Glacial and interglacial refugia within a long-term rainforest refugium: The Wet Tropics Bioregion of NE Queensland, Australia

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Abstract

An artificial neural network is used to classify environments, including climate, terrain and soil variables, according to their suitability for fifteen structural/environmental forest classes in the Wet Tropics Bioregion of north-east Queensland. We map the environments characteristic of these forest classes in four climate regimes (the present and three past climate scenarios), quantify the changes in area of these environments in response to past regional changes in climate and identify areas that would have been environmentally suitable for rainforests at last glacial maximum (glacial refugia). We also identify areas that would have been suitable for upland and highland rainforest classes during the warmest parts of the interglacial (interglacial refugia) and map locations that consistently remain favourable to specific forest classes despite large changes in climate.

In the climate of the last glacial maximum (LGM), rainforest environments are predicted in three relatively distinct refugia in the northern, central and southern Wet Tropics. Only three percent of the total area contains lowland, Mesophyll Vine Forest and the majority of the area of the rainforest refugia supports upland rainforest classes. In the cool, wet climate of the Pleistocene/ Holocene transition (PHT), rainforest environments expand to form a more or less continuous block from the northern limits of the region to the Walter Hill Range, except for discontinuous patches extending through the Seaview and Paluma Ranges in the south. During the Holocene climatic optimum (HCO), rainforest environments become more fragmented, especially in the south. Lowland rainforest environments are very extensive in this climate while upland rainforest classes are restricted to what we term "interglacial refugia".

Estimated distributions and stable locations (consistently predicted in all four climate scenarios) for the various rainforest environment classes are our main, novel contribution. Each forest environment responds individualistically to climate change. Our results confirm the highly dynamic nature of the Wet Tropics landscape and present a much more detailed picture of landscape change since the late Pleistocene than previously has been available. This mapping exercise should be useful in the future for analyses of present-day biogeographic patterns. We argue that empirical modelling approaches have an important role in palaeoecology and global change research that is complementary to the developing mechanistic methods.

1. Introduction

In this paper we describe how the environments of the structural/environmental forest classes within the Wet Tropics Bioregion region have changed in response to

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climate changes since the last glacial maximum (LGM). We show that, while rainforest environments as a whole contracted to several regional refugia at the LGM, the cooler upland and highland rainforest environments are restricted to regional refugia during interglacial times, especially the Holocene climatic optimum (HCO). Our quantitative modelling approach provides much greater resolution of palaeo-biogeographic dynamics, as well as regions of relative stability, than previous bioclimatic analyses and should be of considerable use in the future in explaining current biogeographic patterns of the region's unique flora and fauna.

1.1. The Wet Tropics Bioregion

There are several long-term rainforest refugia in Australia (Adam, 1992), primarily along the east coast. These are thought to be remnants of rainforests that were widely distributed in Australia in the Miocene/Early Tertiary (Truswell, 1993). The Wet Tropics Bioregion (see Fig. 1; Williams et al., 1996), located between 15° and 19°S, long. 145°–146°30′E, is the largest of the tropical to warm-temperate rainforest refugia and is considered to be one of the most significant regional ecosystems in the world (Webb, 1984). It is rich in regionally endemic biodiversity, including 53 genera of vascular plants (Metcalfe and Ford, in press). Only New Caledonia has a greater concentration of endemic plant genera (Webb and Tracey, 1981). While retaining unique tropical rainforests in the lowlands, the richness of its endemic flora and fauna increases with altitude. The rainforest vertebrate fauna includes 66 species endemic to the region (Williams et al., 1996). Land snails are exceptionally diverse and mostly endemic, with 185 out of 222 known Australian species being endemic to the region (Stanisic et al., 1994).

The topography of the region is complex with elevations ranging from sea level to 1615 m and there are steep gradients of temperature and rainfall. Mean annual precipitation varies from greater than 8000 mm at higher altitudes to approximately 600 mm at drier, inland locations. Interannual variability of rainfall is high. Annual mean temperatures vary from above 25.0 °C at some coastal locations to less than 17.0 °C on the higher mountains. The combination of high topographic, edaphic, and climatic variability over the region results in a very complex mosaic of diverse forest types.

