Australian Rainforest Ecology on the Basis of Species Traits

Robert M. Kooyman (Grad.Cert. For.Sc.; M.Sc.)

Department of Biological Sciences, Faculty of Science,

Macquarie University, Sydney, Australia

This thesis is presented for the degree of Doctor of Philosophy

Submitted: 32 January 2013

TABLE OF CONTENTS

3

LIST OF FIGURES

LIST OF TABLES

THESIS ABSTRACT

Objectives: Quantify the influence of species traits, functional and phylogenetic diversity, history, scale, and environmental gradients on community assembly in tropical and sub-tropical rainforests.

Location: Australia

Methods: Three datasets were used. Allometric relationships governing the economy of sapling height gain were investigated for 11,111 individuals from 75 species in sub-tropical rainforest. Trait-gradient analysis partitioned species trait values between alpha (within) and beta (among) components for 231 woody taxa in 216 sub-tropical rainforest assemblages. Community phylogenetic structure was quantified for 596 assemblages, 1137 taxa, four functional traits, and two latitude regions (tropical and sub-tropical). Taxonomic patterns, trait values and structures, phylogenetic structure, and species niche breadth were quantified and compared across selected gradients and scales.

Results: Main-stem mass required to achieve a common height was the product of stem volume and wood density, and not significantly linked to other ecological traits. Correlation structures of species trait values differed across scales. Within sites, dispersal, habitat filtering, and competitive exclusion did not create strong linkages among traits. Across the landscape, abiotic drivers created strong linkages among leaf, stem, and seed traits. Within species height variation showed only a few species moved from lower to higher height ranking as site-mean-height declined. Most declined in unison with, or had a narrower range relative to site-mean-heights. Phylogenetic divergences in moist forest along the latitudinal gradient between the tropics and sub-tropics were older than those along the altitudinal gradient within.

Assemblages of species were more phylogenetically clustered where the effects of historic climatic oscillations had been greater, and less clustered in long-term stable locations.

Conclusions: Historic and recent rainforest contraction and re-expansion resulted in species within regions being more related than by chance. In recolonised areas within regions, species pools and trait ranges were reduced, and assemblages were dominated by widely dispersed species with greater niche breadth.

STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled "Australian rainforest ecology on the basis of species traits" has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University. Where results from previous work have been referred to, cited, or included they constitute a minor component and have been acknowledged in detail.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

The research presented in this thesis did not require approval from the Macquarie University Ethics Review Committee.

Signed:

Robert Michael Kooyman

Date: 10 January 2011

For the rain forest,

and Madeleine.

Dedication

To my dear friend Professor Len Webb (1920-2008), who taught me so much about life, plants, rainforest and ecology, and who never stopped celebrating how much more there was to know. To my mother (Johanna W. Boekema) and father (Gerrit Kooyman): despite never quite understanding my passion for life in the forest and wild places, they would have appreciated and enjoyed this moment.

LIST OF ABBREVIATIONS

AIC – Akaike Information Criteria

BP – before present

C – centigrade

ca. – circa

CA – cover abundance

CART – classification and regression tree (model), linkage model

CMVF – complex mesophyll vine forest

CNVF – complex notophyll vine forest

CO_2 – carbon dioxide

Corr. Coeff. – correlation coefficient

CY – Cape York

D – diameter

dbh – diameter breast height (over bark)

DO – Dorrigo

e.g. – for example

EI – where E is Young's modulus of rupture, and I is the second moment of cross-sectional area

Fig. and Figs – figure(s)

H – height

Hmax – estimated maximum height at maturity

ha – hectare

i.e. – that is

kg – kilogram

KY – thousand years

LA – leaf area

L – volume in litres

LGM – last glacial maxima

m – metre; cm – centimetre; mm – millimetre

MNTD – mean nearest related trait distance

MPD – mean pairwise trait distance

MYA – million years

NB – Nightcap-Border Ranges

n.d. – no date

NMDS – non-metric multidimensional scaling (ordination)

NRI – net relatedness index

NTI – nearest related taxon index

NSW – New South Wales

OLS – ordinary least squares regression

Phylobeta - phylobetadiversity

PP1 and PP2 – permanent plot 1 and 2

Qld - Queensland

R – statistical package R

R.M.K. – Robert M. Kooyman

SDM – seed dry mass

SS – seed size

SES – standardized effect size

Simprof – similarity profile (permutation test)

SMA and SMATR – standardized major axis tests in regression

SNMVF – simple notophyll-microphyll vine forest

SNVF - simple notophyll vine forest

TGA – trait gradient analysis

WD – wood density

WA – Washpool

WT – Wet Tropics

CHAPTER 1

INTRODUCTION

Australian Rainforest Ecology on the Basis of Species Traits

Robert M. Kooyman

1.1 Thesis Introduction

1.1.1 Focus of the study

This thesis is about how plant functional traits that reflect plant strategies in assemblages shift along environmental gradients, and how traits and trait relationships have shaped Australian tropical and sub-tropical rainforest community assembly across space and through evolutionary time.

1.1.2 Why is this of interest?

Comparative studies in community ecology can reveal the substantial contribution of geographic scale (local, regional, continental and global) and historical (biogeographic and evolutionary) processes to the size and taxonomic structure of current-day regional species pools, and to local community assembly (e.g. Ricklefs 1987, 2004, 2008). Understanding how these factors and processes influence the distribution of plant species and plant functional diversity (traits) in assemblages across landscapes is central to plant ecology (Westoby *et al.*, 2002; Westoby and Wright 2006; McGill *et al.*, 2006). The focus on traits and the functional components of communities is a shift away from asking how many or which plant species are present in different locations under different circumstances, to what types of plants are present, what traits they have, and how much trait variation there is at a location. That knowledge may allow a deeper understanding of the processes that influence and shape rainforest species distributions and community assembly across biotic and abiotic gradients. It may also provide insight into the spread of plant strategies, and species performance in relation to co-occurring taxa in assemblages arrayed along environmental gradients. Species abundance is expected to reflect performance in relation to both persistence and dispersal-based traits (McGill *et al.*, 2006).

1.1.3 Factors influencing the evolution of the Australian flora

The two major factors that shaped the evolution of the Australian flora relate to the ancestral origins of the vegetation on the Gondwanan super-continent, and the subsequent break-up of Gondwana and isolation of the Australian continent as it rafted northward into the tropics. While northward rafting triggered significant climate changes on the continent, and had significant implications for the vegetation, it also buffered the continent from glaciation during ensuing ice ages. This allowed ancestral rainforest lineages and the rainforest biome to persist through the evolutionary history of the Australian vegetation.

1.1.4 Gondwanan biogeography

The Australian flora can be divided into two major elements. The first is the original Gondwanan flora, comprised of ancestral stocks derived directly (pre-separation) from the super-continent. The second is a smaller intrusive component, comprised of plants that subsequently entered Australia after separation and as the continent rafted into the tropics (see Webb *et al*., 1986). The Gondwanan flora can be further subdivided into a relictual component representing ecologically conservative taxa that are still mostly confined to humid habitats presumed to have existed on the super-continent; and an autochthonous component that developed post separation in response to cycles of aridity, rainforest contraction, and edaphic development (Specht 1981). Old, low-nutrient soils are thought to have driven the evolution of scleromorphy (e.g. Barlow 1981; Hill 1998). In addition, a detailed history of exchange between the Australian and Indo-Malesian floras has not yet been quantified. While it is acknowledged that elements of both the aseasonal-wet and

seasonal-dry monsoon vegetation of Indo-Malesia have migrated into and out of Australia, the extent of interaction between the floras remains largely undetermined, but of considerable interest (Kershaw *et al*., 2007; and see Specht and Womersley 1979; Crisp *et al*., 1995, 2004; Rowe 2007).

1.1.5 History of the Australian rainforest

Rainforest was once the dominant vegetation on the Australian continent. Rainforest contraction was the outcome of a sequence of palaeogeographic and palaeoclimatic events and oscillations (Webb and Tracey 1981a,b; Webb *et al*., 1984, 1986; Barlow and Hyland 1988; Ziegler *et al*., 2003). Increasing aridity reduced the overall coverage of the ancestral rainforest and fragmented it into an archipelago of small 'islands' isolated by dry-land barriers (Herbert 1967). Palaeobotanical evidence suggests alternation between warm-wet (expansion) and cool-dry (contraction and extinction) phases. Cool-dry phases are regarded as responsible for the long-term trend toward both decreasing extent and diversity of the wet-aseasonal rainforest biome (Christophel and Greenwood, 1989; Crisp *et al*., 2004, 2009; Kershaw *et al*., 2007). The glacial cycles of the Pleistocene reflected a continuation of global climate fluctuations (Flenley 1979, 1998) and contraction of rainforest vegetation across the Australian continent (Farrera *et al*., 1999). More recently the rainforests marginally re-expanded during a warm-wet period commencing around 6K BP (e.g. Hopkins *et al*., 1996).

1.1.6 Implications

Over the last 30 million years increasing aridity and fire incidence (reflecting decreasing rainfall) interacted with topographic and edaphic gradients to reduce (but

not extirpate) the area of available habitat for broad-leafed mesic vegetation on the

Australian continent, and the number of rainforest lineages (Hill 2004; Martin 2006).

Despite currently representing < 1% of the Australian land surface, the extant

rainforests retain many ancient lineages and relatively high levels of biodiversity and

endemism (Webb and Tracey 1981a; Adam 1992). This supports the idea that

rainforest persisted in localized pockets of relative environmental stability through

time (e.g. Greenwood and Christophel 2005; Crisp *et al.*, 2009). Some of Australia's

dry-adapted flora is derived from lineages from the ancestral moist forests, showing

that biome shifts were possible (Webb and Tracey 1981a,b; Hill 1994, 1998, 2004;

Barlow 1981, 1994; Barlow and Hyland 1988). Nevertheless, the history of the mesic

component of the Australian rainforest flora remains predominantly a narrative of

habitat contraction, persistence in small populations, biome conservatism, and

extinction (e.g. Rossetto and Kooyman 2005; Crisp *et al.*, 2009).

1.1.7 Early rainforest descriptions

Early descriptions of rainforests around the world were provided by Humboldt (1805,

1817, 1852) and later by naturalists such as Alfred Russel Wallace, Charles Darwin

and Joseph Dalton Hooker. It was Schimper (1898, 1903) who apparently first coined

the term *tropische Regenweld* for this evergreen forest formation. However, it was not

until 1952 that Paul W. Richards published a book called The Tropical Rainforest.

That was the first detailed account and synthesis of the ecology of rainforest across its

global extent. That publication influenced and shaped the thinking of rainforest

ecologists around the globe, and helped set the research agenda for some years to

come, including in Australia.

1.1.8 Overview of Australian rainforest

Comprehensive and detailed accounts of Australian rainforest are provided in Webb

and Tracey (1981a,b), Beadle (1981), Figgis (1985), Werren and Kershaw (1987),

Kitching (1988), Floyd (1990), Groves (1994) and Adam (1992). Figure 1 (from

Adam 1992) provides an overview of the distribution of rainforest and vine forests

(monsoon forests) on the Australian continent.
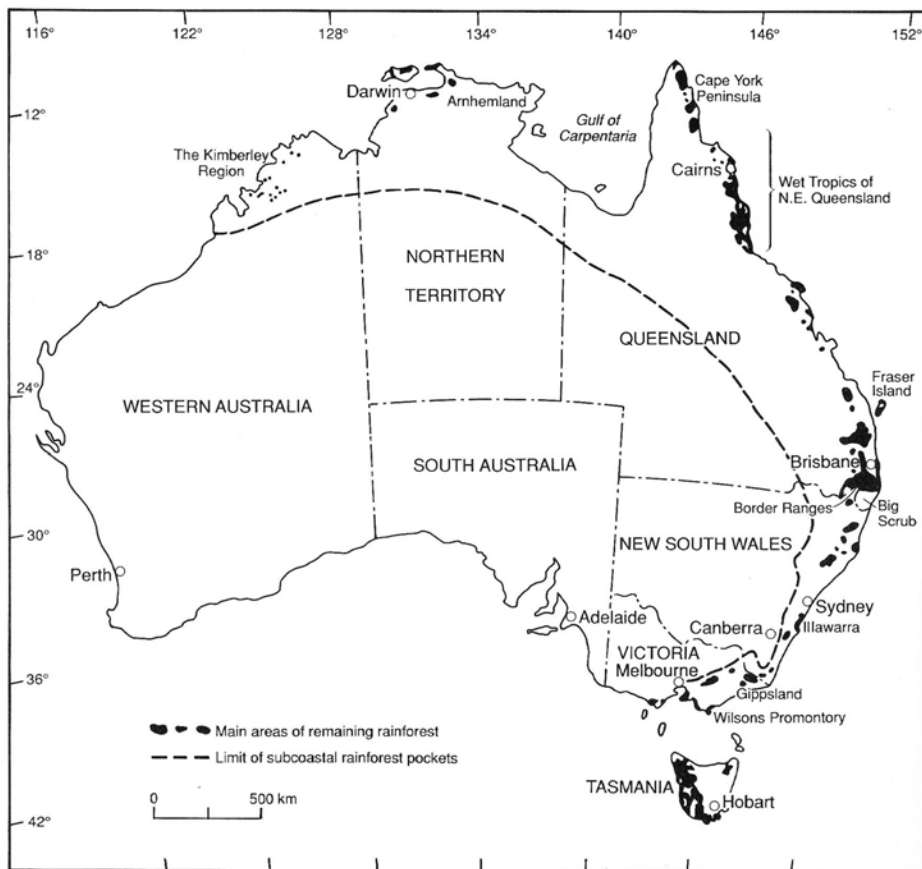
Figure 1.1 Map of Australia showing extent of current day rainforest.

1.1.9 A brief history of ecological research in Australian rainforest

Early botanical collections in Australia included rainforest species (e.g. Daniel Solander and Joseph Banks on the Endeavour voyage, 1770), laying the foundation for much of the systematic work on Australian rainforest trees that followed. Large-scale and systematic surveys of Australian and Papua New Guinea rainforests occurred during and following World War II. These surveys were part of a continuation of the wartime effort to identify important pharmaceutical plants in Australia, and to locate and develop local plants that could act as substitute sources for drugs that were in short supply. The Australian Phytochemical Survey and its extension into Papua New Guinea was conducted by the Council for Scientific and Industrial Research, later to become the Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia (Webb 1948, 1949, 1952, 1955; Simes *et al*., 1959). These surveys laid the foundation for the Rain forest Ecology Unit in the Division of Plant Industry in CSIRO. This unit subsequently developed pivotal ecological research that classified and recognised rainforest types and communities by ranking physiognomic and functional features including leaf size (Fig. 1.2) and characteristics of leaf margins (e.g. leaf teeth), the extent of deciduousness (Figs 1.3-1.4), and the relative incidence and frequency of stem features such as buttresses, bark textures and colours, life form sizes (e.g. trees-shrubs, wiry vines-lianas), and life forms such as epiphytes (Webb 1959, 1968, 1978).
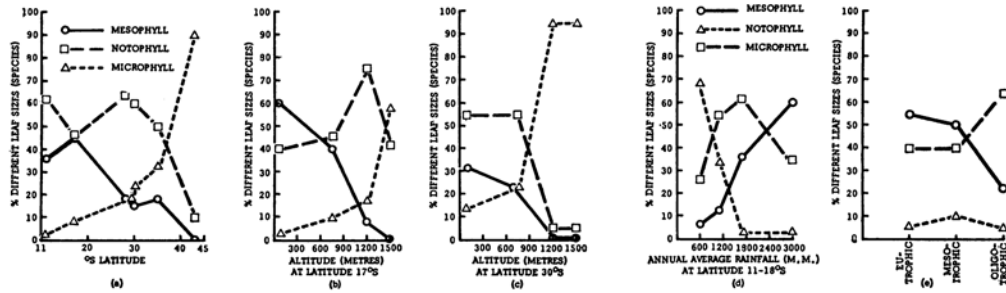
Fig. 1.2 Variation in representation of different leaf-size classes along different environmental gradients in Australian rainforests. Extracted from Webb (1968).
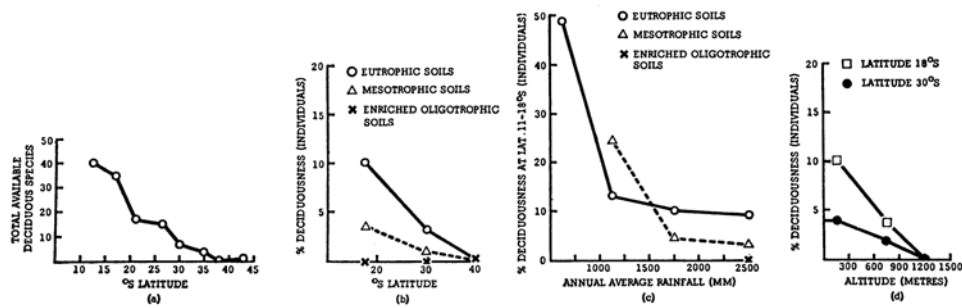
Fig. 1.3 Variation in deciduousness in Australian rainforests with changes in latitude, altitude, and rainfall on different soils. Extracted from Webb (1968).
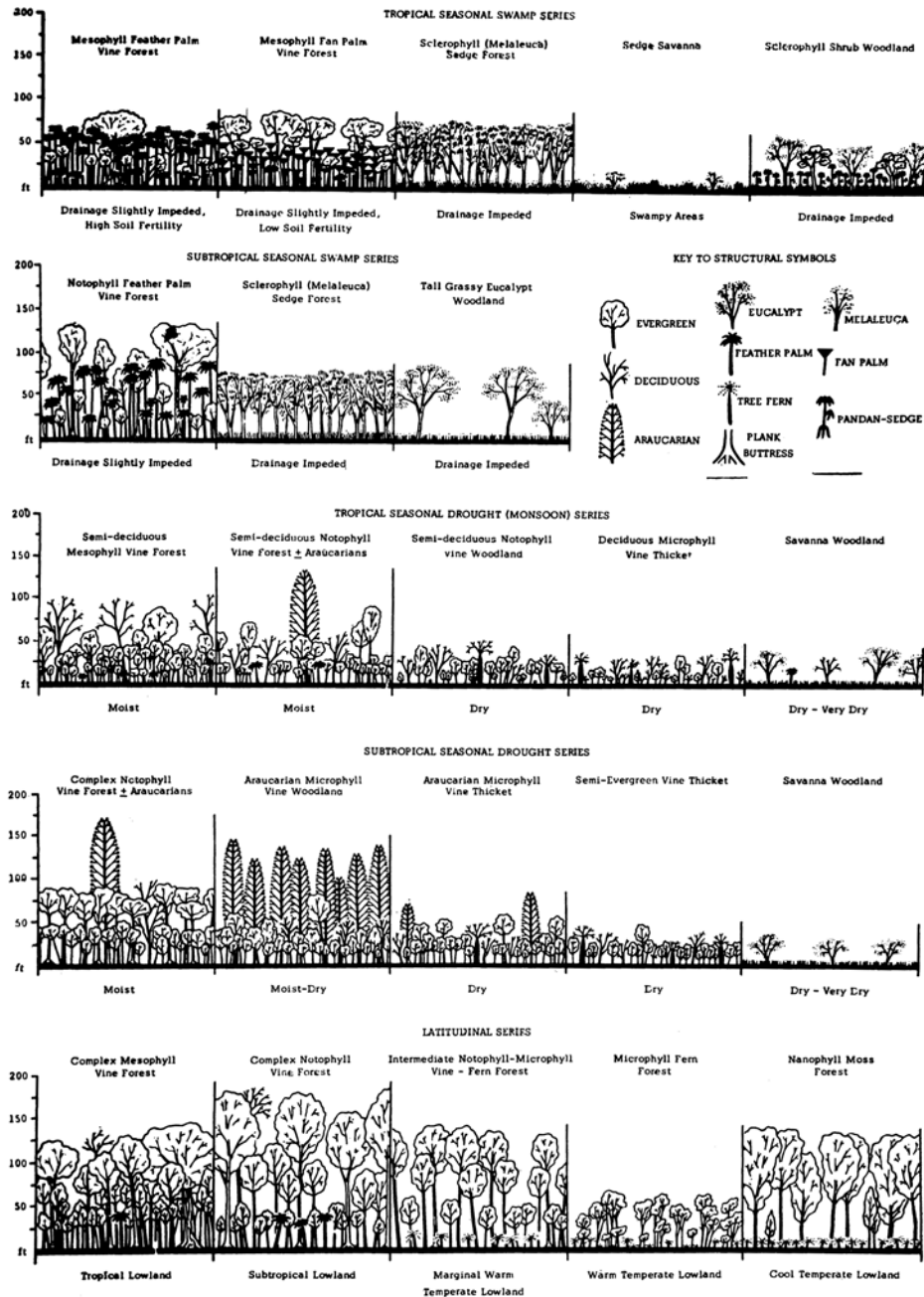
Fig. 1.4 Structural changes in rainforest along environmental gradients (extracted from Webb 1968).

The rain forest ecology unit also positioned species and local assemblages relative to climatic and edaphic gradients (Figs 1.4-1.6; Webb 1968), and to events such as cyclones (Webb 1958). However, at that time discussion of variation within rainforest

30

was constrained by incomplete sampling and resolution of species taxonomic status, and by the shortage of truly quantitative data as distinct from ranks or inferred data (Adam 1992). Also the role of specific traits and trait relationships in species ecology had not been studied so much as subsequently (e.g. Cornelissen 2003; Díaz 2004; Wright *et al*., 2004). One motivation for this thesis was that providing measured values for traits such as leaf area, seed size, wood density, and species maximum height at maturity might help elucidate rainforest community distribution, assembly, and function.
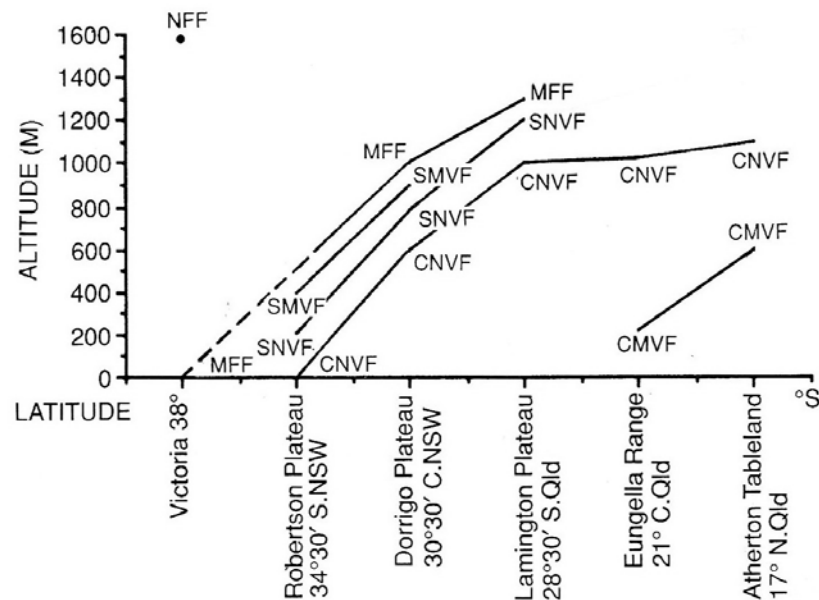
Fig. 1.5 Altitudinal zonation of structural rainforest types under conditions of high rainfall and soil fertility (Webb and Tracey 1981a; Adam 1992). NFF – nanophyll fern forest; MFF – microphyll fern forest; SNVF – simple notophyll vine forest; SMVF – simple microphyll vine forest; CNVF – complex notophyll vine forest; CMVF – complex mesophyll vine forest.

vine forests (VF)

fern forests (FF) and vine-fern forests (VFF)

mossy forests (MF) and fern forests (FF)

raingreen

evergreen

evergreen

evergreen

wet/moist

moist

dry

wet/moist

wet/cloudy wet

everwet/cloudy wet

eutrophic/ mesotrophic soils

eutrophic/ mesotrophic soils

eutrophic mesotrophic/ oligotrophic soils

eutrophic mesotrophic soils

oligotrophic soils

eutrophic/ mesotrophic soils

eutrophic/ mesotrophic/ oligotrophic soils

TROPICAL/ SUB-TROPICAL (rainforests)

TROPICAL/ SUB-TROPICAL (rainforests)

TROPICAL (monsoon forests)

SUB-TROPICAL 'Hoop Pine Scrubs'· 'Bottle tree scrubs'

TROPICAL/ SUB-TROPICAL (rainforests, generally with sclerophyll emergents)

SUBMONTANE/ WARM TEMPERATE (rainforests, generally mixed with wet sclerophyll forests)

MONTANE/ COOL TEMPERATE (rainforests, generally mixed with wet sclerophyll forests)

tropical eutrophic: complex mesophyll, subtropical eutrophic: complex notophyll tropical mesotrophic: mesophyll, sub-tropical mesotrophic: notophyll, (all VFs)

semi-deciduous mesophyll/ notophyll (VFs): deciduous microphyll vine thicket (VT)

complex notophyll VF± Araucarian emergents

low microphyll VF± Araucarian emergents: semi-evergreen microphyll VT

simple notophyll FF evergreen VF; simple semi-evergreen notophyll VF: evergreen notophyll VF

simple microphyll FF and VFF

simple nanophyll MF and FF

Fig. 1.6 Inferred soil nutrient status of major structural rainforest types (Webb 1968, 1978; from Adam 1992).

From the 1950's through the 1980's there was a rapid expansion of rainforest botany and ecology in Australia. Much of the early effort was focused on floristic and structural classification that included intuitive grouping of major types into leagues using climate based terminology (e.g. Baur 1965), grouping by key species (e.g. Forestry Commission of NSW 1989), and definition of floristic associations or alliances (Beadle and Costin 1952; Floyd 1987, 1990; Baur 1989). Perhaps the most interesting and informative of the efforts was undertaken by Len Webb and colleagues. Over a period of 20 years they used quantitative methods and floristic data at various scales and sampling intensities to investigate rainforest community ecology (e.g. Webb *et al*., 1967a,b; 1984; Williams *et al*., 1973; Williams and Tracey 1984). However, much of the focus at that time remained on floristic and physiognomic

classification, with physiognomy including ranked values for leaf size and life form variation (Webb 1968, 1978; Webb *et al*., 1976). Only later was an integrative framework reflecting phytogeographic parameters erected (Webb *et al*., 1984). This framework aligned with the primary gradients of temperature and rainfall in relation to latitude and altitude, recognised the role of edaphic differentiation, and defined plant thermal response groups (Nix 1982, 1991) and eco-floristic regions (Webb and Tracey 1981a; Webb *et al*., 1984). The thermal plant response groups were broad and did not provide for detailed plant physiological assessment or for positioning species and their traits along underlying abiotic gradients.

More recently there has been an explosion in research into Australia's rainforests, aligned with initiatives to improve conservation outcomes and our understanding of these complex terrestrial ecosystems (e.g. Rainforest Co-operative Research Centre; CSIRO; and numerous Universities). Nearly all the plant species have been collected and systematically described (e.g. Floyd 1989; Hyland *et al*., 2003), opening up possibilities for compiling species trait data. Species and forest distributions are now better known in relation to detailed climate data (e.g. Hilbert 2008), and past forest refugia have been modelled in relation to climate (e.g. Graham *et al*., 2006). Despite this considerable research effort, there remains much scope for improving our understanding about factors affecting rainforest community distribution and functioning (Metcalfe and Ford 2008).

1.2 Main aims
The overall aim of the thesis is to quantify and analyse the influence of species traits, functional and phylogenetic diversity, history, scale, and environmental gradients on

community assembly across tropical and sub-tropical latitude regions to improve understanding of rainforest ecology and functioning.

1.3 Study area

The tropical northeast and sub-tropical central eastern latitude regions of the Australian continent form the focus of this study. The tropical latitude region used in the study extends from approximately 10º to 20° S and includes the rainforests of Cape York and the Wet Tropics. In the sub-tropics the range is from ca. 28° to 32° S and includes the Nightcap-Border Ranges, Dorrigo and Washpool areas. The moist forests in the two latitude regions contracted to the east coast by the late Miocene (< 20 MYA BP) (Martin 1987; Greenwood and Christophel 2005), coincident with major increases in continental aridity (Bowler *et al.*, 1976) Within each region current-day rainforests are distributed in an archipelago of patches that have been separated by dry-land corridors and barriers of various extent and effectiveness since at least the last glacial maximum (LGM; 18-12 KY) (e.g. Webb and Tracey 1981a,b; Kershaw *et al.*, 2007).

1.4 Climate

The climate of the study area varies from tropical warm wet on the lowlands to cool wet at higher altitudes in the Wet Tropics, seasonally dry-wet and monsoonal in Cape York, to sub-tropical and seasonal warm wet and cool wet along the elevation gradient in northern New South Wales. Climate data for all assemblage sample locations were obtained from the Australian Bureau of Meteorology. Additional climate modelling was undertaken and details are provided in appendix 5. Nix (1991) provided current-day climate parameters for various rainforest structural types (Fig. 5;

Table 1; from Webb 1968), and Hill (1994) provided details of palaeo-climates relevant to the evolution of the Australian flora, from Cretaceous to recent. More recent updates and alignments with climatic oscillations are provided from ocean drilling off the north Queensland coast (Kershaw *et al.*, 1993; Moss and Kershaw 2007), pollen records from selected sites in north Queensland (Kershaw 1970, 1976, 1978, 1994; Kershaw *et al.*, 2007), and comparisons of macro-fossil assemblages from south-eastern Australia (Christophel 1991, 1988, 1994; Christophel and Greenwood 1987, 1988, 1989; Greenwood and Christophel 2005).

1.5 Research focus: community assembly and plant functional traits

On small spatial scales in heterogenous environments where there is no effective influence from dispersal limitation, the distributions of plant species are expected to reflect the influence of abiotic gradients and biotic interactions. Small-scale here means sufficiently local that over several generations species are effectively dispersed across, and could occur in, all places in the local landscape. Observed species distributions at this scale would therefore reflect the operation of several filters that influence ecological processes. These include: dispersal and germination of seeds and successful establishment of seedlings, physiological tolerances of plants as they establish and grow, demographic effects related to density dependence and response to disturbances, competition with other species in the community, and biotic interactions including both beneficial mutualisms and the potentially harmful effects of herbivores and pathogens (e.g. Janzen 1970; Connell 1971; Bazzaz 1991; Weiher and Keddy 1995; Díaz *et al.*, 1998). Together these assembly processes shape the distribution patterns of species and lead to significant associations between environmental gradients and the functional traits of species (Ackerly 2003; Wright *et*

al., 2004). Relationships between plant form and function, climate, and patterns of trait distribution are also evident at larger spatial scales (Givnish 1999). This is despite the complications of dispersal and the tendency for an increase in species turn-over (replacement) with increasing spatial scale. The identification of similar trait patterns in similar habitats spread across larger scales has played an important role in the development of global plant ecology (e.g. Schimper 1903; Mooney and Dunn 1970; Reich *et al*., 1997, 1999). Examples that have been used in both palaeo- and neo- ecology include the positive relationship between mean leaf size and increasing precipitation, and the decreasing frequency of toothed leaves in assemblages as temperature increases (e.g. Webb 1968; Wolfe 1973, 1995; Wilf 1997; Greenwood 2006).

At local, continental, and global scales, key plant traits exhibit shifts across climatic gradients (e.g. Wright *et al*., 2005; Moles *et al*., 2007). At regional landscape scales species that are more similar (in terms of traits) are filtered into assemblages in similar habitats arranged along major gradients, while co-existing taxa within assemblages can show a broad range of trait variation (e.g. Wright *et al*., 2004; Ackerly and Cornwell 2007). Partitioning trait values into alpha (within assemblage) and beta (among assemblage) components, and quantifying community phylogenetic structure in relation to time since divergence could provide insights into how these factors influence community assembly, and the age and strength of the evolutionary signals. The outcomes of these processes and interactions are reflected in patterns of community phylogenetic structure.

1.6 Theoretical setting and background to research direction

Two contrasting traditions in the study of plant ecology have influenced research in rainforest community ecology. The first reflects plant geography and explores how plant form and function shift along climatic and edaphic gradients (e.g. Schimper 1903; and see for example Webb 1968). The second investigates plant demographic and functional differences and how these reflect competition among co-occurring species in relation to mechanisms of co-existence (e.g. Pacala and Tilman 1993; Tilman 1994; Chesson 2000), and of niche partitioning at assemblage scales (e.g. Hutchinson 1957; MacArthur and Levins 1967). The first tradition links plant functional ecology to community ecology, while the second grapples with the question of how high numbers of species co-exist at small spatial scales (e.g. Phillips *et al.*, 1994; Wright 2002), an issue that has been prominent for rainforests because of their conspicuous diversity. Trait-based approaches to community ecology that link the ecological strategies of plants to community assembly theory and functional diversity have been suggested as having the potential to unify these differing perspectives and paradigms (Grime 2006; McGill *et al.*, 2006; Westoby and Wright 2006; Ackerly and Cornwell 2007).

Factors that shape community assembly processes are influenced both by scale and by the size of regional and local species pools. In turn, the sizes of regional species pools reflect the interaction of biogeographic and evolutionary history with current-day abiotic gradients and biotic interactions (Ricklefs 1987; 2004; 2008; Ricklefs and Schluter 1993). Trait combinations reflect the ecological strategies of present-day plants and can show how they make a living (Westoby 1998; Westoby *et al.*, 2002). Mean values for key traits show significant shifts across climatic gradients at global,

37

continental and local scales (eg. Wright *et al*., 2005; Moles *et al*., 2007), suggesting

habitat filtering and some convergence of plants with functional similarities into

shared habitats. At the same time, high levels of trait disparity are observed within

communities (Wright *et al*., 2004; Ackerly and Cornwell 2007), and there has been

interest in the possibility that co-existing species are less similar than expected by

chance, due to competition and limiting similarity (e.g. Janzen 1970; Connell 1971;

Webb *et al*., 2006).

Community ecology investigates interactions among organisms and their

consequences for community composition. It includes both the evolutionary origins of

those interactions, and their ecology and consequences in the present day. When

placed in a phylogenetic context it combines the study of extant species and the

spread of different ways of making a living with the evolutionary history that has led

up to current-day ecology (Westoby 2006). Phylogenetic community ecology

investigates how interactions among species in communities have fed back to

influence the evolutionary processes that impact species ecological strategies, and

species and trait diversity in regional pools. Community ecology links short-term

local and assemblage level processes to regional, continental and global scale

processes that occur over deep evolutionary timescales (e.g. Losos 1996; Webb 2000;

Webb *et al*., 2002; Ackerly 2003; Ricklefs 2004; Cavender-Bares 2004, 2006;

Gillespie 2004; Fine *et al*., 2006; Pennington *et al*., 2006; Davies *et al*., 2007;

Mittelbach *et al*., 2007; Kraft *et al*., 2007; Swenson *et al*., 2007; Hardy and Senterre

2007; Donoghue 2008; Emerson and Gillespie 2008; Graham and Fine 2008; Vamosi

et al., 2009; Cavender-Bares *et al*., 2009).

1.7 Phylogenetic framework

Quantifying and analysing community phylogenetic structure can help elucidate contemporary ecological interactions, and can link community ecology to biogeography and the study of character evolution (Vamosi *et al*., 2009). Tests of community phylogenetic structure include null models (Webb 2000; Webb *et al*., 2002; Kembel and Hubbell 2006; Kraft *et al*., 2007; Kembel 2009; Vamosi *et al*., 2009), and are implemented across a range of scales that reflect the questions being addressed (e.g. Wiens and Graham 2005; Kembel 2009; Vamosi *et al*., 2009).

Phylogenetic clustering is suggested as evidence for environmental filtering of phylogenetically conserved traits into habitats (e.g. Webb 2000; Vamosi and Vamosi 2007). Phylogenetic evenness is suggested as indicating limiting similarity arising from competition between more closely related taxa in phylogenetically conserved niches (Lovette and Hochachka 2006; Slingsby and Verboom 2006). In addition, random patterns of community phylogenetic structure have sometimes been interpreted as representing the outcome of species-neutral processes during community assembly (Kembel and Hubbell 2006; Swenson *et al*., 2006; Kraft *et al*., 2007). However, it needs to be borne in mind that measures of community phylogenetic structure are net outcomes that are derived both from processes generating clustering and from any processes generating evenness. When the net effect is indistinguishable from random, this may mean that opposing processes are obviating each other's effects rather than the processes are absent.

1.8 Scope of the thesis

This thesis presents a series of five papers investigating the influence of species traits, functional and phylogenetic diversity, history, scale, and environmental gradients on community assembly in Australian tropical and sub-tropical rainforests.

1.9 Thesis Components and Structure

To strengthen the quantification of the main features of Australian rainforests the study combines species-level data on ecological traits, sample data giving co-occurrence and composition of assemblages, and phylogeny expressed as trees of descent and as evolutionary divergences rather than as taxon categories. All are positioned relative to continental scale and well-resolved climate estimates for the assemblages used in the study.

1.9.1 Traits

Four traits and their associated correlations and potential trade-offs were included in this research (e.g. Cornelissen *et al*., 2003; Díaz *et al*., 2004).

Seed size: is related to life history strategy, plant growth form and dispersal mode (Moles *et al*., 2005a,b), potential dispersal distance, and regeneration biology (Leishman *et al*., 2000). It reflects the potential of a species to disperse into a regeneration opportunity, and the capacity of seedlings at the cotyledon-stage to survive various hazards (Westoby 1998). Both the maximum dimensions of seeds (length and width; chapters 2-4) and seed dry mass (chapters 5 and 6) were used as measures of seed size in the thesis. Fruit length was also referred to.

Leaf area: is measured as the surface area of the top side of the leaf, is important for energy balance and whole plant hydraulic architecture, and is known to be associated with a range of other traits (including stem traits), and environmental gradients (such as latitude, altitude and rainfall) (e.g. Ackerly and Cornwell 2007).

Wood density: is significantly related to growth and survival rates. It directly determines the cost of building tissue per volume, it is linked to hydraulic conductance, species performance, and life history strategy variation (Poorter *et al*., 2010), it trades off with mortality and longevity of stem, and it contributes to the costs of height gain (Chave *et al*., 2009).

Height at maturity: describes a species or individual's ultimate stature and position in the canopy, and the transition in relation to allocation of resources from growth to reproductive maturity (Falster and Westoby 2005). Height and size during ontogeny influence survival until maturation, reproductive output, and lifespan.

1.9.2 Data sets

Three main data sets were used in the thesis.

The first data set, used in chapter 2, included height and diameter measurements for 11,111 individuals of 75 species from sub-tropical rainforest. The costs of height gain for rainforest saplings in the understorey were expected to show some relationship to traits that reflect species ecological strategies and shade tolerance. While the results provided an improved understanding of the costs of height gain, this did not link substantially to the selected traits.

The second data set, used in chapter 3, included four traits (described above), 231 woody species (trees and shrubs) and 216 plot-based samples located in sub-tropical eastern Australia. Vegetation types represented complex notophyll vine forest (sub-tropical rainforest) and simple notophyll-microphyll vine forest (warm temperate rainforest) assemblages arrayed across a range of abiotic gradients. This data set was used to look at trait values and correlations across scales in relation to gradients and community assembly processes. Chapter 4 used a subset of these same data, 100 plots and 81 woody species in simple notophyll-microphyll vine forest, to investigate the role of trait variation and within species phenotypic variation (height) relative to abiotic gradients. While organised into separate chapters, chapters 3 and 4 really represent a single body of work that investigated how trait variation and correlations were structured at alpha (within assemblage) and beta (across assemblages in a landscape) scales in rainforest communities in a region. However, the behaviour of trait relationships at larger scales and across latitude regions (sub-tropical and tropical) remained an open question of considerable interest.

The third data set, used in chapters 5 and 6, included 4 traits, 1137 woody taxa and 596 assemblage samples from two latitude regions (tropics and sub-tropics). Chapters 5 and 6 represent a single body of work at continental, regional and local scales that quantifies the influence of community phylogenetic structure and functional traits on community assembly. In chapter 5 the quantification of the trait signal was limited and mostly not significant, however, other aspects were informative. In chapter 6 the relationship between biogeography and functional traits is further investigated. Here the signal for the relationship of seed dry mass and dispersal to species niche breadth,

42

phylogenetic community structure, and biogeographic and climate history becomes more evident. Again, the signal was not strong, but it provided interesting insights into the larger story surrounding evolutionary history and the current-day ecology of Australian rainforests.

Chapter details and topics

More specific information related to each chapter follows, including an overview of expectations, questions, and initial working hypotheses. This is followed by acknowledgements for each chapter and data sources.

1.9.3 Chapter 2: Species growth strategies and community assembly

Coexisting tree species can differ substantially in relation to height-diameter relationships (e.g. Thomas 1996; King 1996; Poorter *et al*., 2003, 2006). The smaller diameter at a common height of some species compared to others could reflect differences between high and low risk growth strategies. It has been suggested that species with dense wood represent the high cost but low risk strategy because dense wood has a higher modulus of rupture and stems are less likely to shatter or break (e.g. Niklas 1994, 1995). Consequently, the costs of height gain for saplings could reflect differences in the safety factors that influence survival through ontogeny, and species ecological strategies that reflect factors such as maximum height at maturity, shade tolerance, and longevity (e.g. Putz *et al*., 1983; van Gelder *et al*., 2006; Falster 2006).

Hypothesis: The allometric relationships of height-diameter for rainforest saplings reflect trade-offs between wood density and diameter that (in turn) reflect differences in species ultimate stature at maturity, ecological strategies, and shade tolerance.

1.9.4 Chapter 3: Functional traits, abiotic gradients and community assembly
To elucidate community assembly requires positioning species, and the traits that reflect their ecological strategies, along environmental gradients. Plant functional traits (as means or frequencies) shift along environmental gradients. They also show considerable diversity within assemblages at particular points along gradients (e.g. Wright *et al*., 2004), species with widely varying functional traits coexisting under

44

similar conditions of macroclimate (Givnish 1987; Westoby *et al*., 2002; Ackerly 2003; Cornwell and Ackerly 2009). This coexistence has most often been interpreted as resulting from niche partitioning of local environments within the community, such as micro-habitats arrayed along topographic gradients (see for example Royer *et al*., 2009). Plant and trait coexistence in communities can also be maintained by colonization-competition trade-offs reflecting the contrasting characteristics and life history strategies of pioneer versus persistent, later successional species (Grime 1977; Bazazz 1979; Tilman 1994; Rees and Westoby 1997; Wright 2002). Under colonization-competition trade-offs traits may not be correlated with the structural components of specific micro-habitats (such as topography and soil types). However, traits might still be correlated to factors such as light environment (e.g. Falster and Westoby 2005; Brodribb and Feild 2010; Lusk *et al*., 2010a,b) and soil nutrient ratios that can shift during the gap-succession process (Tilman 1988).

Trait gradient analysis (TGA) partitions traits into alpha (within assemblage) and beta (among assemblage) components to evaluate the extent and strength of 1) trait correlations in relation to underlying environmental gradients across landscape scales and 2) interactions between co-occurring species (Ackerly and Cornwell 2007). It then becomes possible to ask how much of the trait correlation arises because traits need to be coordinated for species functional effectiveness (within assemblages), versus how much arises because different traits are adjusting in parallel to abiotic gradients?

Hypotheses: Community assembly processes create strong linkages among traits both within assemblages (alpha) and across the landscape (beta). Trait variation is greater

among coexisting species within assemblages than between the assemblages a species occupies along abiotic gradients at landscape scales.

1.9.5 Chapter 4: Strategy shifts along gradients

Plant trait values shift along environmental gradients. Following on from chapter 3, a key question is how closely phenotypic variation within species is aligned with the trait gradient for any particular trait (Ackerly and Cornwell 2007). Adult body size is regarded as the single most important trait of a species (Brown 1995). Plant height, a trait that is known to respond to underlying gradients that reflect site productivity, was used to investigate the influence of phenotypic variation.

In tropical and sub-tropical rainforests light interception by trees is largely dependent on their height in the canopy (e.g. Niklas 1995; King 1996; Westoby 1998; Poorter *et al*., 2003, 2005; Falster and Westoby 2005; Osunkoya *et al*., 2007; van Gelder *et al*., 2007). As assemblage-mean heights shift along the height trait gradient, how does the height vary from site to site within an individual species? If height does not change

much within a species and if the species spans a wide range of assemblages, then the relative height ranking of the species will shift considerably along the gradient, and its ecology might be expected to shift along with relative height. Alternatively the potential height of an individual species might shift in alignment with the assemblage-mean height. Another possibility is that most species might span relatively narrow ranges along the gradient, resulting in little or no height adjustment within species, and relative height rankings not shifting much.

Hypotheses: Shifts in assemblage-mean heights along abiotic gradients include the sign of species turnover. Shifts in the height strategies of species in rainforest communities reflect their performance in relation to abiotic gradients.

1.9.6 Chapter 5: Phylogenetic community structure, history, and scale

Darwin (1859) first articulated the idea that because of competition between taxa that are morphologically, functionally or behaviourally similar, assemblages might include fewer congeners than expected. Linking local community assembly processes to regional and continental scale processes across evolutionary timescales remains a key challenge in ecology (e.g. Westoby 2006; Graham and Fine 2008). By using the full phylogenetic tree, it is possible to quantify more comprehensively whether assemblages are overdispersed phylogenetically (Webb 2000; Webb *et al*., 2002). Where data are also available for ecological traits, it is possible to assess whether any phylogenetic overdispersion is associated with overdispersion of traits. At regional scales, diversity gradients and species pool sizes are strongly influenced by both evolutionary and ecological factors, including the timing and rate of lineage diversification, and the historic and current-day extent of suitable habitat (Wiens and Donoghue 2004; Graham *et al*., 2006; Ricklefs 2006; Weir and Schluter 2007). At local scales, community phylogenetic structure can reflect biotic interactions among co-existing species and their traits (Webb *et al*., 2002, 2006; Cavender-Bares *et al*., 2004; Kembel and Hubbell 2006).

Hypotheses: Phylogenetic divergences between latitude regions (tropics and sub-tropics) are older than divergences along gradients within regions. Community phylogenetic structure values shift in a manner that reflects the historic and current-day extent of habitat, and the size of regional and local species pools.

1.9.7 Chapter 6: Evolution, biogeography and functional diversity of Australian rainforests

Historical differences between regions in climatic stability, geographical configuration and relief, that influence speciation and extinction, can have long-lasting effects on the size and diversity of regional species pools (Ricklefs 2004). Understanding the timescales of the emergence and origin of lineages in relation to the record of global geologic, geographic, and environmental change requires that we place community assembly into a phylogenetic framework (Webb 2000; Webb *et al*., 2002). Biogeographic patterns are often used to generate hypotheses regarding the evolutionary and ecological processes that structure and shape species distributions and diversity (Pianka 1966; Jablonski and Sepkoski 1996; Jablonski *et al*., 2006; Crisci *et al*., 2006). However, on their own they are insufficient to infer historical processes. Biogeographic patterns need to be complemented with molecular, phylogenetic, or functional data to allow inferences about history to be made (e.g. Rossetto and Kooyman 2005; Rossetto *et al*., 2008). Measuring community phylogenetic structure in relation to increasing geographic scales provides indications of the extent to which niche conservatism vs lability, and dispersal limitation are operating within a region (Graham and Fine 2008). Results may then be positioned in relation to independent fossil evidence and palaeo-ecological data to improve or support biogeographic interpretations (Schneider and Williams 2005). The outcome could effectively trace the narrative of Australian rainforest biogeography onto a quantified community phylogenetic structure across latitude regions.

Hypotheses: Trait variation is greater and niche breadth lower (reflecting higher levels of endemism) in larger (more stable) areas that have been geographically isolated and topographically buffered from historic disturbance and change. In less protected areas seed dispersal and dispersal related traits contribute significantly to community phylogenetic structure.

Working Group 69 (Gondwanan Rainforests; palaeo- and neo- perspectives) provided valuable insights into southern latitude rainforest vegetation history.

1.9.8 Chapter 7: Thesis Conclusions

Chapter 7 is a concluding discussion that brings together the findings of the previous chapters, and considers them in aggregate.

1.9.9 Appendices

To avoid inconsistencies with published text, supplementary materials are provided here in the same format as the on-line version of published, and submitted papers. Supplementary materials for chapters 2-6 appear here as appendices 1-5, with the content of each first listed in each paper (chapters 2-6), consistent with journal formats.

1.10 References

Ackerly, D.D. and Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among- community components. *Ecology Letters* 10: 135-14.

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Science* 164(3): 165-184.

Adam, P. (1992) *Australian Rainforests*. Oxford University Press, Oxford. UK.

Barlow, B.A. (1981) The Australian flora: its origin and evolution, pp. 25-75 in *Flora of Australia*. Australian Government Publishing Service, Canberra.

Barlow, B.A. (1994) Phytogeography of the Australian region. In: *Australian Vegetation* (second edition) (ed. R.H. Groves). Cambridge University Press, Cambridge.

Barlow, B.A. and Hyland , B.P.M. (1988) The origins of the flora of Australia's wet tropics. *Proceedings of the Ecological Society of Australia* 15: 1-17.

Baur, G.N. (1965) *Forest Types in New South Wales. Forestry Commission of NSW Research Note 17*. Forestry Commission of NSW. Sydney.

Baur, G.N. (1989) *Notes on the silviculture of major N.S.W. types II. Rainforest types*. Forestry Commission of NSW. Sydney.

Bazazz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10: 351-371.

Bazazz, F.A. (1991) Habitat selection in plants. *American Naturalist* 137: S116-S130.

Beadle, N.C.W. (1981) *The vegetation of Australia*. Fischer, Stuttgart.

Beadle, N.C.W. and Costin, A.B. (1952) Ecological classification and nomenclature. *Proceedings of the Linnean Society of NSW* 77: 61-82.

Bowler, J.M., Hope, G.S., Jennings, J.N., Singh, G. and Walker, D. (1976) Late Quaternary climates of Australia and New Guinea. *Quaternary Research* 6: 359-394.

Brodribb, T.J. and Feild, T.S. (2010) Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters* 13: 175-183.

Brown, J.H. (1995) Macroecology. University of Chicago Press, Chicago, USA.

Burbidge, N.T. (1960) The phytogeography of the Australian region. *Australian Journal of Botany* 8: 75-212.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. and Bazazz, F.A. (2004) Phylogenetic over-dispersion in Floridian oak communities. *American Naturalist* 163: 823-843.

Cavender-Bares, J., Keen, A. and Miles, B. (2006) Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87: 109-122.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. and Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693-715.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. and Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351-366.

Chesson, P.L. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-367.

Christophel, D.C. (1981) Tertiary megafossil floras as indicators of floristic associations and palaeoclimate. Pp. 379-390 in A. Keast (ed.), *Ecological Biogeography of Australia*. Dr. W. Junk, The Hague.

Christophel, D.C. (1988) Evolution of the Australian flora through the Tertiary. *Plant Systematics and Evolution* 162: 63-78.

Christophel, D.C. (1994) The early Tertiary macrofloras of continental Australia. Pp. 262-275 in R. Hill (ed.), *The history of Australian vegetation: Cretaceous to Present*. Cambridge University Press, Cambridge.

Christophel, D.C. and Greenwood, D.R. (1987) A megafossil flora from the Eocene of Golden Grove, South Australia. Transactions of the Royal Society of South Australia 111(3): 155-162.

Christophel, D.C. and Greenwood, D.R. (1988) A comparison of Australian tropical rainforest and Tertiary fossil leaf-beds. Pp. 139-148 in R. Kitching (ed.), *The ecology of Australia's Wet Tropics*. Proceedings of the Ecological Society of Australia, vol. 15. Surrey Beatty and Sons, Sydney.

Christophel, D.C. and Greenwood, D.R. (1989) Changes in climate and vegetation in Australia during the Tertiary. *Review of Palaeobotany and Palynology* 58: 95-109.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. Pp. 298-313, in: den Boer P.J. and Gradwell, G.R. (eds.) *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79(1): 109-126.

Crisci, J.V., Sala, O.E., Katinas, L. and Posadas, P. (2006). Bridging historical and ecological approaches in biogeography. *Australian Systematic Botany* 19: 1-10.

Crisp, M.D., Linder, H.P. and Weston, P.H. (1995) Cladistic biogeography of plants in Australia and New Guinea: congruent pattern reveals two endemic tropical tracks. *Systematic Biology* 44: 457-473.

Crisp, M., Cook, L. and Steane, D. (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philosophical Transactions of the Royal Society London B* 359: 1551-1571.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.A., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P. and Linder, H.P. (2009) Phylogenetic biome conservatism on a global scale. *Nature* 458: 754-756.

Darwin, C.R. (1859) On the origin of species by means of natural selection. J. Murray Publ., London.

Davies, T., Meiri, S., Barraclough, T. and Gittleman, J. (2007) Species co-existence and character divergence across carnivores. *Ecology Letters* 10: 146-152.

Díaz, S.J., Cabido, M. & Casanoves, F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 1113-122.

Díaz, S.J., Hodgson, J.G., Thompson, K., Cabido, M.J., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Prunes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk,V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R.J. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295-304.

Donoghue, M.J. (2008) A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Science* U.S.A. 105: 11549-11555.

Emerson, B.C. and Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution* 23: 619-630.

Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* 93: 521-535.

Falster, D.S. (2006) Sapling strength and safety: the importance of wood density in tropical forests. *New Phytologist* (commentary) 171: 237-239.

Farrera, I., Harrison, S.P., Prentice, I.C., Ramstein, G., Guiot, J., Bartlein, P.J., Bonnefille, R., Bush, M., Cramer, W., von Grafenstein, U., Holmgren, K., Hooghiemstra, H., Hope, G., Jolly, D., Lauritzen, S.E., Ono, Y., Pinot, S., Stute, M. and Yu, G. (1999) Tropical climates at the last glacial maximum: a new synthesis of terrestrial paleoclimate data. I. Vegetation, lake levels and geochemistry. *Climate Dynamics* 15: 823-856.

Figgis, P. (ed.) (1985) *Rainforests of Australia*. Weldon, Sydney.

Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C. and Coley, P.D. (2006) The growth-defence trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87: 150-162.

Flenley, J.R. (1979) The Late Quaternary vegetation history of the equatorial mountains. *Progress in Physical Geography* 3: 488-509.

Flenley, J.R. (1998) Tropical forests under the climates of the last 30,000 years. *Climate Change* 39: 177-197.

Floyd, A.G. (1987) Status of rainforests in northern New South Wales. In: *The rainforest legacy. Australian national rainforest study*, Vol. 1 (eds. G. Werren and P. Kershaw), pp. 95-117. Australian Government Publishing Service, Canberra.

Floyd, A.G. (1990) A*ustralian rainforests in New South Wales*. 2 vols. Surrey Beatty, Sydney.

Forestry Commission of NSW (1989) *Forest Types in New South Wales*. *Forestry Commission of NSW Research Note 17*. Forestry Commission of NSW. Sydney.

Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303: 356-359.

Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* 106: S131-S160.

Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87: 193-210.

Graham, C.H., Moritz, C. and Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Science USA* 103: 632-636.

Graham, C. and Fine, P. (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space and time. *Ecology Letters* 11: 1265-1277.

Greenwood, D.R. and Christophel, D.C. (2005) The origins and tertiary history of Australian "tropical" rainforests. In: (eds. Bermingham, E., Dick, C.W. and Moritz, C.) *Tropical Rainforests, Past, Present, and Future*. Chicago University Press, Chicago.

Greenwood, D.R. (2006) Leaf form and the reconstruction of past climates. *New Phytologist* 166: 355-357.

Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 255-260.

Groves, R.H. (ed.) (1994) Australian Vegetation. University Press, Cambridge, UK.

Hardy, O.J. and Senterre, B. (2007) Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology* 95: 493-506.

Herbert, D.A. (1967) Ecological segregation and Australian phytogeographic elements. *Proceedings of the Royal Society of Queensland* 78: 101-111.

Hilbert, D.W. (2008) The dynamic forest landscape of the Australian Wet Tropics: present, past and future. Pp. 107-122, in: *Living in a Dynamic Tropical Forest Landscape* (eds. Nigel E. Stork and Stephen M. Turton). Blackwell Publishing, UK.

Hill, R.S. (1994) The history of selected Australian taxa. Pp. 390-420 in R.S. Hill (ed.), *The history of Australian vegetation: Cretaceous to Present*. Cambridge University Press, Cambridge.

Hill, R.S. (1998) Fossil evidence for the onset of xeromporphy and scleromporphy in the Australian Proteaceae. *Australian Systematic Botany* 11: 391-400.

Hill, R.S. (2004) Origins of the southeastern Australian vegetation. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 359: 1537-1549.

Hopkins, M.S., Ash, J., Graham, A.W., Head, J. and Hewett, R.K. (1993) Charcoal evidence of the spatial extent of *Eucalyptus* woodland expansions and rainforest contractions in north Queensland during the late Pleistocene. *Journal of Biogeography* 20: 357-372.

Hopkins, M.S., Head, J., Ash, J., Hewett, R.K. and Graham, A.W. (1996) Evidence of a Holocene and continuing recent expansion of lowland rainforest in humid tropical North Queensland. *Journal of Biogeography* 23: 737-745.

Humboldt, A. von (1805) *Essay on the Geography of Plants* (*Essai sur la Geographie des Plantes*). Paris.

Humboldt, A. von (1817) *De distributione geographica plantarum secundum coeli temperium et altitudinem montium prolegomena*. Paris.

Humboldt, A. von (1852) *Personal narrative of travels to the equinoctial regions of America*, 2. Translation by T. Ross, London.

Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22: 415-427.

Hyland, B.P.M., Whiffin, T., Christophel, D.C., Gray, B. and Elick, R.W. (2003) Australian tropical rainforest plants: trees, shrubs and vines. CSIRO Publishing.

Jablonski, D. and Sepkoski, J.J. Jr. (1996) Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77(5): 1367-1378.

Jablonski, D., Roy, K. and Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314: 102-106.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501-528.

Kembel, S. and Hubbell, S.P. (2006) The phylogenetic structure of a neo-tropical forest tree community. *Ecology* 87: 86-99.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12: 949-960.

Kershaw, A.P. (1970) A pollen diagram from Lake Euramoo, northeast Queensland, Australia. *New Phytologist* 69: 785-805.

Kershaw, A.P. (1976) A late Pleistocene and Holocene pollen diagram from Lynch's Crater, north-eastern Queensland, Australia. *New Phytologist* 77: 468-498.

Kershaw, A.P. (1978) A record of the last interglacial-glacial cycle from north-eastern Queensland, Australia. *Nature* 272: 159-161.

Kershaw, A.P. (1994) Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109: 399-412.

Kershaw, A.P., McKenzie, G.M. and McMinn, A. (1993) A Quaternary vegetation history of northeastern Queensland from pollen analysis of ODP site 820. *Proceedings of Ocean Drilling Program, Scientific Results* 133: 107-114.

Kershaw, A.P., Bretherton, S.C. and van der Kaars, S. (2007) A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 23-45.

King, D.A. (1996) Allometry and life history of tropical trees. *Journal of Tropical Ecology* 12: 25-44.

Kitching, R. (ed.) (1988) The Ecology of Australia's Wet Tropics. Proceedings of the Ecological Society of Australia. Vol. 15. Surrey Beatty and Sons, Sydney.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. and Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170(2): 271-283.

Leishman, M.R., Wright, I., Moles, A.T. and Westoby, M. (2000) The evolutionary ecology of seed size. In: *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 31-57. CABI Publishing, Wallingford, UK.

Losos, J.B. (1996) Phylogenetic perspectives on community ecology. *Ecology* 77: 1344-1354.

Lovette, I.J. and Hochachka, W.M. (2006) Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology* 87: 14-28.

MacArthur, R.H. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 167: 377-385.

Lusk, C.H., Onoda, Y., Kooyman, R.M. and Gutie´rrez-Giro´n, A. (2010a) Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *New Phytologist* doi: 10.1111/j.1469-8137.2010.03202.x

Lusk, C.H., Sendall, K. and Kooyman, R. (2010b) Latitude, solar elevation angles and gap-regenerating rainforest pioneers. *Journal of Ecology* (accepted)

Martin, H.A. (1987) Cainozoic history of the vegetation and climate of the Lachlan River region, New South Wales. *Proceedings of the Linnean Society of New South Wales* 109: 213-257.

Martin, H.A. (2006) Cenozoic climate change and the development of the arid vegetation in Australia. *Journal of Arid Environments* 66: 533-563.

McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21: 178-185.

Metcalfe, D.J. and Ford, A.J. (2008) Floristics and plant biodiversity of the rainforests of the Wet Tropics. In: *Living in a Dynamic Tropical Forest Landscape* (eds. Nigel E. Stork and Stephen M. Turton) pp. 123-132. Blackwell Publishing, UK.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H. A., McCain, C.M.,

McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. and Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10: 315-331.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B., Pitman, A.J. and Westoby, M. (2005a) Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences* 102(30): 10540-10544.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. and Westoby, M. (2005b) A brief history of seed size. *Science* 307: 576-580.

Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M., Mayfield, M.M., Pitman, A., Wood, J.T. and Westoby, M. (2007) Global patterns in seed size. *Global Ecology and Biogeography* 16: 109-116.

Mooney, H.A. and Dunn, E.L. (1970) Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. *American Naturalist* 104: 447-453.

Moss, P.T. and Kershaw, A.P. (2007) A late Quaternary marine palynological record (oxygen isotope stages 1 to 7) for the humid tropics of northeastern Australia based on ODP Site 820 *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 4-22.

Niklas, K.J. (1994) The allometry of safety factors for plant height. *American Journal of Botany* 81: 345-351.

Niklas, K.J. (1995) Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* 75: 217-227.

Nix, H.A. (1982) Environmental determinants of biogeography and evolution in Terra Australis. *Evolution of the flora and fauna of arid Australia*, (eds. W.R. Barker and P.J.M. Greenslade), pp. 47-66. Peacock Publications, Frewville, South Australia.

Nix, H.A. (1991) An environmental analysis of Australian rainforests. Pp. 1-26 in G.L. Werren and A.K. Kershaw (eds.) *Australian national Rainforests Study, vol. 2 Flora and fauna of the rainforests*. Australian Government Publishing Service, Canberra.

Osunkoya, O.O., Omar-Ali, K., Amit, N., Dayan, J., Daud, D.S. and Sheng, T.K. (2007) Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* 94(12): 1951-1962.

Pacala, S.W. and Tilman, D. (1994) Limiting similarity in mechanistic and spatial models of plant competition in heterogenous environments. *American Naturalist* 143: 222-257.

Pennington, R.T., Richardson, J.E. and Lavin, M. (2006) Insights into the historical construction of species-rich biomes from dated plant phylogenies, neutral ecological theory and phylogenetic community structure. *New Phytologist* 172: 605-616.

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. and Vásquez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences* 91: 2805-2809.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 65-75.

Poorter, L., Bongers, F., Sterck, F.J. and Hannsjörg W. (2003) Architecture of 53 rainforest trees differing in adult stature and shade tolerance. *Ecology* 84: 602-608.

Poorter, L., Bongers, F., Sterck, F.J. and Woll, H. (2005) Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* 93: 256-267.

Poorter, L., Bongers, L. and Bongers, F. (2006) Architecture of 54 moist forest tree species: traits, tradeoffs, and functional groups. *Ecology* 87(5): 1289-1301.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., licona, J-C., Peńa-Claros, M., Sterck, F., Villegas, Z. and Sass-Klassen, U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest species. *New Phytologist* 185: 481-492.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. and Aiello, A. (1983) Uprooting and snapping in trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research* 13: 1011-1020.

R Development Core Team. (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org.

Rees, M. and Westoby, M. (1997) Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78: 116-126.

Reich, P.B., Walters, M.B. and Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* 94(25): 13730-13734.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., and Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* 80(6): 1955-1969.

Richards, P.W. (1952) *The Tropical Rain Forest*. University Press, Cambridge. U.K.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* 235: 167-171.

Ricklefs, R.E. (2004) History and species-area relationship in Lesser Antillean birds. *American Naturalist* 163: 227-239.

Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* 87: S3-S13.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *The American Naturalist* 172(6): 741-750.

Ricklefs, R.E. and Schluter, D. (eds.) (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.

Rossetto, M. & Kooyman, R.M. (2005) The tension between dispersal and persistence regulates the current distribution of rare paleo-endemic rain forest flora: a case study. *Journal of Ecology* 93: 906-917.

Rossetto, M., Kooyman, R.M., Sherwin, W. & Jones, R. (2008) Dispersal limitations rather than bottlenecks or habitat specificity can restrict the distribution of rare and endemic rainforest trees. *American Journal of Botany* 95(3): 321-329.

Rowe, C. (2007) A palynological investigation of Holocene vegetation change in Torres Strait, seasonal tropics of northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 83-103.

Royer, D.L., Kooyman, R.M., Little, S.A. and Wilf, P. (2009) Ecology of leaf teeth: a multi-site analysis from an Australian sub-tropical rainforest. *American Journal of Botany* 96(4): 1-14.

Schimper, A. F. W. (1898) *Pflanzen-geographie auf physiologischer*. Grundlage. G. Fischer, Jena.

Schimper, A. F. W. (1903) Plant geography upon a physiological basis. Clarendon, Oxford.

Schneider, C.J. and Williams, S.E. (2005) Effects of Quaternary climate change on rainforest diversity: insights from spatial analyses of species and genes in Australia's

Wet Tropics. Pp. 401-424, in E. Bermingham, C.W. Dick and C. Moritz eds. *Tropical Rainforests: past, present, and future*. University of Chicago Press, Chicago.

Simes, J.J.H., Tracey, J.G., Webb, L.J. and Dunstan, W.J. (1959) An Australian phytochemical survey. III. Saponins in eastern Australian flowering plants. Bulletin No. 281, CSIRO, Melbourne.

Slingsby, J.A. and Verboom, G.A. (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *American Naturalist* 168: 14-27.

Specht, R.L. and Womersley, J.S. (1979) Heathlands and related shrublands of Malesia (with particular reference to Borneo and New Guinea). In *Ecosystems of the World*, vol. 9a, *Heathlands and related shrublands. Descriptive studies* (ed. R.L. Specht) pp. 321-338. Elsevier, Amsterdam.

Specht, R.L. (1981) Evolution of the Australian flora: some generalisations. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 783-805. The Hague: W.Junk.

Stanton, P. and Fell, D. (2005) *The Rainforests of Cape York Peninsula*. Cooperative Research Centre for Tropical Rainforest Ecology and Management. Rainforest CRC, Cairns.

Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J. and Zimmerman, J.K. (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology* 87: 2418-2424.

Swenson, N.G., Enquist, B.J., Thompson, J. and Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770-1780.

Thomas, S.C. (1996) Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rainforest trees. *American Journal of Botany* 83: 556-566.

Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, N.J.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.

Tracey, J.G. (1982) *The Vegetation of the Humid Tropical Region of North Queensland*. CSIRO Publications. Melbourne.

Vamosi, J.C. and Vamosi, S.M. (2007) Body size, rarity, and phylogenetic community structure: insights from diving beetle assemblages of Alberta. *Diversity and Distributions* 13: 1-10.

Vamosi, S.M., Heard, S.B., Vamosi, J.C. and Webb, C.O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18: 572-592.

van Gelder H.A., Poorter, L. and Sterck, F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest community. *New Phytologist* 171: 367-378.

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* 156: 145-155.

Webb, C.O., Ackerly, D.D., Peek, M.A. and Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475-505.

Webb, C.O., Losos, J.B. and Agrawal, A.A. (2006) Integrating phylogenies into community ecology. *Ecology* 87: S1-S2.

Webb, L.J. (1948) Guide to the medicinal and poisonous plants of Queensland. Council of Scientific and Industrial Research, Australia, Bulletin No. 232.

Webb, L.J. (1949) Australian Phytochemical Survey – Part 1. Bulletin No. 241. CSIRO, Melbourne.

Webb, L.J. (1952) Australian Phytochemical Survey – Part II. Bulletin No. 268. CSIRO, Melbourne.

Webb, L.J. (1955) A preliminary phytochemical survey of Papua New Guinea. *Pacific Science* 9: 430-441.

Webb, L.J. (1958) Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Australian Journal of Botany* 6: 220-228.

Webb, L.J. (1959) A physiognomic classification of Australian rain forests. *Journal of Ecology* 47: 551-570.

Webb, L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296-311.

Webb, L.J. (1978) A General Classification of Australian Rainforests. *Australian Plants* 9, 349-363.

Webb, L.J. and Tracey, J.G. (1981a) Australian rainforests: patterns and change. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 605-694. The Hague: W.Junk.

Webb, L.J. and Tracey, J.G. (1981b) The rainforests of northern Australia. In: *Australian Vegetation* (ed. R.H. Groves), pp. 67-101. Cambridge University Press, Cambridge.

Webb, L.J., Tracey, J.G., Williams, W.T. and Lance, G.N. (1967a) Studies in the numerical analysis of complex rain-forest communities. I. A comparison of methods applicable to site/species data. *Journal of Ecology* 55: 171-191.

Webb, L.J., Tracey, J.G., Williams, W.T. and Lance, G.N. (1967b) Studies in the numerical analysis of complex rain-forest communities. II. The problem of species sampling. *Journal of Ecology* 55: 525-538.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1976) The value of structural features in tropical forest typology. *Australian Journal of Ecology* 1: 3-28.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1984). A floristic framework of Australian Rainforests. *Australian Journal of Ecology* 9: 169-198.

Webb, L.J., Tracey, J.G. and Jessup, L.W. (1986) Recent evidence for autochthony of Australian tropical and subtropical rainforest floristic elements. *Telopea* 2: 575-589.

Weiher, E. and Keddy, P.A. (1995) The assembly of experimental wetland plant communities. *Oikos* 73: 323-335.

Weir, J.T. and Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315: 1574-1576.

Werren, G.L. and Kershaw, A.P. (eds.) (1987) The rainforest legacy: Australian national rainforests study. Vol. 1-3. Australian Government Publishing Service, Canberra.

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.

Westoby, M, Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125-159.

Westoby, M. and Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21(5): 261-268.

Westoby, M. (2006) Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology* 87: S163-S166.

Wiens, J. and Donoghue, M.J. (2004) Historical biogeography, ecology, and species richness. Trends in Ecology and Evolution 19: 639-644.

Wiens, J. and Graham, C. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics* 36: 519-539.

Williams, W.T., Lance, G.N., Webb, L.J. and Tracey, J.G. (1973) Studies in the numerical analysis of complex rain-forest communities. VI. Models for the classification of quantitative data. *Journal of Ecology* 61: 47-70.

Williams, W.T. and Tracey, J.G. (1984) Network analysis of northern Queensland tropical rainforests. *Australian Journal of Botany* 32: 109-116.

Wilf, P. (1997) When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* 23: 373-390.

Wolfe, J.A. (1979) Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. *U.S. Geological Survey Professional Paper* 1106: 1 – 37.

Wolfe, J.A. (1993) A method of obtaining climatic parameters from leaf assemblages. *U.S. Geological Survey Bulletin* 2040: 1 – 71.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Philip K. Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. and Westoby, M. (2005) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14: 411–421.

Wright, I.J., Westoby, M., Reich, P.B., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lusk, C., Midgley, J.J., Navas, M-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior,

L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature* 428, 821-827.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Paz, H., Pitman, N.C.A., Poorter, L., Silman, M.R., Vriesendorp, C.F., Webb, C.O., Westoby, M. & Wright, S.J. (2007) Relationships among ecologically important dimensions of plant trait variation in seven neo-tropical forests. *Annals of Botany* 99, 1003-1015.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species co-existence. *Oecologia* 130: 1-14.

Ziegler, A.M., Eshel, G., Rees, P.M., Rothfus, T.A., Rowley, D.B. and Sunderlin, D. (2003) Tracing the tropics across land and sea: Permian to present. *Lethaia* 36: 227-254.

CHAPTER 2

Costs of height gain in rainforest saplings: main stem scaling, functional traits and strategy variation across 75 species

Robert Kooyman[1] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, Sydney, NSW 2109*

Australia

ANNALS OF
BOTANY
Founded 1887

Costs of height gain in rainforest saplings: main-stem scaling, functional traits and strategy variation across 75 species

Robert M. Kooyman* and Mark Westoby

Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

• *Background and Aims* Height gain plays an important role in plant life-history strategies and species coexistence. Here main-stem costs of height gain of saplings across species within a rainforest community are compared.

• *Methods* Scaling relationships of height to diameter at the sapling stage were compared among 75 woody rainforest plant species in subtropical eastern Australia using standardized major axis regression. Main-stem costs of height gain were then related to other functional traits that reflect aspects of species ecological strategies.

• *Key Results* Slopes (β) for the height–diameter (H–D) scaling relationship were close to 1·3, in line with previous reports and with theory. Main-stem volume to achieve 5 m in height varied substantially between species, including between species within groups based on adult height and successional status. The variation was largely independent of other species traits, being uncorrelated with mature plant height (H_{max}) and with leaf size, and weakly negatively correlated with wood density and seed size. The relationship between volume to reach 5 m and wood density was too weak to be regarded as a trade-off. Estimated main-stem dry mass to achieve 5 m height varied almost three-fold across species, with wood density and stem volume contributing roughly equally to the variation.

• *Conclusion* The wide range in economy of sapling height gain reported here is presumed to be associated with a trade-off between faster growth and higher mortality rates. It is suggested that wide diameters would have a stronger effect in preventing main-stem breakage in the short term, while high wood density would have a stronger effect in sustaining stem strength over time.

Key words: Allometry, community ecology, diameter, functional traits, height, saplings, stem volume, trait correlations, wood density.

INTRODUCTION

Plant size (measured as mass, height or diameter) can span ten orders of magnitude over the ontogenetic lifetime of an individual tree. Size exerts a powerful influence on plant form, function and life history (Niklas, 1995; Westoby *et al.*, 2002). Coexisting trees can vary considerably in height at similar diameters (diameter at breast height, dbh; Thomas, 1996; King, 1996; Sterck *et al.*, 2001; Kohyama *et al.*, 2003; Poorter *et al.*, 2003, 2006), and diameter–height relationships influence the 'safety factor' of species against buckling (Putz *et al.*, 1983; van Gelder *et al.*, 2006).

Two alternative interpretations can be suggested for the smaller diameter at a given height (e.g. dbh) of some species compared with others. One is that narrow-dbh species reflect a fast-growth strategy with a concomitant high risk of stem breakage. The other possibility is that narrow-dbh species compensate for limited basal thickening by having strong, high-density wood. Dense wood has a higher modulus of rupture (Niklas, 1994) and makes trees less vulnerable to breakage. If narrow-dbh species invested more in wood density, then the biomass cost of height gain and the risk of breakage might be similar across different stem-widening strategies.

Thomas (1996) examined the hypothesis that understorey trees have thicker stems (at a common height) than canopy

trees in the same assemblage because diameter increment continues even after trees attain their maximum height (King, 1990). Interestingly, he found no correlation between diameter at a common height and maximum height at maturity (H_{max}). However, a number of studies have subsequently reported that adult shade-tolerant sub-canopy trees have thicker stems than canopy trees at the same height (King, 1996; Sterck *et al.*, 2001; Kohyama *et al.*, 2003; Poorter *et al.*, 2003, 2006; King *et al.*, 2006*a*), suggesting that the height–diameter (H–D) relationship does vary in relation to H_{max} (Thomas, 1996; King *et al.*, 2006*b*; Poorter *et al.*, 2006; Osunkoya *et al.*, 2007). Because the diameter–height ratio increases progressively with growth, and species ranking can switch with reference to height, a more general approach to addressing this question is to assess the slope and intercept of log diameter versus log height graphs (Kerkhoff *et al.*, 2006; Poorter and Bongers, 2006; Warton *et al.*, 2006).

The functional basis for the expectation that some traits are influenced by growth form (plant size) is well established (see, for example, Moles *et al.*, 2005). In addition, trait-based approaches to community ecology can potentially link ecological strategy variation and functional diversity (via scaling relationships and performance currencies) to community assembly and species coexistence (Westoby and Wright, 2006; Grime, 2006; McGill *et al.*, 2006). Strong correlations across species have been reported for leaf size, specific leaf

* For correspondence. E-mail rkooyman@bio.mq.edu.au

area (SLA) and maximum height (e.g. Fonseca *et al.*, 2000); between leaf size, wood density, seed size and maximum height (Ackerly *et al.*, 2002; Cornwell *et al.*, 2006; Cornwell and Ackerly, 2009); and between shade tolerance (reflecting successional status), wood density and maximum height (Falster and Westoby, 2005; discussed in Poorter, 2008; and see Reich *et al.*, 2003; Wright *et al.*, 2007).

This paper compares investment in main stem at the sapling stage across 75 species in Australian subtropical rain forest. The following questions are addressed: (1) how did species vary in the main-stem investment used to attain a given height, and what were the contributions to this variation from allometry ($H–D$ relationships) and from wood density; and (2) were those architectural traits associated with other species traits for which data were available and that are thought to be ecologically significant, namely adult stature (potential maximum height as H_{max}), shade tolerance, leaf size and seed size?

MATERIALS AND METHODS

Site and selection of species

Diameter at breast height over bark (dbh) and height for plants >1.0 and <10 cm dbh were collected in 2000–2001 for 18 134 individual understorey trees, small trees and shrubs from 20 previously established permanent plots in sub-tropical rain forest in eastern Australia (Kariuki and Kooyman, 2005; Kariuki *et al.*, 2006). The aim at the time was to supplement data for larger trees (3000 individuals >10 cm dbh, representing 117 species) that had been permanently tagged and monitored for growth over decades. Individual trees were removed from the dataset if they belonged to species represented by low numbers of individuals (predominantly shade-tolerant canopy tree species), if their stems were recorded as broken or had measurements that clearly indicated they were damaged, or if they had dbh <1 cm. The resulting data covered a total of 11 111 individual plants representing 75 species from the total of 138 recorded (Supplementary Data Table S1, available online). The species came from 32 families and 62 genera, and varied substantially in adult stature and successional status.

Of the 75 species included in the study 70 were classed as shade-tolerant and five as shade-intolerant, based on local knowledge at seedling and sapling stages (Kooyman, 1996; Kariuki and Kooyman, 2005; Kariuki *et al.*, 2006). Shade-intolerant species included both pioneers and canopy trees, and shade-tolerant species included shrubs, understorey trees and canopy trees. Rather than using these as categories, the continuous trait of maximum height at maturity as a potential predictor was used, along with shade-tolerance.

Diameter was measured at 1.3 m above ground level using a steel diameter tape or calliper. Height was measured to the topmost foliage using an extendable height pole. Species-level data for leaf size, wood traits (including density) and seed size were taken from published floras and other sources, including Bootle (1983), Stanley and Ross (1983–1989, volumes 1–3), Floyd (1989, pp. 268–270), Harden (1990–1993, volumes 1–4 with revisions), Ilic *et al.* (2000) and Cornelissen *et al.* (2003). Minimum and maximum leaf sizes reported in the floras generally reflected

the range of variation in leaf size on mature plants, and juvenile leaf sizes were excluded from consideration. Leaf size reported here is for whole simple leaves and for lateral leaflets of compound leaves. Leaf size was estimated using maximum leaf length and width, where area = length × width × 0.70 (cm^2), which has been shown to correlate well with photographic area estimates of rainforest tree leaves (e.g. Kraft *et al.*, 2008). Seed size was estimated using maximum dimensions of embryo plus endocarp (length + width/2, in millimetres; reflecting average diameter). Wood density estimates for adults [dry kg m^{-3}; van Gelder *et al.* (2006) found that adult and juvenile wood density were well correlated across species, $r = 0.91$, $P < 0.001$] were extracted from published sources. Estimated maximum height at maturity (H_{max}) was based on field information previously collected by R.M.K. that reflects maximum canopy height (m) for species in this location (at largest known diameters, at reproductive maturity). This provides a single value for maximum potential height for each species.

Data analysis

Relationships between height and diameter were described by fitting standardized major axis (SMA) lines, given that the questions were about co-ordination between these two growth measures, rather than about predicting one from the other (Warton *et al.*, 2006). Tests equivalent to analysis of covariance (common slope, different elevations given a common slope, confidence intervals for slopes and elevations) were implemented through SMATR software (Falster *et al.*, 2003, 2006; Warton *et al.*, 2006).

RESULTS

The increase in log$D$ appeared to be linear with log$H$ within this range of size (data shown for six species in Fig. 1; slopes and intercepts included to illustrate the main features). There was substantial scatter in the data, individual saplings within a species having quite a wide range of diameters at a given height. The scatter probably reflected the considerable variation in light and factors associated with forest structure, disturbance, stem density, and interaction effects and competition (Niklas, 1995; King, 1996; Henry and Aarssen, 1999; Niklas *et al.*, 2003; Kariuki *et al.*, 2006; Poorter *et al.*, 2006). Despite the scatter around the height–diameter relationships, some species clearly tended to have greater diameter than others, at a given height (Fig. 1).

There were no consistent or interpretable differences in slopes between species (Fig. 2A, B, and Supplementary Data Table S1). The common scaling slope of the $D–H$ relationship across the 75 species was $\beta = 1.321$, and most slopes fell between the 3/2 expected under elastic similarity and the 1/1 expected under geometric self-similarity models for stem strength and safety (McMahon, 1973; McMahon and Kronauer, 1976; Niklas, 1994, 1995). After Bonferroni correction there were only three species with slopes significantly shallower than $\beta = 1.32$, and five species with slopes significantly steeper. Neither group of species had features that stood out from those of other species (see Supplementary
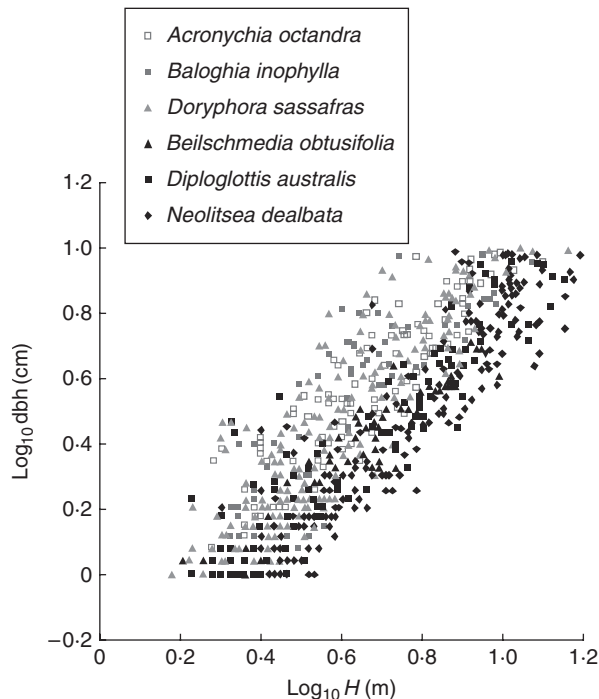
FIG. 1. Scatterplot illustrating the relationships between $\log_{10}$ dbh and $\log_{10}$ height for six species. Each data point is an individual stem in the range 1–9·9 cm dbh for the six species shown in the legend that represent three each with high and low stem volume at a (low) common height. Taxonomic information for all species referred to in this study is provided in the Supplementary Data. SMA slope (β) and intercept (α) values are: *Acronychia octandra* – $\beta = 1·27$, $\alpha = -0·29$, $r^2 = 0·81$; *Baloghia inophyla* – $\beta = 1·33$, $\alpha = -0·35$, $r^2 = 0·75$; *Doryphora sassafras* – $\beta = 1·468$, $\alpha = -0·44$, $r^2 = 0·8$; *Beischmeidia obtusifolia* – $\beta = 1·10$, $\alpha = -0·34$, $r^2 = 0·87$; *Diploglottis australis* – $\beta = 1·17$, $\alpha = -0·37$, $r^2 = 87$; *Neolitsea delabata* – $\beta = 1·31$, $\alpha = -0·51$, $r^2 = 0·84$.

Data Table 3a–b). The extreme low slope shown in Fig. 2 was not among those that were significantly different.

SMA fits to the relationships between diameter and height growth differed between species mainly in elevation (intercept of $\log H$–$\log D$ graphs) rather than in slope. Diameter (dbh) at a reference height of 5 m was calculated using the SMA line fitted for each species, and varied approx. 1·8-fold (2·5–4·4 cm) across the 75 species.

The range of dbh at 5 m height translated into an approx. three-fold range of stem volume (Fig. 2C, D). Stem volumes were approximated as cones at the common height of 5 m, where $V = \pi r^2 h)/3$, $h = 5$ m (500 cm) and r was radius at the base of the cone, calculated as r/dbh $= 5/(5-1·3)$. This approximation is not likely to be exact, but we believe it provides a reasonable relative ranking among species. The approx. three-fold range of main-stem volume used to achieve a common height (in this case 5 m) was consistent with the findings of King *et al.* (2006*a*).

We considered whether either the $\log D$–$\log H$ slope or the estimated main-stem volume to reach 5 m height might be correlated with potential canopy height or with wood density (Fig. 2). Falster and Westoby (2005) and Poorter (2008) had previously noted that species with low potential heights were markedly different depending on whether they were shade-

tolerant (understorey species) or shade-intolerant (pioneer species). Accordingly, we tested for interaction, i.e. for response to maximum height or to wood density having different slope depending on shade tolerance. These interaction terms were not significant (Table 1), and nor were any of the main effects except for a weak ($r^2 = 0·025$) tendency towards shallower slope in species with greater maximum heights (Table 1).

Dry mass investment in the main stem to achieve 5 m sapling height is the product of stem volume and wood density. Consideration was given to whether thicker stemmed species might tend to comprise lighter wood. Larger dbh and hence stem volume at 5 m height was not significantly correlated with lower wood density ($r = 0·17$, $P = 0·14$; Fig. 3).

Contours in Fig. 3 indicate main-stem dry mass at 5 m sapling height calculated as estimated volume × wood density. The numbers should be interpreted comparatively between species more than absolutely because the stem volume is approximate, the wood density has been taken from adult stems elsewhere and some of the volume will be bark rather than wood. The more economical main stems were both narrow in dbh and also fairly low in wood density; more expensive main stems were either wide in dbh or had high wood density. Wood density and main-stem volume were almost equally important as sources of variation across species in estimated dry mass of main stem (54 vs. 46 %, multiple regression). Most species lay within about a two-fold range in each dimension (wood density approx. 0·5–1·0, main-stem volume approx. 2·0–4·0 L).

Sapling main-stem volume at 5 m height was only weakly positively correlated with the size of leaves ($P < 0·1$), and negatively (but not significantly) correlated with seed size (Table 2).

DISCUSSION

In the saplings examined here, diameter generally increased relatively faster than height (SMA common slope across species $\beta = 1·32$, a two-fold increase in height being associated with an approx. 2·5-fold increase in dbh). This happened in a similar way across species, and in shade-intolerant compared with shade-tolerant species. The slope was in line with previously reported results for tropical rain forest species (Kohyama, 1987, 1991; Kohyama and Hotta, 1990; King, 1990; Niklas, 1995) and was consistent with theory (see, for example, Niklas, 1995; Thomas, 1996; Sterck and Bongers, 1998; Sposito and Santos, 2001). Shifting D–H ratios through ontogeny (Sterck and Bongers, 2001; Poorter *et al.*, 2005) are thought to reflect taller stems requiring greater mechanical support, having different respiratory loads and fluid requirements, and eventually in the exposed canopy experiencing different conditions (Givnish, 1988; Niklas, 1994). In addition, as plants approach their maximum height, and with the onset of reproduction and a resultant shift in the allocation of energy, height growth must slow further compared with diameter (Charnov, 1993; Enquist *et al.*, 1999; Koch *et al.*, 2004). Studies including larger size classes have described non-linear diameter–height allometric relationships during ontogeny (Niklas, 1995; Thomas, 1996), and significant differences based on successional status (King, 1981;
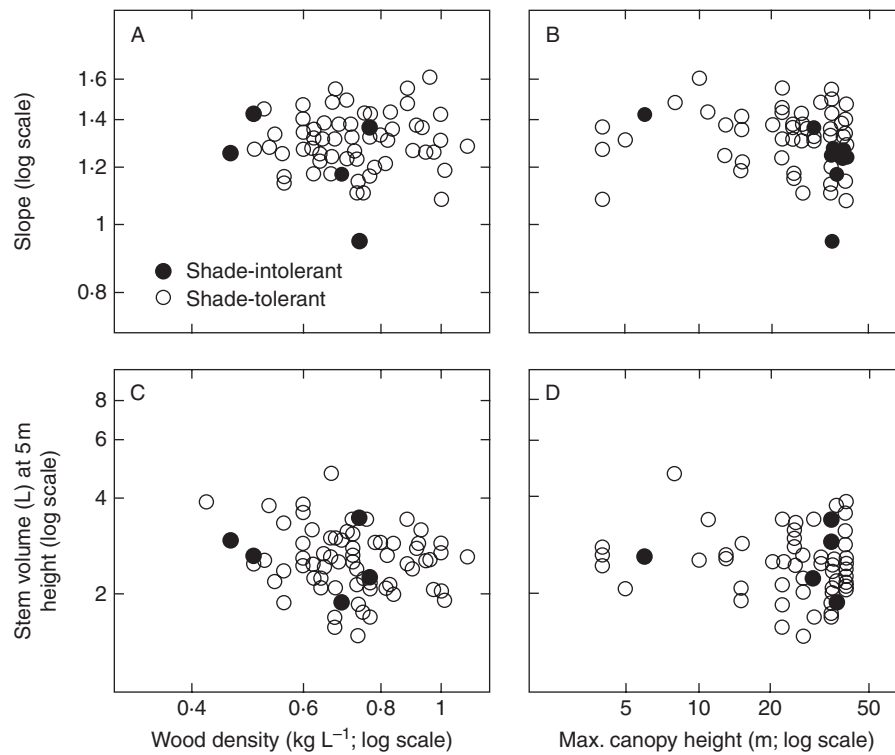
FIG. 2. Scatterplots relating SMA slopes and volume for saplings at a common height (5 metres) to wood density and estimated maximum height at maturity. Two species groups are shown: shade-intolerant and shade-tolerant, as indicated. The species with the shallowest estimated slope is *Alphitonia excelsa*, a shade-intolerant tree with medium wood density. SMA slopes represent $\log_{10}$ dbh-diameter (cm) to $\log_{10}$ height (m) for saplings from 75 species in the range 1–10 cm dbh.

TABLE 1. *Summary data for analyses of covariance corresponding to Fig. 2*

Dependent variable	Source	Type III sum of squares	d.f.	Mean square	F	P-value
Slope	Shade-tolerance	0·003	1	0·003	1·94	0·17
	Wood density	0·003	1	0·003	1·62	0·21
	Shade-tolerance × wood density	0·005	1	0·005	3·00	0·09
	Error	0·114	71	0·002		
Slope	Shade-tolerance	0·003	1	0·003	1·77	0·19
	Maximum height	0·008	1	0·008	4·92	0·03
	Shade-tolerance × maximum height	0·005	1	0·005	3·01	0·09
	Error	0·112	71	0·002		
Main-stem volume at 5 m	Shade-tolerance	0·000	1	0·000	0·03	0·87
	Wood density	0·005	1	0·005	0·56	0·46
	Shade-tolerance × wood density	0·000	1	0·000	0·03	0·85
	Error	0·666	71	0·009		
Main-stem volume at 5 m	Shade-tolerance	0·000024	1	0·000024	0·003	0·96
	Maximum height	0·001	1	0·001	0·07	0·79
	Shade-tolerance × maximum height	0·000067	1	0·000067	0·007	0·93
	Error	0·679	71	0·010		

The predicted variable is either slope of the $\log D$–$\log H$ relationship (log scaled) or estimated main-stem volume at 5 m height (log scaled). Predictor variables are shade-tolerance (categorical) and either wood density or maximum canopy height (log scaled).

Alvarez-Buylla and Martinez-Ramos, 1992; but see Sterck and Bongers, 1998).

The increase in the $\log D$–$\log H$ relationship (unlike its slope) did differ substantially across species among these saplings, corresponding to an estimated three-fold range in main-stem mass required to achieve a common height. King *et al.* (2006*a*) found a similar level of variation in biomass allocation across the 21 rainforest tree species they sampled from Pasoh

Forest Reserve in Peninsular Malaysia, although they compared main-stem biomass at 17 m height.

In the present study, among species that required greater mass, some had higher wood density and others had wider stems. However, the trade-off between stem width and wood density was weak at best (negative correlation, $r = 0.17$, $P = 0.14$). This is somewhat contrary to the expectation of a trade-off between wood density and stem thickness in relation to
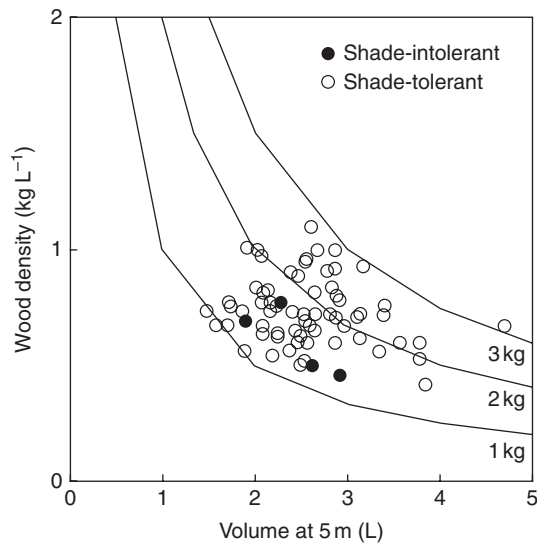
FIG. 3. Scatterplot of stem volume at a common height and wood density for 75 species. The lines represent the contours of main-stem mass (volume × density) for values of 1, 2 and 3 kg, and provide the link between points of equal cost of height growth in relation to the two measures. Shade-intolerant species ($n = 5$) and shade-tolerant species ($n = 70$) are indicated. van Gelder *et al.* (2006) found that adult and juvenile wood density was well correlated across species ($r = 0.91$, $P < 0.001$). Estimates of species sapling strength and safety in the understorey using measures of MR (modulus of rupture) and ME (modulus of elasticity) for adult stems showed strong correlation with (adult) wood density (see Supplementary Data, Appendix S6).

TABLE 2. *Cross-species correlation coefficients (r) between trait values (including stem volume at 5 m height) using species means; n = 75 except for wood density (n = 72).*

	$\log_{10}$ max. height	$\log_{10}$ wood density	$\log_{10}$ leaf area	$\log_{10}$ seed size
$\log_{10}$ max. height	1			
$\log_{10}$ wood density	−0.14	1		
$\log_{10}$ leaf area	**0.25****	**0.30*****	1	
$\log_{10}$ seed size	**0.30*****	**0.22****	0.18	1
$\log_{10}$ stem volume	−0.07	−0.17	**0.20***	−0.18

Significant relationships are in bold: * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$.

safety factors (Enquist *et al.*, 1999; Wright *et al.*, 2003; King *et al.*, 2006*a*; van Gelder *et al.*, 2006).

Whether this range from high to low main-stem costs of height gain was associated with other aspects of plant ecological strategy was assessed. Indicators available were seed size, maximum height, leaf size, wood density and shade-tolerance. These traits were correlated among each other (Table 2) in patterns similar to those previously reported elsewhere. For example, seed and leaf size were positively correlated with H_{max} (Leishman *et al.*, 2000; Moles *et al.*, 2004), and wood density was negatively correlated with leaf size and positively correlated with seed size.

Interestingly, within the species sampled, the range from high to low main-stem costs proved to be unrelated to seed

size, to leaf size and to shade-tolerance. The absence of a relationship to shade-tolerance was especially interesting, as it might be expected that shade-intolerant species typically were growing in higher light, and in general, open-grown stems are expected to be shorter and thicker, whereas stems in high-density stands are taller and thinner (Niklas, 1995; Niklas *et al.*, 2003).

In summary, across the species sampled, main-stem expense to reach 5 m did not show any trend in association with H_{max} or with wood density. Main-stem expense to achieve 5 m height also varied largely independently of the other ecological traits available to us. Higher main-stem expense implies lower allocation to leaves and roots and hence slower growth than might otherwise have been the case. It seems likely that the benefit of higher main-stem expense lies in improved survival. Although continued height gain in the understorey helps trees to avoid overtopping and suppression, this must be balanced against risks of damage from limb and tree falls in order to maximize survival to reproduction (King, 1990; Kohyama and Hotta, 1990; Niklas, 1995; Thomas, 1996; Poorter *et al.*, 2003; Falster, 2006; Osunkoya *et al.*, 2007; Poorter, 2008). Previous studies have found positive correlations across tree species between lower wood density, higher growth rate and increased mortality rate (Enquist *et al.*, 1999; Wright *et al.*, 2003; King *et al.*, 2006*a*; van Gelder *et al.*, 2006). Our results show that stem width contributes as much as wood density to variation in main-stem cost, so growth and mortality rates might be more tightly related to overall main-stem cost than to wood density alone.

In theory, a combination of wider diameters with lighter wood should have a stronger effect on mechanical strength and hence on preventing main-stem breakage in the short term. The flexural stiffness of sapling stems (force required to produce a given deflection) is proportional to EI, where E is Young's modulus of elasticity, and I is the second moment of cross-sectional area, which for circular stems is $\pi r^4/4$. At a given mass per length of stem, flexural stiffness would be substantially greater in sapling species with large diameters, because the fourth-power effect of increasing diameter is expected to outweigh the corresponding decrease in wood density (a strong correlate of modulus of elasticity). On the other hand, stems with high wood density would be expected to suffer less from attack by borers and fungi (e.g. Augspurger, 1984) and to sustain stem strength better over time. Possibly these factors could influence the wide range of alternative ways that a given main-stem cost is incurred.

SUPPLEMENTARY DATA

Supplementary data are available online at www.Aob.oxfordjournals.org and consist of the following information. Table S1: Summary results for species (75) from standardized major axis. Table S2: Trait values, and growth data for 75 species. Table S3: Summary results and trait values for eight species still significant after Bonferroni correction (from standardized major axis results) in relation to tests of the null hypothesis for slope values. Appendix S4: Synthesis of inter-specific comparisons for species-level results for species with 95 % confidence interval that bracketed ($H-D = 1:1$; geometric self-similarity model); and taxa with

low R^2 values. Appendix S5: Binary logistic model for mortality likelihood coefficients, model outputs and mortality statistics (basic by group). Appendix S6: Results of (oridinary least-squares, OLS) regression analysis of relationship between stem safety measures (modulus of rupture and modulus of elasticity) and wood density (for adult wood only). Table S7: Species taxonomic checklist.

LITERATURE CITED

Ackerly DD, Knight CA, Weiss SB, Barton K, Starmer KP. 2002. Leaf size, specific leaf area and microhabitat distribution of woody plants in a California chaparral: contrasting patterns in species level and community level analyses. *Oecologia* **130**: 449–457.

Alvarez-Buylla ER, Martinez-Ramos M. 1992. Demography and allometry of *Cecropia obtusifolia*, a neo-tropical pioneer tree – an evaluation of the climax–pioneer paradigm for tropical rainforests. *Journal of Ecology* **80**: 275–290.

Augspurger CK. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* **72**: 777–796.

Bootle KR. 1983. *Wood in Australia: types, properties and uses*. Sydney: McGraw-Hill.

Charnov EL. 1993. *Life history invariants: some explanations of symmetry in evolutionary ecology*. Oxford: Oxford University Press.

Cornelissen JHC, Lavorel S, Garnier E, *et al.* 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.

Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79**: 109–126.

Cornwell WK, Schwilk DW, Ackerly DD. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**: 1465–1471.

Enquist BJ, West GB, Charnov EL, Brown JH. 1999. Allometric scaling of production and life history variation in vascular plants. *Nature* **401**: 907–911.

Falster DS. 2006. Sapling strength and safety: the importance of wood density in tropical forests. *New Phytologist* **171**: 237–239

Falster DS, Westoby M. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* **93**: 521–535.

Falster DS, Warton DI, Wright IJ. 2003. (S)MATR: standardized major axis tests and routines http://www.bio.mq.edu.au/ecology/SMATR [July 2007].

Falster DS, Warton DI, Wright IJ. 2006. *Updated user's guide to SMATR: standardised major axis tests and routines*, Version 2.0. http://www.bio.mq.edu.au/ecology/SMATR/.

Floyd AG. 1989. *Rainforest trees of mainland south-eastern Australia*, Sydney: Inkata Press.

Fonseca CR, Overton JM, Collins B, Westoby M. 2000. Shifts in trait-combinations along rainfall and phosphorous gradients. *Journal of Ecology* **88**: 964–977.

van Gelder HA, Poorter L, Sterck FJ. 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest community. *New Phytologist* **171**: 367–378.

Givnish TJ. 1988. Adaptations to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology* **15**: 63–92.

Grime JP. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* **17**: 255–260.

Harden GJ. 1990–1993. *Flora of New South Wales*, volumes 1–4. Sydney: UNSW Press.

Henry H, Aarssen LW. 1999. The interpretation of stem diameter–height allometry in trees: biomechanical constraints, neighbour effects, or biased regressions? *Ecology Letters* **2**: 89–97.

Ilic J, Boland D, McDonald M, Downes G, Blakemore P. 2000. *Wood density phase 1: state of knowledge*. National Carbon Accounting System Technical Report No. 18. Australian Greenhouse Office. http://www.greenhouse.gov.au/ncas/reports/pubs/tr18final.pdf.

Kariuki M, Kooyman RM. 2005. Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* **30**: 844–855.

Kariuki M, Rolfe M, Smith RGB, Vanclay JK, Kooyman RM. 2006. Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. *Forest Ecology and Management* **225**: 1–14.

Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorous in the seed plants. *The American Naturalist* **168**: E103–E122.

King DA. 1981. Tree dimensions: maximizing the rate of height growth in dense stands. *Oecologia* **51**: 351–356.

King DA. 1990. Allometry of saplings and understorey trees of a Panamanian forest. *Functional Ecology* **4**: 27–32.

King DA. 1996. Allometry and life history of tropical trees. *Journal of Tropical Ecology* **12**: 25–44.

King DA, Davies SJ, Tan S, Nur NSM. 2006a. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* **94**: 670–680.

King DA, Wright SJ, Connell JH. 2006b. The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. *Journal of Tropical Ecology* **22**: 11–24.

Koch GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. *Nature* **428**: 851–854.

Kohyama T. 1987. Significance of architecture and allometry in saplings. *Functional Ecology* **1**: 399–404.

Kohyama T. 1991. A functional model describing sapling growth under a tropical forest canopy. *Functional Ecology* **5**: 83–90.

Kohyama T, Hotta M. 1990. Significance of allometry in tropical saplings. *Functional Ecology* **4**: 515–521.

Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocap forest. *Journal of Ecology* **91**: 797–806.

Kooyman RM. 1996. *Growing rainforest: rainforest restoration and regeneration – recommendations for the humid sub-tropical region of northern NSW and south-east Qld*. Australia: Greening Australia Queensland.

Kraft NJB, Valencia R, Ackerly DD. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**: 580–582.

Leishman MR, Wright IJ, Moles AT, Westoby M. 2000. The evolutionary ecology of seed size. In Fenner M ed. *Seeds – the ecology of regeneration in plant communities*. Wallingford: CAB International, 31–57.

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**: 178–185.

McMahon TA. 1973. Size and shape in biology. *Science* **179**: 1201–1204.

McMahon TA, Kronauer RE. 1976. Tree structures: deducing the principles of mechanical design. *Journal of Theoretical Biology* **59**: 443–466.

Moles AT, Falster DS, Leishman MR, Westoby M. 2004. Small-seeded plants produce more seeds per square metre of canopy area per year, but not per individual per lifetime. *Journal of Ecology* 92: 384–396.

Moles AT, Ackerly DD, Webb CO, *et al.* 2005. Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences* 102: 10540–10544.

Niklas KJ. 1994. The allometry of safety factors for plant height. *American Journal of Botany* 81: 345–351.

Niklas KJ. 1995. Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* 75: 217–227.

Niklas KJ, Midgley JJ, Rand RH. 2003. Tree size frequency distributions, plant density, age and community disturbance. *Ecology Letters* 6: 405–411.

Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK. 2007. Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* 94: 1951–1962.

Poorter L. 2008. The relationships of wood-, gas- and water fractions of tree stems to performance and life history variation in tropical trees. *Annals of Botany* 102: 367–375.

Poorter L, Bongers F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87: 1733–1743.

Poorter L, Bongers F, Sterck FJ, Hannsjörg W. 2003. Architecture of 53 rainforest trees differing in adult stature and shade tolerance. *Ecology* 84: 602–608.

Poorter L, Bongers F, Sterck FJ, Woll H. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. *Journal of Ecology* 93: 256–267.

Poorter L, Bongers L, Bongers F. 2006. Architecture of 54 moist forest tree species: traits, tradeoffs, and functional groups. *Ecology* 87: 1289–1301.

Putz FE, Coley PD, Lu K, Montalvo A, Aiello A. 1983. Uprooting and snapping in trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research* 13: 1011–1020.

Reich PB, Wright IJ, Cavender-Bares J, *et al.* 2003. The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Sciences* 164: 143–164.

Sposito TC, Santos FAM. 2001. Scaling of stem and crown in eight *Cecropia* (Cecropiaceae) species of Brazil. *American Journal of Botany* 88: 939–949.

Stanley TD, Ross EM. 1983–1989. *Flora of south-eastern Queensland*, volumes 1–3. Brisbane: Queensland Department of Primary Industries.

Sterck FJ, Bongers F. 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany* 85: 266–272.

Sterck FJ, Bongers F. 2001. Crown development in tropical rainforest trees: patterns with tree height and light availability. *Journal of Ecology* 89: 1–13.

Sterck FJ, Bongers F, Newberry D. 2001. Tree architecture in a Bornean lowland rain forest: intra- and inter-specific patterns. *Plant Ecology* 153: 279–292.

Thomas SC. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rainforest trees. *American Journal of Botany* 83: 556–566.

Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line fitting methods for allometry. *Biological Reviews* 81: 259–291.

Westoby M, Wright IJ. 2006. Land plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21: 261–268.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.

Wright IJ, Ackerly DD, Bongers F, *et al.* 2007. Relationships among ecologically important dimensions of plant trait variation in seven neo-tropical forests. *Annals of Botany* 99: 1003–1015.

Wright SJ, Muller-Landau HC, Condit R, Hubbell SP. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.

CHAPTER 3

Plant functional traits in Australian sub-tropical rain forest: partitioning within-community from cross-landscape variation

Robert Kooyman[1,2], Will Cornwell[3] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia;*

[2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;*

[3] *Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada.*

Plant functional traits in Australian subtropical rain forest: partitioning within-community from cross-landscape variation

Robert Kooyman[1,2]*, Will Cornwell[3,4] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia;* [2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;* [3]*Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1Z4, Canada; and* [4]*Department of Integrative Biology, University of California, Berkely, CA 94720, USA*

Summary

1. Plant functional traits are dimensions of ecological strategy variation and provide insights into the assembly of plant communities. For woody rain forest vegetation of northern coastal New South Wales, Australia, we quantified four continuous traits (leaf size, seed size, wood density and maximum height) for 231 freestanding woody species and documented community composition for 216 plots. Using trait-gradient analysis, we partitioned species trait values between alpha (within-site) and beta (among-site) components. This allowed us to identify both trait shifts along gradients and variation among co-occurring species.

2. Alpha trait components consistently varied more widely than beta components, meaning that trait variation among species within plots was wider than variation in the mean trait values of plots where species typically grow.

3. Beta trait components covaried significantly among leaf area, seed size, wood density and maximum height. For example, species found in habitats with a large mean leaf size were consistently also found in plots with large mean seed size ($r = 0.70$). Beta correlations show that these leaf, wood and seed traits respond in parallel to the dominant abiotic gradients: soil types, topographic position, elevation and large-patch disturbances such as those caused by cyclones–storms, landslips or fires.

