistic response curves reflect incorrect physiological relationships between plants and climate predictors (Austin, 2007). Finally, I fitted final models by relating the fitted probabilities to observed proportions. For this step I used a simple linear calibration for each vegetation/shrubland type by applying a linear regression to the predicted probability of a given vegetation type to its observed proportion. Then, I inverted that regression relationship to find a

weighting factor to the predicted probabilities, and excluded all negative values by setting them to zero. These final predicted probabilities were related to each vegetation/shrubland type in each grid cell by selecting the highest predicted probabilities after weighting.

I used the final models to predict the proportional grid cover of each of the major vegetation types and shrubland classes within each grid cell. That is, following (Wang *et al*., 2013), I used a simple linear calibration to relate the GLM-predicted probabilities to observed proportional grid cover. The regression relationship was inverted to obtain a weighting factor to be applied to the predicted values. Negative predicted values were set to 0 and values > 1 were set to 1. The parameter values for the final models are listed in Tables A2.1 and A2.2, respectively, in the Appendix 2.1.

Mapping and assessing goodness of fit

To assess the agreement between observed and projected distributions, I combined projections for the four vegetation types into a single map, where the vegetation type within a given grid cell was that which had the highest predicted proportional grid cover. I refer to these as “ensemble GLMs”. The resulting map was compared to the observed proportional grid cover map (created in the same manner as predicted proportional grid cover, by aggregating the NVIS subtypes according to Table 1). Agreement was assessed using Cohen’s kappa statistic (Cohen, 1960; Prentice *et al*., 1992), the values of which range from 0 to 1, where zero indicates that similarities are most likely obtained by chance while 1 indicates complete agreement between two maps. Generally, kappa > 0.55 are accepted as ‘good’ (see Monserud & Leemans, 1992). Cross tabulation was used to compare observed and predicted values within different vegetation types and Shrubland classes.

Analyses were performed with the R software v 2.2-1 (R Core Team 2012) using the *vegan* package (Oksanen *et al.*, 2013).

Results

Identifying climate variables associated with the distribution of Shrublands

The CCA biplot (Figure 2.1) illustrates relationships between the four vegetation types and climatic gradients in Australia. The first and second axes explain 56% and 29% of variation across the climate variables, respectively (for scores of the two axes see Appendix 2.1, Table A2.3). Annual and seasonal moisture variables, such as α, MAP, SM_1, α_s, and $SM_{1(s)}$, are aligned to the first axis, while temperature and energy variables, particularly PAR_0, GDD_0, GDD_5 and MAT and summer precipitation variables such as SPI and $P_{(conc)}$, are aligned on the second axis. Across a gradient from high to low moisture (left to right along axis 1) major vegetation groups transition from forest, to woodland, and then grassland and shrubland. Similarly, along a gradient of high to low temperature (bottom to top along axis 2) vegetation shifts from grassland, woodland, forest, then shrubland.

Based on AIC analysis the four variables, α, SPI, α_s, and PAR_0, were most important for determining the distribution of the four vegetation types. Correlation coefficients between these variables were < 0.8 which further supported their selection.

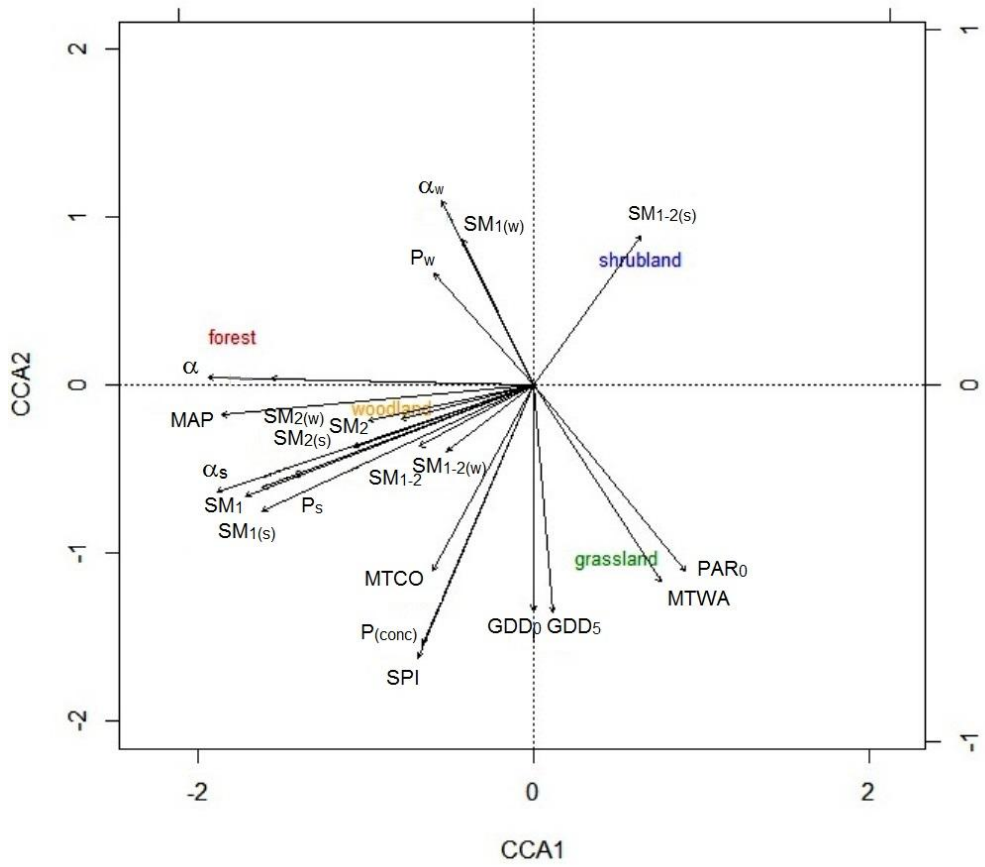

Figure 2.1 CCA biplot of four vegetation types (shrubland, forest, woodland, grassland), and 24 climatic variables. See Table 2.1 for full names of climate variables. CCA1 axis represents a gradient of moisture availability increasing from right to left. CCA2 axis represents a temperature gradient, increasing from the bottom upwards.

The response curves of GLMs of the four major vegetation types show that the proportional grid cover of shrubland vegetation type rapidly declines as α increases (Figure 2.2). There is also a negative relationship between grid cover of shrubland and SPI and PAR_0. Proportional cover of grassland increases the more rainfall is concentrated in summer, but shows unrealistic responses to α and PAR_0. Cover of grassland declines with α_s while shrubland increases. While there is little association between proportion of forest cover and α or PAR_0, higher coverage of woodland is associated with intermediate values of both of these variables. Forest and woodland also differ in their response to SPI: forest cover is greater in areas where rainfall is

concentrated in winter, while woodland is associated with summer concentration (Figure 2.2).

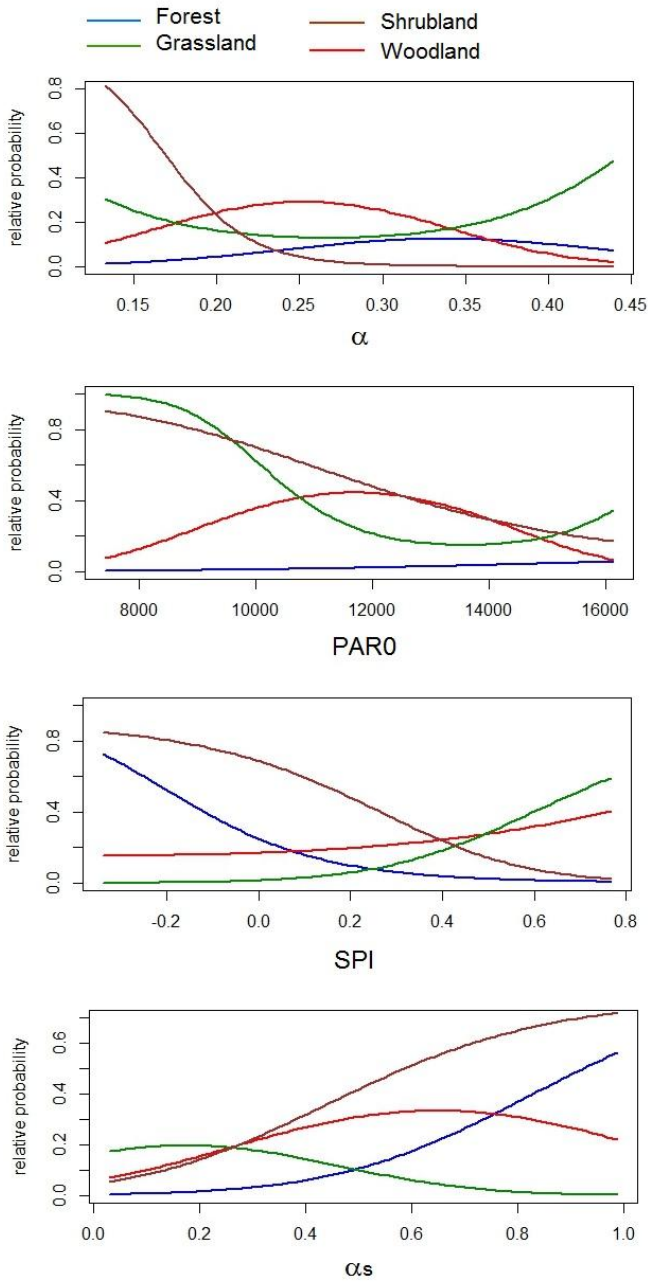

Figure 2.2 Response curves of major vegetation types (forest, grassland, shrubland, and woodland) generated by generalized linear models. The four variables are: α = Cramer-Prentice α index; PAR_0 = photosynthetically active radiation during the period with temperature above 0°C; SPI = summer precipitation index; α_s = mean summer α.

What are the climate envelopes of individual shrubland classes?

The relationship between six shrubland classes and climate in Australia is shown in Figure 2.3. The first and second axes explain 38% and 37% of variation across the

shrubland classes, respectively (for axes scores see Appendix 2.1, Table A2.4). The shrubland classes are separated along the first axis on the basis of temperature and energy (e.g. MAT PAR_0, GDD_0, MTWA) and summer moisture availability (e.g. α_s, P_s). The second axis is based primarily on different measures of seasonal and annual soil moisture availability (e.g. $SM_{1(s)}$, $SM1_{(w)}$, SM_2). Along the gradient of high to low temperature, shrubland classes shift from Acacia, Chenopods, Other shrubland, Mallee, Tall shrubland, and then Heathland. Similarly, along the gradient of high to low moisture availability, shrubland transitions from Heathland, Tall shrubland, Other shrubland, Mallee, Acacia, then Chenopods.

Based on AIC analysis, the two moisture variables, α and $SM_{1\text{-}2(s)}$, and the variable PAR_0, were selected as the most important for determining the distribution of different shrubland classes. Correlation coefficients between these three variables were also low (< 0.45) which further supported their selection.

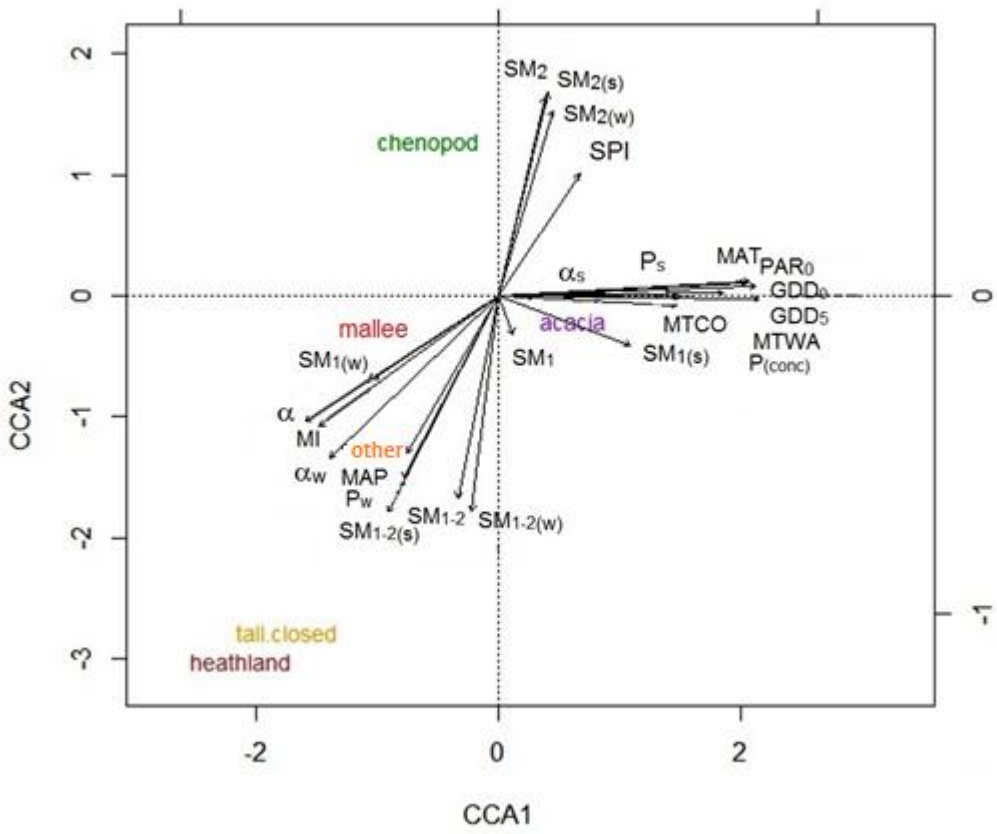

Figure 2.3 CCA biplot of six shrubland classes: Acacia, Chenopods; Heathland; Mallee; Other; Tall closed; and 24 climatic variables. See Table 2.1 for names of variables. Variables separate along the first axis based on temperature and energy, and the second axis mostly on moisture availability.

The response curves of calibrated GLMs for the six shrubland classes demonstrate that coverage of Acacia shrubland is higher in regions with low α (< 0.4) and increases with increasing PAR_0. Cover also increases with higher levels of moisture in deeper, compared to shallower, soils (i.e. lower $SM1_{-2(s)}$). Coverage of chenopods declines increasing α, and positively correlated with PAR_0 and moisture in shallow soil layers. Heathlands show very low probabilities with all three predictor variables with an unrealistic response to PAR_0. In general, Heathland cover is positively associated with α and moisture in shallow soil layers, and is absent from deeper or dry soils. Mallee coverage decreases with increasing α and PAR_0 but increases in slightly moist deeper soil layers. Tall closed shrublands occur in relatively low α (0.25 – 0.35) and PAR_0 (12500 – 15000) and in moister shallow soil layers. Coverage of Other shrublands increases with increasing α and PAR_0 and has a non-realistic response to $SM1_{-2(s)}$ (Figure 2.4).

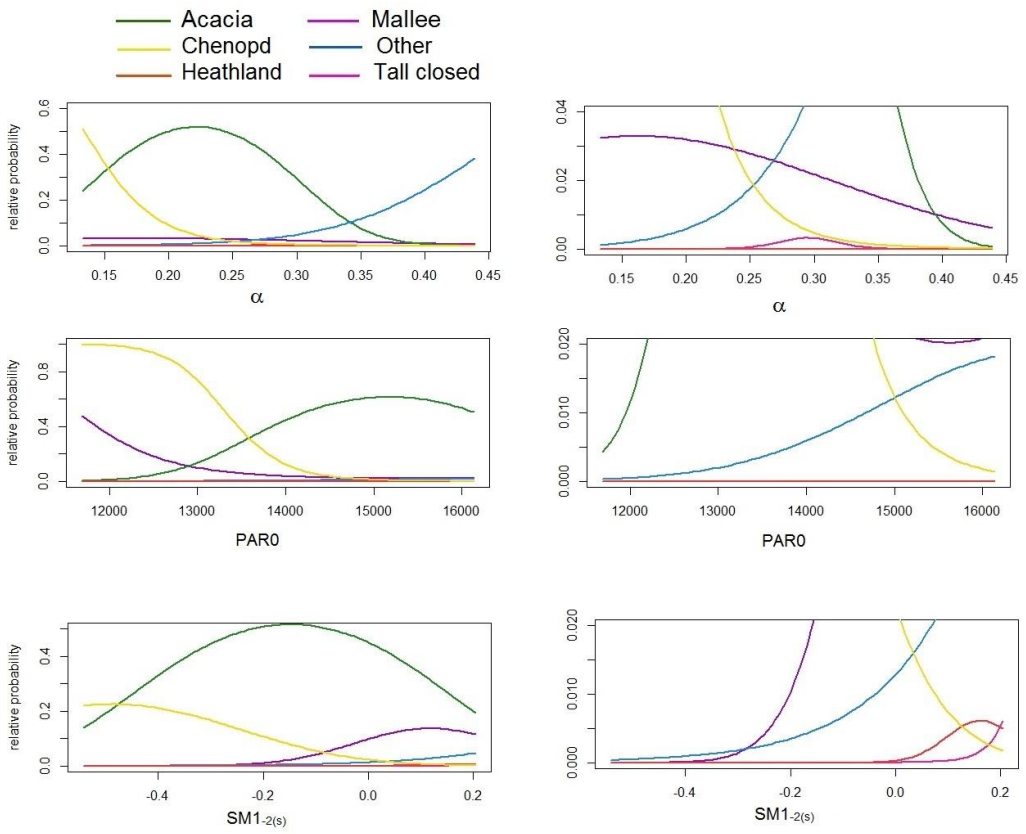

Figure 2.4. Response curves of six shrubland classes (Acacia, Chenopod, Heathland, Mallee, and tall closed) found across Australia, modelled with generalized linear models. α = Cramer-Prentice α index; PAR_0 = Photosynthetically active radiation during the period with temperature above 0 ºC; $SM1_{-2(s)}$ = Mean difference between soil layers 1 and 2 in summer. Plots on the left are fully sized, whereas plots on the right show smaller section at finer probability scales.

Model performance

GLM models for the first ensemble had a Kappa value of 0.7. According to Monserud & Leemans (1992), this indicates that the predictive power of the models were between “Good” to “Excellent” (Figure 2.6). 74% of grid cells were correctly predicted to be shrubland (Figure 2.5). The ensembled map indicates that the GLM correctly predicted much of the southern range of shrubland, although shrubland in parts of western Australia, and in scattered regions in south-western Queensland and the Northern Territory were incorrectly predicted to be grassland (Figure 2.6). Rarely was shrubland predicted to be forest (< 1%) or woodland (< 6%). Forest was poorly predicted, with only 38% of grid cells correct. Approximately 51% of forest was predicted as woodland particularly in south-eastern New South Wales/Victoria and Tasmania. In contrast, ~ 57% of woodland was correctly predicted with < 8% incorrectly classified as Forest, although regions of south-western and central Australia were misclassified as shrubland and grassland, respectively.

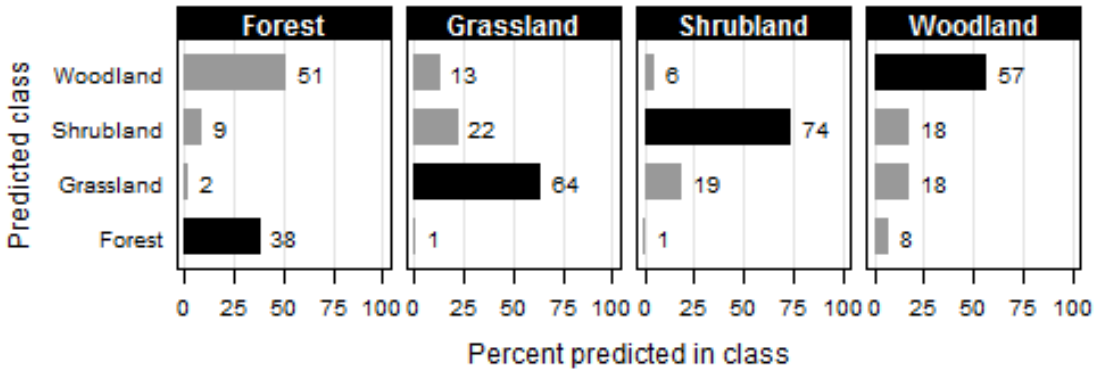

Figure 2.5 Results of an ensemble of four general linear models, predicting the distribution of four dominant vegetation types across Australia, compared to the observed dominant vegetation type. Each section sums to 100% and shows the proportional of cells for which the dominant vegetation type was predicted correctly, as well as the breakdown of incorrect predictions.