1.2. Quaternary climate change and rainforests

It is now widely recognized that climates changed appreciably in the tropics throughout the glacial cycles of the Pleistocene (Farrera et al., 1999). In the Neotropics, climate changes during the late Tertiary and Quaternary periods indicate low-latitude temperature fluctuations of up to 5 or 6 °C (Colinvaux et al., 1996; Burnham and Graham, 1999; Heine, 2000) and similar glacial cooling was widespread throughout the tropics (van der Kaars and Dam, 1997). In general, glacial cooling and aridity restricted the extent and altered the spatial distribution of tropical rainforests and depressed altitudinal zones while warmer and wetter conditions during the Holocene allowed marked expansion of rainforests (Walker and Chen, 1987; Flenley, 1998). African lowland rainforest, for example, may have contracted to 25% of its present area at last glacial maximum (LGM), ca. 20 to 18 kyr BP, and expanded to three times its present area during the Holocene climatic optimum (HCO), ca. 5 kyr BP (Hamilton, 1976). During glacial periods, these rainforests may have been replaced by tropical seasonal forest, seasonal or dry forests were replaced by savanna or steppe and mountain forests occurred at lower elevations than today (Elenga et al., 2000).

In Mesoamerica, during the late Pleistocene, lowland rainforest species may have been limited to riparian habitats and expanded with increased temperature and rainfall approximately 12 kyr BP (Aide and Rivera, 1998). In contrast, rainforest remained in the Amazonian lowlands throughout the Pleistocene and the main effect of climate changes may have been on the distribution of heat intolerant plants responding to Holocene warming (Haberle, 1999; Colinvaux et al., 2000; Colinvaux and De Oliveira, 2001). In the Sunda shelf of Southeast Asia, drier climates during the peak of the last ice age led to a reduction in the extent of rainforests (Taylor et al., 1999). Rainforests in central New Guinea contracted to 75% of their present area at LGM (Walker and Chen, 1987) and tree line in the central highlands was 1500 m lower than today (Walker and Flenley, 1979; Walker and Hope, 1982).

