Relative importance of fire regimes and environmental gradients for the distribution of rainforests in the Sydney region

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ABSTRACT

While Australian rainforests have been classified as fire intolerant, studies conducted in Australian environments over the past few years indicate that rainforest species, as a group, are able to regenerate following fires. These discrepancies—combined with past studies which identified several different environmental variables as the principal environmental controls for rainforest distribution—may be the result of the use of different definitions of rainforests, varying scales of investigation and the use of proxies for fire regimes.

This study compared the environmental controls for rainforest distribution using a uniform floristic definition of rainforests at two scales—map or topo-scale and plot or meso-scale—and observed fire regime data in the Sydney region. General Linear Models and Generalised Additive Models were used to construct the rainforest models. Best models were selected by ranking the Akaike information criteria (AIC), receiver operator area under the curve (ROC AUC), kappa statistic and deviance explained.

Preliminary results indicate that, as a general rule, precipitation is the main environmental control for all rainforest types in the Sydney region at both scales. These results also indicate that varying vegetation types have different levels of sensitivity to the scale used in modelling.

Scale differences can be observed for the secondary environmental controls of rainforest occurrence. Warm temperate rainforests and cool temperate rainforest models did not show different responses to scale and indicate that a combination of temperature and precipitation are most important for both rainforest types. Temperate rainforest models are susceptible to scale differences: map-scale models identified time since fire as an influential variable while plot-scale models identified landscape position as more important following precipitation. Finally, the scale sensitivity of dry rainforests and subtropical rainforests could not be determined conclusively. Preliminary results indicate that these rainforest types may be controlled by fire regimes following precipitation. Additional analyses—currently in progress—will clarify this.

1. INTRODUCTION

Australian rainforests have been classified as fire intolerant (Bowman, 2000a, Bowman, 2000c). As such, it has been proposed that fire regimes made of frequent and intense fires will result in a loss of rainforest species and communities from the landscape (Jackson, 1968). However, rainforests species, as a group, have been reported to be as resilient as sclerophyllous species with the exception of individual fire-intolerant species. These studies also reported that rainforests were able to regenerate above-ground biomass by coppicing based on the length of time between fire events, productivity and disturbance gradients (Campbell and Clarke, 2006, Williams et al., 2006). This suggests that factors other than fire regimes alone are interacting to determine the current distribution of rainforests.

Numerous investigations—ranging from experimental glass house studies to landscape observational studies—have proposed several environmental gradients as the main environmental controls for the distribution of rainforests. These variables range from soil fertility (Florence, 1996) to precipitation (Banfai et al., 2007), fire frequency (Crockett et al., 2006), landscape position (Floyd, 1990) and successional stage (Baur, 1957) among many others. All environmental controls proposed can be classified as climatic, topographic, edaphic, fire regimes or other disturbances and ecological processes.

Reported differences in environmental controls for rainforest distribution in the literature can be attributed to the use of diverse rainforest definitions, the study of rainforests in varying environments which may result in differences in observed rates of change in rainforest boundaries; and analysis of communities at different scales. This study compared the relative importance of climatic, topographic, edaphic and fire regime variables for the distribution of rainforests in the Sydney region using the same definition for rainforest at two scales (map or topo-scale and plot or micro-scale) and across two climatic regions (temperate and subtropical).

Specifically, this study tested the following three hypotheses:

> **Ho_1:** Fire regime variables are the most important environmental controls of rainforest occurrence at the map scale.
>
> **Ho_2:** Fire regime variables are the most important environmental controls of rainforest occurrence at the plot scale.
>
> **Ho_3:** The main environmental controls for rainforest distribution are the same for rainforests measured at the map and plot scale.

Previous studies into the effects of fire regimes on the distribution of rainforests used proxies for fire regime data such as the presence of charcoal on the forest floor (Helman, 1983) or indices of aspect. This study used observed fire regime data recorded in the Sydney region from 1977 to 2006 by the New South Wales Department of Environment and Conservation.

