Identifying Climate Refugia for Australian Rainforest Plant Species: from the Last Glacial Maximum to 2070

A thesis submitted for the degree of Master of Research

October 2017

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Date of submission: 30 October 2017

To the examiners,

This thesis represents a nine-month project undertaken for a Masters of Research. The thesis is written in the form of a journal article for the *Journal of Biogeography*. Link for the Author guidelines for this journal can be found at the end of my thesis. Any deviations from this journal style are in accordance with the Macquarie University Masters of Research thesis guidelines. For ease of reading, all tables and figures are embedded within the text rather than at the end of the document.

Declaration

I certify that this work has not been submitted for a higher degree to any other university or institution. However, this work has been undertaken as a collaboration with individuals at Macquarie University and the Royal Botanic Gardens, Sydney. The project was conceived and designed by Maurizio Rossetto, Peter Wilson, Linda Beaumont, John Baumgartner and Manuel Esperon-Rodriguez. John Baumgartner and Peter Wilson developed custom R code used to fit species distribution models. Both provided advice on using R. Peter Wilson downscaled the climate data. Maurizio Rossetto provided advice on the adequacy of projected distributions for each species. I undertook all species distribution modelling and post-hoc analyses and wrote the manuscript.

Abstract:

Aim Historically, climate refugia – areas that have remained suitable for species during periods of climate disruption – have played an important role in species persistence. Identifying and protecting climate refugia is a key climate change adaptation approach for conservation planning. This study aims to identify climate refugia for Australian rainforest flora, from the Last Glacial Maximum to 2070.

Location Australia

Taxon Angiosperms

Method Models of habitat suitability for 30 plant species were calibrated using Maxent, and projected onto climate data for the Last Glacial Maximum (LGM, ~22,000 ybp), mid-Holocene (MH, ~6,000 ybp), current period and 2070. The intersection of suitable habitat over consecutive periods was assessed, identifying a) paleo refugia (LGM – MH – Current), b) future refugia (Current – Future) and c) High Value Refugia (HVR, suitable over all four periods). Centres of refugia (regions suitable for multiple species) were identified.

Result Predictive performance of models was acceptable, with maps of current suitable habitat verified by experts. Generally, habitat suitability spans the greatest extent now compared to past or future time periods. Four centres of paleo refugia were located in the Wet Tropics, Central Mackay Coast, South Eastern Queensland and North Coast of New South Wales bioregions. Ranges for most species were projected to decline by 2070 (mean = 52%, SD = 22%). HVR were identified for all species to at least 2070, although these occupy, on average, 16% of current habitat (SD = 11%). Future refugia were projected to occur elsewhere for all species, but may be well beyond species' dispersal ranges.

Main conclusions HVR are likely to be highly important for the conservation of these rainforest species, given generation times, limited dispersal capabilities and anthropogenic barriers to movement. This study may assist in understanding long-term spatial shifts in rainforest flora in response to climate change, and for designing future conservation strategies.

Introduction

Life on earth has repeatedly been subjected to large fluctuations in climate (VanDerWal *et al.*, 2009a; Pecl *et al.*, 2017). Most recently, climate oscillations during the glacial-interglacial cycles that characterised the late Quaternary period drove major re-organisation in community structure and composition, species' abundances and distributions (Bennett & Provan, 2008; VanDerWal *et al.*, 2009a).

The world is currently undergoing another period of climate change, primarily as a result of human activities, at a pace more rapid than natural variability (Karl & Trenberth, 2003). Since the pre-industrial age (~1750), carbon dioxide concentrations have increased > 40%, methane by > 150%, and nitrous oxide by > 20% (IPCC, 2013). Carbon dioxide concentrations are now higher than anytime during the past 800,000 years (IPCC, 2013). This scenario has driven an increase in global average temperature of ~0.85°C since 1880, and should greenhouse gas emissions continue at their current rate temperatures may increase 4.3 ± 0.7°C by 2100, relative to 1986-2005 (Collins *et al.*, 2013).

Myriad studies from around the world have already identified substantial impacts of climate change on biodiversity, from an organismal to biome level (Chen *et al.*, 2011; Bellard *et al.*, 2012; Pecl *et al.*, 2017). Species can respond to climate change by shifting their distribution, changing life history traits or via genetic adaptation (Bellard *et al.*, 2012). However, if species' tolerances to environmental conditions are exceeded and they cannot adapt or migrate, then populations may be extirpated (Thomas *et al.*, 2004; Berg *et al.*, 2010; Urban, 2015).

Substantial evidence from the paleo record indicates that a common biological response to past major climatic transitions was for species to undergo range shifts to track spatial changes in their climate envelope (Willis & MacDonald, 2011; Hampe *et al.*, 2013). Species' survival was facilitated by some locations retaining suitable climatic conditions during periods of climate disruption (Ashcroft, 2010; Dobrowski, 2011), such as the glacial-interglacial oscillations over which time modern taxa evolved (Bennett & Provan, 2008). These locations are referred to as "climate refugia". For instance, glacial refugia were areas in which populations of warm adapted species survived during the Last Glacial Maximum (LGM; ~22,000 years before present, ybp) (Dahl, 1946; Keppel *et al.*, 2012). In contrast,

interglacial refugia retained the cooler habitats that were required by some cold-adapted species during warmer interglacial periods (Cornejo-Romero *et al.*, 2017). The presence of glacial and interglacial refugia has played a pivotal role in shaping the current distribution of many species and patterns of regional biodiversity (Médail & Diadema, 2009).

Given the impact that anthropogenic climate change will likely have on biodiversity, identifying geographic regions that may serve as climate refugia is viewed as an increasingly important conservation action (Reside *et al.*, 2014). These regions may be a valuable addition to protected area networks (Keppel & Wardell-Johnson, 2012). Future refugia can be defined by their location with respect to a species' current range. Areas that are both currently suitable and projected to remain so in the future may be termed *in situ* refugia (Ashcroft, 2010). Such areas may be of key importance for the persistence of species with poor dispersal abilities that occur in fragmented landscapes or that have limited suitable habitat elsewhere. In contrast, *ex-situ* refugia will be areas located outside the species' former distribution (Ashcroft, 2010). Species with certain functional traits, such as high dispersal ability, may be able to move unaided to these regions. For other species, ex-situ refugia might only become reachable via assisted colonization.

Australia's rainforests
Australia's rainforests are a mix of ancient Gondwanan relicts and more recent immigrants from south-eastern Asia. These communities are currently found in northern Australia, from the Kimberley region of Western Australia eastward across the Northern Territory, extending down the east coast of Queensland, New South Wales (NSW) and Victoria, to the cool temperate region of Tasmania (Metcalfe & Green, 2017). Although rainforests occupy a mere 0.3% of the Australian landmass, they contain around 20% of all native Australian plant families (Metcalfe & Green, 2017). During the Pleistocene glacial-interglacial cycles, rainforests in Australia were heavily fragmented and declined in area (Schneider & Moritz, 1999). However, climatic conditions became more favourable ~7500 ybp, and rainforests expanded over a broader area (Hopkins *et al.*, 1996). Hence, there is a clear fingerprint of past climate oscillations on the current distribution of Australia's rainforest communities.

Since the arrival of Europeans in the 18th century, rainforest communities have undergone substantial declines, with approximately one-third of their estimated pre-European extent being cleared (Dunstan & Fox, 1996; Metcalfe & Green, 2017). Today,

many rainforest communities are isolated remnants surrounded by agricultural lands (Fox *et al.*, 1997). These characteristics of their distribution, along with long generation times and poor dispersal capabilities of many plant species, impose limits on the ability of rainforest plants to shift their distributions to track anthropogenic climate change (Holl, 1999; Ingle, 2003). As such, the goal of the current study is to examine the geographical congruence of past, present and future refugia for 30 tropical and sub-tropical rainforest plant species using the species distribution model (SDM) Maxent (Phillips *et al.*, 2006).

SDMs have become a common tool to identify climate refugia. These models assess the relationship between locations where a species occurs and the environmental (frequently climatic) characteristics of those regions, to define the range of suitable conditions for the species (Elith & Leathwick, 2009; Franklin, 2010). This relationship can then be used to assess the distribution of suitable habitat under past or future climate scenarios, while assuming a constant biotic response or niche stability (Nogués-Bravo, 2009; Keppel *et al.*, 2012).

In this study, I identified: a) regions that have remained, or will likely remain, climatically suitable for each species from the Last Glacial Maximum (LGM, ~ 22,000 ypb) and the mid-Holocene (MH, ~6000 ybp), to the current period and into the future; b) congruence in the spatial location of past and future refugia for each species; and c) regions that are likely to be refugia for multiple rainforest species in the future (to 2070). By identifying the location of refugia throughout space and time I highlight regions likely to be important for long-term conservation and management actions for key rainforest plant species.

Materials and methods

Study area

The study region covers areas characterized by the presence of rainforests. Australian tropical and sub-tropical rainforests are found across the north and south-east coast of Queensland, and the central and southern coast of New South Wales (Catterall *et al.*, 2004; Metcalfe & Green, 2017) (Figure 1).

Table 1. List of species used in this study, with details about their taxonomic identity (matched with Australian Plant Name Index (APNI)) and life form.

Species	Scientific authority	Family	Life form
Argyrodendron trifoliolatum	F. Muell.	Malvaceae	Tree
Callicoma serratifolia	Andrews	Cunoniaceae	Shrub or tree to 20 m
Castanospermum australe	A. Cunn.	Fabaceae	Tree
Castanospora alphandii	(F. Muell.) F.Muell.	Sapindaceae	Tree
Cinnamomum oliveri	F.M. Bailey	Lauraceae	Tree
Cryptocarya glaucescens	R.Br.	Lauraceae	Tree
Cryptocarya obovata	R.Br.	Lauraceae	Tree
Diploglottis australis	(Hook.) Hook.f. ex Benth	Sapindaceae	Tree
Doryphora sassafras	Endl.	Atherospermataceae	Tree
Dysoxylum mollissimum	(Miq.) Mabb	Meliaceae	Tree
Elaeocarpus angustifolius	Blume	Elaeocarpaceae	Tree
Elaeocarpus obovatus	G. Don	Elaeocarpaceae	Tree
Elaeocarpus reticulatus	Sm.	Elaeocarpaceae	Shrub or small tree
Ficus rubiginosa	Desf. ex Vent.	Moraceae	Tree
Flindersia australis	R.Br.	Rutaceae	Tree
Flindersia schottiana	F. Muell.	Rutaceae	Tree
Gmelina leichhardtii	(F. Muell.) Benth.	Lamiaceae	Tree
Karrabina benthamiana	(F. Muell.)	Cunoniaceae	Tree
Neolitsea dealbata	(R.Br.) Merr.	Lauraceae	Shrub or tree to 12 m
Orites excelsus	R.Br.	Proteaceae	Tree
Pittosporum multiflorum	(A. Cunn. ex Loudon) L.W.Cayzer et al.	Pittosporaceae	Shrub
Polyscias murrayi	(F. Muell.) Harms	Araliaceae	Tree
Sloanea australis	Benth. & F.Muell.	Elaeocarpaceae	Tree
Sloanea woollsii	(F. Muell.)	Elaeocarpaceae	Tree
Stenocarpus salignus	R.Br.	Proteaceae	Tree
Stenocarpus sinuatus	(Loudon) Endl.	Proteaceae	Tree
Toona australis	M. Roem.	Meliaceae	Tree
Tristaniopsis collina	Peter G. Wilson & J.T. Waterh.	Myrtaceae	Shrub or tree to 30 m
Tristaniopsis laurina	(Sm.) Peter G. Wilson & J.T. Waterh.	Myrtaceae	Tree
Wilkiea huegeliana	(Tul.) A.DC.	Monimiaceae	Shrub or small tree