In Australia, during the last glacial cycle, the most important climatic feature has been variation in precipitation with the driest conditions occurring during the transition from the peak of the last glacial to the Holocene (Kershaw and Nanson, 1993). The major change in the vegetation of Australia, occurring within the last 140 kyr BP, involved the replacement of extensive moist rainforest by open eucalypt woodland, postulated to have been caused by the burning activities of Aboriginal people (Kershaw, 1994). In the central Wet Tropics, volcanic activity within and adjacent to the catchments of the Barron, Mulgrave and Tully Rivers (Whitehead et al., in press) would have initiated forest fires during this period. Over long-term and continental
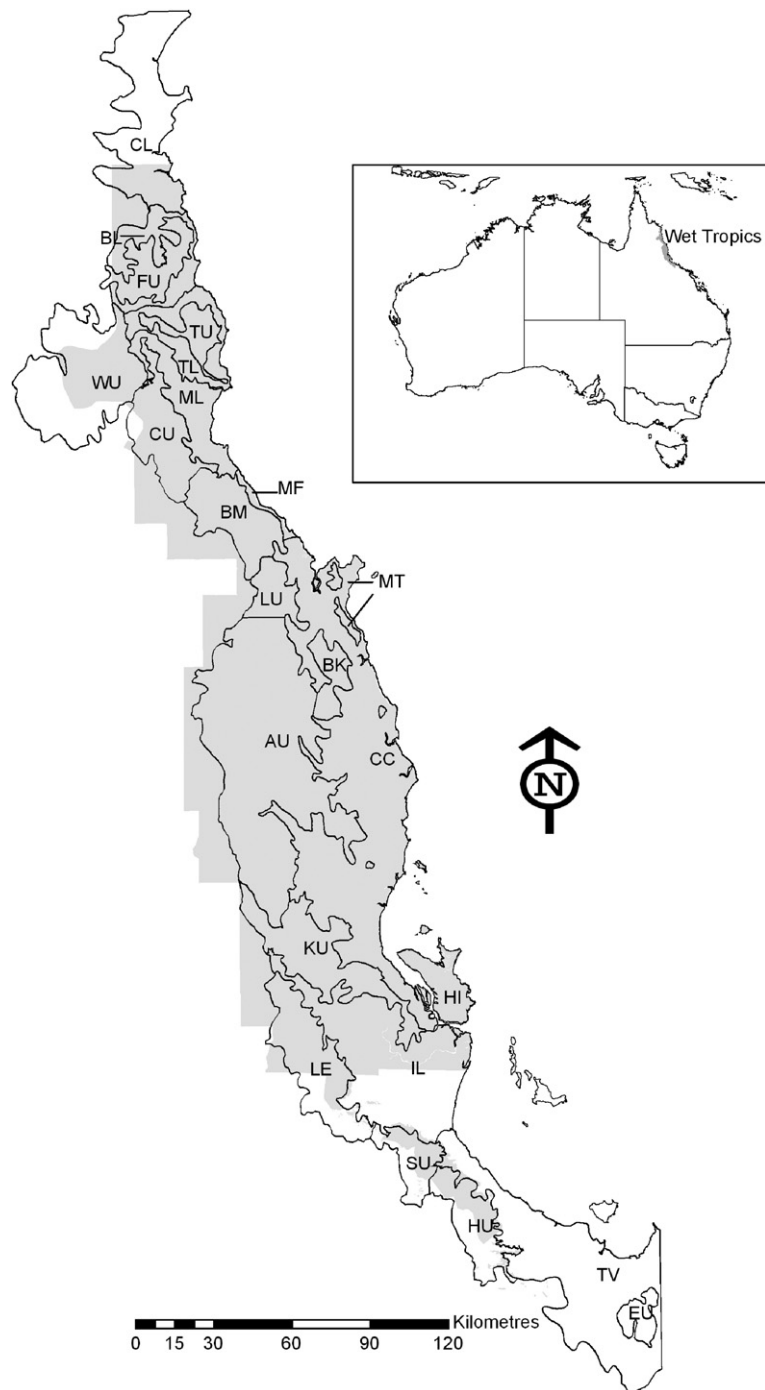
Fig. 1. The Wet Tropics Bioregion, its subregions (Williams et al., 1996) and the extent of the vegetation mapping used in our analyses in grey (Hilbert and van den Muyzenberg, 1999). Subregion abbreviations: Atherton Uplands (AU), Bellenden-Ker/Bartle-Frere (BK), Bloomfield Lowlands (BL), Black Mountain Corridor (BM), Cairns–Cardwell Lowlands (CC), Cooktown Lowlands (CL), Carbine Uplands (CU), Elliot Uplands (EU), Finnegan Uplands (FU), Halifax Uplands (HU), Hinchinbrook Island (HI), Ingham Lowlands (IL), Kirrama Uplands (KU), Lee Uplands (LE), Lamb Uplands (LU), McAlister Foothills (MF), Mossman Lowlands (ML), Malbon Thompson Uplands (MT), Spec Uplands (SU), Thornton Lowlands (TL), Thornton Uplands (TU), Townsville Lowlands (TV), Windsor Uplands (WU).

scales, all the extant rainforests in Australia can be thought of as refugia (Webb and Tracey, 1981).

At the spatial scale of the Wet Tropics, it is well established that rainforest refugia have expanded and contracted throughout the Pleistocene. Webb and Tracey (1981) subjectively identified a large number of Pleistocene rainforest refugia in the Wet Tropics including all the presently cloudy and wet mountains and high tablelands and the very wet lowlands that now receive greater than 2500 mm annual rainfall. Gallery forests are assumed to have been present in drier areas near the permanent rivers and wet coastal gorges and most of these rivers are also likely rainforest refugia. Nix and Switzer (1991) postulated two large refugia at the LGM, centred on Thornton Peak in the North and the Atherton Tablelands with a smaller refugium in the Paluma Range.

Charcoal collected from the Windsor Tableland, now dominated by Simple Notophyll and Mesophyll Vine Forests, demonstrates the existence of pyrophytic forests dominated by *Eucalyptus* in the late Pleistocene, 26.86 to 12.75 kyr BP (Hopkins et al., 1990). Further evidence from charcoal fragments collected throughout the rainforests of the Wet Tropics suggest that *Eucalyptus* woodlands or forests reached a maximum extent toward the end of the Pleistocene, between 13 and 8 kyr BP (Hopkins et al., 1993). Palynological evidence from Lynch's crater indicates sclerophyll forests and woodlands in that location from as early as 38 to ca. 8 kyr BP (Kershaw, 1985, 1989). This expansion of sclerophyll forest has been attributed to both increasing aridity in the late Pleistocene and to burning by Aborigines (Kershaw, 1986). Further analysis of pollen and charcoal from Lynch's Crater suggest an increase in fire frequency at 45 C_{14} kyr BP supporting the view that human occupation of Australia occurred by at least 45–55 kyr BP (Turney et al., 2001). Analysis of a sediment core from Lake Xere Wapo, New Caledonia, shows a decline in *Araucaria* species at around 45 kyr BP, as is seen at Lynch's Crater, but this could not have been caused by anthropogenic fires as humans had not yet reached this island (Stevenson and Hope, 2005). The pollen and charcoal record from Lake Euramoo suggests the presence of dry sclerophyll woodland between 23 and 16.8 kyr BP; wet sclerophyll woodland (Tall Open Forest and Woodland) between 16.8 and 8.6 kyr BP; warm temperate rainforest between 8.6 and 5 kyr BP; dry subtropical rainforest between 5000 and 70 yr BP, followed by degraded dry subtropical rainforest (Haberle, 2005).