1.1. Defining rainforests

Many definitions of rainforests have been proposed over the years. A review of the literature on the definition of rainforests suggests that there is only consensus on the *lack* of agreement about what constitutes a rainforest. In general, rainforests are considered tree-dominated plant formations where the tallest stratum is usually closed. Rainforest have been defined using physiognomic, floristic, environmental and mixed definitions of rainforests (Bowman, 2000b).

Environmental definitions merit special attention. For example, Lynch and Nelder (2000) defined rainforest species as those that are able to regenerate under low light conditions in the absence of fire. For this study, environmental definitions of rainforests were specifically excluded as their use would have resulted in a circular argument.

In this study, rainforests are defined as forest areas where the dominant overstorey species are those listed by Tozer *et al.* (2006). This definition was selected over other definitions available because it provided the means to identify rainforests in an objective manner, and the use of this definition allowed for the use of Tozer *et al.* (2006)'s vegetation maps for the map-scale analysis. Vegetation communities identified by Tozer *et al.* (2006)—including rainforests—were identified using cluster analysis and classification of extant vegetation plots held by land management authorities. Tozer *et al.* (2006) used the resulting vegetation communities, geographical information systems (GIS) data and remote sensing data to construct tree models to generate the final vegetation maps.

1.2. The Sydney region

The study area is located on the central coast of New South Wales and parts of the southern coast. It covers an area of 12,101,329 ha, approximately 15% of New South Wales (Figure 1). It is located between -31° 16' 36.25"and 149° 14' 10.04", and -36° 38' 54.08" and 152° 57' 25.80". It contains the entire Sydney Basin Bioregion, and parts of the New South Wales North Coast Bioregion, New England Tablelands Bioregion and Nandewar Bioregion. Small sections of the Brigalow Belt South Bioregion, New South Wales Western Slopes Bioregions, South-east Highlands Bioregion, and South-east Corner Bioregion are also contained within the study area (NSW National Parks and Wildlife Service, 2003). The climate in this region is variable because of its large geographic extent and diverse topography. It can be generally described as temperate although it exhibits substantial variation according to its proximity to coastal and mountainous regions (NSW National Parks and Wildlife Service, 2003).

This area was selected because it has a high density of rainforest patches, which are subject to significant management pressures. Due to the area's high population density, fire management practices in the region aim to protect people and property, while simultaneously maintaining biodiversity values. These objectives are often in conflict as hazard reduction prescribed burning can eliminate rainforest species that require long periods to reach maturity. Some of the rainforest communities present are endangered ecological communities, for example littoral rainforests and dry rainforests.

Figure 1. Study area in relation to the Sydney Basin bioregion.

1.3. Species distribution modelling

Species Distribution Models (SDM) are used to test ecological theory, to explore the outcomes of different management approaches, and to explore the effects of environmental changes (such as Climate Change) on the survival and distribution of species of interest. SDM are empirical models that relate field observations to environmental predictor variables (Guisan and Thuiller, 2005). They range from statistical models such as generalised linear models to predictive species distribution packages such as Bioclim (Houlder et al., 2000) and LAMOS (Lavorel et al., 2000). SDM rely on the concept of the environmental niche.

The environmental niche is defined as the 'n' dimensional space where a population's intrinsic growth rate is equal to or greater than 1 (at least self-replacement) (Soberon, 2007). Two types of environmental niches have been proposed. The first is the Grinellian niche (Grinnell, 1917) which suggests that the environmental niche is defined by non-interactive variables such as edaphic or climatic variables (hereafter scenopoetic variables). This niche can be further subdivided into Grinellian realised niche and Grinellian fundamental niche. The Eltonian niche (Elton, 1927), suggests that the niche is defined by interaction of resource-consumer dynamics (hereafter bionomic variables).