4. In contrast, the alpha components of traits were largely uncorrelated among species. Alpha leaf area was not associated with alpha larger seeds, meaning that leaf area and seed size act as independent axes of differentiation among coexisting species.

5. *Synthesis.* The different correlation structures for alpha and beta components of traits reflect community assembly processes at different scales. Within sites, assembly processes have not created strong linkages among these traits. But across different sites in the landscape, abiotic drivers have created strong linkages.

Key-words: alpha and beta scales, community assembly, functional traits, height, leaf size, seed size, subtropical rain forest, trait correlation structures, trait-gradient analysis, wood density

Introduction

Trait-gradient analysis (TGA) (Ackerly & Cornwell 2007) partitions species traits into within-site (alpha) versus between-site (beta) components, providing an improved approach to the question of how correlations between different traits across

species arise. The utility of the method is that it arrays communities along a one-dimensional trait gradient reflecting the mean trait value of co-occurring taxa, and then partitions individual species mean trait values into alpha and beta components. The community ordination and the units of the resulting species parameters are explicitly framed in terms of trait values. The beta trait component is a measure of a species position across the range of sites in which it occurs, and the alpha trait

*Correspondence author. E-mail: rkooyman@bio.mq.edu.au

component measures how the traits of each species differ from those of co-occurring species. In TGA, trait plot means provide an integrated measure of the abiotic and biotic interactions that may influence community assembly. The partitioning of species trait values into alpha and beta components is achieved by describing across-site variation in relation to the trait itself, rather than by reference to environmental variables. As a consequence, the analysis can be conducted even when environmental data are not available or the factors underlying gradients in particular traits remain unknown (Ackerly & Cornwell 2007).

Ecologists have long been interested in the role of functional traits in structuring communities and in sorting species along environmental gradients (Schimper 1898; Cowles 1899; Clark, Palmer & Clark 1999; Lavorel & Garnier 2002; Ackerly 2003, 2004; Phillips *et al*. 2003; Ackerly *et al*. 2006; Grime 2006; McGill *et al*. 2006; Westoby & Wright 2006; Mouillot, Mason & Wilson 2007). Traits reflect both ecological and evolutionary processes of community assembly (Cavender-Bares *et al*. 2009). This study uses TGA to partition trait variation and focuses on correlation structures among traits at different scales in order to elucidate plant functional diversity and community assembly.

As an example of correlation between traits, consider the 'leaf economic spectrum': where several leaf functional traits are correlated across species world-wide (Reich, Walters & Ellsworth 1997; Reich *et al*. 1998, 1999; Westoby *et al*. 2002; Wright *et al*. 2004). The leaf economic spectrum can be considered part of a spectrum from acquisitive (fast) to retentive (slow and persistent) strategies (Grime 1974, 1977, 1979; and see Grubb 1998). The question is how much of the trait correlation arises because different traits need to be coordinated for functional effectiveness, even within sites, versus how much arises because different traits are adjusting in parallel in response to physical geography, geomorphology and soils, and temperature and rainfall gradients?

In large data sets spanning a range of sites, strong correlations across species have been reported between leaf size, specific leaf area, and maximum height (e.g. Fonseca *et al*. 2000), and between leaf size, wood density, seed size and maximum height (Ackerly *et al*. 2002; Cornwell, Schwilk & Ackerly 2006; Cornwell & Ackerly 2009). These correlations could arise because: (i) traits respond in parallel to abiotic gradients across sites, while being decoupled within each site (correlated beta components, uncorrelated alpha components); (ii) traits may be correlated within sites, but respond independently to gradients across sites (correlated alpha, uncorrelated beta); or (iii) traits could be correlated at multiple scales (both beta and alpha correlated). In the particular case of the leaf economic spectrum, it is known that the traits involved are indeed correlated both across sites and across species within sites. More generally, robust quantitative answers are not yet available about the contributions of different spatial scales to trait correlation across species.

This study applied TGA to a large subtropical data set (231 species, 216 plots, 4 traits) that captures significant variation in rain forest communities across a regional scale. Our expecta-tion was that partitioning trait components across these scales should identify the extent and strength of trait correlations in relation to both environmental gradients and interactions between co-occurring species. Our aim was to find which trait correlations were general across scales and which were a product only of shared responses to landscape-scale gradients. Traits chosen were seed size, leaf size, height and wood density (Cornelissen *et al*. 2003). These traits influence the structure, dynamics and assembly of communities (Ackerly *et al*. 2002; Cornwell, Schwilk & Ackerly 2006). Three of the traits have previously been linked to identified strategy dimensions: (i) seed size is correlated positively with fruit size and negatively with seed output (regeneration strategy); (ii) species with larger leaves tend to have larger twigs, less frequent branching and larger fruits (Corner's Rules, Corner 1949); and (iii) typical maximum height is connected with light interception strategy (Westoby 1998; Westoby *et al*. 2002; Wright *et al*. 2007; Kraft, Valencia & Ackerly 2008; Poorter *et al*. 2008). Wood density is the fourth trait considered here. It is linked to several inter-related aspects of ecological strategy variation that reflect growth, mortality and succession (Chave *et al*. 2009). Contributing factors are thought to include allocation to growth versus strength and resistance to pathogen attack (Turner 2001; Falster & Westoby 2005; van Gelder, Poorter & Sterck 2006; Kooyman & Westoby 2009), and the hydraulic properties of species (Wright *et al*. 2007).

Materials and methods

STUDY SYSTEM

The study area in eastern Australia (Fig. 2) has subtropical climate with high rainfall (> 2000 mm yearly average) and generally mild temperatures (approx. mean max. 22 °C, mean min. 12 °C) (Bureau of Meteorology (Australia), n.d.). Mean annual precipitation does not vary substantially across the sample. The data represent two broad rain forest community types from the study area, Complex Notophyll Vine Forest (CNVF) and Simple Notophyll–Simple Noto-phyll Microphyll Vine Forest (SNVF–SNMVF) (nomenclature follows Webb 1978).

Simple Notophyll Vine Forest and CNVF can reach similar stature under optimum conditions. SNMVF is a variant of SNVF that often occurs in more exposed mountain areas on shallow to skeletal soils. It is less species-rich and lower in stature. Most species in SNMFV are shared with SNVF, including all the dominant species. The SNVF data include some minor presence of adjacent eucalypt-dominated wet sclerophyll communities. Following large-scale disturbances that include mineral soil exposure, regeneration in both SNVF and CNVF can include long-lived sclerophyll species from genera such as *Acacia* (Fabaceae) and *Eucalyptus* (Myrtaceae).

The SNVF–SNMVF assemblage samples are from the southern flanks of the eroded Mt. Warning (Wollumbin) volcanic caldera and occur mostly on rhyolite-derived soils. The CNVF samples are drawn from a larger geographic area of the far north-east of NSW, and occur predominantly on basalt-derived soils. There is some minor overlap of these soil types (and communities) in the sample, and a number of species are shared between the communities (and across the range of abiotic variables). SNVF is often referred to as Warm Temperate Rainforest. It is dominated by just a few canopy species
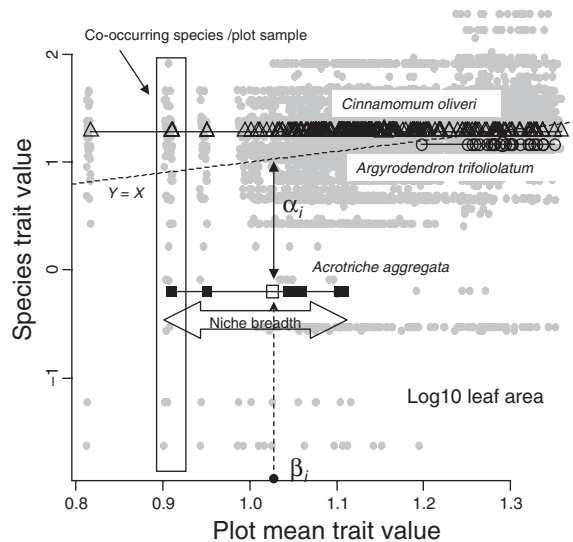
Fig. 1. Scatterplot of species trait values versus abundance-weighted plot-mean trait values for $\log_{10}$ leaf area cm^{-2} in 216 woody plant assemblages (representing two main rain forest communities in north-east New South Wales). Values for three species are highlighted for illustration: *Argyrodendron trifoliolatum* – Malvaceae (most common species in Complex Notophyll Vine Forest on basalt-derived soils); *Cinnamomum oliveri* – Lauraceae (occurs in almost all sites across all gradients); *Acrotriche aggregata* – Ericaceae (occurs only in lowest stature Simple Notophyll Microphyll Vine Forest on skeletal rhyolite-derived soils). *Acrotriche aggregata* is represented as a large open square, and the plots it occupies are shown as solid grey squares. Using only *A. aggregata* as an illustration, the large symbol represents the intersection of the mean trait value for the plots occupied by the species (the β_i trait value on abcissa) and the mean species trait value (on ordinate). The distance of the large symbol from the $Y = X$ dashed line is the species α_i trait value. This represents the difference between the species mean trait value and its beta value. The $Y = X$ dashed line represents the slope of the trait gradient defined by the mean trait values of the species co-occurring in assemblages. The range of occupied plots on the *x*-axis is the niche breadth, shown here as the labelled open arrow and representing the range of plots occupied by the species along and across the gradient of trait variation represented in the sample.

mostly in Cunoniaceae (dominant), Lauraceae, Myrtaceae and Atherospermataceae. Trees mostly lack buttresses, and vines are generally thin and wiry. CNVF is more structurally complex than SNVF, and has high floristic diversity in all strata. Canopy trees come from many families, notably Malvaceae (Sterculioideae), Meliaceae, Myrtaceae, Lauraceae, Rutaceae, Fabaceae, Sapindaceae, Sapotaceae, Elaeocarpaceae, and Ebenaceae. Many tree species have plank buttresses. Lianas (large woody vines) are common.

The volcanic activity (Focal Peak and Mt Warning) that gave rise to both basalt and rhyolite parent materials occurred *c*. 30–20 Ma (Stevens 1977). Soils derived from basalt are free-draining fine grained deep red earths (clay loam), and those from rhyolite generally form shallower brown clay loams (Appendix S1 in Supporting Information). The terrain is mountainous and the study sites ranged from *c*. 200 to 1000 m a.s.l. The upland plateaus are deeply dissected by numerous streams. The streams form a network of large river valleys. Cliffs and deep gorges feature in the headwaters of the major streams.

The most important environmental influences on communities in this landscape (see Appendix S1 and Baur 1957; Beckman & Thompson 1977; Turner & Kelly 1981; Floyd 1990; Kariuki & Kooyman

2005; Rossetto & Kooyman 2005; Kariuki *et al.* 2006) are (i) topographically mediated variation in soil depth on rhyolite substrates, with shallow to skeletal soils on upper slopes and crests; (ii) increasing soil depth and nutrient concentration moving from rhyolite to basalt parent materials; (iii) altitude; and (iv) disturbances that include wind and storm effects, logging history and fire.

PLOT SAMPLING

The 216 plots were established in 2000–05 as part of a larger project to sample regional rain forest diversity and dynamics. A complete species list was compiled (by R.M.K.) for all established plants taller than 1 m, and a Braun-Blanquet cover abundance rank was recorded (1 = < 5% cover and rare, 2 = < 5% cover and more common, 3 = 6–20%, 4 = 21–50%, 5 = 51–75%, 6 = 76–100%).

The TGA presented here deal with the 231 freestanding native tree and shrub species. Herbs, sedges, ferns, epiphytes, orchids, vines, palms and cordylines were removed because trait data for wood density and maximum height were not available or not comparable. Alpha diversity ranged from 18 to 78 species per plot, and there were a total of 7575 species-plot observations. Plots were 0.1 ha except for the geographically constrained SNMVF (100 samples), where plot size was 0.04 ha. In that case, increasing plot size (from 0.04 to 0.1 ha) made little difference to woody species diversity accumulation. Sampling for all plots proceeded from an initial (nested) subplot quadrat sample size of (20×20 m) 0.04 ha, and was expanded to 50×20 m for the SNVF and CNVF samples. Woody species accumulation with increasing plot size was negligible for SNMVF, low for SNVF, and high for CNVF. Information about abiotic gradients was collected as ranked environmental variables for each plot at the time of sampling. This included information for topographic position, altitude, slope, aspect, soil texture, soil depth and fire frequency (time interval). Altitude was obtained from topographic maps.

TRAIT DATA

Trait data for leaf area (LA), wood density (WD) and seed size (SS) were extracted from published floras and other sources including Bootle (1983); Stanley & Ross (1983–89, volumes 1–3); Floyd (1989); Ilic *et al.* (2000); Harden (1990–2002, volumes 1–4 with revisions). A limitation of this study was that a single value for each trait was allocated to each species, irrespective of site. Leaf size was for the whole area of simple leaves or phyllodes and for the leaflets of compound leaves. Juvenile leaf sizes were excluded from consideration. Leaf size (cm^2) was estimated as maximum length $\times$ maximum width $\times$ 0.70. This formula has been shown to correlate well with photographic area estimates of rain forest tree leaves (e.g. Kraft, Valencia & Ackerly 2008). Leaf material was collected for > 100 of the species in this study and was consistent with dimensions reported in the floras. Seed size was estimated using maximum dimensions of embryo plus endocarp (length + width/2, in millimetres; average diameter). Wood density estimates (as dry weight in kg m^{-3}) were taken from published sources. Estimated maximum height at maturity (H_{max}) was based on field information previously collected by R.M.K., which reflected maximum canopy height (m) for species (at largest known diameters, at reproductive maturity). This provided a single value for maximum potential height for each species, irrespective of site.

ANALYSIS

Leaf area, maximum height at maturity and seed size were $\log_{10}$-transformed to reduce skew. Wood density was not transformed.

Analyses were carried out in ʀ version 2.7 (R Development Core Team 2006)

Trait-gradient analysis (Ackerly & Cornwell 2007) decomposes trait values into alpha (within sites or plots) and beta (among sites or plots) components. A mean trait value for each plot is calculated across all species at the plot (eqn 1). The plots are then arranged along a spectrum or gradient according to their trait means, forming the *x*-axis of Fig. 1 (the 'trait-gradient' of TGA). Each species at each plot has a point-location in Fig. 1. The *x*-axis location is the plot mean for the trait, and the *y*-axis location is the trait value for the individual species. The vertically arranged points at a particular value of p_j represent the species co-occurring in a plot (Figs 1 and 2). The ordinary least-squares regression line of t_{ij} versus p_j (representing the $Y = X$ line) has, by definition, slope 1 and intercept 0.

Abundance-weighted plot-mean trait values (eqn 1), species mean trait values (eqn 2), and mean of plot means for plots occupied by each species (eqn 3) are defined as follows:

$$\overline{p_j} = \frac{\sum_{i=1}^{S} a_{ij} t_{ij}}{\sum_{i=1}^{S} a_{ij}}, \qquad \text{eqn 1}$$

$$\overline{t_i} = \frac{\sum_{j=1}^{P} a_{ij} t_{ij}}{\sum_{j=1}^{P} a_{ij}}, \qquad \text{eqn 2}$$

$$\beta_i = \frac{\sum_{j=1}^{P} \overline{p_j} a_{ij}}{\sum_{j=1}^{P} a_{ij}}, \qquad \text{eqn 3}$$

where t_{ij} is the trait value and α_{ij} is the abundance for species *i* in plot *j*, the total number of plots in the study is *P*, and the species richness of plot *j* is S_j. The analyses presented here use cover abundance-weighted values. Analyses were repeated using presence/absence data only and the general patterns and results (not presented) were very similar, as also found by Ackerly & Cornwell (2007).

Beta components (β_i, eqn 3) are the *x*-axis means for each species, illustrated in Fig. 1 by larger symbols (black outline square) for *Acrotriche aggregata* (R.Br.) Sprengel (Ericaceae) and (black outline triangle) *Cinnamomum oliveri* F.M. Bailey (Lauraceae). Beta components describe the habitats where each species occurs, in units of the mean trait value across all species at those sites. The niche breadth of a species is then characterized as the range of plots occupied (p_j-values;
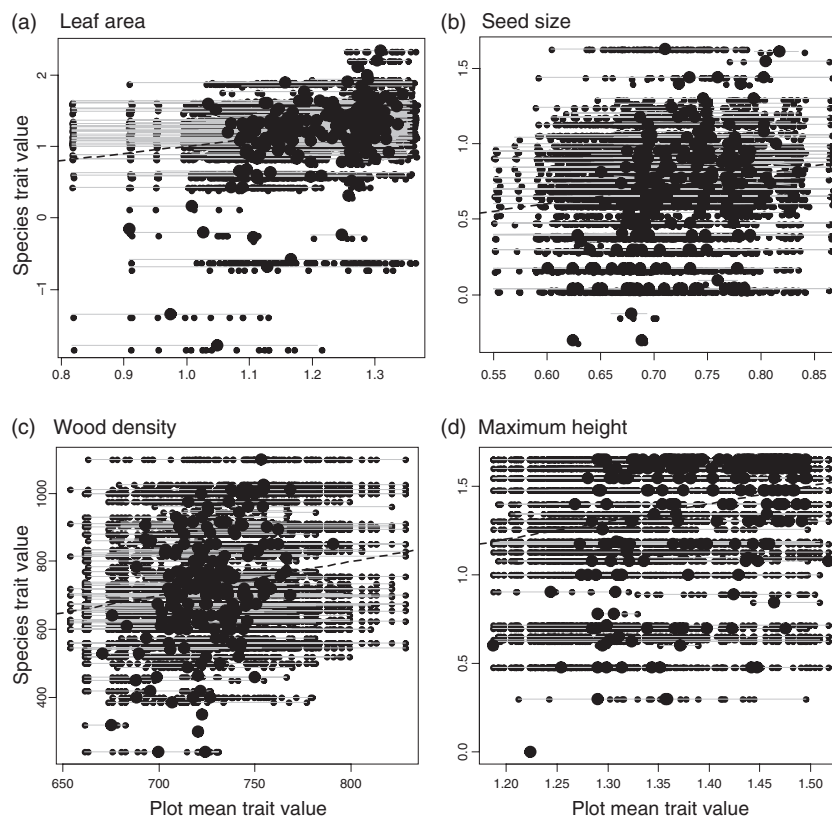
Fig. 2. Scatterplots of species trait values versus abundance-weighted plot-mean trait values for: (a) $\log_{10}$ leaf area cm^{-2}, (b) $\log_{10}$ seed size (mm), (c) (actual) wood density (kg m^{-3}), and (d) $\log_{10}$ maximum height (m); in 216 woody plant assemblages from two rainforest communities in north-east New South Wales. The larger, solid black circles represent the intersection of the mean trait value for the plots occupied by each species (the species β_i trait value on abcissa) and the species mean trait value (on ordinate). The small black symbols represent species occurrences. The vertical alignment of the latter represents the species in a plot (Fig. 1 shows this as a vertically aligned rectangle marked as 'co-occurring species/plot sample'). The horizontal alignment joined by the grey lines represents a species occurrence across the range of plots in which it occurs. The distance of the large black symbol from the $Y = X$ dashed line is the species α_i trait value (that represents the difference between the species mean trait value and its beta value). The $Y = X$ dashed line represents the slope of the trait gradient defined by the mean trait values of the species co-occurring in assemblages. The range of occupied plots on the *x*-axis, represented as the length of the grey line, is the species niche breadth. This represents the range and spread of plots occupied by the species along the gradient of trait variation represented in the sample.

illustrated in Fig. 1 for *A. aggregata*). Alpha components (α_i) measure the deviation of species trait values from the cross-species mean at the site, that is, the deviation in the y dimension from the $Y = X$ line in Fig. 1. Alpha components reflect the differentiation of each species from co-occurring taxa with regard to the trait. The partitioning into components in TGA is made possible by describing across-site variation by reference to the trait itself, rather than by reference to any single environmental variable, which might not be the sole or main cause of trait variation.

In some studies, trait values for each species may be measured separately at each site. Then a slope b_i of t_{ij} versus p_j can be calculated for each species, and this slope measures how closely phenotypic variation within the species is aligned with the trait gradient (Ackerly & Cornwell 2007). However, in other studies, including this one, only a single average trait value is available for each species, so point locations for a species across different sites all lay in a horizontal row (Figs 1 and 2). In situations where large geographic areas are sampled, trait measures from a range of sites that capture the extent of variation may be included.

Results

Across the 231 species sampled, traits ranged > 1000-fold for leaf area, almost 100-fold for seed size, > 20-fold for maximum height at maturity and 5-fold for wood density.

Niche breadths describe species distributions in units of plot means for the trait (Table 1, Fig. 1). Some species occurred only once and consequently had niche breadth measured as zero, while others spanned virtually the whole gradient (Figs 1 and 2). Correlation values were mostly low between niche breadth and species trait means except for wood density; generally negative and high between niche breadth and beta trait values; and low between niche breadth and alpha trait values (Table 2).

The range of alpha (α_i) was much wider than the range of beta (β_i) components for all traits (Fig. 3, Table 1), meaning that trait values varied much more across co-occurring species than across means for plots where they occurred. Nevertheless, the covariance between traits was stronger for the beta components (β_i) (Fig. 3).

PAIRWISE TRAIT CORRELATIONS

Correlations among plot means for traits (p_j) (column a in Fig. 3) indicate whether a pair of trait shifts in parallel along the dominant environmental gradient. Plot means were negatively correlated between leaf area (LA) and wood density (WD) ($r = -0.52$), positively correlated between leaf area and

Table 1. Summary statistics for four traits measured across 231 species and 216 plots in north-east New South Wales, Australia. (a) All results and measurements of the various components of TGA in $\log_{10}$-transformed units of the trait(s) except for WD; (b) back-transformed (actual) trait values

(a)	Traits (units, transformations)			
Parameter	LA (cm^2, $\log_{10}$)	SS (mean) (mm, $\log_{10}$)	H_{max} (m, $\log_{10}$)	WD* (kg m^{-3})
Species characteristics				
t_{is} mean	1.18	0.67	1.34	724
t_{is} minimum–maximum	−1.78, 2.34	−0.30, 1.63	0.30, 1.65	240, 1100
β_{is} minimum–maximum	0.90, 1.34	0.59, 0.83	1.19, 1.52	670, 790
α_{is} minimum–maximum	−2.80, 1.03	−0.98, 0.92	−1.22, 0.36	−483, 346
R_{is} mean	0.21	0.14	0.16	77
R_{is} minimum–maximum	0, 0.54	0, 0.32	0, 0.33	0, 174
Plot characteristics				
p_{js} mean	1.15	0.69	1.33	739
p_{js} minimum–maximum	0.81, 1.35	0.54, 0.86	1.19, 1.50	653, 827

(b)	Traits (units, back-transformed $\log_{10}$)			
Parameter	LA (cm^2)	SS (mean) (mm)	H_{max} (m)	WD (kg m^{-3})
Species characteristics				
t_{is} mean	15.1	4.7	21.88	724
t_{is} minimum–maximum	0.02, 218.8	0.5, 42.7	2, 44.67	240, 1100
β_{is} minimum–maximum	7.9, 21.9	3.9, 6.8	15.49, 33.11	670, 790
α_{is} minimum–maximum	0.001, 10.7	0.1, 8.3	0.06, 2.29	−483, 346
R_{is} mean	1.6	1.4	1.45	77
R_{is} minimum–maximum	0, 3.5	0, 2.1	0, 2.14	0, 174
Plot characteristics				
p_{js} mean	14.1	4.9	21.38	739
p_{js} minimum–maximum	6.5, 22.4	3.47, 7.2	15.49, 31.62	653, 827

LA, leaf area; SS, seed size; H_{max}, estimated maximum height; WD, wood density; t_{is}, species trait mean; β_{is}, beta trait value; α_{is}, alpha trait value; R_{is}, niche breadth; p_{js}, plot-mean trait value.
*A total of 206 species with data available for WD.

Table 2. Correlation coefficients across species among mean trait values, beta, alpha, and niche breadth (*Rs*) for four traits (leaf area; seed size; wood density; maximum height – estimated maximum height at maturity) in the northern New South Wales data set. Species that occurred only once (singletons) were removed from the analysis, as niche breadth values for such species using the trait gradient method are '0'; leaving 204 from the 231 species. *$P > 0.05$–0.1; **$P < 0.001$; ***$P < 0.0001$

		Species mean (t_i)	Beta trait (β_i)	Alpha trait (α_i)
Maximum height	β_i	0.33***	1	
	α_i	0.98***	0.13	1
	R_s	0.01	−0.52***	0.11
Leaf area	β_i	0.42***	1	
	α_i	0.98***	0.26**	1
	R_s	−0.10	−0.62***	0.01
Seed size	β_i	0.37***	1	
	α_i	0.99***	0.26**	1
	R_s	0.08	−0.40***	0.14*
Wood density	β_i	0.82***	1	
	α_i	0.59***	0.03	1
	R_s	0.39***	0.48***	−0.01

seed size (SS) ($r = 0.37$) and uncorrelated between seed size and wood density ($r = 0.15$) (Fig. 3a).

Beta trait components (β_i) (among-site species trait values) were strongly correlated among the same trait pairs (leaf area and wood density $r = -0.75$; leaf area and seed size 0.70) (Fig. 3b), while alpha components (α_i) (within-site species trait values) showed much weaker correlations among these traits (Fig. 3c). The LA–WD and LA–SS trait correlations across species (Fig. 3d) therefore predominantly reflected the beta correlation.

For the relationship of wood density with seed size, the direction of the beta-component correlation was opposite to the alpha-component correlation. However, because both components were relatively weak, the overall correlation among species means was only very weakly positive.

Across plot means (Fig. 3a) and across species (Fig. 3d), H_{max} was positively correlated with leaf area and seed size. H_{max} was negatively correlated with wood density across plot means and uncorrelated across species. Species beta trait values (β_i) were the most strongly correlated among the same traits (Fig. 3b), while species alpha trait values (α_i) showed much weaker correlations (Fig. 3c). The species mean H_{max}–LA–SS–WD trait correlations therefore predominantly reflected beta trait values (β_i) (Fig. 3d).

ABIOTIC FACTORS

Topographic positions lower downslopes tended to be associated with larger plot-mean leaf size and lower wood density (Table 3).

Higher altitude tended to be associated with lower height and seed size. Deeper soils and basalt soils were associated with

taller plant heights, larger leaf size and larger seed size, and lower wood density (data not shown). All this is consistent with higher productivity sites in the study area (including sites in lower slope to gully topographic positions; and those with basalt-influenced soils) carrying taller species, with larger leaves and seeds, and lower wood density. Lower wood density on higher nutrient (more productive) sites has also been observed in the American tropics (Muller-Landau 2004). A trend to smaller leaves and higher wood density in upslope topographic positions has previously been noted in a study of an Amazonian forest plot (Kraft, Valencia & Ackerly 2008).

Discussion

PARTITIONING OF SPECIES TRAIT VALUES

Here, as elsewhere, the range of trait variation within plots (α_i) was wider than variation across-site means (β_i), meaning that much of the trait variation between species was associated with different functional strategies within a shared environment (Wright *et al.* 2004; Westoby & Wright 2006). The emphasis here was on between species trait variation relative to community assembly. We did not include values for phenotypic (within-species) variation in this study.

Although alpha components contributed more variation than beta components, correlations between these traits arose predominantly from correlations between beta components. This means that despite the wide scatter among species within each site, correlations between these traits were predominantly driven by their tendency to vary in parallel along wider scale abiotic gradients. The coordinated shifts in mean trait values across abiotic gradients can be thought of as habitat filtering (Díaz, Cabido & Casanoves 1998; Ackerly 2004; Díaz *et al.* 2004; Cornwell, Schwilk & Ackerly 2006). In contrast, alpha components were largely uncorrelated between traits across species, suggesting that they act as independent axes of differentiation among coexisting species.

In community ecology, a restricted range of trait values is often viewed as evidence for habitat filtering (Cornwell, Schwilk & Ackerly 2006). The convergence of form and function in relation to edaphic and climatic conditions results in stronger trait correlations but reduced trait breadth at landscape (beta) scales. In essence, species that are more similar (i.e. with shared trait attributes) are filtered into habitats along abiotic gradients. In contrast, at local scales (alpha), a broader range of trait variation (and weaker trait correlations) may be interpreted as reflecting the signal of various mechanisms of species coexistence (e.g. Tilman 1994). The explicit partitioning of alpha and beta trait components in TGA provides a clear conceptual basis to interpret trait correlations at different scales, which reflect both trait shifts along gradients and variation among co-occurring species (Ackerly & Cornwell 2007).

TRAITS, ABIOTIC GRADIENTS AND HABITATS

In this Australian subtropical forest vegetation, there is a history of classifying communities by reference to leaf size (Webb
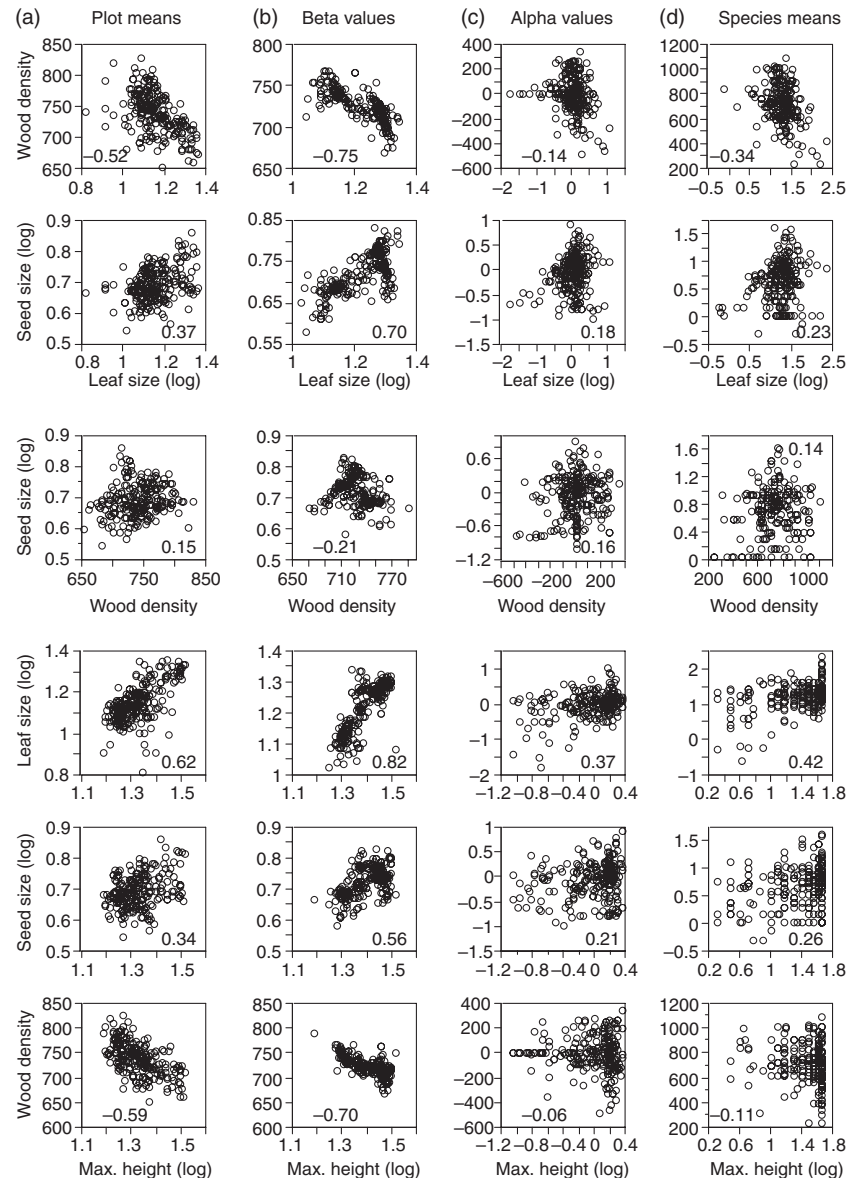
Fig. 3. Scatterplots of (a) plot-mean trait values (p_j), (b) species beta trait values (β_i), (c) species alpha trait values (α_i), and (d) species mean trait values for pairwise combinations of leaf size (log), wood density (actual), seed size (log) and maximum height (log). Correlation (r) values are shown.

1978), giving confidence that the axis of plot-mean leaf area reflects a major environmental gradient related to community differentiation. Previous studies in these forests have confirmed the influence of soils, topography and altitude (e.g. Baur 1957; Horne & Gwalter 1987; Rossetto & Kooyman 2005; Kariuki *et al.* 2006; Rossetto *et al.* 2008), and the differentiation of the CNVF and SNVF communities along a productivity gradient that reflects soil type (Webb, Tracey & Williams 1972; Turner & Kelly 1981).

Across the abiotic gradients sampled, sites with taller species generally also had larger leaves and seeds, and lower wood density. Within each plot, these correlations were much weaker or absent. At alpha scale, no relationship was evident between wood density and height at maturity, indicating that coexisting species use a broad range of wood densities to reach a given height.

Within the whole data set, there was a weak positive correlation across species between seed size and leaf size (Fig. 3d). This might seem to contrast with earlier findings by Ackerly &

Cornwell (2007), where seed size varied independently from leaf and wood traits in woody plant communities of coastal California, and by Rossetto & Kooyman (2005), where seed size varied independently from leaf and wood traits within SNVF–SNMVF rain forest. However, the correlation across species in this study arose predominantly from the beta component (Fig. 3b), with species having larger leaves and larger seeds tending to co-occur in the higher productivity community (CNVF). This illustrates how sensitive trait correlations can be to the spread of vegetation types included in a data set and highlights the value of separating alpha from beta components.

Species with larger leaves and lower wood density contributed to the spread of variation within most plots. At the same time, species with this combination of traits were more abundant at some plot-types than others. A partial explanation for this was that some of these species were pioneers (Bazzaz 1979) and were more abundant at recently disturbed plots. However, species with a similar combination of traits were also relatively

Table 3. Correlation values for plot trait means (leaf area – tp LA; seed size – tp SS; maximum height – tp H_{max}; and wood density – tpWD) for 216 plot-based samples in northern New South Wales, Australia, by eight environmental variables [Topog., topographic position; Altitud., altitude; Soil Te., soil texture; Soil Dep., soil depth; Fire, fire frequency (interval)]

	tp H_{max}	tp LA	tp SS	tp WD	Topog.	Altitud.	Slope	Aspect	Soil Te.	Soil Dep.	Fire
tp LA	0.35										
tp SS	0.41	0.38									
tp WD	−0.27	−0.52	0.15								
Topog.	−0.02	0.23	−0.02	−0.29							
Altitud.	−0.41	−0.08	−0.31	0.10	−0.28						
Slope	−0.21	0.08	−0.07	−0.06	0.08	0.15					
Aspect	−0.07	−0.05	−0.16	0.12	−0.22	0.35	0.19				
Soil Te.	−0.27	−0.27	−0.18	0.41	−0.11	0.26	−0.11	0.15			
Soil Dep.	0.44	0.56	0.30	−0.50	0.24	−0.25	−0.20	−0.34	−0.37		
Fire	0.09	−0.22	−0.06	0.03	−0.04	−0.33	−0.12	−0.10	−0.24	−0.06	
Disturbance	0.16	0.04	−0.06	−0.19	−0.11	−0.14	−0.21	−0.16	−0.32	0.28	0.57

common at undisturbed plots on more productive soils derived from basalt or deeper rhyolite, while few such species were found in the SNVF–SNMVF communities on poorer soils regardless of disturbance levels (Horne & Mackowski 1987).

The different correlation structures for alpha and beta components of traits reflect processes at different scales. Within sites, community assembly did not create strong linkages among traits. Across the landscape, abiotic drivers created strong linkages among traits. Grime (2006) suggested that the physical and chemical traits that drive ecosystems would in most cases be linked to the site productivity gradient, while disturbance-related traits would be less differentiated across wider scales. Our results were consistent with that prediction. Our study shows how partitioning variation in trait values across different scales can help clarify the linkages among traits that characterize plant functional diversity.

Acknowledgements

References

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, **164**(Suppl. 3), 165–184.

Ackerly, D.D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, **75**, 25–44.

Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135–145.

Ackerly, D.D., Schwilk, D.W. & Webb, C.O. (2006) Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, **87**, S50–S61.

Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K. & Starmer, K.P. (2002) Leaf size, specific leaf area and microhabitat distribution of woody plants in a California chaparral: contrasting patterns in species level and community level analyses. *Oecologia*, **130**, 449–457.

Baur, G.N. (1957) Nature and distribution of rain-forests in New South Wales. *Australian Journal of Botany*, **5**, 190–233.

Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.

Beckman, G.G. & Thompson, C.H. (1977) The soils. *The Border Ranges: A Land Use Conflict in Regional Perspective* (eds R. Monroe & N.C. Stevens), pp. 7–10. Royal Society of Queensland, Brisbane, Qld.

Bootle, K.R. (1983) *Wood in Australia: Types, Properties and Uses.* McGraw-Hill, Sydney, NSW, Australia.

Bureau of Meteorology (Australia). *Climate Data Files for NENSW and Whian Whian SF (Rummery Park) Weather Recording Station (1943 to 2001).* Available at: http://www.bom.gov.au.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Clark, D.B., Palmer, M.W. & Clark, D.A. (1999) Edaphic factors and the landscape-scale distributions of tropical forest trees. *Ecology*, **80**, 2662–2675.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Corner, E.J.H. (1949) The Durian theory, or the origin of the modern tree. *Annals of Botany*, **13**, 367–414.

Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465–1471.

Cowles, H.C. (1899) The ecological relations of the vegetation of the sand dunes of Lake Michigan. *Botanical Gazette*, **27**, 95–117.

Díaz, S.J., Cabido, M. & Casanoves, F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, **9**, 1113–1122.

Díaz, S.J., Hodgson, J.G., Thompson, K., Cabido, M.J., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, **93**, 521–535.

Floyd, A.G. (1989) *Rainforest Trees of Mainland South-eastern Australia.* Inkata Press, Sydney, NSW.

Floyd, A.G. (1990) *Australian Rainforests in New South Wales*, Vols 1 and 2. Surrey Beatty and Sons, Chipping Norton, NSW.

Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, **88**, 964–977.

van Gelder, H.A., Poorter, L. & Sterck, F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367–378.

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, **250**, 26–31.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK.

Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.

Grubb, P. (1998) A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics*, **1**, 3–31.

Harden, G.J. (1990–2002 with revisions) *Flora of New South Wales*, Vols 1–4. UNSW Press, Sydney, NSW, Austalia.

Horne, R. & Gwalter, J. (1987) The recovery of rainforest overstorey following logging. 2. Warm temperate rainforest. *Forest Ecology and Management*, **22**, 267–281.

Horne, R. & Mackowski, C. (1987) Crown dieback, overstorey regrowth and regeneration response in warm temperate rainforest following logging. *Forest Ecology and Management*, **22**, 283–289.

Ilic, J., Boland, D., McDonald, M., Downes, G. & Blakemore, P. (2000) *Wood Density Phase 1: State of Knowledge*. National Carbon Accounting System Technical Report No. 18. Australian Greenhouse Office. Available at: http://www.greenhouse.gov.au/ncas/reports/pubs/tr18final.pdf.

Kariuki, M. & Kooyman, R.M. (2005) Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology*, **30**, 844–855.

Kariuki, M., Rolfe, M., Smith, R.G.B., Vanclay, J.K. & Kooyman, R.M. (2006) Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. *Forest Ecology and Management*, **225**, 1–14.

Kooyman, R.M. & Westoby, M. (2009) Costs of height gain in rainforest saplings: main-stem scaling, functional traits and strategy variation across 75 species. *Annals of Botany*, **104**, 987–993.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

Mouillot, D., Mason, N.W.H. & Wilson, J.B. (2007) Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia*, **152**, 729–737.

Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20–32.

Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.-E.C., Sanchez, W.G., Yli-Halla, M. & Rose, S. (2003) Habitat association among Amazonian tree species: a landscape scale approach. *Journal of Ecology*, **91**, 757–775.

Poorter, L., Hawthorne, W., Bongers, F. & Sheil, D. (2008) Maximum size distributions in tropical forest communities: relationships with rainfall and disturbance. *Journal of Ecology*, **96**, 495–504.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730–13734.

Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C. & Bowman, W.D. (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, **114**, 471–482.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.

Rossetto, M. & Kooyman, R.M. (2005) The tension between dispersal and persistence regulates the current distribution of rare paleo-endemic rain forest flora: a case study. *Journal of Ecology*, **93**, 906–917.

Rossetto, M., Kooyman, R.M., Sherwin, W. & Jones, R. (2008) Dispersal limitations rather than bottlenecks or habitat specificity can restrict the distribution of rare and endemic rainforest trees. *American Journal of Botany*, **95**, 321–329.

Schimper, A.F.W. (1898) *Pflanzen-geographie auf physiologischer*. Grundlage. G. Fischer, Jena.

Stanley, T.D. & Ross, E.M. (1983–89) *Flora of south-eastern Queensland*, Vols 1–3. Queensland Department of Primary Industries, Brisbane, Qld, Australia.

Stevens, N.C. (1977) Geology and landforms. *The Border Ranges: A Land Use Conflict in Regional Perspective* (eds. R. Monroe & N.C. Stevens), pp. 1–6. Royal Society of Queensland, Brisbane, Qld.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Turner, I.M. (2001) *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge, UK.

Turner, J. & Kelly, J. (1981) Relationships between soil nutrients and vegetation in a North Coast forest, New South Wales. *Australian Forest Research*, **11**, 201–208.

Webb, L.J. (1978) A general classification of Australian rainforests. *Australian Plants*, **9**, 349–363.

Webb, L.J., Tracey, J.G. & Williams, W.T. (1972) Regeneration and pattern in the subtropical rain forest. *Journal of Ecology*, **60**, 675–695.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Wright, I.J., Westoby, M., Reich, P.B., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M. *et al.* (2007) Relationships among ecologically important dimensions of plant trait variation in seven neo-tropical forests. *Annals of Botany*, **99**, 1003–1015.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Soil analysis results from Baur (1957) for several of the northern NSW locations and rainforest floristic alliances used in this study.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

CHAPTER 4

Traits and gradients explain the distribution and performance of a clonal Australian rainforest tree species

Robert M. Kooyman[1,2]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109 Australia; [2]National Herbarium of NSW, Sydney, NSW 2000 Australia; [3]University of New England, Armidale, NSW 2351, Australia

ABSTRACT

Premise: Shifts in mean trait values for assemblages arrayed along abiotic gradients include the sign of species turnover, and shifts in species growth strategy and performance. Clonal tree species that rely on in-situ persistence show distinct trait and demographic values relative to environmental gradients and co-occurring taxa.

Methods: Values for four traits (leaf area, seed size, wood density, maximum height) were quantified for 82 woody species in 100 rainforest assemblages arrayed along environmental gradients, and partitioned into within- and among- assemblage components. Clonal tree growth performance was quantified. Comparisons to co-occurring taxa used the continuous trait variable of maximum height.

Key Results: Floristic variation across assemblages, decreasing canopy height, and increasing abundance of *Uromyrtus australis* A.J.Scott Myrtaceae in the canopy were linked to decreasing soil depth in upslope topographic positions. Clonal growth was slow, seed production did not result in recruitment, and mortality was not detected. Other traits were within the range of variation of co-occurring species in assemblages.

Conclusions: Changes in plot means for trait values across abiotic gradients reflect species turnover in assemblages, and shifts in co-occurring species performance related to fecundity, plasticity and stem architecture. Clonal species performance improved in lower stature forest habitats on lower productivity sites. Allocation to seed production was lower for smaller stems and isolated populations. However, there was no evidence of a trade-off between sexual reproduction and vegetative growth. For conservation assessment, environmental variance should be dissected into

components that affect recruitment from seed versus those that affect vegetative growth and persistence.

Key Words: Australian rainforest; clonal tree; environmental gradients; fecundity; functional traits; growth; mortality; performance; persistence; stem size, abundance, and architecture

INTRODUCTION

In closed canopy rainforests the capacity of trees to intercept light depends on their height (e.g. Westoby, 1998; Falster and Westoby, 2005). The vertical distribution of leaves and the volume occupied influence the intensity of shading and competition for light among individuals. The height-light trajectory of species is influenced by the costs of height gain during ontogeny (e.g. Kooyman and Westoby, 2009) and by the important trait of maximum height achieved at maturity. Together these reflect key components of species ecological strategies (Westoby et al., 2002).

Shifts in plant trait values along environmental gradients reflect both evolutionary history and present-day ecological competence (e.g. Westoby, 2006). Plant functional trait values vary along landscape-scale environmental gradients and among co-occurring species in habitats (e.g. Ackerly and Cornwell, 2007). The dichotomy across scales inherent in this creates a challenge for the synthesis of functional and community ecology: with trait variation at larger scales reflecting the filtering of species into habitats, representing shifts in plant form and function along climatic and edaphic gradients (Schimper, 1903); and within assemblage trait variation reflecting finer scale niche partitioning (Hutchinson, 1957), and demographic and functional differences among co-occurring species interacting with

mechanisms of co-existence such as competition (e.g. Pacala and Tilman, 1994) and limiting similarity (eg. MacArthur and Levins 1967).

Demography and functional traits—Plant functional traits are directly responsible for the acquisition of resources required for growth (e.g. light, water, nutrients, CO_2), the regulation of conditions that influence metabolism (e.g. temperature, turgor and vascular-vessel pressure), the repair of damage, holding and occupying habitat, and the production of seeds (or other propagules) (Ackerly, 2003). During their lifetime, plants can experience different levels of stress and resource availability, including in relation to height in the canopy and access to light. Optimal life history research involves measurement of traits that reflect the effectiveness and intensity of resource gathering, and the allocation of energy and biomass to sustain the organism (Enquist et al., 2007). The trajectories of demographic functions such as growth, fecundity, senescence, and mortality, reflect the interaction of life history traits, environmental variables that regulate resource availability, and species ecological strategies (Caswell, 1985, 1989; Monaghan et al., 2008; Mangel et al., 2008).

Clonal species performance and persistence—*Uromyrtus australis* A.J.Scott (Myrtaceae) is a multi-stemmed (integrated) clonal rainforest tree. Here I describe the species distribution in relation to abiotic variables and co-occurring taxa; and performance as measurable variation in genet architecture that includes stem size (height and diameter), stem density (spacer lengths between integrated ramets) (Klimes et al., 1997), and fecundity (as seed production per unit area of crown) (e.g. Henery and Westoby, 2001). The elements of species performance represent two key components of optimal life history, reflecting behavioural traits and allocation processes that contribute directly to organism and species persistence (Bond and

Midgley, 2001; Vesk and Westoby, 2004; Rossetto et al., 2004; Rossetto and

Kooyman, 2005).

Clonality as a trait—It has been postulated that clonal life histories constitute

adaptations to environmental factors. However, genetic evidence of heritable variation

leading to evolutionary adaptation (in clonal species) is mostly lacking (Fischer and

Van Kleunen, 2002). It has also been suggested that sexual reproductive output (e.g.

number of seeds) is inversely proportional to genet longevity (Klekowski, 1997), and

that there is a trade-off between allocation to sexual reproduction versus vegetative

growth (e.g. Silvertown et al., 1993).

What is known is that the physical and physiological integration of ramets

allows clonal plants to plastically place stems in benign or advantageous positions in

heterogenous landscapes (reflecting foraging behaviour in response to resource

availability) (Hutchings and de Kroon, 1994; Fischer and Van Kleunen, 2002). This

suggests that clonal tree species may be less influenced by detrimental environmental

variation within the habitats they occupy, and more able to capitalise on advantageous

conditions than individuals of species that are filtered into habitats across landscapes

by dispersal and regeneration from seed, and tightly constrained to a single 'point'

location. In contrast, clonal species may be more vulnerable to drastic stochastic

events because recolonisation from seed sources is less likely. Reflecting the effects

of small population size (limited number of genets) and/or trade-offs between

vegetative growth and sexual reproduction.

Environmental gradients—Functional traits are considered adaptive in

situations where the phenotype occurring in a particular environment improves

species performance in that environment (e.g. by improved resource acquisition,

growth, fecundity, survival and / or reproduction) (Ackerly, 2003). Hypotheses related

to environmental gradients as potential filters for rainforest tree species capable of clonal growth include that: The density, size and arrangement of stems follow similar patterns under similar conditions across a species range. Populations show significant variation in demographic parameters (including fecundity) along environmental gradients, and across geographical distance. Clonal species trait values differ from those of co-existing taxa in assemblages arrayed along environmental gradients.

The study tests those hypotheses by addressing the following questions: What factors (or combination of factors) influence species distributions and assemblage level variation in these habitats? Do the same factors influence clonal species architecture, population size, stem size and density, fecundity, competitiveness and persistence in the habitats occupied? Are shifts in the demographic parameters for *U. australis* directional along environmental gradients, and consistent across populations separated by geographic distance? Do the traits of clonal rainforest species differ from those of co-existing taxa in the assemblages in which they occur? Are clonal tree species traits that influence performance less or more influenced by environmental variation within the habitats they occupy than species that disperse and regenerate from seed?

MATERIALS AND METHODS

Australian rainforest history—Over millions of years the movement of continental landmasses and changing climatic conditions have influenced the evolution of the Australian flora and caused significant adjustments to species distributions (Hill, 1994, 2004; Hewitt, 2000). The impacts of major climatic changes in Australia included a large contraction in area and distribution of rainforest

(Kershaw et al. 1991, 2007; Hill, 2004). Local rainforest species responded to change in the environment in a variety of ways. Some expanded their range, others dispersed to more suitable locations, persisted in the remaining suitable sections of their former range (sometimes reduced to small refugia; Rossetto and Kooyman, 2005), became functionally immortal (Dreschler et al. 1999), turned into ancient clones (Lynch et al., 1998), or went extinct (Lande, 1993; Hewitt, 2000; Sjöström and Gross, 2006).

Study area—The study area in eastern Australia has a sub-tropical coastal climate with high rainfall especially during summer-autumn (>2350 mm yearly average), and generally mild temperatures (mean max. 22.4^{o} C, mean min. 12.7^{o} C). This is based on a 57-year record for Rummery Park weather station, altitude 370 m, 28.5988 S, 153.3783 E, located within Nightcap NP (Bureau of Meteorology, n.d.). Nix (1991) placed the area in the Mesotherm bioclimatic region. It is positioned on the southern flanks of the eroded Mt. Warning (Wollumbin) volcanic caldera. Volcanic activity was from 23-20 Ma (Stevens, 1977). There is mountainous terrain and upland plateaus deeply dissected by eroded stream bases. These streams form an almost semi-circular radiating network of valleys. Rhyolite cliffs and deep gorges in the headwaters of the major creeks and rivers are a feature. Study sites ranged between approximately 300-800 m asl. Stevens (1977), and Beckman and Thompson (1977) described the Mt. Warning landscape, and Morand (1994, 1996) provided detailed soil mapping. Details of the study area (Rossetto et al., 2008) and locations were provided previously (Royer et al., 2009).

Study species—*Uromyrtus australis* A.J. Scott is a multi-stemmed clonal rainforest tree with height at maturity ranging between 6 and 20 m. Most large stems are <25 cm in diameter at breast height (dbh), and ramet stems are integrated, though distances between them vary. The species has opposite leaves, whitish flowers turning

pink to purple with age, and globose black multi-seeded berries around 6-8 mm
diameter (Snow and Guymer, 2001; Floyd, 1989). It is listed on Schedule 1
(Endangered) of the *Threatened Species Conservation Act NSW* (1995)*,* is listed as
Endangered on the Commonwealth *Environment Protection and Biodiversity
Conservation Act,* 1999, and has a Rare or Threatened Australian Plant (ROTAP)
conservation code of 2Eci, where 2 = geographic range <100 kms; E = endangered; c
= occurs in reserved land; i = <1000 plants known from reserved areas (Briggs and
Leigh, 1996).

     Study species habitat—Species in the genus *Uromyrtus* generally occur in
association with upland cool rainforest at higher elevations. Such sites provide moist
forest habitat for a range of taxa, including rare and narrowly endemic species. *U.
australis* is patchily distributed in natural habitat areas of differing sizes (<0.1-30 ha)
across a relatively large continuum of forest at altitudes from 350-800 m. Typical *U.
australis* sites are in and on the margins of the simple evergreen notophyll and
microphyll vine forest communities (following the typology of Webb 1978) that are
often referred to as warm-temperate rainforest (e.g. Baur, 1957; Floyd 1973, 1989;
Wilson, 1991). These rainforest areas are generally fringed by eucalypt-dominated
(sclerophyll) forest on exposed slopes, and the margins may periodically be affected
by fire (Adam, 1992). Floyd (1990) provided detail of the floristic sub-alliances
within the broad community type. The species distribution may be coarsely defined
by the mountainous terrain and by the distribution and extent of rhyolite dominated
volcanics (Nimbin Rhyolite) and rhyolite-derived soils, on the southern flanks of the
Mt. Warning shield volcano (Floyd, 1973, 1989).

     Habitat surveys and floristic data analysis—The full floristic sample was
comprised of 150 species from 100 quadrats (50 x 20 m, with 20 x 20 m nested sub-

plots) established in the species 'core' habitats in Nightcap and Mt Jerusalem National Park areas (Fig. 1). Plots were located within a constrained altitudinal range (ca. 600-800 m) representing the species 'core' habitat. Fifty quadrats were established at each of the locations and were located in different topographical positions representing 10 in each of: crest, upper slope, mid-slope, lower slope, creek/gully. A complete species list was compiled for all established plants taller than 1 m, and a Braun-Blanquet cover abundance rank was recorded for each (1 = < 5% cover and rare, 2 = < 5% cover and more common, 3 = 6-20%, 4 = 21-50%, 5 = 51-75%, 6 = 76-100%). Environmental data were collected at each plot location (refer to Rossetto and Kooyman, 2005; Royer et al., 2009; and on-line appendix S1, Table S1.1; see Supplemental data with the online version of this article).