Unlike the early Holocene re-expansion of upland rainforests, the sclerophyll forests in the lowland,

Daintree region were present until at least 1.40 kyr BP (Hopkins et al., 1996). These authors suggest that rapid sea level rise concentrated aboriginal populations in the area of the present coastline and that their burning activities were sufficient to re-establish sclerophyll forests during the latter part of the Holocene from approximately 4 kyr BP, following a warmer and wetter period which would have been conducive to rainforest re-expansion. This rainforest expansion may have accelerated since the arrival of Europeans and the concomitant decrease in fire.

1.3. Approach

Knowledge of the past distribution of vegetation and climates are frequently based on palynology. While this is often the only direct, empirical approach possible, biogeographic interpretations from pollen records are limited by the typically sparse spatial samples and the difficulties associated with the variable production and spatial redistribution of pollen from various taxa. Macrofossils combined with radiocarbon dating, such as the charcoal studied by Hopkins et al. (1993), have the advantage that taxa can be placed at specific locations at specific times. Our approach is more like the bioclimatic analyses of Nix (1991) who used similar palaeo-climate reconstructions and mapped the spatial distribution of two climate classes (mesothermal and megathermal) throughout the Wet Tropics. He used these bioclimatic patterns to qualitatively infer the extent and distribution of rainforests at various periods in the past. Unlike Nix, our model, PFANN (Hilbert and Ostendorf, 2001; Hilbert et al., 2001), quantitatively classifies environments based on the present associations between forest structural classes and environmental variables. Unlike purely bioclimatic analyses, soil parent material and terrain related indices are also included. This is important because past changes in vegetation pattern are best interpreted in relation to the total habitat, including edaphic and topographic factors (Webb and Tracey, 1981). The result is conceptually similar to Nix's bioclimatic analyses but is more refined in the sense that the environments of many forest classes are distinguished and the classification is objective and quantitative.

Here, we estimate detailed environmental patterns in the recent geological past that describe forest environments of the Wet Tropics in three past climates that are representative of the range of environments experienced by the region's biota since LGM at approximately 18 kyr BP. Our primary objectives are to: (1) map the environments characteristic of several structural forest

classes in four climate regimes (the present and three past climate scenarios); (2) quantify the changes in area of these environments in response to regional changes in climate; (3) identify areas that would have been environmentally suitable for rainforests at last glacial maximum (glacial refugia); (4) identify areas that would have been suitable for upland and highland rainforest classes during the warmest parts of the interglacial (interglacial refugia); (5) map locations that consistently remain favorable to specific forest classes despite large changes in climate; and (6) illustrate the utility of empirical models to objectively identify environmental patterns in the past. A motivation for this study is that the biogeography and ecology of a region are often as dependent on the area's history as on the current environmental conditions. Thus, the study of past environments and distributions of biota is essential in order to understand present-day patterns of biodiversity. Here, we restrict ourselves to a very detailed description of past forest environment while future papers will explore its relationship with the biogeography of the region's flora and fauna.

2. Methods

2.1. Forest classes and environments

Our approach involves classification of the environments characteristic of a large number of forest classes and estimating their distributions in past climates. Since the general consensus is that plant species respond individualistically to climate, plant communities are not thought to be stable in response to large and long-term climate change. Thus it is important to understand the nature of the forest classification and mapping that is fundamental to our approach.