Soberón (2007) proposed an updated environmental niche model which combines both Grinellian and Eltonian niche concepts to explain the interactions between scenopoetic and bionomic variables as well as dispersal (Figure 2). In order to be able to understand the main environmental controls of a species of interest, researchers can endeavor to define and understand the area occupied by 'Jo' in Figure 2. This area is where the rainforest population sources are located and therefore where modeled environmental conditions will result in the best estimates of environmental controls for communities of interest. However, the identification of population sources is difficult for long-lived species such as rainforest species because their identification requires the ability to follow individuals thorough an entire life cycle and to confirm that the individuals are able to self-replace in the same location.

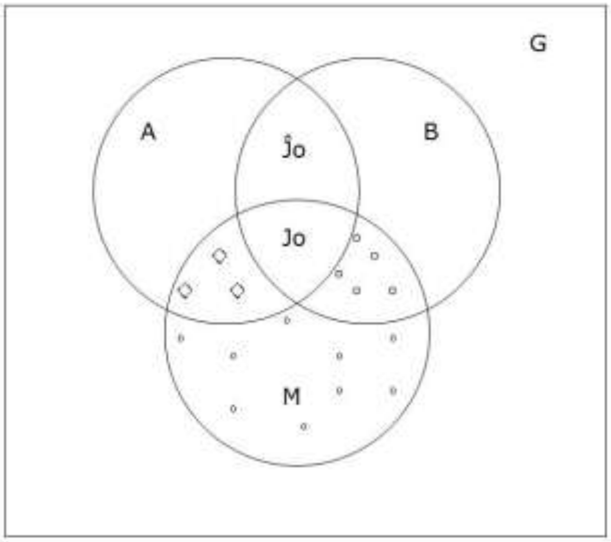


Figure 2. Soberón's environmental niche model (simplified from Sóberon (2007)). G represents the environmental space. A represents the geographic area where the scenopoetic conditions allow for a species to persist and self-replace. B is the area where the bionomic conditions allow a species to compete successfully. M is the area where the species can disperse successfully. Jo represents population sources. Ĵo represents areas where the bionomic and scenopoetic conditions are optimal but are not available for dispersal. Geometric shapes represent population sinks due to competitive exclusion (◊), negative intrinsic growth rate (□) or a combination of both sink types (○).

A coarse method to determine if an area is a population source or sink for long-lived species involves searching for evidence of environmental equilibrium, defined as constancy over time (Turner et al., 1993). Equilibrium analyses may include the identification of contractions or expansions in the distribution of a species or community in an area of interest over a period of time, where the area has experienced the same environmental conditions during the period studied. Areas where the species range decreases may be indicative of population sinks while areas remaining static or expanding under the same environmental conditions and over the same time period may be indicative of sources. This type of analysis is beyond the scope of this study.

The environmental niche has been typically defined in terms of the resource utilisation of individual species where the optimal distribution of a species will coincide with the area where the species achieves maximum resource utilisation. Studies quantifying the environmental niche of individual species are typically conducted at the micro-scale—*sensu* Mackey (1996)—where individual species are recorded in the field. In this sense, the overall environmental niche of a species can be quantified by measuring the between phenotypic component (BPC) to account for variations in resource utilisation by several individuals (within phenotypic component WPC) of the same species (Figure 3a).