Multivariate analysis—The site by species data were classified by grouping similar plots using a simple numerical hierarchical agglomerative clustering process, and the Bray-Curtis association measure. Similarity profile permutation tests (Simprof) were used to test the groupings (1000 permutations). Similarity among quadrats/sites was further investigated through non-metric multidimensional scaling (nMDS) ordination using the underlying resemblance matrix as input. Spearman rank correlation tests (999 permutations) were used to test the influence of environmental variables on multivariate patterns. A classification and regression tree (CART) model was used to further investigate the influence of abiotic factors on the grouping of assemblages in multivariate space based on similarity (De'ath, 2002).

Cover abundance and population census data for **U. australis**—Measured population data for *U. australis* included number of ramet stems (6817 in total) in each nominated size-class (height classes: 0-1m, >1-5m, >5-10m, >10m), and diameter at breast height over bark (dbh) for all stems in the 5-10m and >10m height

categories (898 stems). Population data were based on the 100 / 20 x 20 m nested sub-plots. Rank abundance data (modified Braun-Blanquet cover code described above) were collected for the species at all sites.

Life history parameters—Life history parameters for growth, survivorship, and mortality were generated from long time-scale (16 year) demographic studies of populations of *U. australis* and associated (co-existing) species. Deterministic matrix projection models and elasticity values (De Kroon et al., 1986) for life history parameters were developed using the methods described in Enright and Ogden (1979) and Enright et al. (1995). In 1986 two 1600m^2 permanent plots (PP1 and PP2) were established in the Nightcap Range (only) as part of a larger study (established by RMK; Kooyman, 2005) on rainforest dynamics that included a number of rainforest ecosystem types. Permanent Plot 1 (PP1) was located outside the main Nightcap population of *U. australis* on deeper soils, and had a tall forest canopy height (>30 m). Permanent Plot 2 (PP2) was surrounded by the larger Nightcap population of the species, had skeletal soil, and a low (<6-12 m) forest canopy. Both sites were on mid- to upper- slopes with similar aspects. Fecundity (seed production) was measured in seed trapping experiments (three year duration) in five sites in each of two locations (this time including an outlier population at Mt. Jerusalem, and the core population in Nightcap).

Trait data—Available traits were leaf area, seed size, wood density, and estimated maximum height at maturity. Species were allocated a single value for each trait, and variation due to assemblage level shifts in plot trait means along gradients were interpreted. In the 50-plot sample from Nightcap, measured data for H$_{max}$ were available for each species in each plot, allowing within and between species (phenotypic) variation across gradients to be included and interpreted. These data

represent the 79 freestanding native tree and shrub species in the Nightcap sample. Herbs, sedges, ferns, epiphytes, orchids, vines, palms and cordylines were removed from consideration in all trait analyses.

Trait data compilation—The trait data for leaf area (LA), wood density (WD) and seed size (SS) were extracted from published floras and other sources including Bootle (1983); Floyd (1989); Ilic et al. (2000); Harden (1990-2002, volumes 1-4 with revisions). Leaf size was for the whole area of simple leaves or phyllodes and for the leaflets of compound leaves. Juvenile leaf sizes were excluded from consideration. Leaf size (cm^2) was estimated as maximum length x maximum width x 0.70. This formula has been shown to correlate well with photographic area estimates of rain forest tree leaves (e.g. Kraft et al., 2008). Seed size was estimated using maximum dimensions of embryo plus endocarp (length + width / 2, in millimetres; average diameter). Wood density estimates (as dry weight in kg m^{-3}) were taken from published sources. Estimated maximum height at maturity (H$_{max}$) was based on data collected by RMK, and (in Nightcap) included maximum canopy height (in metres) for each species at each site. Heights were measured using a digital height meter (Haglof, Vertex III).

Trait Gradient Analysis—The trait gradient analysis (TGA) methods used here follow those described in Ackerly and Cornwell (2007) and Kooyman et al. (2010). Traits were log$_{10}$-transformed to reduce skew. Analyses were carried out in R version 2.8.1. Trait gradient analysis (TGA) decomposes trait values into alpha (within sites or plots) and beta (among sites or plots) components (Appendix S1; see Supplemental data with the online version of this article).

Interpreting TGA results—A mean trait value for each plot is calculated across all species at the plot. Plots are arranged along a spectrum or gradient

according to their trait means, forming the *x*-axis (the 'trait-gradient' of TGA). Each species at each plot has a point-location in the graph. The *x*-axis location is the plot mean for the trait, and the *y*-axis location is the trait value for the individual species. The vertically arranged points at a particular value for the plot trait mean (p_j) along the *x*-axis represent the species co-occurring in a plot. The ordinary least squares regression line of t_{ij} vs. p_j (species trait mean versus plot trait mean; representing the Y = X line) has, by definition, slope 1 and intercept 0.

Beta components (β_i, eqn 3 in appendix S1; see Supplemental data with the online version of this article) are the *x*-axis means for each species, illustrated in Fig. 2 by larger symbols (black outline square) for *Uromyrtus australis* A.J.Scott Myrtaceae, (black outline triangle) *Ceratopetalum apetalum* D.Don Cunoniaceae, and (black outline circle) *Acrotriche aggregata* (R.Br.) Sprengel (Ericaceae). Beta components describe the habitats where each species occurs, in units of the mean trait value across all species at those sites. The niche breadth of a species is then characterized as the range of plots occupied (p_j values). Alpha components (α_i) measure the deviation of species trait values from the cross-species mean at the site, that is, the deviation in the y dimension from the Y=X line (the labelled dotted line in Fig. 2). Alpha components reflect the differentiation of each species from co-occurring taxa with regard to the trait. The partitioning into components in TGA is made possible by describing across-site variation by reference to the trait itself, rather than by reference to any single environmental variable, which might not be the sole or main cause of trait variation.

TGA for height—In this study values for H_{max} were measured for each species separately at each site (in the Nightcap sample), and the slope b_i of t_{ij} vs. p_j was calculated for each species. This slope measures how closely phenotypic variation

within the species is aligned with the trait gradient for any particular trait (Ackerly and Cornwell, 2007).

RESULTS

Multivariate analyses—What were the major floristic patterns? Across the full sample, floristic patterns showed strong similarities between areas in relation to the distribution of taxa along abiotic gradients. However, the non-metric multidimensional scaling ordination of floristic data showed separation between the two geographically separated (ca. 5 km) and different sized areas of rainforest, Mt. Jerusalem and Nightcap. Key floristic differences between these areas reflect species turnover and the absence of canopy trees such as *Endiandra introrsa* C.T.White Lauraceae and *Canarium australasicum* F.M.Bailey Burseracaeae from Mt. Jerusalem. These locations are the main habitat areas for the study species (*U. australis*). The largest population of this species occurs in Nightcap, while Mt. Jerusalem has a smaller isolated population (Fig. 1).

What factors influenced species distributions and assemblage level variation in these habitats? Spearman Rank correlation (Mantel coefficient) was used to test the relationship (correlations) between ranked environmental variables and the extent to which abiotic gradients could explain the position of samples in the ordination space (Clarke and Gorley, 2006). For the combined 100 quadrat sample and the two most influential and correlated variables (topography and soil depth) Spearman's r = 0.305, $P < 0.001$. A linkage tree model was used to test that result (De'ath, 2002). The model that best explained species composition in assemblages relative to abiotic variables used two variables (topographic position and soil depth). After 1000 permutations, the

108

first major split in plot grouping was for topographic position (analysis of similarity r = 0.33; with the absolute measure of group differences (B%) = 73%), and the second split was for soil depth (r = 0.19, (B%) = 59%).

Did the same factors influence the clonal species? The clonal species was mostly absent from tall forest on deeper soils and more abundant on shallow soils. This is illustrated in the nMDS ordination (Fig. 1) that shows increasing abundance (as increasing number values) of *U. australis* relative to the direction of influence of soil depth (correlated with topographic position) in the combined (100-plot) sample.

Life history parameters—*Were demographic shifts directional along environmental gradients?* As canopy height decreased along the abiotic gradient of decreasing soil depth in upslope topographic positions, the number of stems of *U. australis* greater than 5cm diameter increased significantly across the sample (OLS; r^2 = 0.175, $P < 0.0001$).

Were shifts in the demographic parameters for U. australis *consistent across small and large sub-populations?* Within the Nightcap population, no large stem mortalities were recorded, and there were no significant differences in the other parameters (vegetative growth and mortality) between larger and smaller (sub) populations (Table S1.2). In contrast, seed production per unit area of canopy was greater in Nightcap, a larger population area with more stems (Table S1.2), and increased with stem size and in relation to position in the canopy versus sub-canopy (results not presented). Overall, smaller population size was a significant influence on seed production.
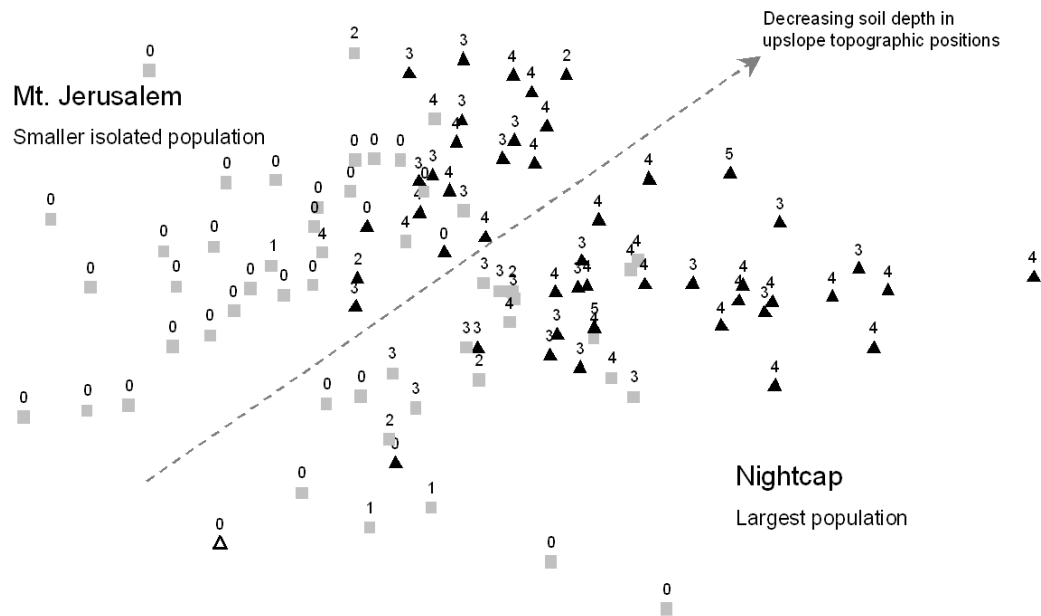
Figure 1 Constrained 2-dimensional nMDS (non-metric multidimensional scaling) ordination of 100 sites based on full floristics and representing 50 plots (each 20 x 20 m) in each of the two areas, Nightcap (below dotted line) and Mt Jerusalem (above dotted line). Numbering represents abundance of *Uromyrtus australis* at sites; 0-absent, numbers 1-5 represent sequentially increasing abundance. Solid black triangles – shallow to skeletal soils; grey squares – moderate depth soils; outline black triangle – deeper soil. Overall stress in the 2-dimensional ordination (0.16).

Did any of the demographic parameters for U. australis *differ between geographically separated areas?* Significant variation in fecundity was detected between the two areas separated by a geographic distance of ca. 5 km (Table S1.2). ANOVA results for number of seeds from equal sized samples from the two locations (Nightcap and Mt. Jerusalem) over two years of seed trapping showed significant differences between the areas ($F_{1, 4427} = 55.6$, $P < 0.0001$) (Kooyman 2005). There

was no sign of a significant difference between populations in relation to stem sizes or numbers (abundance) relative to abiotic gradients (Fig. 1), and therefore no evidence of a trade-off between allocations to vegetative growth versus seed production.

Trait correlations —For plot trait means, ordinary least squares (OLS) regression showed that plots with taller trees had larger leaves (Corr. Coef. = 0.61, r^2 = 0.37, $P < 0.0001$), smaller seeds (SS) (Corr. Coef. = -0.53, $r^2 = 0.27$, $P < 0.0001$) and lower wood density (Corr. Coef. = -0.53, $r^2 = 0.28$, $P < 0.0001$). Plots with lower wood density had larger leaves (Corr. Coef. = -0.62, $r^2 = 0.38$, $P < 0.0001$), and plots with smaller seeds had higher wood density (Corr. Coef. = 0.48, $r^2 = 0.23$, $P < 0.0001$). Previous results confirmed that both leaf size and the incidence of leaf teeth increased in assemblages in lower slope topographic positions in this rainforest community sample (Royer et al., 2009).

Trait gradient analysis—Variation in H_{max} is represented as within and between species variation (i.e. the phenotypic component) in relation to plot mean height (Fig. 2). The slope of the relationship of height to the underlying gradients for the dominant co-occurring canopy species *Ceratopetalum apetalum* (highlighted in green in Fig. 2) and *Endiandra introrsa* C.T.White Lauraceae (the latter in Nightcap only) was very similar to the Y=X line in both cases. However, several smaller tree species (e.g. *Uromyrtus australis*, *Anopterus macleayanus* F.Muell. Escalloniaceae and *Helicia ferruginea* F.Muell. Proteaceae) tended to stay at similar heights throughout, and consequently shifted from sub-canopy to canopy status as forest stature diminished (e.g. this is shown for *U. australis* in Fig. 2). Among such species only *U. australis* increased in stem abundance and biomass (as performance measures) to become a co-dominant canopy species as stand height decreased. In other cases, taxa favoured by those conditions (e.g. *Acrotriche aggregata* R.Br.

Ericaceae) were present only at the extremes of the gradient (i.e. in low stature forest

on skeletal, rocky soils) (Fig. 2).

plot mean trait value
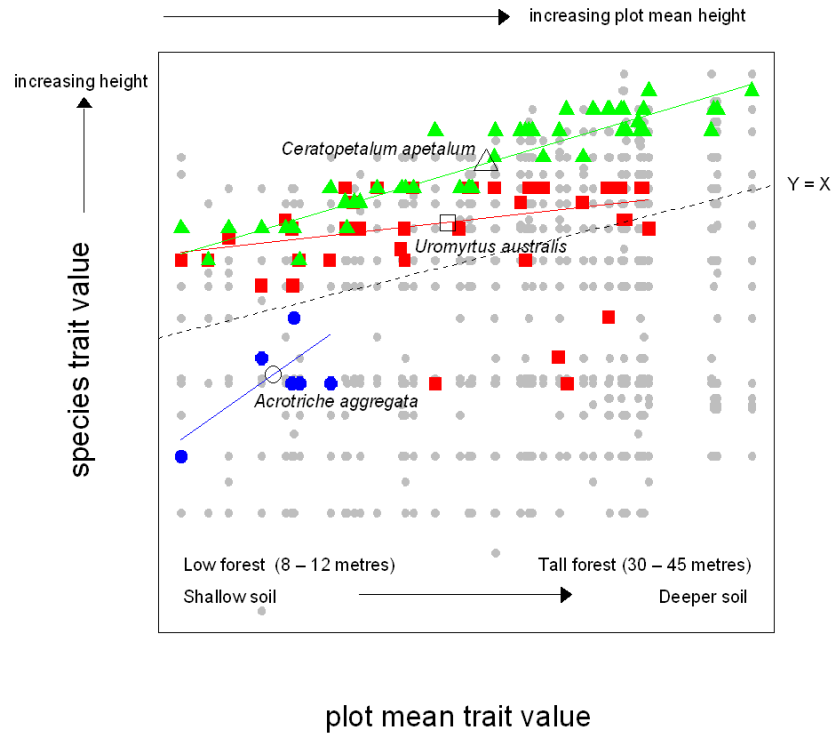
Figure 2 Scatterplot of species trait values vs. abundance-weighted plot mean trait

values for log10 actual (measured) Hmax (maximum height) in metres in 50 woody

plant assemblages (from Nightcap National Park in the simple notophyll vine forest

community type in north-east New South Wales). Values for three species are

highlighted: *Ceratopetalum apetalum* - Cunoniaceae (most common canopy species

in Simple Notophyll-Microphyll Vine Forest on rhyolite derived soils); *Uromyrtus*

australis – Myrtaceae (the clonal study species); *Acrotriche aggregata* – Ericaceae

(low shrub to very small tree that occurs only in lowest stature Simple Notophyll-

Microphyll Vine Forest on skeletal rhyolite derived soils). *Ceratopetalum apetalum* is

represented as a large black outline triangle (species mean). The green triangles show

the plots occupied by the species. *Uromyrtus australis* is represented as a large black

outline square (species mean), and occupied plots as red squares. *Acrotriche aggregata* is represented as a large open circle, and the plots it occupies are shown as blue circles. Using *A. aggregata* as a conveniently constrained illustration of the trait gradient analysis, the large symbol (open circle) represents the intersection of the mean trait value for the plots occupied by the species (the β_i beta trait value on abcissa) and the mean species trait value (on ordinate). The distance of the large symbol from the $Y = X$ dashed line is the species α_i alpha trait value. This represents the difference between the species mean trait value and its beta value. The $Y = X$ dashed line represents the slope of the trait gradient defined by the mean trait values of the species co-occurring in assemblages. The range of occupied plots on the *x*-axis is the species niche breadth, representing the range of plots occupied by the species along and across the gradient of trait variation represented in the sample (Ackerly and Cornwell 2007; Kooyman *et al.*, 2010).

Do the trait values of clonal rainforest tree species differ from those of co-occurring taxa? Across the range of available traits, and compared to co-occurring species, *U. australis* trait values differed from those of co-existing taxa in assemblages arrayed along environmental gradients only in terms of clonal architecture, and shifts in stem abundance. In relation to number of stems of *U. australis* and trait means for plots, numbers increased on plots with smaller leaves ($r^2 = 0.36$, $P < 0.0001$) and higher wood density ($r^2 = 0.41$, $P < 0.0001$) reflecting upslope topographic positions (e.g. Kraft et al., 2008; Kooyman et al., 2010). Overall, trait values for *U. australis* are nested within the range of co-occurring taxa. The species has small leaves and seeds, mid range stature, and high wood density (Table 1).

Table 1 Trait values (log10) for four traits (maximum height at maturity, leaf area, seed size, and wood density) as range for plots (Tp_min – trait plot minimum; Tp_max – trait plot maximum), range for species (STr_min – species trait range minimum; STr_max – species trait range maximum), for *Uromyrtus australis* (Uro_STr_val - *Uromyrtus australis* species trait value), and for plots in which *U. australis* occurs (Uro_Tp_min - trait plot minimum for plots with *U. australis*; Uro_Tp_max - trait plot maximum for plots with *U. australis*).

TRAITS	Tp_min	Tp_max	STr_min	STr_max	Uro_STr_val	Uro_Tp_min	Uro_Tp_max
Maximum Height	1.19	1.37	0.30	1.65	1.30	1.19	1.34
Leaf Area	0.91	1.31	-0.68	1.90	0.43	0.91	1.17
Seed Size	0.57	0.78	0.04	1.63	0.48	0.60	0.78
Wood Density	2.18	2.91	2.59	3.04	2.93	2.84	2.91

The results confirm that shifts in trait means in assemblages can include species turnover (the arrival or loss of taxa) along abiotic gradients and across geographic distance, and shifts in species performance (abundance and biomass) relative to canopy height in assemblages arrayed along gradients. In this case, shifts in performance along the gradient of declining soil depth (and productivity) were more apparent and greater for the clonal study species than for co-occurring species with predominantly seed-based regeneration strategies.

DISCUSSION

Traits, species turnover and gradients—Community level turnover of species was most evident for canopy trees, and between the two areas separated by geographic distance (ca. 5 kms). However, in both areas assemblage level turnover of

species at finer scales resulted in increased floristic similarity of assemblages positioned along the environmental gradients (soil depth and topographic position) that influence forest canopy height. Assemblage level trait values were shown to shift along the gradients, suggestive of the filtering of species into habitats (or alternatively the filtering of species by abiotic factors resulting in the exclusion of species from certain habitats).

Life history parameters—For *U. australis*, bigger stems had greater reproductive output, but this varied substantially across populations in relation to abiotic gradients, and population size and isolation. Growth rate was very slow across all size classes (Table S1.2; Kooyman, 2005). Multi-stemmed clonal genets could not be ascribed a particular asymptotic size, unlike individual ramet stems. Damage to individual stems in stands was not observed to accumulate or lead to an increase in senescence and mortality in surrounding stems in the stand. Thus, the likelihood of genet mortality was not observed to increase with number and size of stems, or age. In relation to the hypotheses, both genet size and longevity remained undetermined, and could not be linked to (life-time) reproductive output. However, ramet stem size did influence seed production (per unit area of canopy and overall), and reflected position in the landscape relative to abiotic gradients, and position in the canopy. Viable seed production did not result in population growth over the two decades of observation (most likely due to fruit and seed predation; e.g. Janzen, 1970; Connell, 1971; Crawley, 1992; Wright, 2002; Moles and Westoby, 2003). In this case plant mortality is apparently decoupled from age, but the study provided no insights into the circumstances that might cause mortality, or precipitate seed-based regeneration (e.g. Romme et al., 1997).

Environmental gradients—Localised variation in environmental gradients reflecting soil depth and topographic position influenced all taxa, but resulted in different outcomes for co-existing taxa (along the same abiotic gradients). For *U. australis* patterns associated with abiotic gradients were consistent across the two populations separated by geographic distance (e.g. Weiher and Keddy, 1995). Species performance (measured as clonal stem abundance, and size-height in canopy) increased as soil depth decreased in upslope topographic positions. No other taxa in these assemblages simultaneously shifted height strategy (from understorey to canopy) and stem abundance relative to abiotic gradients and co-occurring taxa in this way (e.g. Küppers, 1989). Broadly speaking, this supports the 'environmental gradients as filters' hypothesis because the density, size and arrangement of stems followed similar patterns under similar conditions across the species range.

Performance and traits—Species performance in assemblages arrayed along abiotic gradients was quantified by measuring two key components of plant performance; variation (plasticity) in genet architecture that includes stem size (height and diameter) and stem density, and fecundity (as seed production per unit area of crown). The interaction of the axes of maximal tree stature (H_{max}) and light demand reflects the partitioning of the vertical light gradient and tree stratification, that are known to be important influences on rainforest tree species trait variation and architecture (Poorter et al., 2006). Patterns of clonal architecture and ramet stem size and numbers were similar in smaller and larger populations under similar conditions of environment. In the case of sexual reproductive output (as seed produced year-year) there was an increase with stem size (but only in the largest population and habitat area, Nightcap), but this could not be related to number of stems, and did not result in successful seed-based regeneration. In addition, there was no evidence of a

116

trade-off between allocation to sexual reproduction and vegetative growth, but considerable variation in seed production was detected in relation to population size. In terms of the latter, the localised (geographical) variation in allocation of resources to seed production may reflect constraints on sexual reproduction as a consequence of lower numbers of individual genets in smaller populations. Recent genetic work on other rainforest tree taxa in these and nearby habitats shows the potential consequences of reduced population size on both population level heterozygosity (Rossetto et al., 2008) and seed production and viability (e.g. Rossetto et al., 2004).

Conclusions—Both species turnover, and shifts in species performance and ecological strategies contribute to the sign of trait shifts in assemblages arrayed along abiotic gradients. For *U. australis* increased vegetative growth and competitiveness in lower productivity habitats resulted in a shift from low abundance in the understorey, to high abundance in the canopy (e.g. Murray and Lepschi 2004; and see Sagarin et al., 2006), while fecundity decreased in smaller populations and was decoupled from sexual reproductive success (e.g. Cody and Mooney, 1978). Clonality and vegetative suckering increase longevity and allow species to survive to take advantage of stochastic or other events (e.g. Romme et al., 1997; Bond and Midgley, 2001) that provide the conditions and opportunities for seed-based regeneration. For *U. australis* it seems likely environmental filtering has favoured clonality (e.g. May *et al*., 2009), however, future environmental changes may yet enable a resumption of sexual reproduction. Confirming that for conservation assessment, environmental variance should be dissected into components that affect recruitment from seed versus those that affect persistence (Rossetto and Kooyman, 2005; Kooyman and Rossetto, 2008).

LITERATURE CITED

Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Science* 164(3): S165-S184.

Ackerly, D.D. and W.K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135-145.

Adam, P. 1992. Australian Rainforests. Oxford Biogeography Series No. 6. Oxford University Press, Oxford, UK.

Baur, G.N. 1957. Nature and distribution of rain forests in New South Wales. *Australian Journal of Botany* 5(2): 190-233.

Beckman, G.G. and C.H. Thompson. 1977. The Soils. In: R. Monroe and N.C. Stevens [eds.], The Border Ranges: a Land Use Conflict in Regional Perspective, 7-10. Royal Society of Queensland, Brisbane, Australia.

Bond, W.J. and J.J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16(1): 45-51.

Bootle, K.R. 1983. Wood in Australia: types, properties and uses. McGraw-Hill Sydney, Australia.

Braun-Blanquet, J. 1932. Plant Phytosociology. McGraw-Hill, New York.

Briggs, J.D. and J.H. Leigh. 1996. Rare or Threatened Australian Plants. Revised Edition. CSIRO/Australian Nature Conservation Agency, Canberra, Australia.

Bureau of Meteorology (Australia). Climate data files for Whian Whian SF (Rummery Park) weather recording station: 1943 to 2001. <www.bom.gov.au>.

Caswell, H. 1985. The evolutionary demography of clonal reproduction. In: J.B.C. Jackson, L.W. Buss and R.E. Cook [eds.], Population biology and evolution of clonal organisms, 187-224. Yale University Press, New Haven, USA.

Caswell, H. 1989. Matrix Population Models. Sinauer, Sunderland, Massachusetts, USA.

Clarke, K.R. and R.N. Gorley. 2006. Primer v6 user manual. Primer-E Ltd. Plymouth Marine Laboratory, Plymouth, UK.

Commonwealth Environment Protection and Biodiversity Conservation Act 1999, Australian Government, Canberra, Australia.

Cody, M.L. and H.A. Mooney. 1978. Convergence versus non-convergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9: 265-321.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. In: P.J. den Boer and G.R. Gradwell [eds.], Dynamics of Numbers in Populations, 298-312. Advanced Study Institute, Osterbeek Wageningen, Netherlands.

Crawley, M.J. 1992. Seed predators and plant population dynamics. In: M. Fenner [ed.], Seeds: the ecology of regeneration in plant communities, 157-191. CAB International, Wallingford, UK.

De'ath, G. 2002. Multivariate regression trees: a new technique for modelling species-environment relationships. *Ecology* 83: 1105-1117.

De Kroon, H., A. Plaiser, J. van Groenendal and H. Caswell. 1986. Elasticity: the
relative contribution of demographic parameters to population growth rate.
Ecology 67: 1427-1431.

Drechsler, M., B.B. Lamont, M.A. Burgman, H.R. Akcakaya, E.T.F. Witkowski and
Supriyadi. 1999. Modelling the persistence of an apparently immortal *Banksia*
species after fire and land clearing. *Biological Conservation* 88: 249-259.

Enquist, B.J., A.J. Kerkhoff, S.C. Starck, N.G. Swenson, M.C. McCarthy and Price,
C.A. 2007. A general integrative model for scaling plant growth, carbon flux,
and functional trait spectra. *Nature* 449: 218-222.

Enright, N. and J. Ogden. 1979. Application of transition matrix models in forest
dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand.
Australian Journal of Ecology 4: 3-23.

Enright, N.J., M. Franco and J. Silvertown. 1995. Comparing plant life histories using
elasticity analysis: the importance of life span and the number of life-cycle
stages. *Oecologia* 104: 79-84.

Falster, D. and M. Westoby. 2005. Alternative height strategies among 45 dicot
rainforest species from tropical Queensland, Australia. *Journal of Ecology* 93:
521-535.

Fischer, M. and M. Van Kleunen. 2002. On the evolution of clonal plant life histories.
Evolutionary Ecology 15: 565-582.

Floyd, A.G. 1973. N.S.W. Rainforest Trees, Part III, Family Myrtaceae. Research
note 28. Forestry Commission of N.S.W., Coffs Harbour, New South Wales,
Australia.

Floyd, A.G. 1989. Rainforest Trees of Mainland South-eastern Australia, pp. 268-270.
Inkata Press, Sydney, Australia.

Floyd, A.G. 1990. Australian Rainforests in New South Wales. Vol. 1 and 2. Surrey

    Beatty and Sons, Chipping Norton, NSW, Australia.

Harden, G.J. 1990-2002 with revisions. Flora of New South Wales (vol. 1-4). UNSW

    Press, Sydney, Australia.

Henery, M. and M. Westoby. 2001. Seed mass and seed nutrient content as predictors

    of seed output variation between species. *Oikos* 92: 479-490.

Hewitt, G. 2000. The genetic legacy of the quaternary ice ages. *Nature* 405: 907-913.

Hill, R.S. 1994. History of the Australian vegetation: Cretaceous to Recent.

    Cambridge University Press, Cambridge, UK.

Hill, R.S. 2004. Origins of the southeastern Australian vegetation. *Philosophical*

    *Transactions of the Royal Society London B***,** 359: 1537-1549.

Hutchings, M.J. and H. de Kroon. 1994. Foraging in plants: the role of morphological

    plasticity in resource acquisition. *Advances in Ecological Research* 25: 159-

    238.

Hutchinson, G. 1957. Concluding remarks. *Cold Spring Harbour Symposium on*

    Quantitative Biology 22: 415-457.

Ilic, J., D. Boland, M. McDonald, G. Downes, and P. Blakemore. 2000. Wood

    Density Phase 1: State of Knowledge. National Carbon Accounting System

    Technical Report No. 18. Australian Greenhouse Office.

    http://www.greenhouse.gov.au/ncas/reports/pubs/tr18final.pdf

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests.

    American Naturalist 104: 501-508.

Kershaw, A.P., I.R. Sluiter, J. McEwan Mason, B.E. Wagstaff and M. Whitelaw.

    1991. The history of rainforest in Australia – evidence from pollen. In: G.

Werren and P. Kershaw [eds.], The Rainforest Legacy, Vol. 3, 1-16. Australian Government Press. Canberra, Australia.

Kershaw, A.P., S.C. Bretherton and S. van der Kaars. 2007. A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251: 23-45.

Klekowski, E.J.,Jr. 1997. Somatic mutation theory of clonality. In: H. de Kroon and J. van Groenendael [eds.], The Ecology and Evolution of Clonal Plants, 227-241. Backhuys Publishers, Leiden, Netherlands.

Klimes, L., J. Klimesova, R. Hendricks and J. van Groenendael. 1997. Clonal architecture: a comparative analysis of form and function. In: H. de Kroon and J. van Groenendael [eds.], The Ecology and Evolution of Clonal Plants, 1-30. Backhuys Publishers, Leiden, Netherlands.

Kooyman, R.M. 2000. Results of field surveys to determine the distribution of *Uromyrtus australis*. Report (*unpubl.*) prepared for NSW NPWS, Australia.

Kooyman, R.M. 2005. The ecology and population biology of *Uromyrtus australis* A.J. Scott. MSc dissertation, University of New England, Armidale, NSW, Australia.

Kooyman, R.M. and M. Rossetto. 2008. Definition of plant functional groups for informing implementation scenarios in resource-limited multi-species recovery planning. *Biodiversity Conservation* 17: 2917-2973.

Kooyman, R.M. and M. Westoby. 2009. Costs of height gain in rainforest saplings: main-stem scaling, functional traits and strategy variation across 75 species. *Annals of Botany* 104: 987-993.

Kooyman, R.M., W. Cornwell and M. Westoby. 2010. Plant functional traits in
Australian sub-tropical rain forest: partitioning within community from cross-
landscape variation. *Journal of Ecology* 98: 517-525.

Kraft, N.J.B., R. Valencia and D.D. Ackerly. 2008. Functional traits and niche-based
tree community assembly in an Amazonian forest. *Science* 322: 580-582.

Küppers, M. 1989. Ecological significance of above-ground architectural patterns in
woody plants: a question of cost-benefit relationships. *Trends in Ecology and
Evolution* 4(12): 375-379.

Lande, R. 1993. Risks of population extinction from demographic and environmental
stochasticity and random catastrophes. *American Naturalist* 142(6): 911-927.

Lynch, M. and W. Gabriel. 1983. Phenotypic evolution and parthenogenesis.
American Naturalist 122: 745-764.

Lynch, A.J.J., R.W. Barnes, J. Cambacedes and R.E. Vaillancourt. 1998. Genetic
evidence that *Lomatia tasmanica* (Proteaceae) is an ancient clone. *Australian
Journal of Botany* 46: 25-33.

MacArthur, R.H. and R. Levins. 1967. The limiting similarity, convergence, and
divergence of coexisting species. *American Naturalist* 167: 377-385.

Mangel, M. 2008. Environment, damage and senescence: modelling the life-history
consequences of variable stress and caloric intake. *Functional Ecology* 22:
422-430.

May, M.R., M.C. Provance, A.C. Sanders, N.C. Ellstrand and J. Ross-Ibarra. 2009. A
Pleistocene clone of Palmer's oak persisting in southern California. *PloS ONE*
4, e8346.

Moles, A.T. and M. Westoby. 2003. Do large seeds suffer higher levels of pre- or
post-dispersal seed predation than small seeds? *Ecology* 84: 3148-3161.

Monaghan, P., A. Charmantier, D.H. Nussey and R.E. Ricklefs. 2008. The evolutionary ecology of senescence. *Functional Ecology* 22: 371-378.

Morand, D.T. 1994. Soil Landscapes of the Lismore - Ballina 1:100,000 Sheet. Department of Conservation and Land Management, Sydney, Australia.

Morand, D.T. 1996. Soil Landscapes of the Murwillumbah - Tweed Heads 1:100,000 Sheet. Department of Conservation and Land Management, Sydney.

Murray, B.R. and B.J. Lepschi. 2004. Are rare species abundant elsewhere in their geographical range? *Austral Ecology* 29(3): 287-293.

New South Wales Threatened Species Conservation Act 1995. Lists of Schedule 1 and 2, threatened species, NSW, Australia. <www.environment.nsw.gov.au>.

Nix, H.A. 1991. An environmental analysis of Australian rainforests. In: Gerry Werren and Peter Kershaw [eds.], The Rainforest Legacy, Australian National Rainforest Study Vol. 2, 1-26. Australian Government Publishing Service, Canberra, Australia.

Poorter, L., L. Bongers and F. Bongers. 2006. Architecture of 54 moist forest tree species: traits, tradeoffs, and functional groups. *Ecology* 87(5): 1289-1301.

Ricklefs, R.E. 2008. The evolution of senescence from a comparative perspective. *Functional Ecology* 22: 379-392.

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain and R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. *Natural Areas Journal* 17: 17-25.

Rossetto, M., C.L. Gross, R. Jones and J. Hunter. 2004. The impact of clonality on an endangered tree (*Elaeocarpus williamsianus*) in a fragmented rainforest. *Biological Conservation* 117: 33-39.

Rossetto, M. and R.M. Kooyman. 2005. The tension between dispersal and persistence regulates the current distribution of rare palaeo-endemic rain forest flora: a case study. *Journal of Ecology* 93: 906-917.

Rossetto, M., R.M. Kooyman, W. Sherwin and R. Jones. 2008. Dispersal limitations rather than bottlenecks or habitat specificity can restrict the distribution of rare and endemic rainforest trees. *American Journal of Botany* 95(3), 321-329.

Royer, D.L., R.M. Kooyman, S.A. Little and P. Wilf. 2009. Ecology of leaf teeth: a multi-site analysis from an Australian sub-tropical rainforest. *American Journal of Botany* 96(4): 1-14.

Sagarin, R.D., S.D. Gaines and B. Gaylord. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* 21(9): 524-530.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Clarendon, Oxford.

Silvertown, J., M. Franco, I. Pisanty and A. Mendoza. 1993. Comparative plant demography: relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465-476.

Sjöström, A. and C.L. Gross. 2006. Life history characters and phylogeny are correlated with extinction risk in the Australian angiosperms. *Journal of Biogeography* 33: 271-290.

Snow, N. and G.P. Guymer. 2001. Revision of Australian species of *Uromyrtus* (Myrtaceae) and two new combinations for New Caledonia. *Systematic Botany* 26(4): 733-742.

Stevens, N.C. 1977. Geology and landforms. In: R. Monroe and N.C. Stevens [eds.], The Border Ranges: a Land Use Conflict in Regional Perspective, 1-6. Royal Society of Queensland, Brisbane, Australia.

Takhtajan, A.L. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Botanical Review* 46: 225-359.

Vesk, P.A. and M. Westoby. 2004. Sprouting ability across diverse disturbances and habitats worldwide. *Journal of Ecology* 92: 310-320.

Webb, L.J. 1978. A General Classification of Australian Rainforests. *Australian Plants* 9: 349-363.

Weiher, E. and P.A. Keddy. 1995. The assembly of experimental wetland plant communities. *Oikos* 73: 323-335.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.

Westoby, M, D.S. Falster, A.T. Moles, P.A. Vesk and I.J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125-159.

Westoby, M. 2006. Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology* 87(7): S163-S165.

Wilson, P.G. 1991. 'Uromyrtus', In: G.J. Harden [ed.], Flora of New South Wales, Vol. 2 (revised), 230-231. NSW University Press, Sydney, Australia.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species co-existence. *Oecologia* 130: 1-14.

ON-LINE SUPPLEMENTAL MATERIALS

Appendix S1 – Additional details of methods (multivariate, trait gradient, seed trapping), and results (multivariate, *U. australis* population data, life history values and demographic parameters). Table S1.1 Environmental variables; Table S1.2 Annual demographic transition probabilities; Table S1.3 List of rainforest types across the sample area on rhyolite soils, and key to nomenclature used in Webb (1978); Table S1.4 Correlation values for alpha and beta trait components of 82 woody (tree and shrub) species from 100 plot samples.

CHAPTER 5

Phylogenetic tests of community assembly across regional to continental scales in tropical and sub-tropical rainforests

Robert Kooyman[1,2], Maurizio Rossetto[2], William Cornwell[3,4] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia;*

[2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;* [3]*Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada.* [4]*Department of Integrative Biology, University of California, Berkeley, CA, USA.*

ABSTRACT

Aim: Measure and quantify community phylogenetic structure to evaluate how evolutionary, ecological and biogeographic processes have shaped the distributions and assemblage of tropical and sub-tropical rainforest tree species across local, regional and continental scales.

Location: Australia.

Methods: We used 596 assemblage-level samples and 1137 woody species in rainforest vegetation sampled across two latitude regions (tropics and sub-tropics) and five distinct areas. Based on this dataset, we obtained and analysed species level trait values (for leaf size, seed size, wood density and maximum height at maturity), measures of community phylogenetic structure, and species turnover across space (beta) and evolutionary time (phylobeta).

Results: Species replacement and turnover through time (phylobeta) was by less closely related taxa across the regions combined, and by more closely related taxa within each latitude region. Assemblages of species were more phylogenetically clustered across the whole phylogeny (net relatedness index, NRI) and with respect to more recent divergences (nearest related taxon index, NTI) where the effects of historic disturbance (climatic oscillations) had been greater, and less clustered in long-term stable (refugial) locations. Local species composition in the stable wet tropics showed significant phylogenetic evenness, but there was no corresponding evenness in distributions of the ecological traits measured.

Main Conclusions: Despite a shared evolutionary and biogeographic history the two regions diverged from each other before the development of internal divergences. Phylogenetic evenness is more evident in long-term stable habitats (refugia) where species interact in conserved niches. Phylogenetic clustering is more evident where

131

recolonization of more highly disturbed areas from historically reduced species pools reflects filtering of species into phylogenetically preferred habitats.

INTRODUCTION

Phylogenetic community ecology links evolutionary and biogeographic history to present-day ecology (eg. Westoby 2006; Emerson & Gillespie, 2008). Regional species pools are comprised of species and lineages shaped by the influence of history on community interactions and trait evolution (eg. Ackerly, 2003; Ricklefs, 1987, 2008). The assembly of local communities from regional pools reflects contemporary interactions among co-occurring species, and the spread of species traits across abiotic gradients. Investigating the phylogenetic relatedness of interacting species and their traits (Webb, 2000; Webb *et al*., 2002), and the turnover of species in assemblages across spatial (beta) and temporal (phylobeta) gradients (Cavender-Bares *et al*., 2009), can provide important insights into the climatic, geological and topographic factors shaping rainforest community assemblage.

The incidence of species in communities may be mediated by their physical and behavioural characteristics interacting with abiotic gradients (eg. Westoby & Wright 2006). The ecological similarity of recently diverged taxa and their tendency to compete for limiting resources (Darwin 1859; Lord *et al*., 1995; Wiens & Graham, 2005) suggests there may be a strong link between the evolutionary relatedness of species in assemblages, species characters (traits), and the ecological processes that

determine their distribution and abundance (Kraft *et al*., 2007). The interaction of these factors can result in non-random patterns of community phylogenetic structure (reviewed in Webb *et al*., 2002; Vamosi *et al*., 2009). The link between species fidelity to habitats through time (phylogenetic niche conservatism; eg. Wiens & Graham, 2005) and different community assembly processes that reflect species relatedness (eg. competition and limiting similarity) provides the basis for interpretations of community assembly processes (Webb *et al*., 2002; Kembel & Hubbell, 2006; Kraft *et al*., 2007; Kembel, 2009). The focus of such studies is on understanding how short-term processes that affect local community assembly interact with, and link to, regional, continental and global scale processes that occur over deep evolutionary timescales (eg. Hardy & Senterre, 2007; Swenson *et al*., 2007; Graham & Fine 2008).

Phylogenetic clustering (defined as the local co-occurrence of taxa that are more phylogenetically related than expected by chance) is suggested as evidence for environmental filtering of phylogenetically conserved traits into habitats (eg. Webb, 2000; Vamosi & Vamosi, 2007). Phylogenetic evenness (defined as the local co-occurrence of taxa that are less phylogenetically related than expected by chance) is suggested as the outcome of limiting similarity and competition between more closely related taxa in phylogenetically conserved niches (Lovette & Hochachka, 2006; Slingsby & Verboom, 2006; Webb *et al*., 2006), or environmental filtering of convergently evolved traits (eg. Cavender-Bares *et al*., 2004). As an example, we might expect older more stable rainforest regions with a continuous history to show either phylogenetic evenness because of the influence of limiting similarity in conserved niches (in refugial areas), or clustering based on dispersal limitation,

localized clade divergences, and habitat specialisation. In contrast, areas within more substantially disturbed regions that have been recolonised by dispersal of species with phylogenetically conserved traits are expected to show clustering.

The tropical and sub-tropical rainforests of northern and eastern Australia emerged from a sequence of palaeogeographic and palaeoclimatic events and oscillations (e.g. Webb & Tracey, 1981a, b; Webb *et al.*, 1984, 1986; Barlow & Hyland, 1988; Kershaw *et al.*, 2007). Indigenous tertiary rainforest covered much of the Australian continent up to around the mid Miocene but contracted to the high-rainfall east coast by the Pliocene (Martin, 1987; Greenwood & Christophel, 2005). During the Pleistocene (2.8 MYA to 12 KY BP) climatic oscillations generated a series of contractions to refugia of persistent moist forest habitat followed by re-expansions of refugial patches into more continuous distributions (e.g. Kershaw *et al.*, 2007). The most recent cycle of refugial re-expansion followed the last glacial maximum (LGM; around 18 KY BP). However, even under the current more favourable interglacial conditions, rainforests occupy only about 1% of the continent and are relegated to a natural archipelago of heterogeneous remnants. Despite this history of attrition they still retain high levels of biodiversity.

Previous interpretations of floristics and endemism in Australian rainforests have mostly invoked this biogeographic history in a qualitative way (Hooker, 1860; Burbidge, 1960; Barlow & Hyland, 1988; Adam, 1994; but see Crisp *et al.*, 2001). Here our aim is to move interpretation to a more quantitative basis using community phylogenetic methods. Quantification is based on: 1) species composition data from a total of 596 assemblage-level samples and 1137 woody species in rainforest

vegetation sampled across two latitude regions (tropics and sub-tropics); 2) species level trait values (for leaf size, seed size, wood density and maximum height at maturity), 3) phylogenetic trees to summarize the history of evolutionary divergence among species; 4) indices that compare the spatial (beta) and temporal (phylobeta) turnover of species across abiotic gradients; and 5) indices quantifying phylogenetic dispersion as clustering and evenness among species and traits coexisting at sites.

Based on the biogeographic history described above and predicted patterns for community phylogenetic structure we propose three hypotheses. 1) The phylogenetic signal of the influence of continental scale biogeographic history is deeper across latitude regions combined than within each region where filtering of species and traits along key local gradients (such as altitude) is more prevalent. 2) Because local competitive exclusion operates more powerfully between closely related species with similar traits in conserved niches, phylogenetic evenness is more evident in long-term stable habitats (refugia). 3) In contrast, phylogenetic clustering of traits is more evident where species are filtered into phylogenetically preferred habitats by dispersal-based re-colonization from reduced species pools.

To empirically test those hypotheses we address the following questions:

1. Are phylogenetic divergences along the latitudinal gradient between the tropics and subtropics deeper (i.e. older) in the phylogenetic tree than divergences along within-region elevation gradients?

2. Do assemblages in regions regarded as having the oldest continuous history show phylogenetic clustering or evenness compared to null models? How does this compare to results for areas that share the same origins but have experienced

135

greater disturbance histories; and globally to other tropical forests? Do the available trait data show similar patterns?

METHODS

Floristic data and sampling

Presence-absence data were available for 286 community samples from Cape York and the Wet Tropics in Queensland (Qld) (Tracey, 1982; Williams & Tracey, 1984; Stanton & Fell, 2005), and for 310 community samples from three areas in northern New South Wales (NSW), Nightcap-Border Ranges, Dorrigo and Washpool (Kooyman personal data; and YETI vegetation survey data base) (Table 1). The two latitudinal regions (tropics and sub-tropics) are separated by more than 1100 km (Fig.1). All species in all samples (full pool 1744 taxa, trees and shrubs only; with 1137 included in the study) were taxonomically checked (Hyland *et al*., 2003) and updated, and reconciled where necessary with collection records using the Australian Virtual Herbarium database (http://www.rbg.vic.gov.au/avh). Incorrect, redundant and duplicate names were removed, and data were entered into matrices (presence / absence by sample by area and region) and merged at various scales. Across the sample, alpha diversity ranged from 7-117 species and was similar in each area and region (Table 1). The assemblage samples referred to here represent samples of all trees, shrubs and saplings >1m in height in a constrained area (eg. the area defined by ca. 30 nearest-neighbour canopy to sub-canopy trees, that can vary from ca. 0.1 to 0.5 ha under different circumstances related to stem size; on-line Appendix S1 provides details, including additional background information on vegetation history).Vamosi *et al*. (2009) found that plot area was not a significant predictor of community phylogenetic structure in the studies they compared, but emphasised the desirability of

using samples that were small enough for individuals to interact. Palms, ferns, vines, and other (non woody) life forms were excluded from the data used in the analyses presented here (refer to Kembel & Hubbell, 2006).

Focal communities and species pools

Climate varies from highly seasonal tropical lowlands to ever-wet tropical mountains at low latitudes, to seasonal moist sub-tropical at higher latitudes. Across this large geographical region the sampled rainforest habitats include coastal sand dunes, estuaries and headlands, near-coast coral atolls and islands, alluvial floodplains and riparian edges, foothills, uplands, and highland mountains. In the tropical region, Wet Tropics has high mountains and dramatic relief (0-1650m) with large river valleys and deeply dissected terrain, while Cape York has more constrained relief (0-500m). In the sub-tropics all areas have significant mountain ranges (up to and > 1100m) and relatively heterogenous topographic gradients. Offshore islands associated with the Wet Tropics sample, and the extensive low coastal plains of Cape York, are absent in the sub-tropics.

Rainforest vegetation across the sample varies from drier deciduous and semi-deciduous vine thickets in parts of Cape York (Kikkawa *et al*., 1981) to the warm lowland and cool wet tropical forests of the Wet Tropics, and the warm lowland and cool wet sub-tropical to warm-temperate forests of northern NSW (refer to Webb *et al*., 1984; Nix, 1991). Species pools (for free-standing woody taxa only) were defined at three scales (Table 1): 1) full pool (all rainforest taxa north of Townsville to Torres Strait in Qld, plus all of NSW); 2) regional pool (the full pool split by region; Qld and NSW); and 3) local sample pool, based on those species that occur in each of the five

areas; Cape York (CY) and Wet Tropics (WT) in Qld, and Nightcap-Border Ranges (NB), Dorrigo (DO) and Washpool (WA) in NSW.

Figure 1 Map of Australia showing State boundaries; NSW-New South Wales (sub-tropics) and Qld-Queensland (tropics). Areas within latitude regions are labelled in relation to position and approximate extent of sample is indicated. Cape York (black dots) and Wet Tropics (dark grey) in the tropics; Nightcap Border Ranges (medium grey), Dorrigo (light grey) and Washpool (black) in the sub-tropics.

Table 1 Attributes including (n-species) total number of species, genera and families
(trees and shrubs only) in the study and by area (Qld – Queensland; NSW – New
South Wales; CY – Cape York; WT – Wet Tropics; NB – Nightcap-Border Ranges;
DO – Dorrigo; and WA – Washpool). Other information includes number of
assemblage samples used in the study (n-samples) (details in Appendix S1) and alpha
diversity for each area (alpha-divers.). Data sources: YETI data base Department
Environment Climate Change and Water, New South Wales (257 samples); Kooyman
personal data (53 samples); Tracey, J.G. (1982; 146 samples Wet Tropics); CSIRO
Canberra; Stanton & Fell (2005; 140 samples Cape York); Rainforest CRC; Hyland *et
al*., (2003) CSIRO.

AREA	n-species	Scale	Genera	Families	n-samples	alpha-divers.
Qld+NSW	1137	full sample	406	98	596	7 to 117
Qld+NSW	1744	full pool	519	104		
Qld+NSW	>150 shared					
CY+WT	921	regional sample	369	88	286	7 to 110
Qld	1452	regional pool	504	102		
CY	531	area sample	268	77	140	9 to 61
	780	local pool	355	88		
WT	662	area sample	299	83	146	7 to 110
	1316	local pool	466	101		
NB+DO+WA	396	regional sample	195	61	310	12 to 117
NSW	448	regional pool	229	69		
NB	318	area sample	191	60	140	24 to 117
	371	local pool	212	63		
DO	232	area sample	152	54	127	19 to 99
	253	local pool	158	55		
WA	131	area sample	93	45	43	12 to 55
	148	local pool	104	46		

Phylobetadiversity

To determine the relationship of species turnover to spatial, temporal and
environmental variation, assemblage sample-based beta and pairwise
phylobetadiversity (Graham & Fine, 2008) values were generated using the PICANTE
package (R 2.8.1 and *Phylocom*). Beta represents the fraction of species found in one
sample but not another (the spatial turnover of species across samples). Phylobeta
represents the mean phylogenetic tree distance between species in two samples; it is
an evolutionary time measure in the sense that higher phylobeta means that species
diverged further into the past, on average. To evaluate correlations among beta
diversity, phylobetadiversity, and environmental / geographic factors we developed an
integrated model in R (R version 2.8.1 and the PICANTE package) and used the Akaike
Information Criterion (AIC; Akaike, 1973) to identify the most important
environmental factors (see Appendix S1 in Supporting Information). From these
(isothermality, elevation, seasonality of precipitation, soil types) we selected elevation
(altitude) as the focus here because it is the most significant habitat gradient within
each region; because it can easily be measured on the same scale in the two regions;
because temperature change is a major component of both the elevation gradients
within regions and the latitudinal differentiation between regions; because rainfall
generally increases with altitude (in these coastally aligned sites) and cloud stripping
buffers vegetation from seasonal dryness; and because soil information was only
available as categories for available soil nutrients by type (Nix, 1991). We looked at
three key components in the analyses relative to gradients in our data set: 1) what
explains beta; 2) what explains phylobeta; and 3) what explains phylobeta given beta.

Supertrees

Phylogenetic supertrees representing each of the focal communities (and scales) described above were generated using *Phylomatic* (www.phylodiversity.net/phylomatic/). The BLADJ algorithm implemented in *Phylocom 3.4.1* (Webb *et al*., 2008) was used to age the nodes of each species-pool supertree by applying the molecular and fossil dates of Wikstrom *et al*. (2001). This process minimised branch-length variance on the supertrees by applying dates to nodes where an estimate was available in Wikstrom *et al*. (2001) and then evenly spacing dates from these 'known' nodes to populate 'unknown' nodes. These dates are far from perfect, but this approach is the best available at present and represents an improvement over the default that sets all branch lengths equal (Webb, 2000). See Appendix S1.

Phylogenetic community structure metrics

To measure relatedness of species within samples we used *Phylocom* to calculate mean phylogenetic distance (MPD) and mean nearest phylogenetic taxon distance (MNTD). MPD measures mean pairwise phylogenetic distance between each taxa within the sample (i.e. a tree-wide assessment of relatedness among co-occurring taxa), while MNTD measures the average distance to closest relative for each taxon (i.e. an assessment of terminal relatedness among co-occurring taxa). These two measures were standardised into net relatedness index (NRI) and nearest related taxon index (NTI) respectively (Webb *et al*., 2002). For NRI and NTI, positive values reflect clustering (species are more related than by chance) and negative values reflect evenness (species are less related than by chance) relative to a null model.

Because different size species pools and different null models can influence results (see Appendix S1) we compared the outputs from the different models (representing different pool sizes and null models) and tabulated the means for NRI and NTI. Four null models were tested for all metrics. All combinations of metrics and null models were run on *Phylocom* using 999 randomizations. Null models and results of additional statistical tests (t-tests, and SMA; Falster *et al*., 2003) are described in Appendix S1 and S2.

Functional trait data

Continuous measures for species leaf size (surface area), seed size (seed dry mass), fruit size (length; maximum dimension), wood density (basic), and maximum height at maturity were used in the study. Appendix S1 includes descriptions of the trait data sources and methods.