The combination of high topographic, edaphic, and climatic variability in the Wet Tropics Bioregion results in a diverse regional mosaic of many forest types that were mapped at 1:100,000 scale (Tracey and Webb, 1975). The extent of this vegetation map (c. 1,700,000 ha of forest) and subsequent mapping of rainforests in the Paluma Range defines the extent of the Wet Tropics region that we modelled. A structural typology for rainforests (Webb, 1959, 1968, 1978) and non-rainforest vegetation (Specht, 1970) was used in the vegetation mapping. Detailed descriptions of the rainforest types are given in Tracey (1982). The vegetation classes are largely based on structural attributes such as canopy height, degree of canopy closure, complexity of the forest profile, the relative abundance of epiphytes and lianas, and average leaf size of the canopy trees. Fine-grained vegetation mosaics that could not be mapped in detail at the 1:100,000 scale are classified as several classes of coastal complexes or mountain rock pavements.

The structural types can be broadly correlated with climatic zones and soil patterns, with some effect of disturbance, especially fire (Webb and Tracey, 1981). While there are floristic correlations with structural types (Graham et al., 2006), and sometimes diagnostic species (Webb and Tracey, 1981), the floristic composition at different locations of the same structural type can be very distinct. Thus, these forest classes are *not* floristic communities. They are structural/physiognomic classes that are a more or less direct expression of the local environment. Thus, they can be expected to be similarly controlled in the past.

Statistical analyses (Hilbert, in press) indicate that the overall vegetation pattern of the Wet Tropics is most strongly influenced by mean annual precipitation and mean annual temperature. Individually, most forest types are best predicted by a combination of some temperature and a precipitation variable. Soil parent material and topography play a more significant role for some vegetation types, such as coastal complexes, and particularly in areas of lower rainfall. Overall, these analyses demonstrate the strong climatic control of the tropical forests in the region. The distribution of rainforest versus sclerophyll forests and woodland is largely controlled by rainfall while the type of rainforest depends on temperature as well as rainfall.

2.2. Modelling

Our mapping of past forest environments relies on an artificial neural network model (PFANN) that estimates the relative suitability of environments for 15 forest classes (see Table 1). The model is documented fully by Hilbert and van den Muyzenberg (1999), methods for applying the model for a number of purposes are described by Hilbert and Ostendorf (2001) and the model has been used successfully to study past changes in the extent of woodlands and tall open forests (Hilbert et al., 2000) and the sensitivity of the Wet Tropics' forests to future climate change (Hilbert et al., 2001). The model is a feedforward artificial neural network with one hidden layer. The independent, environmental variables include seven climate variables, nine soil parent material classes, and seven terrain variables. Climate variables were estimated spatially by the ANUCLIM software (McMahon et al., 1995) using a digital elevation model (AUSLIG, 1994), meteorological data from a large number of stations, and a thin-plate

Table 1

Vegetation classes used in the modelling, class number and abbreviation, the corresponding types in the Tracey and Webb maping, and a brief description of each class (modified from Hilbert and Ostendorf, 2001)

Class number and abbreviation	Tracey and Webb (1975) classes	Description
1 MVF	1 and 2	Mesophyll Vine Forests – complex structure, high diversity of vascular epiphytes, and a canopy dominated by mesophyllous species
2 MVFP	3	Mesophyll Vine Forests with Palms – canopy dominated by palms, occurring on poorly drained soils near the coast
3 SDMVF	4	Semideciduous Mesophyll Vine Forest – mesophyll vine forest with canopy emergents often deciduous
4 CNVF	5, 6	Complex Notophyll Vine Forests – rainforests of cooler uplands, structurally complex, canopy dominated by notophyll species
5 NVF	7	Notophyll Vine Forests – rainforest found in drier coastal zones, simple structure, low canopy
6 SNSM	8, 9, 10	Simple Notophyll and Simple Microphyll Forests and Thickets – highland rainforest in the coolest and wettest parts of the study area, structure from complex to simple
7 DMVT	11	Deciduous Microphyll Vine Thicket – rainforest with low canopy of mainly drought deciduous species
8 VFAE	12, 13	Vine Forest with *Acacia* and/or *Eucalyptus* – rainforest with sclerophyll canopy emergents, transitional from sclerophyll to rainforest classes
9 TOFTW	14	Tall Open Forest and Woodland – sclerophyll forests with high canopies in moist environments
10 MOFW	15	Medium Open Forest and Woodlands – medium height sclerophyll forests, including poorly drained coastal locations
11 MLW	16	Medium and Low Woodlands – dry, open sclerophyll woodlands
12 CC	17 to 20, 22, 23	Coastal Complexes – variety of fine grained mosaics of several rainforest and sclerophyll classes near the coast
13 MRP	21	Mountain Rock Pavements – fine grained mosaic of dry rainforest and sclerophyll classes on steep mountain slopes with thin soils
14 AVF	25	Araucarian Vine Forests – rainforest and woodland with dominant *Araucaria* spp.
15 NSEVF	26, 27	Notophyll Semi-evergreen Vine Forests – notophyll vine forest where many tree crowns become sparse in the dry season, true deciduous species generally absent