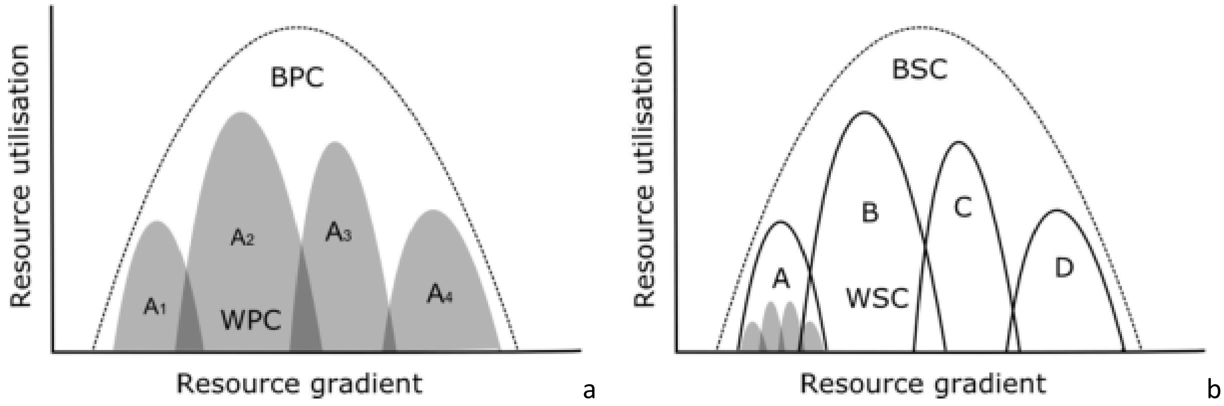


Figure 3. Schematic representations of the environmental niche for a. individual species; and b. a community. BCP = between phenotypic component, WPC = within phenotypic component, BSC = between species components; and WSC = within species component.

The same idea can be used to model the environmental niche of vegetation communities, where the environmental niche of each individual species can be modelled if we assume that a species BPC is the same as a community within species component (WSC). Therefore, the environmental niche of the community becomes the between species component (BSC) (Figure 3b). Environmental niche studies quantifying the environmental niche of communities are conducted at the topo-scale and may use vegetation maps derived from satellite imagery or vegetation modelling.

2. METHODS

The methodology for this study was conducted in three stages: i) construction of the Sydney region environmental database, 2) preliminary analyses; and 3) rainforest modelling.

2.1. Sydney region environmental database

The Sydney Region Environmental Database (SRED) is a geographically-referenced database consisting of raster surfaces representing 109 environmental variables and indexes of environmental variables covering the extent of the study area. With the exception of the climatic variables—derived from a 100 by 100 metre digital elevation model (DEM)—all the rasters contained in the database have a spatial resolution of 25 by 25 metres and are projected on GDA94 AMG Zone 56.

The SRED database contains raster surfaces for the dependent and independent variables required to model the presence and absence of rainforest species. The dependent variables—namely rainforest presence absence—were derived at the map and plot scales. The map-scale rainforest data was derived from Tozer *et al.* (2006) vegetation map data as binomial rasters where rainforest areas where given a value of 1 while areas where rainforests were absent were given a value of 0. Plot-scale rainforest data was obtained from BIOGRAD (BIOlogical Georeferenced RelAtional Database (Cawsey, 2004)) from the CSIRO Division of Sustainable Ecosystems. Plots containing rainforest species—as defined by Tozer *et al.* (2006)—were identified using data matching.

The SRED database also contains raster surfaces created to capture the spatial variability of thermal, disturbance and resource gradients (Figure 4). These include various temperature and precipitation variables, fire regime variables, soil fertility and depth, primary and secondary topographic variables including solar radiation on sloping surface and land use. All variables, with the exception of land use, were derived from digital elevation models or extant geology maps. The methods used to derive most variables followed Wilson and Gallant (2000), Summerell *el al.* (2004), Gallant (1997) and Turvey (1987) and were completed in ArcInfo (ESRI, 2006).