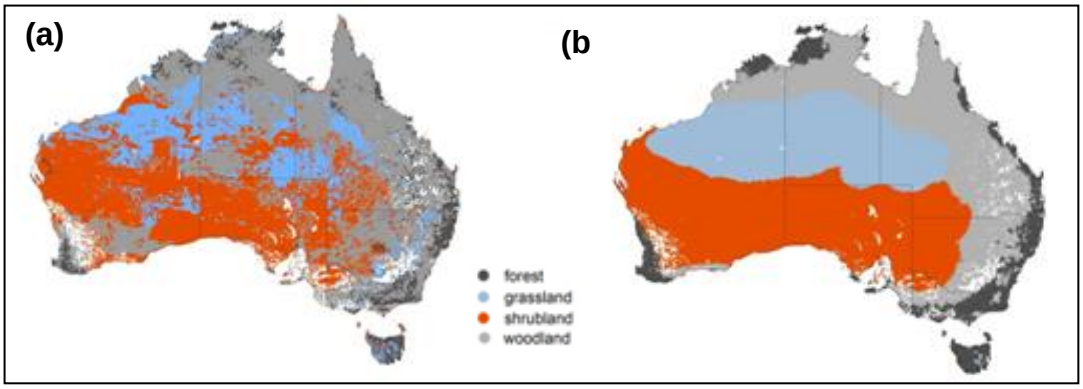

Figure 2.6 Observed (a) and predicted (b); distribution of the four major vegetation types (forest, woodland, shrubland, grassland). The observed map is based on aggregation of the NVIS data set. For each grid cell, the predicted vegetation type was that with the highest predicted probability based on four generalised linear models that used some or all of the following as predictors (refer to Table 2.3): α, PAR_0, SPI, α_s. Predictors are defined in Table 2.2 and described in text in the Methods section.

The ensembled model of the six shrubland classes was less successful, as predictive power of the GLM was only fair (Kappa: 0.4) with the distribution of mallee, acacia and other shrubland being over-estimated (Figure 2.8). Although Acacia and Chenopods were predicted quite accurately (~ 74% and 68%, respectively), and Mallee was reasonable (53%), the remaining classes were poorly predicted (Figures 2.7 and 2.8). The most frequent misclassification for Acacia was as Chenopods (14%), and vice versa (18%). 27% of Mallee grid cells were classified as Acacia. Less than 20% of Tall shrublands were correctly predicted, with 48% being classified as Other and 24% as Mallee. Other shrubland was frequently classified as Mallee (22%), Acacia (23%) or Chenopods (21%). There was no agreement between observed and predicted distributions of Heathland. Rather, these areas were primarily classified as Other shrubland (49%), Mallee (36%) or Tall shrubland (20%).

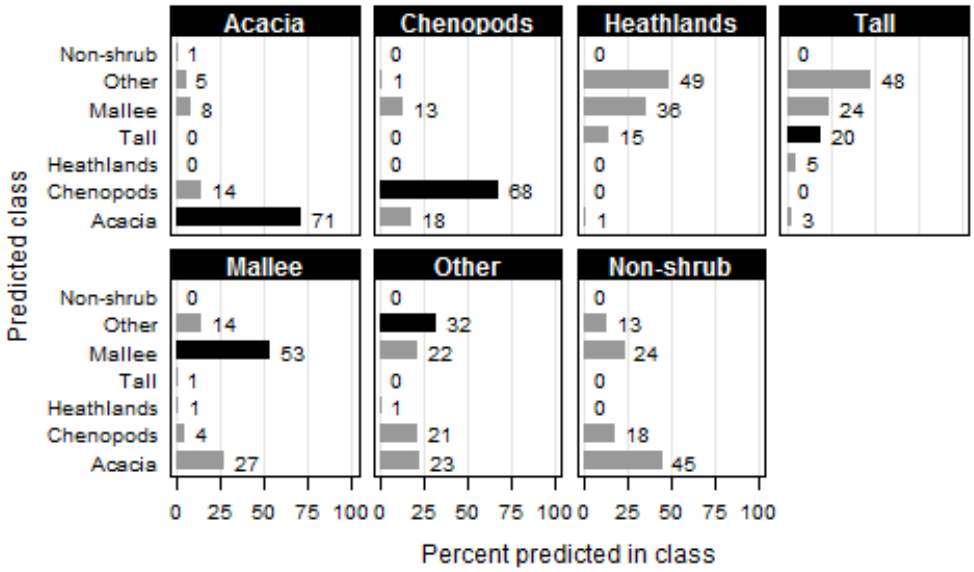

Figure 2.7 Results of an ensemble of six general linear models, predicting the distribution of shrubland classes. Each section sums to 100% and shows the proportional of cells for which shrubland was predicted correctly (in bold), and the breakdown of errors. Acacia = Acacia shrubland; Chenopods = Chenopod shrubland, samphire shrubland and forblands; Heathlands = Heathland; Tall = Low closed forests and tall closed shrubland; Mallee = Mallee shrubland and woodland; Other = other shrublands; Non-shrub = vegetation types other than shrubland.

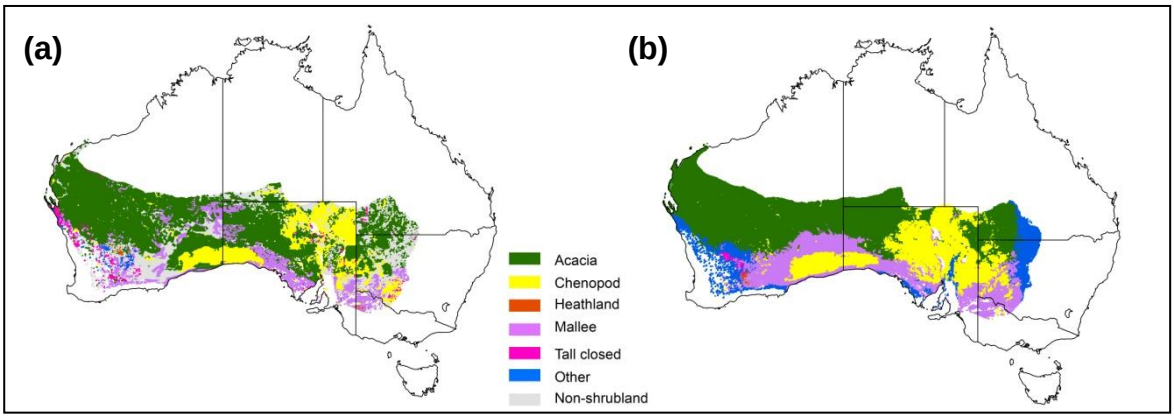

Figure 2.8 Observed map (a) of aggregated MSVs representing six shrublands that are located within the area predicted to contain shrubland (see Figure 2.3). (b) Predicted distribution of six shrubland classes, based on an ensemble of six generalised linear models (GLM). Acacia (Acacia shrubland); Chenopods (Chenopod shrubland, samphire shrubland and forblands); Heathlands (Heathland); Mallee (Mallee shrubland and woodland); Other shrubland; Tall closed (Low closed forests and tall closed shrubland); Non-shrubland (Other vegetation types). GLMs were calibrated using α, PAR_0, and $SM1_{-2(S)}$ as predictors. Predictors are defined in Table 2.2 and described in text in the Methods section.

Discussion

Climate controls of Australian shrublands

Across Australia, the four major vegetation types (shrubland, forest, woodland and grassland) can be separated according to their climate space, as defined by gradients of annual and summer soil moisture, and temperature availability. My analyses indicated that soil moisture is a primary factor distinguishing shrubland from other vegetation growth forms. Physiologically, this is explained by forest and woodland requiring relatively higher values of soil moisture than shrubland and grassland, in order to support higher levels of photosynthetic activity (Briggs *et al*., 2005; Meng *et al*., 2009). However, while GLMs predicted the distribution of

shrubland relatively well, it was harder to distinguish forest from woodland (51% of observed forest was predicted as woodland).

As indicated by CCA, both shrubland and grassland occur in environments with low annual moisture. The primary difference between these vegetation types is that higher shrubland occurrence is associated with higher summer soil moisture. This supports previous research suggesting that shrubs' efficient use of irregular or low water enables them to dominate these regions (e.g. Mooney, 1981; Burgess, 1995). Shrubs can extract rainfall more efficiently than grasses due to their deep, branched roots (Burgess, 1995).

Although other studies have suggested that seasonal moisture is a driver of shrubland distribution, or have commented on the ability of shrublands to utilise soil moisture from deep layers (Mooney, 1981; Burgess, 1995; Reynolds *et al*., 1999), this is the first study to explicitly demonstrate that deep soil moisture is an important predictor for shrubland classes such as Acacia and Chenopods. It is known however, that competition with perennial grasslands in arid regions may negatively impact the distribution of shrubland (Harrington, 1991). For instance, Hummock grasslands in central arid Australia are dominated by *Triodia* species (Griffin & Hodgkinson, 1986; DEWR, 2007). These grasses are functionally similarly to shrubs with roots reaching a depth of 10 m (Reid *et al*., 2008), enabling plants to withstand harsh conditions and live longer.

Different classes of shrubland also occupy different climate space, with moisture availability again being the primary factor distinguishing these classes. In general, the climate niches of Chenopod, Acacia and Mallee shrublands differ from each other and from Heathlands and Tall shrublands, with the latter two occupying similar climate niches (based on the variables I have used). With the exception of

Acacia shrubland, temperature variables have little effect on the Australian distribution of shrubland classes.

Modelling limitations

While predicting the distribution of shrubland was a goal of this study, it was met with only moderate success. This may be because shrubland in general occupies a very wide climate niche. While mostly found in arid and semi-arid regions of central and southern Australia, Heathland and Tall shrubland also occur in temperate regions of Western Australia, Tasmania and eastern Australia. The ensemble GLM of the four major vegetation types did not predict shrubland to have the greatest proportional grid cover within Tasmania or eastern regions of the continent. Secondly, Heathland in Western Australia occurs in semi-arid regions in contrast to the temperate Heathlands of the east. Separating these communities into different categories for modelling may result in higher accuracy.

Model inaccuracies may be related to two reasons: Firstly, level of NVIS data accuracy likely differs across states. This could occur due to incorporating non-NVIS data from different databases across states in order to fill spatial gaps in MVGs and MVSs (NSW VIS, 2008). Secondly, combining MVS of smaller vegetation components other than shrubs in each vegetation group may have declined the quality of the model prediction. For instance, Acacia shrubland was an aggregate of nine MVSs, most of which were classified in NVIS as open woodlands and sparse shrubland (Table 1). Thus, in many instances “shrubland” may constitute mixed communities: whether these MVSs should be excluded from Acacia shrubland and combined with Woodland classes requires further exploration. Similar difficulties occur with the class “Other Shrublands”. For the most part these consist of shrubland

communities that do not fit within the definitions of the other five classes, and there is no indication that these communities form a cohesive unit.

Finally, factors other than climate can play important roles in defining shrubland distribution, diversity and composition. These include fire frequency and physical soil properties (Bowmana *et al*., 2008; Nicholas *et al.*, 2011) and grazing (Tiver *et al.,* 2008; Daryanto *et al.*, 2013). Heathland distribution, for instance, appears to be strongly influenced by soil nutrient status, and in particular the concentration of phosphate (Specht, 1994). Similarly, soil physical and chemical properties, along with soil moisture, are key factors governing Chenopod distribution (Groves, 1994).

Comparison with previous results

Few studies have described explicit relationships between climate and the distribution of shrublands in Australia. However, there is an agreement between my findings and the NVIS (DSEWPaC, 2012) description of climatic requirements for shrubland, which suggests that three major climatic factors control shrubland distribution: annual and seasonal moisture availability, and high temperature.

My results suggested that coverage of shrublands increases with lower soil moisture, while forests increase with higher α. High coverage of grassland is mostly associated with high temperature. This is in agreement with Barboni *et al*. (2004) who reported higher abundance of Mediterranean shrubs in low α (< 0.5) environments while tree abundance increased with higher α. They suggested that grasses occur more in regions of lowest winter temperature (i.e. higher abundances with higher temperature).

My results are relatively consistent with other studies, which have also identified the importance of moisture in controlling shrubs and shrubland growth (e.g.

Harrington, 1991; Lavorel & Cramer, 1999; Dallmeyer *et al*., 2011). For instance, annual precipitation was suggested to be a vital component for predicting the global distribution of shrubland (Zeng *et al*., 2008). There is a high correlation (~ 90%) between the mean annual precipitation (MAP) and summer seasonal soil moisture variable (α_s), the latter of which was included in the GLMs in this Chapter.

Cavanaugh *et al*. (2011) also found shrub distribution to be positively correlated with concentrated rainfall events and the availability of moisture in deep soil layers, while Harrington (1991) identified summer moisture as important for shrub establishment. He also noted that perennial grasses with deep roots (~ 90 cm) can be strong competitors to shrub species. As a consequence, unless factors such as overgrazing and fire suppress grassland distribution, competition with grasses may restrict the distribution of shrubland in semi-arid Australia (Harrington, 1991).

Previous studies have found temperature variables to be important for defining the distribution of shrubland in cool climate regions. For example, mean annual temperature in warmest month (MTWA) was a key variable explaining cold shrubland distribution in China (Dallmeyer *et al*., 2011), mean annual temperature (MAT) for boreal shrubland globally (Zeng, 2010), and accumulated growing degree days above 0°C and above 5°C (GDD_0 and GDD_5 respectively) for cold and cool shrubland globally, along with soil moisture variables) (Prentice *et al*., 1992). In Australia, shrubland occurs mostly in semi-arid and arid regions; hence, temperature has less influence on shrubland distribution than moisture. However, my analyses identified PAR_0 as one of the most important variables for the distribution of shrubland classes, and this is strongly correlated with MTWA and GDD.

Conclusions

The major Australian vegetation types are separated along gradients of annual and seasonal moisture and energy, with shrubland occurring in regions that are drier compared with forest and woodland, and with cooler mean temperature and higher seasonality of soil moisture compared to grassland. I also identified summer moisture availability within deep soil layers as playing an important role in controlling the distribution of different shrubland classes, such as Acacia and Chenopod shrublands. These results are consistent with knowledge of shrub morphology and physiology; shrubs have deeper roots than grasses, enabling efficient access to soil moisture in environments prone to drought or low rainfall. I used models to successfully distinguish climate space occupied by shrublands from that occupied by other Australian vegetation types. However, my approach has failed to separate the Heathland class from the other shrubland classes. This may be due to mosaicking of vegetation groups within NVIS. Modelling the potential distribution of shrublands under current climates is an important step for understanding responses to climate and environmental change.

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Appendix 2.1

Table A2.1 Regression intercepts and coefficients of predictors for a Generalised Linear Model developed for each vegetation type. **B**: terms excluded due to lack of realism in the fitted model. All other coefficients are significant ($P < 0.001$). Coefficient values reflect the ascending effect of climate over plant type (+ve) or (-ve) sign indicates the direction of relationship between plant and climatic term. α = Cramer-Prentice α index; PAR_0 = Photosynthetically active radiation during the period with temperature above 0°C; SPI = Summer precipitation index; α_s = Mean summer alpha.

Vegetation type		**α**		**PAR_0**		**SPI**		**α_s**	
	Intercept	**Linear**	**Quadratic**	**Linear**	**Quadratic**	**Linear**	**Quadratic**	**Linear**	**Quadratic**
Forest	-12.71	10.9	-7.781	0.00	0.00	-5.76	4.29	8.28	-5.87
Grassland	29.4	**B**	**B**	0.00	0.00	7.81	-2.35	2.54	-7.34
Shrubland	-7.9	16.5	2.881	0.00	-0.01	-2.88	-0.77	6.96	-2.93
Woodland	-21.37	10.4	-11.23	0.00	0.00	0.68	1.18	6.44	-4.97

Table A2.2 Regression intercept and coefficients of predictors from a Generalised Linear Model developed for each shrubland class. **A**: terms excluded due to lack of statistical significance. **B**: terms excluded due to lack of realism in the fitted model. All other coefficients had $P < 0.01$, α = Cramer-Prentice α index; PAR_0 = photosynthetically active radiation during the period with temperature above 0ºC; $SM1_{-2(s)}$ = Mean difference between soil layers 1 and 2 in summer.

Shrubland class		**α**		**PAR_0**		**$SM_{1-2(s)}$**	
	Intercept	**Linear**	**Quadratic**	**Linear**	**Quadratic**	**Linear**	**Quadratic**
Acacia shrubland	-119.6	69.2	-156.2	0.01	-0.00	-3.53	-11.99
Chenopods & Samphire shrubland or	94.29	-43.9	26.91	-0.01	0.00	-0.31	-10.58
Heathlands	7.20	72.6	-90.34	**A**	**A**	38.28	-117.6
Low closed forests & tall closed	-445.3	515	-874.9	0.05	-0.00	18.53	30.52
Mallee woodlands and shrubland	56.87	7.21	-22.25	-0.01	0.00	6.35	-26.76
Other shrubland	-57.27	29.12	-15.12	0.01	0.00	6.53	**B**

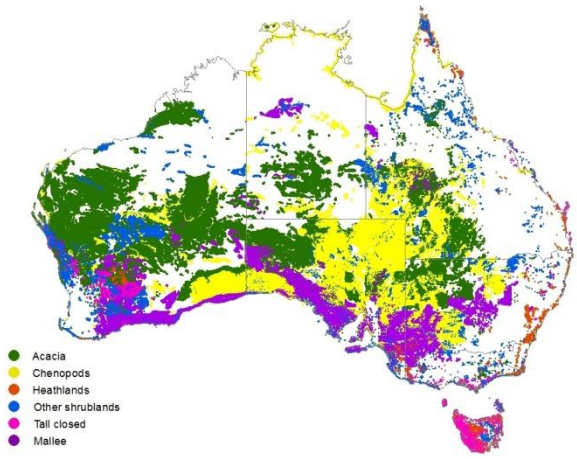
Table A2.3 Canonical correlation *analysis* scores of first and second axes, (CCA1) and (CCA2) respectively. CCA analysis includes 24 climate variables used to assess the distribution of four major vegetation types across Australia.

Variable	CCA1	CCA2
MAP	-0.879049	-0.08389
MAT	-0.0008103	-0.63116
α	-0.9139317	0.02258
MTCO	-0.2834318	-0.51963
MTWA	0.3567609	-0.5511
GDD_0	-0.0024063	-0.63115
PAR_0	0.4267412	-0.52072
SPI	-0.3243638	-0.76438
MI	-0.7379797	0.02006
α_w	-0.2601154	0.51749
α_s	-0.8917799	-0.29701
$P_{(conc)}$	-0.3123227	-0.72692
P_w	-0.2810469	0.31478
P_s	-0.7637128	-0.28798
GDD_5	0.0525825	-0.63852
SM_2	-0.3740945	-0.09542
$SM_{2(w)}$	-0.4654793	-0.09979
$SM_{1(s)}$	-0.7648624	-0.35148
$SM_{1(w)}$	-0.202043	0.40993
SM_1	-0.8103176	-0.30995
$SM_{2(s)}$	-0.5062768	-0.17202
$SM_{1-2(s)}$	0.3009803	0.42059
$SM_{1-2(w)}$	-0.2455999	-0.18566
SM_{1-2}	-0.3220786	-0.17118

Table A2.4 Canonical correlation *analysis* scores of first and second axes, (CCA1) and (CCA2) respectively. CCA analysis includes 24 climate variables used to assess the distribution of six classes of shrubland in Australia.