Species data

For this study, I selected 24 tree and six shrub species typically associated with tropical and sub-tropical Australian rainforests. The species included members of the families Elaeocarpaceae (n = 5), Lauraceae (4), Proteaceae (3), Cunoniaceae (2), Meliaceae (2), Myrtaceae (2), Rutaceae (2), Sapindaceae (2), Araliaceae (1), Monimiaceae (1), Moraceae (1), Atherospermataceae (1), Fabaceae (1), Lamiaceae (1), Malvaceae (1), and Pittosporaceae (1) (Table 1). I collected occurrence records for each of the 30 species from the Atlas of Living Australia (ALA; http://ala.org.au), an online natural history database of Australian specimens (accessed in April 2017). In total, 55,773 records were downloaded. To reduce spatial uncertainty and improve the quality of the data, I applied the following data-cleaning procedures, removing records that were: i) non-georeferenced; ii) located beyond the terrestrial zone of Australia; iii) located in botanic gardens or classified as cultivated material; iv) collected prior to 1950; and/or v) categorized by ALA as environmental or spatial outliers. Additionally, to reduce sampling bias I removed duplicate records for a given species, classified as more than one record within a 1 × 1 km area. Thus, I retained a total of 6824 unique occurrences for all species (average = 227, SD = 155).
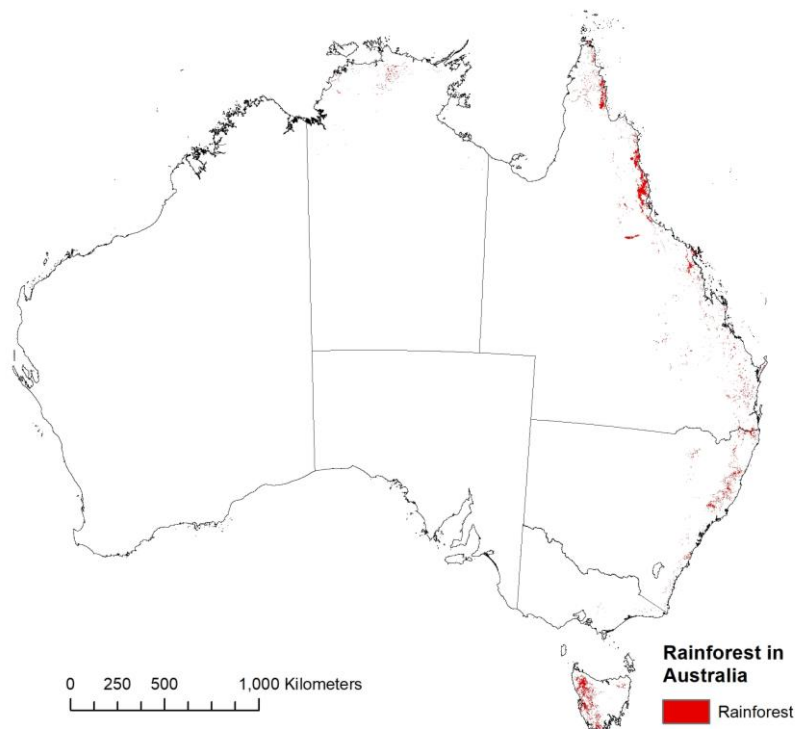

Figure 1: Spatial distribution of rainforest in Australia (source: Australia's State of the Forests Report 2013, http://www.agriculture.gov.au/abares/forestsaustralia/sofr/sofr-2013*).*

Environmental data

Initially, 17 environmental variables were selected to model suitable habitat of each species: 15 climate and two topographic variables (Supplementary Information Table S1). To generate baseline bioclimatic variables monthly data from the Ecosystem Modelling and Scaling Infrastructure Facility (eMAST; http://www.emast.org.au) were downloaded for (i) near surface daily minimum air temperature (tasmin), (ii) near surface daily maximum temperature (tasmax), and (iii) precipitation (pr), for the period 1983-2012, at 0.01 degree spatial resolution. Using these monthly data 19 standard bioclimatic variables, *sensu* ANUCLIM (Xu & Hutchinson, 2011) were calculated. From these 19 variables, I excluded Mean Temperature of the Wettest Quarter (Bio 08), Mean Temperature of the Driest Quarter (Bio 09), Precipitation of the Warmest Quarter (Bio 18) and Precipitation of the Coldest Quarter (Bio 19), as they showed spatial discontinuities across our study region.

The two topographic variables were used to characterise topography and its relationship to species occurrences: the Topographic Position Index (TPI) and the Topographic Wetness Index (TWI). The former, TPI, uses relative elevation as a fraction of local relief to classify cells into classes corresponding to upper, middle and lower slopes, while TWI estimates the relative wetness within a catchment. TPI and TWI data were downloaded from the CSIRO data portal (https://data.csiro.au) at the original grid resolution of 3 arc seconds (~0.00083 degrees) and later resampled to the 0.01 degree grid of the climate data by taking the average of values falling in the larger grid cells.

Past and Future Climate Scenarios

Climate scenarios for the Last Glacial Maximum (LGM, 22,000 ybp), the Mid-Holocene (MH, 6000 ybp) and for the 30-year period centred on 2070, were obtained from the Climate Model Inter-comparison Project 5 (CMIP5) data repository maintained by the Earth Survey Grid Federation (ESGF), which was accessed via the Lawrence Livermore National Laboratory node at https://esgf-node.llnl.gov/projects/esgf-llnl. Alternate climate scenarios, either past or future, comprise substantial uncertainty due to the wide range and variability of physical processes in the atmosphere, which is expressed differently by alternate Global Climate Models (GCM) (Buisson *et al.*, 2010). The climate simulated by different GCMs varies due to their parameterization, the attributes of their input data (e.g. the spatial resolution and physical characteristics of atmospheric and/or oceanic processes), and the resolution of their output (Whetton *et al.*, 2015). Hence, GCMs may differ in their simulations of past or

future conditions. Generally, higher confidence will be placed in GCMs that can satisfactorily simulate current climate in the region of interest, although identifying this subset of GCMs is not straightforward. As such, I referred to the analysis by Whetton *et al.* (2015), who assigned skill scores to multiple GCMs by comparing their ability to simulated observed temperature, rainfall and mean sea level pressure across different regions of the Australian continent. I selected the subset of these GCMs with skill scores above the median for eastern Australia. This process resulted in four GCMs for each of the past time periods and seven GCMs for the future (Table 2).

Minimum and maximum monthly surface temperature and monthly precipitation for the two paleo and future climate periods were also downloaded from the CMIP5 data repository (https://esgf-node.llnl.gov/projects/esgf-llnl). The future climate data were based on the 30 years centred on 2070 (i.e. average of 2056-2085), for two Representative Concentration Pathways (RCPs): 4.5 (representing equivalent radiative forcing of 4.5 W/m^2); and 8.5 (i.e., 8.5 W/m^2). RCPs indicate a set of trajectories that consider some of the main forcing agents of climate change, i.e. land-use change, rate of emission and concentration of radiative forcings (Van Vuuren *et al.*, 2011). RCP 4.5 is considered an intermediate pathway and RCP 8.5 is considered a high energy-intensive pathway (Van Vuuren *et al.*, 2011). The R package *ncdf4* (Pierce, 2017) was used to extract the data for each month between January 2056 and December 2085. Data were averaged to provide monthly 30-year means, and were then spatially downscaled and corrected for anomalies following the delta method based on thin plate spline spatial interpolation (Ramirez-Villegas & Jarvis, 2010). The interpolated anomalies were added to the baseline data (the eMAST-derived dataset for 1983-2012) and the final bioclimatic variables for each GCM were calculated. All environmental datasets were projected to Australia Albers Equal Area GDA 1994 (EPSG:3577) and clipped to eastern Australia (extending from 140.5 to 154° longitude and -43.74 to -9° latitude) (see Figure S3 for average mean annual temperature and annual precipitation anomalies for each time period).

Table 2. List of selected General Circulation Models (GCMs) for which paleo and future climate scenarios were obtained. The selection of GCMs was based upon skill score assessments undertaken by Whetton et al. (2015).

Last Glacial Maximum	Mid-Holocene	Future (RCP 4.5)	Future (RCP 8.5)
CNRM-CM5	BCC-CSM1-1	ACCESS1-0	ACCESS1-0
COSMOS-ASO	CNRM-CM5	CanESM2	CanESM2
MPI-ESM-P	MPI-ESM-P	GFDL-CM3	GFDL-CM3
MRI-CGCM3	MRI-CGCM3	MPI-ESM-LR	MPI-ESM-LR
		MPI-ESM-MR	MPI-ESM-MR
		MRI-CGCM3	MRI-CGCM3
		NorESM1-M	NorESM1-M

Species distribution modeling (SDM)

I used the maximum entropy algorithm, Maxent (ver. 3.3.3k) (Phillips *et al.*, 2006), to model habitat suitability for each species. Maxent is a machine learning algorithm widely applied for modeling species' distributions with presence-only data (Phillips *et al.*, 2006). This SDM generally has good predictive performance, including for species represented by few presence records (Wisz *et al.*, 2008; Zhang *et al.*, 2016). Maxent provides a measure of environmental suitability for the target species (Elith *et al.*, 2011). Locations with higher values are hypothesised to have greater suitability for the modelled species (Phillips *et al.*, 2006; Phillips & Dudík, 2008).

Pair-wise Pearson's correlations among the variables and the variance inflation factor (VIF) (Dormann *et al.*, 2013) were calculated using R package *usdm* (Naimi, 2013), applied within R version 3.1.2 (R Development Core Team 2014). When two variables were highly correlated (i.e. |r| > 0.7), I removed the variable with the higher VIF (Powney *et al.*, 2011), then reassessed the remaining predictors for their contribution to the model for each species (described below). Following Ikeda *et al.* (2014) and Sahlean *et al.* (2014), any variable with a contribution below 5% was iteratively removed from the respective model until all variables had contributions greater than 5% or only five variables remained. Thus, different sets of non-correlated climate variables were selected for each species. I modified Maxent's default settings to improve model performance by disabling hinge and threshold features to avoid locally overfit response curves, hence using only linear, product and quadratic features.

Following VanDerWal *et al.* (2009b), for each study species, background points were obtained using a target-species approach, selecting 10,000 random points from all plant

records held in the Australasian Virtual Herbarium (AVH; https://avh.chah.org.au/) that fell within a 200 km buffer of our target species. These analyses were undertaken using customized R code, based on the packages *dismo* (Hijmans *et al.*, 2017) and *rmaxent* (Baumgartner *et al.*, 2017). After modeling, I also used gdalUtils (Greenberg & Mattiuzzi, 2015), *rgeos (*Bivand & Rundel, 2017), *sp* (Pebesma & Bivand, 2005) and *raster* (Hijmans, 2016) packages, in addition to custom R code, for representation, comparison and manipulation of spatial data. Model performance was estimated for each model by calculating the average test AUC (the area under the receiver operating characteristic curve (Swets, 1988). Although AUC has some limitations and caution is advised when using it (Lobo *et al.*, 2008), this statistic is often used to measure model performance (Allouche *et al.*, 2006). A higher AUC indicates a better classification of suitable and unsuitable areas (Phillips *et al.*, 2006). I also utilized the true skill statistic (TSS) to evaluate model performance. TSS ranges from -1 to 1 and gives equal weight to model sensitivity and specificity (Allouche *et al.*, 2006; Shabani *et al.*, 2016). In addition, I generated Multivariate Environmental Similarity Surface (MESS) maps for each species, to assess the extent to which models extrapolated outside the training range of the data (Elith *et al.*, 2011).

Climate refugia

Binary distribution maps for all species across each time period and climate scenario were created by applying the threshold corresponding to the maximum sum of training specificity and sensitivity. This threshold has been found effective for presence-only data (Liu *et al.*, 2013; Liu *et al.*, 2016) and has been used in numerous Maxent-based studies (Weber, 2011; Razgour, 2015). For each species and time period, I stacked maps of habitat suitability to assess concordance across the climate scenarios, i.e. to identify those grid cells classified suitable across all scenarios. This represents a very conservative approach to accounting for variation between climate scenarios.

Using the concordance maps, species-specific refugia were then identified through the intersection of cells classified as suitable over consecutive time periods. These areas are interpreted as macro-refugia due to the resolution of the predictor variables used in this study (i.e. 1 km x 1 km). That is, any grid cell classified as suitable from the LGM and MH to the present day were interpreted as areas of climatic stability, and were termed "paleo refugia". I also identified two types of putative future macro-refugia. The first of these represented the intersection of current and future suitable habitat (termed "future refugia'),

while the second identified grid cells suitable throughout all four time periods (LGM, MH, current and 2070). I refer to the latter as "high value refugia" (HVR), hypothesizing that these sites may be particularly valuable from a conservation perspective, as they may enable the persistence of populations with high genetic diversity. Finally, I stacked species-specific macro-refugia maps, for each of the three categories described above, to identify geographic regions (Interim Biogeographic Regionalisation for Australia) (IBRA, 2012) projected to be putative macro-refugia for multiple species.