Trait-based phylogenetic community structure metrics

We used *Phylocom* to measure trait dispersion within samples across a range of communities and species pools (COMTRAIT). The metrics used for these calculations were mean pairwise trait distances among taxa (MPD), and mean distances to nearest neighbour trait distance (MNTD). Dispersion values in observed and null communities (similar to those calculated for the phylogenetic measures) were used in conjunction with standardised effect size (SES) of the trait dispersion metrics and the rank of the observed trait dispersion relative to that of null communities. These provided indicative values of trait clustering or evenness. Values for SES MNTD and SES MPD less than zero indicate clustering and values greater than zero equate with evenness. In very few cases the results for MNTD for a trait at assemblage level

returned a zero value (in the *Phylocom* outputs), indicating lower statistical support. In general, and in cases where we report means, we compared results with and without the 0 values and found they had no influence.

RESULTS

Phylogenetic differentiation along latitude and elevation gradients

Species dissimilarity across spatial scales as beta diversity (Fig. 2a) increased with elevation difference as expected, and in a similar manner within the tropics and subtropics (latitude regions), from below 0.80 to above 0.95. Beta dissimilarity between latitude regions was higher than within. Beta dissimilarity has a ceiling at 1.0, which most likely explains the apparently shallower slope of the response to elevation in terms of the difference between latitude regions compared to within latitude regions.

Phylobeta (mean phylogenetic tree distance between species in a pair of plots; Fig. 2b) similarly increased with elevation difference and was very similar at different latitudes. Phylobeta between latitudes was greater, at a given elevation difference, than within latitudes.

To measure the depth of divergence in the phylogenetic tree we modelled the phylobeta residuals after extracting the correlation with beta (i.e. by removing the residue of the spatial signal). The phylobeta residuals were positive for plot-pairs compared across latitudes (tropical versus sub-tropical regions), and negative for plot-pairs within latitudes (Fig. 2c), showing that phylogenetic differentiation along the

latitudinal gradient tended to be older than along the elevation gradient within a latitude region.
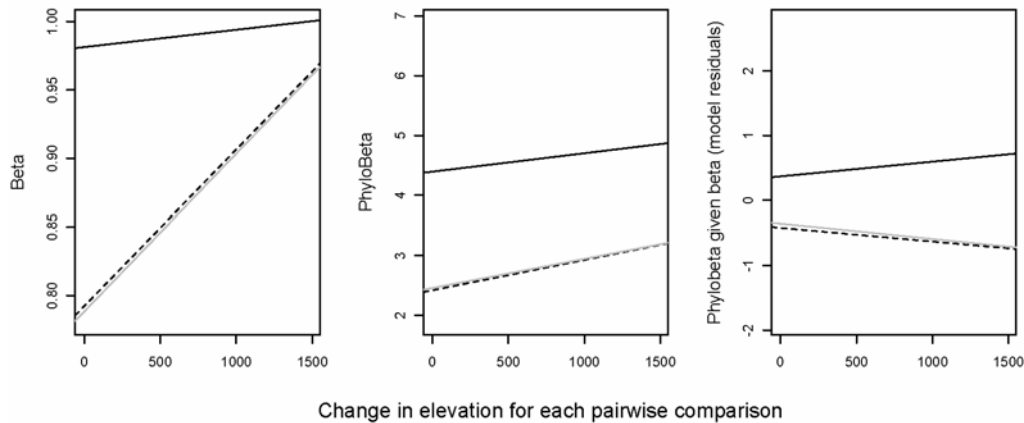
Figure 2 (a-c) Pairwise comparisons between and within New South Wales (NSW) and Queensland (Qld) samples in relation to change in elevation for: a) beta; b) phylobeta; and c) phylobeta given beta (model residuals). Solid black line – comparisons of NSW and Qld samples; black dashed line – comparisons within NSW; grey line – comparisons within Qld. In graph a) species turnover across plot samples (the spatial component; beta) increases with elevation, changes similarly within the latitude regions, and the difference is greatest between the regions. In graph b) phylobeta increases similarly with elevation within latitude regions, and is greater between latitudes. For graph c) that represents only the temporal component of species turnover (depth of divergence) in the model, values greater than zero (greater than expected relative to the null) for phylobeta show that species are replaced by more distantly related taxa across the two regions (solid black line) and by more closely related taxa within each area (grey and dashed- black lines). This shows that phylogenetic differentiation along the latitudinal gradient is older than along the elevation gradient within the latitude regions.
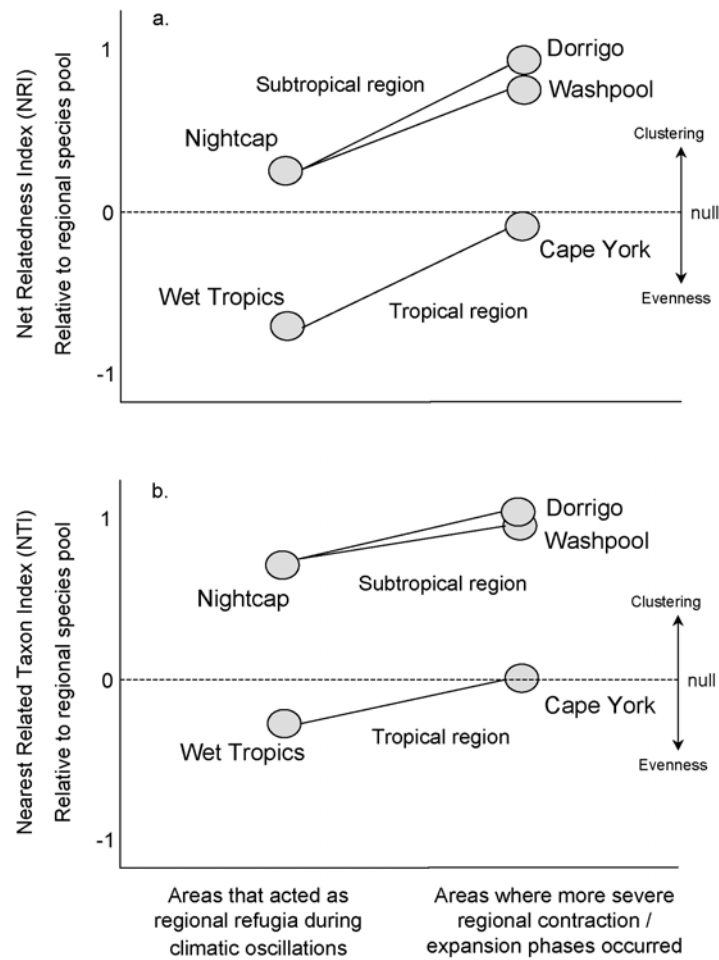
Figure 3 (a-b) Schematic of mean values for net relatedness index (NRI) (a) and

nearest related taxon index (NTI) (b) by area and latitude region (tropical and sub-

tropical) in relation to regional species pools, and the null. Grey filled circles

represent areas in each latitude region and show different outcomes relative to climate

history and the LGM (last glacial maximum). In the tropical region, negative values

(evenness) for Wet Tropics indicate in-situ persistence of moist forest (refugia); while

more neutral values for Cape York indicate more severe contraction of rainforest. For

the sub-tropics, more neutral values for Nightcap-Border Ranges indicate higher in-

situ persistence and regional refugia; while more positive values (stronger clustering)

for Washpool and Dorrigo indicate more severe contraction of rainforest, and subsequent re-colonisation and re-expansion following the LGM.
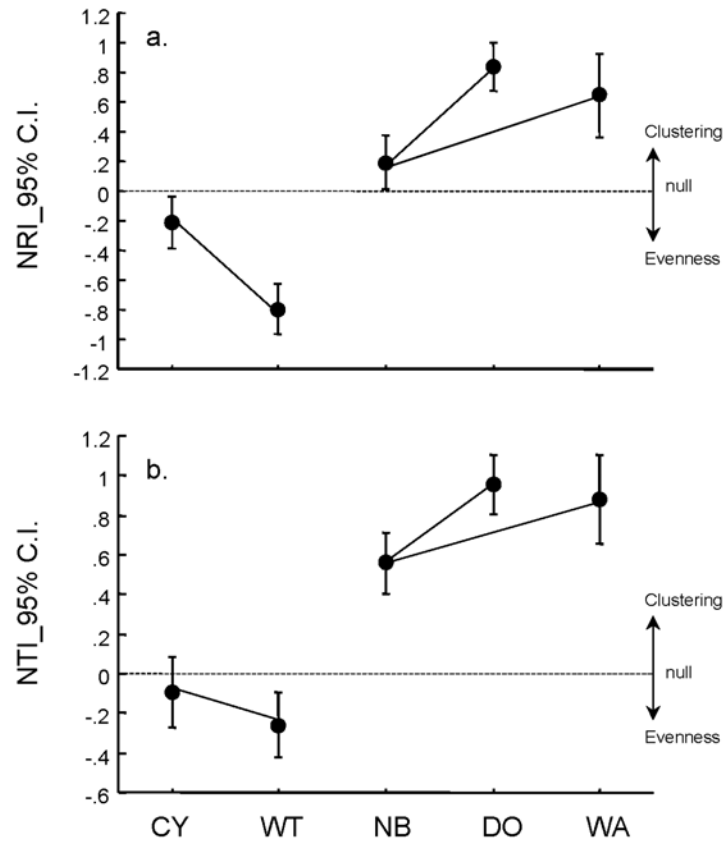
Figure 4 (a-b) Interaction line plots for net relatedness index (NRI) and nearest related taxon index (NTI) by area relative to regional species pools and null model 2 (*Phylocom*). CY – Cape York and WT – Wet Tropics in far north Queensland; NB - Nightcap-Border Ranges, DO – Dorrigo, and WA - Washpool in northern New South Wales. Positive values equate with clustering and negative with evenness. Highest order effects; upper and lower 95% confidence limits shown. Lines connect regional refugia (WT in tropics and NB in sub-tropics) to other areas in each latitude region. Table 1 shows number of samples by area and details of relative pool sizes.

Phylogenetic structure in refugial rainforests compared to those that substantially re-established since the last glacial maximum

Assemblages in Washpool and Dorrigo had a composition that was more phylogenetically clustered than Nightcap - Border Ranges, and assemblages in Cape York had composition that was less even phylogenetically than in the Wet Tropics (Figs 3 and 4). The differences were somewhat more marked when measured as NRI (across the whole depth of the phylogeny) (Figs 3a and 4a) than as NTI (at the tips of branches representing more recent divergences) (Figs 3b and 4b). This is consistent with the idea that they arise from the absence of whole clades from the re-established forests, not only from the absence of individual species within speciose clades.

Table 2. Mean values for NRI – net relatedness index (derived from mean pairwise phylogenetic distance metric, MPD) and NTI – nearest related taxon index (derived from mean nearest related taxon distance metric, MNTD) for the five areas; CY – Cape York, WT – Wet Tropics, NB – Nightcap / Border Ranges, DO – Dorrigo, and WA – Washpool by regional pool size and null model 2. Positive values represent clustering (species more related than expected relative to the null); negative values reflect evenness (species less related).

Metric - Null	CY	WT	N	B	DO	WA
NRI_2	-0.212			-0.795	0.190	0.835	0.648
NTI_2	-0.091			-0.258	0.560	0.958	0.883

Phylogenetic evenness or clustering

Among Australian rainforests significant evenness was found for the Wet Tropics only. Dorrigo and Washpool in the subtropics showed distinct phylogenetic clustering. Cape York and Nightcap-Border Ranges were closer to neutral (Figs 3-4).

Trait clustering or evenness

The measures of trait clustering or evenness (see Appendix S2; Table S2.5) are expressed in standard deviation units. Among the 50 observations (Table S2.5, at full pool size), only one deviates from zero by more than two standard deviation units (-2.19 indicating a tendency to cluster relative to the null model for canopy height in Wet Tropics; but this could easily arise by chance among 50 tests). Thus there is little or no evidence for either clustering or evenness of distributions of any of the traits. In particular, there is no evidence for trait evenness in Wet Tropics where phylogenetic distribution tended towards evenness (Fig. 3); and no evidence for trait clustering in Dorrigo and Washpool where phylogenetic distribution tended towards clustering.

DISCUSSION

Regional and continental divergences along the latitudinal gradient

The two latitude regions (tropics and sub-tropics) have a shared evolutionary and biogeographic history, and share a substantial number of taxa (Table 1). Phylogenetic divergences along the latitudinal gradient between the tropics and subtropics are older than divergences within-region along the elevation gradient (Fig. 2c). This evidence supports the scenario of lineages primarily being structured by geographic distance (latitude) and dispersal limitation over long time-scales. Figure 2c shows that species turnover through time was by more distantly related taxa across the two regions

combined (solid black line with values >0) and by more closely related taxa within each latitude region (grey and dashed- black lines with values <0).

Two measures of dissimilarity were used in combination to investigate this. The beta diversity between a pair of samples (Fig. 2a) is a spatial measure of species turnover that represents the fraction of species present at one location that are absent from the other. Phylobetadiversity (Graham & Fine, 2008) is a temporal measure of species turnover that represents the phylogenetic distance between two assemblages of species (Fig. 2b); it is the average phylogenetic tree distance between all possible pairs of species that have one member at one sample location and the other member at another (location). We tested the actual depth of divergence in the phylogenetic tree by modelling phylobeta residuals along the elevation gradient after extracting any remaining correlation with beta (i.e. by removing the residue of the spatial signal; Fig. 2c). The extent to which phylobetadiversity patterns differ from neutrality in relation to geographic scale is represented on the y-axis (neutrality equates with scenarios where phylobeta values are the same for all components - eg. within the Qld tropics, within the NSW sub-tropics, and between the tropics and sub-tropics). Environmental heterogeneity (in this case the elevation gradient that represents variation in each region and is correlated with some climatic variables) is represented on the x-axis. Theoretically the difference between the within-area and between-area lines in relation to habitat (elevation on the x-axis) identifies the extent to which different factors (niche conservatism vs. lability, and dispersal limitation and dispersal linkage) are operating and influencing community assembly in the study regions (Graham and Fine, 2008).

Stability versus re-expansion and re-colonization

The subtropical and warm temperate samples (NSW) were more phylogenetically clustered (NRI and NTI, Fig. 3), reflecting their narrower phylogenetic distribution compared to the tropical rainforest floras. Within NSW, Dorrigo and Washpool were more phylogenetically clustered than Nightcap-Border Ranges. This reflects relative differences in dispersal and re-colonisation processes that followed more severe (historic) rainforest contractions and loss of both species richness and taxonomic breadth in those areas. A taxonomic indicator of these events across the two latitude regions was the higher incidence of the family Myrtaceae in sub-tropical compared to tropical assemblages. This suggests both overall floristic simplification and a shift in taxonomic structure. Within the sub-tropics the disturbance-related signal from this family was differentiated still further. For example, Washpool had higher representation of the disturbance related sclerophyll genus *Eucalyptus*, while the more refugial Nightcap-Border Ranges area had a higher incidence of several rainforest tree genera in the family Myrtaceae, including *Syzygium*.

The tropical Queensland sample shows phylogenetic evenness. The evenness is strongest in the Wet Tropics and weaker in Cape York. This is consistent with stronger rainforest contractions in the latter caused by lack of topographic variation compared to the Wet Tropics. The contrasts are somewhat stronger for nearest-relative indices than for indices of overall phylogenetic tree depth (Fig. 3; Table 2). This is expected on the basis that the time since recolonization of Cape York sites has not been sufficient for the colonization events to give rise to whole clades. Taxonomically, differences between these two tropical areas are highlighted by Wet Tropics having many species in families such as Lauraceae, Myrtaceae, Sapindaceae,

Proteaceae, Rutaceae, Cunoniaceae, Elaeocarpaceae, and Monimiaceae that have

strong Gondwanan representation. For Cape York families that are described as

'southern or Gondwanan' in origin such as Cunoniaceae, Elaeocarpaceae and

Monimiaceae are relatively poorly represented, and tropical elements of Annonaceae,

Fabaceae, Rubiaceae, Sapotaceae, Combretaceae and Clusiaceae increase in

importance. This suggests a greater role in Cape York for colonization by (northern)

tropical monsoon forest elements of the Indo-Malesian flora in seasonally dry areas

(see Webb and Tracey, 1981).

Phylogenetic structure

Indices of dispersion represent the net effect of opposing processes, with habitat

specialization and the extinction-colonization history of particular clades giving rise

to clustering, and competitive exclusion of phylogenetically-related taxa giving rise to

evenness. Phylogenetic dispersion metrics for local land plant assemblages (collected

and reviewed in Vamosi *et al.*, 2009) have so far documented all three possible

patterns (clustering, evenness, and not significantly different from random). Studies

from lowland tropical rainforests variously report clustering (Swenson *et al.*, 2006),

evenness (Webb *et al.*, 2006) or a mixture of both depending on habitat (Kembel &

Hubbell, 2006). However, to date, most studies have found either clustering or no net

effect (Vamosi *et al.*, 2009). Where evenness has been shown, the tests have mostly

been within particular genera rather than for the whole assemblage (Cavender-Bares

et al., 2004; 2006). The detection of evenness in rainforest studies that include

multiple taxonomic groups has to date mostly been reported at smaller spatial scales

than used here (eg. Webb *et al.*, 2006; Kembel & Hubbell, 2006).

The phylogenetic evenness in the Australian Wet Tropics might have arisen from competitive exclusion among more closely related species, or because the Wet Tropics have persisted continuously as rainforest habitat so there has been relatively less historical extinction of clades. Despite the selected traits not showing evenness for Wet Tropics (see Appendix S2: Table S2.5), other traits (eg. defensive chemistry) are likely to be more effective at showing the influence of competition and limiting similarity. Therefore, the competitive exclusion hypothesis for evenness in Wet Tropics remains plausible, especially as herbivores or pathogens supported by each species might still reasonably be expected to inflict more damage (eg. graze more heavily, or cause increased seedling mortality from fungal outbreaks) on species in the same clade (Webb *et al*., 2006).

Quantifying community phylogenetic structure provided empirical data and evidence that allowed us to investigate and test long-standing hypotheses about the history of rainforest community assembly in Australia. The patterns quantified here, at continental scales and through evolutionary time, confirm the shared history of the Australian tropical and sub-tropical rainforests and their divergence deep in the past. Historic differentiation of the vegetation type across continental scales in relation to climate history provides important insights into large-scale vegetation processes. These include the tendency within each latitude region to stronger phylogenetic clustering of species in assemblages in areas subjected to more extreme (historic) contraction and recolonization phases, and the tendency to phylogenetic evenness in areas that acted as refugia. The results demonstrate that the questions phylogenetic community structure measures address in relation to key processes are fundamental to elucidating community assembly processes across temporal and spatial scales in many

contexts. Understanding the causes and consequences of community structure, including which traits are ecologically important and phylogenetically conserved, remains an important research challenge across this and many other systems and circumstances in Australia and globally.

References

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Science*, **164**(3): 165-184.

Adam, P. (1994) *Australian Rainforests*. Oxford Biogeography Series No. 6. (eds. A. Hallam, B.R. Rosen and T.C. Whitmore). Oxford University Press, Oxford.

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *2nd International Symposium on Information Theory* (eds. B.N. Petrov and F. Czáki), pp. 267-281. Akademiai Kiadó, Budapest.

Barlow, B.A. and Hyland, B.P.M. (1988) The origins of the flora of Australia's wet tropics. *Proceedings of the Ecological Society of Australia*, **15**, 1-17.

Burbidge, N.T. (1960) The phytogeography of the Australian region. *Australian Journal of Botany,* **8**, 75-212.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. and Bazzaz, F.A. (2004) Phylogenetic over-dispersion in Floridian oak communities. *American Naturalist*, **163**, 709-721.

Cavender-Bares, J., Keen, J.A. and Miles, B. (2006) Phylogenetic structure of Floridian plant communities depends on spatial and taxonomic scale. *Ecology*, **87**, S109-S122.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. and Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693-715.

Crisp, M.D., Laffan, S., Linder, H.P. and Munro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183-198.

Darwin, C.R. (1859) On the origin of species by means of natural selection. J. Murray, London.

Emerson, B.C. and Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, **23**, 619-630.

Falster, D.S., Warton, D.I. and Wright I.J. (2003) (S)MATR: standardized major axis tests and routines http://www.bio.mq.edu.au/ecology/SMATR [July 2007].

Graham, C.H. and Fine, P.V.A. (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters*, **11**, 1265-1277.

Greenwood, D.R. and Christophel, D.C. (2005) The origins and tertiary history of Australian "tropical" rainforests. *Tropical Rainforests, Past, Present, and Future*, (eds. Bermingham, E., Dick, C.W. and Moritz, C.) pp. 336-373. Chicago University Press, Chicago.

Hardy, O.J. and Senterre, B. (2007) Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *Journal of Ecology*, **95**, 493-506.

Hooker, J.D. (1860) Introductory essay. *Botany of the Antarctic voyage of H.M. Discovery Ships 'Erebus' and 'Terror' in the years 1830-1843. III. Flora Tasmaniae.* Reeve, London.

Hyland, B.P.M., Whiffin, T., Christophel, D.C., Gray, B. and Elick, R.W. (2003) Australian Tropical Rain Forest Plants – Trees, Shrubs and Vines. CSIRO Publishing. Melbourne.

Kembel, S.W. and Hubbell, S.P. (2006) The phylogenetic structure of a Neotropical forest tree community. *Ecology*, **87**, S86-S99.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, **12**, 949-960.

Kershaw, A.P., Bretherton, S.C. and van der Kaars, S. (2007) A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 23-45.

Kikkawa, J., Webb, L.J., Dale, M.B., Monteith, G.B., Tracey, J.G. and Williams, W.T. (1981) Gradients and boundaries of monsoon forests in Australia. *Proceedings of the Ecological Society of Australia*, **11**, 39-52.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. and Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist*, **170**(2), 271-283.

Lord, J., Westoby, M. and Leishman (1995) Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *American Naturalist*, **146**, 349-364.

Lovette, I.J. and Hochachka, W.M. (2006) Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology*, **87**, 14-28.

Martin, H.A. (1987) Cainozoic history of the vegetation and climate of the Lachlan River region, New South Wales. *Proceedings of the Linnean Society of New South Wales*, **109**, 213-257.

Nix, H.A. (1981) The environment of Terra Australis. *Ecological Biogeography of Australia*, (ed. A. Keast), pp. 105-133. Junk, The Hague.

Nix, H.A. (1991) An environmental analysis of Australian rainforests. *Australian National Rainforests Study, vol. 2, Flora and fauna of the rainforests*, (eds. G.L. Werren and A.K. Kershaw), pp. 1-26. Australian Government Publishing Service, Canberra.

R Development Core Team. (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167-171.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *The American Naturalist*, **172**(6), 741-750.

Slingsby, J.A. and Verboom, G.A. (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: Evidence from the schoenid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *American Naturalist*, **168**, 14-27.

Stanton, P. and Fell, D. (2005) *The Rainforests of Cape York Peninsula*. Cooperative Research Centre for Tropical Rainforest Ecology and Management. Rainforest CRC, Cairns.

Swenson, N.G., Enquist, B.J., Pither, J., Thompson,J. and Zimmerman, J.K. (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology*, **87**, 2418-2424.

Swenson, N.G., Enquist, B.J., Thompson, J. and Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770-1780.

Tracey, J.G. (1982) *The Vegetation of the Humid Tropical Region of North Queensland*. CSIRO Publications. Melbourne.

Vamosi, J.C. and Vamosi, S.M. (2007) Body size, rarity, and phylogenetic community structure: insights from diving beetle assemblages of Alberta. *Diversity and Distributions*, **13**, 1-10.

Vamosi, S.M., Heard, S.B., Vamosi, J.C. and Webb, C.O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, **18**, 572-592.

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145-155.

Webb, C. O., Ackerly, D. D., McPeek, M.A. and Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475-505.

Webb, C. O., Losos, J.B. and Agrawal, A.A. (2006) Integrating phylogenies into community ecology. *Ecology*, **87**, S1-S2.

Webb, C. O., Ackerly, D. D. and Kembel, S. W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *BioInformatics*, **24**, 2098-2100.

Webb, L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology*, **49**, 296-311.

Webb, L.J. and Tracey, J.G. (1981a) Australian rainforests: patterns and change. In: *Ecological Biogeography of Australia* (ed. A. Keast), pp. 605-694. The Hague: W.Junk.

Webb, L.J. and Tracey, J.G. (1981b) The rainforests of northern Australia. In: *Australian Vegetation* (ed. R.H. Groves), pp. 67-101. Cambridge University Press, Cambridge.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1984) A floristic framework of Australian rainforests. *Australian Journal of Ecology*, **9**, 169-198.

Webb, L.J., Tracey, J.G. and Jessup, L.W. (1986) Recent evidence for autochthony of Australian tropical and subtropical rainforest floristic elements. *Telopea*, **2**, 575-589.

Westoby, M. (2006) Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology*, **87**, S163-S166.

Westoby, M. and Wright, I.J. (2006) Land-plant ecology on the basis of species traits. *Trends in Ecology and Evolution*, **21**, 261-268.

Wiens, J. and Graham, C. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics*, **36**, 519-539.

Wikstrom, N., Savolainen, V. and Chase, M.W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London B*, **268**, 2211-2200.

Williams, W.T. and Tracey, J.G. (1984) Network analysis of northern Queensland tropical rainforests. *Australian Journal of Botany*, **32**, 109-116.

Supplementary Material

Additional Supporting Information may be found in the online version of this article:

Appendix S1

Background on history of the Australian vegetation; Detail of assemblage samples; Climate data sources; Discussion in relation to: phylogenetic structure metrics and background tree resolution; null models and null model selection. Trait data compilation and methods.

Appendix S2

Additional tests of phylogenetic structure indices; including Tables S2.1 & S2.2 Results of un-paired t-tests to compare significance values for NRI and NTI; Table S2.3 Results of SMA tests for comparisons of slope and intercept for NRI (x-axis) vs NTI (y-axis) across five areas; SMA methods and discussion of results in Table S2.4. Figure S2 (a-c) Bivariate graphs for 596 samples and discussion related to multidimensional approaches. Table S2.5 SES MPD and MNTD values for 5 traits at full pool size.

Appendix S3 References cited in Appendices (and not included in main text).

CHAPTER 6

Australian tropical and sub-tropical rainforest: functional biogeography, phylogeny, and environmental gradients

Robert Kooyman[1,2], Maurizio Rossetto[2], Chris Allen[2] and William Cornwell[3,4]

[1]Department of Biological Sciences, Macquarie University, NSW 2109, Australia; [2]National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia; [3]Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada. [4]Department of Integrative Biology, University of California, Berkeley, CA, USA.

Abstract

Aim: Quantifying the distribution of functional trait values for woody taxa in tropical and sub-tropical rainforests relative to environmental gradients and biogeographic history will link community assembly to evolutionary processes and enhance our understanding of both.

Location: Tropical northeastern and sub-tropical central eastern Australia.

Methods: To compare community assemblage patterns across selected gradients and scales we tested the relationship of species traits to phylogenetic structure, and niche breadth. We considered correlations across current-day species in assemblages in relation to species pool sizes, and trait values along gradients including altitude and latitude. Trait values were quantified across scales for seed size, leaf area, wood density and maximum height at maturity for 1137 species and 596 assemblages using trait gradient analysis.

Results: Species pool sizes were larger in the tropics than the sub-tropics, but regional shifts in size were not co-ordinated with latitude. As a group, species drawn from the smaller sub-tropical pool and filtered into re-expansion areas spanned a narrower trait range, but had higher niche breadth values measured in units of the traits and reflecting the site-mean trait values where the species occurred. Relationships between community phylogenetic structure and selected traits were most significant for seed traits in the sub-tropics, reflecting dispersal and recolonisation processes. Altitude accounted for little of the variance in community phylogenetic structure or trait variation across local and regional scales.

Main Conclusions: Regional species pool sizes were larger, trait breadth across co-existing species was higher, and species niche breadths were narrower in the tropics. Within latitude regions these values shifted in relation to environmental gradients that

reflected climatic, topographic and edaphic variation, and biogeographic history. Historic and recent rainforest contraction and re-expansion can result in recolonised areas being dominated by species with smaller more widely dispersed seeds and greater niche breadth.

Key Words: Australian tropical and sub-tropical rainforest, altitude, biogeography, community phylogenetic structure, evolutionary history, functional traits, latitude regions, niche breadth, seed size, scale

Introduction

Quantifying trait variation across current day gradients (e.g. Westoby *et al*., 2002) and in relation to assemblage level phylogenetic structure (e.g. Webb, 2000) can identify the factors that influence community assembly processes across scales, and in time (Webb *et al*., 2002; Westoby, 2006; Kembel, 2009). Combining these factors to elucidate rainforest community assembly processes invokes a functional biogeographic approach that links two key elements. The trait relationships that shape plant strategies and influence community assembly processes across scales (e.g. McGill *et al*., 2006; Westoby & Wright, 2006), and the phylogenetic relatedness of co-occurring species and their traits (Webb, 2000; Webb *et al*., 2002). The latter includes the turnover of species in assemblages across spatial and temporal gradients (Cavender-Bares *et al*., 2009) that can provide insights into the climatic, geological and topographic factors that shape rainforest communities (Kooyman *et al*., 2010a).

Rainforest vegetation once dominated the Australian continent. Increasing aridity reduced the size of the ancestral rainforests and fragmented them into a long coastally

aligned latitudinal archipelago of small habitat 'islands' separated by dry-land barriers (Herbert, 1967). Further rainforest contraction occurred as a consequence of Quaternary climatic events and oscillations (Bowler *et al.*, 1976; Webb & Tracey, 1981; Webb *et al.*, 1984, 1986; Barlow & Hyland, 1988; Ziegler *et al.*, 2003). Palaeobotanical evidence suggests alternation between warm-wet (expansion) and cool-dry (contraction and extinction) phases. The latter regarded as responsible for the long-term trend toward both decreasing extent and diversity of the wet-aseasonal rainforest biome (Christophel & Greenwood, 1989; Crisp *et al.*, 2004, 2009; Kershaw *et al.*, 2007; Moss & Kershaw 2007). By influencing the way scale and geographic variation interacted with the spatial aspects of populations (Jablonski & Sepkoski, 1996; Ricklefs & Schluter, 1993; and see Ricklefs, 2008) this complex history isolated the tropical and sub-tropical rainforest regions of the continent, and shaped levels of species richness, the spatial and temporal turnover of taxa, community phylogenetic structure patterns, and community assembly processes (Kooyman *et al.*, 2010a).

Centres of species richness and endemism have been identified for the Australian continent (Crisp *et al.*, 2001). These show that plant species richness is highest in the low relief Mediterranean climate southwest (Hopper and Gioia, 2004), next highest in the tropical northeast (that includes the rainforests of Wet Tropics and Cape York), followed by the central-eastern sub-tropical rainforest area of the Border Ranges-Nightcap, the northwest wet-dry (monsoonal) tropics (Kimberley), and the Sydney Basin. This pattern runs somewhat counter to expectations based on hypotheses of the low latitude tropics as the engine and source of global biodiversity (Jablonski *et al.*, 2006), and the latitudinal gradient in species richness as one of the most important,

consistent, and conspicuous global diversity patterns (Whittaker *et al.*, 2001; Willig *et al.*, 2003; Weiser *et al.*, 2007). As a consequence, quantifying and clarifying the effects of both latitude and altitude on the distribution and phylogenetic structure of rainforest plant diversity on the Australian continent is important for testing the evidence surrounding different biogeographic interpretations.

The time and area hypothesis suggests that tropical rainforests have more species because they are older and historically larger, allowing for more diversification (Stephens & Wiens, 2003; Wiens *et al.*, 2010). In the tropics, high speciation rates and levels of species maintenance have been hypothesized as reflecting the effects of temperature, high rainfall, relative climatic stability, and a continuous and largely invariant growing season (Givnish, 1999). These factors can influence individual survivorship, species level demographic turnover and generation times, potential mutation rates, and speed of selection (Rohde, 1992). Under those conditions, higher tree species richness should also result in a greater range of woody plant strategies and 'lifestyles', reflecting a larger potential range of morphological and character (trait) variation relative to environmental gradients (Ricklefs, 1977; Loehle, 2000; Webb, 2000; Ackerly, 2003; and see Brodribb & Feild, 2010; Lusk *et al.*, 2010).

Vegetation zonation across the altitudinal gradient and movement up and down slope, have been used as an indicator of historic climatic oscillations (Flenley, 1979; and see Greenwood & Christophel, 2005). In Australia discussion about altitudinal zonation of rainforest vegetation has mostly focused on vegetation structure that also varies in relation to latitude, climatic (temperature and rainfall), topographic, and edaphic factors (Webb, 1968; Webb & Tracey, 1981). The potentially important role of

topographic variation (relief) and altitude in influencing species richness and endemism in near coastal regions functioning as refugia in Australia was partly quantified and briefly discussed in Crisp *et al.*, (2001).

It has been suggested that species losses occurred as a result of rainforest contracting during drier-cooler climate periods associated with the glacial maxima of the Quaternary. Differential adaptation and filtering of species through time would also have occurred along shifting gradients of altitude and climate (Kershaw *et al.*, 1994; Martin, 1994; Kershaw, 1997). For example, in the Australian Wet Tropics species losses were conjectured to be mostly of taxa from cool-adapted clades, restricted to a chain of upland ($\geq$300m) rainforest patches in isolated topographic areas at higher elevations (Moritz, 2005), and referred to as the "mesotherm archipelago" (Nix, 1991). Two hypotheses are presented that potentially explain the projected patterns of distribution of cool-adapted taxa.

The cool-adapted hypothesis suggests that the surviving components of the (ancestral) aseasonal-wet biome flora were filtered by and adapted to cooler conditions during the northward migration of the continent prior to (and during) the early Miocene to Pleistocene. Survival during the Quaternary glacial maxima was facilitated by retreat to, or isolation in, cooler upland areas (>300m altitude) surrounded by warmer and drier environments.

The poor competitor hypothesis suggests that conservative ancestral clades (genera and families) were less competitive in higher productivity (tropical lowland; <300m altitude) environments that reflect climatic and edaphic factors, and physiological constraints.

Aims

Quantifying rainforest plant species and assemblage level phylogenetic structure and trait variation across local and regional scales and gradients will allow us to explore the history and distribution of functional diversity in Australian tropical and sub-tropical rainforest assemblages. Here we use a functional trait and biogeographic approach based on species composition data for 596 assemblage (plot) samples of woody species in rainforest vegetation; measures of assemblage level phylogenetic structure; species and sample level values for the ecologically important traits of seed size, leaf size, wood density and canopy height at maturity; and species values for niche breadth; to address the following hypotheses, questions and expectations.

1) Latitude is the primary determinant of regional species richness and species pool sizes. The expectation is for a co-ordinated shift in rainforest species pool sizes across latitude. 2) Functional diversity is greater in areas with larger regional species pools. 3) Assemblage values for trait and niche breadth shift along regional abiotic gradients. If that is the case, how do the relationships between trait values, niche breadth and community phylogenetic structure differ between and within latitude regions, and/or along the altitudinal gradient within regions? 4) Is the detected trait variation (if any) stronger across the whole phylogeny (NRI – net relatedness index) or for measures of more recent divergence (NTI – nearest related taxon index)? 5) Are the signs of historical biogeographic processes reflected in the differential distribution of functional traits across current-day assemblages? If so what is the relationship between trait values, community phylogenetic structure and assembly processes?

Methods

Details of phylogenetic methods, assemblage samples, environmental variables, and trait data compilations are provided in chapter 5.

Background to the study system

The currently prevailing concepts of Gondwanan biogeography position the Australian flora in relation to two major elements: 1) the original Gondwanan flora, comprising ancestral stocks derived directly (pre-separation) from the super-continent, and 2) a smaller 'intrusive' component, comprising plants that have subsequently entered Australia after separation and as the continent 'drifted' into the tropics. The Gondwanan flora is then further divided into the 'relict' component representing conservative taxa that are still mostly confined to humid habitats (aseasonal-wet biome; Crisp *et al*., 2004, 2009) similar to those presumed to have existed on the super-continent; and the 'autochthonous' component that developed post separation in response to cycles of aridity, rainforest contraction, and edaphic development that resulted in the widespread evolution of scleromorphy (e.g. Barlow, 1981; Hill, 1998). The actual extent of migration into Australia of different elements (aseasonal-wet versus seasonal-dry monsoon) of the Indo-Malesian flora remains uncertain, particularly in relation to late Miocene-Pleistocene-Holocene proximity and contact between the landmasses (Truswell *et al*., 1987; Kershaw *et al*., 2007; and see Specht and Womersley, 1979; Crisp *et al*., 1995, 2004; Rowe, 2007).

Floristic data and sampling

Estimates and comparisons of species richness, phylogenetic structure, and functional trait values of rainforests in northern tropical and sub-tropical latitude regions of eastern Australia were developed using presence-absence data for 596 community

samples; 286 from the tropics (Cape York - CY and the Wet Tropics - WT); and 310
from three areas in the sub-tropics (Nightcap-Border Ranges - NB, Dorrigo – DO, and
Washpool – WA). Species pools were based on the full sample (Queensland - Qld and
New South Wales - NSW combined), regional samples (NSW and Qld), and local
samples. Details of taxonomic structure and richness for each area, region, and for the
southern pool (not used in the analyses presented) are provided in Table 1.
Relationships between number of species, genera and families across two latitude
regions and five areas were tested and compared using regression and standardized
major axis tests (SMA; Warton *et al.*, 2006; refer to on-line Appendix S2, Tables
S2.1-S2.3, Fig. S2.1).

Topography and altitudinal range of study area

In the tropical region, Wet Tropics has high mountains and dramatic relief (0-1650m)
with large river valleys and deeply dissected terrain, while Cape York has more
constrained relief (0-500m). In the sub-tropics all areas have significant mountain
ranges (up to and > 1100m) and relatively heterogenous topographic gradients.
Consistent with Kooyman *et al.*, (2010a) we focus here on elevation (altitude) because
it is the most significant habitat gradient within each region; because it can easily be
measured on the same scale in the two regions; because temperature change is a major
component of both elevation gradients within regions and latitudinal differentiation
between regions; and because rainfall generally increases with altitude (in these
coastally aligned sites), and cloud stripping buffers vegetation from seasonal dryness.

Table 1 Attributes including (n-species) total number of species (followed by number of species with single occurrences in sample by area in brackets), genera and families in study and by area (Qld – Queensland; NSW – New South Wales; CY – Cape York; WT – Wet Tropics; NB – Nightcap-Border Ranges; DO – Dorrigo; and WA – Washpool). Other information includes number of samples (n-samples) and alpha diversity for each area (alpha-divers.) at species, genus, and family taxonomic levels. Data sources: YETI database DECC NSW; Kooyman *personal data*; Tracey, J.G. (1982) CSIRO Canberra; Briggs & Leigh (1996) CSIRO; Hyland *et al*., (2003) CSIRO; Cooper & Cooper (2004); Stanton & Fell (2005) Rainforest CRC.

AREA	n-species	Scale	Genera	Families	Samples	Alpha-divers.		
						species	genera	family
NSW	448	regional pool	229	69				
Qld	1452	regional pool	504	102				
Qld+NSW	1137	on plots	406	98	596	7 to 117	7 to 88	6 to 50
Qld+NSW	1744	full pool	519	104				
Qld+NSW	>150 shared							
CY+WT	921	on plots	369	88	286	7 to 110	7 to 80	6 to 50
CY	526 (47)	on plots	268	77	140	9 to 61	9 to 53	8 to 31
	780	local pool	355	88				
WT	661 (55)	on plots	299	83	146	7 to 110	7 to 80	6 to 50
	1316	local pool	466	101				
NB+DO+WA	396	on plots	195	61	310	12 to 117	12 to 88	10 to 40
NB	318 (20)	on plots	191	60	140	24 to 117	22 to 88	12 to 40
	371	local pool	212	63				
DO	232 (5)	on plots	152	54	127	19 to 99	17 to 79	11 to 39
	253	local pool	158	55				
WA	131 (0)	on plots	93	45	43	12 to 55	12 to 47	10 to 29
	148	local pool	104	46				
Southern Aust.	56	full pool	40	23				
Victoria	20	regional pool	17	15				
Tasmania	41	regional pool	30	18				

Phylogenetic community structure

To measure relatedness of species within samples we used *Phylocom* to calculate mean phylogenetic distance (MPD) and mean nearest phylogenetic taxon distance (MNTD). These two measures were standardised respectively into net relatedness index (NRI) and nearest taxon index (NTI) (Webb *et al*., 2002). Assemblage level values by area and region are positioned relative to a 'null or neutral community assembly value' and show random (neutral), positive (clustering) or negative (evenness) values.

Functional trait data

Four functional traits for which we had continuous measures for 1137 woody species were included in the study (leaf area, seed dry mass, wood density and maximum height at maturity; referred to as LA, SDM, WD and Hmax). These represent a subset of traits previously suggested as informative, that include (as examples) traits associated with leaf economics, wood density, xylem anatomy and physiology, maximum height, and seed size and dispersal (Westoby *et al.*, 2002; Reich *et al.*, 2003; Cornelissen *et al*., 2003; Wright *et al.*, 2004; Poorter *et al.*, 2010). Where species values for WD in the tropics were not available for a species, genus values were used.

Functional trait values: partitioning trait variation across scales

To explore the distribution and range of trait variation across gradients, and to look at trait relationships across scales we used Trait Gradient Analysis (TGA; Ackerly & Cornwell, 2007; Kooyman *et al*. 2010b). Outputs of TGA include means and range of

variance for species and assemblages, and species trait values partitioned into alpha (within) and beta (among) community components for all taxa across all the assemblages in the study.

Niche breadth

Measures of species 'niche breadth' in units of the trait(s) are an output of the trait gradient analysis (TGA) method. Potential limitations of measures of niche breadth reflect factors such as the adequacy (of coverage) of the assemblage level sample relative to species actual distributions. For example, in the case of both poorly sampled and truly rare taxa niche breadth values will be lower than actual values. Table 1 provides details of the spread and richness of the sample(s) and number of singletons by area, providing confidence that for this study this is not a significant constraint on interpretation, particularly for areas in the sub-tropics. Phylogenetic trait and niche conservatism were tested for using a model constructed in the statistical package R, the PICANTE package and Phylocom, and the K-statistic of Blomberg *et al*., (2003) relative to environmental factors ranked in importance using AIC (Akaike, 1973). Environmental variables are listed and results presented in on-line Appendix S1, Tables S1.1 and S1.2.

Results

Species richness

The size of the regional pools of woody species (trees and shrubs) increased from the sub-tropics (448 species; NSW regional pool in Table 1) to the tropics (1452 species; Queensland regional pool in Table 1). However, the relationship of species richness to latitude was not uniform along the gradient (see also Crisp *et al*., 2001). For example,

in the tropics, Wet Tropics at higher latitude had higher richness than Cape York

(lower latitude). In the southern temperate rainforests, Tasmania at higher latitudes

has higher diversity than Victoria at lower latitudes (Table 1). This suggests that a

range of factors (likely including areal extent, topographic relief and biogeographic

history) have influenced the distribution of tree diversity across the latitudinal

gradient in these rainforest habitats. Comparisons of taxonomic patterns by region and

area are provided in on-line Appendix 1 (refer to Warwick & Clarke, 1995; Enquist *et*

al., 2002).

Traits by latitude region and area

Assemblage level trait means for leaf area and seed dry mass were highest in the

tropics and for Wet Tropics, followed by Cape York (Table 2). Leaves and seeds

showed significant increase in size (means by assemblage) along the latitudinal

gradient from the sub-tropics to the tropics (ordinary least squares - OLS regression:

for leaves $r^2 = 0.617$, $P < 0.001$; and for seeds $r^2 = 0.574$, $P < 0.001$) (see Lord *et al*.,

1997). Leaf size variation based on comparisons of areas within the two latitude

regions was minor, and not significant. Seed dry mass within the sub-tropics was

highest in Nightcap-Border Ranges and lowest in Washpool. Overall, forests were a

little taller (Hmax) in the moist sub-tropics than the tropics, with only slightly higher

wood density. Within the tropics, variation in Hmax was most evident in relation to

differences between the tall moist forests of Wet Tropics and the seasonally dry

monsoon vine forests and thickets of Cape York (Table 2; Figs S2.2-2.5). Strong

seasonality of rainfall and lack of relief in some areas of Cape York results in

increased deciduousness. Compared to the (moist) evergreen types, the seasonally

drier semi-deciduous and deciduous (monsoonal) assemblages of Cape York had

shorter stature, smaller leaves and seeds, but similar wood density to the evergreen assemblages (Table S2.4). Results for wood density included some genus and family level values so interpretations need to take account of that lack of resolution for some taxa. However, removing those taxa from the analyses generally made little difference, except in the few instances where assemblage samples in the tropics were dominated by taxa with genus level values.

Trait range by latitude regions and areas

Cape York (tropics) had the widest variation in leaf area, followed by Nightcap-Border Ranges (sub-tropics). For seed dry mass Wet Tropics had the largest trait range followed by Cape York (tropics), and Nightcap-Border Ranges (sub-tropics). Washpool (sub-tropics) had the lowest values for trait range (across all traits), and this was most evident for seed size (as SDM) (Table 2). Although mean trait values shifted in some cases, shifts in trait range (Table 2) and frequency distributions (Figs S2.2-2.5) across the rainforest biome more broadly were not large.

Table 2 Synthesis of results from Trait Gradient Analysis across two latitude regions (tropical and sub-tropical); and five areas: CY – Cape York and WT – Wet Tropics (tropical); and NB – Nightcap-Border Ranges, DO – Dorrigo and WA – Washpool (sub-tropical). LA – leaf area; SDM – seed dry mass; Hmax – maximum estimated height at maturity; and WD – wood density; min., minimum; max., maximum; t_{is} species trait mean; β_{is} beta trait value; α_{is} alpha trait value; p_{js} plot mean trait value; n = number of species by area / region; n = number of plot samples. * Wood density includes some genus level values.

175

			Traits (units, transformations)			
			LA	SDM	Hmax	WD*
Region	Area	Parameter	$(cm^2, \log10)$	$(mg, \log10)$	$(m, \log10)$	$(mg\ cm^{-3})$
Tropics	CY	Species (n=526)				
		t_{is} mean	1.83	1.7	1.18	0.56
		t_{is} min-max	-1.52, 3.19	-1.02, 4.44	0, 1.78	0.21, 0.88
		β_{is} min-max	1.50, 2.11	1.24, 2.23	0.96, 1.40	0.50, 0.61
		α_{is} min-max	-3.25, 1.23	-2.86, 2.57	-1.21, 0.56	-0.36, 0.31
		Plots (n=140)				
		p_{js} mean	1.88	1.82	1.22	0.57
		p_{js} min-max	1.44, 2.13	0.98, 2.23	0.96, 1.47	0.46, 0.61
		p trait value (range)	0.79, 2.62	-0.05, 3.39	0.54, 1.62	0.33, 0.76
	WT	Species (n=661)				
		t_{is} mean	1.87	1.82	1.23	0.57
		t_{is} min-max	-1.15, 3.19	-1.02, 4.48	0.30, 1.70	0.21, 0.88
		β_{is} min-max	1.57, 2.08	1.39, 2.33	1.09, 1.42	0.53, 0.62
		α_{is} min-max	-3.01, 1.20	-3.02, 2.34	-1.03, 0.46	-0.35, 0.31
		Plots (n=146)				
		p_{js} mean	1.93	1.96	1.31	0.57
		p_{js} min-max	1.57, 2.13	1.13, 2.60	1.09, 1.54	0.50, 0.62
		p trait value (range)	0.92, 2.73	-0.37, 3.87	0.52, 1.63	0.31, 0.78
Sub-trop.		Species (n=396)				
		t_{is} mean	1.57	1.45	1.27	0.59
		t_{is} min-max	-1.40, 3.19	-1.00, 4.17	0, 1.70	0.21, 0.87
		β_{is} min-max	1.37, 1.75	1.10, 1.73	1.20, 1.41	0.55, 0.63
		α_{is} min-max	-2.87, 1.45	-2.46, 2.65	-1.31, 0.40	-0.37, 0.26
		Plots (n=310)				
		p_{js} mean	1.59	1.38	1.32	0.59
		p_{js} min-max	1.21, 1.91	0.78, 1.93	1.12, 1.48	0.50, 0.68
		p trait value (range)	-0.22, 2.38	-0.47, 3.00	0.46, 1.66	0.32, 0.84
	NB	Species (n=319)				
		t_{is} mean	1.6	1.46	1.28	0.59
		t_{is} min-max	-1.40, 3.19	-1.00, 4.17	0, 1.70	0.21, 0.87
		β_{is} min-max	1.43, 1.75	1.10, 1.73	1.20, 1.39	0.55, 0.63
		α_{is} min-max	-2.87, 1.45	-2.46, 2.65	-1.31, 0.40	-0.37, 0.26
		Plots (n=140)				
		p_{js} mean	1.64	1.48	1.33	0.59
		p_{js} min-max	1.33, 1.91	0.99, 1.93	1.11, 1.48	0.53, 0.65
		p trait value (range)	-0.01, 2.51	-0.55, 3.13	0.46, 1.67	0.28, 0.84
	DO	Species (n=234)				
		t_{is} mean	1.58	1.33	1.3	0.59
		t_{is} min-max	-1.40, 2.92	-1.00, 3.82	0, 1.70	0.21, 0.87
		β_{is} min-max	1.37, 1.72	1.10, 1.65	1.21, 1.40	0.55, 0.63
		α_{is} min-max	-2.87, 1.25	-2.46, 2.30	-1.30, 0.40	-0.37, 0.26
		Plots (n=127)				
		p_{js} mean	1.53	1.28	1.3	0.6
		p_{js} min-max	1.21, 1.79	0.78, 1.86	1.15, 1.43	0.55, 0.67
		p trait value (range)	-0.59, 2.27	-0.39, 2.63	0.46, 1.66	0.36, 0.85

WA	Species (n=131)				
	t_{is} mean	1.62	1.27	1.32	0.57
	t_{is} min-max	-1.40, 2.58	-1.00, 3.52	0, 1.65	0.21, 0.87
	β_{is} min-max	1.45, 1.73	1.16, 1.57	1.24, 1.38	0.55, 0.61
	α_{is} min-max	-2.87, 0.90	-2.46, 1.95	-1.31, 0.36	-0.37, 0.26
	Plots (n=43)				
	p_{js} mean	1.62	1.32	1.34	0.57
	p_{js} min-max	1.39, 1.76	1.08, 1.70	1.19, 1.45	0.50, 0.64
	p trait value (range)	0.18, 2.31	-0.34, 2.90	0.49, 1.65	0.31, 0.81

Means for niche breadth

Means for niche breadth were highest in Washpool for all traits (Table 3), reflecting that all species in the Washpool sample occurred more widely.

Alpha and beta trait components

Cape York (tropics) had the greatest range in alpha (within assemblage α_{is} min-max) trait values, meaning that the spread of trait values across species within site was widest there. This was true across all traits. Wet Tropics was next highest, and then Nightcap-Border Ranges (sub-tropics). For the spread of beta values (across landscape β_{is} min-max), rankings among regions were different depending on which trait was considered. Cape York had the greatest range in beta values for leaf area, followed by Wet Tropics, and then Nightcap-Border Ranges (sub-tropics). For seed dry mass Wet Tropics had the greatest range for beta values, followed by Cape York (tropics), and then Nightcap-Border Ranges (sub-tropics). Washpool (sub-tropics) had consistently lower values for both alpha (within assemblage) and beta (among assemblage) trait ranges across all traits (Table 2). Across the full sample there was a positive correlation (r = 0.23) between alpha trait values for height and seed size, with taller trees in assemblages having larger seeds. This was consistent with patterns

177

previously identified for the Australian sub-tropical rainforest (Kooyman *et al*.,
2010b; and see Butler *et al*., 2007), and globally (Eriksson *et al*., 2000; Moles *et al*.,
2005b). However, it also clearly demonstrates the wide range of variation in seed size
at a given plant height (Reich *et al*., 2003).

Traits and altitude

None of the traits showed a significant relationship to altitude. This was interesting
because leaf size dominance and margin characters (e.g. teeth) in Australian rainforest
have previously been reported as shifting along altitudinal, latitudinal, and
topographic gradients (Webb, 1968), and used for palaeobotanical interpretations of
climate (e.g. Greenwood, 2006; Royer *et al*., 2009). The difference between our
results and those reported by Webb may be a consequence of using presence-
absence rather than abundance-weighted data, and reporting assemblage level
variation rather than overall percentage variation in leaf size classes by rainforest type
(Webb 1968). In addition, the patterns reported by Webb may reflect the abundance
or dominance of particular leaf sizes in assemblages, rather than the mixture of
variation in species present with each weighted equally. For example, using plot
samples and abundance-weighted floristic data from the sub-tropical rainforest area of
this study, Royer *et al*. (2009) showed strong connections between leaf size, toothed
margins and lower slope topographic positions in an altitudinally constrained sample;
and decreasing leaf size and increasing leaf teeth in relation to increasing elevation
across a larger geographic sample (in the same area).

Table 3 Niche breadths in units of the traits from across tropical and sub-tropical latitude regions in Australia. The niche breadth for a species in relation to a trait is the spread of site means for the trait across sites where the species occurs, from Trait Gradient Analysis. Five areas: CY – Cape York and WT – Wet Tropics (tropical); and NB – Nightcap-Border Ranges, DO – Dorrigo and WA – Washpool (sub-tropical) are included. Trait units for LA – leaf area; SDM – seed dry mass; Hmax – maximum estimated height at maturity; and WD – wood density are shown. R_{is} niche breadth as means, minimum and maximum by area and (where indicated) for the full sample combined; Singletons removed from consideration for quantitative comparisons of means and min-max.