2.2. Preliminary analyses

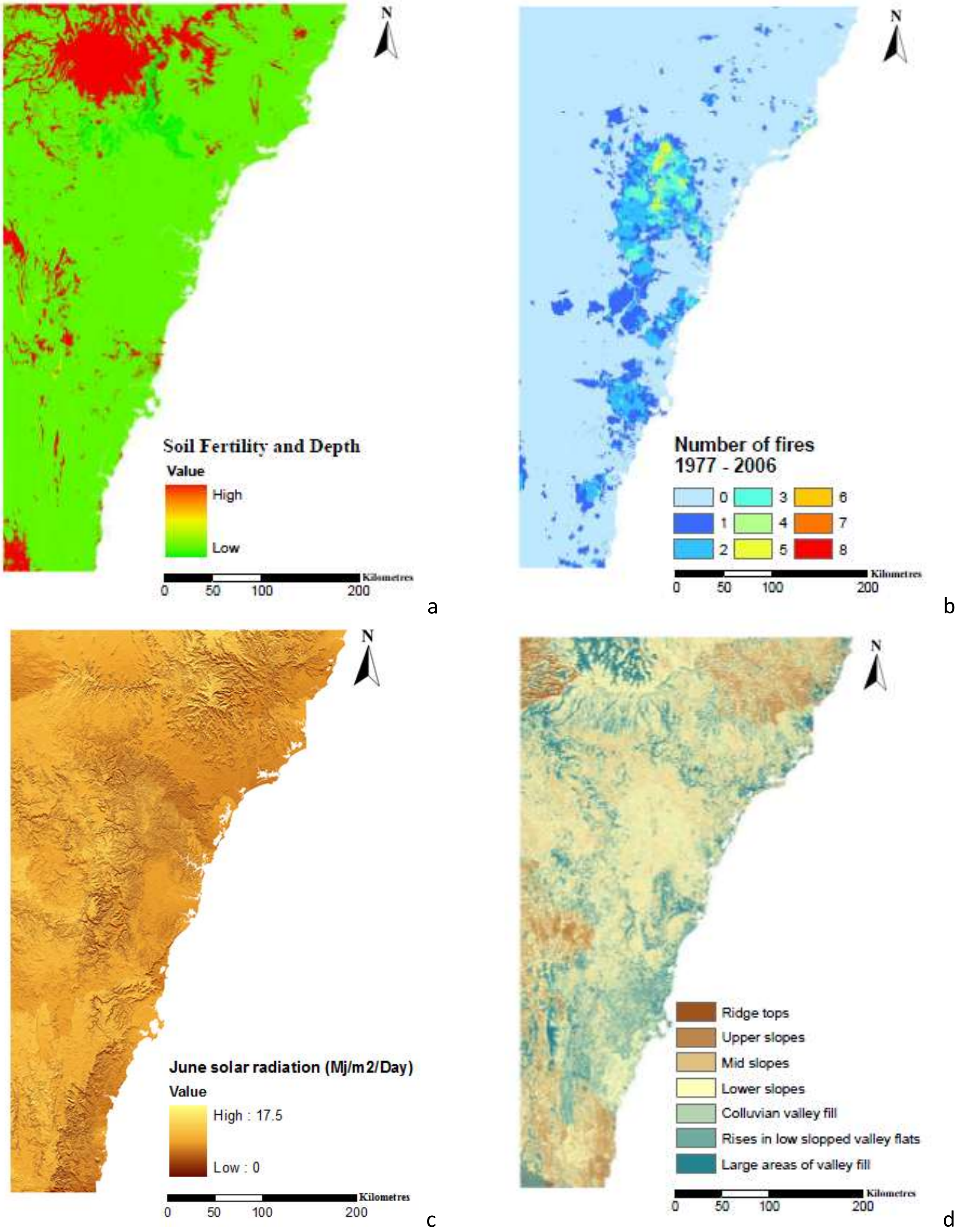
Preliminary analyses were conducted in two stages including map-scale sampling and plot-scale classification and sampling. Classification analyses were completed using the software PATN (Belbin, 2004) while additional statistical analyses were conducted in R (R Core Development Team, 2008).