Results

Across the 30 species, the average cross-validated test AUC and TSS were 0.844 (SD = 0.056) and 0.552 (SD = 0.111), respectively. Values ranged from 0.727 (AUC) and 0.331 (TSS) for *Ficus rubiginosa* to 0.928 (AUC) and 0.726 (TSS) for *Sloanea woollsii* (Table 3), which indicates good to high classifier performance (Swets, 1988). The most important predictor variables for each SDM varied from species to species (for details see Supplementary Information Table S2), with Precipitation of Driest Month providing the greatest contribution to the models for 22 species. MESS maps indicated that extrapolation beyond the training range of the data occurred in some regions for all time periods, particularly the Cape York Peninsula, central Queensland and Tasmania, although to different extents for different species (for examples, see Figure S4). Note that these regions occur outside of the known current geographic region of each species.

For most species, models of current habitat are generally compatible with expert knowledge of their distributions (M. Rossetto, pers. comm). Exceptions are over-predictions of suitable habitat in south-western New South Wales and Victoria for *Flindersia australis*, and western Tasmania for *Argyrodendron trifoliolatum*, *Cryptocarya glaucescens*, and *Pittosporum multiflorum* (for details, see Supplementary Information Figure S1*)*. Over-prediction of current suitable habitat beyond species' known distributions may occur as factors in addition to be because of the factors in addition to predictor variables used in model calibration will influence species' range limits. Further, considerable fragmentation of many rainforests has occurred since European arrival. On average, suitable habitat spanned 188,496 km^2 (SD = 138,867 km^2), ranging from 47,648 km^2 for *Dysoxylum mollissimum* to 702,443 km^2 for *F. australis* (Table 3), and was largest under current conditions compared with the three other time periods considered in this study.

Which areas were suitable under paleo-climate?

In general, concordance maps indicated that suitable habitat spanned a smaller spatial extent in both previous time periods compared to the present (Table 3). Indeed, during the cooler-drier conditions of the LGM suitable habitat was projected to be 65% smaller, on average, than under current climate (SD = 19%). For two species, *Stenocarpus salignus* and *D. mollissimum*, suitable habitat was > 90% smaller than at present.

However, by the mid-Holocene both rainfall and temperature had increased substantially, as had the size of suitable habitat, although it was still smaller than present for most species (average = 21%, SD = 26%). Exceptions were *Tristaniopsis laurina, D. mollissimum, Elaeocarpus reticulatus, F. australis*, and *A. trifoliolatum*, for which suitable habitat during the mid-Holocene was between 3 to 42% larger than in the present.

Table 3. Suitable habitat for 30 tropical or sub-tropical rainforest plant species were modelled using Maxent. For each species, predictive power (AUC [area under the receiver operator curve] and TSS [true skill sensitivity]) is given, as is the number of unique occurrence records and the areal size of suitable habitat under past (LGM [Last Glacial Maximum] and MH [mid-Holocene]), current and future (2070, RCP 4.5 and RCP 8.5) climate scenarios.

Species	AUC	TSS	No. records	Area of suitable habitat (km^2)				
				LGM	MH	Current	2070 (RCP 4.5)	2070 (RCP 8.5)
Argyrodendron trifoliolatum	0.804	0.453	154	78,813	268,116	188,472	57150	62378
Callicoma serratifolia	0.838	0.555	367	44,922	91,536	108,205	38581	29072
Castanospermum australe	0.798	0.466	178	18,537	91,536	109,725	23248	20470
Castanospora alphandii	0.913	0.696	123	31,786	92,809	152,340	83486	42529
Cinnamomum oliveri	0.881	0.666	141	49,751	151,615	152,112	115336	103771
Cryptocarya glaucescens	0.883	0.593	226	51,885	90,639	104,548	62896	51731
Cryptocarya obovata	0.885	0.629	83	194,649	174,851	246,055	41262	29885
Diploglottis australis	0.815	0.501	106	26,437	52,201	100,394	77489	101983
Doryphora sassafras	0.835	0.515	308	26,180	88,977	119,697	65789	60729
Dysoxylum mollissimum	0.888	0.646	126	1,538	50,615	47,648	17431	15493
Elaeocarpus angustifolius	0.891	0.635	80	30,848	137,517	145,669	104541	104072
Elaeocarpus obovatus	0.801	0.439	281	29,939	86,222	208,325	137480	130992
Elaeocarpus reticulatus	0.785	0.418	634	47,105	233,005	205,142	94744	78284
Ficus rubiginosa	0.727	0.331	701	219,636	415,908	498,401	475746	442126
Flindersia australis	0.769	0.451	205	199,541	893,860	702,443	269341	309117
Flindersia schottiana	0.848	0.566	195	13,159	89,046	124,423	84335	72043
Gmelina leichhardtii	0.917	0.714	93	72,088	125,087	136,090	70281	56190
Karrabina benthamiana	0.92	0.723	57	76,353	60,634	117,270	32149	25752
Neolitsea dealbata	0.847	0.530	484	57,424	34,585	129,365	38354	22949
Orites excelsus	0.872	0.578	211	125,602	93,593	177,176	94336	74983
Pittosporum multiflorum	0.806	0.493	324	143,241	223,429	230,543	136023	102895
Polyscias murrayi	0.857	0.542	130	54,493	137,301	211,532	101410	87928
Sloanea australis	0.88	0.617	246	44,052	91,728	140,261	64491	55526
Sloanea woollsii	0.928	0.726	88	44,882	29,005	90,074	15398	8030

Stenocarpus salignus	0.751	0.372	232	8,566	163,231	168,479	133414	146955
Stenocarpus sinuatus	0.914	0.690	97	22,606	38,219	54,318	20220	11736
Toona australis	0.768	0.392	227	223,293	444,707	479,784	270180	218354
Tristaniopsis collina	0.867	0.578	173	51,767	101,864	143,122	70397	55551
Tristaniopsis laurina	0.773	0.437	333	44,007	229,449	222,284	101513	97548
Wilkiea huegeliana	0.87	0.612	221	31,634	119,660	140,995	108849	100111
Mean	0.84	0.55	227	68,824	163,364	188,496	100195	90639
SD	0.06	0.11	155	63,740	170,460	138,866	93462	91533

Which areas may be suitable in the future?

I projected Maxent models onto multiple climate scenarios for 2070, for RCP 4.5 and 8.5. Under RCP 4.5, which projects a modest increase in temperature and decline in precipitation, suitable habitat was projected to decrease for all species (average decrease = 53%, SD = 20%) (Table 3). The decline was projected to decrease at least 70% for six species.

Climate scenarios under RCP 8.5 simulate a substantially warmer and drier future for the study area (Supplementary Information Figure S3) than RCP 4.5. While suitable habitat for the 30 species was projected to be an average 48% smaller than at present (SD = 23%), slight increases were simulated for one species - *Diploglottis australis* (1.5%) (Table 3). For this species, the spatial extent of suitable habitat by 2070 is likely to be larger than at any time since the LGM, although this does not mean that either species will be able to occupy all areas projected to be suitable. In contrast, eight species were projected to experience substantial declines in suitable habitat (> 70%). Among them, *Sloanea woollsii* is projected to lose ~91% of its current suitability in 2070 under the RCP 8.5 scenario (Table 3).

Distribution of paleo refugia for rainforest species

Paleo refugia, areas that have been historically stable, were identified based on the intersection of suitable habitat over three time periods: LGM, mid-Holocene, and the current period. On average, paleo refugia spanned 23% of species' current ranges (SD = 12%), representing an area of 49,150 km^2 (SD = 53,237 km^2) (Table 4). The species with the smallest paleo refugia was *D. mollissimum* (1485 km^2, spanning 3% of current suitable habitat), and can be contrasted to *A. trifoliolatum,* which had the largest paleo refugia relative to the size of current suitable habitat (42%). Maps of paleo refugia for the 30 species were stacked to identify centres of paleo refugia: areas that have historically been suitable for multiple species. These centres, suitable for at least 15 species, are located across four of Australia's IBRA (Interim Biogeographic Regionalisation for Australia) Bioregions: the Wet Tropics in north-east Queensland; Central Mackay Coast; South Eastern Queensland; and North Coast of New South Wales (Figure 2).
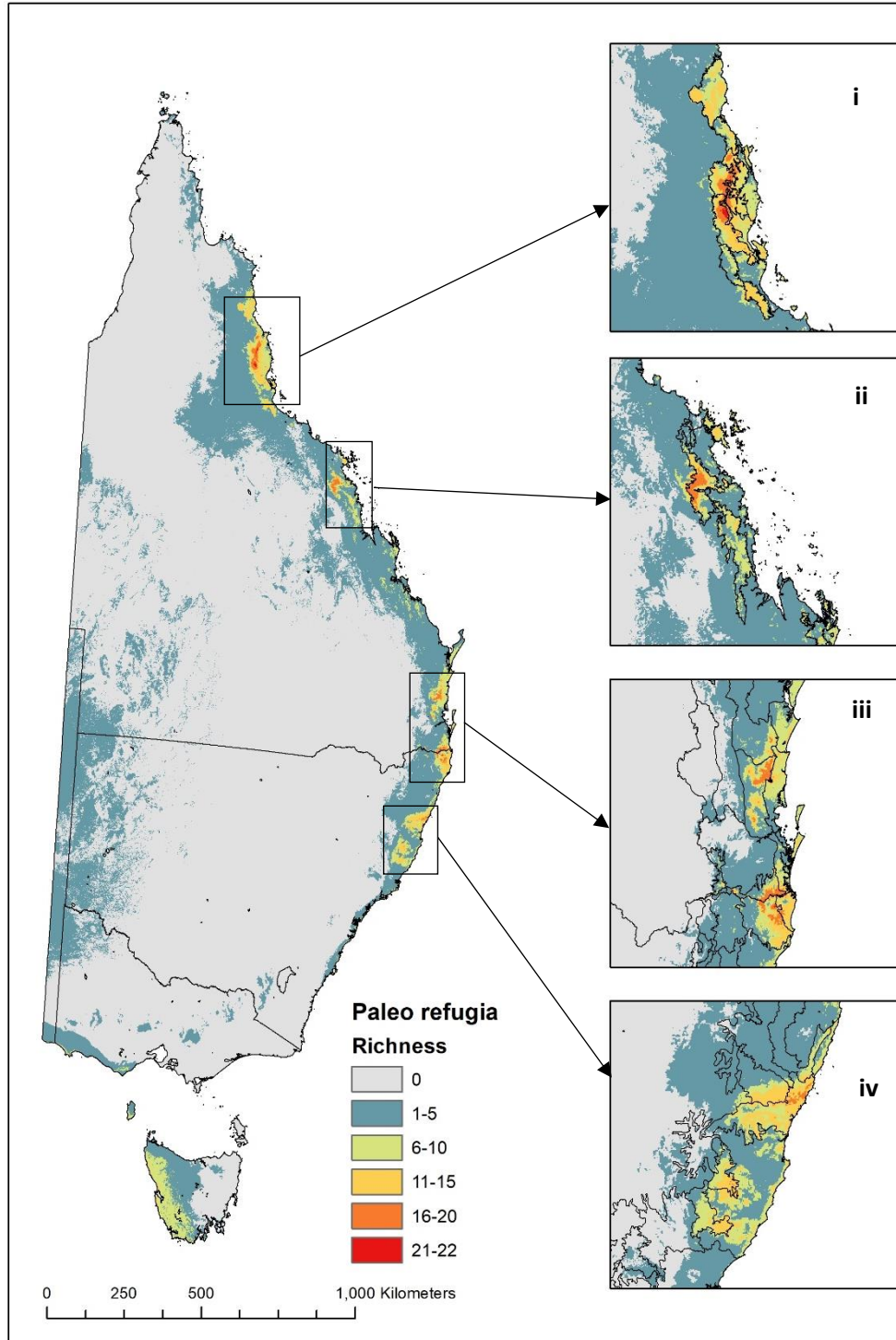
Figure 2: Centres of paleo refugia (inset map showing four IBRA [Interim Biogeographic Regionalisation for Australia] bioregions i. Wet Tropics, ii. Central Mackay Coast, iii. South Eastern Queensland, and iv. North Coast of New South Wales) for 30 tropical and subtropical Australian rainforest plant species, based on habitat suitability maps generated with Maxent. Paleo refugia are defined as the intersection of areas classified as suitable over consecutive time periods: the Last Glacial Maximum (LGM), the mid-Holocene and the current period.