Variable	CCA1	CCA2
MAP	-0.28673	-0.493241
MAT	0.77575	0.0404956
α	-0.60843	-0.39399
MTCO	0.56026	-0.028315
MTWA	0.80522	0.0297745
GDD_0	0.77539	0.040675
PAR_0	0.81828	-0.010427
SPI	0.25382	0.3830535
MI	-0.5648	-0.410635
α_w	-0.53068	-0.507791
α_s	0.11163	-0.003406
$P_{(conc)}$	0.70645	0.0080428
P_w	-0.30032	-0.570087
P_s	0.38575	0.0003266
GDD_5	0.78752	0.0452366
SM_2	0.14304	0.622804
$SM_{2(w)}$	0.16851	0.5815042
$SM_{1(s)}$	0.4114	-0.154424
$SM_{1(w)}$	-0.48087	-0.314967
SM_1	0.04421	-0.120893
$SM_{2(s)}$	0.15589	0.6383527
$SM_{1-2(s)}$	-0.35016	-0.679685
$SM_{1-2(w)}$	-0.08431	-0.674702
SM_{1-2}	-0.12948	-0.633181

Figure A2.1 Six major shrubland vegetation groups (MVGs) classified by the National Vegetation Information Systems (NVIS). Shrubland groups are: Acacia (Acacia shrubland); Chenopods (Chenopod shrubland, samphire shrubland and forblands); Heathlands (Heathland); Mallee (Mallee shrubland and woodland); Other shrubland; Tall closed (Low closed forests and tall closed shrubland)



Chapter 3

Soil, climate or both? Which variables are better predictors of the distributions of Australian shrub species?

Chapter 3: Soil, climate or both? Which variables are better predictors of the distributions of Australian shrub species?

Introduction

Whilst not a strict botanical category, shrubs are generally regarded as low height, woody perennial plants with several base-stems (Zeng *et al*., 2008; Meng *et al*., 2009). As the dominant flora in arid regions, shrubs play a key role in enhancing soil fertility, reducing runoff, soil loss (Pressland, 1973; Xu *et al*., 2008; Song *et al*., 2013), dust emissions (Engelstaedter, 2003), and facilitate carbon sequestration in grassland ecosystems (Yashiro *et al*., 2010). Further, by providing fodder for livestock (Lefroy *et al*., 1992) shrubs can enhance economic returns for dryland farms by providing an 'out-of-season' food source (Monjardino *et al*., 2010).

The distribution of shrub species is strongly influenced by environmental conditions, such as climate, and physical and chemical soil properties (Pedley, 1979; Westman, 1991; Kienast *et al*., 1998). Species occurring in arid to semi-arid regions have evolved several strategies enabling them to tolerate extended periods of lower precipitation and high temperature. These include small leaves (Smith *et al*., 1997), slower growth rates, and more horizontal, rather than vertical, growth (Zeng *et al*., 2008). During the hot, dry season stomata may be partly closed, reducing transpiration, leaves may be shed (Smith *et al*., 1997) and physiological activity limited (Reynolds, 1999). Following rare rainfall event leaves may fully open (Zeng *et al*., 2008) and negative impacts of the dry season may be compensated for via enhanced physiology and growth (Reynolds, 1999). In addition, shrubs have a deeper and wider rooting system than grasses, enabling the efficient extraction of

water in low moisture environments (Burgess, 1995). Desert shrubs often accumulate their organic matter beneath their canopies, thereby enriching the nutrient pool horizontally, enabling these species to grow in infertile soils (Zinke, 1962; Jackson & Caldwell, 1993; Schlesinger *et al*., 1996; Burke *et al*., 1998).

Shrubs occupy a substantial part of the Australian landmass, mainly in semi-arid and arid regions which form approximately 70% of the continent. As with shrub species elsewhere around the globe (Song *et al*., 2013), both physical and chemical soil properties, in addition to climate, play a major role in controlling the distribution of shrub species and communities across Australia (Pedley, 1979). Shrubs usually occur on shallow, coarse and infertile soils (Groves, 1994), and are adapted to live on sandy soils with limited soil moisture.

Australia's National Vegetation Information System defines five categories of shrub growth forms (ESCAVI, 2003): shrubs, mallee, heath, chenopods or saltbush, and samphire. Shrubs, i.e. "Woody plants multi-stemmed at the base (or within 200 mm from ground level) or if single stemmed, less than 2 m" (ESCAVI, 2003, pg 87) are distinguished from mallee shrubs, which are described as multi-stemmed species from the genus *Eucalyptus* which may be up to 8 m in height, and typically occur in subhumid and semi-arid areas. The canopy of mallee channels water down the stem to the soil-root interface and to depths as great as 28 m, where it is stored for utilisation in the dry summer (Nulsen *et al*., 1986), enabling mallee to survive in water-limited environments.

Heath shrubs are sclerophyllous species (typically belonging to Epacridaceae, Myrtaceae, Fabaceae and Proteaceae), mainly occurring on nutrient-poor substrates in the south-eastern/western quarters of the continent. Chenopods or salt bush species are semi-succulent, single- or multi-stemmed members of the family Chenopodiaceae, which are drought and salt tolerant. These species are widespread

in semi-arid and arid regions mostly in southern Australia. Finally, samphire shrubs are primarily members of Tribe Salicornieae from the family Chenopodiaceae, and generally occur in environments regarded as hostile (e.g., high temperature and salinity, frost, waterlogged soils). Other dominant shrubs are members of the *Acacia* genus. For instance, *Acacia aneura* (mulga) is a key shrub species, strongly associated with regions of low moisture availability and light textured soils that have very low phosphorus content (Groves, 1994).

Modelling the distributions of shrub species

Species distribution models (SDM) are increasingly used to assess the spatial distribution of potentially suitable habitat for species, and how this may shift under different environmental conditions. These tools generally correlate species' occurrence records with environmental variables, which are frequently selected from a common set of 19 'bioclimatic' indices available in WorldClim (Hijmans *et al*., 2005), and which can be attributed to Nix (1986).

To date, relatively few SDM studies have incorporated other environmental variables such as soil properties, irradiance, topography and landuse (Table 3.1). This may partly reflect difficulties with obtaining appropriate data sets at relevant spatial scales, particularly with regards to soil variables that are related to plant functionality. However, climate variables may not be the only relevant predictors of species distributions (Chatfield *et al*., 2010; Austin & Van Niel, 2011), as plant survival and reproduction is dependent on light, temperature, nutrients, water, CO_2, as well as disturbance and biotic interactions (Guisan & Zimmermann, 2000; Austin & Van Niel, 2011). Since incorporation of physiologically-related environmental variables should lead to more robust SDMs (Williams *et al*., 2012), greater predictive

power may be achieved by expanding the set of predictors to include more than climate.

In this chapter I assessed the extent to which soil variables, in conjunction with climate, may increase the predictive power of models of the distributions of Australian shrub species. I used the species distribution model, MaxEnt, to predict the distribution of 29 shrub species, which together span the distribution of shrublands across the continent. MaxEnt enables models to be developed based on presence-only data (such as that found in the Atlas of Living Australia, which was utilised for this study). In contrast, the approach used in my previous chapter (General Linear Models) requires absence data, which were unavailable for the shrub species. I hypothesised that the inclusion of climate and soil properties as predictor variables will lead to greater predictive power of SDMs, compared with models that incorporate only climate variables.

Table 3.1 Most studies using species distribution models have relied primarily on climate variables as predictors of species distributions. This table provides some examples of studies that have incorporated other predictor variables such as soil, radiation, and topographic characteristics. Full names of predictor variables are given in Table 3.3.

Environmental predictor variables	**Taxa**	**SDM**	**Highest and lowest contributed variables**	**Reference**	**Region**
Dry-season moisture Resin phosphorus, Calcium concentration, Potassium concentration, Aluminum concentration, Iron concentration, Zinc concentration, Inorganic nitrogen concentration	550 tree species	Gaussian logistic regression	Dry-season moisture and soil phosphorus	Condit *et al*., 2013	central Panama
MAT, MTCM, MTWM, MAP, Summer precipitation, winter precipitation, index of growing season length Soil texture, Total plant-available nitrogen and phosphorus, Saturated hydraulic conductivity, Plant available water capacity	100 *Banksia* species	MaxEnt		Fitzpatrick *et al*., 2008	South-west Australia
MAP, MTCM, MTWM Solar insulation in winter & spring Slope angle related to soil depth	20 species of coastal & chaparral sage shrubs	Generalized additive (GAM), generalized linear (GLM) and classification tree models	Precipitation, temperature and topography	Franklin, 1998	North America
Elevation, Aspect, Slope, Gypsum, Lime, Available moisture, EC Clay, Gravel, Organic matter, pH	Two shrub species	MaxEnt	Lime and elevation variables contributed the highest	Hosseini *et al*., 2013	Iran
Air saturation deficit, Annual integral of root zone water deficit	33 New- Zealand tree species	GAM		Leathwick & Whitehead, 2001	New Zealand
MAT, ISO, TS, MTCM, TAR, MTDQ, MTCQ, PWQ, PCQ, pH Clay content concentration, Total organic carbon,	30 species of grasses and woody plants	MaxEnt	Temperature variables	Martinson e*t al.,* 2011	North America
Land use data Water-holding capacity, Soil texture, Percentage of clay & sand, CEC Slope, Aspect, Topographic position Minimum winter temperature, Degree-days with a 5.5°C threshold, Summer precipitation [April–September]	30 tree species	GLM	Degree-days, minimum winter temperature and slope	Meier *et al*., 2012	Europe
MTCM, MTWM, PDM, PWM Human population density Crop and pasture layers Soil type Vegetation cover	3 species	MaxEnt	Including static variable (soil) with climate improved model performance.	Stanton *et al*., 2012	North America
MAT, MAP Solar radiation Soil clay content, Soil pH	584 native & not wet plant species	Regression, GAM, and MaxEnt		Summers e*t al.*, 2012	Australia
Climate change and soil drainage	One shrub species	CLIMAX	Climate change and soil drainage	Taylor & Kumar, 2013	Australia
MAT, MDR, TS, TAR, MAP, PDM, PS, CEC, C:N ratio class topsoil, Organic carbon pool topsoil, Effective soil depth, Soil drainage class, Nitrogen % top soil, pH top soil, Soil production index, Textural class subsoil	2319 woody species	MaxEnt		Zhou *et al*., 2012	China

Methods

Species data

As discussed previously, Australia's National Vegetation Information System (NVIS, http://www.environment.gov.au/erin/nvis, ESCAVI, 2003) has classified vegetation across the continent into 23 major groups, of which six are shrublands: Acacia shrubland; low closed forests and tall closed shrublands; chenopod or samphire shrubland and forblands; mallee shrublands; heathlands; other shrublands. The most dominant endemic shrubs within each of these shrublands were identified from NVIS descriptions (Table 3.2). For the resulting 29 species, I obtained occurrence records from the Atlas of Living Australia (ALA, see http://www.ala.org.au/). I removed records that did not contain coordinates (an average of 2% of records), were collected before 1960, or that were identified by ALA as 'outlier records' given the climatic envelope of the species. This resulted in an average 3,523 (± 3,214 standard deviation) records per species.

Climate and soil data

I obtained data for 19 bioclimatic variables at a resolution of 5 km x 5 km (Table 3.3), developed for the Wallace Initiative (http://wallaceinitiative.org). These data were derived from monthly precipitation and temperature values (covering the time period 1976 - 2005) obtained from the Australia Water Availability Project (AWAP, Raupach *et al*., 2009, Raupach *et al*., 2012; http://www.bom.gov.au/jsp/awap/). They were converted to the bioclimatic variables using the "climates" package (VanDerWal *et al.,* 2011) in R (http://www.r-project.org/).

Table 3.2 Dominant Australian shrub species included in this study.

Acacia	Chenopods	Heathlands	Mallee	Tall closed	Other
Acacia aneura	*Atriplex angulata*	*Epacris impressa*	*Eucalyptus diversifolia*	*Allocasuarina campestris*	*Atalaya hemiglauca*
A. sclerosperma	*A. eardleyae*		*E. dumosa*	*Leptospermum continental*	*Eremophila freelingii*
A. tetragonophylla	*A. holocarpa*		*E. gracilis*	*L. glaucescens*	*Ozothamnus turbinatus*
A. victoriae	*A. nummularia*		*E. incrassata*	*L. laevigatum*	
	A. vesicaria		*E. oleosa*	*L. lanigerum*	
	Maireana aphylla		*E. socialis*	*L. scoparium*	
				Melaleuca ericifolia	
				M. squamea	
				M. squarrosa	

Table 3.3 19 bioclimatic variables assessed for inclusion in models of shrub distributions.

Abbreviation	Climate Variable
MAT	Annual Mean Temperature
MDR	Mean Diurnal Range (Mean of monthly (max temp - min temp))
ISO	Isothermality (MDR/MAT) (* 100)
TS	Temperature Seasonality (standard deviation *100)
MTWA	Maximum Temperature of Warmest Month
MTCO	Minimum Temperature of Coldest Month
TAR	Temperature Annual Range (MTWA-MTCO)
MTWetQ	Mean Temperature of Wettest Quarter
MTDryQ	Mean Temperature of Driest Quarter
MTWQ	Mean Temperature of Warmest Quarter
MTCQ	Mean Temperature of Coldest Quarter
MAP	Mean Annual Precipitation
PWM	Precipitation of Wettest Month
PDM	Precipitation of Driest Month
PS	Precipitation Seasonality (Coefficient of Variation)
PWetQ	Precipitation of Wettest Quarter
PDryQ	Precipitation of Driest Quarter
PWQ	Precipitation of Warmest Quarter
PCQ	Precipitation of Coldest Quarter

Soil data

I identified 10 soil variables that reflect physical and chemical properties that influence soil functionality (Sauer *et al*., 2006; Fisher *et al*., 2011; Meier *et al*., 2012), and for which I could obtain data. Four variables were downloaded from the Australian Soil Resource Information System (ASRIS, 2011) at a resolution of ~ 1 km. These were clay content percentage [Clay]; bulk density [BD] which reflects soil porosity; pH $CaCl_2$ [pH] which reflects soil salinity; and soil water capacity [PWAC]. The first three relate to soil characteristics from a depth of 0 – 30 cm while the fourth is from 0 – 100 cm.

Six additional variables were obtained from the Global Soil Dataset for Earth System Modelling (GSD; http://globalchange.bnu.edu.cn/research/soilw), at a resolution of ~ 1 km: organic carbon [OC]; total nitrogen [TN]; the amount of phosphorus using the Bray1 method [P]; electrical conductivity [EC]; cation exchange capacity [CEC] and base saturation [BS]. The GSD provides data for each variable at eight depths through the soil profile (4.5, 9.1, 16.6, 28.9, 49.3, 82.9, 138.3, 229.6 cm). For consistency with ASRIS data, I calculated the average of the first four depths (i.e. to ~ 30 cm), as most nutrients are concentrated in topsoil to a depth of ~ 20 cm (Tyler, 1996; Jobbágy & Jackson, 2001). Using ArcGIS (ESRI Inc., 2010) I extracted soil data from GSD to match the spatial extent of the ASRIS data. All soil data were then aggregated to a resolution of ~ 5 km, by calculating the mean of the underlying grid cells, thereby matching the resolution of the climate data.

Selection of predictor variables

The incorporation of physiologically-related environmental variables should lead to more robust model performance (Williams *et al.,* 2012). Hence, I initially considered

19 climate and 10 soil variables known to influence the distribution of shrubs, for inclusion in the species distribution model, MaxEnt (version 3.3.3k; Phillips *et al*., 2004, 2006). The use of a large number of variables can reduce MaxEnt performance and cause over-fitting of the model prediction (Elith *et al*., 2010; Williams *et al*., 2012; Zhou *et al*., 2012). Therefore, I assessed correlations among the variables and excluded those with a Pearson's correlation coefficient > 0.85. This reduced the number of climate variables to a set of five: MAT, MTWA, MAP, PWQ, and PCQ, which reflect annual and seasonal temperature and precipitation variables.

Only two soil variables had a correlation coefficient > 0.85 (BS and EC). Hence, to further reduce the set of predictors, I ran MaxEnt (version 3.3.3k; Phillips *et al*., 2004, 2006) for all 29 shrub species using nine soil variables (i.e. excluding BS), to investigate the relative contribution of each variable to the models. Model settings were similar to the final settings described in the following section. Four variables that frequently contributed < 5% to the models were identified and excluded from the final models. The remaining variables used in the models were: pH, Clay, BD, EC, and OC. Combined, these reflect physical and chemical soil characteristics.

Generating MaxEnt models of shrub species' distributions

Using the approach described below, three sets of models were calibrated for each species. Models referred to as V_{C+S} were calibrated with both climate and soil variables; those referred to as V_C were calibrated with only climate variables while V_S models used only soil variables.

MaxEnt is a presence only modelling approach that produces a continuous probability field that can be interpreted as a relative index of environmental suitability.

Higher values represent greater suitability of a region for the target species (Phillips *et al*., 2004, 2006).

In place of absence data, MaxEnt contrasts characteristics of the species' occurrences to other sample locations called background points. By default, the program selects 10,000 background locations randomly from the extent of the environmental layers. Resulting models, however, can be influenced by the number of background points (VanDerWal *et al*., 2009) and the extent of their climate space, relative to occurrence records (Elith *et al*., 2010; Merow *et al*., 2013). Hence, selection of background points can alter the gradient between observed and potential climatically suitable habitat (Chefaoui & Lobo, 2008). Because this study aimed to identify environmental conditions that defined the distribution of species, I selected background points from the occurrence records of all 29 species. This "targeted background" approach aims to balance biases between the focal species and the background records that MaxEnt requires to create the models (Warren *et al*., 2008; Merow *et al*., 2013).

Studies using MaxEnt frequently accept default values recommended by Philips *et al*., (2004, 2006). However, selection of model settings can cause substantial variation in the output (Syfert *et al*., 2013), and so should be selected to suit the specific research questions (Merow *et al*., 2013). Therefore I initially explored how different mathematical transformations of predictor variables ("features") influenced model predictions (described in Appendix 3.2). I concluded that superior models were obtained when linear, quadratic, product and threshold features were used. The results described throughout this chapter are based on models developed with these features.

The random selection of occurrence records for model training versus testing can influence the resulting prediction. To reduce this bias I used the 'cross-validation' option within MaxEnt to generated five runs each species, using a different selection of 20% of occurrence records to test each run.

Model performance

I used two approaches to assess model performance. The area under the receiver-operator curve (AUC) is the probability that randomly chosen presence locations are ranked higher than randomly chosen background points (Merow *et al*., 2013). High AUC scores indicate that the model can distinguish between presence and background points, and model performance is generally considered good when the AUC score is > 0.75 (Pearce & Ferrier, 2000; Elith *et al*., 2006). I assessed the maximum AUC_{Test} value, which is based on the model with the highest AUC value for test data that is excluded from model calibration: this approach generally does not result in over-fitting problems that can occur when using the AUC of training data to select models (Warren & Seiferi, 2011). I also calculated the sample-size corrected Akaike Information Criteria (AIC_c) (Akaike 1974; Burnham & Anderson, 2002) using ENMTools software (version 1.4.2) (Warren & Seifert, 2011). This approach accounts for model complexity: some features within MaxEnt can produce numerous suitability functions and these models are penalised more severely by AIC_c (Warren & Seifert, 2011). Currently, there is no agreed approach for evaluating model performance, hence different methods should be utilised. Although AUC is the most common measure of the performance of MaxEnt (Merow et al. 2013), AIC is suggested to be used in models that apply the cross-validation sampling process (Warren & Seifert, 2011).