2.2.1. Map-scale sampling

Individual map-scale rainforest types were classified according to patch size and sampled using a stratified random sampling scheme. The minimum sample per patch size was determined using proportional allocation. Map-scale sampling was completed in three stages: i) classifying rainforest patches by size, ii) calculating minimum sample size using proportional allocation; and iii) data sampling. Firstly, rainforest patches for each rainforest type were classified into three groups according to the patches' area. The classes included patches of up to one hectare (small), patches between one to ten hectares (medium); and patches with an area greater than ten hectares (large). Secondly the sample size for each map-scale rainforest type was calculated using proportional allocation where small, medium and large patch classes were treated as separate strata (Thompson, 2002). Finally, a raster surface recording presence and absence of rainforest types were derived for the 13 rainforest types and sampled using the sampling tool of the Spatial Analyst tool box of ArcInfo (ESRI, 2006).

2.2.2. Plot-scale sampling

BIOGRAD points were classified into distinct rainforest communities using Gower Metric as association measure and an Agglomerative Hierarchical Fusion – Average Linkage classification strategy employing the Flexible Unweight Pair-Groups Method Using Arithmetic Averages (UPGMA) technique. This resulted in six vegetation communities: marginal rainforests, warm temperate rainforests, cool temperate rainforests, dry temperate rainforests, warm temperate or intermediate subtropical rainforests, and complex subtropical rainforests.



a b c d

Figure 4. Examples of SRED independent variables derived for this study. a. Soil fertility and depth, b. Number of fires from 1977 to 2006, c. June solar radiation on sloping surface (Mj/m²/year); and d. Landscape position.

Plot-scale rainforest presences were sampled by randomly selecting sixty per cent of the total number of available plots for each rainforest type. The same number of points were randomly selected as rainforest absences using a random selection tool (Beyer, 2004). Absences were selected from areas where the specific rainforest type was found to be absent. The remaining presences (40% per rainforest type) and equivalent number of absences were used to test the model's predictive ability and performance.

2.3. Model construction

Map scale and plot scale models were constructed in four stages. Firstly, Pearson's correlations tests were used to identify and remove highly correlated variables from the analysis. When two variables were correlated, direct and resource variables—*sensu* Austin—were selected in preference to indirect variables as these allow for better understanding of the processes determining rainforest occurrence.

Secondly, exploratory Generalised Additive Models (GAM) (Yee and Mitchell, 1991) were used to determine the shape of the response of independent variables to the dependent variables. To build the exploratory GAMs, each continuous independent variable was tested on its own against the dependent variable and the shape of the response curve was identified and recorded. This approach was selected in preference to testing all variables simultaneously because exploratory analyses indicated that changes in the observed shape of the response curve—when additional variables were added to a model—were the result of changes in the scale at which the curves where displayed.

For the third stage, candidate models were built using Generalised Linear Models (GLM) (Nelder and Wedderburn, 1972) with a binomial distribution of errors and a logit link. When GAMs identified variables with non-linear responses, the appropriate response curve was included in the model for that variable. For each rainforest type, up to eight candidate models were constructed using either a forward stepwise or a backwards elimination approach and four decision rules: i) including variables explaining at least 1% of the model deviance, ii) including variables explaining at least 5% of the model deviance, iii) including variables and interactions explaining at least 1% of the model deviance; and iv) including variables and interactions explaining at least 5% of the model deviance. These different approaches were tested for each model as this provided the opportunity to identify variables that become important in the presence of another variable, or to identify highly influential variables on their own.

Finally, four model performance metrics were calculated for each model and ranked to identify the best model for each vegetation type. The model performance metrics used include the Akaike Information Criteria (AIC) (Akaike, 1973), the Receiver Operator Area Under the Curve (ROC AUC) (Fawcett, 2006), the kappa statistic (kappa) (Cohen, 1960) and deviance explained (D^2) (Guisan and Zimmermann, 2000). The four selection metrics were used jointly as each metric tests for different aspects of each model's robustness including parsimony (AIC), performance (ROC AUC), predictive ability (Kappa statistic and ROC AUC) and explanatory power (D^2). All model performance metrics were ranked from best (1) to worst (4) and added for each candidate model. The model with the lowest overall performance score per vegetation type was selected as the best model for that rainforest type.