Detailed descriptions of rainforest classes are given in Tracey (1982). In the mapping, type 24 was used for cleared land and is not included in the model.

spline method to interpolate between observations. The climate variables include means of annual temperature, minimum temperature of coldest period, temperature of warmest quarter, temperature of coldest quarter, annual precipitation, precipitation of the wettest quarter, and precipitation of the driest quarter. The original model (Hilbert and van den Muyzenberg, 1999) used distance to the coast as one of the terrain variables. For the purposes of studying palaeo-environments, a new model (PFANN) was trained that did not use this variable but was otherwise identical and has similar accuracy (Hilbert and Ostendorf, 2001; Hilbert et al., 2001). Output from the model is a vector of fifteen real numbers in the range zero to one that measure the relative suitability of a local environment for each of the forest classes. All rainforest types (types 1 to 8, 14, and 15) have closed canopies while sclerophyll forests are more or less open, forest types 9 and 10 being more closed than woodlands (type 11). Coastal complexes (type 12) include a broad range of vegetation complexes and mosaics with rainforest and sclerophyll components that occur on the coastal plains where microtopography and soil type affect soil water drainage. This type includes the saline littoral zone dominated by mangroves. Mountain Rock Pavements (type 13) are also a fine-grained vegetation mosaic (scrub, shrubland, heath, and some vine forest) occurring largely on steep, granitic mountain slopes with very shallow soils.

Table 2

Palaeoclimate scenarios for the Wet Tropics Bioregion

	Climate scenario		
	LGM	PHT	HCO
All temperature variables	−3.5	−2.0	+2.0
Mean annual precipitation	0.5	1.2	1.25
Precipitation of the wettest quarter	0.5	1.2	1.25
Precipitation of the driest quarter	0.5	2.0	1.5