Table 4. Climate refugia for 30 tropical and sub-tropical rainforest plant species calculated by stacking the thresholded habitat suitability maps. Three types of refugia have been measured - Paleo refugia (concordance between Last Glacial Maximum (_LGM), mid-Holocene (MH) and the current period), high value refugia (concordance between LGM, MH, current and future) and future refugia (concordance between current and future). For each species, estimate of area (km²) is given for respective refugia, as is the percent of the current range that contains refugia based on data in Table 3.

| Species | Size of refugia km² (% of current range) | | | | |
	Paleo refugia	High value refugia RCP 4.5	High value refugia RCP 8.5	Future refugia RCP 4.5	Future refugia RCP 8.5
Argyrodendron trifoliolatum	78,358 (42%)	21,389 (11%)	35,182 (19%)	57116 (30%)	62326 (33%)
Callicoma serratifolia	30,218 (28%)	17,351 (16%)	26,887 (25%)	38372 (35%)	28779 (27%)
Castanospermum australe	18,469 (17%)	13,035 (12%)	17,557 (16%)	23168 (21%)	20335 (19%)
Castanospora alphandii	31,591 (21%)	26,339 (17%)	31,501 (21%)	60705 (40%)	35695 (23%)
Cinnamomum oliveri	46,096 (30%)	44,952 (30%)	45,266 (30%)	115139 (76%)	103622 (68%)
Cryptocarya glaucescens	44,609 (43%)	42,508 (41%)	44,335 (42%)	62885 (60%)	51731 (49%)
Cryptocarya obovata	106,295 (43%)	19,509 (8%)	13,065 (5%)	41099 (17%)	29614 (12%)
Diploglottis australis	14,876 (15%)	8,531 (8%)	11,336 (11%)	59404 (59%)	59846 (60%)
Doryphora sassafras	8,494 (7%)	4,957 (4%)	3,799 (3%)	63176 (53%)	54839 (46%)
Dysoxylum mollissimum	1,485 (3%)	1,352 (3%)	1,462 (3%)	17291 (36%)	15189 (32%)
Elaeocarpus angustifolius	30,836 (21%)	30,328 (21%)	30,061 (21%)	104534 (72%)	103778 (71%)
Elaeocarpus obovatus	23,389 (11%)	21,910 (11%)	15,728 (8%)	117243 (56%)	81387 (39%)
Elaeocarpus reticulatus	47,015 (23%)	38,567 (19%)	46,702 (23%)	91957 (45%)	74047 (36%)
Ficus rubiginosa	176,211 (35%)	168,790 (34%)	155,521 (31%)	420475 (84%)	350895 (70%)
Flindersia australis	195,599 (28%)	123,470 (18%)	168,435 (24%)	246230 (35%)	250214 (36%)
Flindersia schottiana	12,330 (10%)	12,305 (10%)	12,317 (10%)	71924 (58%)	56050 (45%)
Gmelina leichhardtii	49,465 (36%)	42,878 (32%)	38,518 (28%)	70281 (52%)	56190 (41%)
Karrabina benthamiana	26,376 (22%)	7,639 (7%)	4,397 (4%)	31779 (27%)	25051 (21%)
Neolitsea dealbata	21,405 (17%)	12,836 (10%)	7,316 (6%)	33839 (26%)	16673 (13%)
Orites excelsus	67,929 (38%)	56,903 (32%)	49,560 (28%)	93016 (52%)	74718 (42%)
Pittosporum multiflorum	84,902 (37%)	58,371 (25%)	51,286 (22%)	134845 (58%)	102489 (44%)
Polyscias murrayi	22,581 (11%)	12,317 (6%)	6,734 (3%)	96479 (46%)	77046 (36%)
Sloanea australis	27,566 (20%)	14,497 (10%)	9,739 (7%)	62984 (45%)	52027 (37%)

Sloanea woollsii	15,332 (17%)	9,181 (10%)	8,811 (10%)	15225 (17%)	7730 (9%)
Stenocarpus salignus	6,773 (4%)	5,186 (3%)	4,869 (3%)	130100 (77%)	128845 (76%)
Stenocarpus sinuatus	19,982 (37%)	3,864 (7%)	4,788 (9%)	19005 (35%)	11366 (21%)
Toona australis	194,868 (41%)	140,695 (29%)	114,852 (24%)	268644 (56%)	215365 (45%)
Tristaniopsis collina	31,389 (22%)	28,855 (20%)	28,166 (20%)	70355 (49%)	55522 (39%)
Tristaniopsis laurina	8,677 (4%)	8,457 (4%)	8,667 (4%)	101309 (46%)	96996 (44%)
Wilkiea huegeliana	31,388 (22%)	27,030 (19%)	27,221 (19%)	107595 (76%)	98442 (70%)
Mean	49,150	34,133	34,135	94,205	79,894
SD	53237	40,842	41,681	84,863	74,723

Distribution of future refugia

Future refugia, defined as the intersection between current and future suitable habitat, were projected to be substantially larger in spatial extent than paleo refugia, spanning an average 94,205km^2 (SD = 84,863km^2) and 79,894km^2 (SD = 74,723km^2), under RCP 4.5 and 8.5, respectively (Table 4). However, the size of putative future refugia were ~48% (SD = 18%) and 40% (SD = 18%) of species' current ranges, under the two RCPs, respectively. Centres of future refugia were projected to be more extensive than centres of paleo refugia, and extend further south such as the Sydney Basin the South East Coastal Plain bioregions, and also includes regions beyond species' known ranges, e.g. western Tasmania (Figure 3). These areas are projected to be currently suitable, and remain so in the future, but are currently unoccupied.
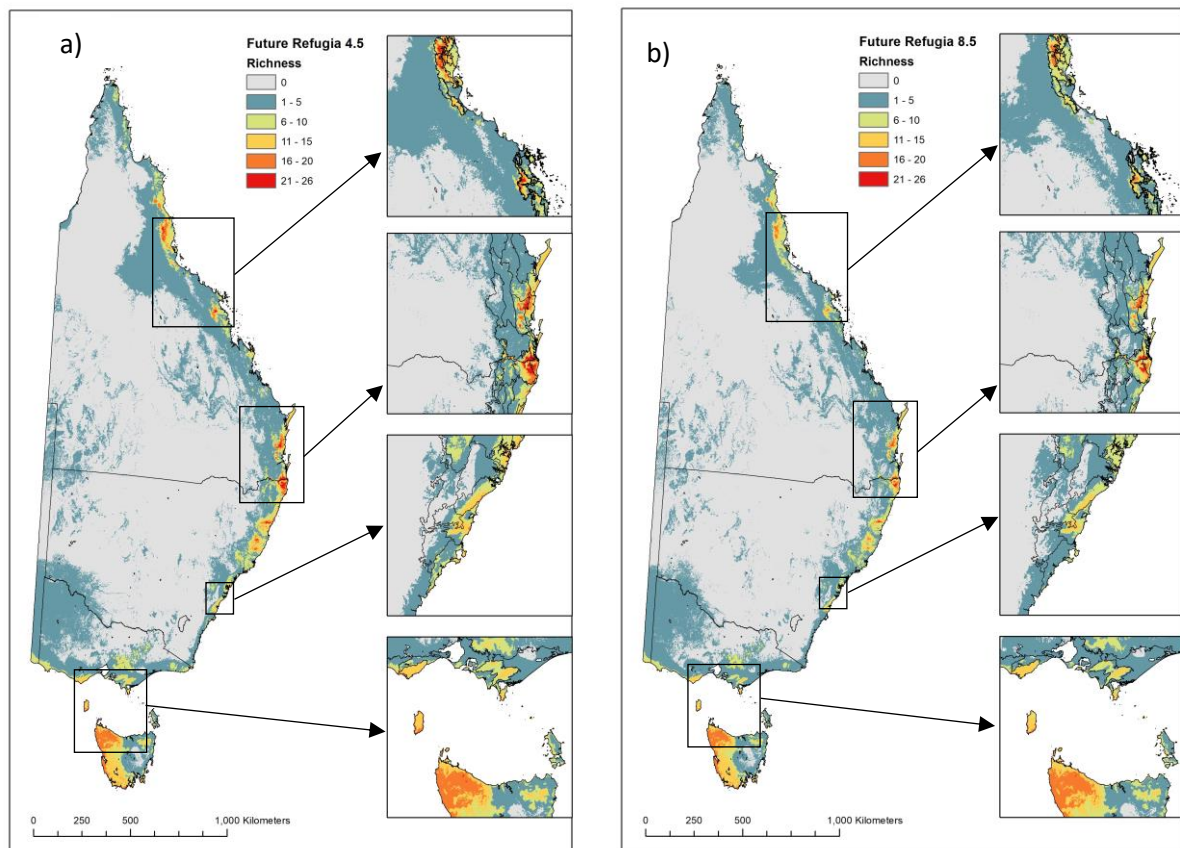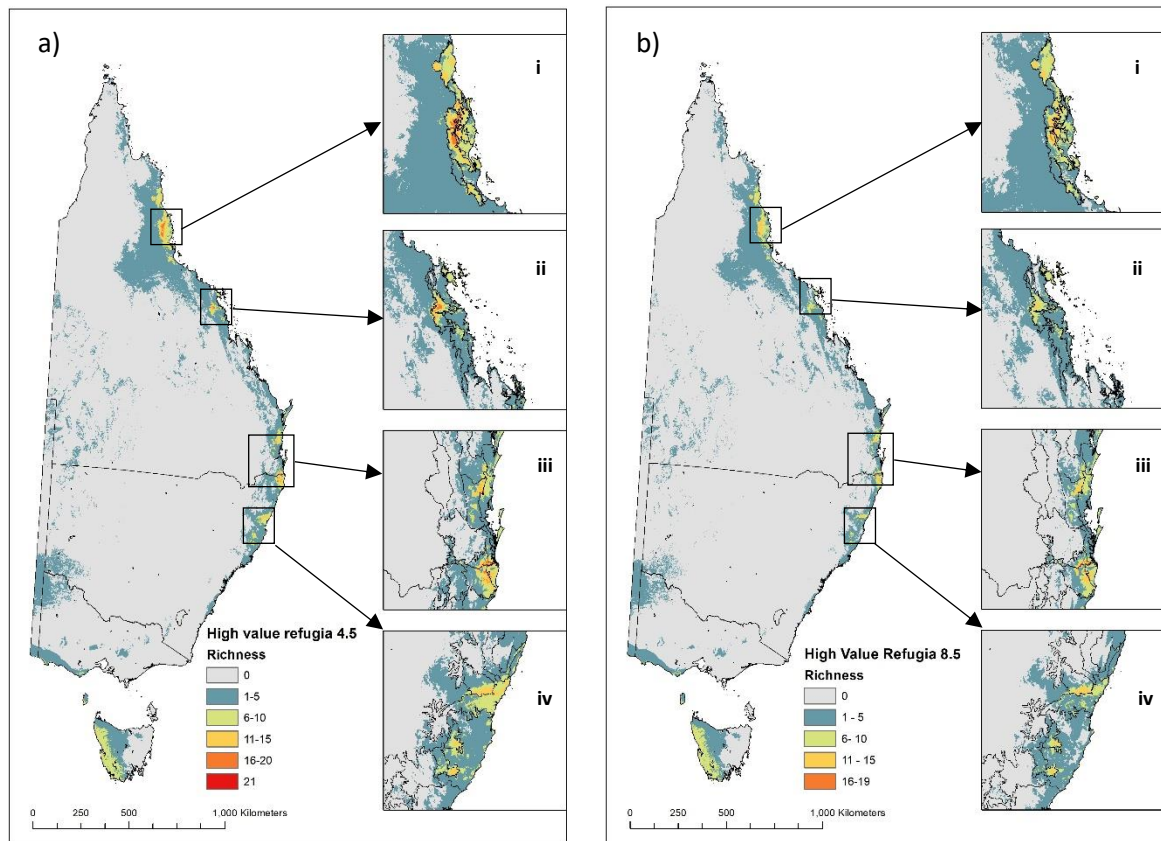

Figure 3: Centres of future refugia for (inset map showing four IBRA [Interim Biogeographic Regionalisation for Australia] regions i. Wet Tropics and Central Mackay Coast, ii. South Eastern Queensland and North Coast of New South Wales, iii. Sydney Basin, and iv. South East Coastal Plain) for 30 tropical and subtropical Australian rainforest plant species, based on habitat suitability maps generated with Maxent. Future refugia were defined as the intersection of areas classified as suitable under current climate as well as scenarios for 2070 under (a) RCP 4.5 and (b) RCP 8.5.

Distribution of high value refugia (HVR) for rainforest species

By definition, HVR must be the same size or smaller than, and contained within, areas identified as paleo refugia. On average, HVRs were projected to be 29% smaller than paleo refugia (SD = 26%), meaning that centres of high value refugia will also be restricted (Figure 4). The size of HVR under both RCPs was similar, spanning an average 16% (SD 11%) of current ranges (RCP 4.5 average = 34,133 km^2, SD 40,842 km^2; RCP 8.5 average = 34,136 km^2, SD = 41,681 km^2) (Table 4). Again, the smallest HVR was identified for *D. mollissimum* (1352 km^2 and 1462 km^2 for RCP 4.5 and RCP 8.5, i.e. ~3% of its current range). The largest, relative to current suitable habitat, was estimated for *C. glaucescens* (42,508 km^2 RCP 4.5 [41%] and 44,335 km^2 RCP 8.5 [42%]).