3. RESULTS

Eleven map-scale models (Table 1) and six plot-scale models (Table 2) were built for rainforest communities in the Sydney region. The models explained from 35 per cent to 100 per cent of the total model deviance for each rainforest type.

Based on these results, it was proposed to:

> **Reject Ho_1:** Fire regime variables are the most important environmental control of rainforest occurrence at the map scale.

Precipitation variables were found to be the main environmental controls for rainforest occurrence in eight out of eleven models constructed at the map scale. Temperature variables were most important for three map-scale rainforests.

> **Reject Ho_2:** Fire regime variables are the most important environmental control of rainforest occurrence at the plot scale.

Precipitation variables were found to be the main environmental controls for rainforest occurrence at the plot scale for four of the six map-scale models. Temperature was the most important environmental control for one plot-scale rainforest type—warm intermediate/subtropical rainforest—while landscape position was the most important environmental control for marginal rainforests.

> **Results pending - Ho_3:** The main environmental controls for rainforest distribution are the same for rainforests measured at the map and plot scale.

Preliminary results suggest that this hypothesis can be accepted for specific environmental conditions. However, detailed analyses of comparable rainforest types in relation to identified response curves and known vital attributes are required to make meaningful comparisons between the results for map and plot-scale models.

Table 1. Percentage deviance explained for map-scale rainforest models. Grey shading indicates a principal environmental control for a rainforest type.

Vegetation name	Resource Gradient				Direct Gradient			Indirect gradient			Interactions	
	Soil fertility	June solar radiation	Precipitation	TWI	Temperature	Number of fires	TSF	Slope	Landscape Position	Westness	Interactions	Total
Far south coast fig dry rainforest	Insufficient data											
Far south east warm temperate rainforest		3.93	18.42		12.88		5.21	1.88	2.08		1.18	**45.58**
Subtropical dry rainforest			77.88							8.91	6.7	**93.49**
Subtropical complex rainforest			94.37			5.63						**100**
Coastal warm temperate rainforest		6.53	17.46	1.08			4.8		5.13			**35**
Sandstone scarp warm temperate rainforest		2.7	30.12		3.93		1.22	1.32				**39.29**
Intermediate temperate rainforest		4.14	4.14		22.02		10.24		1.88		5.23	**47.65**
Temperate littoral rainforest	1.53	3.56	73.3				5.38				4.14	**87.91**
Budderoo Temperate rainforest			67.32		28.11							**95.43**
Clyde-Deua cool temperate rainforest		1.44	13.35		21.51		6.5	2.29	2.66		2.85	**50.6**
Grey Myrtle dry rainforest	1.72		40.61				3.75				4.35	**50.43**
Temperate dry rainforest		1.29	9.57		16.1		11.65				1.03	**39.64**
Yarrawarra temperate rainforest	Insufficient data											

Table 2. Percentage deviance explained for plot-scale rainforest models. Grey shading indicates a principal environmental control for a rainforest type.

Vegetation name	Resource Gradient				Direct Gradient			Indirect gradient				
	Soil fertility	June solar radiation	Precipitation	TWI	Temperature	Number of fires	TSF	Elevation	Slope	Landscape Position	Westness	Total
Marginal rainforest		2.54	8.2		11.76					20.26		**42.76**
Warm temperate rainforest		6.01	54.79		14.46							**75.26**
Cool temperate rainforest			54.47		45.53							**100**
Dry temperate rainforest / creek lines			86.06		11.73							**97.79**
Warm temperate / Intermediate subtropical rainforest	11.58				41.7	6.75		18.44		17.8		**69.27**
Complex sub tropical rainforest			36.82						18.63			**55.45**

4. DISCUSSION

Analyses completed to date indicate that precipitation variables—including mean annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter and precipitation of the warmest quarter—are the most important environmental controls of rainforest distribution in the Sydney region. Exceptions to this include map-scale intermediate temperate rainforests, Clive-Deua cool temperate rainforests and temperate rainforests; and plot-scale warm temperate/intermediate subtropical rainforests. Personal observations of the dataset indicate that, as a general rule, temperature and precipitation tend to be positively correlated. However, it is very probable that the differences between precipitation-rainforests and temperature-rainforests are the results of different biological processes rather than the result of confounded variables because highly correlated variables (with an $r^2 \geq 0.5$) were removed from the analysis.