Region	Area	Niche Breadth	LA (cm^2, log10)	SDM (mg, log10)	Hmax (m, log10)	WD* (mg cm^{-3})
Tropics	CY	R_{is} mean - CY, (all)	0.31	0.59	0.22	0.06
		R_{is} min-max - CY, (all)	0.0004, 0.93	0.004, 1.78	0.005, 0.52	0.003, 0.17
		R_{is} mean - CY only	0.24	0.42	0.18	0.05
		R_{is} min-max - CY only	0.0001, 0.63	0.004, 1.25	0.00005, 0.43	0.00009, 0.15
	WT	Ris mean - WT, (all)	0.3	0.63	0.21	0.06
		Ris min-max - WT, (all)	0.0003, 0.93	0.006, 1.48	0.0005, 0.51	0.0007, 0.18
		Ris mean - WT only	0.21	0.52	0.16	0.05
		Ris min-max - WT only	0.0003, 0.52	0.006, 1.30	0.0005, 0.39	0.0002, 0.11
Sub-tropics		Ris mean - NSW, (all)	0.4	0.71	0.23	0.09
		Ris min-max - NSW, (all)	0.032, 0.934	0.36, 1.48	0.008, 0.52	0.004, 0.18
		Ris mean - NSW only	0.32	0.59	0.2	0.08
		Ris min-max - NSW only	0.25, 0.70	0.002, 1.15	0.008, 0.35	0.004, 0.18
	NB	R_{is} mean NB	0.33	0.6	0.2	0.08
		R_{is} min-max - NB	0.025, 0.70	0.002, 1.15	0.008, 0.35	0.004, 0.18
	DO	R_{is} mean DO	0.37	0.66	0.22	0.09
		R_{is} min-max - DO	0.10, 0.70	0.05, 1.15	0.07, 0.35	0.01, 0.18
	WA	R_{is} mean WA	0.41	0.75	0.25	0.11
		R_{is} min-max - WA	0.10, 0.70	0.13, 1.15	0.08, 0.35	0.03, 0.18
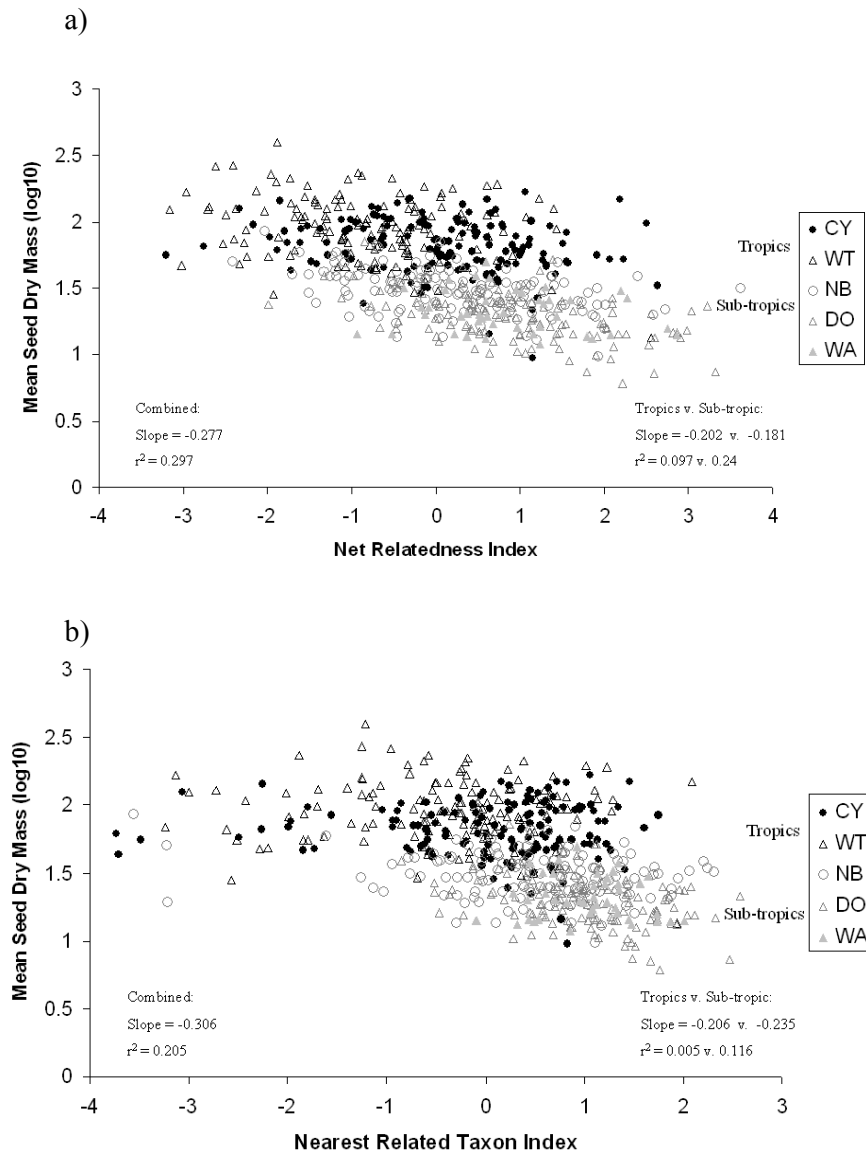
Figure 1a-b Community phylogenetic structure values as a) Net Relatedness Index

(NRI) and b) Nearest Related Taxon Index (NTI) versus seed dry mass (SDM) for 596

assemblage samples of woody taxa in Australian rainforests. For NRI and NTI on the

x-axes, positive values equate with clustering and negative with evenness. Values for

assemblage level means for SDM on the y-axes; tropics (black fill and outline shapes)

and sub-tropics (grey fill and outline shapes). Two-letter code for areas in graph

legend: CY-Cape York; WT-Wet Tropics; NB-Nightcap-Border Ranges; DO-

Dorrigo; WA-Washpool. Null (2) at full pool size.

Community phylogenetic structure, latitude, and traits

Tests of the relationship of community phylogenetic structure (NRI and NTI) to assemblage level log-scaled values for traits (using SMA, standardized major axis methods in regression, and based on the full sample) showed mostly weak relationships, with the strongest being for seed dry mass (SDM) followed by leaf area (LA). When split by latitude region the same traits showed a stronger and more significant relationship to phylogenetic community structure in the sub-tropics than tropics (Table S2.5). For seed dry mass, variance explained was greater for NRI for the full sample and in the sub-tropics, and significantly greater for NTI in the sub-tropics than tropics (Fig. 1a-b). This suggests a low overall turnover of clades within and across regions as a whole, some loss of trait range (and species) within clades in areas of the sub-tropical region that historically contracted more severely, and assemblages in those areas of the sub-tropics having more closely related taxa with similar traits (e.g. smaller seeds).

Table 4 Synthesis of results from SMA (standardised major axis tests in regression) for comparisons among groups of the relationship of NRI and NTI to log scaled values for altitude across the full sample, two latitude regions (tropics and sub-tropics), and five areas: CY – Cape York; WT – Wet Tropics; NB – Nightcap Border Ranges; DO – Dorrigo; WA – Washpool. Metric – net relatedness index (NRI), nearest related taxon index (NTI); n – number of assemblage level samples; R^2 – r-squared values; p-val. – p-values representing statistical significance (<0.05); and values for slope and intercept.

Altitude						
Metric	Group	n	R^2	p-val.	Slope	Intercept
NRI	all (596)	596	0	0.632	0.003762	-1.3
NTI	all (596)	596	0.014	0.004	0.003396	-0.9781
NRI	tropics	286	0.063	<0.001	-0.00336	0.5404
NTI	tropics	286	0.012	0.069	-0.00329	0.7045
NRI	sub-tropics	310	0	0.81	0.003983	-1.3068
NTI	sub-tropics	310	0.007	0.148	0.003057	-0.6786
NRI	CY	140	0.058	0.004	-0.01024	0.9429
NTI	CY	140	0.035	0.026	-0.01053	0.92499
NRI	WT	146	0	0.799	-0.00267	0.4198
NTI	WT	146	0.001	0.673	0.00281	-1.66254
NRI	NB	140	0.002	0.634	-0.00475	2.2816
NTI	NB	140	0	0.86	-0.00423	2.3376
NRI	DO	127	0.001	0.718	-0.0039	2.6088
NTI	DO	127	0.011	0.235	0.002514	-0.09737
NRI	WA	43	0	0.995	-0.00407	4.0273
NTI	WA	43	0	0.981	-0.00233	2.85087

Community phylogenetic structure and altitude

Altitude accounted for little of the variance in community phylogenetic structure

values (NRI and NTI) at full sample, regional sample (tropical and sub-tropical), and

within region (area) levels (Table 4). Overall, the regressions using SMA

(standardized major axis tests) showed some significance but mostly low explanatory

power for altitude in relation to NRI and NTI. Results were significant for the full

sample, for the tropics compared to sub-tropics, and for Cape York (within the

tropics) compared to the other areas (Table 4). Cape York differs physically from the

other areas in having a smaller altitudinal range (0-500m) and mostly low topographic

relief, coupled with more extreme seasonality of rainfall. Within Cape York

community phylogenetic structure values (NRI and NTI) were more neutral (than Wet

Tropics), likely reflecting stronger environmental filtering of taxa with similar traits

into seasonally drier habitats, though balanced by the continued operation of the

opposing processes that create evenness (e.g. limiting similarity). The signal of

environmental filtering includes the more recently arrived and (as yet) largely non-

diversified Indo-Malesian floristic element present at lower altitudes in the seasonally

drier deciduous and semi-deciduous monsoon forest components of the vegetation

(Crisp *et al.*, 1995).

Phylogenetic trait and niche conservatism

Phylogenetic trait and niche conservatism were tested for, confirmed, and quantified

for the rainforest vegetation using K-statistics (Blomberg *et al.*, 2003) (Table S1.2).

Consistent with the biome conservatism previously identified by Crisp *et al.*, (2009),

the results suggest low rates of change, and relative stasis over long evolutionary and

biogeographic time scales. Comparisons of methods and limitations for interpretation

are discussed in more detail in Wiens *et al.*, (2010).

Discussion

Latitude: are northern rainforests more species rich?

At continental scales our findings support the hypothesis of increasing species

richness with decreasing latitude (Willig *et al.*, 2003; Jablonski *et al.*, 2006), with

both the lowland tropics and sub-tropics more species rich (regionally and at plot

scales) than cool temperate rainforests at high latitudes (Table 1). Nevertheless, the

pattern was not consistent within latitude regions. For example, within the tropics

species pool size was significantly larger at higher latitudes in association with the

largest rainforest area (Wet Tropics).

The fossil evidence for several important Gondwanan families (Proteaceae and

Lauraceae) does not support the hypothesis of (low latitude) tropical origins for higher

diversity, or later development of diversity in the Australian tropics (Vadala &

Greenwood, 2001). The high latitude (presumably low light angle) tropical origins of

the flora, and large-scale climatically induced and latitudinally differentiated

rainforest contractions during northward continental drift appear to be the most likely

explanation for extant rainforest diversity patterns across the Australian continent.

The outcome of those processes was a reduced continental species pool, long time-

scale separation and isolation of the tropics and sub-tropics (Kooyman *et al*., 2010a),

and different sized regional and local species pools. In summary, the patterns reflect

high latitude rainforest origins, differential reduction in area across latitude regions

through time, and higher rates of extinction at temperate latitudes; rather than

diversification as the major historic processes influencing the current-day distribution

of rainforest diversity (see Mittelbach *et al*., 2007). This is supported by the signal of

trait and niche conservatism detected in this study and previously (Crisp *et al*., 2009).

We suggest that for the Australian rainforests, low latitude origin has not been the

primary factor influencing the distribution of diversity.

Altitude as a gradient: history and importance

In the Wet Tropics, a clear phylogenetic signal might have been expected from mass

retreat of ancestral cool-adapted plant species to stable upland refugia (the cool-

adapted hypothesis), or from a consistent lack of competitiveness of that component

of the flora at low elevations (the poor-competitor hypothesis). These expectations

were not supported by our data. No difference was detected in community

phylogenetic structure (NRI and NTI) values between altitude zones (0-300m and

>300m) or along the elevation gradient (as a continuous variable) in Wet Tropics, or

more generally in relation to altitude across our study areas and sites. One explanation

for these patterns is that within each latitude region species turnover along the

elevation gradient (that reflects edaphic and climatic gradients) was by more closely

related taxa (Kooyman *et al*., 2010a). This reflects a more widespread distribution of clades across the gradients, despite some species within clades having restricted distributions that are tied to specific habitat conditions or locations.

Do assemblages drawn from larger species pools have a wider range of trait variation? Do co-existing species in these assemblages have higher or lower niche breadth?

Assemblages drawn from larger species pools (in both the tropics and sub-tropics) had greater trait breadth for some traits (leaf area, seed dry mass), but not for others (wood density, maximum height). Co-existing species in these assemblages had lower mean niche breadth, reflecting higher species turnover along gradients. In contrast, species assemblages drawn from smaller pools and filtered into post-glacial re-colonization areas had lower trait range, but higher niche breadth values. These species represent a pool of more widespread taxa that have dispersal related traits (fruit type, fruit size, SDM) that allow them to cross 'barriers' and establish successfully in newly available habitat (Rossetto & Kooyman, 2005; Moles *et al*., 2005a; Rossetto *et al*., 2008, 2009). Our data demonstrate that areas that were re-colonised following more extreme historic rainforest contractions (such as Washpool) had smaller local species pool size, and lower taxonomic breadth (i.e. were more clustered relative to NRI). Assemblages drawn from the smaller species pool had reduced trait range, and were dominated by species with higher niche breadth values.

Phylogenetic structure and seed trait patterns

Community phylogenetic structure can shift in response to environmental gradients that include impacts from climate disturbances associated with biogeographic history

(Kooyman *et al*., 2010a). Seed mass is related to dispersal syndrome and potential

dispersal distance (Moles *et al*., 2005b), and forms part of the link between evolution

in spatially structured populations and ecological dynamics in spatially structured

communities (Urban *et al*., 2008). Simulations designed to assess the performance of

community phylogenetic structure tests have highlighted the need for interpretations

of the causes of community phylogenetic structure to take account of the influence of

dispersal and dispersal related traits (Kembel, 2009). Consistent with that

recommendation, we compared patterns of distribution of community phylogenetic

structure (NRI and NTI) and seed dry mass (Fig. 1a-b). We found that taxa with the

largest seeds were less common or absent from sub-tropical areas where rainforest

contraction phases had been more severe (e.g. Dorrigo and Wahspool in the sub-

tropics; Table 2), and this was evident both across the full depth of the phylogeny

(NRI) and in relation to more recent divergences (NTI). The signal was most evident

in relation to NTI in Washpool where the rainforest tree flora is dominated by taxa

with smaller seeds that are more widely dispersed. In contrast, in the more stable

tropical and sub-tropical areas larger seeded taxa persisted, and likely expanded their

range when conditions improved. Quantifying the relationship of seed mass to

community phylogenetic structure across scales helped define the influence of

biogeographic history and climate impacts on functional trait and niche breadth values

that shape current day community assembly.

Conclusions

The Australian rainforest flora had its origins in higher latitudes at a time when global

climates were more similar to current tropical and sub-tropical climates (see for

example, Ziegler *et al*., 2003). The persistence of higher diversity in the Australian

tropics and sub-tropics is generally regarded as an artefact of the continent drifting northward into the tropical belt during (and including) the time when climatic oscillations (and rainforest contractions) were occurring. The retention of areas of suitable habitat in the northern Australian tropics and central-eastern sub-tropics allowed ancestral rainforest lineages to persist through the Quaternary oscillations. With contraction and loss of diversity subsequently greatest at higher latitudes and in locations with less relief. The tropical and sub-tropical uplands and some areas at lower elevations most likely acted as regional refugia because they included a greater range of altitudinal, topographic and edaphic variation, had higher and less seasonal rainfall patterns, and were protected from fire/disturbance during drier climate periods (Hopkins *et al*., 1993, 1996). Repeated rainforest contractions likely resulted in assemblages in the uplands and other protected areas differentiating as a consequence of isolation (e.g. on mountains separated by dry eucalypt forest or deep gorges), drift and vicariance. Current day distribution and genetic (Rossetto *et al*., 2008, 2009) patterns reflect the results of that history, subsequent re-expansion and environmental filtering (including in relation to rainfall and edaphic gradients), and interactions between co-existing species (likely including competition and limiting similarity). Interestingly we found no evidence for a direct link between temperature and the spread of functional (trait) and taxonomic diversities.

As species pools were reduced, trait range and variation were constrained for some traits, and niche breadth increased in locations where contractions were greatest. This highlights the role of seed size in relation to recolonization of isolated areas by more widely and easily dispersed taxa. At the other end of the spectrum, the importance of the Wet Tropics and the sub-tropical rainforests of Nightcap-Border Ranges as stable

phylogenetic (Whiffin and Hyland 1986), functional, and moist forest refugia were confirmed by our results. With both areas retaining many species from ancestral rainforest lineages across a range of temporally conserved and more recently re-expanded habitats.

References

Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Science*, **164**(3), 165-184.

Ackerly, D.D. and Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among- community components. *Ecology Letters*, **10**, 135-145.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: *2nd International Symposium on Information Theory* (ed. by B.N. Petrov and F. Czáki), pp. 267-281. Akademiai Kiadó, Budapest.

Barlow, B.A. (1981) The Australian flora: its origin and evolution. *Flora of Australia*. Australian, pp. 25-75. Government Publishing Service, Canberra.

Barlow, B.A. and Hyland , B.P.M. (1988) The origins of the flora of Australia's wet tropics. *Proceedings of the Ecological Society of Australia*, **15**, 1-17.

Blomberg, S.P., Garland, T. and Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* **57**, 717-745.

Bowler, J.M., Hope, G.S., Jennings, J.N., Singh, G. and Walker, D. (1976) Late Quaternary climates of Australia and New Guinea. *Quaternary Research*, **6**, 359-394.

Brodribb, T.J. and Feild, T.S. (2010) Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters* **13**, 175-183.

Butler, D.W., Green, R.J., Lamb, D., McDonald, W.J.F. and Forster, P.I. (2007) Biogeography of seed dispersal syndromes, life-forms and seed sizes among woody rain-forest plants in Australia's sub-tropics. *Journal of Biogeography* **34**, 1736-1750.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. and Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693-715.

Christophel, D.C. and Greenwood, D.R. (1989) Changes in climate and vegetation in Australia during the Tertiary. *Review of Palaeobotany and Palynology*, **58**, 95-109.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Crisp, M.D., Linder, H.P. and Weston, P.H. (1995) Cladistic biogeography of plants in Australia and New Guinea: congruent pattern reveals two endemic tropical tracks. *Systematic Biology*, **44**, 457-473.

Crisp, M.D., Laffan, S., Linder, H.P. and Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183-198.

Crisp, M., Cook, L. and Steane, D. (2004) Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philosophical Transactions of the Royal Society London B*, **359**, 1551-1571.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.A., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P. and Linder, H.P. (2009) Phylogenetic biome conservatism on a global scale. *Nature*, **458**, 754-756.

Enquist, B.J., Haskell, J.P. and Tiffney, B.H. (2002) General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature*, **419**, 610-613.

Eriksson, O., Friis, E.M. and Lofgren, P. (2000) Seed size, fruit size, and dispersal systems in angiosperms from the early Cretaceous to the late Tertiary. *The American Naturalist*, **156**(1), 47-58.

Flenley, J.R. (1979) The Late Quaternary vegetation history of the equatorial mountains. *Progress in Physical Geography*, **3**, 488-509.

Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology*, **87**, 193-210.

Greenwood, D.R. and Christophel, D.C. (2005) The origins and tertiary history of Australian "tropical" rainforests. *Tropical Rainforests, Past, Present, and Future* (ed. by E. Bermingham, C.W. Dick, and C. Moritz), pp. 336-373. Chicago University Press, Chicago.

Greenwood, D.R. (2006) Leaf form and the reconstruction of past climates. *New Phytologist*, **166**, 355-357.

Herbert, D.A. (1967) Ecological segregation and Australian phytogeographic elements. *Proceedings of the Royal Society of Queensland*, **78**, 101-111.

Hill, R.S. (1998) Fossil evidence for the onset of xeromporphy and scleromporphy in the Australian Proteaceae. *Australian Systematic Botany*, **11**, 391-400.

Hopkins, M.S., Ash, J., Graham, A.W., Head, J. and Hewett, R.K. (1993) Charcoal evidence of the spatial extent of *Eucalyptus* woodland expansions and rainforest

contractions in north Queensland during the late Pleistocene. *Journal of Biogeography,* **20**, 357-372.

Hopkins, M.S., Head, J., Ash, J., Hewett, R.K. and Graham, A.W. (1996) Evidence of a Holocene and continuing recent expansion of lowland rainforest in humid tropical North Queensland. *Journal of Biogeography*, **23**, 737-745.

Hopper, S.D. and Gioia, P. (2004) The southwest Australian floristic region: evolution and conservation of global hot spot of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **35**, 623-650.

Humboldt, F.H.A. von (1817) De Distributione Geographica Plantarum Secundum Coeli Temperiem et Altitudinem Montium Prolegomena. Paris.

Jablonski, D. & Sepkoski, J.J. Jr. (1996) Paleobiology, community ecology, and scales of ecological pattern. *Ecology*, **77**(5), 1367-1378.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102-106.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters*, **12**, 949-960.

Kershaw, A.P. (1997) A bioclimatic analysis of early to middle Miocene brown coal floras, Latrobe Valley, south-eastern Australia. *Australian Journal of Botany* **45**, 373-387.

Kershaw, A.P., Martin, H.A. and McEwen Mason, J. (1994) The Neogene: a period of transition. *Australian vegetation history: Cretaceous to Recent* (ed. by R. Hill), pp. 435-462. Cambridge University Press, Cambridge.

Kershaw, A.P., Bretherton, S.C. and van der Kaars, S. (2007) A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 23-45.

Kooyman, R.M., Rossetto, M., Cornwell, W. and Westoby, M. (*accepted* 2010a) Phylogenetic tests of community assembly across regional to continental scales in tropical and sub-tropical rainforests. *Global Ecology and Biogeography* DOI:

Kooyman, R.M., Cornwell, W. and Westoby, M. (2010b) Plant functional traits in Australian sub-tropical rain forest: partitioning within community from cross-landscape variation. *Journal of Ecology*, **98**, 517-525.

Liddle, D.T., Russell-Smith, J., Brock. J., Leach, G.J. and Connors, G.T. (1994) Atlas of the Rainforest Plants of the Northern Territory. Australian Biological Resources Study, Canberra.

Loehle, C. (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *American Naturalist*, **156**, 14-33.

Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D. and Westoby, M. (1997) Larger seeds in tropical floras: consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*, **24**, 205-211.

Lusk, C.H., Sendall, K. and Kooyman R.M. (*accepted* 2010) Latitude, solar elevation angles and gap-regenerating rainforest pioneers. *Journal of Ecology*

Martin, H.A. (1994) Australian Tertiary phytogeography: evidence from palynology. *Australian vegetation history: Cretaceous to Recent* (ed. by R. Hill) pp. 104-142. Cambridge University Press, Cambridge.

McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**(4), 178-185.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H. A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. and Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315-331.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B., Pitman, A.J. and Westoby, M. (2005a) Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences*, **102**(30), 10540-10544.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. and Westoby, M. (2005b) A brief history of seed size. *Science*, **307**, 576-580.

Moritz, C. (2005) Overview: rainforest history and dynamics in the Australian Wet Tropics. In: *Tropical Rainforests, Past, Present, and Future*, (ed. by E. Bermingham, C.W. Dick, and C. Moritz), pp. 313-321. Chicago University Press, Chicago.

Moss, P.T. and Kershaw, A.P. (2007) A late Quaternary marine palynological record (oxygen isotope stages 1 to 7) for the humid tropics of northeastern Australia based on ODP Site 820 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 4-22.

Nix, H.A. (1991) An environmental analysis of Australian rainforests. *Australian National Rainforests Study, vol. 2 Flora and fauna of the rainforests*, (ed. by G.L. Werren and A.K. Kershaw), pp. 1-26. Australian Government Publishing Service, Canberra.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., licona, J-C., Peńa-Claros, M., Sterck, F., Villegas, Z. and Sass-Klassen, U. (2010) The importance of wood traits

and hydraulic conductance for the performance and life history strategies of 42 rainforest species. *New Phytologist*, **185**, 481-492.

R Development Core Team. (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. and Walters, M.B. (2003) The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Science*, **164**(3), 143-164.

Ricklefs, R.E. (1977) Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist*, **111**, 376–381.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *The American Naturalist*, **172**(6), 741-750.

Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514-527.

Rossetto, M. and Kooyman, R.M. (2005). The tension between dispersal and persistence regulates the current distribution of rare palaeo-endemic rainforest flora: a case study. *Journal of Ecology*, **93**, 906-917.

Rossetto, M., Kooyman, R.M., Sherwin, W. and Jones, R. (2008) Dispersal limitations rather than bottlenecks or habitat specificity can restrict the distribution of rare and endemic rainforest trees. *American Journal of Botany*, **95**(3), 321-329.

Rossetto, M., Crayn, D., Ford, A., Mellick, R. and Sommerville, K. (2009) The influence of environment and life-history traits on the distribution of genes and

individuals: a comparative study of 11 rainforest trees. *Molecular Ecology*, 18, 1422-1438.

Rowe, C. (2007) A palynological investigation of Holocene vegetation change in Torres Strait, seasonal tropics of northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 83-103.

Royer, D.L., Kooyman, R.M., Little, S.A. and Wilf, P. (2009) Ecology of leaf teeth: a multi-site analysis from an Australian sub-tropical rainforest. *American Journal of Botany*, **96**(4), 1-14.

Specht, R.L. and Womersley, J.S. (1979) Heathlands and related shrublands of Malesia (with particular reference to Borneo and New Guinea). In *Ecosystems of the World*, vol. 9a, *Heathlands and related shrublands. Descriptive studies* (ed. by R.L. Specht) pp. 321-338. Elsevier, Amsterdam.

Stephens, J.R. and Wiens, J.J. (2003) Explaining species richness from continents to communities: the time for speciation effect in emydid turtles. *American Naturalist*, **161**, 112-128.

Truswell, E.M., Kershaw, A.P. and Sluiter, I.R. (1987) The Australian-southeast Asian connection: evidence from the palaeobotanical record. *Biogeographical Evolution of the Malay Archipelago* (ed. by T.C. Whitmore), pp. 32-49. Clarendon Press, Oxford.

Urban, M.C., Leibold, M.A., Amarasekare, P., de Meester, L., Gomulkiewicz, R., Hochberg, M.E., Klausmeier, N.L., de Mazancourt, C., Norberg, J., Pantel, J.H., Strauss, S.Y., Vellend, M. and Wade, M.J. (2008) The evolutionary ecology of metacommunities. *Trends in Ecology and Evolution* 23(6): 311-317.

Vadala, A.J. and Greenwood, D.R. (2001) Australian Paleogene vegetation and environments: evidence for palaeo- Gondwanic elements in the fossil records of

Lauraceae and Proteaceae. *Faunal and floral migrations and evolution in S.E. Asia-Australasia*, (ed. by I. Metcalfe, J.M.B. Smith, and I. Davidson), pp. 196-221. Swets & Zeitlinger Publishers, Lisse.

Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M. (2006) Bivariate line fitting methods for allometry. *Biological Reviews*, **81**(2), 259-291.

Warwick, R.M. and Clarke, K.R. (1995) New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series*, **129**, 301-305.

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145-155.

Webb, C.O., Ackerly, D.D., Peek, M.A. and Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475-505.

Webb, L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology*, **49**, 296-311.

Webb, L.J. and Tracey, J.G. (1981) Australian rainforests: patterns and change. *Ecological Biogeography of Australia* (ed. by A. Keast), pp. 605-694. The Hague: W.Junk.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1984). A floristic framework of Australian Rainforests. *Australian Journal of Ecology*, **9**, 169-198.

Webb, L.J., Tracey, J.G. and Jessup, L.W. (1986) Recent evidence for autochthony of Australian tropical and subtropical rainforest floristic elements. *Telopea*, **2**, 575-589.

Weiser, M.D., Enquist, B.J., Boyle, B., Killeen, T.J., Jørgensen, P.M., Fonseca, G., Jennings, M.D., Kerkhoff, A.J., Lacher Jr., T.E., Monteagudo, A., Núñez Vargas, M.P., Phillips, O.L., Swenson, N.G. and Vásquez Martínez, R. (2007) Latitudinal

patterns of range size and species richness of New World woody plants. *Global Ecology and Biogeography*, **16**, 679-688.

Westoby, M, Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125-159.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**(5), 261-268.

Westoby, M. (2006) Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology*, **87**, S163-S166.

Whiffin, T. and Hyland, B.P.M. (1986) Taxonomic and biogeographic evidence on the relationships of Australian rainforest plants. *Telopea*, **2**, 591-610.

Whittaker, R.J., Willis, K.J. and Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J-A., Harrison, S.P., Hawkings, B.A., Holt, R.D., McCain, C.M. and Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310-1324.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology and Systematics*, **34**, 273-309.

Wright, I.J., Westoby, M., Reich, P.B., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lusk, C., Midgley, J.J., Navas, M-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior,

L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821-827.

Ziegler, A.M., Eshel, G., Rees, P.M., Rothfus, T.A., Rowley, D.B. and Sunderlin, D. (2003) Tracing the tropics across land and sea: Permian to present. *Lethaia*, **36**, 227-254.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Climate and environmental variables used for model selection. Tables S1.1 (environmental variables), and S1.2 (K-statistics).

Appendix S2 Taxonomic and trait patterns including additional statistical tests (SMA) (Fig. S2.1; Tables S2.1-S.2.3); TGA results for Cape York deciduous, semi-deciduous and evergreen components (Table S2.4); SMA tests of the relationships between measures of community phylogenetic structure (NRI and NTI) and four traits (Table S2.5); and trait frequency graphs for four traits, five areas and two regions (Figs S2.2-S2.5).

CHAPTER 7

THESIS CONCLUSIONS

7.1 Aim and focus

The aim of the study was to quantify the influence of species traits, functional and phylogenetic diversity, history, scale, and environmental gradients on community assembly in tropical and sub-tropical rainforests. The focus was on how plant functional traits that reflect plant strategies in assemblages shift along environmental gradients, and how traits and trait relationships have shaped Australian tropical and sub-tropical rainforest community assembly across space and in time.

The use of quantified data for species traits, updated phylogenies expressed as trees rather than categories, a large number of assemblage samples that included the tropics and sub-tropics, good environmental surfaces (climate data), and the convergence of new analytical methods, provided the means to investigate Australian rainforest ecology and biogeography from a quantitative and functional perspective.

7.2 Synthesis

The study examined the distribution of trait values at different scales across tropical and sub-tropical latitude regions and within areas and assemblages arrayed along environmental gradients. In the introduction to the thesis, hypotheses were presented for each component (and chapter) of the study. These were framed to test ideas about the links between functional diversity, evolutionary and biogeographic history, and community assembly processes relative to species ecological strategies. In the context of those hypotheses and the thesis structure outlined in the introduction, the study provided the following insights into rainforest community ecology and assembly on the basis of species traits.

7.2.1 Species growth strategies and community assembly

The allometric relationships of height to diameter for sub-tropical rainforest saplings did not reflect direct trade-offs between wood density and diameter. If density and diameter had traded off strongly, the stem mass required to achieve 5m in height might have been rather similar across species, though achieved in different ways. In the absence of a clear trade off, some species achieved the height of 5 m almost 3-fold more cheaply than others. Presumably these more cheaply constructed saplings were at higher risk of damage or early mortality, otherwise cheaper stems would consistently have been advantaged in the race for light. Nevertheless, no correlation was evident between the costs of height gain for saplings in the understorey and traits such as ultimate stature at maturity, leaf size, seed size, and shade tolerance, that might reflect species regenerative and ecological strategies.

The provisional interpretation of the decoupling between wood density and stem diameter was that wider diameters might have a stronger effect on preventing main-stem breakage in the shorter term, and higher wood density might have a stronger effect in sustaining stem strength over time.

7.2.2 Functional traits, abiotic gradients and community assembly

Trait variation was partitioned into alpha (within assemblage) and beta (among assemblage) components. This in turn allowed correlations between different traits to be traced to within-assemblage versus across-assemblage components. The focus was on the traits (leaf area, seed size, wood density, and height at maturity) of freestanding woody taxa in sub-tropical rainforest assemblages. Variation of traits was wider among coexisting species (alpha component) in assemblages than across the range of

assemblages in which species occurred (beta component); however, correlations between traits were stronger in the beta component. The different correlation structures for alpha and beta components of traits reflected community assembly processes at different scales. Within-site assembly processes did not create strong linkages among traits, but the filtering of species into different sites across the landscape, created relatively strong trait correlations. Within-species variation in trait values (maximum height) in rainforest assemblages reflected species performance along abiotic gradients. Plant responses that include architectural plasticity as change in stem height, size, and numbers can shift the relative ranking of species in assemblages. It seems likely that other traits such as SLA (specific leaf area) that are know to reflect plant performance under different circumstances (Fonseca *et al*., 2000; Wright et al., 2004; Díaz *et al*., 2004) would also shift along the same gradients.

7.2.3 Phylogenetic community structure, history, and scale

Phylogenetic divergences between latitude regions (tropics and sub-tropics) were found to be older than divergences along gradients within regions. In addition, co-occurring species tended to be more phylogenetically clustered in forests subjected to more severe historic contractions compared with the signal for forests that had been more stable. Signals of phylogenetic evenness have previously been described as rare or absent in studies of tropical forest, whereas phylogenetic clustering has been described as relatively common (Kraft *et al*., 2009). Since both evenness and clustering reflect a net outcome from opposing processes (limiting similarity and filtering), it is not possible to tell whether the previously reported rarity of signal means that the processes are weak, or rather that they are strong but often cancel each other out. In this study, quantifying community phylogenetic structure measures

provided insights into mechanisms underlying community assembly that included both historic and current-day factors. However, shifts in community phylogenetic structure values were not significantly co-ordinated with shifts in trait values, reflecting the need for careful selection of traits that link to key ecological processes.

7.2.4 Evolution, functional biogeography and diversity of Australian rainforests

Trait variation across species was greater and niche breadth within species narrower in larger areas that had historically been topographically buffered from climate-based events, impacts, and change. In areas with greater levels of historic climate-induced impacts the pattern was reversed, with lower values for trait breadth and higher values for niche breadth. Lower trait breadth reflected a reduced range of functional diversity, and higher niche breadth reflected species that were distributed more widely across sites, where the spread of occupied sites was measured in units of site means for the trait. Quantifying the relationship of traits to measures of community phylogenetic structure provided a measure of the importance of seed size and dispersal for ecological and evolutionary interpretations of community assembly (Kembel 2009) in the different regions and areas. As expected (Ricklefs 1977; 2008; Ricklefs and Schluter 1993), historical differences between regions in terms of climatic stability and relief had long-lasting effects on the size and diversity of regional species pools, presumably by influencing speciation and extinction, the spread of trait variation in the pool(s), and species distributions. In summary, evolutionary and biogeographic history interacting with climatic, edaphic and topographic gradients influenced the distribution of species, species richness, and functional diversity. Historic and recent rainforest contraction and re-expansion resulted in woody plant assemblages in recolonised areas having a reduced trait range

and being dominated by assemblages of species with greater niche breadth that are good dispersers.

7.3 Quantitative measures

Physiognomic features and traits including leaf size (as ranked categories), plant stature (as life form categories), canopy structure (texture, depth, and layers), and stem features (including bark textures and incidence of buttresses) have previously been used to assess assemblage level variation in rainforest vegetation (Webb 1959, 1968, 1978; Webb *et al*., 1976). These previous quantifications were limited by the categorical and sometimes arbitrary nature of the ranked data (discussed in Adam 1992). Variation within traits, the strength of correlations between traits, and the extent of orthogonality among traits were not assessed. Other methods used previously to investigate the Australian rainforest vegetation were based on the grouping (classification) of assemblages based on floristic similarity (or dissimilarity) and the partitioning of the subsequent dendrogram into eco-floristic regions (e.g. Webb *et al*., 1984). Eco-floristic regions were aligned with the plant thermal response groups described in Nix (1982).

In the current study there was no intention to classify the vegetation per se. By using species level values for specific traits, and phylogenetic trees rather than taxonomic categories, species functional attributes and phylogenetic relationships were quantified in relation to community assembly, and positioned in relation to shifts in scale and abiotic gradients. Shifts in scale included temporal and spatial components, and described both evolutionary and biogeographic history. Abiotic gradients included continuous measures for altitude and latitude, and modelled climate surfaces (chapter 6 appendices) for assemblage sample sites.

7.4 Implications for elucidating community assembly

Plant outcomes such as growth performance and demography are linked to species architectures, ecological strategies, and functional traits in several ways. By virtue of their architecture and tissue properties, rainforest trees control ecosystem processes and define the habitat available for other taxa, making them a high priority for research aimed at understanding ecosystem functioning at a site. In relation to traits, quantifying the trait values expressed at a site and coupling these to knowledge of trait costs and benefits promises to provide an improved understanding of how vegetation properties and species ecological strategies change along key gradients of physical geography (e.g. Westoby and Wright 2006). In addition, measuring species and community phylogenetic structure in assemblages arrayed along 'real world' gradients can provide insights into how multiple ecological processes and environmental gradients affect community structuring, and the shifting abundance of species and ecological strategies in communities in space and time.

The trait-based approaches to rainforest community ecology used in this study linked the ecological strategies of plants to community assembly theory by quantifying functional diversity and community phylogenetic structure, and positioning species and assemblage level values for these relative to evolutionary and biogeographic history. Quantifying the various components of community assembly across spatial and temporal scales helped elucidate the influence of a range of variables. These included the evolutionary origins and relatedness of species, historic biogeography, latitude, altitude, topographic relief, edaphic variation, and climate variables such as temperature and rainfall on current-day species assemblage patterns. This provided

insights into the spread of functional trait values (that reflect how plants make a living) along environmental gradients at various scales, and the relative contribution of both historic and current-day processes to rainforest community functioning and assembly.

7.5 Future directions

Several areas of this research deserve further exploration, beginning with the inclusion of traits that reflect performance currencies (e.g. photosynthetic rates as units of species energy, or the nutrients, such as nitrogen, required to acquire, allocate, and maintain biomass), the 'leaf economics spectrum' (Wright *et al*., 2004), plant ecological strategies in relation to light (e.g. Lusk *et al*., 2010a,b), and stem traits. Stem traits reflect the connection between soil, water, and leaf hydraulics. Whole plant carbon budgets are linked to leaf vein density and architecture, and capacity to assimilate CO_2 (e.g. Brodribb and Feild 2010). A related question has to do with interactions between co-occurring species physiological rates, and how competitive advantage and dominance can shift under differing environmental or climatic conditions (McGill *et al*., 2006). The outcomes of those interactions help shape relationships among co-occurring species at smaller scales (reflecting the interaction milieu), and potentially define the distribution of ecological strategies at larger scales. An interesting question in that regard relates to whether interactions between the northern Australian and Indo-Malesian rainforest flora have been constrained by barriers of physical geography and dispersal limitation or alternatively by physiological barriers reflecting species competitive ability under different conditions.

In relation to scale, the inclusion of the high latitude temperate rainforests and the testing of patterns of phylogenetic structure and trait values for those forests could provide additional insights into Australian rainforest biogeography. For example, Tasmania has a relatively large area of rainforest and a small species pool with a relatively high proportion of Gymnosperms relative to Angiosperms. Assemblages in refugial areas might show either clustering (closely related taxa dominate assemblages) or evenness (taxa within assemblages phylogenetically overdispersed). Similar effects could be expected for Patagonia in South America where, for example, species from Nothofagaceae and Araucariaceae can dominate some areas (potentially resulting in clustering). The dry vine forests of Central Queensland and the monsoon forests of the tropical north and northwest are other areas of interest that could be added. Such lines of research could help clarify aspects of global distribution patterns related to latitudinal climate zones, and the spread of plant ecological strategies under differing circumstances. Use of abundance-weighted data could also improve community ecology analyses based on measures of community phylogenetic structure and functional trait variation by linking to species performance (abundance) under different conditions.

Palaeoecological interpretations of the Gondwanan fossil record in relation to temporal climate shifts and events, and environmental gradients, have the potential to inform current-day interpretations of community phylogenetic structure and assembly processes. The reverse is also true (Royer *et al*., 2009; Wilf *et al*., 2009). Constraints on linking neo- and palaeo- ecology include uncertainties associated with defining the spatial extent and topographic arrangement of the source floras contributing to fossil assemblages, and in relating species from fossil assemblages to present-day floras.

For example, leaves can accumulate from multiple biomes or community types into a single fossil bed, complicating and potentially distorting interpretations. Another example would be if abundant tree taxa from a past forest community were absent from the fossil assemblage due to say some aspect of leaf morphology that led to poor preservation. Then the fossil record might over represent shade tolerant understorey trees and shrubs, and the fossil leaf signals for the relationship to climate or other variables could be significantly misinterpreted.

These are critical factors that potentially influence phylogenetic and trait signals through the nature and type of taphonomic filters at work in different landscapes. Quantifying the variation in current-day floristic and trait patterns across sites in relation to statistically modelled taphonomic filters could substantially improve and provide tests of fossil flora trait patterns, phylogenetic structures, and interpretations.

The emerging need to integrate palaeo- and neo- ecology to test a range of factors related to community assembly requires new data compilations drawn from across the fossil record and new models and methods to address key questions. For example, do we see temporally and spatially coherent and interpretable shifts in associations, traits, functional ecology, major environments and even biomes in the fossil record? Can we link the functional role and attributes of taxa seen in fossil assemblages to the occurrence of near relatives (ecologically equivalent or even the same taxa) in living habitats, and what does this tell us about the past? How will dating key fossils improve the phylogenies used for community phylogenetic structure analysis? Will this alter the overall phylogenetic signal, or just provide greater confidence for interpretation? Can we confirm trait and niche conservatism? Is the idea of persistence

of associations in Gondwanan forest communities real, or simply imagined on the basis of accumulated impressions?

Another key area of interest is the distribution of traits within and between distinct communities. Trait range was quantified in this study in relation to the rainforest biome. However, questions remain in regard to the potentially different ways in which traits may be dispersed within different communities (e.g. Weiher *et al.*, 1998; McGill *et al.*, 2006). For example, both phylogenetic community structure and functional trait measures could provide greater insight into the interactions between rainforest and sclerophyll forest communities and help clarify what has been described in Australia as "the problem of mixed forests" (Adam 1992). These are mixtures of eucalypt forest with rainforest. The issue about mixed forest has historically mostly been one of commercial logging management, though the discussion has extended into the ecological realm (Dale *et al.*, 1980; Smith and Guyer 1983), and earlier ecological authors included eucalypt dominated wet sclerophyll forest as rain forest (Schimper 1903; Richards 1952). From a trait perspective the potentially interesting ecological question is the extent to which (along the continuum between rainforest and eucalypt forest) there are recognisable transition points or thresholds that are closer to one community than the other, and for which traits under what conditions. Recent fossil evidence suggests an evolutionary origin for *Eucalyptus* in the tropical rainforests to the north of Australia, and a broad Gondwanan distribution including Patagonia in the past (Peter Wilf pers. com.). Suggesting no clear dichotomy between eucalypt forests and rainforests.

7.6 Benefits and limitations of the trait-based approach to rainforest ecology

The approach through functional traits (seed weight being closely related to dispersal), when combined with information about evolutionary and biogeographic history and the quantification of community phylogenetic structure, helped to elucidate community assembly processes in these Australian tropical and sub-tropical rainforests. However, all interpretation so far has been based on realized niches rather than on fundamental niches. It remains to be answered which traits were most important in deciding competitive outcomes among co-occurring taxa, and in shaping the translation from fundamental to realized niche.

The trait-based approach to rainforest ecology provided an improved understanding of these species rich rainforest communities, especially in relation to comparisons across a large range of species, environmental gradients and physical geography. The inclusion of traits that link to plant physiology and allocation processes is complementary to single species or pairwise comparisons based on population demography, and signals significant progress in rainforest community ecology. McGill *et al.* (2006) pointed to the potential for a more predictive ecology, and for a synthesis across scales between community and ecosystem ecology. For prediction, they argued that it is more fundamental in ecology to be able to predict what traits species have at a site (i.e. what sort of species are likely to be present under certain conditions) than how many species are likely to be present. For synthesis between community and ecosystem ecology, they argued that morphological and physiological traits link to performance currencies. Through traits, assemblage level variation in communities arrayed along abiotic gradients could potentially be translated into an

ecosystem-based perspective. When linked to the evolutionary history that has led up to present-day ecology (Westoby 2006) those constitute exciting prospects.

7.7 References

Adam, P. (1992) *Australian Rainforests*. Oxford University Press, Oxford. UK.

Brodribb, T.J. and Feild, T.S. (2010) Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters* 13: 175-183.

Dale, M., Kershaw, P., Kikkawa, J., Parsons, P. and Webb, L. (1980) Resolution by the Ecological Society of Australia on Australian rainforest conservation. *Bulletin of the Ecological Society of Australia Inc*. 10(3): 6-7.

Díaz, S.J., Hodgson, J.G., Thompson, K., Cabido, M.J., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Prunes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk,V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. and Zak, M.R.J. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295-304.

Kembel, S.W. (2009) Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12: 949-960.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. and Ackerly, D.D. (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* 170(2): 271-283.

Lusk, C.H., Onoda, Y., Kooyman, R.M. and Gutie´rrez-Giro´n, A. (2010a) Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. *New Phytologist* doi: 10.1111/j.1469-8137.2010.03202.x

Lusk, C.H., Sendall, K. and Kooyman, R.M. (2010b) Latitude, solar elevation angles and gap-regenerating rainforest pioneers. *Journal of Ecology* (accepted)

McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21: 178-185.

Nix, H.A. (1982) Environmental determinants of biogeography and evolution in Terra Australis. *Evolution of the flora and fauna of arid Australia*, (eds. W.R. Barker and P.J.M. Greenslade), pp. 47-66. Peacock Publications, Frewville, South Australia.

Nix, H.A. (1991) An environmental analysis of Australian rainforests. Pp. 1-26 in G.L. Werren and A.K. Kershaw (eds.) *Australian national Rainforests Study, vol. 2 Flora and fauna of the rainforests*. Australian Government Publishing Service, Canberra.

Richards, P.W. (1952) *The tropical rain forest*. Cambridge University Press, Cambridge.

Ricklefs, R.E. (1977) Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist* 111: 376–381.

Ricklefs, R.E. (2008) Disintegration of the ecological community. *The American Naturalist* 172(6): 741-750.

Ricklefs, R.E. and Schluter, D. (1993) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Royer, D.L., Kooyman, R.M., Little, S.A. and Wilf, P. (2009) Ecology of leaf teeth: a multi-site analysis from an Australian sub-tropical rainforest. *American Journal of Botany* 96(4): 1-14.

Schimper, A.F.W. (1903) *Plant-geography upon a physiological basis*. Clarendon Press, Oxford.

Smith, J.M.B. and Guyer, I.J. (1983) Rainforest-eucalypt forest interactions and the relevance of the biological nomad concept. *Australian Journal of Ecology* 8: 55-61.

Webb, L.J. (1959) A physiognomic classification of Australian rain forests. *Journal of Ecology* 47: 551-570.

Webb, L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296-311.

Webb, L.J. (1978) A General Classification of Australian Rainforests. *Australian Plants* 9, 349-363.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1976) The value of structural features in tropical forest typology. *Australian Journal of Ecology* 1: 3-28.

Webb, L.J., Tracey, J.G. and Williams, W.T. (1984). A floristic framework of Australian Rainforests. *Australian Journal of Ecology* 9: 169-198.

Weiher, E., Clarke, E.D.P. and Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81: 309-322.

Wilf, P., Little, S.A., Iglesias, A., del Carmen Zamaloa, M., Gandolfo, M.A., Cúneo, R. and Johnson, K.R. (2009) Papuacedrus (Cuppressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. *American Journal of Botany* 96(11): 2031-2047.

Westoby, M. (2006) Phylogenetic ecology at world scale, a new fusion between ecology and evolution. *Ecology* 87: S163-S166.

Westoby, M. and Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21(5): 261-268.

Wright, I.J., Westoby, M., Reich, P.B., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lusk, C., Midgley, J.J., Navas, M-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature* 428, 821-827.

APPENDIX 1

Supplementary Materials for:

CHAPTER 2

Costs of height gain in rainforest saplings: main stem scaling, functional traits and strategy variation across 75 species

Robert Kooyman[1] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, Sydney, NSW 2109*

Australia

Supplemental information

Appendix S1. Table S1 Summary results from SMA (standardized major axis) regression of the relationship between log10 DBH (cm) and log10 height (m) for 75 species grouped by shade tolerance at the sapling stage (1 - <10cm DBH) in 20 permanent plots (8-ha in total) in northern New South Wales, Australia. Tests of the null hypothesis (H_0) of slope (β) = 1.32 are included. 95% CI (confidence intervals) are provided for slope values. YgrandX – diameter (Y) at the Grand Mean of (X) height; N - number of stems; R^2 – from SMA; *, $P < 0.05$; **, $P < 0.005$; ***, $P < 0.0001$; NS, not significant; P-b, P-values bonferroni corrected.

Species and Groups	N	R^2	P	YgrandX	Intercept	Slope	95% LowCI	95% UppCI	Test of H_0 of slope (β) = 1.32 F ratio	P	P-b
Ackama paniculata	436	0.819	***	0.341	-0.425	1.347	1.294	1.402	0.853	NS	NS
Acmena (Syzygium) ingens	30	0.759	***	0.305	-0.453	1.335	1.106	1.613	0.012	NS	NS
Acronychia octandra	124	0.81	***	0.428	-0.292	1.274	1.178	1.377	0.879	NS	NS
Acronychia pubescens	55	0.807	***	0.341	-0.314	1.174	1.041	1.325	3.864	*	NS
Acronychia suberosa	22	0.814	***	0.331	-0.434	1.349	1.104	1.647	0.044	NS	NS
Actephila lindleyi	248	0.869	***	0.388	-0.426	1.435	1.371	1.502	12.689	***	***
Akania bidwillii	96	0.907	***	0.394	-0.275	1.175	1.104	1.25	14.116	***	***
Alangium villosum	181	0.728	***	0.341	-0.504	1.493	1.383	1.613	9.887	**	NS
Alectryon subcinereus	35	0.686	***	0.264	-0.375	1.103	0.906	1.344	3.461	NS	NS
Anthocarapa nitidula	307	0.84	***	0.365	-0.388	1.328	1.27	1.39	0.051	NS	NS
Archidendron grandiflorum	16	0.855	***	0.315	-0.43	1.312	1.057	1.628	0.006	NS	NS
Argyrodendron actinophyllum	283	0.738	***	0.35	-0.391	1.306	1.23	1.387	0.153	NS	NS
Argyrodendron trifoliolatum	701	0.856	***	0.331	-0.383	1.263	1.228	1.299	10.128	**	NS
Arytera divaricata	59	0.841	***	0.283	-0.419	1.235	1.112	1.373	1.638	NS	NS
Atractocarpus benthamianus	923	0.748	***	0.347	-0.456	1.424	1.379	1.471	20.401	***	***
Baloghia inophylla	126	0.749	***	0.401	-0.353	1.328	1.215	1.452	0.012	NS	NS
Beilschmiedia elliptica	32	0.913	***	0.312	-0.379	1.216	1.089	1.356	2.424	NS	NS
Beilschmiedia obtusifolia	48	0.865	***	0.277	-0.338	1.101	0.988	1.228	11.46	**	NS
Brachychiton acerifolius	34	0.799	***	0.449	-0.148	1.073	0.914	1.26	6.999	*	NS
Capparis arborea	102	0.836	***	0.37	-0.506	1.549	1.429	1.678	15.401	***	***
Cinnamomum oliverii	314	0.838	***	0.335	-0.374	1.247	1.192	1.304	6.556	**	NS
Cinnamomum virens	23	0.811	***	0.295	-0.345	1.136	0.934	1.382	2.571	NS	NS
Claoxylon australe	47	0.765	***	0.336	-0.447	1.372	1.186	1.586	0.263	NS	NS
Cleistanthus cunninghamii	291	0.846	***	0.357	-0.425	1.379	1.318	1.443	3.379	NS	NS
Croton verreauxii	146	0.868	***	0.301	-0.382	1.221	1.15	1.296	6.907	**	NS
Cryptocarya erythroxylon	112	0.84	***	0.374	-0.339	1.252	1.161	1.35	2.029	NS	NS
Cryptocarya obovata	161	0.796	***	0.314	-0.426	1.305	1.216	1.401	0.12	NS	NS
Cupaniopsis flagelliformis var. *australis*	40	0.864	***	0.288	-0.489	1.361	1.206	1.536	0.242	NS	NS
Cyclophyllum longipetalum	40	0.838	***	0.293	-0.447	1.305	1.144	1.489	0.036	NS	NS
Daphnandra apatela	180	0.823	***	0.337	-0.444	1.381	1.298	1.47	1.958	NS	NS
Denhamia celastroides	26	0.849	***	0.356	-0.409	1.353	1.15	1.593	0.089	NS	NS
Diospyros pentamera	234	0.872	***	0.333	-0.382	1.261	1.204	1.321	4.001	*	NS
Doryphora sassafras	309	0.803	***	0.384	-0.44	1.468	1.397	1.543	17.228	***	***
Dysoxylum fraserianum	53	0.812	***	0.39	-0.31	1.242	1.1	1.403	1.051	NS	NS

Dysoxylum rufum	33	0.84	***	0.301	-0.402	1.248	1.079	1.444	0.635	NS	NS
Elattostachys xylocapa	18	0.662	***	0.24	-0.569	1.425	1.052	1.931	0.271	NS	NS
Endiandra crassiflora	28	0.667	***	0.365	-0.297	1.199	0.952	1.51	0.745	NS	NS
Endiandra muelleri ssp. *muelleri*	34	0.869	***	0.309	-0.346	1.166	1.024	1.328	3.844	*	NS
Eupomatia laurina	198	0.781	***	0.339	-0.441	1.377	1.289	1.471	1.516	NS	NS
Flindersia australis	20	0.769	***	0.348	-0.365	1.256	0.992	1.59	0.203	NS	NS
Geissois benthamii	321	0.804	***	0.33	-0.415	1.313	1.251	1.379	0.067	NS	NS
Guilfoylia monostylis	110	0.852	***	0.382	-0.388	1.357	1.261	1.46	0.508	NS	NS
Halfordia kendack	24	0.82	***	0.35	-0.377	1.281	1.063	1.545	0.116	NS	NS
Helicia glabriflora	65	0.82	***	0.332	-0.519	1.48	1.33	1.647	4.5	*	NS
Ixora beckleri	51	0.911	***	0.314	-0.609	1.607	1.476	1.75	21.409	***	***
Litsea reticulata	68	0.87	***	0.339	-0.378	1.268	1.161	1.385	0.87	NS	NS
Mischocarpus australis	23	0.894	***	0.298	-0.51	1.424	1.229	1.65	1.1	NS	NS
Myrsine subsessilis	13	0.527	**	0.34	-0.425	1.371	0.881	2.133	0.032	NS	NS
Neolitsea australiensis	76	0.826	***	0.256	-0.492	1.315	1.194	1.448	0.011	NS	NS
Neolitsea dealbata	206	0.841	***	0.238	-0.509	1.313	1.243	1.388	0.049	NS	NS
Notelea johnsonii	43	0.834	***	0.301	-0.375	1.183	1.041	1.345	3.041	NS	NS
Orites excelsus	71	0.883	***	0.352	-0.44	1.4	1.29	1.52	1.961	NS	NS
Pittosporum multiflorum	157	0.362	***	0.342	-0.381	1.267	1.116	1.437	0.439	NS	NS
Polyosma cunninghamii	317	0.793	***	0.36	-0.382	1.31	1.245	1.378	0.121	NS	NS
Pouteria australis	150	0.807	***	0.314	-0.524	1.476	1.374	1.585	9.405	**	NS
Psychotria simmondsiana	21	0.6	***	0.429	-0.231	1.08	0.801	1.456	1.968	NS	NS
Quintinia sieberi	20	0.632	***	0.383	-0.239	1.16	0.863	1.56	0.835	NS	NS
Quintinia verdonii	200	0.852	***	0.334	-0.502	1.451	1.375	1.532	11.78	**	NS
Sarcopteryx stipata	194	0.781	***	0.304	-0.407	1.253	1.172	1.339	2.482	NS	NS
Sloanea australis	1378	0.749	***	0.422	-0.327	1.326	1.291	1.362	0.06	NS	NS
Sloanea woollsii	125	0.859	***	0.393	-0.328	1.269	1.187	1.356	1.471	NS	NS
Stenocarpus sinuatus	53	0.754	***	0.308	-0.443	1.323	1.151	1.52	0	NS	NS
Synoum glandulosum	66	0.793	***	0.346	-0.533	1.544	1.378	1.729	7.509	*	NS
Syzygium corynanthum	58	0.758	***	0.383	-0.304	1.231	1.08	1.404	1.162	NS	NS
Syzygium crebrinerve	89	0.879	***	0.308	-0.324	1.146	1.065	1.234	14.691	***	***
Syzygium francisii	19	0.918	***	0.339	-0.454	1.382	1.194	1.599	0.413	NS	NS
Tasmannia insipida	40	0.512	***	0.298	-0.442	1.306	1.04	1.64	0.011	NS	NS
Wilkiea austroqueenslandica	125	0.727	***	0.431	-0.387	1.478	1.347	1.622	5.657	*	NS
Wilkiea huegeliana	400	0.77	***	0.354	-0.352	1.243	1.186	1.303	6.516	**	NS
Zanthoxylum brachyacanthum	51	0.898	***	0.308	-0.523	1.428	1.303	1.565	2.874	NS	NS
Shade intolerant											
Alphitonia excelsa	16	0.604	***	0.329	-0.083	0.945	0.663	1.345	4.14	NS	NS
Clerodendrum tomentosum	24	0.804	***	0.347	-0.476	1.426	1.174	1.732	0.65	NS	NS
Diploglottis australis	118	0.867	***	0.285	-0.369	1.169	1.093	1.250	13.208	***	***
Guioa semiglauca	92	0.715	***	0.311	-0.458	1.356	1.213	1.516	0.206	NS	NS
Polyscias elegans	162	0.9	***	0.368	-0.331	1.252	1.191	1.315	4.742	*	NS

Appendix S2. Table S2 Mean values for stem, leaf, and seed traits for the 75 study species. WD - wood density; MR – modulus of rupture; ME – modulus of elasticity; SS – seed size; LA – leaf area; H_{max} – estimated adult height; Growth – annual DBH increment in cm; # denotes growth values derived from means from other plot sources in the study area, or ## consistent with another species in the genus on site; YgrandX – diameter (*Y*) at the Grand Mean of (*X*) height; Slender (Slenderness) = height/diameter ratio; Vol_5m – stem volume at a common height (5metres).