I compared the predictive power (AUC and AIC_c) of the three sets of models (V_{C+S}, V_C, V_S) using one-way ANOVAs, and applied a post-hoc analysis using Fisher's least significant difference (LSD) test where group variances are assumed equal. MaxEnt suitability scores were converted to presence/absence using the maximum training sensitivity plus specificity threshold (as recommended by Liu *et al*., 2013). I then calculated pair-wise differences in the area of suitable habitat predicted by the three sets of MaxEnt models using the ArcGIS extension SDMtoolbox (Brown, 2014). Also, I calculated species richness, i.e. sum of unique species per grid cell using those binary maps.

Results

Which set of variables results in higher predictive power of MaxEnt models?

Whilst all models had AUC scores > 0.75, a one-way ANOVA indicated there were significant differences between the three sets of models ($F_{(2,86)} = 3.936$, $P = 0.023$). Post-hoc analyses found V_S models (M = 0.89, SD = 0.047) to be significantly different to the others, while there was no significant difference between V_C (M = 0.91, SD = 0.046) and V_{C+S} models (M = 0.92, SD = 0.040) (Table 3.4). In contrast, there were no significant differences in AIC_c values between the three sets of models ($F_{(2,86)} = 0.030$, $P = 0.971$) (Table 3.4).

Table 3.4 Mean AUC_{Test} (SD) and AICc (SD) scores of MaxEnt models calibrated with different sets of environmental variables. Scores were assessed with a one-way ANOVA and Fisher's post hoc LSD test, for which P values are reported.

Environmental variable set	AUC	P	AICc	P
Climate vs Soil	0.91 (0.046) 0.89 (0.047)	0.083	69,006 (74,281) 68,535 (75,691)	0.981

Climate vs Climate & Soil	0.91 (0.046) 0.92 (0.040)	0.311	69,006 (74,281) 64,643 (73,898)	0.824
Soil vs Climate & Soil	0.89 (0.047) 0.92 (0.040)	0.007	68,535 (75,691) 64,643 (73,898)	0.843

Visual inspection of maps generated by MaxEnt also indicated that V_{C+S} and V_C models resulted in more realistic predictions of potential climatically suitable habitat than those calibrated with only soil variables (Figure 3.1). The size of suitable habitat predicted by V_{C+S} models ranged from 47,220 km² (*Leptospermum glaucescens*) to 3,767,910 km² (*Atalaya hemiglauca*). V_C models predicted habitats to range from 56,280 km² (*L. glaucescens*) to 3,995,850 km² (*A. hemiglauca*) (Table 3.6), hence, V_S predictions tended to cover a smaller spatial extent and have greater fragmentation of suitable habitat. Maps from V_{C+S} and V_C models were similar for most species. Exceptions were: *Acacia tetragonophylla, A. victoriae, Atriplex angulate* (Figure 3.1F and H), *A. eardleyae, Eremophila freelingii, Eucalyptus socialies,* and *Maireana aphylla*.

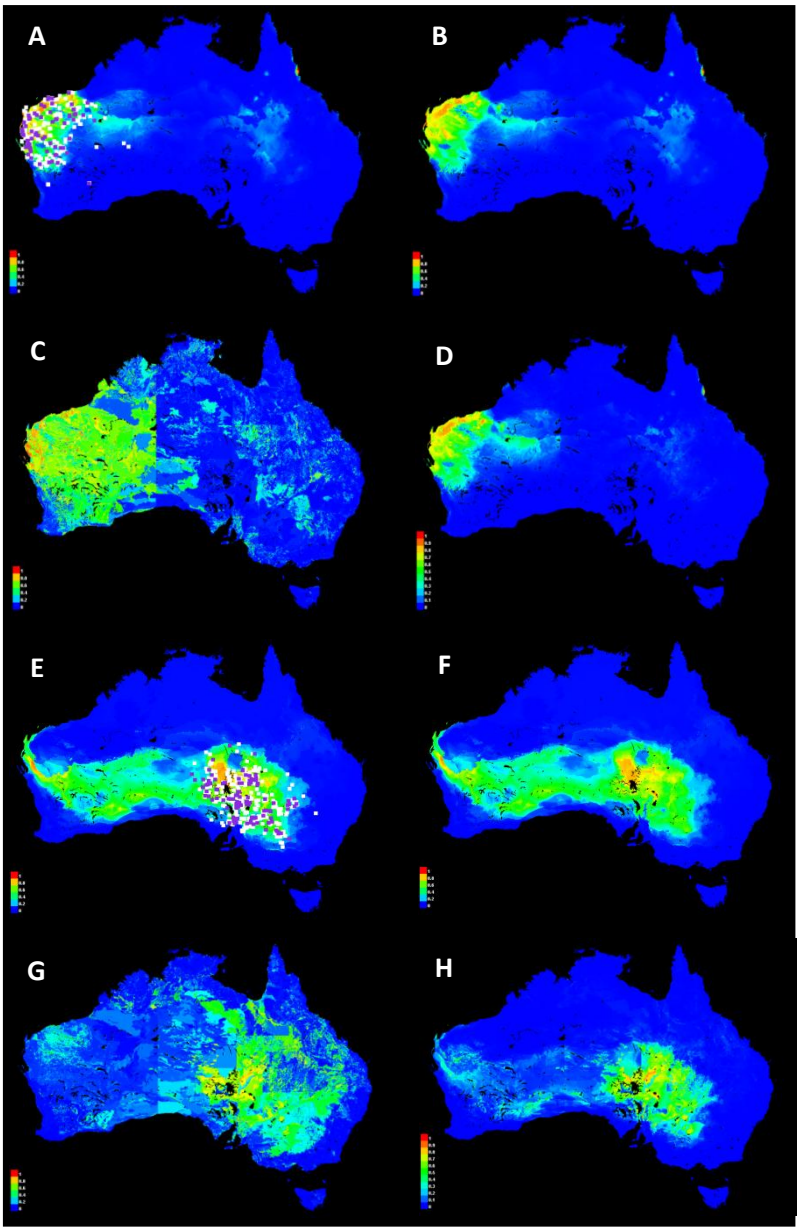


Figure 3.1 MaxEnt predictions of potential suitable habitat for *Acacia sclerosperma* (A-D) and *Atriplex angulata* (E-H) modelled with different sets of environmental conditions. Warmer colours (red) show areas predicted to have higher suitability. Bright blue represents unsuitable areas. (A, E) Indicates occurrence records (white dots show the presence locations used for training, while violet dots show test locations). Remaining maps show suitable habitat derived from models calibrated with (B, F) climate variables only, (C, G) soil variables only and (D, H) climate and soil variables.

Table 3.5 Comparison of potential size of suitable habitat predicted by MaxEnt when calibrated with different sets of predictor variables. First column represents predicted size based on models calibrated with only climate variables (V_C) while the remaining two columns show relative additional area (Expansion) or loss (Contraction) of the climate variables model (V_c) when predicted by models calibrated with climate and soil variables (V_{C+S}).

Species	Suitable habitat V_C (Km²)	Expansion V_{C+S} (Km²)	Contraction V_{C+S} (Km²)
Acacia aneura	3,638,250	168,398	109,939
A. sclerosperma	970,350	523,417	110,722
A. tetragonophylla	2,954,730	266,219	64,803
A. victoriae	3,795,990	222,737	419,010
Allocasuarina campestris	406,680	56,383	240,990
Atalaya hemiglauca	3,995,850	142,026	170,683
Atriplex angulata	1,301,220	212,542	509,284
A. eardleyae	131,220	348,313	590,205
A. holocarpa	1,107,120	66,728	271,271
A. nummularia	2,116,380	48,204	525,041
A. vesicaria	1,919,400	150,686	510,968
Epacris impressa	338,670	8,751	8,360
Eremophila freelingii	1,529,610	158,595	327,083
Eucalyptus diversifolia	164,340	2,676	66,607
E. Dumosa	648,240	28,778	97,972
E. gracilis	684,360	35,724	111,383
E. incrassate	421,770	73,704	54,669
E. oleosa	529,380	163,226	41,408
E. socialis	1,220,940	710,459	331,293
Leptospermum continental	363,030	82,305	5,653
L. glaucescens	56,280	4,330	5,593
L. laevigatum	416,700	96,618	54,369
L. lanigerum	266,430	15,607	8,781
L. scoparium	94,020	25,260	601
Maireana aphylla	1,885,710	289,585	815,257
Melaleuca ericifolia	185,880	27,575	14,464
M. squamea	123,450	35,063	42,911
M. squarrosa	144930	15,757	4,481
Ozothamnus turbinatus	57,390	30,402	55,150

At a continental scale patterns of species richness differed depending on which set of variables were used for model calibration (Figure 3.2). Highest richness was achieved by V_S models, which predicted a total area of ~36,600 km^2 to contain 11 – 13 species (Table 3.5). However, this map also showed substantial spatial discontinuities (i.e. smaller contiguous areas of high richness). In contrast, V_{C+S} predicted only 3,750 km^2 to contain 11 – 13 species. Although broadly similar patterns were predicted by both V_C and V_{C+S} models, richness of shrub species was

higher based on VC models, particularly in central Western Australia (see region approximately 118 - 129º E, 25 – 28º S).

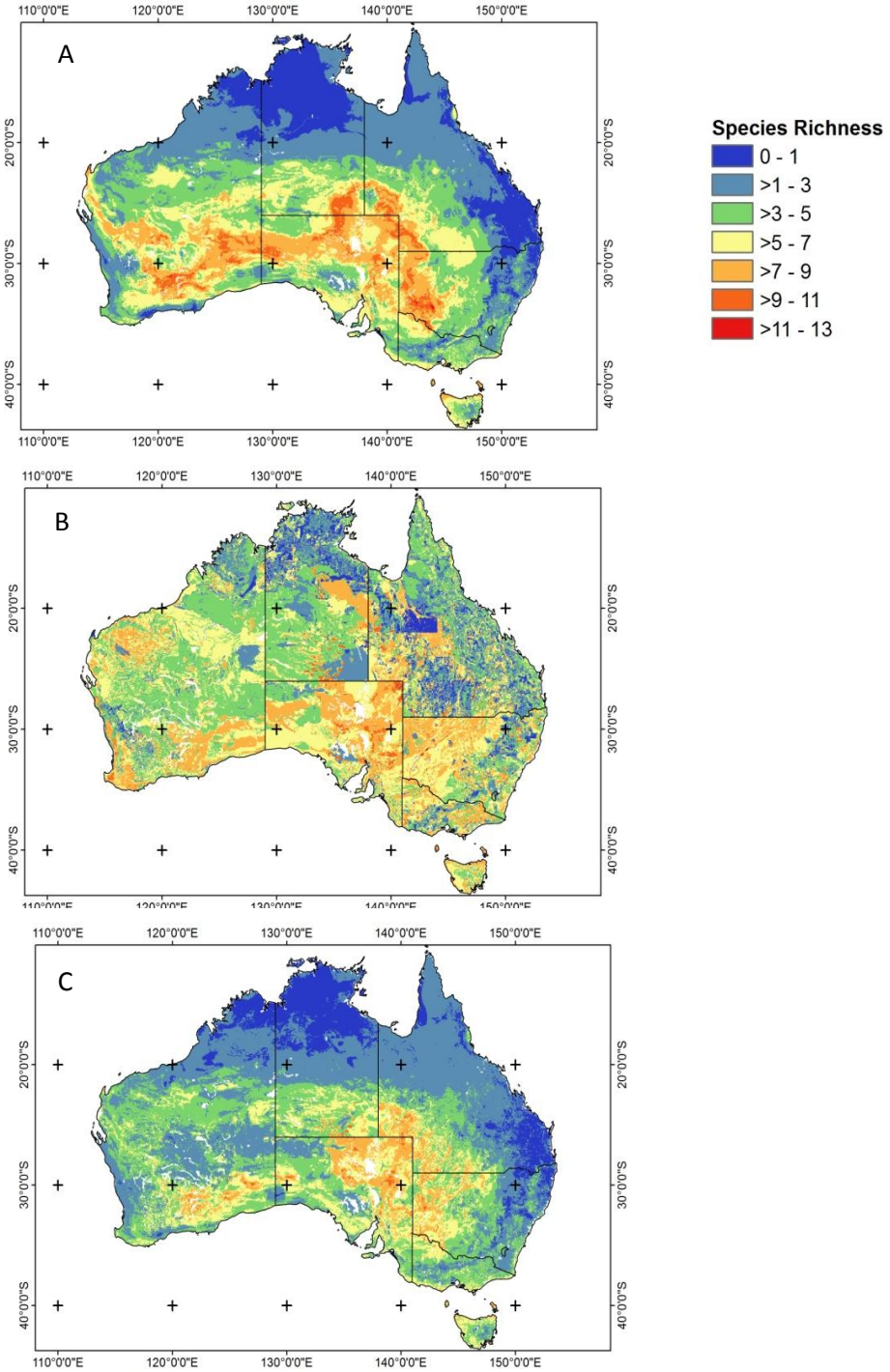


Figure 3.2 Richness maps of 29 shrub species based on models predicted by MaxEnt calibrated with (A) climate variables only, (B) soil variables only and (C) climate and soil variables. Warmer colours show areas with higher predicted richness.

Contribution of climate and soil variables to models of shrub distributions

For all 29 shrub species, climate variables contributed more to calibration of V_{C+S} models than soil variables (Table 3.6). In total, contribution of climate variables exceeded 80% for 21 species (maximum 97.9%, *L. scoparium*) and was < 60% for only one species (52.3%, *Maireana aphylla*). Of the individual climate variables, MTWA and MAP contributed the highest percentage to models for eight and seven species, respectively, while PCQ contributed the most for two species. Of the soil variables, clay contributed > 20% to models for three species (*A. angulata*, *A. nummularia*, *M. aphylla*) while pH did so for only one species (*Allocasuarina campestris*). Neither EC nor OC contributed > 10% to the models of any species.

Table 3.6 Percent contribution of the five climate variables and five soil variables used to calibrate MaxEnt models for 29 shrub species. Full names of variables are given in Table 3.3. For each species, the variable contributing the most to the model is in bold.

Species	MTWA	MAT	MAP	PWQ	PCQ	BD	Clay	EC	OC	pH
Acacia aneura	**40.3**	20	9.7	1.7	18.3	0.9	5.9	0.2	0.5	2.5
A. sclerosperma	4.5	**58.8**	7.5	0.9	20.9	1.3	5	0.1	0.1	1
A. tetragonophylla	**37.4**	19.4	16.8	4.1	4.1	2.1	4	2.5	0.8	8.8
A. victoriae	**46.6**	2.2	0.8	13.9	2.7	15	1	9.6	1.6	6.6
Allocasuarina campestris	9.8	14.1	11.4	18	11.7	3.6	8.2	0.4	0.6	**22.2**
Atalaya hemiglauca	8.1	**45.8**	7	27.9	7.3	0.5	0.9	0.5	0.5	1.3
Atriplex angulata	13.6	1.2	**34.5**	9.1	10.5	1.1	22.7	0.5	5.2	1.6
A. eardleyae	26.6	2.3	10.3	3	**26.8**	2.8	19	1.9	2.5	4.8
A. holocarpa	29.3	10.4	**35.8**	6.4	2.9	2.1	11.9	0.4	0.4	0.4
A. nummularia	3.8	3.7	14.2	8.1	**33.4**	1	20.1	4.3	8.8	2.6
A. vesicaria	2.7	2.1	**47.2**	14.4	17.2	1.3	7.5	4.1	0.9	2.5
Epacris impressa	10.1	**69.5**	15.7	1.5	0.2	0.3	0.2	0.9	1.1	0.5
Eremophila freelingii	**17.4**	0.6	15.2	15	16.4	12.5	0.9	7.6	0.3	14.1
Eucalyptus diversifolia	22.6	1.2	0.9	**44.9**	25.7	0.4	2.3	0.4	0.4	1.2
E. Dumosa	8	32.4	**35.6**	1.7	8.8	2.5	2.8	2.8	3	2.5
E. gracilis	17.2	14.9	20.2	**30.3**	1.6	5.8	2.4	1.6	4.8	1.2
E. incrassate	4.6	23.1	13.4	**33.4**	7.9	0.7	6.4	6.3	0.4	3.7
E. oleosa	12.5	20	7.1	**38.1**	2.9	1.6	4.9	1.7	9.1	2.1
E. socialis	20.3	16.5	**46.2**	2.6	1.2	1.7	5.7	3.5	0.9	1.6
Leptospermum continental	**33.4**	5.3	35.3	0.6	18.1	6.4	0	0.4	0.1	0.3
L. glaucescens	**72.2**	4.1	5.8	2.5	4.9	2	4.7	1.4	1.2	1.2
L. laevigatum	3.9	**29**	26.9	2.2	25.9	0.5	5.3	2.5	3.6	0.2
L. lanigerum	22.3	**58.8**	9.7	0.4	0.6	2.8	1.1	1	1.5	1.8
L. scoparium	**52.4**	40.4	0.6	3.1	1.4	0.9	0.1	0.4	0.3	0.5
Maireana aphylla	25.1	3.9	10.1	7.7	5.5	0.1	**39.3**	0.6	1.1	6.5
Melaleuca ericifolia	20.3	14.1	25.5	**27.9**	7.1	0.3	0.5	0	1.2	3
M. squamea	28.4	2	**42.8**	2.3	16.1	2.5	1.5	0.6	1.4	2.4
M. squarrosa	24.5	9	**33.2**	4.9	24.5	0.5	0.4	0	1.8	1.2
Ozothamnus turbinatus	27.7	16.2	0.8	0.4	**34.3**	4.9	3.9	7.8	2.4	1.6

For V_C models MTWA and MAP were the most important variables for nine and seven species respectively, while PCQ contributed the most to models for four species (Appendix 3.1 Table A3.1.1). When calibrated with soil variables only (V_S), Clay and pH were the most important for six and five species, respectively, while OC contributed > 70% to the model for *Epacris impressa.* BD did not contribute substantially to any model (Appendix 3.1 Table A3.1.2).

Discussion

Species distribution models are frequently calibrated with only climate variables. But for plant species, does the addition of soil properties as predictors improve model performance? For 29 Australian shrub species, I found that a) *on average* models calibrated with both climate and soil variables (V_{C+S} models) did not perform significantly better than those calibrated solely with climate variables (V_C) (Table 3.4); b) models calibrated with only soil variables (V_S) had significantly lower AUC scores and frequently resulted in unrealistic prediction (which unsurprising given the coarse spatial resolution of this study; c) for 27 species, a precipitation or temperature variable was the most important contributor to V_{C+S} models (Table 3.6); and d) for some species the inclusion of soil properties along with climate variables resulted in predictions of current suitable habitat that more closely approximately the realized distribution, compared to models calibrated with climate variables only. As a consequence, at a regional scale species richness patterns were similar regardless of whether they were derived from V_{C+S} or V_C models, but at finer spatial scales these patterns may diverge substantially (Figure 3.2).

While species richness is a convenient way to describe or compare the biodiversity of different areas, there are concerns that estimates of species richness

using combined or so-called stacked-SDMs may be over-estimated (Guisan & Rahbek, 2011; Hortal et al., 2012). It has been suggested that the bias may be corrected by linking stacked SDMs to macroecological models: however, early comparisons indicate that this approach has not yielded much improvement in reducing overestimates of richness (Calabrese, *et al.* 2014). The issue of how best to estimate richness from stacked SDMs will undoubtedly be a key area of research over the next few years.

Climate and soil as predictors of species distributions

To date, few studies have explicitly assessed whether the inclusion of soil variables increases predictive power of SDMs, although several studies have included these variables in model calibration (see Table 3.1). By themselves the soil variables included in this study did not result in biologically realistic maps of the realised distribution of the shrub species, with predictions frequently being fragmented or having abrupt boundaries (Figure 3.2C, G).