Once precipitation is accounted for, differences in the next most influential environmental variables can be identified for specific rainforest groups: subtropical, warm temperate, temperate, cool temperate and dry rainforests. These variables can then be compared at the map and plot scale.

Identical or almost identical responses between map-scale and plot-scale models were found for warm-temperate and cool-temperate rainforests, while important variations in the processes determining rainforest distribution were found for temperate rainforests. Ambiguous interpretations of map and plot-scale models can be made for subtropical and dry temperate rainforests.

4.1. Similarities between scales

After precipitation, the main environmental control for warm temperate rainforests at both scales was temperature, with the exception of June solar radiation on sloping surface (Mj m^{-1} $year^{-1}$) for coastal warm temperate rainforest. June solar radiation can act as a proxy for temperature as higher solar radiation can be expected to result in higher temperatures. This relationship needs to be confirmed by a detailed examination of the temperature and radiation response curves in relation to warm temperate rainforest presence and absence.

In the case of cool temperate rainforests, map-scale models indicate that the main environmental controls for this rainforest type are, in order of importance, temperature and precipitation variables. The plot-scale model for cool temperate rainforests indicates that the main environmental controls are precipitation and temperature. This suggests that both variables are important for this rainforest type regardless of the scale investigated.

4.2. Differences between scales

Markedly different results were found between map-scale and plot-scale models for temperate rainforests. All models indicated that temperature is an important environmental control for this rainforest type as temperature variables have been found to be either the most important environmental control or second in importance for all temperate rainforests at all scales—with the exception of map-scale temperate littoral rainforest. However, after temperature, time since fire is most important for map-scale rainforests while elevation and landscape position are most important for plot-scale models.

4.3. Ambiguous results

After precipitation, map-scale subtropical rainforests were controlled by either the number of fires over 30 years or westness. Westness is an index of aspect, which can be used as an indirect variable for temperature, solar radiation and fire regimes. Plot-scale subtropical rainforests were controlled by slope following precipitation. Slope can be used as an indirect variable for physical disturbance; soil, water and nutrient retention and fires. The identification of the actual variable represented by westness and slope will require experimentation or detail analysis of the vital attributes of diagnostic species to allow interpretation. This analysis is currently in progress.

Equally, following precipitation, the main environmental controls of map-scale dry rainforests include time since fires in years or westness. In contrast, the plot-scale model for dry rainforests identified temperature as the main environmental control for rainforest distribution following precipitation. As discussed above, westness can be used as both a proxy for fire regime and temperature variables. Additional analyses are required to elucidate further interpretation.

4.4. Future analyses and applications

Detailed analyses of vital attributes for map and plot-scale diagnostic species and the characteristics of each model’s response curves are currently in progress. These will provide additional insight into the main environmental controls of rainforest in the Sydney region, the implications of the use of different scales for conservation studies and recommendations for rainforest management.

One of the main contributions of this study to further the mission of the Australian Flora Foundation is highlighting methodological efficiencies for conservation studies. For example, given the similarities in the results for map and plot-scale warm temperate and cool temperate rainforest models, regional studies can consider the use of less resource intensive map-scale vegetation mapping—such as medium-scale satellite imagery or modelling—for these vegetation types. This will free resources to conduct detailed experimental studies for vegetation communities that are scale sensitive such as temperate rainforests.

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