Figure 4: Centres of high value refugia (HVR) (inset map showing four IBRA [Interim Biogeographic Regionalisation for Australia] regions i. Wet Tropics, ii. Central Mackay Coast, iii. South Eastern Queensland, and iv. North Coast of New South Wales) for 30 tropical and subtropical Australian rainforest plant species, based on habitat suitability maps generated with Maxent. HVR were defined as the intersection of areas classified as suitable over consecutive time periods: Last Glacial Maximum, mid-Holocene, the current period, and 2070 under (a) RCP 4.5 and (b) RCP 8.5.

Of the four centres of paleo refugia (Figure 2), higher elevation areas of the Wet Tropics will remain as refugium for numerous species, while the Central Mackey Coast, South Eastern Queensland and North Coast of New South Wales are projected to support fewer species (Figure 4).

Discussion

The distribution of suitable habitat for 30 rainforest plant species has shifted substantially over geological time, and anthropogenic climate change will likely result in contractions to the extent of suitable habitat for most species. However, high value refugia – geographic regions projected to be climatically stable over past, current and future time periods – will exist for most species until at least 2070. These refugia are likely to play an important role in the conservation of rainforest plants and biodiversity during this current period of rapid climate change.

Shifts in suitable habitat since the Last Glacial Maximum
Of the time periods considered in this study, suitable habitat was most constrained during the Last Glacial Maximum (LGM, ~ 22,000 ybp), a period of high aridity, increased evapotranspiration, and cooler temperatures (Bowler *et al.*, 1976; Dodson & Ono, 1997; Petherick *et al.*, 2008). Such conditions restricted rainforest vegetation cover and resulted in severe contractions of rainforest species from their previous ranges (Williams & Pearson, 1997; Costion *et al.*, 2015). SDM hindcasts to the LGM demonstrate that suitable habitat during this period was between 21-97% smaller than the size of current suitable habitat.

By the mid-Holocene, temperature had increased considerably (~4°C) as had precipitation (Kershaw & Nix, 1988; Moritz *et al.*, 2009). SDMs indicate that suitable habitat expanded from the LGM to the mid-Holocene for all but five species (*Cryptocarya obovata*, *Karrabina benthamiana*, *Neolitsea dealbata*, *Orites excelsus*, *S. woollsii*). However, with the exception of *A. trifoliolatum*, *D. mollissimum*, *E. reticulatus*, *F. australis*, *T. laurina*), suitable habitat covered a smaller geographic range than during the present day.

As the 21st century progresses, most species' ranges are once again likely to contract with increases in temperature and shifts in precipitation. While the decline in spatial extent projected for 2070 under RCP 8.5 averages 40% (SD = 28%), for nine species this extent may be smaller in size than prior to the LGM. Such declines may be even more profound, however, as my analysis does not consider whether habitat

is likely to be within the dispersal range of these species, or meets other requirements for establishment and persistence.

Distribution of paleo-climate refugia

The congruence of areas projected to have suitable habitat over consecutive time periods can be used to identify future climate refugia. I defined paleo refugia as areas that have remained suitable from the LGM and mid-Holocene to the present day. On average, only 23% (SD = 12%) of species' current ranges were suitable in both the LGM and mid-Holocene. These refugia are mostly concentrate in four IBRA bioregions (IBRA Version 7; IBRA, 2012) along the north-eastern and central-eastern coastline of Australia (Figure 2): Wet Tropics, Central Mackay Coast, South-Eastern Queensland and North Coast of New South Wales. Indeed, the Wet Tropics supports an incredible diversity of rainforest plant genera and is well recognized as a biodiversity hotspot (Williams *et al.*, 2011). Patches of the wet tropics including higher elevation areas have been also identified as climate refuge (Adam, 1992; Hilbert *et al.*, 2007; VanDerWal *et al.*, 2009a).

It is generally assumed that since paleo refugia have been stable for considerable time, these regions may harbour unique and highly diverse genetic materials (Abbott *et al.*, 2000; Petit *et al.*, 2003; Provan & Bennett, 2008; Thomas *et al.*, 2012; Russell *et al.*, 2014; Havrdová *et al.*, 2015). Compared to areas that recolonize from the refugia, paleo refugia have a low risk of genetic bottlenecks (Ehrich *et al.*, 2007) and hence extinction of paleo refugia can result in a substantial loss of genetic diversity (Alsos *et al.*, 2009).

Refugia from anthropogenic climate change

Identifying and protecting climate refugia is a key climate change adaptation approach for conservation planning, and is frequently undertaken using SDMs (Schmitz *et al.*, 2015; Jones *et al.*, 2016). Such studies typically assess the congruence of suitable habitat under current and future conditions, and may distinguish between 'in situ' and 'ex situ' refugium (Ashcroft, 2010). The former refers to regions suitable in both time periods whereas the latter identifies areas presently unsuitable for the target species. From the perspective of rainforest plant species, identifying in situ refugia is more likely to present a viable conservation strategy given dispersal limitations (Holl, 1999; Ingle,

2003) and barriers and other biotic requirements. Furthermore, in situ refugia – particularly in regions that have also been paleo refugia – may enable the persistence of populations with high genetic diversity.

In this study, I identified High Value Refugia (HVR), i.e. areas likely to have been climatically stable since the LGM through to the present and until at least 2070. HVR are projected to be less than one-third of the size of paleo refugia, spanning an average 16% (SD = 11%) of species' current suitable habitat. Four species are likely to have HVR spanning < 5% of their current range (*Doryphora sassafras*, *D. mollissimum*, , *S. salignus*, *T. laurina*). While each of the four centres of refugia will continue to remain as key locations for tropical and sub-tropical rainforest plant species, they are projected to harbour conditions suited to fewer species. For instance, the Wet Tropics is projected to no longer be suitable for *D. sassafras* or *Wilkiea huegeliana*, while there will be no refugia in NSW for *K. benthamiana* and *C. obovata* (for details see Supplementary Information Figure S2).

HVR can be distinguished from other future refugia that have become climatically stable more recently. These areas were identified by the intersection of only current and future suitable habitat. Although conservation of HVR may be preferable if these areas harbour populations with high genetic diversity, should insufficient HVR exist then other refugia may be necessary to secure the survival of some species over the long term. Indeed, three of the four species projected to have greatly constrained HVR have future refugia spanning > 40% of their current range (*D. sassafras*, *D. mollissimum*, *S. salignus*, and *T. laurina*). However, much of these areas are projected to lie considerably further south than the species' current ranges e.g. in Victoria and Tasmania, making it exceedingly unlikely that populations will establish there without human intervention.

Note that since SDMs are representations of suitable habitat only, as opposed to occupancy, it is possible that some HVRs occur in areas in which there is no current population of the target species. This is a limitation of my modelling approach, although one potential solution to this would be to restrict projections of suitable habitat to grid cells within a given proximity of known populations. Even this approach would still assume that sites have been continuously occupied since the LGM. It should also

be recognised that, under future climate scenarios, some species may be able to exist in localised micro-refugia that are at a resolution too small to be identified by my study.

Variable contribution to SDMs

A general approach when modelling the distribution of suitable habitat for multiple species has been to use a single set of predictor variables for all species. In this study, however, a variable selection procedure was undertaken, the end result of which was that a) variables incorporated into the final model had a correlation coefficient of < 0.7 and b) a unique set of variables was selected for each species, based on the contribution of each variable to the model and collinearity of variables.

Analysis of variable contribution indicated that precipitation of the driest month, precipitation of the wettest month and annual precipitation frequently had the greatest influence on habitat suitability (Supplementary Information Table S2). Indeed, rainfall is a key driver of rainforest distribution (McJannet *et al.*, 2007; Wallace & McJannet, 2013) and future changes in rainfall are suggested to have a greater impact on rainforest structure than changes in temperature (Wallace & McJannet, 2012). However, temperature is also an important variable for predicting rainforest distribution (Zhang *et al.*, 2016). My results reveal that after precipitation, mean diurnal range and mean temperature of warmest quarter also contribute substantially to models.

Soil nutrients also plays crucial role in limiting and regulating the distribution of rainforest community (Sollins, 1998; John *et al.*, 2007; Vleminckx *et al.*, 2015). Different regions of Australia are geologically distinct, and the aggregated effect of climate, geology or landscape history has driven the distribution of different vegetation types (Orians & Milewski, 2007; Bowman *et al.*, 2010). In my study, soil characteristics were not included as predictor variables: these have changed substantially over the time periods included in this study, and spatial data for these variables for paleo periods were not available. This does represent an unavoidable limitation to my modelling approach.

Future research

The identification of climate refugia can be further advanced with the incorporation of additional dimensions, such as by combining genetic data with SDMs (McCallum *et*

al., 2014; Reside *et al.*, 2014). This integrated approach can detect refugia for genetic and lineage diversity, which could not be identified with classical methods (Keppel *et al.*, 2012; Ikeda *et al.*, 2017). Furthermore, the study of genetic diversity can reveal significant information about the underlying patterns of population spread and establishment (Zhou *et al.*, 2013; Assis *et al.*, 2016). For example, gene flow due to dispersal traits of a population is an indicator of a species' range-shifting ability in response to historical climate change (McCallum *et al.*, 2014). Thus, knowledge on evolution of genetically adaptive traits (Franks & Hoffmann, 2012) can uncover consequences of future climate change and infer the effect of past climatic history on genetic variation (Alsos *et al.*, 2009).

While the current study identifies numerous refugia for rainforest species, projections indicate that in the future there will be a broad-scaled reduction of the spatial extent of climatically suitable habitat. Consequent population extirpations may have substantial implications for the genetic diversity of these species. Presently, the Royal Botanic Gardens (Sydney) is assessing genetic diversity for up to 30 populations of each of the species included in this study (M. Rossetto, pers. com). The genetic signature left behind from the biotic and abiotic interaction of populations with refugia may help to pinpoint the origin of historical refugia (Hewitt, 2004; Brito, 2005; Assis *et al.*, 2016). Such genetic information can also help to infer possible effects of past climate change (Keppel *et al.*, 2012), which is responsible for current genetic patterns (McCallum *et al.*, 2014), and suggest future adaptive actions to preserve suitable conditions for speciation (Willis & Birks, 2006). Our goal is to assess the extent to which centres of genetic diversity for these species coincide with paleo climate refugia, assess the consequences of climate change for genetic diversity, and undertake spatial prioritization for conservation planning.

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Supplementary materials

Table S1: *List of environmental variables used to model habitat suitability species distributions in SDM of in this study, with their code names and description.*

Environmental variables	Description
Bio01	Annual mean temperature (°C)
Bio02	Mean diurnal temperature range (mean (period max-min)) (°C)
Bio03	Isothermality (Bio02 ÷ Bio07)
Bio04	Temperature seasonality (Coefficient of variance)
Bio05	Max temperature of warmest week (°C)
Bio06	Min temperature of coldest week (°C)
Bio07	Temperature annual range (Bio05-Bio06) (°C)
Bio10	Mean temperature of warmest quarter (°C)
Bio11	Mean temperature of coldest quarter (°C)
Bio12	Annual precipitation (mm)
Bio13	Precipitation of wettest week (mm)
Bio14	Precipitation of driest week (mm)
Bio15	Precipitation seasonality (Coefficient of variance)
Bio16	Precipitation of wettest quarter (mm)
Bio17	Precipitation of driest quarter (mm)
TPI	Topographic Position Index
TWI	Topographic Wetness Index

Table S2: *Permutation importance (%) of environmental variables used in the Maxent modeling for 30 tropical and subtropical Australian rainforest species.*