V_{C+S} models suggested that the distributions of *Acacia* and *Leptospermum* species are strongly limited by temperature, while moisture variables are key determinants for others, such as the saltbushes (*Atriplex* spp.) which inhabit arid and semi-arid regions of Australia. This indicates that at the scale of this study climate plays a greater role in defining the distribution of these shrub species than soil characteristics. Similarly, Martinson *et al*., (2011) used MaxEnt to model the distributions of 30 species at 10 km x 10 km spatial resolution, including shrubs, in arid areas of North America, using climate and soil variables. Temperature variables, mainly Annual Mean Temperature, contributed the most to models, with none of the three soil variables being the most important for any species. Soil variables, such as

CEC (cation exchange capacity) and texture, were also found to contribute little to models of the distributions of European trees (Meier *et al*., 2012).

However, the V_C model over-predicted the realized distribution of some shrub species, whereas the V_{C+S} model provided a closer approximation (e.g. *Atriplex angulata* Figure 3.2F vs H). For these species, although climate variables contributed the most to the models, soil variables (mostly clay) were the second or third highest contributing variable. Indeed, heavy clay soils are known to be favoured by some *Atriplex* spp. such as *A. angulata*, *A. eardleyae* and *A. nummularia* (Cunningham *et al*., 1992). Similarly, *Allocasuarina campestris* occurs in gravely laterite soil which contains high quantities of aluminium and iron compounds and is highly affected by pH (Osuolale *et al*., 2012). For this species, pH was the highest contributing variable in the V_{C+S} model.

Caveats

The accuracy of species distribution models is influenced by a number of factors, including a) accuracy and availability of environmental data used to calibrate the model, b) biases in occurrence records and c) selection of model parameters (Beaumont *et al*., 2008).

Environmental data frequently has to be manipulated in order to be useable in SDMs, and this often involves converting the data to a different resolution. Aggregation or interpolation to a coarser or finer resolution, respectively, can alter the accuracy of data. In order to match the spatial resolution of the climate data, both soil datasets used in this study, ASRIS (Australian) and GSD (global), were aggregated from 1 km to 5 km. In some areas there are obvious disparities in the values of soil variables along state borders, potentially a result of different state agencies using

different classification methods. These inconsistencies may have been magnified when I aggregated soil data to a coarser resolution, and are apparent in the distribution maps for some species. For example, the maps from V_S models for *Acacia sclerosperma* (Figure 3.1C) and *Atriplex angulata* shows clear patchiness or sharp boundaries at state borders, and even within states. Similarly, the species richness map calculated from V_S models (Figure 3.2B) shows abrupt changes along some state borders (e.g., see Queensland and NSW border). It is worth mentioning the recently released Soil and Landscape Grid of Australia dataset (http://www.clw.csiro.au/aclep/soilandlandscapegrid/ProductDetails-SoilAttributes.html), which contains 14 gridded physical and chemical soil and landscape attributes at high resolution (~ 90 m) and with estimates of reliability. The dataset is promising as it provides accurate, comprehensive nation-wide soil and landscape data and will be a useful option to explore in future.

Similar interpolation and accuracy issues may also occur with climate data. For instance, although new high-resolution climate data (1 km) have recently become available (e.g. e-MAST data products; http://www.emast.org.au/), precipitation-related variables may suffer accuracy problems when interpolating to areas with complex topography (ANUCLIM v 6.1 Hutchinson & Xu, 2010).

It is also likely that patterns in climate and soil do not vary at the same spatial scale. For example, different mallee species (*Eucalyptus*) in Western Australia broadly occupy the same hot, dry climatic conditions. Within these climate zones, soil varies at a finer scale, and as such, *Eucalyptus diversifolia* is restricted to the limestone coastal dunes and cliffs while *E. incrassata* occurs on sand plains such as in South Australia (Specht, 1966). Therefore, trade-offs will occur when selecting the

most appropriate spatial scale and environmental variables for studies utilising models (Guisan & Zimmermann, 2000).

An additional hindrance for some studies may be that predictions of a variable under alternative scenarios, such as climate change, may be required (e.g. see Chapter 4 where potential climate impacts are analysed). However, these may be difficult to obtain. For instance, while scenarios for the standard 19 bioclimatic variables included in WorldClim (Hijmans *et al*., 2005) and similar products are readily available, they may not be for less-frequently used variables. Models developed in Chapter 2 used a number of moisture-related indices, such as the Cramer-Prentice α index of plant-available moisture and soil moisture at different depths. Future scenarios of these variables were not available, precluding their use in this chapter. As such, although I found little difference between V_{C+S} and V_C models, an alternate set of variables that included soil moisture may have led to different conclusions.

Accuracy of occurrence records and sampling biases associated with them may affect SDM performance (Hefley *et al*., 2013). To reduce the likelihood of errors I applied filters to the ALA records to exclude outliers, while to reduce sampling bias duplicate records in grid cells were removed. However, I point out that sampling across arid and semi-arid zones of Australia has typically been poor and very clumped in space and time (Haque *et al*., in review). Hence, although I selected dominant, easily-identified species for this study, it is not possible to determine whether their entire realized distribution has been sampled.

Conclusion

This chapter demonstrates that for some shrub species, the inclusion of soil properties may result in more realistic predictions of the distribution of current potential habitat. Problems occur, however, with the use of soil data, due to historic inconsistencies with the measurement of soil properties across different management regions (such as State boundaries). I also demonstrate how maps of species distributions can diverge substantially depending on whether models were calibrated with only climate variables or with climate and soil variables – even though AUC scores were very similar. Of interest, then, is just how far model predictions may continue to diverge when applied to scenarios of future climate. This problem will be explored in Chapter 4.

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Appendix 3.1

Table A3.1.1 Percent contribution of the five soil properties predictor variables used in developing MaxEnt models of the distributions of 29 shrub species. Variables are: Maximum Temperature of Warmest Month (MTWA); Mean Annual Temperature (MAT); Mean annual Precipitation (MAP); Precipitation of Warmest Quarter (PWQ); and Precipitation of Coldest Quarter (PCQ).

Species name	MTWA	MAT	MAP	PWQ	PDQ
Acacia aneura	43.5	22.8	10.6	3	20.2
A. sclerosperma	4.8	61.6	8.9	1.3	23.3
A. tetragonophylla	45.1	20.4	22	6	6.5
A. victoriae	65.8	3.1	1.8	21.9	7.4
Allocasuarina campestris	24	12.5	18.1	22.7	22.7
Atalaya hemiglauca	9.1	46.5	8.5	27.7	8.2
Atriplex angulata	24.9	2	41.2	19.2	12.7
A. eardleyae	36.3	3.8	13.4	7.1	39.4
A. holocarpa	35.8	11.4	39.9	8.9	4
A. nummularia	7.9	4.5	24.1	16	47.4
A. vesicaria	3.8	4.3	54.6	17.7	19.6
Epacris impressa	10.5	70.8	16.4	2	0.3
Eremophila freelingii	24.1	5.9	22.5	18.6	29
Eucalyptus diversifolia	23.5	1.3	1.1	47.3	26.8
E. dumosa	9.2	34.8	40.3	6.1	9.6
E. gracilis	22	14.5	26	35.4	2
E. incrassate	7.1	26.8	17	39.2	9.9
E. oleosa	17.2	25.5	11.3	43.2	2.8
E. socialis	22.4	18.8	51.6	5.4	1.8
Leptospermum continental	36.6	7.4	35.5	1.4	19.2
L. glaucescens	74.5	7.1	7.5	2.9	7.9
L. laevigatum	5.7	32.4	29.2	3.2	29.6
L. lanigerum	21.1	65.6	11.1	0.6	1.5
L. scoparium	53.3	41.2	0.6	3.3	1.6
Maireana aphylla	37.9	6.8	23.3	19.3	12.6
Melaleuca ericifolia	20.2	15.1	27.8	30.2	6.7
M. squamea	31.9	1.5	44.8	3.1	18.7
M. squarrosa	24.7	9.4	35.2	5.5	25.2
Ozothamnus turbinatus	33.7	18	2.1	0.4	45.9

Table A3.1.2 Percent contribution of the five soil predictor variables used developing MaxEnt models of the distributions of 29 shrub species. Variables are: Bulk density (BD); Clay content percentage (Clay); Cation exchange capacity (CEC); Organic carbon (OC); pH $CaCl_2$ (pH); and Electrical conductivity (EC).

Species name	BD	CLAY	ECE	OC	PH
Acacia aneura	14.3	4.7	5.1	45.1	30.7
A. sclerosperma	23.1	17.5	7.8	31.0	20.6
A. tetragonophylla	23.4	2.7	11.4	36.2	26.3
A. victoriae	25.8	10.8	28.9	26.0	8.6
Allocasuarina campestris	27.9	15.0	6.5	14.4	36.1
Atalaya hemiglauca	8.2	26.5	24.2	26.9	14.4
Atriplex angulata	6.0	45.9	8.2	24.6	15.4
A. eardleyae	12.6	32.8	2.2	27.8	24.5
A. holocarpa	7.5	34.3	3.3	26.7	28.2
A. nummularia	3.2	34.0	8.4	33.6	20.7
A. vesicaria	14.3	17.5	21.4	3.1	43.8
Epacris impressa	1.0	0.6	14.4	77.5	6.5
Eremophila freelingii	22.9	11.0	30.0	2.7	33.4
Eucalyptus diversifolia	5.0	29.7	21.1	18.5	25.6
E. Dumosa	14.6	12.8	16.7	16.1	39.8
E. gracilis	13.1	13.1	19.3	17.4	37.1
E. incrassate	10.6	22.6	34.9	11.5	20.4
E. oleosa	4.3	20.3	15.5	25.9	34.0
E. socialis	16.5	13.2	17.2	9.1	44.0
Leptospermum continental	23.0	1.1	18.9	31.4	25.7
L. glaucescens	39.2	10.0	1.5	29.4	19.8
L. laevigatum	3.5	22.7	29.2	22.7	22.0
L. lanigerum	18.8	1.2	6.7	70.9	2.5
L. scoparium	35.1	1.4	3.6	52.8	7.0
Maireana aphylla	2.6	53.5	4.7	13.3	25.9
Melaleuca ericifolia	11.7	6.9	21.0	53.0	7.4
M. squamea	16.5	5.3	2.7	40.6	34.9
M. squarrosa	12.0	3.7	8.0	57.8	18.5
Ozothamnus turbinatus	14.7	11.6	31.5	37.3	4.8

Appendix 3.2

Feature selection in MaxEnt

I initially explored how different mathematical transformations of predictor variables ("features") influenced the predictive power of MaxEnt predictions. These features are important in defining model complexity: selecting more features may result in complex non-linear response curves while fewer features may generate simpler response curves (Merow *et al*., 2013). In this study, I compared models calibrated with four feature types (all but hinge, as hinge and threshold features are well correlated, Elith *et al*., 2011) versus those calibrated with linear and quadratic features. These two sets of models are referred to as F_1 and F_2, respectively. In total, for each shrub species I calibrated six models, i.e. three sets of predictor variables (V_{C+S} [climate and soil variables]; V_C [climate variables only]; V_S [soil variables only]) * two feature groups (F_1: linear, quadratic, product and threshold; F_2: linear and quadratic).

Whilst all models had AUC scores > 0.75, on average those generated using a combination of linear, quadratic, product and threshold features (F_1) resulted in significantly higher AUC scores than those generated with linear and quadratic features (F_2), regardless of the predictor variables used ($P < 0.05$; Table A3.3). However, while mean AIC_c values were generally lower for F_1 models compared to F_2, this was not significant across the three sets of predictor variables (Table A3.4).

Table A3.2.1 Average AUC_{Test} scores for two sets of MaxEnt models generated for 29 shrub species (standard deviations in brackets), and results of one-way ANOVA (F-stat and P value). F_1, indicates linear, quadratic, product and threshold features used to calibrate models; F_2, indicates linear and quadratic features used. df = 1,56.

Environmental variable set	Mean AUC F_1	Mean AUC F_2	F-stat	P-value
Climate	0.91 (0.046)	0.87 (0.069)	5.930	0.018
Soil	0.89 (0.047)	0.82 (0.063)	19.630	0.000
Climate & Soil	0.92 (0.040)	0.89 (0.054)	5.469	0.023

Table A3.2.2 Average AIC_C scores from two sets of MaxEnt models generated for 29 shrub species (standard deviations in brackets), and results of one-way ANOVA (F-stat and P value). F_1, indicates linear, quadratic, product and threshold features used to calibrate models; F_2, indicates linear and quadratic features used. df = 1,56.

Environmental variable set	Mean AIC_c F_1	Mean AIC_c F_2	F-stat	P-value
Climate	69,006 (74,281)	71,258 (75,511)	0.013	0.909
Soil	64,643 (73,898)	66,967 (75,400)	0.037	0.849
Climate & Soil	68,535 (75,691)	72,386 (77,615)	0.014	0.906

Chapter 4

Potential impacts of climate change on the distributions of Australian shrubs

Chapter 4: Potential impacts of climate change on the distributions of Australian shrubs

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Introduction

Globally, mean annual temperature has risen 0.85 ºC (0.65 to 1.06 ºC) since 1880 (IPCC, 2013). Precipitation patterns have shifted, however while there is considerable evidence of increased precipitation across Northern Hemisphere mid-latitude land masses, trends elsewhere are not well understood (IPCC, 2013).

Similar to global trends, mean annual temperature in Australia has increased, particularly over the period 1970 – 2010 (CSIRO & BOM, 2011). While annual precipitation has increased in the north-west of the continent (IPCC, 2013), the eastern and south-eastern regions have experienced prolonged drought (Tiver *et al*., 2008; CSIRO & BoM, 2011), with rainfall also declining substantially in south-western Western Australia (SoE 2011).

Although there is international recognition that actions need to be undertaken to ensure that the magnitude of climate change does not exceed 2 ºC (Meinshausen *et al*., 2009), it is likely that global mean temperature will increase by 1.0 to 3.7 ºC by the late 21st century, relative to 1986 – 2005 (IPCC, 2013). By 2030, median warming across Australia is projected to be 0.7 – 1.2 ºC (relative to 1980 – 1999), with greater warming occurring inland than along coastal regions (CSIRO & BoM, 2007). By 2050, best estimates suggest an increase of 1.2 – 2.2 ºC, rising to 2.2 – 3.4 ºC by 2070 (CSIRO & BoM, 2007). Projections of precipitation vary spatially and

seasonally, with considerable uncertainty in many regions. By 2030, estimates of annual changes range from -15% to +10% in northern regions and -10% to no change in the south. By 2070, estimates for central, eastern and northern areas range from -30% to +20%, while the southwest may be faced with changes ranging from -30% to +5% (CSIRO and BoM, 2007). The dry end of these scenarios would have severe impacts on all natural and human-managed systems (Reisinger *et al*., 2014). Multi-model comparisons indicate that under the most severe emission scenario, representative concentration pathway (RCP8.5) assumes that the concentration of greenhouse gas emissions (GHG) will significantly increase over time, resulting in a radiative forcing of 8.5 W m^2 by 2100 (Riahi *et al*., 2011) (RCP8.5) there is substantial agreement on the direction and magnitude of precipitation changes in several regions of Australia: substantial drying in the south-western corner of Western Australia, slight drying along south eastern Queensland, and higher precipitation in north-eastern Western Australia and north-western Northern Territory (Reisinger *et al*., 2014). In contrast, projections are divergent in north-east Queensland, north-eastern New South Wales and much of northern-central region of Australia (Reisinger *et al*., 2014).

As with taxa elsewhere, anthropogenic climate change has already had a discernible impact on Australia's terrestrial and marine fauna and flora (Cabrelli *et al*., 2015). These responses include shifts in the distributions of species, changes to the timing of life cycle events, morphological and behavioural changes, as well as genetic adaptations (see reviews by Cabrelli *et al*., 2015 and Beaumont *et al*., 2015).

Distribution shifts have also been reported for Australian shrub species. For example, recent encroachment of *Leptospermum scoparium* in southern Australia is suggested to have occurred due to availability of soil moisture during wet periods,

which enable shrub seedlings to compete with grasses (Price & Morgan, 2008). In contrast, substantial mortality of *Eucalyptus* species across the semi-arid savanna of north and central Queensland has been reported because of drought (Fensham & Fairfax, 2003; Fensham *et al*., 2005). Similarly, growth of the shrub species *Eremophila sturtii* and *Dodonaea viscosa* subsp. *angustissima* have been suppressed in semi-arid eastern Australia due to severe drought conditions (Norman *et al*., 2014).

The goal of this chapter is to explore how climate change may impact the distributions of Australian shrub species modelled in Chapter 3. In doing so, I continue exploring how variation in the output of species distribution models (SDM) is driven by the choice of predictor variables. Although soil properties perform an important role in limiting the growth and distribution of shrub species, changes to these variables generally occur over geological time (Stanton *et al*., 2012). This contrasts to the rate at which climate is currently changing and is projected to change over coming decades. As discussed by Stanton *et al*. (2012) it is unclear whether static variables (i.e. soil properties) should be incorporated with dynamic variables (i.e. climate scenarios) in SDMs. This is because models calibrated with static and dynamic variables may fit current distributions well but may be ill-suited to projecting responses to future climate change because climate variables are given less weight in the model. In contrast, excluding static variables may result in models that are particularly sensitive to climate change. A useful comparison of these alternatives would be to test the ability of models to predict recent range shifts by calibrating them with data from the mid-20th century. Unfortunately, there are insufficient data to do so for Australian shrub species. Hence, I compare how the spatial extent of suitable habitat may diverge under future climate scenarios, when

SDMs are calibrated with both climate and soil variables (referred to as V_{C+S} models) versus models calibrated with only climate variables (V_C).

The objectives of this chapter therefore, were to assess:

1. How may climate change alter the spatial distribution of suitable habitat for 29 Australian shrub species?
2. To what extent may projections of suitable habitat diverge when SDMs calibrated with climate and soil variables versus only climate variables are projected onto scenarios of future climate change?

Methods

Climate change scenarios

In Chapter 3 I developed models of the distributions of 29 Australian shrub species, based on five climate variables: Mean annual temperature [MAT]; Mean temperature of warmest month [MTWA]; Mean annual precipitation [MAP]; Precipitation of warmest quarter [WPQ], and Precipitation of coldest quarter [CPQ]. These variables were derived from data developed for the Australian Water Availability Project (AWAP; http://www.bom.gov.au/jsp/awap/, Raupach *et al*., 2009; Raupach *et al*., 2012), and were at a resolution of ~ 5 km.

For the current chapter, I downloaded two climate scenarios available from the Wallace initiative (http://climascope.wwfus.org). This initiative developed downscaled scenarios of future climate based on projections from 18 global climate models (GCM). For each GCM, anomalies were downscaled to 5 km via a cubic spline interpolation (VanDerWal *et al*., 2011) and added to AWAP baseline data (1976 to 2005). The standard 19 bioclimatic variables (sensu Nix, 1986) were then calculated.

From the 18 GCM projections included in climascope, I selected simulations from two models, under a single RCP (RCP8.5). Of the four RCPs for which climate simulations are readily available, RCP8.5 assumes the highest increase in GHG emissions, and is also the pathway that is closest to the trajectory currently being followed (Peters *et al*., 2013).

I selected scenarios projected by MIROC 3.2 medres (http:// www-pcmdi.llnl.gov/ipcc/model_documentation/MIROC3.2_hires.pdf) and IPSL–CM4 (http://www.ipcc-data.org/ar4/model-IPSL-CM4-change.html), specifically because multi-model comparisons of skill-score (i.e. how well a model captures the observed probability density function for temperature and precipitation variables, e.g. Evans *et al*., (2012) and Perkins *et al*., (2008)) found these models to have high performance and independency. Note, however, that there is little agreement as to the best method of scoring GCM performance, and models may perform well for some variables, across some temporal scales, and less well for others (Beaumont *et al*., 2008).