Species	WD	MR	ME	log10_SS	log10_LA	Hmax	Growth	YgrandX	Slender	Vol_5m
Shade tolerant										
Ackama paniculata	0.6	97	13	0.041	1.368	37	0.188	0.341	1.672	2.573
Acmena ingens	0.54	-	-	1.267	1.447	40	0.272	0.305	1.881	2.181
Acronychia octandra	0.53	75	11	0.176	1.699	37	0.246	0.428	1.342	3.76
Acronychia pubescens	0.63	-	-	0.653	1.639	25	0.04	0.341	1.628	2.463
Acronychia suberosa	0.63	-	-	0.602	0.943	35	0.183	0.331	1.802	2.485
Actephila lindleyi	0.76	-	-	0.903	1.265	10.6	0.02	0.388	1.558	3.41
Akania bidwillii	0.67	-	-	1.041	1.615	25	0.066	0.394	1.542	2.96
Alangium villosum	0.71	-	-	1	1.279	35	0.101	0.341	1.786	2.87
Alectryon subcinereus	0.74	-	-	0.74	1.389	27	0.134	0.264	2.142	1.479
Anthocarapa nitidula	0.8	-	-	1.13	1.368	35	0.071	0.365	1.673	2.884
Archidendron grandiflorum	0.63	-	-	0.699	1.146	30	0.074	0.315	1.848	2.247
Argyrodendron actinophyllum	0.82	124	21	0.778	1.482	40	0.259	0.35	1.746	2.641
Argyrodendron trifoliolatum	0.85	118	18	0.903	1.166	40	0.208	0.331	1.722	2.383
Arytera divaricata	0.74	-	-	0.903	1.273	22	0.012	0.283	1.989	1.853
Atractocarpus benthamianus	1	-	-	0.602	1.523	15.5	0.053	0.347	1.771	2.869
Baloghia inophylla	0.72	-	-	0.875	1.426	30	0.128	0.401	1.519	3.378
Beilschmiedia elliptica	0.82	-	-	0.954	1.166	35	0.241	0.312	1.87	2.088
Beilschmiedia obtusifolia	0.75	118	18	1.301	1.166	35	0.14	0.277	1.914	1.748
Brachychiton acerifolius	0.42	34	7	0.954	2.342	40	0.184	0.449	1.314	3.831
Capparis arborea	0.89	-	-	0.954	1.211	22	0.045	0.37	1.661	3.406
Cinnamomum oliverii	0.56	93	14	1	1.283	35	0.377	0.335	1.785	2.363
Cinnamomum virens	0.56	-	-	0.954	1.151	35	0.143	0.295	1.881	1.89
Claoxylon australe	0.69	-	-	0.398	1.322	20	0.12	0.336	1.667	2.528
Cleistanthus cunninghamii	0.92	-	-	0.398	1.079	25	#0.036	0.357	1.663	2.86
Croton verreauxii	0.64	-	-	0.301	1.106	15	0.076	0.301	1.755	2.088
Cryptocarya erythroxylon	0.72	130	19	1.079	1.279	35	0.197	0.374	1.664	2.819
Cryptocarya obovata	0.64	-	-	0.903	1.255	40	0.16	0.314	1.796	2.243
Cupaniopsis flagelliformis var. *autralis*	0.84	-	-	1.041	1.38	35	0.212	0.288	1.85	2.015
Cyclophyllum longipetalum	1	-	-	0.477	1.067	27	0.008	0.293	1.94	2.038
Daphnandra apatela	0.65	112	17	0.301	1.284	27	0.161	0.337	1.776	2.634
Denhamia celastroides	0.84	-	-	0.477	1.239	15	0.079	0.356	1.72	2.838
Diospyros pentamera	0.73	-	-	0.929	1.021	35	0.15	0.333	1.733	2.387
Doryphora sassafras	0.6	99	14	0.301	1.114	40	0.162	0.384	1.653	3.562
Dysoxylum fraserianum	0.72	-	-	0.845	1.176	40	0.179	0.39	1.491	3.125
Dysoxylum rufum	0.64	-	-	0.699	1.462	40	0.177	0.301	1.796	2.089
Elattostachys xylocapa	0.77	-	-	0.778	1.004	35	#0.019	0.24	2.178	1.713
Endiandra crassiflora	0.79	-	-	0.954	1.271	35	0.238	0.365	1.465	2.891
Endiandra muelleri ssp. *muelleri*	0.77	-	-	1.204	1.38	37	0.126	0.309	1.806	2.07

Eupomatia laurina	0.72	-	-	0.176	1.346	12.5	0.09	0.339	1.763	2.641
Flindersia australis	0.95	135	17	0.875	1.276	40	0.149	0.348	1.725	2.54
Geissois benthamii	0.65	108	14	0.477	1.429	40	0.231	0.33	1.778	2.424
Guilfoylia monostylis	0.93	-	-	0.954	1.205	25	0.091	0.382	1.597	3.163
Halfordia kendack	1.1	198	21	0.845	1.362	40	0.197	0.35	1.717	2.61
Helicia glabriflora	0.67	-	-	0.954	1.263	32	0.081	0.332	1.715	2.572
Ixora beckleri	0.96	-	-	0.74	1.455	10	#0.019	0.314	1.809	2.558
Litsea reticulata	0.5	74	11	0.978	1.193	37	0.263	0.339	1.701	2.482
Mischocarpus australis	0.76	-	-	0.778	1.23	27	0.135	0.298	1.912	2.232
Myrsine subsessilis	0.91	-	-	0.653	1.217	4.5	#0.019	0.34	1.925	2.783
Neolitsea australiensis	0.68	-	-	0.903	1.404	30	0.154	0.256	1.868	1.709
Neolitsea dealbata	0.68	-	-	0.653	1.641	22	0.172	0.238	1.978	1.574
Notelea johnsonii	1.01	-	-	1.041	1.204	15.3	#0.019	0.301	1.951	1.917
Orites excelsus	0.6	96	13	0.699	1.222	40	0.252	0.352	1.701	2.857
Pittosporum multiflorum	0.6	-	-	0.041	-0.581	4.2	#0.019	0.342	1.914	2.441
Polyosma cunninghamii	0.72	-	-	1	0.903	25	0.095	0.36	1.658	2.792
Pouteria australis	0.88	145	17	1.176	1.447	32	0.106	0.314	1.851	2.473
Psychotria simmondsiana	1	-	-	0.699	0.631	4.3	#0.019	0.429	1.623	2.669
Quintinia sieberi	0.56	-	-	0.041	1.265	25	0.094	0.383	1.333	3.329
Quintinia verdonii	0.52	-	-	0.041	1.336	22	0.215	0.334	1.678	2.534
Sarcopteryx stipata	0.98	-	-	0.699	1.108	35	0.119	0.304	1.937	2.068
Sloanea australis	0.6	83	12	0.813	1.904	40	0.14	0.422	1.521	3.786
Sloanea woollsii	0.62	107	15	0.699	1.54	40	0.262	0.393	1.586	3.133
Stenocarpus sinuatus	0.77	-	-	1.217	1.669	37	0.11	0.308	1.838	2.196
Synoum glandulosum	0.68	122	15	0.778	1.021	35	0.096	0.346	1.723	2.955
Syzygium corynanthum	0.71	-	-	0.74	1.38	40	0.146	0.383	1.432	3.101
Syzygium crebrinerve	0.74	-	-	0.74	1.314	40	0.201	0.308	1.719	2.148
Syzygium francisii	0.72	-	-	0.813	1	38	0.075	0.339	1.614	2.523
Tasmannia insipida	0.68	-	-	0.398	1.368	5.2	#0.019	0.298	1.993	2.089
Wilkiea austroqueenslandica	0.67	-	-	0.875	1.591	7.8	##0.092	0.431	1.526	4.679
Wilkiea huegeliana	0.67	-	-	0.903	1.322	13.5	0.093	0.354	1.715	2.58
Zanthoxylum brachyacanthum	0.83	-	-	0.778	1.13	22	0.152	0.308	1.685	2.13
Shade intolerant										
Alphitonia excelsa	0.74	134	19	0.544	1.346	35.000	0.416	0.329	1.403	3.418
Clerodendrum tomentosum	0.50	-	-	0.740	1.346	5.800	-	0.347	1.577	2.625
Diploglottis australis	0.70	-	-	1.146	1.934	37.000	0.188	0.285	1.880	1.885
Guioa semiglauca	0.77	-	-	0.778	1.035	30.000	0.362	0.311	1.859	2.274
Polyscias elegans	0.46	-	-	0.602	1.430	35.000	0.199	0.368	1.419	2.924

Appendix S3. *Interspecific comparisons of sapling stature: D-H allometry*

Tables S1 and S2 provide a summary of results for species and groups from the SMA regressions, and species values for traits. Table S6a belows shows that when bonferroni corrections were made to the p values from the SMA regression for the test of the null hypothesis (H_0) of no difference in slope (for the common scaling exponent $\beta=1.32$; close to 4/3) 8 species remained with significant values. These included three with lower and five with higher slope values (than the common $\beta = 1.32$). (By way of explanation, where $\beta > 1.32$ this indicates greater DBH gain per height increment, and thicker stems.) We looked at these two groups of species to determine what, if anything, the species in them had in common (Table S6b). The three species with lower β include the shade tolerant canopy tree *Syzygium crebrinerve* (Myrtaceae); a shade tolerant sub-canopy tree *Akania bidwillii* (Akanianceae); and a shade intolerant tree species *Diploglottis australis* (Sapindaceae). The five species with higher β include the large shade tolerant canopy tree *Doryphora sassafras* (Atherospermataceae); a smaller (occasional) canopy tree *Capparis arborea* (Capparaceae) that displays a sprawling liana like growth habit early in ontogeny that is only later consolidated into tree form; and three shade tolerant understorey species *Actephila lindlyei* (Euphorbiaceae), *Atractocarpus benthamianus* (Rubiaceae), and *Ixora beckleri* (Rubiaceae) that have the whole of their species potential height variation (including H_{max}) sampled in the data. *Atractocarpus benthamianus* represents the most abundant sub-canopy smaller understorey tree in the assemblages. When the 8 species are compared on the basis of the other values and traits (excluding H_{max}) no significant patterns or groupings are evident.

S3. Tables S3 a. & b. Summary data from Tables 1 & 2 for 8 species; representing 3 with lower and 5 with higher (β) slope values. Life Form groups (1-4) as above (Tables S1 & S2).

a)

Species	N	Life Form	Interc.	Slope	Low. CI	Upp. CI
β < 1.32						
Akania bidwillii	96	2	-0.275	1.175	1.104	1.250
Syzygium crebrinerve	89	3	-0.324	1.146	1.065	1.234
Diploglottis australis	118	4	-0.369	1.169	1.093	1.250
β > 1.32						
Capparis arborea	102	3	-0.506	1.549	1.429	1.678
Doryphora sassafras	309	3	-0.440	1.468	1.397	1.543
Atractocarpus benthamianus	923	2	-0.456	1.424	1.379	1.471
Ixora beckleri	51	2	-0.609	1.607	1.476	1.750
Actephila lindleyi	248	2	-0.426	1.435	1.371	1.501

b)

Species	WD	log10_SS	log10_LA	Hmax	Growth	YgrandX	Slenderness	Vol_5m
β < 1.32								
Akania bidwillii	0.67	1.041	1.615	25.0	0.066	0.394	1.542	2.960
Syzygium crebrinerve	0.74	0.740	1.314	40.0	0.201	0.308	1.719	2.148
Diploglottis australis	0.70	1.146	1.934	37.0	0.188	0.285	1.880	1.885
β > 1.32								
Capparis arborea	0.89	0.954	1.211	22.0	0.045	0.370	1.661	3.406
Doryphora sassafras	0.60	0.301	1.114	40.0	0.162	0.384	1.653	3.562
Atractocarpus benthamianus	1.00	0.602	1.523	15.5	0.053	0.347	1.771	2.869
Ixora beckleri	0.96	0.740	1.455	10.0	#0.019	0.314	1.809	2.558
Actephila lindleyi	0.76	0.903	1.265	10.600	0.020	0.388	1.558	3.410

Appendix S4.

Table S1 shows that ten species had lower 95% CI (confidence interval) values for slope less than unity, including the shade tolerant shrubs *Myrsine subsessilis* (Myrsinaceae) and *Psychotria simmondsiana* (Rubiaceae); the shade tolerant tree *Alectryon subcinereus* (Sapindaceae); the shade intolerant tree *Alphitonia excelsa* (Rhamnaceae); the partly shade tolerant canopy tree *Brachychiton acerifolius* (Malvaceae); and the shade tolerant canopy trees *Beilschmedia obtusifolia* (Lauraceae), *Cinnamomum virens* (Lauraceae), *Endiandra crassiflora* (Lauraceae), *Flindersia australis* (Rutaceae), and *Quintinia sieberi* (Quintiniaceae). The phylogenetic signal from the 3 shade-tolerant canopy trees species in Lauraceae is of interest, but was not explored further. The remaining species had lower CI slope values between 1.01-1.5.

The strength (r^2) of the *D-H* relationship from SMA regression was lower (though still significant) for the three shade tolerant shrubs *Pittosporum multiflorum* (Pittosporaceae) (~0.36), *Myrsine subsessilis* (Myrsinaceae) (~0.52) and *Psychotria simmondsiana* (Rubiaceae) (~0.6); the shade tolerant understorey species *Tasmannia insipida* (Winteraceae) (~0.51), *Alectryon subcinereus* (Sapindaceae) (~0.68) and *Ellatostachys xylocarpa* (Sapindaceae) (~0.66); the shade intolerant tree *Alphitonia excelsa* (Rhamnaceae) (~0.60); and the canopy trees *Endiandra crassiflora* (Lauraceae) (~0.66) and *Quintinia sieberi* (Quintiniaceae) (~0.63). Values were high for all the remaining species (>0.70).

Appendix S5

Binary logistic model (provided by Maina Kariuki) to estimate the mean annual probability of a tree (> 10 cm DBH) from a particular group or size class dying:

$$\left.\begin{array}{l} \text{prop}_{ij} \sim \text{Binomial}(\text{denom}_{ij}, \pi_{ij}) \\ \text{prop}_{ij} = \pi_{ij} + e_{0ij}\text{pcons}^* \end{array}\right\}$$

$$\text{logit}(\pi_{ij}) = \beta_{1j}\text{cons} + -1.504374(0.153139)\text{spp2}_{ij} + -1.829048(0.209825)\text{spp3}_{ij} + -3.349973(0.508327)\text{spp4}_{ij} + $$
$$-0.421865(0.117340)\text{spp5}_{ij} + -0.204273(0.101746)\text{d2}_{ij} + -0.903466(0.237933)\text{d3}_{ij} + $$
$$-1.106815(0.388755)\text{d4}_{ij}$$

$$\beta_{1j} = -4.490106(0.134795) + u_{1j}$$

$$\left[u_{1j}\right] \sim N(0, \Omega_u) \; : \; \Omega_u = \left[0.224028(0.091371)\right]$$

$$\text{pcons}^* = \text{pcons}\left[\pi_{ij}(1 - \pi_{ij})/\text{denom}_{ij}\right]^{0.5}$$

$$\left[e_{0ij}\right] \sim (0, \Omega_e) \; : \; \Omega_e = \left[0.628723(0.023630)\right]$$

Table S5.1 Parameter estimates, standard errors, and Wald tests of significance (* significant at the 95% confidence level) for a binary logistic model, estimating the mean annual probability of a tree (> 10 cm DBH) dying in various species and size class groups (3) in subtropical rainforest in north-east NSW, Australia. Consistent with the groups in Table 1 & 2; shade tolerant small trees; shade tolerant canopy trees; shade intolerant canopy trees.

Variable description	Coefficient	Std error	|Z|	P-value
Intercept (β_{1j} cons)	-4.490106	0.134795	33.311	0
Shade tolerant mid canopy trees (2); (β_{1j} spp2)	-1.504374	0.153139	9.824	0
Shade tolerant understorey trees (2): (β_{1j} spp3)	-1.829048	0.209825	8.717	0
Moderate shade tolerant and persistent trees (3); (β_{1j} spp4)	-3.349973	0.508327	6.590	2.21E-11
Shade intolerant pioneer trees (4); (β_{1j} spp5)	-0.421865	0.117340	3.595	0.000162
DBH class (20-39cm); (β_{1j}d2)	-0.204273	0.101746	2.008	0.022322
DBH class (40-59cm); (β_{1j} d3)	-0.903466	0.237933	3.797	7.33E-05
DBH class ($\geq$ 60cm); (β_{1j} d4)	-1.106815	0.388755	2.847	0.002207
Plot level residual variance $\sigma 2$ (u_{1j})	0.224028	0.091371	2.452	0.007103
Tree level residual $\sigma 2$ (e $_{0ij}$)	0.628723	0.023630	26.607	0

Mortality model

(1+exp(-("probability of a tree dying")))^ -1 (that is, the probability of the target species group and size class divided by the total probability of all species plus 1).

Thus, (1+exp(-(4.490106)))^ -1 (that is, the probability of the target species group and size class divided by the total probability of all species plus 1).

By way of explanation of model: Group 1 is embedded in the intercept β_{1j} = -4.49016. The model outputs show that the (coefficient of) likelihood of mortality in these assemblages across all ontogenetic stages decreases with size; and is (predictably) highest overall for the canopy tree group that has the largest number of species and individuals; and then for the (faster growing) shade intolerant species. Sub-canopy and smaller trees of the understorey have lower (coefficients of) likelihood of mortality. Percentage occurrence of mortality by group reflects synthesis of raw species level data:

Table S5.2 Percent (%) occurrence of mortality by group (3) based on raw species level data.

% yearly mortality by group	
4.429931	Shade tolerant canopy
5.396246	Shade tolerant small trees
6.838186	Shade intolerant canopy

We then merged the groups described in Kariuki et al. (2006) to reflect species life form groups, and generated the following values for the likelihood (as coefficients) of mortality by species and size class groups (note that the overall canopy tree model slope is merged with the moderate shade tolerant persistent canopy trees to form a single canopy tree group):

Table S5.3 Coefficient of likelihood of mortality by life form and size group.

Co-efficient of likelihood of mortality	Group
0.011095	model canopy tree slope (β_{1j})
0.005744	shade tolerant canopy trees
0.002142	shade tolerant understorey trees
0.007304	shade intolerant (pioneer) trees
0.009064	DBH class (20-39cm)
0.004525	DBH class (40-59cm)
0.003696	DBH class ($\geq$ 60cm)

Appendix S6

Wood density and safety factors

Consistent with van Gelder et al. (2006) the main stem structural properties of modulus of rupture (MOR) and modulus of elasticity (MOE) (extracted from Bootle 1983) were found to be tightly correlated with wood density (WD) for 20 of the species included in the data presented here ($r^2 = 79.37$; $r^2 = 72.33$); and 44 species that occur in the rainforest assemblages of the study area ($r^2 = 80.6$; $r^2 = 67.2$). Refer to S3, Table S3 for values for WD, MR and ME for a subset of species in this study.

Appendix S7. Table S7 Species taxonomic checklist.

Species	Family
Ackama paniculata (F.Muell.) Hoogland (syn. *Caldcluvia paniculosa*)	Cunoniaceae
Acmena ingens (F.Muell. Ex C.Moore) Guymer & B.Hyland	Myrtaceae
Acronychia octandra (F. Muell.) T.G. Hartley	Rutaceae
Acronychia pubescens (Bailey) C.T. White	Rutaceae
Acronychia suberosa C.T. White	Rutaceae
Actephila lindleyi (Steud.) Airy Shaw	Phyllanthaceae
Akania bidwillii (Hogg) Mabb.	Akaniaceae
Alangium villosum (F.Muell.) Bloemb.	Cornaceae
Alectryon subcinereus (A.Gray) Radlk.	Sapindaceae
Alphitonia excelsa (A.Cunn. ex Fenzl) Resissek ex Benth.	Rhamnaceae
Anthocarpa nitidula (Benth.) T.D.Penn. ex Mabb.	Meliaceae
Archidendron grandiflorum (Sol. ex Benth.) I.C.Neilsen	Fabaceae
Argyrodendron actinophyllum (F.M.Bailey) Edlin.	Malvaceae
Argyrodendron trifoliolatum F.Muell.	Malvaceae
Arytera divaricata F.Muell.	Sapindaceae
Atractocarpus benthamianus ssp *glaber* Puttock	Rubiaceae
Baloghia inophylla (G. Forst.) P.S. Green	Euphorbiaceae
Beilschmiedia elliptica C.T.White & W.D. Francis	Lauraceae
Beilschmiedia obtusifolia (F.Muell. ex Meisn.) F.Muell.	Lauraceae
Brachychiton acerifolius (A.Cunn. ex G.Don) Macarthur	Malvaceae
Capparis arborea (F.Muell.) Maiden	Capparaceae
Cinnamomum oliverii F.M.Bailey	Lauraceae
Cinnamomum virens R.T.Baker	Lauraceae
Claoxylon australe Baill. ex Muell. Arg.	Euphorbiaceae
Cleistanthus cunninghamii Muell. Arg.	Phyllanthaceae
Clerodendrum tomentosum (Vent.) R.Br.	Lamiaceae
Croton verreauxii Baill.	Euphorbiaceae
Cryptocarya erythroxylon Maiden & Betche ex Maiden	Lauraceae
Cryptocarya obovata R.Br.	Lauraceae
Cupaniopsis flagelliformis var. *autralis* S.T.Reynolds	Sapindaceae
Cyclophyllum longipetalum (*Canthium coprosmoides*) F.Muell.	Rubiaceae
Daphnandra apatela ms. (sp. Mc Pherson Range W.D.Francis)	Atherospermataceae
Denhamia celastroides (F.Muell.) Jessup	Celastraceae
Diospyros pentamera (Woolls & F.Muell.) F.Muell	Ebenaceae
Diploglottis australis (G.Don) Radlk.	Sapindaceae
Doryphora sassafras Endl.	Atherospermataceae
Dysoxylum fraserianum (A.Juss.) Benth.	Meliaceae
Dysoxylum rufum (A.Rich.) Benth.	Meliaceae
Elattostachys xylocarpa (A.Cunn. ex F.Muell.) Radlk.	Sapindaceae
Endiandra crassiflora C.T.White & W.D. Francis	Lauraceae
Endiandra muelleri Meisn. (ssp *muelleri*)	Lauraceae
Eupomatia laurina R.Br.	Eupomatiaceae
Flindersia australis R. Br.	Rutaceae
Geissois benthamii F.Muell.	Cunoniaceae
Guilfoylia monostylis (Benth.) F.Muell.	Surianaceae
Guioa semiglauca (F.Muell.) Radlk.	Sapindaceae
Halfordia kendack (Montrouz.) Guillaumin	Rutaceae
Helicia glabriflora F.Muell.	Proteaceae
Ixora beckleri Benth.	Rubiaceae

Litsea reticulata (Meisn.) F.Muell.	Lauraceae
Mischocarpus australis S.T.Reynolds	Sapindaceae
Myrsine subsessilis (*Rapanea subsessilis*) F.Muell. Mez	Primulaceae
Neolitsea australiensis Kosterm.	Lauraceae
Neolitsea dealbata (R.Br.) Merr.	Lauraceae
Notelaea johnsonii P.S.Green	Oleaceae
Orites excelsus R.Br.	Proteaceae
Pittosporum multiflorum (A.Cunn. ex Loudon) L.Cayzer, Crisp & I.Telford	Pittosporaceae
Polyosma cunninghamii Benn.	Polyosmaceae
Polyscias elegans (C.Moore & F.Muell.) Harms	Araliaceae
Pouteria australis (R.Br.) Baehni	Sapotaceae
Psychotria simmondsiana F.M.Bailey	Rubiaceae
Quintinia sieberi A.DC.	Quintiniaceae
Quintinia verdonii F.Muell.	Quintiniaceae
Sarcopteryx stipata (F.Muell.) Radlk.	Sapindaceae
Sloanea australis (Benth.) F.Muell.	Elaeocarpaceae
Sloanea woollsii F.Muell.	Elaeocarpaceae
Stenocarpus sinuatus (Loudon) Endl.	Proteaceae
Synoum glandulosum (Sm.) A.Juss. (ssp *glandulosum*)	Meliaceae
Syzygium corynanthum (F.Muell.) L.A.S.Johnson	Myrtaceae
Syzygium crebrinerve (C.T.White) L.A.S.Johnson	Myrtaceae
Syzygium francisii (F.M.Bailey) L.A.S.Johnson	Myrtaceae
Tasmannia insipida R.Br. ex DC.	Winteraceae
Wilkiea austroqueenslandica Domin	Monimiaceae
Wilkiea huegeliana (Tul.) A.DC.	Monimiaceae
Zanthoxylum brachyacanthum F.Muell.	Rutaceae

APPENDIX 2

Supplementary Materials for:

CHAPTER 3

Plant functional traits in Australian sub-tropical rain forest: partitioning within-community from cross-landscape variation

Robert Kooyman[1,2], Will Cornwell[3] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia;*
[2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;*
[3] *Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada.*

Table S1 Soil analysis results from Baur (1957) for several of the northern NSW locations and rainforest floristic alliances used in this study. CNVF – complex notophyll vine forest on basalt soils; SNVF – simple notophyll vine forest on rhyolite soils.

Community	Exch. Cations (m-equiv. / 100g)	Exch. Ca (m-equiv. / 100g)	Exch. K (m-equiv. / 100g)	Total PO$_4$ p.p.m.
Argyrodendron alliance - CNVF	15.8 – 62.0	10.5 – 47.2	0.8 – 2.8	2940 - 7620
Ceratopetalum – Schizomeria - SNVF	2.3 - 11.3	1.1 – 3.5	0.6 – 1.0	520 - 1090
Ceratopetalum – Sloanea - SNVF	5.0	3.5	0.2	510 - 1290

Additional analysis results for selected soil sampling data for the study area are available from Turner & Kelly (1981); and the Dept of Natural Resources web site
<www.naturalresources.nsw.gov.au/soils/data>

Turner, J. & Kelly, J. (1981) Relationships between soil nutrients and vegetation in a
North Coast forest, New South Wales. *Australian Forest Research* 11, 201-
208.

APPENDIX 3

Supplementary Materials for:

CHAPTER 4

Traits and gradients explain the distribution and performance of a clonal Australian rainforest tree species

Robert M. Kooyman[1,2,3]

[1]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109 Australia; [2]National Herbarium of NSW, Sydney, NSW 2000 Australia; [3]University of New England, Armidale, NSW 2351, Australia

METHODS

Multivariate analyses

No transformation (or weighting) of the species abundance measures was undertaken as the intention was to preserve as much of the information in the full floristic samples as possible.

The environmental variables used for ordination analyses were derived from the field-collected environmental data. The relative values and allocated rankings of the environmental variables are described in Table S1, and in Rossetto and Kooyman (2005) and Royer et al. (2009). Transformation of variables included replacement of all measured environmental variables by ranks for PCA, and the use of the Spearman Rank coefficient for subsequent tests of results (Global Tests) and multivariate regression tree analyses (Clarke & Gorley 2006).

The site by species data were classified by grouping similar plots using a simple numerical hierarchical agglomerative clustering process, and the Bray-Curtis association measure. Similarity profile permutation tests (Simprof) were used to test the groupings (1000 permutations). Similarity among quadrats/sites was further investigated through non-metric multidimensional scaling (nMDS) ordination using the underlying resemblance matrix as input. Principal component analysis (PCA; Euclidean distance) was also used to examine the position of group members in component space relative to the influence of environmental variables (not presented).

Trait Gradient Analysis

Abundance-weighted plot mean trait values (eqn. 1), species mean trait values (eqn. 2), and mean of plot means for plots occupied by each species (eqn. 3) are defined as follows:

$$\overline{p_j} = \frac{\sum_{i=1}^{S} a_{ij} t_{ij}}{\sum_{i=1}^{S} a_{ij}}, \quad \text{(eqn 1)}$$

$$\overline{t_i} = \frac{\sum_{j=1}^{P} a_{ij} t_{ij}}{\sum_{j=1}^{P} a_{ij}}, \quad \text{(eqn 2)}$$

$$\beta_i = \frac{\sum_{j=1}^{P} \overline{p_j} a_{ij}}{\sum_{j=1}^{P} a_{ij}}, \quad \text{(eqn 3)}$$

where t_{ij} is the trait value and α_{ij} is the abundance for species i in plot j, the total number of plots in the study is P, and the species richness of plot j is S_j. The analyses presented here use cover abundance weighted values (Ackerly and Cornwell 2007).

Seed trapping and fecundity

Three seed traps were located under the canopy of each of ten stems at five sites at each of two locations (Nightcap and Mt. Jerusalem). Seed traps (ca. 1 x 0.5 m) were constructed of shade cloth and attached to four lightweight steel stakes at a height of approximately 1m above ground level. A 25 x 25mm steel mesh (bird-wire) vertebrate fruit / seed predator excluder was fitted over the 'trap' area. The fine weave shade cloth formed an enclosed shallow sling net that allowed adequate drainage in what is a very high rainfall area, but was fine enough to retain all trapped *U. australis* seeds. The total crown area of the 20 trees sampled was 309.7 m^2, while the 60 seed traps

established represented a total sample area of ca. 30 m^2. Total seed trap area at each

stem was 1.5 m^2, while the mean crown area for all stems sampled was 15.5 m^2.

Results of seed experiments (germination and survivorship) are presented in

Kooyman (2005).

RESULTS

Additional tests of multivariate patterns

Additional analyses and tests undertaken included ANOSIM permutation tests (for the

R statistic), the Global BEST match test, and a modified MRT (multivariate

regression tree) analysis (De'ath 2002) referred to as the Linkage Tree procedure, in

PRIMER v6 (Clarke & Gorley 2006). The outputs from these analyses provided a

range of opportunities to interrogate and test the pattern of relationships of the

available environmental (abiotic) variables to assemblage patterns (floristic variation)

in the data, and confirmed the results presented.

Population data for U. australis relative to gradients

Kruskal-Wallis tests of the relationship of number of stems and basal area of *U.*

australis to soil depth showed a significant relationship for both (number of stems H =

44.265, 2 d.f., *P* < 0.0001; and basal area H = 47.95, 2 d.f., *P* < 0.0001). Fig. S1.1.

Uromyrtus australis distribution in sample

Uromyrtus australis was detected on 68 of the 100 quadrats, with 24 locations from

Mt. Jerusalem and 44 from Nightcap. The geographical pattern of the species

distribution and the abundance data show that the core areas of the species range in

Nightcap NP have the highest population density (Fig. S1.1).

Life history parameters

The deterministic matrix projection model based on measured transition probabilities (Table S1.2; Kooyman, 2005), with fecundity levels set at 0.001 for 1000 time steps resulted in a finite population growth value (eigenvalue) of ca. 1.000007 for both large and small populations. Elasticities for fecundity were (F) = 0.0 (no seeds germinated in the field, despite large numbers of seeds being produced), for growth (G) = ca. 0.0007 (for ramet stem diameter increment in small and large populations), and for survivorship (longevity) (L) > 0.999 (based on small ramet stem turnover) (De Kroon et al., 1986).

Trait Gradient Analysis

Consistent with previous results from the study area and these forests (Kooyman et al., 2010) the range of alpha (α_i) was much wider than the range of beta (β_i) trait components for all traits. Confirming that trait values varied more across co-occurring species than across means for plots where they occurred. However, covariance was stronger between beta trait components (β_i) for leaf (LA) and stem traits (H_{max}, WD) (Table S1.4).
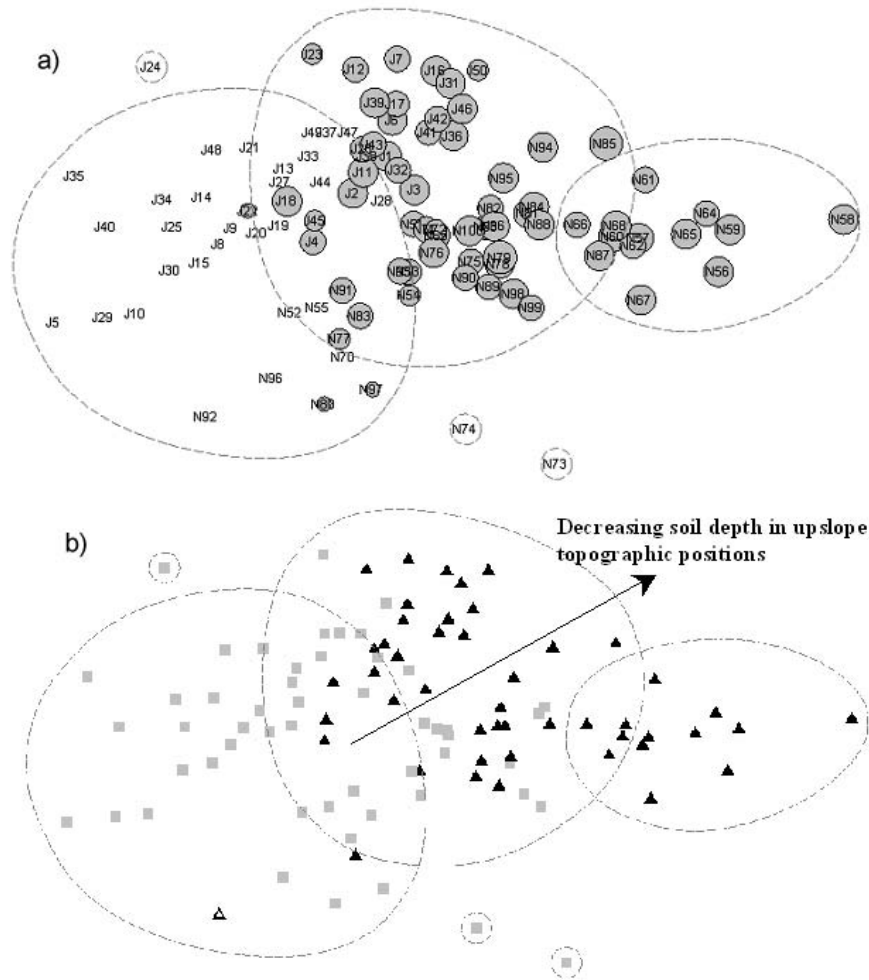
Figure S1.1 (a-b) Constrained 2-dimensional nMDS ordinations of 100 sites representing 50 / 20 x 20 m plots from each area, Nightcap and Mt Jerusalem. a) Grey-scale bubbles indicate sites with *Uromyrtus australis* present; and relative cover abundance (by bubble size). Sites at Nightcap NP are labelled with the prefix 'N'; Mt Jerusalem the prefix 'J'. Note the split between the two geographic areas and the much larger population at Nightcap. b) Shows the influence of the mostly correlated gradients of decreasing soil depth, and upslope topographic positions. Solid black triangles - skeletal / rocky soils; solid grey squares - shallow soils; open triangle – medium depth soils. The broken grey line(s) represent the 60-percent resemblance level derived from the clustering routine (and subsequent dendrogram) using the Bray-Curtis distance measure. Overall stress in the 2-D ordination(s) (0.16).

Table S1.1 Environmental variables and rankings used in data collection and subsequent analyses. Fire frequency and disturbance were ranked using floristic and visual indicators and known disturbance and fire history.

Topographic Position	Fire Freq. (yrs)	Disturbance	Soil Depth	Soil Type	Altitude	Slope	[1]Aspect
1. crest *1*.	0-100 *1*.	none *1*.	skeletal *1*.	clay/loam	*Actual A*	*ctual*	*Actual*
2. upperslope *2*.	100-250 *2*.	light *2*.	shallow *2*.	peaty/clay			
3. mid-slope *3*.	250-500 *3*.	moderate *3*.	medium *3*.	alluvium			
4. lowerslope *4*.	>500 *4*.	heavy *4*.	deep				
5. creek/gully *5*.	no fire						

Table S1.2 Annual transition probabilities and fecundity for a stage-based model based on 16 years of measurement of two 1600m^2 plot samples (ISD = initial size-class distribution for small and large population areas in Nightcap NP; permanent plot 1 - small, and permanent plot 2 - large). Fecundity values are based on values from populations in two locations (#Nightcap and *Mt. Jerusalem).

Vital Rates	Pop. Size L=large S=small	0 Propagules	1 Seedlings (planted)	2[#] >0-1cm	3[#] >1-5cm	4[#] >5-10cm	5[#] >10-25cm	6 Clonal Division
ISD	L	0	0	456	91	17	7	0
	S	0	0	115	26	3	2	0
Fecundity (F)	L	0	0	0	0	0	600#	0
	S	0	0	0	0	0	78*	0
Mortality (M)	L	1(0.999)	0.62	0	0	0	0	0
	S	1(0.999)	0.62	0	0	0	0	0
Recruitment (V)	L	0	0(0.001)	0.029	0(0.001)	0.007	0	0
	S	0	0(0.001)	(0.029)	0(0.001)	(0.007)	0	0
Remaining (P)	L	0(0.001)	0.38	0.977	0.959	1 (0.977)	1	0
	S	0(0.001)	0.38	(0.977)	0.959	1 (0.977)	1	0
Growth (G)	L	0	0	0.0035	0.0055	0.018	0.037	0
	S	0	0	(0.0035)	(0.0055)	(0.018)	(0.037)	0

Fecundity values reflect mean number of seeds produced per unit area of canopy for individual trees in small and large population areas in Nightcap and Mt. Jerusalem. Mortality =1-P, and in the case of seeds indicates post-dispersal predation levels, and for seedlings indicates survivorship of translocated seedlings after 13 months for a single experiment. Pop. Size = population size. (Bracketed values) = no change in the small population through time so large population values used or values adjusted from 1.0 or 0.0 to represent (for example) stochastic events (resulting in seed-based recruitment), or other hypothetical transition probabilities. [#] = size-classes based on measured diameter at breast height in centimetres.

Table S1.3 Forest type descriptions representing broad floristic groupings for the full extent of Coachwood dominated warm temperate rainforest on rhyolite derived soils in the study area. The 100-plot sample is dominated by SNVF-SNMVF-SNMVT.

Forest Type	*i*	*ii*	*iii*	*iv v*		*vi v*	*ii*
Typology[1]	NVF	SNVF	SNMVF to SNMVT	SNVF-SNMVF disturbed	SNVF-SNMVF	SNVF with *Caldcluvia* and *Schizomeria*	*Eucalyptus* spp. with SNVF-SNMVF
Description	Complex forest with emergents: *Ficus* sp., *Sloanea woolsii*	Dominated by: *Ceratopetalum / Endiandra / Canarium*	Includes: *Ceratopetalum / Endiandra* with emergent: *Tristaniopsis collina*	Includes: *Acacia orites*	With or without: *Lophostemon confertus, Callitris macleayana,* or *Syncarpia glomulifera* as emergents	Disturbed, with: *Acacia orites*, gullies with *Sloanea* spp.	Transitions and overlaps between forest communities. Fire influence.

[1] Based on Webb (1978): NVF = notophyll vine forest; SNVF = simple notophyll vine forest; SNMVF = simple notophyll-microphyll vine forest; SNMVT = simple notophyll-microphyll vine thicket.

Botanical authority: Flora of NSW (vols. 1-4 with revisions)

Table S1.4 Correlation values for alpha and beta trait components of 82 woody (tree and shrub) species from 100 plot samples. LA – leaf area; SS – seed size; Hmax – estimated maximum height at maturity; WD – wood density.

	beta_LA	alpha_LA	beta_SS	alpha_SS	beta_Hmax	alpha_Hmax	beta_WD	alpha_WD
beta_LA	1							
alpha_LA	0.53	1						
beta_SS	-0.01	-0.08	1					
alpha_SS	0.22	0.28	0.40	1				
beta_Hmax	0.88	0.42	-0.08	0.19	1			
alpha_Hmax	0.23	0.33	0.01	0.18	0.39	1		
beta_WD	0.10	0.10	-0.10	0.02	0.22	0.44	1	
alpha_WD	-0.09	0.03	0.16	0.17	-0.16	-0.09	-0.03	1

APPENDIX 4

Supplementary Materials for:

CHAPTER 5

Phylogenetic tests of community assembly across regional to continental scales in tropical and sub-tropical rainforests

Robert Kooyman[1,2], Maurizio Rossetto[2], William Cornwell[3,4] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia;*

[2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;* [3]*Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada.* [4]*Department of Integrative Biology, University of California, Berkeley, CA, USA.*

Background

Within the northern tropical region rainforests persisted in moist refugia through the LGM, with the rainforests in Wet Tropics occupying larger areas than the Cape York forests that were constrained to several key but smaller refugia. The evidence for this is based on interpretation of fossil pollen (eg. Kershaw *et al.*, 2007; Moss & Kershaw, 2007), macro-fossils (eg. Greenwood & Christophel, 2005), charcoal (Hopkins *et al.*, 1993, 1996), vegetation responses to environmental gradients (Webb, 1968; Kikkawa *et al.*, 1981) and floristic analysis (Webb *et al.*, 1984) that includes levels of endemism (Crisp *et al.*, 2001). Similar patterns have been assumed for the subtropical region of our study area where some rainforests (Nightcap-Border Ranges in particular) are conjectured to have persisted in larger areas through the LGM while others contracted more severely to small remnants (Adam, 1994). In both regions, inter-glacial expansion and re-establishment must have been either by dispersal from larger moist forest refugia, or from small remnants within local areas.

Additional detail of assemblage samples

Samples from Queensland included data collected from the area defined by the 30 nearest neighbour canopy – sub-canopy trees (largest stems) (Stanton & Fell, 2005), and similar sized spot-listed samples from Tracey (1982). Additional species data (for smaller free-standing woody species >1m only) were collected within the area defined by the larger tree sample. In New South Wales a 0.1 ha plot size was used with all woody species >1m included in the inventory (as for Qld). An examination and comparison of plot data for NSW (50 x 0.1ha plots with measured diameters included; Kooyman personal data) showed (on average) between 3-4 canopy and large sub-

canopy trees per 10m x 10m subplot. This provided confidence that the number of stems in each sample aligned closely across the two regions.

Climate data

Climate surfaces for Australia were generated in the program MATLAB (v. 7.0) from average monthly data for current conditions (1950-2000) (Hijmans *et al*., 2005). Raw climate data were based on weather station observations made by the Bureau of Meteorology in Australia (http://www.bom.gov.au/climate/cdo/about/supply.shtml). Data were interpolated to a resolution of 2.5 arc minutes and species and sample occurrences were matched to climate observations using Hawth's Tools for Spatial Ecology in Arc GIS (v. 7.2). At large scale, isothermality is correlated with latitude; at regional scales temperature and rainfall gradients are mostly tightly correlated with altitude (the most informative factor at that scale). Altitude can be correlated with soil type within regions, but generally not with nutrient ranking.

Phylogenetic structure metrics and background tree resolution

The response of phylogenetic structure metrics to variation in the background tree (resolution) has previously been investigated. Swenson (2009) found that unresolving the terminal nodes of a phylogeny had relatively little effect on NTI and NRI. Letcher (2009) further tested this at increased taxonomic scales (more taxa) and found that NRI values were minimally affected by terminal changes in tree resolution but NTI values were more sensitive. In that case, NTI revealed less phylogenetic structure than NRI, suggesting that care should be taken in interpreting results from NTI as the metric can underestimate non-random phylogenetic structure patterns in some cases (i.e. Type I errors).

Null models

Null model 0: species labels (or trait values) are shuffled across the entire phylogeny pool. Null model 1: random draw from the sample pool (only). Null model 2: random draw from the whole phylogeny pool selected (redundant for traits). Null model 3: matrix based independent swap algorithm (SIM9; Gotelli, 2000; Gotelli and Entsminger, 2003). Null models 0 and 2 behaved similarly across all pool sizes for both NRI and NTI. In contrast, null models 1 and 3 showed considerable variation across the range of combinations of null models in relation to pool sizes, and identified a considerably higher number of significant between-pool differences (online Appendix S2; Table S2.1). In our study null model 3 was very conservative (potential Type I errors), and null model 1 tended to reduce the phylogenetic structure signal of clustering (leading to reversed signals and potential Type II errors). SMA tests of the slope of the relationship between NRI and NTI relative to the null hypothesis ($H_0 = 1.0$) and null models (0,2) show opposing trends in relation to pool sizes in Qld (CY) versus NSW (NB, DO, and WA) that suggest the influence of different processes of community assembly (Table S2.4).

Null model selection

In relation to phylogenetic structure methods, null models allow us to detect and compare the signature and strength of niche-based processes in relation to different scenarios of trait evolution and community assembly. In empirical scenarios null models need to reflect underlying biological realities. Our findings show that (in this case) null model 1 (that shuffles species and trait values in the full sample) had a tendency to over randomise and thus reduce the signal of clustering, particularly at

smaller pool sizes. Null model 2 is based on random draws of species from the full phylogeny pool. This reflected what we thought was the closest to a test of the biological reality and our intended questions relative to the pool of available species. In general null model 2 provided similar results to null model 0 where species labels (or trait values) are shuffled across the entire phylogeny pool. Null model 3 retains row and column totals in the overall matrix and was very conservative in our study. This reflects the nature of the abundance sensitive matrix-based swap algorithm used in the model. Cavender-Bares *et al*. (2006) suggested this null model as more biologically realistic. However, the patterns in our data for null model 3 confirm their prediction of lower power to detect non-random phylogenetic structure when presence / absence data only are used.

Functional trait data

Species-level data for leaf size, wood traits (including density) and seed and fruit size were taken from published floras and other sources for all species in the sample (Cooper & Cooper, 2004; Hyland *et al*., 2003; Cornelissen *et al*., 2003). Minimum and maximum leaf sizes reported in the floras generally reflected the range of variation in leaf size on mature plants, and juvenile leaf sizes were excluded from consideration. Leaf size (as surface area) reported here is for whole simple leaves (and phyllodes) and for lateral leaflets of compound leaves. Leaf size (LA) was estimated using maximum leaf length and width, where Area = length*Width*0.70 (cm^2) which has been shown to correlate well with photographic area estimates of rainforest tree leaves (e.g. Kraft *et al*., 2008). Seed volume was calculated using maximum dimensions of embryo plus endocarp, and converted to dry weight mass (SDM) (following Moles *et al*., 2005). Wood density (WD) estimates for adults were

extracted from published sources, and where necessary converted from dry weight (kg m^{-3}) to basic density (Chave *et al*., 2009). In general Van Gelder *et al*., (2006) found that adult and juvenile wood density were well correlated across species, $r = 0.91$, P<0.001, giving confidence that trends are consistent across the range of variation in the size classes sampled. Where species-level data were missing for wood density we used genera and occasionally family level values (for some Qld species), so results for this trait should be viewed in that light. Estimated maximum height at maturity (H$_{max}$) was based on field information previously collected by RK for NSW that reflects maximum canopy height (m) for species (at largest known diameters, at reproductive maturity). For Qld the data for maximum height were extracted from the sources cited above for the other traits, and supplemented by RK where known. This provided a single value for maximum potential height for each species. Other traits available to us included maximum fruit length – FL (as a continuous measure).

Appendix S2

Table S2.1 Mean values for NRI (MPD metric) and NTI (MNTD metric) for the five areas; CY – Cape York, WT – Wet Tropics, NB – Nightcap / Border Ranges, DO – Dorrigo, and WA – Washpool by three species pool sizes (fp – full; r – regional; - loc – local) and four null models (3,2,1,0). Positive values represent clustering (grey); negative evenness.

Metric - Null - Pool	CY	WT	NB	DO	WA
NRI_3_f	0.056	-0.766	0.241	0.889	0.822
NRI_2_f	0.050	-0.789	0.254	0.916	0.825
NRI_1_f	-0.015	-0.831	0.164	0.820	0.740
NRI_0_f	0.007	-0.780	0.212	0.878	0.794
NRI_3_r	0.049	0.093	0.097	0.057	0.018
NRI_2_r	-0.212	-0.795	0.190	0.835	0.648
NRI_1_r	-0.222	-0.438	-0.354	0.195	-0.278
NRI_0_r	-0.208	-0.796	0.186	0.841	0.639
NRI_3_l	0.040	0.055	0.063	0.044	0.026
NRI_2_l	-0.481	-0.855	0.514	0.719	0.714
NRI_1_l	-0.288	-0.524	-0.477	-0.658	-0.462
NRI_0_l	-0.469	-0.868	0.454	0.631	0.613
NTI_3_f	-0.306	-0.851	0.245	0.897	0.912
NTI_2_f	0.006	-0.391	0.530	0.994	1.023
NTI_1_f	-0.205	-0.686	0.309	0.875	0.919
NTI_0_f	0.038	-0.390	0.556	1.003	1.034
NTI_3_r	-0.067	0.060	0.228	0.020	0.004
NTI_2_r	-0.091	-0.258	0.560	0.958	0.883
NTI_1_r	-0.148	-0.397	-0.126	0.192	-0.156
NTI_0_r	-0.080	-0.255	0.554	0.988	0.888
NTI_3_l	-0.011	0.045	0.191	0.024	-0.045
NTI_2_l	-0.140	-0.397	0.625	0.751	0.922
NTI_1_l	-0.135	-0.437	-0.317	-0.525	-0.240
NTI_0_l	-0.112	-0.380	0.605	0.712	0.866

Additional tests of phylogenetic structure indices

Two-dimensional comparisons of phylogenetic structure metrics were used to visualise and test for variation across the three pool sizes (Vamosi *et al*., 2009) (see S2; Fig. S2.1). T-tests were used to test the null hypothesis of no difference between the metrics in relation to null models and pool sizes (S2; Table S2.2), and no difference between areas (S2; Table S2.3). The fitting of standardised major axis (SMA) lines was undertaken to look at relationships within and between NRI / NTI, species pool sizes, and selected null models (Falster *et al*., 2003, 2006; Warton *et al*., 2006) (Table S2.4).