Species	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	TPI	TWI
Argyrodendron trifoliolatum	-	32.9	20.6	-	-	-	-	-	-	-	4	14.8	27.7	-	-	-	-
Callicoma serratifolia	-	-	-	15.3	-	-	-	7.6	-	0.3	-	68.8	8	-	-	-	-
Castanospermum australe	-	20.4	28.9	-	-	-	-	7	-	-	12	31.7	-	-	-	-	-
Castanospora alphandii	-	4.4	-	-	-	-	-	-	-	-	55.1	14.5	24.3	-	-	-	1.7
Cinnamomum oliveri	-	11.7	-	14.2	-	-	-	-	-	58.5	-	3.6	-	-	-	-	12
Cryptocarya glaucescens	-	-	-	15.3	-	-	-	3.8	-	-	62.5	-	16.4	-	-	-	1.9
Cryptocarya obovata	23.2	-	6.7	-	36.6	-	-	-	-	-	-	2.8	30.7	-	-	-	-
Diploglottis australis	-	13.1	6.2	-	-	-	-	25.5	-	48.4	-	-	-	-	-	-	6.7
Doryphora sassafras	28.5	24	-	-	-	-	-	-	-	23.2	-	18.5	5.8	-	-	-	-
Dysoxylum mollissimum	-	38.7	22.6	-	-	-	-	8.3	-	9.6	-	-	20.9	-	-	-	-
Elaeocarpus angustifolius	-	36.5	7.2	-	-	-	-	-	-	-	18.7	5.8	-	-	-	-	31.8
Elaeocarpus obovatus	-	17.6	10	-	-	-	-	37.9	-	27.8	-	6.8	-	-	-	-	-
Elaeocarpus reticulatus	12.2	-	-	63.5	-	-	-	-	-	1.7	-	19.7	-	-	-	-	2.8
Ficus rubiginosa	-	30.1	-	-	-	-	-	-	21.8	16.7	-	-	16.7	-	-	-	14.7
Flindersia australis	-	10.6	6.2	-	-	-	-	7.8	-	-	7.7	25.9	32.1	-	-	-	9.7
Flindersia schottiana	-	15.8	-	-	-	-	-	37.3	-	35.9	-	8	-	-	-	-	3
Gmelina leichhardtii	-	-	-	36.5	-	-	-	5.1	-	7.3	-	10.5	32.7	-	-	-	7.8
Karrabina benthamiana	23	-	4.5	-	56	-	-	-	-	-	-	-	15	-	-	1.5	-
Neolitsea dealbata	-	5.6	-	-	-	-	-	19	-	62.3	-	12.5	-	-	-	-	0.7
Orites excelsus	-	4.8	-	-	-	-	-	21.1	-	48.9	-	8	17.2	-	-	-	-
Pittosporum multiflorum	-	-	-	42.3	-	-	-	14.4	-	28.3	-	7.8	7.2	-	-	-	-
Polyscias murrayi	-	27	-	-	-	-	-	30.1	-	10.1	-	2.3	30.5	-	-	-	-
Sloanea australis	-	9.9	-	-	-	-	-	19.4	-	64.7	-	2.2	-	-	-	3.8	-
Sloanea woollsii	-	-	-	-	12.4	19.2	-	-	-	-	-	6.7	59.9	-	-	-	1.8
Stenocarpus salignus	-	49.7	-	-	-	-	-	18.7	-	-	-	-	10.6	-	-	1.9	19.1
Stenocarpus_sinuatus	-	21.3	5.9	-	-	-	-	8.7	-	-	26.3	9.7	28.1	-	-	-	-
Toona australis	-	1	-	66.5	-	-	-	17.2	-	4.4	-	-	-	-	-	-	10.9
Tristaniopsis collina	-	-	8.5	31	-	-	-	24	-	26.9	-	9.7	-	-	-	-	-
Tristaniopsis laurina	22	-	6.4	32.3	-	-	-	-	-	17.3	-	-	21.9	-	-	-	-
Wilkiea huegeliana	-	21.2	-	-	-	-	-	4.2	-	49.3	-	4	21.3	-	-	-	-

Figure S1: *Current habitat suitability maps for 30 tropical and sub-tropical Australian rainforest plant species generated by the species distribution model (SDM) Maxent.*
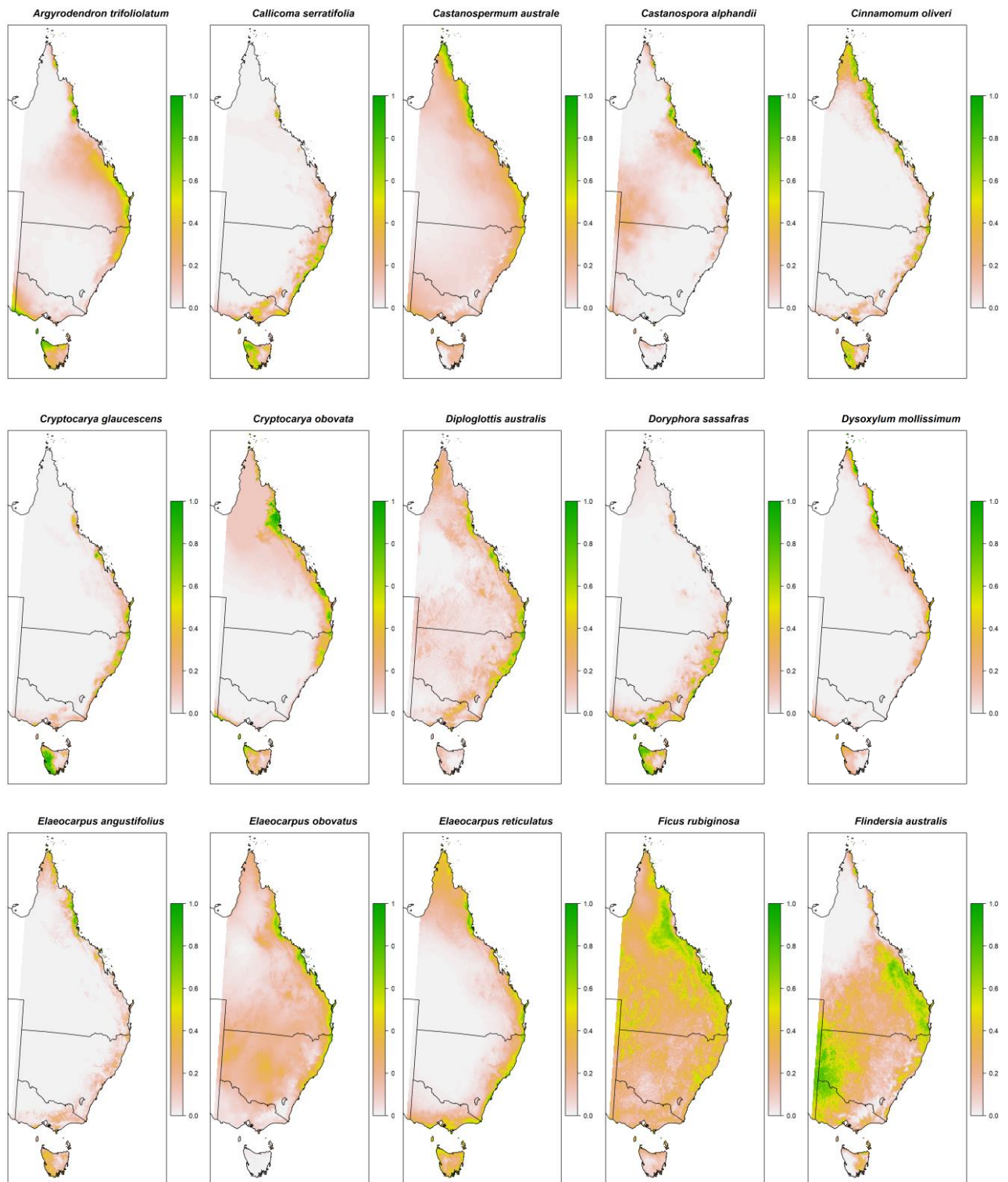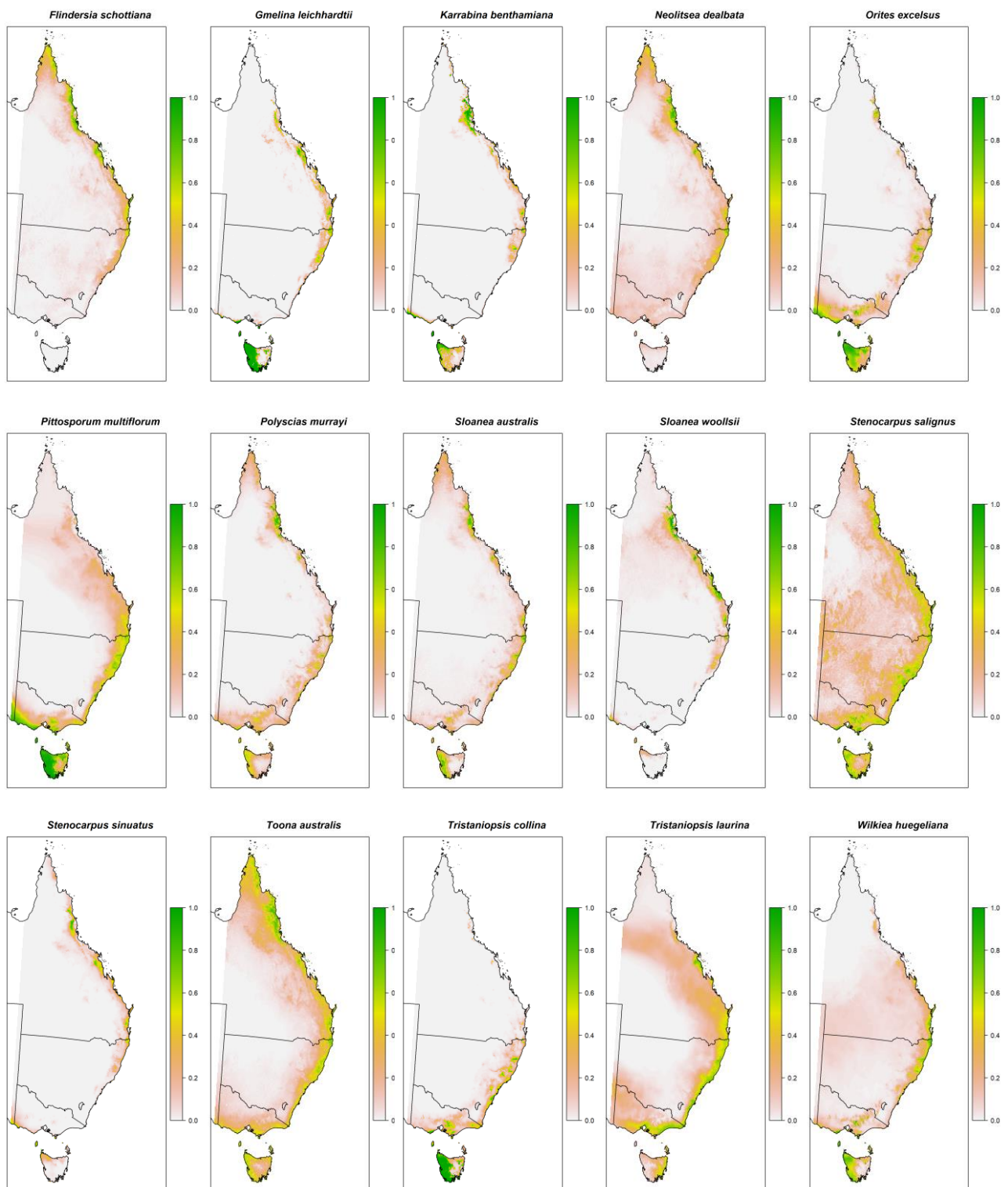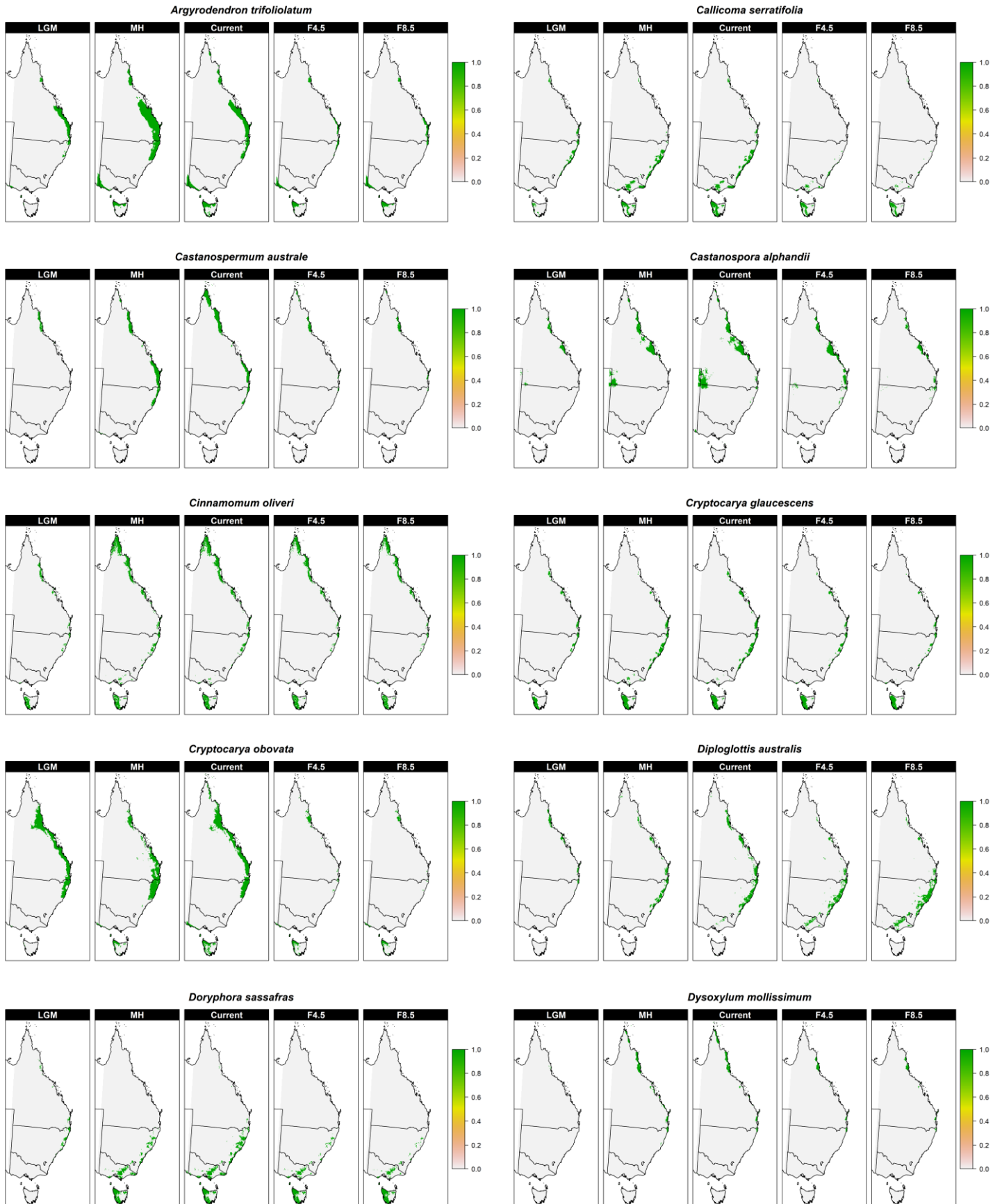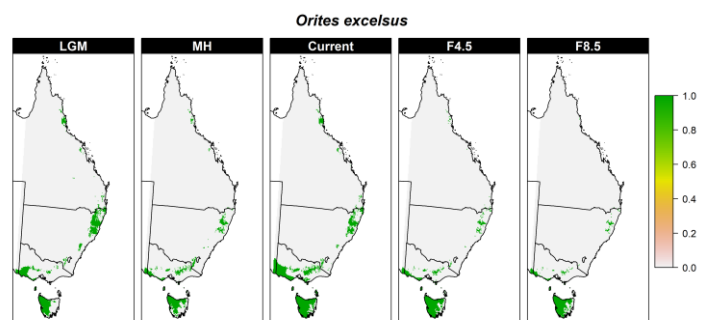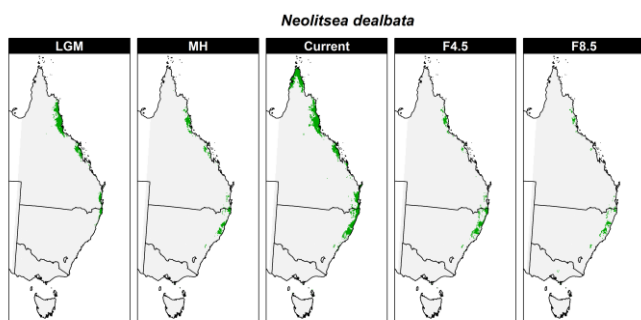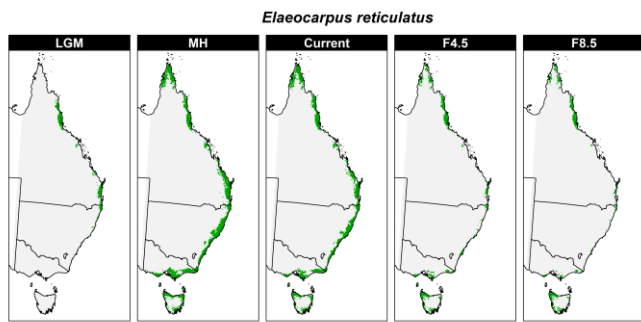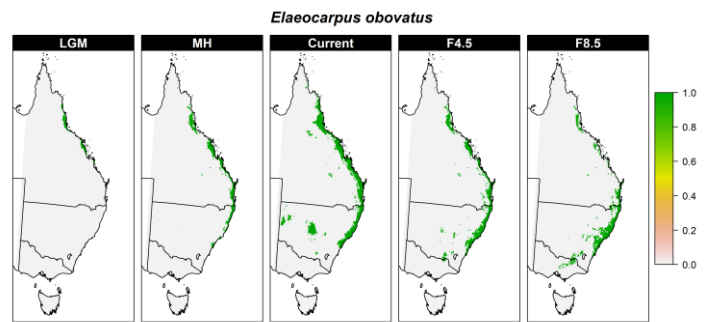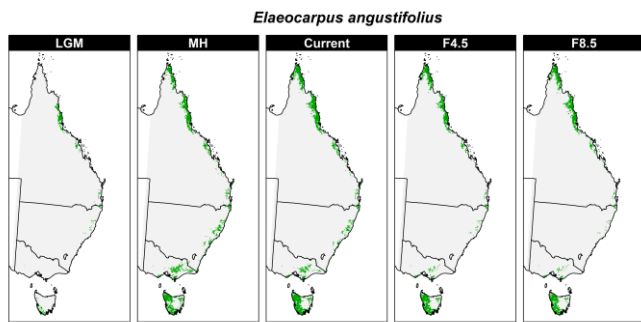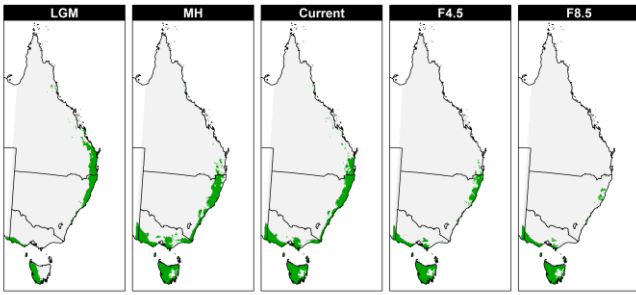
Figure S2: Binary distribution maps of habitat suitability for 30 tropical and subtropical Australian rainforest plant species for the across Last Glacial Maximum (LGM), mid-Holocene (MH), the current period (Current), and future period (2070) under two representative concentration pathways, RCP 4.5 (F4.5) and RCP 8.5 (F8.5). Binary maps were generated, by applying the maximum sum of training specificity and sensitivity threshold.