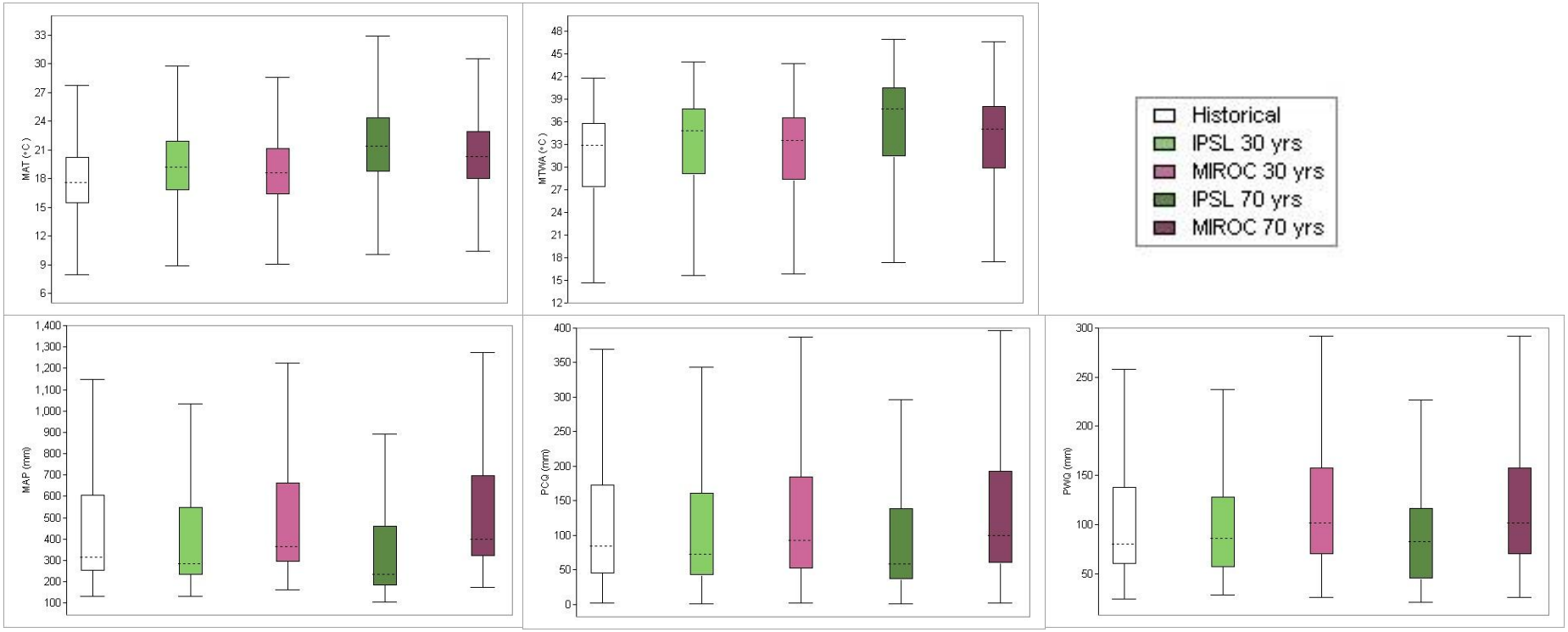
Although GCMs unanimously project temperature increases throughout this century, there is substantial uncertainty in the direction and magnitude of precipitation changes (IPCC, 2013). From a conservation or land management perspective it may be more informative to use scenarios that represent different, but plausible, futures. To summarise, for the decades centred on 2035 and 2075, IPSL projects MAT to increase by an average 2 ºC and 5 ºC, respectively, while MIROC projects a rise of 1 and 3 ºC (Appendix 4, Figure 4.1). Averaged across the continent IPSL projects a decline in MAP by 50 mm and 250 mm by 2035 and 2075, respectively, whilst MIROC projects an increase of ~75 mm (2035) and 125 mm

(2075) (Figure 4.1). Hence, IPSL represents a hot, dry future in contrast to MIROCs warm, wet future. These scenarios will be referred to as hot/dry and warm/wet.

Static soil variables

I projected two sets of SDMs developed in Chapter 3 onto the climate scenarios, enabling me to examine the extent to which future suitable habitat may vary, depending on selection of predictor variables. These were models calibrated with the five climate variables only (V_C: Mean annual temperature [MAT]; Mean temperature of warmest month [MTWA]; Mean annual precipitation [MAP]; Precipitation of warmest quarter [WPQ], and Precipitation of coldest quarter [CPQ]) and those calibrated with the five climate variables in addition to five soil variables (V_{C+S}: Clay content percentage [Clay]; bulk density [BD] which reflects soil porosity; pH $CaCl_2$ [pH] which reflects soil salinity; Electrical conductivity [ECE]; and Organic carbon [OC]. Combined, the soil variables reflect physical and chemical soil characteristics to a depth of ~ 30 cm, and were at a resolution of 5 km (see Chapter 3 for a description of how these variables were developed). Unlike temperature and precipitation, the soil variables are static, remaining constant with time.

Figure 4.1 Box plots of baseline and future climate scenarios across Australia, for the five climate variables used to model species distributions (Mean annual temperature [MAT]; Mean temperature of warmest month [MTWA]; Mean annual precipitation [MAP]; Precipitation of warmest quarter [WPQ], and Precipitation of coldest quarter [CPQ]). Baseline climate was averaged over the period 1976 – 2005 (white box). Future climate scenarios were based on simulations from two global climate models downscaled to 5 km. IPSL (IPSL-CM4, green box) simulates a hot/dry future while MIROC (CCSR-MIROC medres, pink box) simulates a warm/wet future. Scenarios were for the 20-year period centred on 2035 (light colour) and 2075 (darker colour). Within each box, dashed lines represent the median while the boxes represent the interquartile range.



Generating scenarios of the future distribution of suitable habitat

Previously, I generated models of suitable habitat for 29 Australian shrub species using Maximum Entropy Species Distribution Modelling Software (MaxEnt version 3.3.3k; Phillips *et al*., 2004, 2006) (Chapter 3). To summarise, these models (V_C and V_{C+S}) used four feature types (hinge excluded), with five runs of each model generated using a different selection of 20% of occurrence records. In the current chapter, I have projected both sets of models onto four scenarios of future climate (i.e. from two GCMs and for two time periods, 2035 and 2075).

MaxEnt projections were converted to binary maps representing suitable or unsuitable habitat for the species in question, using the ArcGIS (ESRI, 2010) extension, SDMtoolBox (Brown, 2014), and the R software v 2.2-1 (R Core Team 2013) with the 'raster' package (Hijmans, 2015). The threshold for conversion to binary data was based on the value that maximised training sensitivity plus specificity, as recommended by Liu *et al*. (2013). From the binary maps I calculated a) size (km^2) of suitable habitat under each climate scenario (current and future) and area of contraction (loss of currently suitable habitat) and expansion (new areas projected as suitable in the future), b) species richness, i.e. sum of unique species per grid cell and c) differences between MaxEnt projections calibrated from V_{C+S} models vs V_C models, for each GCM and time period.

Results

How may climate change alter the distribution of suitable habitat for Australian shrub species?

For MaxEnt models calibrated with only climate variables (V_C) suitable habitat for 24 of 29 species was projected to decline in size under the warm/wet scenario for 2035

(Table 4.1). By 2075, contractions were projected for 22 species. Under the hot, dry scenario, suitable habitat for 25 and 26 species was projected to decline by 2035 and 2075, respectively. On average, smaller changes in the size of suitable habitat were projected for the warm/wet scenario (2035 -9 ± 30%; 2075 -25 ± 71%) compared with hot/dry (2035 -21 ± 28%; 2075 -42 ± 61% Table 4.1).

Suitable habitat for Chenopods (e.g. *Atriplex eardleyae, A. nummalaria*, Figure 4.2) and *Eucalyptus* species was projected to contract from northern regions and to a greater extent under the hot/dry scenario compared to the warm/wet future. In contrast, suitable habitat for *Acacia tetragonophylla* and *A. sclerosperma* increased and shifted eastward under the hot/dry scenario, while new regions in western Western Australia were projected to become suitable for *Maireana aphylla*.

The tall shrubs, *Melaleuca ericifolia, M. squarrosa* and *Leptospermum laevigatum*, were projected to have suitable habitat expand by 2075, and shift from eastern NSW to the southern reaches of Victoria under the warm/wet future. In the hot/dry scenario for 2075, these species were projected to be faced with declines in range size of between 49 – 74% relative to current sizes (Table 4.1). The heath species, *Epacris impressa*, was projected to lose all suitable habitat in Western Australia in a hot/dry future (2075). Similarly, both *Eucalyptus dumosa* and *E. gracilis* were projected to lose all suitable habitat in South Australia under both climate scenarios for 2075. Among the mallee shrubs (*Eucalyptus* species), almost all currently suitable habitat (96.9 – 99%) was projected to be unsuitable by the hot/dry scenario for 2075, meaning that suitable habitat in the future will not only be smaller but also in a different location than current. These values were slightly lower under warm/wet scenario (83.7 – 94.4%). Conversely, > 75% of currently suitable habitat was projected to remain suitable by 2075 for three species (*Acacia tetragonophylla*,

A. *sclerosperma*, *Atalaya hemiglauca*) under the hot/dry scenario, and five species under the warm/wet scenario (*A. sclerosperma*, *Leptospermum laevigatum*, *Atalaya hemiglauca*, *Allocasuarina campestris*, *Maleleuca squarrosa*).

Although species richness at a continental scale was projected to decline with time, patterns differed under the hot/dry versus warm/wet scenarios (Figure 4.3). Richness of species in a hot/dry future will be highest in central-southern parts of Australia, with richness along the eastern and western margins of the continent declining. Under the warm/wet scenario, richness was projected to remain highest in South Australia, but decline in Western Australia and New South Wales and Victoria.

Figure 4.2 Projections of potential current and future suitable habitat modelled using MaxEnt, for two climate scenarios representing a hot/dry future from (IPSL-CM4) and a warm/wet future (CCSR-MIROC32MED) for 2035 and 2075. Maps show suitable habitat for *Acacia aneura, Atriplex nummalaria* and *Eucalyptus incrassata*. Warmer colours show areas projected to have higher suitability. Models were calibrated using five climate variables only (V_C models).

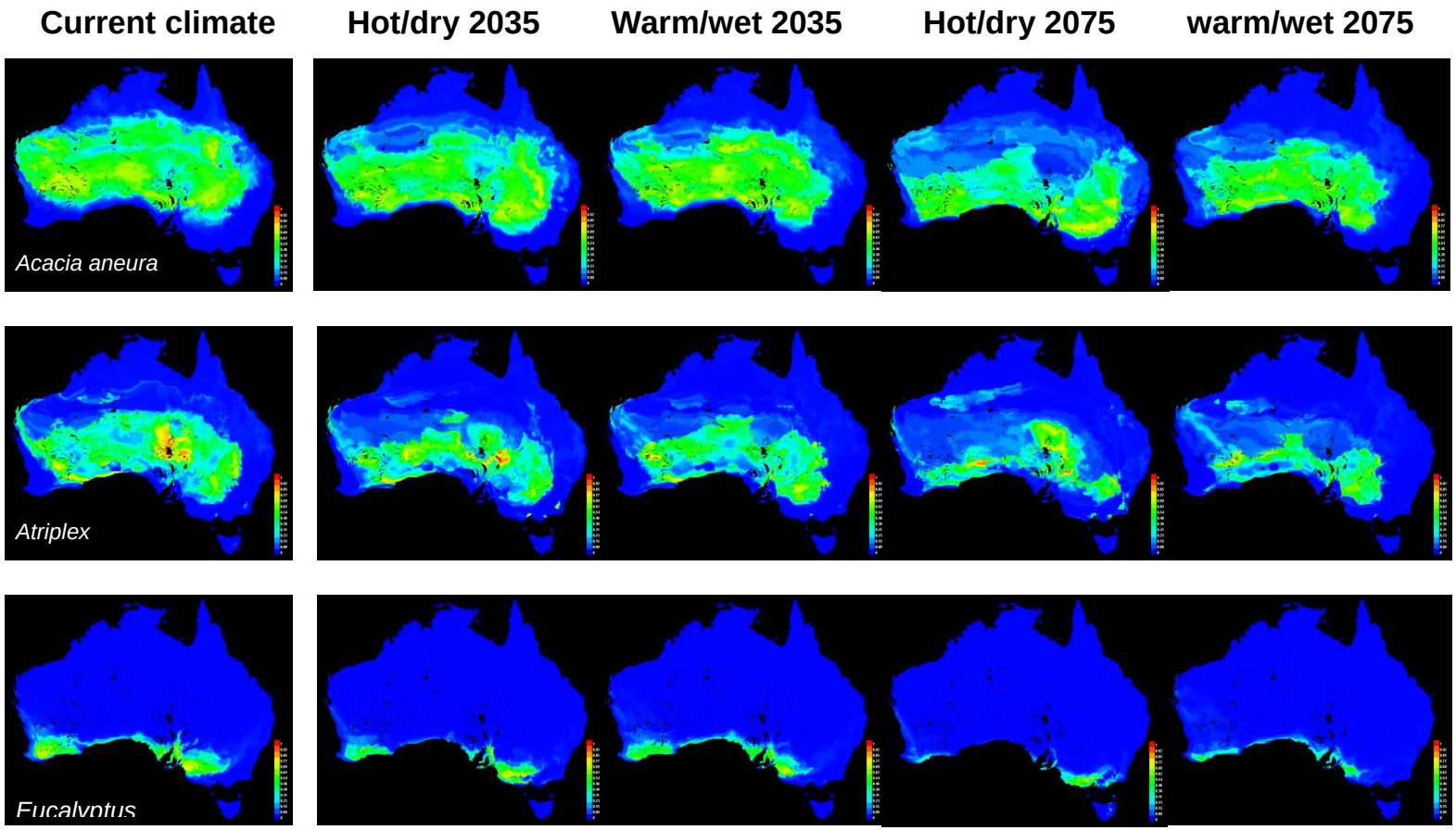


Table 4.1 Comparison of potential size of suitable habitat projected by MaxEnt for 29 Australian shrub species. "Current climate" was based on models calibrated with climate data from 1976 – 2005. Remaining columns show size (km^2) under future scenarios, percent of current habitat remaining suitable in the future (Overlap), percent of current habitat projected to be unsuitable in the future (Loss), percent of future habitat that is in new locations (Gain). The future scenarios represent a hot/dry future from (IPSL-CM4) and a warm/wet future (CCSR-MIROC32MED) for 2035 and 2075. Models were calibrated using five climate variables only (V_C models).

		Hot/dry scenario for 2035				Hot/dry scenario for 2075				Warm/wet scenario for 2035				Warm/wet scenario for 2075			
Species name	**Current climate (Km²)**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**
Acacia aneura	3638250	3205470	74.7	25.3	15.2	2143740	37.3	62.7	36.6	3021480	74.7	25.3	10.0	2238270	50.8	49.2	17.5
A. sclerosperma	970350	1912710	90.3	9.7	54.2	2991210	87.2	12.8	71.7	1774170	89.3	10.7	51.2	3372840	97.7	2.3	71.9
A. tetragonophylla	2954730	3346410	91.8	8.2	19.0	3677250	91.8	8.2	26.3	2630430	77.0	23.0	13.5	2375100	62.0	38.0	22.9
A. victoriae	3795990	3473040	64.5	35.5	29.5	2911830	46.8	53.2	39.0	3727950	70.5	29.5	28.2	3430290	57.8	42.2	36.1
Allocasuarina campestris	406680	446610	66.6	33.4	39.3	291840	23.0	77.0	68.0	628590	86.0	14.0	44.3	711570	78.1	21.9	55.3
Atalaya hemiglauca	3995850	3694620	84.0	16.0	9.1	3434040	76.5	23.5	11.0	4309350	92.8	7.2	14.0	4767720	94.8	5.2	20.5
Atriplex angulata	1301220	1025190	53.6	46.4	32.0	502740	18.6	81.4	51.8	845160	47.6	52.4	26.7	478980	24.9	75.1	32.5
A. eardleyae	1107120	828630	53.5	46.5	28.6	365190	12.5	87.5	62.0	1014240	63.8	36.2	30.4	728010	38.1	61.9	42.0
A. holocarpa	2116380	1802640	64.8	35.2	23.9	1245900	34.4	65.6	41.6	1621590	65.0	35.0	15.1	1017060	34.8	65.2	27.5
A. nummularia	1919400	1383570	48.0	52.0	33.4	876030	28.1	71.9	38.3	1397550	50.0	50.0	31.3	789810	22.8	77.2	44.7
A. vesicaria	1721070	1278660	63.0	37.0	15.3	805260	31.2	68.8	33.2	964170	51.8	48.2	7.6	345510	17.2	82.8	14.4
Epacris impressa	338670	217920	60.2	39.8	6.4	96870	23.3	76.7	18.5	268800	76.8	23.2	3.2	126330	33.8	66.2	9.4
Eremophila freelingii	1529610	674670	34.1	65.9	22.7	99960	1.9	98.1	71.3	764280	39.2	60.8	21.5	154470	5.6	94.4	44.1
Eucalyptus diversifolia	164340	112380	47.3	52.7	30.9	64740	12.2	87.8	69.0	107580	53.8	46.2	17.9	48540	20.3	79.7	31.3
E. dumosa	648240	356550	37.8	62.2	31.2	120120	1.0	99.0	94.4	505380	60.0	40.0	23.1	96990	7.0	93.0	53.2
E. gracilis	684360	391680	42.4	57.6	25.8	135840	3.1	96.9	84.3	460950	55.8	44.2	17.2	82620	7.5	92.5	37.5
E. incrassata	421770	250860	43.6	56.4	26.7	91950	2.1	97.9	90.2	300750	61.3	38.7	14.1	79050	16.3	83.7	12.9
E. oleosa	529380	345930	43.3	56.7	33.8	135480	2.4	97.6	90.7	404010	58.4	41.6	23.4	147810	18.2	81.8	34.7
E. socialis	1220940	754050	26.9	73.1	56.4	223350	1.8	98.2	89.9	1157970	49.5	50.5	47.8	518130	11.2	88.8	73.6
Leptospermum continental	363030	219090	54.5	45.5	9.7	83580	11.3	88.7	51.0	333060	83.0	17.0	9.5	237060	50.0	50.0	23.5
L. glaucescens	56280	42390	70.0	30.0	7.1	24210	40.2	59.8	6.6	46680	76.1	23.9	8.3	29160	46.0	54.0	11.2
L. laevigatum	416700	336300	62.5	37.5	22.6	210870	31.5	68.5	37.8	636630	98.1	1.9	35.8	854220	96.1	3.9	53.1
L. lanigerum	266430	155550	56.4	43.6	3.5	70020	26.1	73.9	0.8	201930	74.7	25.3	1.5	97980	36.7	63.3	0.1
L. scoparium	94020	65850	65.7	34.3	6.2	39480	41.5	58.5	1.2	72720	71.9	28.1	7.1	42120	42.8	57.2	4.5
Maireana aphylla	1885710	2053560	68.1	31.9	37.5	3670320	64.8	35.2	66.7	1772490	56.7	43.3	39.7	2269860	33.7	66.3	72.0
Melaleuca ericifolia	185880	136170	41.9	58.1	42.8	47880	5.4	94.6	78.9	183750	72.8	27.2	26.4	194640	54.7	45.3	47.8
M. squamea	123450	77610	56.0	44.0	10.9	49890	37.4	62.6	7.5	108300	69.4	30.6	20.9	87630	46.7	53.3	34.2
M. squarrosa	144930	99570	59.0	41.0	14.1	66840	36.3	63.7	21.3	178410	86.8	13.2	29.5	172350	78.1	21.9	34.4
Ozothamnus turbinatus	57390	42720	49.3	50.7	33.8	37890	36.2	63.8	45.2	56520	65.7	34.3	33.3	50400	44.3	55.7	49.6