SMA methods

In relation to the fitting of standardised major axis (SMA) lines, key questions were about isometry (1:1) representing the null hypothesis (H_0; no difference between the metrics in relation to parameters) and coordination and comparisons within and between these measures in relation to null models and pool sizes; rather than about predicting one from the other (Warton *et al*., 2006). Tests equivalent to analysis of covariance (common slope, confidence intervals for slopes, and tests of the H_0) were implemented through the SMATR software (Falster *et al*., 2003, 2006; Warton *et al*., 2006).

Table S2.2 Results of un-paired t-tests to compare significance values for NRI and NTI across five areas (CY – Cape York; WT – Wet Tropics; NB – Nightcap-Border Ranges; DO – Dorrigo; WA – Washpool) in relation to four null models (0,1,2,3), and three species pool sizes (as combinations of full, regional and local). P-values in grey are significant at the ≤ 0.05 level.

Area	Pools_compare_	NRI_3	NTI_3	NRI_2	NTI_2	NRI_1	NTI_1	NRI_0	NTI_0
CY	full - regional	0.953	0.105	0.040	0.451	0.101	0.678	0.095	0.360
CY	full - local	0.902	0.042	0.000	0.260	0.033	0.608	0.000	0.241
CY	regional - local	0.952	0.682	0.041	0.701	0.616	0.923	0.050	0.800
WT	full - regional	0.000	0.000	0.960	0.270	0.001	0.026	0.891	0.262
WT	full - local	0.000	0.000	0.578	0.960	0.008	0.065	0.462	0.936
WT	regional - local	0.761	0.905	0.617	0.252	0.455	0.754	0.551	0.301
NB	full - regional	0.255	0.899	0.618	0.790	0.000	0.001	0.842	0.988
NB	full - local	0.168	0.706	0.052	0.450	0.000	0.000	0.073	0.696
NB	regional - local	0.798	0.801	0.016	0.603	0.316	0.170	0.048	0.685
DO	full - regional	0.000	0.000	0.512	0.704	0.000	0.000	0.763	0.873
DO	full - local	0.000	0.000	0.135	0.021	0.000	0.000	0.060	0.005
DO	regional - local	0.921	0.977	0.355	0.074	0.000	0.000	0.091	0.017
WA	full - regional	0.000	0.000	0.363	0.307	0.000	0.000	0.432	0.284
WA	full - local	0.000	0.000	0.584	0.529	0.000	0.000	0.370	0.288
WA	regional - local	0.973	0.827	0.749	0.828	0.371	0.688	0.895	0.900

Table S2.3 Results of un-paired t-tests to compare significance values for NRI and NTI across five areas (CY – Cape York; WT – Wet Tropics; NB – Nightcap-Border Ranges; DO – Dorrigo; WA – Washpool) in relation to null model 2 and the regional species pool.

	NRI_2_reg	NTI_2_reg
CY - DO	0.000	0.000
CY - NB	0.002	0.000
CY - WA	0.000	0.000
CY - WT	0.000	0.167
DO - NB	0.000	0.000
DO - WA	0.252	0.612
DO - WT	0.000	0.000
NB - WA	0.012	0.040
NB - WT	0.000	0.000
WA - WT	0.000	0.000

Table S2.4 Results of SMA tests for comparisons of slope and intercept for NRI (x-axis) vs NTI (y-axis) across five areas (1=CY – Cape York; 2=WT – Wet Tropics; 3=NB – Nightcap-Border Ranges; 4=DO – Dorrigo; 5=WA – Washpool) in relation to two null models (0,2), three species pool sizes (fp – full; reg – regional; loc – local), and the null hypothesis $H_0 = 1.0$ for slope (β). P-values in grey are significant after Bonferroni correction.

AREA	Group	R2	Slope	Intercept	F-value	p-value
	NRI vs NTI by group					$H_0 = 1.0$
CY	0_fp	0.640	0.988	0.031	0.061	0.806
CY	2_fp	0.641	1.029	-0.045	0.308	0.580
CY	0_r	0.634	1.010	0.131	0.034	0.854
CY	2_r	0.643	1.006	0.122	0.013	0.908
CY	0_loc	0.712	0.919	0.319	3.400	0.067
CY	2_loc	0.706	0.932	0.308	2.336	0.129
WT	0_fp	0.591	1.056	0.433	1.037	0.310
WT	2_fp	0.580	1.052	0.439	0.884	0.349
WT	0_r	0.639	0.957	0.507	0.784	0.377
WT	2_r	0.640	0.947	0.495	1.175	0.280
WT	0_loc	0.672	1.051	0.532	1.087	0.299
WT	2_loc	0.661	1.066	0.514	1.749	0.188
NB	0_fp	0.561	0.866	0.372	6.604	0.011
NB	2_fp	0.558	0.892	0.303	4.111	0.045
NB	0_r	0.565	0.852	0.396	8.251	0.005
NB	2_r	0.562	0.871	0.394	6.013	0.015
NB	0_loc	0.833	0.987	0.157	0.138	0.711
NB	2_loc	0.826	0.989	0.117	0.098	0.755
DO	0_fp	0.721	0.623	0.456	107.889	0.000
DO	2_fp	0.715	0.645	0.404	90.002	0.000
DO	0_r	0.808	0.924	0.211	4.128	0.044
DO	2_r	0.817	0.927	0.183	3.901	0.050
DO	0_loc	0.809	0.923	0.130	4.247	0.041
DO	2_loc	0.820	0.920	0.089	4.884	0.029
WA	0_fp	0.816	0.551	0.596	89.121	0.000
WA	2_fp	0.831	0.571	0.552	84.817	0.000
WA	0_r	0.878	0.798	0.378	17.439	0.000
WA	2_r	0.884	0.807	0.360	16.431	0.000
WA	0_loc	0.847	0.929	0.297	1.442	0.237
WA	2_loc	0.860	0.924	0.263	1.856	0.181

Discussion of results in Table S2.4

Comparisons between NRI and NTI using major axis tests (SMATR package; Falster *et al*. 2006) across all scales and for different null models and pool sizes provided some statistically significant values in relation to line fitting and the null hypothesis ($H_0 = 1.0$) that equates with isometry (1:1). In relation to NRI vs. NTI and null models (0,2) significant shifts (after Bonferroni correction) occurred in relation to slope (β) at full pool size for DO, and for WA at full and regional pool size (Table S2.4 includes R^2 values). When the level of significance was relaxed to ≤0.05 all areas in NSW at regional and full pool sizes (null models 0,2) returned significant P-values for tests of the null hypothesis. In Qld only CY got close to significance at local pool size.
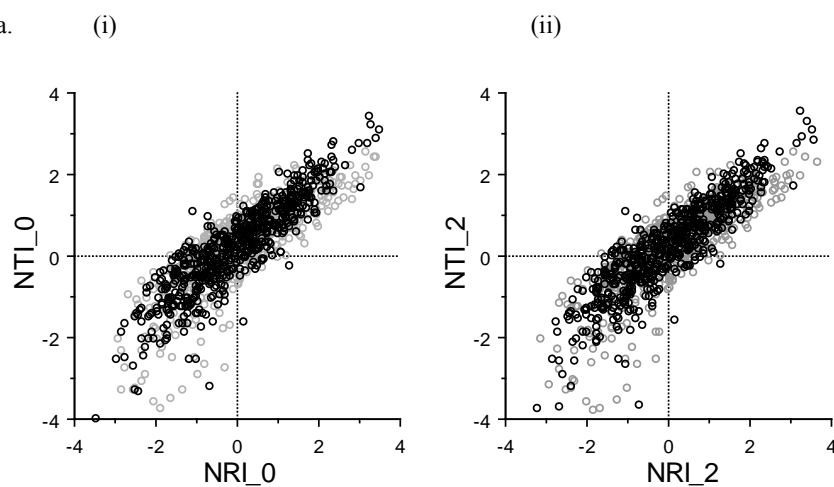
Appendix S2 (Fig. S2)

Figure S2a.   (i)   (ii)

Figure S2b.   (i)   (ii)
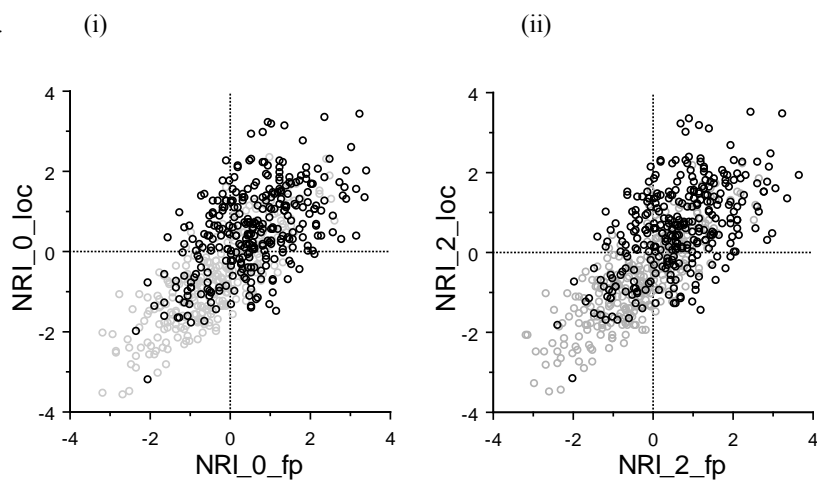

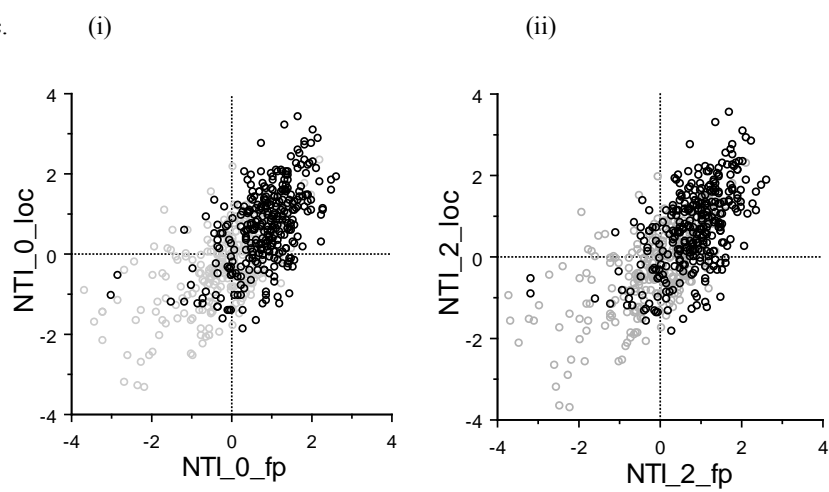Figure S2c.   (i)   (ii)

Figure S2 (a-c) Bivariate graphs for 596 samples. a. (i) NRI vs NTI; null model 0 and two pool sizes (full pool grey circles; local pool black circles); a. (ii) NRI vs NTI; null model 2 and two pool sizes (full pool grey circles; local pool black circles); b. (i) NRI full pool size, null model 0 (NRI_0_fp) vs NRI local pool size, null model 0 (NRI_0_loc); b. (ii) NRI full pool size, null model 2 (NRI_2_fp) vs NRI local pool size, null model 2 (NRI_2_loc) for two regions (far north Queensland grey circles; northern New South Wales black circles); c. (i) NTI full pool size, null model 0 (NTI_0_fp) vs NTI local pool size, null model 0 (NTI_0_loc); and c. (ii) NTI full pool size, null model 2 (NTI_2_fp) vs NTI local pool size, null model 2 (NTI_2_loc); for two regions (far north Queensland open grey circles; northern New South Wales open black circles). Scales on graph A were truncated at –4 to allow direct comparison with other graphs; only a small number of plots were removed by doing so.

Discussion related to multidimensional approaches

The overview of patterns of the relationship of NRI to NTI in relation to full to local pool sizes and null models 0,2 (Appendix S2; Fig. S2a-c) shows little difference across the whole sample. The absence of clumping of clusters in the comparisons between NRI and NTI suggests that the underlying tree is balanced, providing confidence that the measures of NRI derived from MPD do not simply reflect the behaviour of the metric in response to sample size (Vamosi *et al.*, 2009).

Table S2.5 Mean trait dispersion values as SES (standardised effect size) for MNTD (mean nearest taxon trait distance) and MPD (mean pairwise trait distance) for five traits (FL- fruit length as largest dimension; Hmax – estimated maximum height at maturity; LA – leaf area, SDM – seed dry mass, WD – wood density) at full species

pool size (full) and null model (0) in the five areas (CY – Cape York, WT – Wet Tropics, NB – Nightcap-Border Ranges, DO - Dorrigo,WA - Washpool). In the case of SES values: negative values represent clustering; positive evenness (opposite to NRI and NTI). Data sources: Kooyman *personal data*; Hyland *et al.*, (2003) CSIRO; Cooper and Cooper (2004); Kanowski *unpubl.* for WD synthesis in Qld.

Trait	Sample	mntd_full	mpd_full
FL	CY	0.460	-0.563
FL	WT	0.146	-0.496
FL	NB	-0.325	-1.134
FL	DO	-0.373	-0.863
FL	WA	-0.884	-1.175
Hmax	CY	0.437	-1.343
Hmax	WT	0.408	-2.185
Hmax	NB	0.330	-1.010
Hmax	DO	0.461	-0.438
Hmax	WA	0.477	-0.963
LA	CY	0.359	-0.790
LA	WT	0.383	-1.326
LA	NB	-0.090	-0.525
LA	DO	-0.140	-0.071
LA	WA	-0.003	-0.725
SDM	CY	0.152	-1.342
SDM	WT	0.227	-0.425
SDM	NB	-0.066	-0.151
SDM	DO	-0.385	0.143
SDM	WA	-0.403	-0.002
WD	CY	0.044	-0.308
WD	WT	-0.064	-0.265
WD	NB	-0.108	0.773
WD	DO	0.138	0.036
WD	WA	0.176	-0.009

Appendix S3 References cited in Appendices (but not included in main text)

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. and Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351-366.

Cooper, W. and Cooper, W.T. (2004) *Fruits of the Australian Tropical Rainforest*. Nokomis Editions. Melbourne.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. and Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G,J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P. and Linder, H.P. (2009) Phylogenetic biome conservatism on a global scale. *Nature*, doi:10.1038/nature07764.

Falster, D.S., Warton, D.I. and Wright I.J. (2006) Updated user's guide to SMATR: Standardised Major Axis Tests and Routines, Version 2.0.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606-2621.

Gotelli, N.J. and Entsminger, G. (2003) Swap algorithms in null model analysis. *Ecology*, **84**, 532-535.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Hopkins, M.S., Ash, J., Graham, A.W., Head, J. and Hewett, R.K. (1993) Charcoal evidence of the spatial extent of *Eucalyptus* woodland expansions and rainforest contractions in north Queensland during the late Pleistocene. *Journal of Biogeography*, **20**, 357-372.

Hopkins, M.S., Head, J., Ash, J., Hewett, R.K. and Graham, A.W. (1996) Evidence of a Holocene and continuing recent expansion of lowland rainforest in humid tropical North Queensland. *Journal of Biogeography*, **23**, 737-745.

Hyland, B.P.M., Whiffin, T., Christophel, D.C., Gray, B. and Elick, R.W. (2003) Australian Tropical Rain Forest Plants – Trees, Shrubs and Vines. CSIRO Publishing. Melbourne.

Kraft, N.J.B., Valencia, R. and Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580-582.

Letcher, S.G. (2009) Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society - Biology* doi: 10.1098/rspb. 2009.0865

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B., Pitman, A.J. and Westoby, M. (2005) Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences*, USA **102**(30), 10540-10544.

Moss, P.T. and Kershaw, A.P. (2007) A late Quaternary palynological record (oxygen isotope stages 1 to 7) for the humid tropics of northeastern Australia based on ODP site 20. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 4-22.

Swenson, N.G. (2009) Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. (doi:10.1371/journal.pone.0004390)

van Gelder H.A., Poorter, L. and Sterck, F.J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest community. *New Phytologist*, **171**, 367-378.

Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M. (2006) Bivariate line fitting methods for allometry. *Biological Reviews*, **81**(2), 259-291.

APPENDIX 5

Supplementary Materials for:

CHAPTER 6

Australian tropical and sub-tropical rainforest: functional biogeography, phylogeny, and environmental gradients

Robert Kooyman[1,2], Maurizio Rossetto[2], William Cornwell[3,4], Chris Allen[2] and Mark Westoby[1]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109, Australia;* [2]*National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia;* [3]*Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver BC, Canada.* [4]*Department of Integrative Biology, University of California, Berkeley, CA, USA.*

Table S1.1 Climate and environmental variables used for model selection (AIC) in relation to determination of trait and niche conservatism.

Environmental Factors
 Precipitation of Wettest Month
 Precipitation of Driest Quarter
 Max Temperature of Warmest Month
 Min Temperature of Coldest Month
 Mean Temperature of Warmest Quarter
Annual Mean Temperature
 Mean Temperature of Coldest Quarter
 Mean Temperature of Wettest Quarter
 Temperature Seasonality (standard deviation *100)
 Precipitation of Warmest Quarter
 Annual Precipitation
 Mean Temperature of Driest Quarter
 Precipitation of Wettest Quarter
 Temperature Annual Range
 Precipitation of Driest Month
 Precipitation of Coldest Quarter
 Mean Diurnal Range (Mean of monthly (max temp - min temp))
 Isothermality
 Precipitation Seasonality (Coefficient of Variation)
 Soil Types
 Altitude

Climate data

Climate surfaces for Australia were generated in the program MATLAB (v. 7.0) from average monthly data for current conditions (1950-2000) (Hijmans *et al*. 2005). Raw climate data were based on weather station observations made by the Bureau of Meteorology in Australia (http://www.bom.gov.au/climate/cdo/about/supply.shtml). Data were interpolated to a resolution of 2.5 arc minutes and species and sample occurrences were matched to climate observations using Hawth's Tools for Spatial Ecology in Arc GIS (v. 7.2). At large scale, isothermality is correlated with latitude; at regional scales temperature and rainfall gradients are mostly tightly correlated with altitude (the most informative factor at that scale). Altitude can be correlated with soil type, but generally not with nutrient ranking.

Soil rating as potential rainforest plant nutrient supply in Australia

Basalt – 9.0; basic volcanics – 8.0; alluvium – 7.0 (or source rock plus 1.0); acid volcanics – 6.0; granite – 5.5; metamorphics – 4.5; limestone – 4.0; sandstone – 3.0; sand – 1.5; laterite – 1.0; bauxite – 0.7 (Nix 1991).

Results of tests for trait and niche conservatism

Table S1.2. Outputs from model as *K* statistics. Trait conservatism was described quantitatively: $K = 1$ indicates that traits perfectly met a (random) Brownian motion expectation, while $K > 1$ indicates that traits are more conserved than that expectation. Values > 1.0 indicate trait and species conservatism across the full sample relative to the phylogeny. Cases where $K < 1$ indicate that traits are less conserved (more convergent) than a Brownian expectation. Code: ts = species trait means. Niche conservatism is evident where $K < 1$ for environmental 'traits'. Species with similar conserved traits occur in similar habitats (i.e. they are convergent in conserved habitats).

TRAIT	K
ts_Leaf Area	1.457
ts_Seed Dry Mass	1.329
ts_Wood Density	1.832
ts_Height maximum	0.881
Species mean altitude	0.856
Species mean precipitation seasonality	0.457
Species mean isothermality	0.451
Species mean soil	0.456

Appendix S2

Taxonomic relationships, tropics versus sub-tropics

Taxonomic patterns

The mean ratio of genera to species in the Australian tropical and sub-tropical assemblage samples (0.89) was only slightly lower than the mean reported for the neo-tropics (0.94; Enquist *et al*., 2002; and see *Rice and Westoby 1983). Across the two latitude regions and five areas the ratios and slopes of the relationships of numbers of families to number of genera and species were broadly similar (Table S2.1; Fig. S2.1). However, significant shifts in taxonomic relationships between the latitude regions and areas within regions were identified using standardized major axis tests (SMA; Warton *et al*., 2006). Differences were evident as shifts along the common slopes, and in relation to elevation from the slopes (Tables S2.2 & S2.3). In contrast, SMA tests showed no significant relationship between altitude and species richness, and altitude and taxonomic ratios, in relation to the full sample, the latitude regions, or areas within the regions (results not presented).

Table S2.1 Taxonomic ratios for number of genera to species, family to species and family to genera for two latitude regions (tropics and sub-tropics) and five areas. CY-Cape York; WT-Wet Tropics; NB-Nightcap Border Ranges; DO-Dorrigo; WA-Washpool.

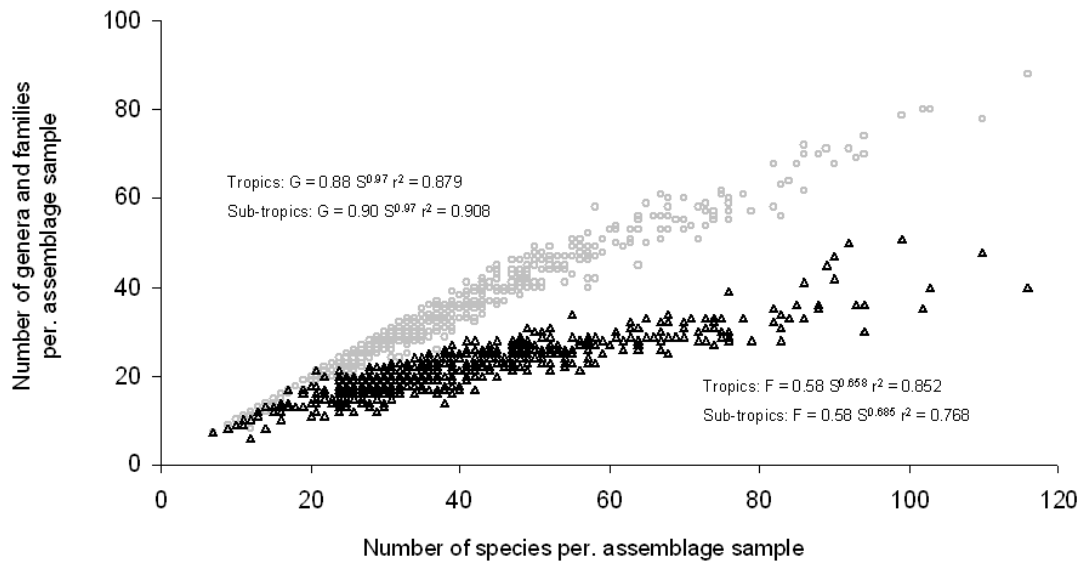| Area	Genera-species	Family-species	Family-genera	Region
CY	0.92	0.64	0.69	tropics
WT	0.84	0.54	0.62	tropics
NB	0.89	0.53	0.59	sub-tropics
DO	0.92	0.61	0.66	sub-tropics
WA	0.91	0.66	0.72	sub-tropics

Figure S2.1 Scatterplot showing number of species by number of genera and number of families for 596 assemblage samples across two latitude regions (tropics and sub-tropics). G – genus to species ratio as mean by region (open grey symbols); F – family to species ratio as mean by region (open black symbols); S – slope (as part of SMA outputs for group comparisons); r^2 – r-squared values. Tables S2.1 & S2.2 provide details of comparisons (using log scaled values for species, genera and families), including slopes and intercepts, and tests for common slope (including movement along and away from the common slope) for all areas in the two regions.

Tables S2.2 & S2.3 provide results of SMA tests of taxonomic relationships across regions and areas.

*Rice, B. and M. Westoby (1983) Plant species richness at the 0.1 hectare scale in the Australian vegetation compared to other continents. *Vegetatio*, **52**(3), 129-140.

Table S2.2 Synthesis of results from SMA (standardised major axis tests in regression) for slope and intercept values for relationships of log scaled values of number of species, genera and families in five areas: CY – Cape York; WT – Wet Tropics; NB – Nightcap Border Ranges; DO – Dorrigo; WA – Washpool; and two latitude regions – tropics and sub-tropics. Results of tests for common slope and R-squared (R^2) values shown.

AREA	R^2	Slope	Intercept
genera x species			
CY	0.975	0.905	0.109
WT	0.970	0.897	0.093
NB	0.963	0.874	0.152
DO	0.950	0.975	0.002
WA	0.982	0.903	0.099
common slope		0.905	
families x species			
CY	0.851	0.649	0.332
WT	0.877	0.714	0.183
NB	0.757	0.658	0.271
DO	0.699	0.862	-0.014
WA	0.864	0.749	0.177
common slope		0.704	
families x genera			
CY	0.876	0.717	0.254
WT	0.906	0.796	0.109
NB	0.801	0.752	0.157
DO	0.743	0.884	-0.016
WA	0.898	0.829	0.096
common slope		0.780	
TWO GROUP			
genera x species			
tropics	0.97	0.879	0.136
sub-tropics	0.97	0.908	0.098
common slope		0.894	
families x species			
tropics	0.852	0.658	0.296
sub-tropics	0.768	0.685	0.241
common slope		0.669	
families x genera			
tropics	0.891	0.749	0.195
sub-tropics	0.806	0.755	0.167
common slope		0.751	

Table S2.3 Synthesis of results from SMA (standardised major axis tests in regression) for comparisons among groups for common slope of relationships of log scaled values for number of species, genera and families in five areas: CY – Cape York; WT – Wet Tropics; NB – Nightcap Border Ranges; DO – Dorrigo; WA – Washpool; and two latitude regions – tropics (trop.) and sub-tropics (sub-t.). Results in order shown for each of the five areas are: common slope, test statistic (F), p-value (0.05 significant). For the two latitude regions: as above for genera by species; and as difference, standard error, df, and p-value (for shifts along the common slope) for family by species, and family by genera.

| | Area interactions: | Comm-slope, f, p-val. | | | |
	CY	WT	NB	DO	WA
	genera x species				
CY	1	(0.901 ,0.177 ,0.680)	(0.892 ,2.636 ,0.103)	(0.926 ,9.319 ,0.001)	(0.904 ,0.004 ,0.944)
WT	(0.901 ,0.177 ,0.680)	1	(0.887 ,1.449 ,0.210)	(0.922 ,11.027,0.001)	(0.899 ,0.067 ,0.815)
NB	(0.892 ,2.636 ,0.103)	(0.887 ,1.449 ,0.210)	1	(0.912 ,17.162,0.001)	(0.885 ,1.506 ,0.222)
DO	(0.926 ,9.319 ,0.001)	(0.922 ,11.027,0.001)	(0.912 ,17.162,0.001)	1	(0.941 ,6.677 ,0.010)
WA	(0.904 ,0.004 ,0.944)	(0.899 ,0.067 ,0.815)	(0.885 ,1.506 ,0.222)	(0.941 ,6.677 ,0.010)	1
	families x species				
CY	1	(0.684 ,4.728 ,0.032)	(0.652 ,0.070 ,0.789)	(0.706 ,22.092,0.001)	(0.671 ,4.479 ,0.031)
WT	(0.684 ,4.728 ,0.032)	1	(0.695 ,2.559 ,0.112)	(0.749 ,10.558,0.003)	(0.721 ,0.523 ,0.457)
NB	(0.652 ,0.070 ,0.789)	(0.695 ,2.559 ,0.112)	1	(0.736 ,16.959,0.001)	(0.688 ,3.201 ,0.080)
DO	(0.706 ,22.092,0.001)	(0.749 ,10.558,0.003)	(0.736 ,16.959,0.001)	1	(0.812 ,3.397 ,0.059)
WA	(0.671 ,4.479 ,0.031)	(0.721 ,0.523 ,0.457)	(0.688 ,3.201 ,0.080)	(0.812 ,3.397 ,0.059)	1
	families x genera				
CY	1	(0.762 ,6.928 ,0.010)	(0.730 ,1.005 ,0.313)	(0.762 ,14.390,0.001)	(0.744 ,5.902 ,0.013)
WT	(0.762 ,6.928 ,0.010)	1	(0.782 ,1.485 ,0.221)	(0.816 ,4.051 ,0.040)	(0.802 ,0.514 ,0.467)
NB	(0.730 ,1.005 ,0.313)	(0.782 ,1.485 ,0.221)	1	(0.804 ,7.317 ,0.006)	(0.780 ,2.316 ,0.133)
DO	(0.762 ,14.390,0.001)	(0.816 ,4.051 ,0.040)	(0.804 ,7.317 ,0.006)	1	(0.858 ,0.922 ,0.317)
WA	(0.744 ,5.902 ,0.013)	(0.802 ,0.514 ,0.467)	(0.780 ,2.316 ,0.133)	(0.858 ,0.922 ,0.317)	1

| | Regional comparisons: | |
	tropics	sub-tropics
	genera x species	Comm-slope, f, p-val.
trop	1	(0.894 ,5.187 ,0.017)
sub-t.	(0.894 ,5.187 ,0.017)	1
	families x species	Diff., SE., df., p-val.
trop	1	(0.070 ,12.520,1 ,0.000)
sub-t.	(0.070 ,12.520,1 ,0.000)	1
	families x genera	Diff., SE., df., p-val.
trop	1	(0.064 ,10.431,1 ,0.001)
sub-t.	(0.064 ,10.431,1 ,0.001)	1

Table S2.4 Synthesis of results from Trait Gradient Analysis for evergreen, semi-deciduous and deciduous components of the tree and shrub flora of CY – Cape York in far north Queensland. LA – leaf area; SDM – seed dry mass; Hmax – maximum estimated height at maturity; and WD – basic wood density; min., minimum; max., maximum; t_{is} species trait mean; β_{is} beta trait value; α_{is} alpha trait value; R_{is} niche breadth as means, minimum and maximum by area and for all combined; R_{is} *Nos. singletons* number of species in area that occur only once in samples; p_{js} plot mean trait value.

		Traits (units, transformations)			
		LA	SDM	Hmax	WD*
Area	Parameter	(cm^2, log10)	(mg, log10)	(m, log10)	(mg cm^{-3})
CY	Non-deciduous (evergreen)				
	Plot characteristics				
	p_{js} mean	1.89	1.84	1.24	0.57
	p_{js} min-max	1.45, 2.11	0.98, 2.23	0.96, 1.40	0.50, 0.61
	p trait value (range)	0.76, 2.59	-0.18, 3.43	0.51, 1.63	0.35, 0.77
CY	Semi-deciduous				
	Plot characteristics				
	p_{js} mean	1.88	1.84	1.22	0.54
	p_{js} min-max	1.50, 2.13	1.39, 2.17	1.01, 1.47	0.46, 0.61
	p trait value (range)	0.76, 2.64	-0.04, 3.47	0.58, 1.63	0.31, 0.75
CY	Deciduous				
	Plot characteristics				
	p_{js} mean	1.83	1.71	1.12	0.56
	p_{js} min-max	1.67, 2.08	1.34, 2.07	0.96, 1.28	0.51, 0.61
	p trait value (range)	0.97, 2.70	0.35, 3.06	0.56, 1.55	0.31, 0.74

Table S2.5 Synthesis of results from SMA (standardised major axis tests in regression) for comparisons among groups of the relationship of NRI and NTI to log scaled values for four traits, seed dry mass, leaf area, maximum height at maturity, and (basic) wood density across the full sample, and two latitude regions (tropics and sub-tropics). Phylo-meas. – phylogenetic measures as net relatedness index (NRI), and nearest related taxon index (NTI); n – number of assemblage level samples; R^2 – r-squared values; values for slope and intercept of the linear relationship of the variables; and p-val. – p-values representing statistical significance (<0.05).

Seed Dry Mass	phylo- meas.	R^2	slope	intercept	p-values
Full Sample (n=596)	NRI	0.297	-0.2765	1.659	< 0.001
	NTI	0.205	-0.3063	1.719	< 0.001
Latitude Regions					
Tropics (n=286)	NRI	0.097	-0.2019	1.813	< 0.001
	NTI	0.005	-0.2059	1.849	0.257
sub-tropics (n=310)	NRI	0.24	-0.1807	1.484	< 0.001
	NTI	0.116	-0.2354	1.561	< 0.001
Leaf Area					
Full Sample (n=596)	NRI	0.193	-0.16	1.761	< 0.001
	NTI	0.147	-0.1772	1.796	< 0.001
Latitude Regions					
Tropics (n=286)	NRI	0.018	-0.1027	1.862	0.022
	NTI	0.004	0.1047	1.922	0.294
sub-tropics (n=310)	NRI	0.073	-0.105	1.655	< 0.001
	NTI	0.024	-0.1368	1.699	0.007
Maximum Height					
Full Sample (n=596)	NRI	0.002	-0.07101	1.302	0.301
	NTI	0.018	0.07866	1.268	0.001
Latitude Regions					
Tropics (n=286)	NRI	0.107	-0.08532	1.229	< 0.001
	NTI	0.005	-0.08699	1.244	0.247
sub-tropics (n=310)	NRI	0.004	-0.05738	1.356	0.223
	NTI	0.002	0.07475	1.262	0.427
Wood density					
Full Sample (n=596)	NRI	0.027	0.01734	2.761	< 0.001
	NTI	0.008	0.01921	2.757	0.027
Latitude Regions					
Tropics (n=286)	NRI	0.009	-0.01604	2.748	0.114
	NTI	0.035	-0.01636	2.751	0.001
sub-tropics (n=310)	NRI	0.002	0.01814	2.761	0.385
	NTI	0.006	-0.02364	2.791	0.189

Trait frequencies

Within latitude regions local area differences were evident but relatively weak for shifts in trait frequencies in size classes, except for SDM (frequency distribution and range) in Washpool (Table 2 main article; Figs S2.2 and S2.4) and height in Cape York (Fig. S2.5).
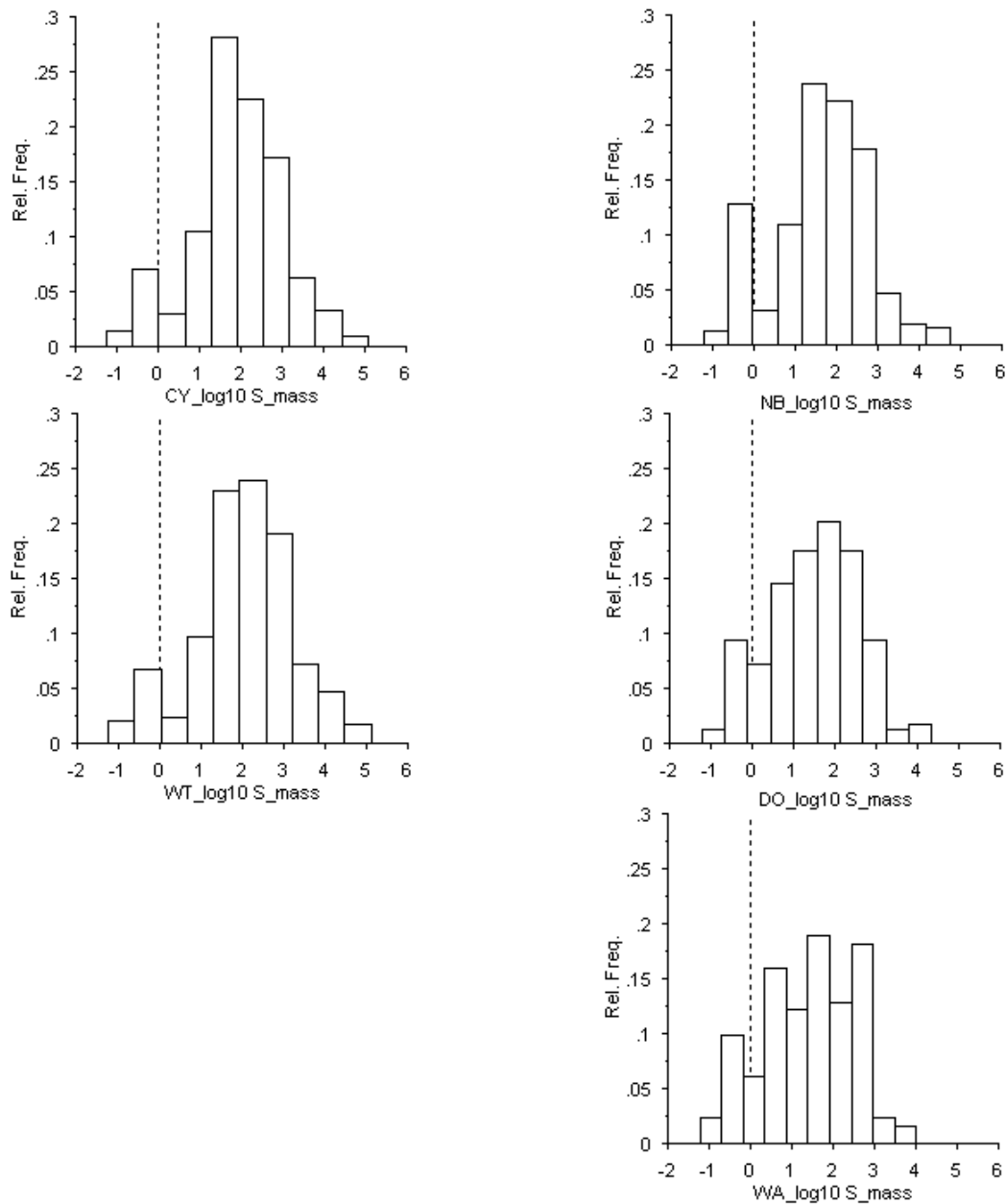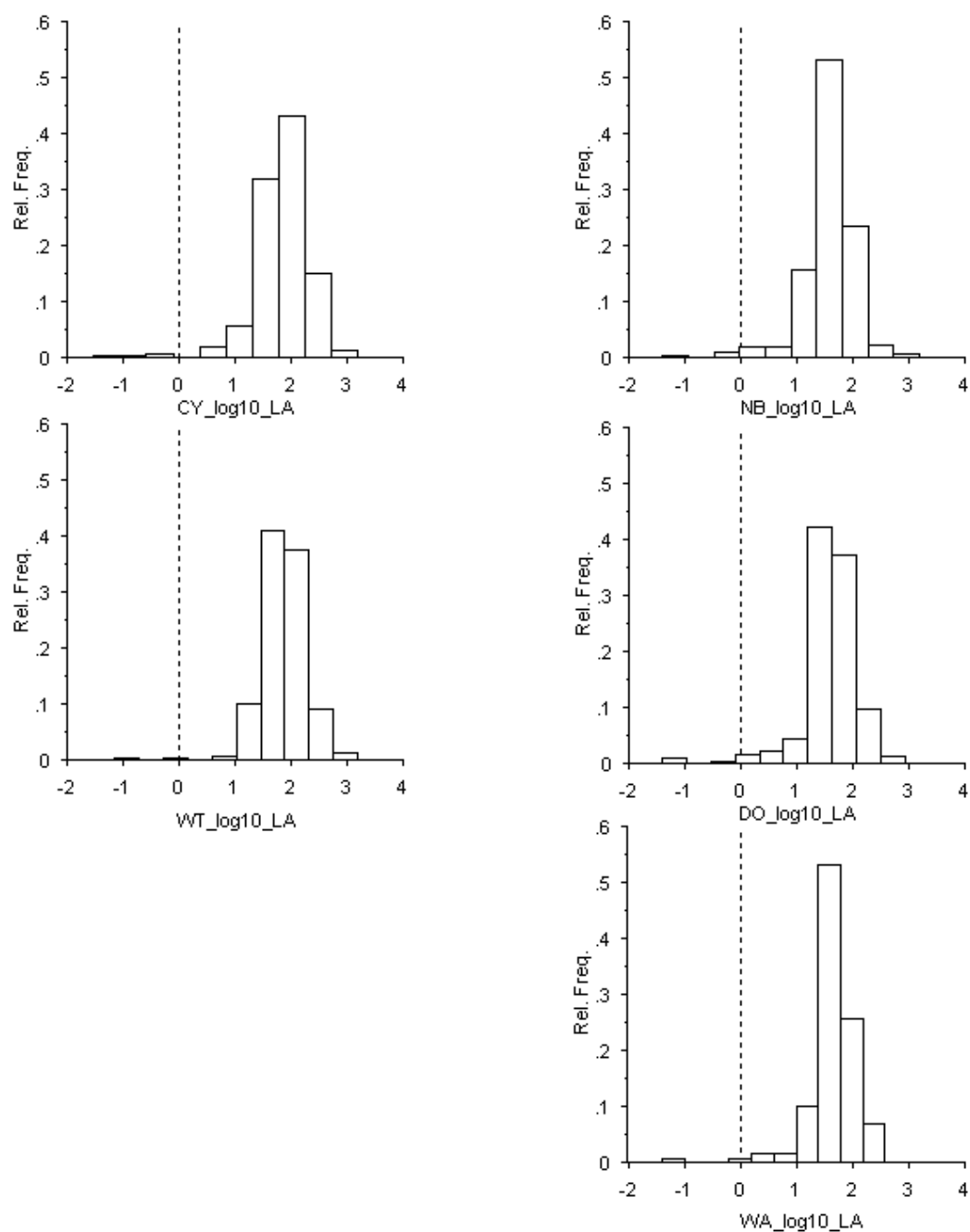

Figure S2.2 Histograms of relative frequency (Rel. Freq.) of log10 seed dry mass (S_mass) in ten size classes in each of five areas in two latitude regions: CY - Cape York and WT – Wet Tropics in the tropics; and NB – Nightcap Border Ranges, DO – Dorrigo and WA - Washpool in the sub-tropics.

Figure S2.3 Histograms of relative frequency (Rel. Freq.) of log10 leaf area (LA) in ten size classes in each of five areas in two latitude regions: CY - Cape York and WT – Wet Tropics in the tropics; and NB – Nightcap Border Ranges, DO – Dorrigo and WA - Washpool in the sub-tropics.
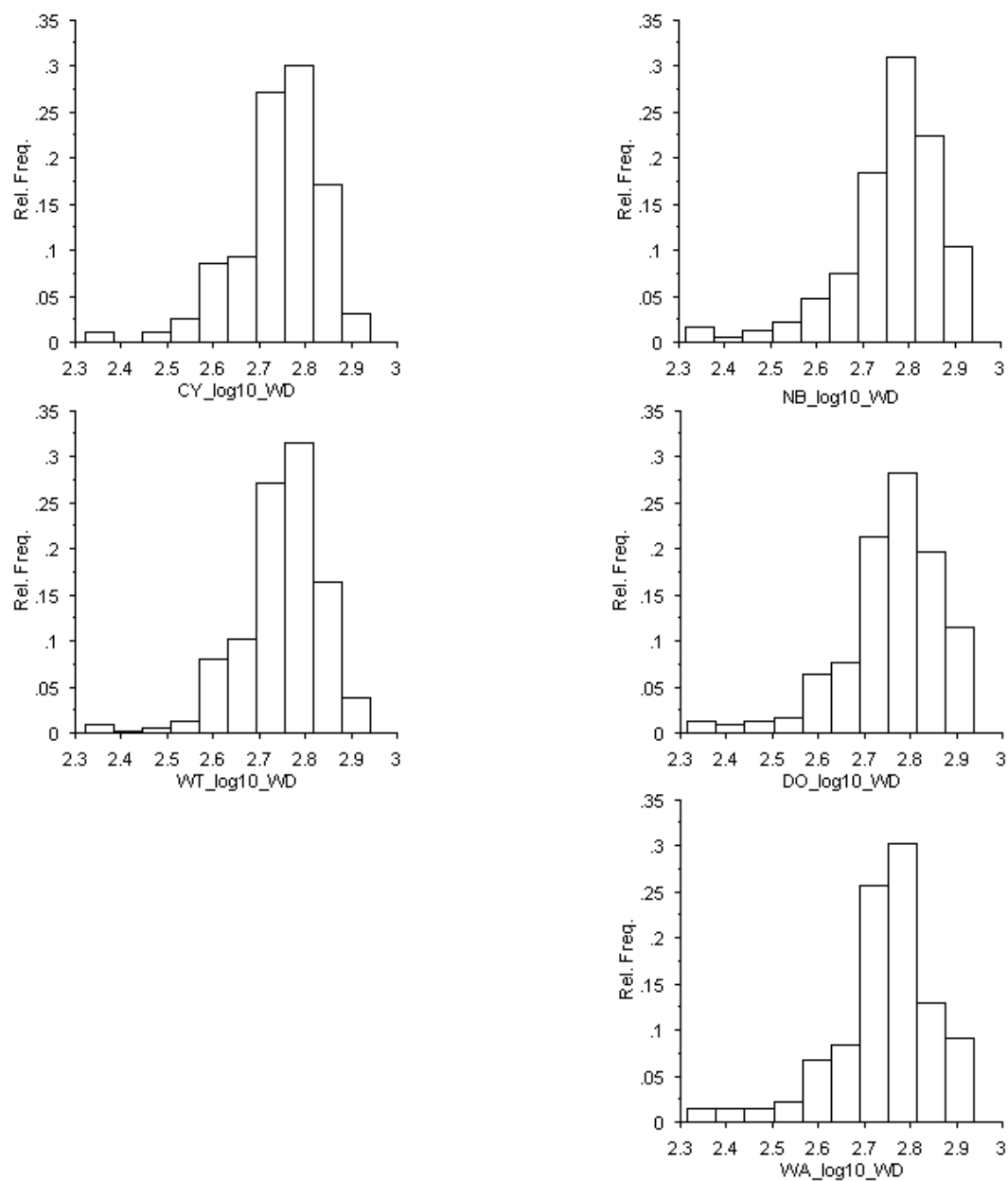
Figure S2.4 Histograms of relative frequency (Rel. Freq.) of log10 wood density (WD) in ten size classes in each of five areas in two latitude regions: CY - Cape York and WT – Wet Tropics in the tropics; and NB – Nightcap Border Ranges, DO – Dorrigo and WA - Washpool in the sub-tropics.
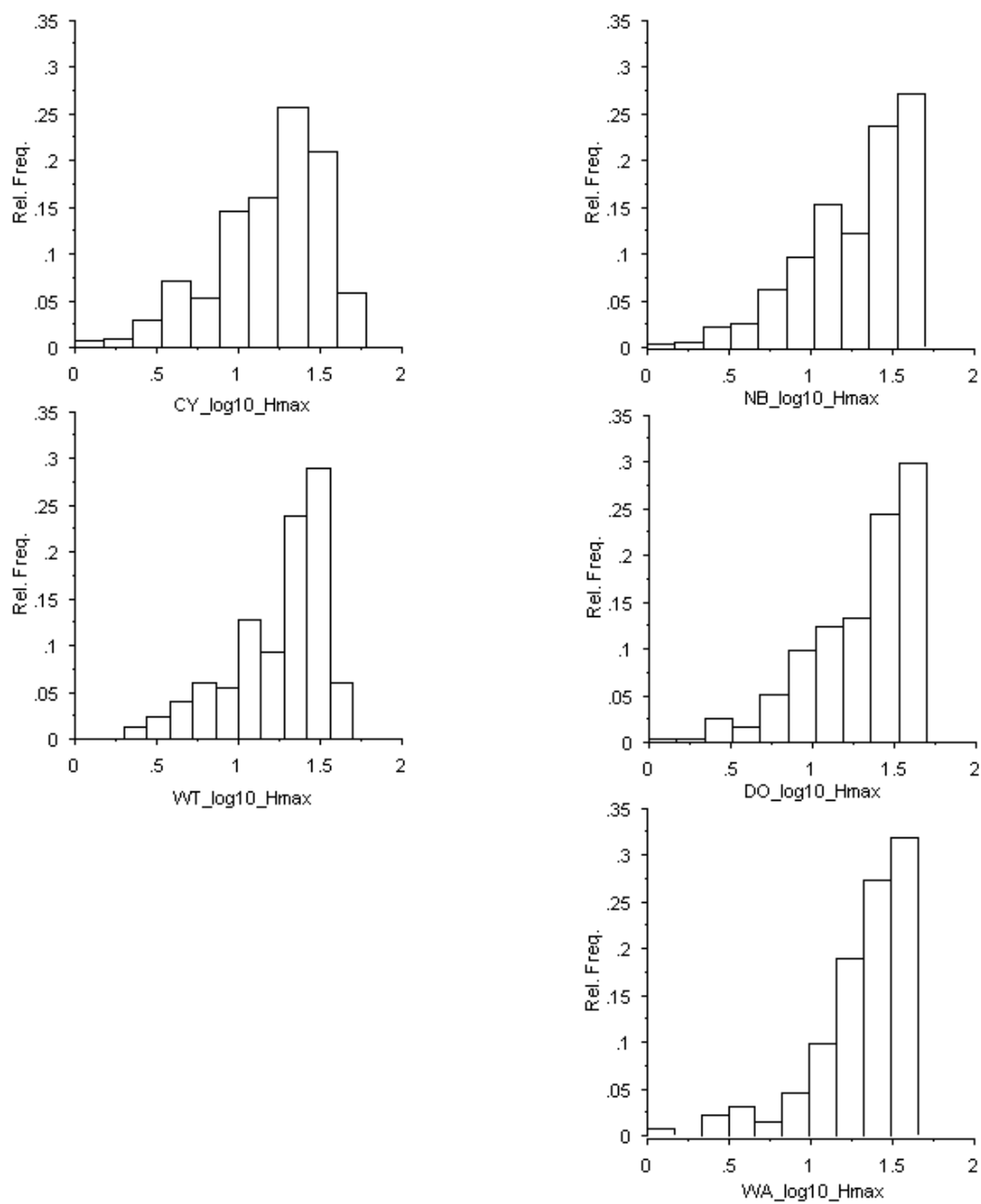
Figure S2.5 Histograms of relative frequency (Rel. Freq.) of log10 estimated maximum height at maturity (Hmax) in ten size classes in each of five areas in two latitude regions: CY - Cape York and WT – Wet Tropics in the tropics; and NB – Nightcap Border Ranges, DO – Dorrigo and WA - Washpool in the sub-tropics.
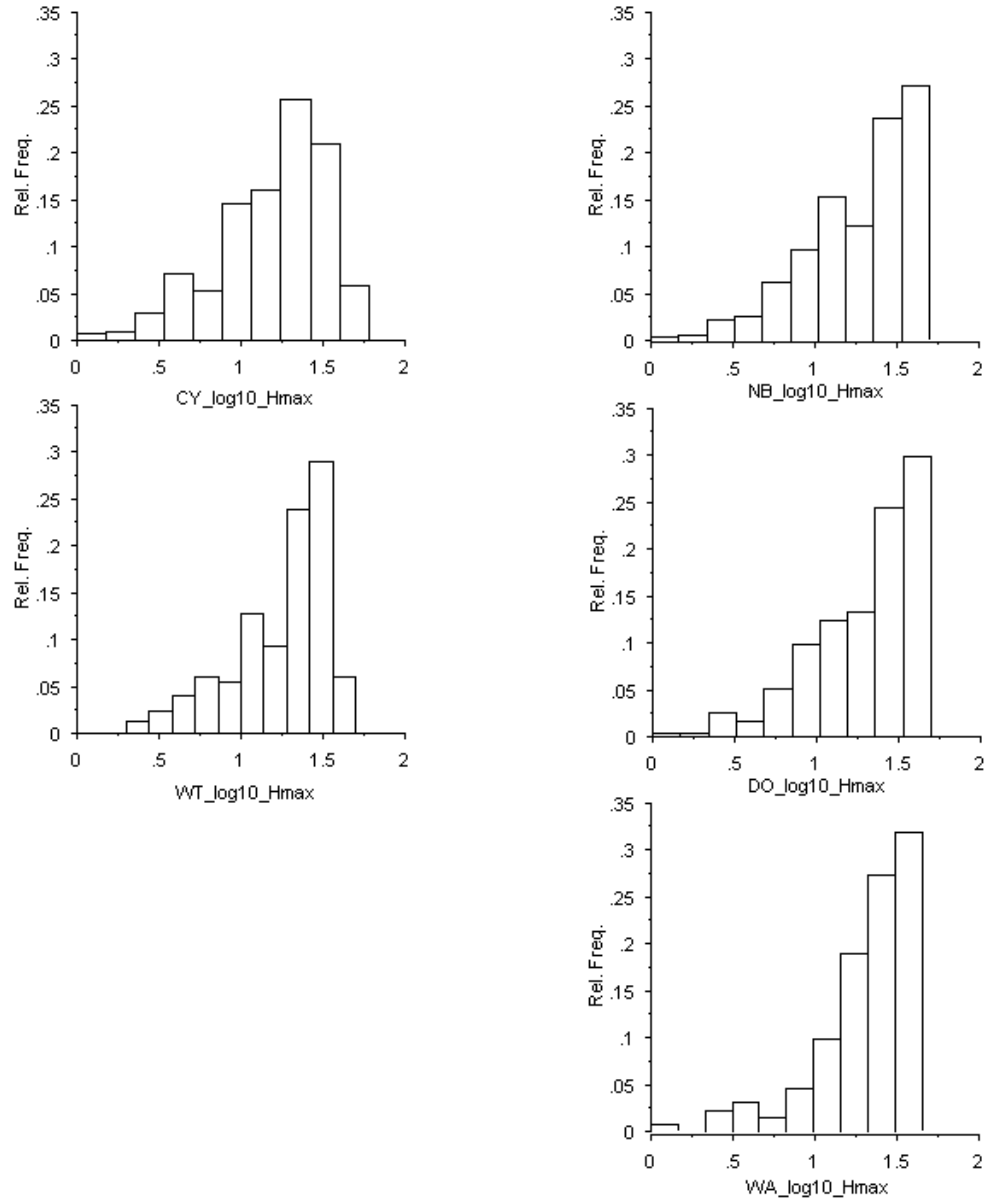
Figure S2.5 Histograms of relative frequency (Rel. Freq.) of log10 estimated maximum height at maturity (Hmax) in ten size classes in each of five areas in two latitude regions: CY - Cape York and WT – Wet Tropics in the tropics; and NB – Nightcap Border Ranges, DO – Dorrigo and WA - Washpool in the sub-tropics.