Elaeocarpus angustifolius

Elaeocarpus obovatus

Elaeocarpus reticulatus

Ficus rubiginosa

Flindersia australis

Flindersia schottiana

Gmelina leichhardtii

Karrabina benthamiana

Neolitsea dealbata

Orites excelsus
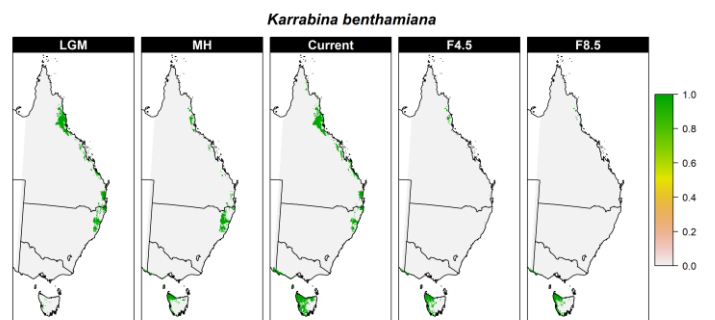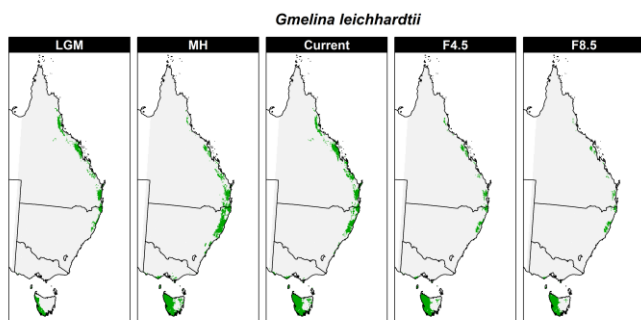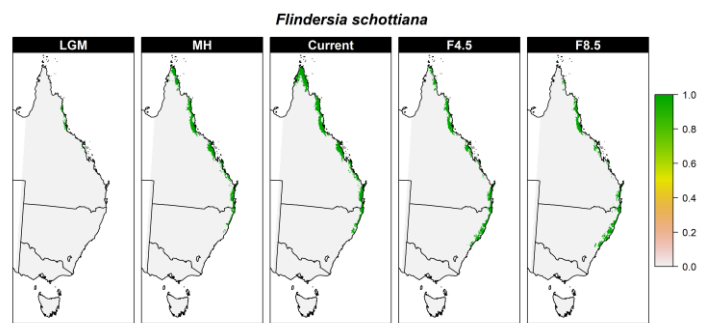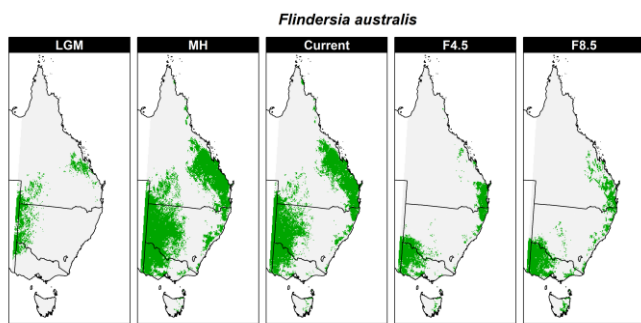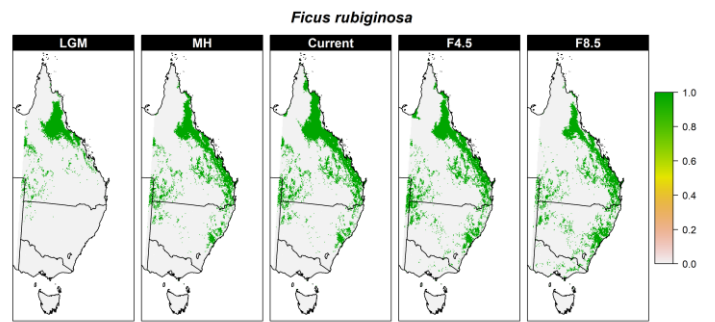
Pittosporum multiflorum