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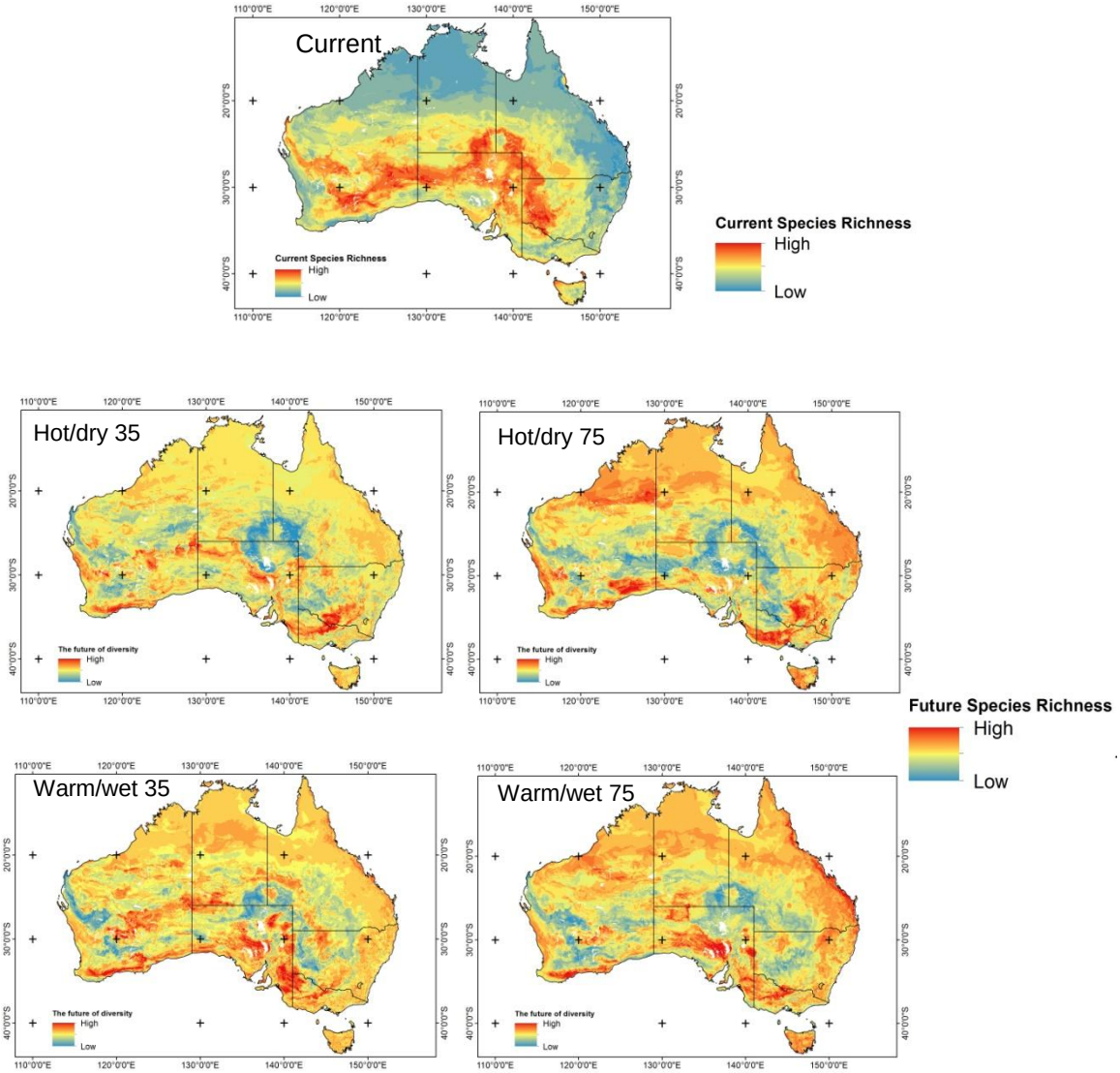


Figure 4.3 Biodiversity maps for 29 shrub species modelled using MaxEnt. Maps are richness map of species are modelled onto current climate (first map) and species differences between current and two scenarios (hot/dry [IPSL-CM4] and warm/wet [CCSR-MIROC32MED]) for 2035 and 2075. Models were calibrated using five climate variables only (V_C models).

How do projections of future distributions vary when soil properties are included in models?

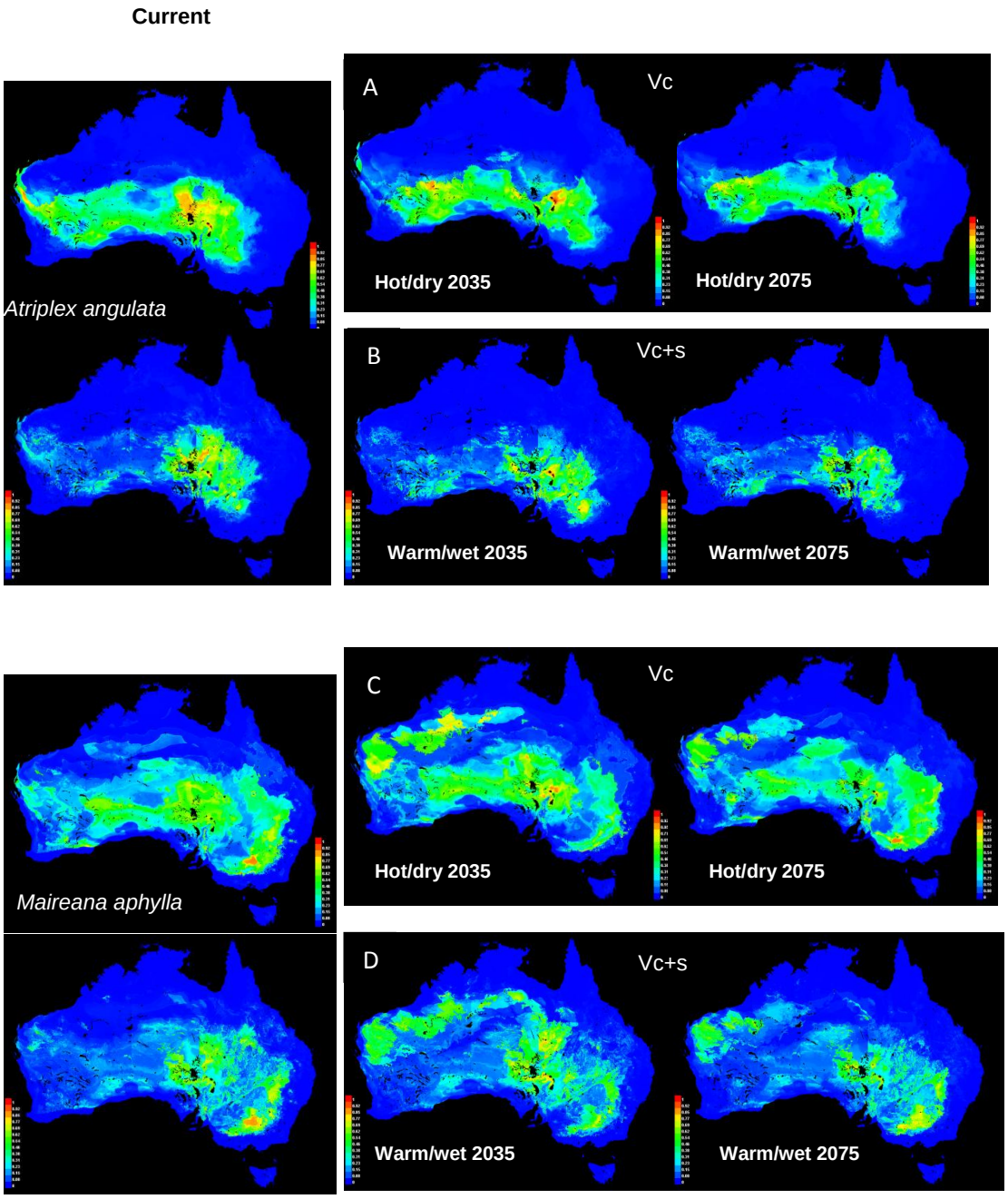
Under the warm/wet scenario suitable habitat for 21 of the 29 species was projected to decline in size by 2035 (Table 4.2). Declines continued for all 21 species under this scenario for 2075. While suitable habitat for six species was projected to expand by 2035 under the hot/dry scenario, expansions continued to occur for only three by 2075. As with V_C models, on average smaller changes in the size of suitable habitat were projected for the warm/wet scenario (2035 -9 ± 26%; 2075 -23 ± 64%) compared to the hot/dry scenario (2035 -19 ± 29%; 2075 -37 ± 64%, Table 4.2).

For some species, projections of range changes simulated by V_{C+S} models differed in direction and magnitude from V_C models. As a result, twice as many species were projected to experience range expansions in the V_{C+S} models (8 species) compared to V_C models (4 species), for the warm/wet scenario. For instance, when soil properties were included in models, habitat suitable for *Acacia victoriae* was projected to increase under the warm/wet scenario (15.3% and 18.4% for 2035 and 2075, respectively, compared to the baseline period). In contrast, declines of 2% and 10% were projected by V_C models (2035, 2075). However, for *A. sclerosperma* similar range changes were simulated by both sets of models – as demonstrated in Chapter 3 soil variables had little importance in defining the distribution of this species (see Table 3.7). Clay, however, was identified as the most important variable for *Maireana aphylla*. V_{C+S} models compared to V_C models simulated substantially greater increases in the size of suitable habitat (55.5% and 20%, respectively) under future scenarios for 2075.

Table 4.2 Comparison of potential size of suitable habitat projected by MaxEnt for 29 Australian shrub species. "Current climate" was based on models calibrated with climate data from 1976 – 2005. Remaining columns show size (km^2) under future scenarios, percent of current habitat remaining suitable in the future (Overlap), percent of current habitat projected to be unsuitable in the future (Loss), percent of future habitat that is in new locations (Gain). The future scenarios represent a hot/dry future from (IPSL-CM4) and a warm/wet future (CCSR-MIROC32MED) for 2035 and 2075. Models were calibrated using five climate variables and five soil variables (V_{C+S} models).

		Hot/dry scenario for 2035				Hot/dry scenario for 2075				Warm/wet scenario for 2035				Warm/wet scenario for 2075			
Species name	**Current climate (Km²)**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**	**Future (Km²)**	**Overlap %**	**Loss %**	**Gain %**
Acacia aneura	3447660	2820720	69.9	30.1	14.6	1928430	35.6	64.4	36.4	2854050	74.1	25.9	10.5	2056950	48.9	51.1	18.1
A. sclerosperma	933450	1638930	97.4	2.6	44.5	2558790	97	3	64.6	1518180	95.9	4.1	41.1	2875590	97	3	68.5
A. tetragonophylla	2907990	3339630	95.1	4.9	17.2	3708000	95.3	4.7	25.3	2847990	85.8	14.2	12.4	2747910	74.9	25.1	20.8
A. victoriae	3050670	3404520	74.9	25.1	32.9	2928720	58.4	41.6	39.2	3517050	80.8	19.2	29.9	3613230	70.9	29.1	40.2
Allocasuarina campestris	367350	377190	76.1	23.9	25.8	287220	35.3	64.7	54.9	472590	92.8	7.2	27.9	491970	83.7	16.3	37.5
Atalaya hemiglauca	3767910	3704640	89.2	10.8	9.3	3629040	83.3	16.7	13.5	4109730	93.8	6.2	14	4487700	95.7	4.3	19.6
Atriplex angulata	807150	681810	63.8	36.2	24.4	556590	43.2	56.8	37.3	545670	55.5	44.5	17.9	357240	27.5	72.5	37.8
A. eardleyae	1047840	917550	64.8	35.2	26	511890	28.8	71.2	41	930600	65.5	34.5	26.3	752640	43.4	56.6	39.6
A. holocarpa	1613370	1669980	76.7	23.3	25.9	1461180	59.4	40.6	34.5	1313790	66.2	33.8	18.6	881640	35.5	64.5	35
A. nummularia	1194360	984480	56	44	32.1	623250	38.9	61.1	25.4	806160	51.5	48.5	23.6	442440	26.4	73.6	28.7
A. vesicaria	1287180	1104930	73.6	26.4	14.3	850860	46.6	53.4	29.5	947820	67.8	32.2	7.9	499110	35	65	9.6
Epacris impressa	311370	200160	59.2	40.8	7.9	87840	21.4	78.6	24.1	242430	75.6	24.4	2.9	115590	34.1	65.9	8.1
Eremophila freelingii	733350	391890	43.3	56.7	19	193860	19.1	80.9	27.7	446520	42	58	31	262680	19.2	80.8	46.4
Eucalyptus diversifolia	151830	97560	41.8	58.2	34.9	46830	6.6	93.4	78.7	94080	50.3	49.7	18.9	42210	19.5	80.5	29.9
E. dumosa	505500	281790	44	56	21.2	52410	1.8	98.2	82.9	379470	62.9	37.1	16.2	70890	11.1	88.9	20.7
E. gracilis	579600	291990	42.3	57.7	15.9	46980	1.5	98.5	80.9	382650	60.5	39.5	8.4	38070	5.8	94.2	11.9
E. incrassata	430650	259710	45.1	54.9	25.2	122220	6.2	93.8	78.1	283620	61.2	38.8	7.1	94080	19	81	13.1
E. oleosa	643590	376860	51.1	48.9	12.7	47340	2.6	97.4	64.4	458010	66.2	33.8	7	162270	22.4	77.6	11.1
E. socialis	1402680	701430	29	71	42	231180	4.6	95.4	72	1199730	56.3	43.7	34.2	629700	19	81	57.6
Leptospermum continental	371910	225840	56.3	43.7	7.3	85800	13.3	86.7	42.4	338100	84.1	15.9	7.5	249120	54.7	45.3	18.4
L. glaucescens	47220	35550	70.8	29.2	5.9	20520	39.7	60.3	8.6	39000	78.3	21.7	5.2	24030	46.8	53.2	8
L. laevigatum	391890	316320	63	37	22	194340	32	68	35.5	585810	96.4	3.6	35.5	793950	93.7	6.3	53.7
L. lanigerum	267300	151860	56.6	43.4	0.4	67470	25.2	74.8	0.4	209100	77.7	22.3	0.7	107880	40.3	59.7	0.1
L. scoparium	99480	71310	64.6	35.4	9.9	42360	41.5	58.5	2.6	79650	72.7	27.3	9.2	46080	42.2	57.8	9
Maireana aphylla	1458780	2119590	74.8	25.2	48.5	3875670	78.1	21.9	70.6	1501110	65.7	34.3	36.2	2267790	50	50	67.8
Melaleuca ericifolia	169530	128820	45.5	54.5	40.1	45150	5.3	94.7	80.3	192270	80.8	19.2	28.8	211470	62.6	37.4	49.9
M. squamea	92190	58290	55.8	44.2	11.7	45150	38.4	61.6	21.7	74130	71.3	28.7	11.3	53100	49.3	50.7	14.5
M. squarrosa	139170	97230	60.9	39.1	12.8	64650	36.6	63.4	21.2	170850	88.5	11.5	27.9	165150	77.6	22.4	34.6
Ozothamnus turbinatus	60600	41550	49.9	50.1	27.2	29430	31.8	68.2	34.6	59070	62.7	37.3	35.7	46470	39.2	60.8	48.9

Figure 4.4 Projections of potential current and future suitable habitat modelled using MaxEnt, for two climate scenarios representing a hot/dry future from (IPSL-CM4) and a warm/wet future (CCSR-MIROC32MED) for 2035 and 2075. Maps show suitable habitat for *Atriplex angulata* under historical climates (upper column) and *Maireana aphylla* (lower column) modelled with different sets of environmental conditions. Panels A, C are based on models calibrated with climate variables only (Vc), while panels B, D are based on models calibrated with climate and soil variables (Vc+s). Warmer colours show areas projected to have higher suitability. Bright blue represents unsuitable areas.



Patterns of species richness are broadly similar under both climate scenarios for 2035, but diverge by 2075 (Figure 4.5). That is, under scenarios for 2035, V_{C+S} models project richness to be greatest in eastern South Australia and south-west Queensland/western New South Wales, although there an area of high richness in southern Western Australia (Figure 4.5). By 2075, areas with greatest richness under the warm/wet scenario are mostly in South Australia. Conversely, several small regions of high richness are projected under the hot/dry scenario: south-east Western Australia, east South Australia and central New South Wales.

Therefore to summarise, the primary difference between projections from V_C and V_{C+S} models for 2035, is that rather than having a broad band of high richness extending from Western Australia through to New South Wales (V_C models, Figure 4.3) V_{C+S} models project two geographically separated areas of high richness: one in Western Australia and one in South Australia/Queensland/New South Wales (Figure 4.5). For 2075, under the hot/dry scenario there are broad similarities to the richness patterns projected by V_C and V_{C+S} models, while under the warm/wet scenario patterns in Western Australia diverge.

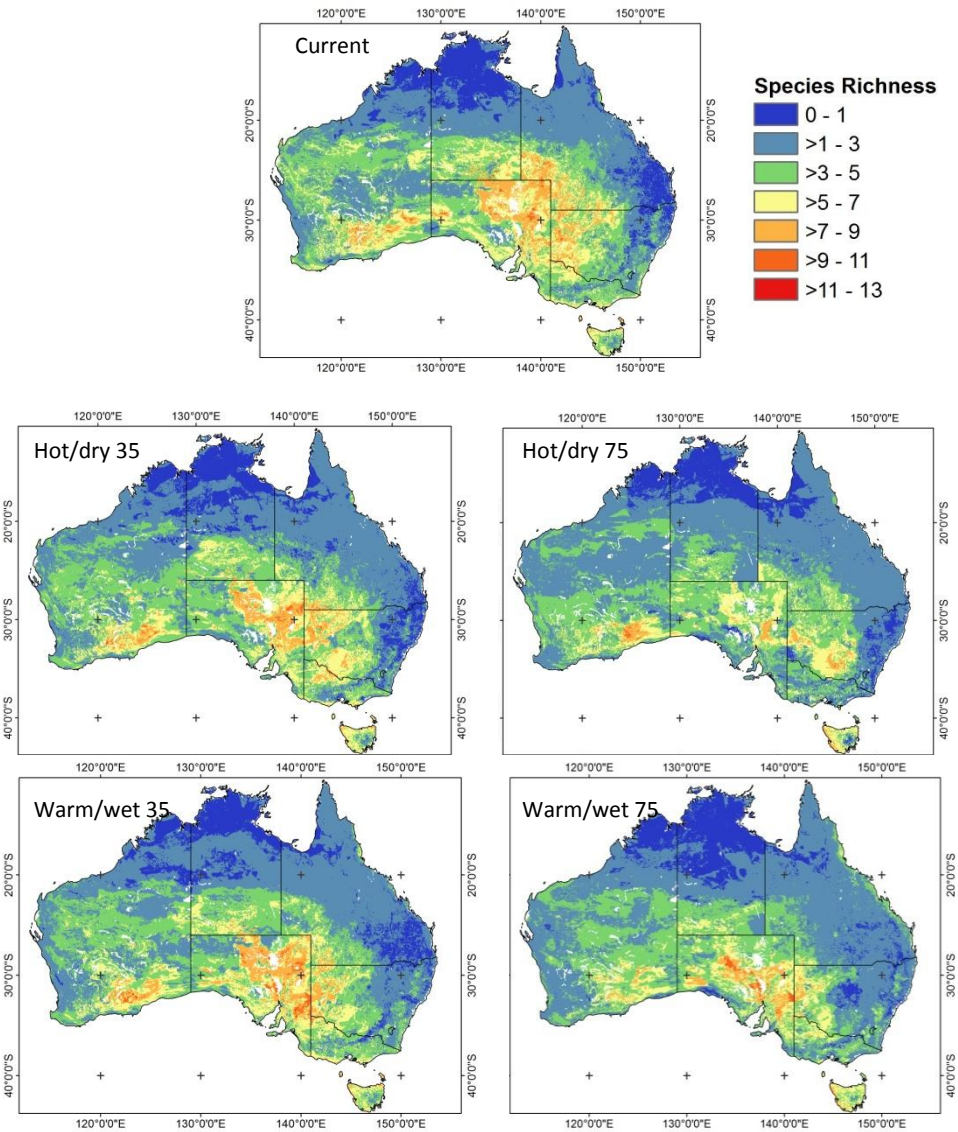


Figure 4.5 Richness maps for 29 shrub species modelled using MaxEnt and projected onto current climate and two scenarios (hot/dry [ipsl-cm4] and warm/wet [ccsr-miroc32med]) for 2035 and 2075. Models were calibrated using five climate and five soil variables (V_{C+S} models).