Changes are relative to today's climate and rainfall changes are given as a multiplier.
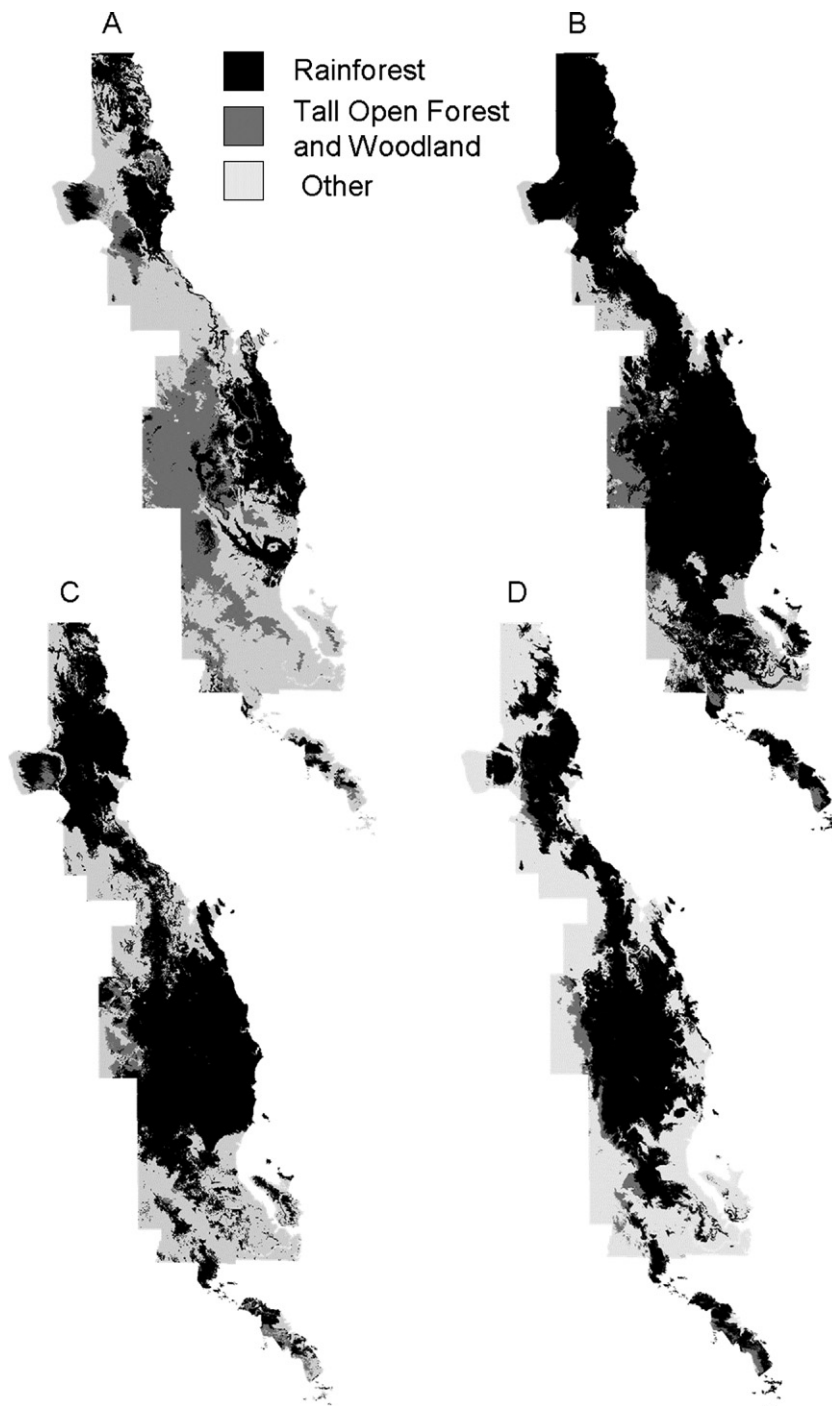
Fig. 2. Areas occupied by rainforest (types 1–8, 14 and 15), Tall Open Forests and Tall Woodlands, and all other classes, primarily Medium and Low Woodlands, in each of the three, palaeoclimate scenarios (A=LGM, B=PHT, C=HCO) and their potential distributions in today's climate (D).

The spatial distribution of forest environments is mapped by providing all the inputs at each location (defined on a grid with a one hectare resolution) and classifying the environment at that location as the forest environment class with the highest output value. With the present climate, there is an overall correspondence of 75% between the classification of forest environments and the mapped distribution of the region's forests at a

1-ha resolution. Hilbert and van den Muyzenberg (1999) and Hilbert and Ostendorf (2001) provide further assessments of the model's accuracy and generality and compare it with maximum likelihood and general additive modeling methods.

Palaeo-climate scenarios were developed from previously published estimates (Nix and Kalma, 1972; Nix, 1991) and are presented in Table 2. These scenarios represent estimates of rainfall and temperature in three different climates thought to have been present in the Wet Tropics since the late Pleistocene. The earliest period is the last glacial maximum (LGM) when the region was the driest and coolest during the last ca. 100 000 years. During the Pleistocene/Holocene transition to early Holocene (PHT) the climate had warmed somewhat and is believed to have been wetter than today's climate. Following this, the Holocene "climatic optimum" (HCO) or "altithermal" was both warmer and wetter than present conditions.

3. Results

3.1. Distribution of major forest classes

The spatial pattern of forest environments is strongly influenced by climate and different responses are predicted for each forest class. The distributions of rainforests, Tall Open Forest and Woodland, and all remaining classes combined (mostly Medium and Low Woodland) for each of the climate scenarios and the present are presented in Fig. 2. At the LGM, rainforest environments occur in three relatively distinct refugia in the northern, central and southern Wet Tropics. In the south, rainforest environments are mostly restricted to the higher elevations of the Paluma Range (Spec and Halifax Uplands) and are well isolated from the central block. A tenuous connection between the northern and

central blocks exists along the coast, east of the so-called Black Mountain corridor. It is likely that gallery forest also occurred on the extensive coastal plain that then extended many kilometers to the east. Roughly 75% of the region has environments most suitable to pyrrhic, sclerophyll vegetation at the LGM. Tall Open Forest and Woodland environments are approximately three times as extensive at this time as in any of the other climates, including today's, and are very extensive in the west-central part of the Wet Tropics (likely extending west of the study area) and also occur on the Carbine and Windsor Uplands and the Lee Uplands.