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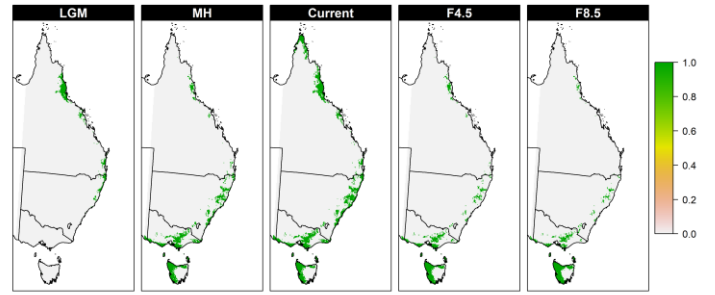
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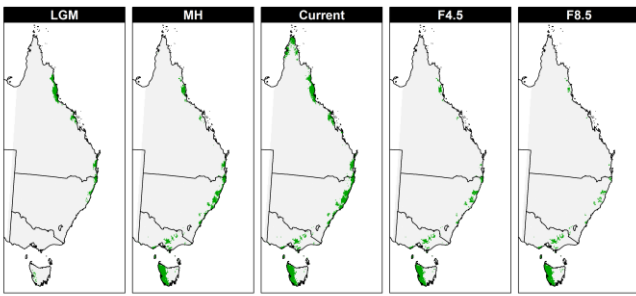
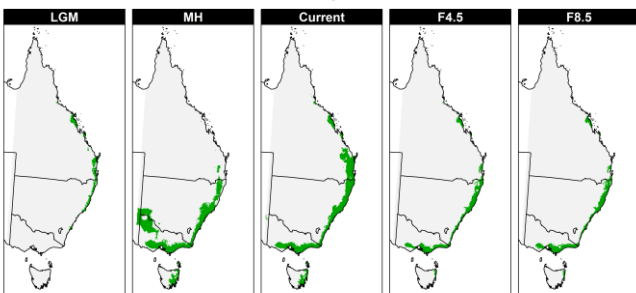*Sloanea woollsii*
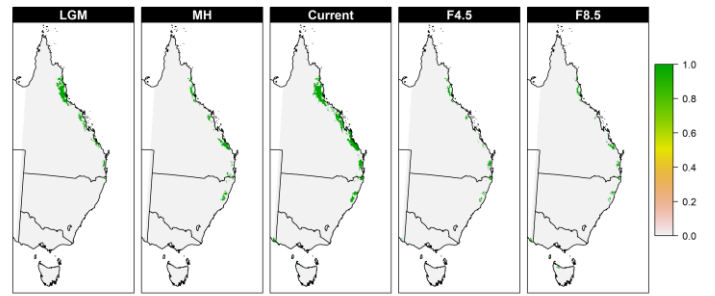
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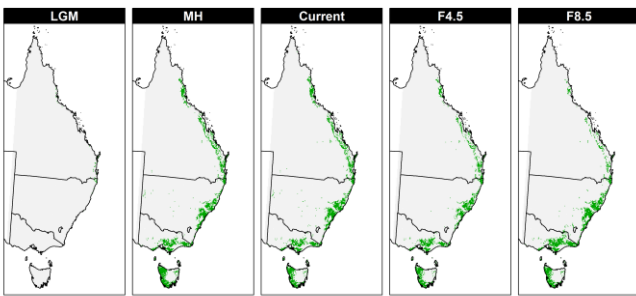
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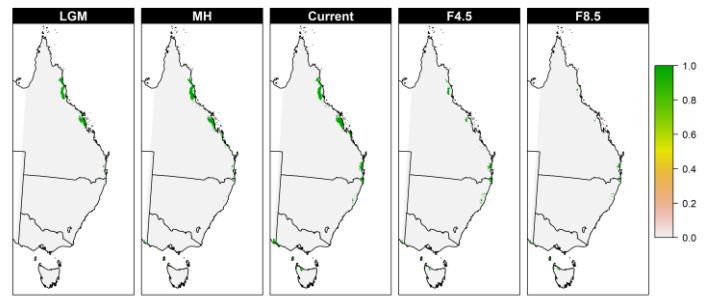
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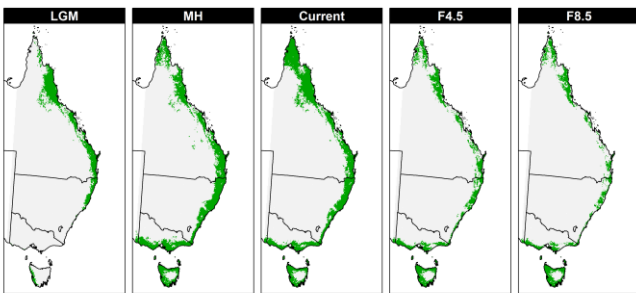
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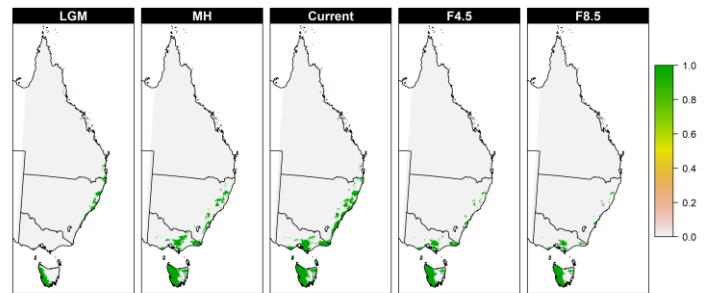
Tristaniopsis laurina

Wilkiea huegeliana
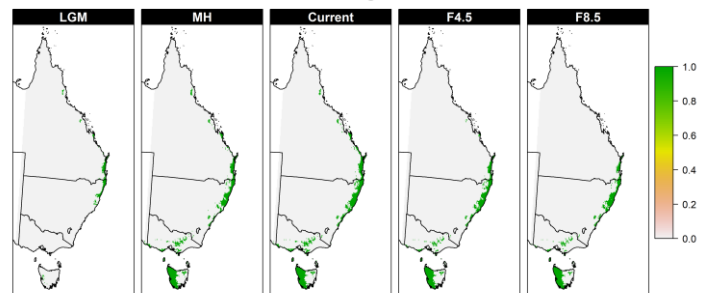
Figure S3: *Anomalies for i) mean annual temperature (MAT) and ii) mean annual precipitation (AP) across the Last Glacial Maximum (LGM), Mid-Holocene (MH) and future period (2070) under RCP 4.5 (F 4.5) and RCP 8.5 (F 8.5), with respect to current climate. Anomalies were averaged over four scenarios for the paleo time periods and seven scenarios for the future*
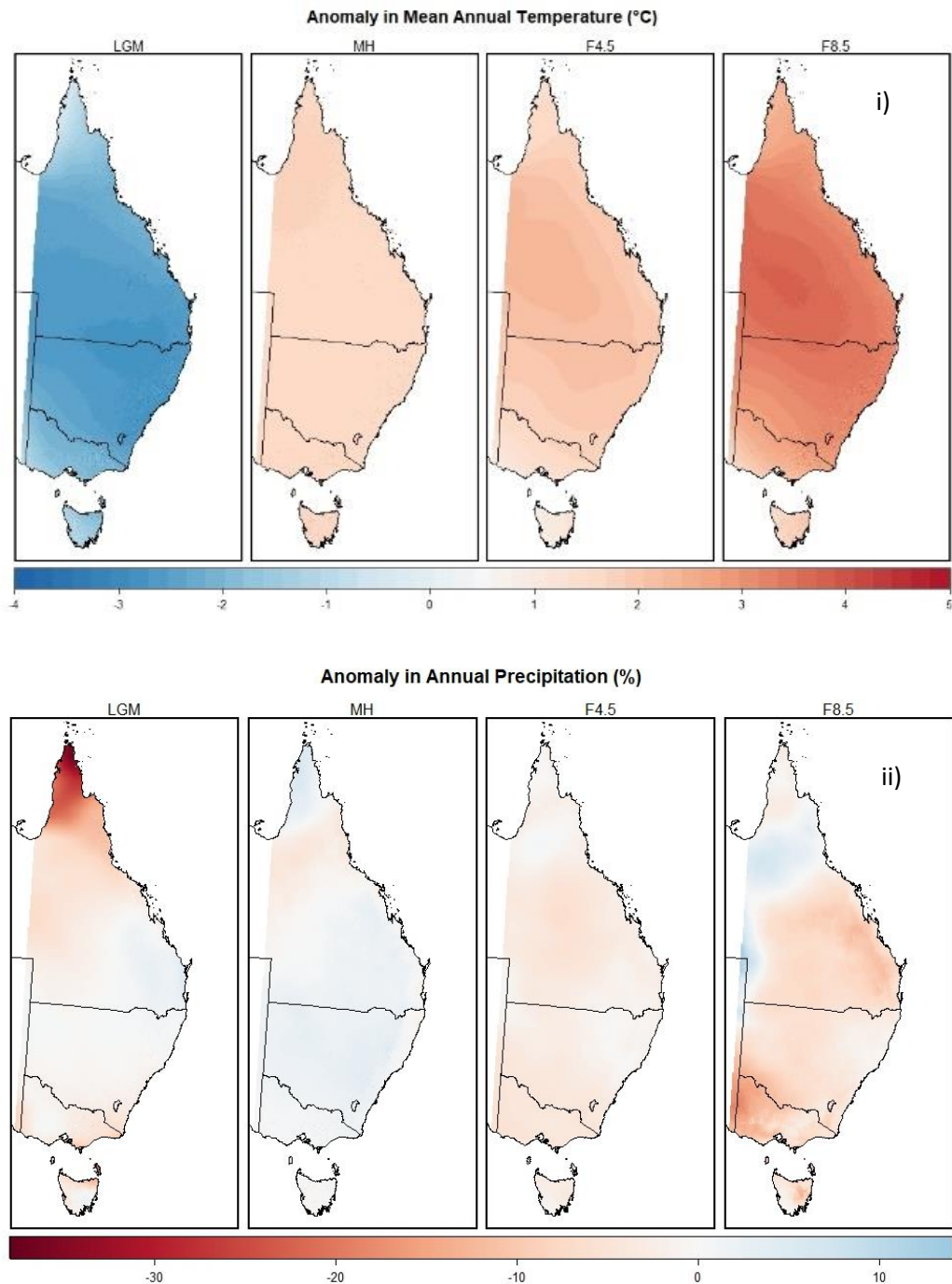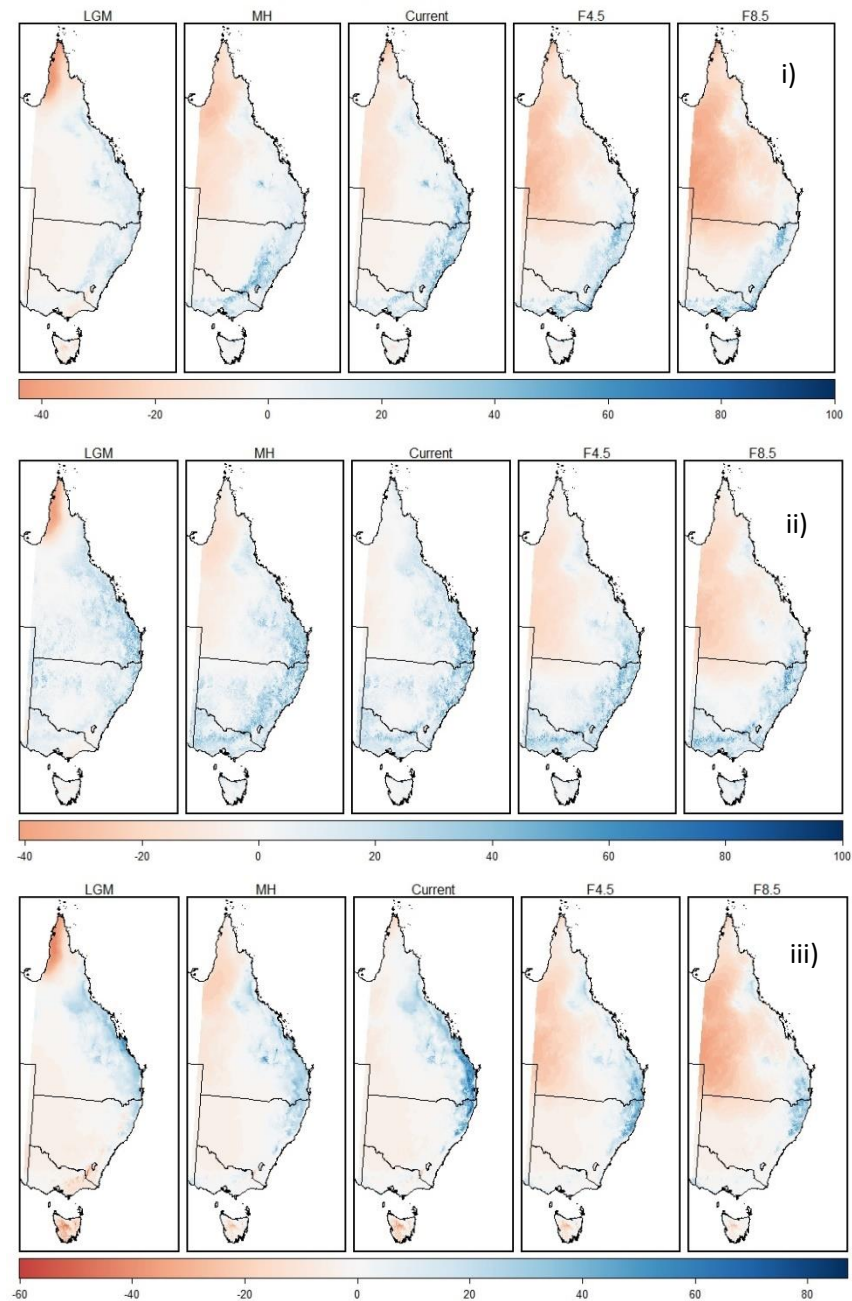
Figure S4: *Multivariate Environmental Similarity Surface (MESS) maps for i) Diploglottis australis ii) Stenocarpus salignus and iii) Stenocarpus sinuatus across the Last Glacial Maximum (LGM), Mid-Holocene (MH), current and future (2070) period under RCP 4.5 (F 4.5) and RCP 8.5 (F 8.5)*

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