Discussion

The impact of climate change on Australian shrub species

Over the course of this century, should climate change follow a trajectory of “hot/dry”, regions of Australia with the highest richness of the shrub species in this study may contract to small areas in south-eastern Western Australia, eastern South Australia

and central New South Wales. However, neither the magnitude of temperature increases nor future precipitation patterns are certain, and should the future be one characterised as “warm/wet” than South Australia may harbour the largest area of habitat suitable for the greatest number of shrub species. Indeed, consistent with other studies (e.g. 100 Banksia species in south-west Western Australia (Fitzpatrick *et al*., 2008); 584 plant species across southern Australia (Summers *et al*., 2012)), the extent of suitable habitat for the majority of species was projected to decline, irrespective of climate scenario.

Averaged across the continent, the hot/dry scenario projected an increase in temperature and decrease in precipitation compared to historical climate (1976 – 2005). More specifically, under this scenario annual and seasonal temperature was projected to rise substantially in central Australia and western regions of Western Australia. These areas are currently inhabited by shrub species for which temperature variables were identified by MaxEnt as the most important, for instance *Acacia aneura*. The hot/dry scenario also projected declines in annual precipitation in central Australia of ~129 – 370 mm, with summer and winter rainfall projected to be between ~ 42 and 111 mm by 2035, respectively, and drier still by 2075. This may result in the elimination of suitable habitat for species inhabiting these areas, although for some, such as *Atriplex nummularia* and *Eucalyptus incrassate,* new areas in the south-east may become more suitable. Hence, although these shrubs can survive in high temperature environments, they are unlikely to withstand higher temperatures and further declines in precipitation. In this case, these species are located at the margins of their distributions based on their physiological tolerance of climatic extremes.

In contrast, suitable habitat for shrubs under the warm/wet scenario fell into two categories: arid species with projected declines in habitat (e.g. *Atriplex angulata*

and *Eucalyptus oleosa)* versus temperate shrubs (such as *Epacris impressa*) whose distributions in eastern Australia may expand while habitat in the west may be eliminated.

Although averaged across the continent, precipitation was projected to increase under the warm/wet scenario, this may be insufficient to offset the impact of higher temperatures on shrub species. As temperature increases, water stress may occur causing injuries to plants (Liu *et al*., 2005) via increased water loss from transpiration. This results in lower moisture availability which may suppress the distribution of shrubs (Huang *et al*., 2011).

Selection of climate scenarios

The differences in suitable habitat under the two future climate scenarios emphasize the uncertainties associated with projections of future climate. The selection of climate scenarios for impacts assessments is an important consideration, yet there is little published guidance on which climate models to obtain simulations from (as discussed in Beaumont *et al*., 2008; Harris *et al*., 2014). Given that no single 'best' climate model exists, it is highly recommended to use simulations from multiple GCMs (Beaumont *et al*., 2008), although this may not be realistic given computational limitations. Scenarios may be averaged to create an ensemble, and while this is useful for removing some biases and reducing reliance on a single scenario, the ensemble may not reflect a state that could actually occur. Consider the two scenarios I used in this Chapter: IPSL has simulated a future where, averaged across the country, precipitation declines. In contrast, MIROC has projected a future where average MAP increases. Averaging these two scenarios, one dry (0) and the other wet (1), would create an ensemble that is not indicative of either model (0.5). Therefore, while multiple climate scenarios should be used for impacts assessments,

from a management and adaptation perspective it may be more informative to report results of contrasting futures (e.g. wet/dry) rather than averaging these.

Incorporating soil properties as predictor variables

The addition of soil properties with climate predictor variables in MaxEnt models (V_{C+S}) resulted in greater fragmentation of suitable habitat than models calibrated with only climate variables (V_C models). This fragmentation could be a result of converting abiotic variables operating at different spatial scales (i.e. climate and soil) to the scale necessary for modelling. These results are consistent with Taylor & Kumar's (2013) assessment of climate change impacts on the distribution of *Lantana camera* in Queensland. The authors found a substantial reduction in the extent of suitable habitat for this shrub species, and greater patchiness but higher suitability, when soil drainage variables were included in SDM calibration.

Approaches for combining dynamic and static variables in SDM projections under future climate scenarios remains poorly investigated (Brook *et al.,* 2009). However, numerous authors have recommended the inclusion of soil variables in these models (e.g. Fitzpatrick *et al*., 2008; Austin & Van Neil 2011; Martinson *et al*., 2011; Meier *et al*., 2012; Stanton *et al*., 2012; Condit *et al*., 2013; Hosseini *et al*., 2013; Taylor & Kumar, 2013).

Other factors limiting the distribution of shrub species

Although I included several precipitation variables (annual precipitation, precipitation of the wettest quarter and precipitation of the coldest quarter), there are other measures of moisture availability that may play a role in limiting the distributions of shrubs. For instance, the number of days without rainfall, which is projected to increase (CSIRO & BoM, 2007). As projections of daily data from global climate

models become more assessable to ecologists, variables representing the number of days before a given threshold is reached, may be useful in assessing climate impacts.

Finally, there are other factors, such as grazing and fire regimes, that may play an important role in defining the distributions of species. Inclusion of these variables in the modelling approach, and separating the effect of climate and soil from these, may improve the reliability of results (Pearson *et al*., 2004).

Conclusion

My results have provided a first approximation as to the impact of climate change on shrub species at a national level and this approach may be useful for land management plans and decision-making. In general, shrub species in arid and semi-arid regions of Australia are likely to be negatively impacted by climate change, particularly should a hotter and drier future occur. In contrast, temperate shrubs may be able to withstand slightly warmer conditions. Ultimately, however, richness of shrub communities may decline as the century progresses with suitable habitat contracting towards the southern-central regions of the continent.

For some species combining soil properties with climate variables may result in more realistic simulations of climate impacts. The addition of soil properties provides a foundation for future studies investigating the role of abiotic factors on the distribution of plants.

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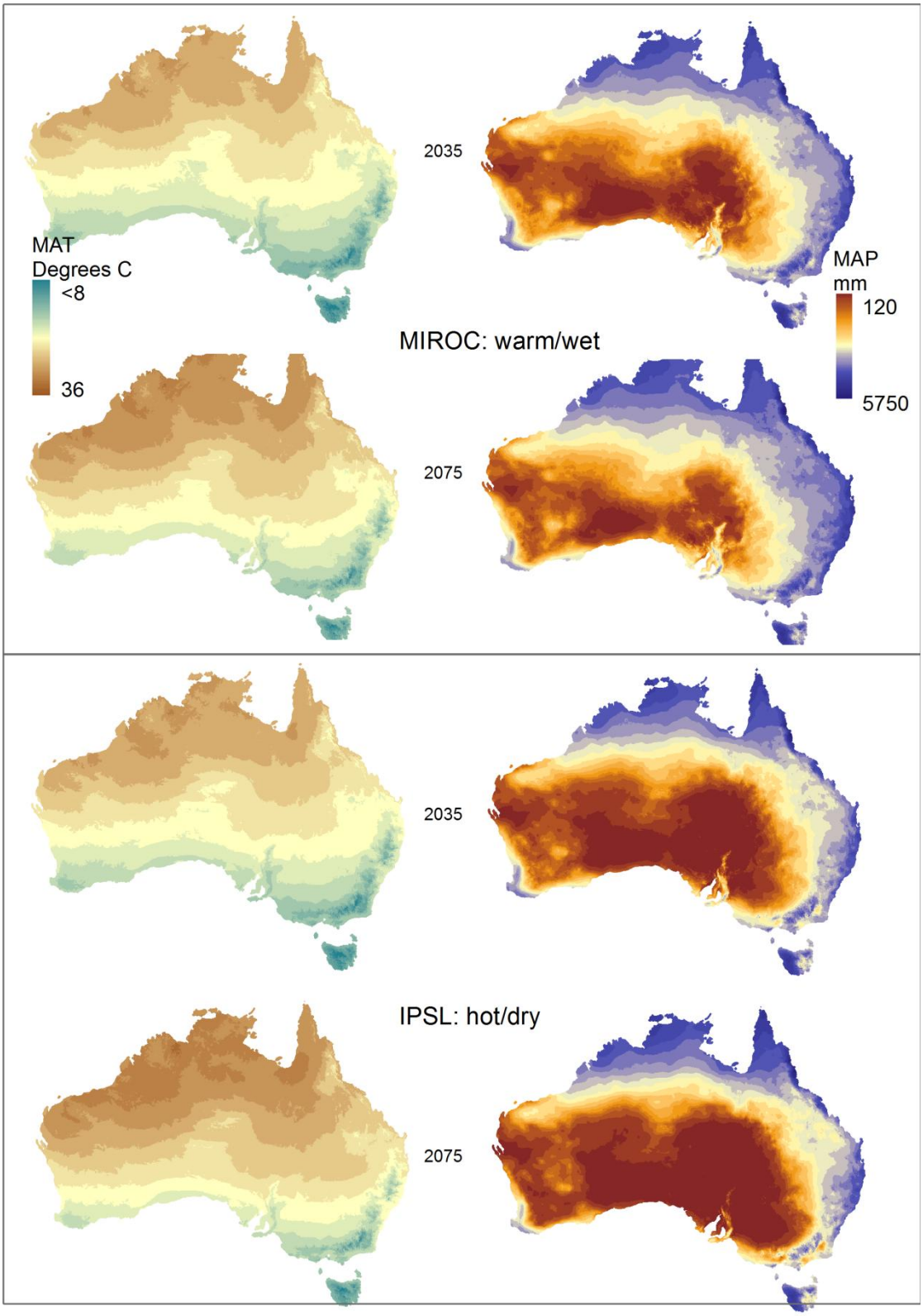
Appendix 4

Figure 4.1 Simulations of mean annual temperature (MAT) and precipitation (MAP) based on two scenarios (MIROC: warm/wet [ccsr-miroc32med]; IPSL: hot/dry [ipsl-cm4]) for twenty year periods centred on 2035 and 2075.



Chapter 5

Conclusions

Chapter 5: Conclusions

The goal of this thesis was to evaluate the role of environmental conditions, in particular climate and soil, in controlling the distribution of Australian shrublands and shrub species. The thesis also aimed to explore variation in projections of species distributions that may occur due to inclusion of soil parameters in model calibration. To this end, I first identified how the climate envelope of shrublands differed from other major vegetation groups, i.e. forest, grassland and woodland (**Chapter 2**), and differences in the climate envelopes of six recognised classes of shrubland. While previous studies have focused on physiological adaptations of shrubs to climate (e.g. Reynolds *et al.*, 1999; Jiang & Li, 2008; Huang *et al*., 2011) assessment of climate envelopes has received much less attention. This may in part be due to inconsistencies in the definition of 'shrubs', particularly as some species are able to grow as trees or shrubs depending on the environmental conditions (e.g. *Acacia aneura*). Thus, this chapter represents the first assessment of the role of climate and soil properties in defining the distribution of different classes of shrubland.

Chapter 2 highlighted the key role that soil moisture plays in distinguishing the climate envelope of shrublands from other vegetation types. Australian shrublands occur in regions with low moisture availability. Physiological mechanisms of shrubs, such as long root systems, enable them to utilise moisture stores in deep soil layers during hot, dry seasons (Cavanaugh *et al*., 2011). Although grasses can tolerate high temperature, they depend mainly on moisture from shallower soil layers, which restricts their growth during dry periods. Shrubs can also utilize water efficiently during the growth season by maximizing their growth rate (Reynolds *et al*., 1999). Therefore, seasonality of soil moisture along with variables such as annual soil

moisture and temperature in the warmest month are good predictors of distribution of shrublands.

I was also able to predict the distributions of five out of six shrubland classes, with varying accuracy. For three classes (Acacia shrubland; Chenopod shrublands, samphire shrublands and forblands; Mallee woodlands and shrublands) which mainly inhabit arid and semi-arid regions, distributions were predicted with a reasonable level accuracy, according to the Kappa statistic (> 53% correctly predicted), although for two other classes occurring in temperate regions (Low closed forests and tall closed shrublands; Other shrublands) models were less accurate (20% and 32%, respectively, correctly predicted). Predictions for heathlands, however, were very poor, potentially due to the mixing of different groups of vegetation within polygons of extant MVG and MVS of NVIS (DSEWPaC, 2012). Modelling the potential distribution of shrublands under current climates is an important step for understanding responses to climate and environmental change. While it would be highly useful to project these models onto scenarios of future climate, a primary limitation was that scenarios were not available for all moisture-related variables. Indeed, the availability of environmental data is a key factor limiting climate impacts assessments.

Although a number of studies have modelled the relationship between climate and particular shrub species (e.g. Altamirano *et al*., 2010; Sardans *et al*., 2013), few have incorporated soil properties (Condit *et al.*, 2013) and fewer still have explicitly compared the relative importance of climate versus soil in defining species distributions (Taylor & Kumar, 2013). In **Chapter 3** I used a species distribution model, MaxEnt, to evaluate whether models calibrated with only climate variables produced more accurate simulations of current suitable habitat for 29 dominant shrub species, than when climate and soil variables are combined, or when only soil variables are used. Limitations in soil datasets meant that variables had to be

selected from two sources, the Australian Soil Resource Information System (ASRIS: Wood & Auricht, 2011; http://www.asris.csiro.au) and the Global Soil Dataset for Earth System Modelling (GSD; http://globalchange.bnu.edu.cn/research/soilw).

For most of the 29 species, climate variables contribute more than soil to defining species distributions, however for some species models, calibration with both climate and soil resulted in more realistic predictions of potential climatically suitable habitat. Soil variables were important for four species in particular: clay contributed > 20% to models for *Atriplex angulata*, *A. nummularia*, *M. aphylla*) while pH did so for *Allocasuarina campestris*. This result supports previous research that has documented the importance of these soil variables for these species (Cunningham *et al*., 1992; Osuolale *et al*., 2012). Furthermore, a promising recent application of SDMs is to connect them with stochastic population models to estimate extinction risk (Keith *et al*., 2008; Stanton *et al*., 2012). Such estimates are dependent on reasonable predictions of suitable habitat as a function of climate conditions and other parameters such as soil type. My analysis validates the approach of incorporating soil variables into SDMs, and I recommend that future studies explore the contribution of soil variables when modelling the distributions of plant species.

SDMs are frequently used to predict potential changes in species distributions under climate change. The degree to which climate change may impact the distribution of shrub species at a regional scale is unclear as most studies have explored areas of interest at finer scales (e.g. Summers *et al*., 2012; Taylor & Kumar, 2013). Therefore, the primary goal of **Chapter 4** was to estimate climate-driven changes in habitat suitability of shrubs at regional scales using MaxEnt.

Rather than projecting MaxEnt models onto an ensemble of future climate scenarios, I specifically identified two contrasting models which is more robust for

interpretation than the use of ensembles. These two models had been shown to have high skill in simulating current conditions (Perkins *et al*., 2007; Evans *et al*., 2012). Compared to historical climate, MIROC (ccsr-miroc32med, http://www-pcmdi.llnl.gov/ipcc/model_documentation/MIROC3.2_hires.pdf), projects warmer and wetter conditions, averaged across the continent, while IPSL (IPSL–CM4, http://www.ipcc-data.org/ar4/model-IPSL-CM4-change.html) projects hotter and drier conditions.

In general, most shrub species were projected to be faced with declines in the size of suitable habitat, regardless of climate scenario. Suitable habitat for shrubs in arid central-southern Australia was projected to contract to a greater extent than for shrub species in temperate regions in models calibrated for species versus vegetation types. My results provide additional support for the sensitivity of ecosystems in arid regions (Austin, 2011) and suggests that severe drought periods could suppress shrub distribution, which has been documented previously (e.g. Fensham *et al*., 2005; Norman *et al*., 2014).

An additional goal of **Chapter 4** was to assess the extent of divergence in projections of future suitable habitat predicted when models were calibrated with only climate variables versus climate and soil variables. Changes in soil characteristics occur over geological time and are thus undetectable over the time period of projections of climate used in SDMs (Stanton *et al*., 2012). I treated soil as unchanging (static) variables. Approaches for combining dynamic and static variables in SDMs have not been well investigated (Brook *et al.,* 2009). However, the inclusion of soil properties in SDMs, to assess current and future distributions, has been found useful in several studies (e.g. Stanton *et al*., 2012; Condit *et al*., 2013; Hosseini *et al*., 2013; Taylor & Kumar, 2013).

Addition of soil variables generally constrained the distribution of shrub species, and resulted in smaller changes to the size of future suitable habitat compared to projections from V_C models. For those species for which soil characteristics strongly influence distribution, inclusion of these variables in models may be constructive in terms of management, as model outputs can help identify areas that meet a broader range of requirements for that species. However, it is disconcerting that for some species the direction and magnitude of range changes may differ depending on whether or not soil variables were included in model calibration. Therefore, I suggest calibrating models with climate and soil variables to explore their relative contributions, then rerunning models excluding unimportant variables. This will assist with reducing uncertainty in model projections.

Of course, plants persist in heterogeneous environments where their distributions are constrained not only by climate and soil properties, but also disturbances such as fire and grazing (Keeley *et al*., 2011). Frequent fires may lead to a more open canopy and patchy distributions in shrublands, and may prevent the establishment of some species, such as *Acacia aneura* (Bowman *et al*., 1995; Bowman *et al*., 2007). Fire may also facilitate the introduction of annual plants, which may be highly flammable and promote hotter and more frequent fires, while grazing may reduce cover and abundance of annuals (Liedloff *et al*., 2001).

Grazing may also impact the distributions of shrub species. For instance, there is evidence of grazing reducing the distribution of shrubs in arid regions of southern Australia (Tiver *et al*., 2008), whereas fires and grazing have facilitated the establishment of shrub species (e.g., *Acacia sophorae*) in south-eastern coastal grasslands (Costello *et al*., 2000) to the detriment of grasses (Costello *et al*., 2000; Lunt *et al*., 2010). Thus, combining climate and soil data with disturbances such as fire and grazing may allow a greater approximation of species niches and provide

insight on how future distributions may be driven by the interaction of biotic and abiotic factors. Tiver *et al*. (2008) for instance, incorporated grazing and future climate scenarios in models and projected the extinction of *Acacia aneura* species within 500 years under scenarios of moderate and heavy grazing by sheep. Similarly, heavy grazing was projected to result in the extirpation of populations of *Atriplex vesicaria* growing along watering points (Hunt, 2001). It would therefore be highly useful to incorporate different land use interactions into assessments of climate impacts.

This thesis has presented a comprehensive analysis of Australian shrub distributions and their relationships to climatic and soil processes. Defining shrubs as a distinct plant functional type in dynamical vegetation models (e.g, Prentice *et al.*, 2007) has been hampered due to a lack of information on the climate envelope of shrublands. This thesis has produced explicit results based on observations of climate data and vegetation in Australia. This analysis can be extended to other continents and ecosystems, making use of widely available climate observations and global shrubland types and shrub species that resemble the Australian arid and temperate shrubs. Finally, the thesis illustrated the importance of exploring the contribution of soil properties when modelling species distributions, highlighting how SDM projections of future suitable habitat may diverge depending on the selection of predictor variables.

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