In the cool, wet PHT scenario, rainforests environments expand to form a more or less continuous block from the northern limits of the region to the Walter Hill Range, with discontinuous patches extending south through the Seaview and Paluma Ranges (LE, SU and HU). Rainforest may have extended beyond the study region to the north-west. Tall Open Forest and Woodland environments are drastically reduced, but may have extended further west in the central part of the study region. With further warming during the HCO, rainforest environments become somewhat more fragmented, especially in the south. Tall Open Forest and Woodland environments are most restricted at this time. Reduced rainfall and cooling since HCO further reduce rainforest environments somewhat in today's climate.

Refugia for rainforests can be identified from their extent in the various subregions of the Wet Tropics Bioregion (Table 3). In terms of total area in rainforest at LGM, the Cairns–Cardwell Lowlands and Atherton Uplands are the two most important refugia which, when combined with the Bellenden-Ker/Bartle-Frere uplands, form the central rainforest refugium. In the northern group of refugia, the Mossman and Thornton Lowlands are most important in terms of area. Additional refugia in the north are the Thornton and

Table 3
Presence of rainforests of any type in Wet Tropics subregions (Williams et al., 1996) where the minimum area of rainforest present in the past climate scenarios is greater than 100 km^2

Subregion	% of area in rainforests			Min area (km^2)	Max area (km^2)	Total area (km^2)
	LGM	PHT	HCO			
Cairns–Cardwell Lowlands	50.4	81.0	74.3	2087	3353	4238
Atherton Uplands	15.1	85.1	81.1	575	3244	3909
Mossman Lowlands	71.5	71.2	73.5	463	478	662
Thornton Lowlands	62.0	96.6	91.7	330	514	545
Bellenden-Ker/Bartle-Frere	79.2	100.0	100.0	245	309	309
Mt. Finnegan Uplands	33.2	65.9	94.2	168	477	524
Bloomfield–Helenvale Lowlands	60.6	26.1	64.8	142	354	560
Carbine Uplands	17.3	89.7	88.5	131	678	807
Thornton Uplands	34.1	100.0	100.0	103	302	302

Table 4
Area (km^2) occupied by each forest class in each climate scenario along with the potential distribution in today's climate

Forest class	LGM	PHT	HCO	Today
MVF	608	3969	9682	4815
MVFP	0	1	0	65
SDMVF	82	1329	19	42
CNVF	1567	1296	445	1123
NVF	1	0	37	10
SNSM	1356	8378	786	2159
DMVT	2	45	0	11
VFAE	1866	447	1123	1479
TOFTW	4897	1298	672	656
MOFW	0	494	43	705
MLW	10 059	2044	4666	6889
CC	0	916	1961	2230
MRP	0	187	720	185
AVF	1	26	45	43
NSEVF	0	9	240	27

Carbine Uplands and the Bloomfield–Helenvale Low-lands. In the south, small amounts of rainforest exist in the Spec and Halifax Uplands (Paluma Range).

With the exception of the Bloomfield–Helenvale Lowlands, the subregions that retain greater than 100 km^2 of rainforest in all of the climate scenarios have a minimum rainforest extent at the LGM. The Mossman Lowlands retain roughly the same extent of rainforest in all scenarios which indicates a very high degree of stability in response to large climate changes. The Bellenden-Ker/Bartle-Frere subregion is also very stable and, as a proportion of its area, retains the most rainforest at the LGM. The Thornton Lowlands are also quite stable.

3.2. Areas of each forest type

Each rainforest environment responds individually to climate change (Table 4). Mesophyll Vine Forest environments cover 47% of the area in the warm, wet climate (HCO) while they are quite restricted (3% of the study area) at the LGM. Complex Notophyll Vine Forest environments are rare in all climates with a maximum extent at the LGM and a minimum at HCO. Simple Notophyll and Microphyll environments are less restricted at the LGM (6.7% of total area) than at HCO when they have a minimum extent of 4% of the region. Their maximum occurs in the cool, wet climate of the PHT (41% of the study region). Thus each of these three most extensive rainforest environments has a maximum extent in a different climate scenario. Tall open forests and woodland environments have declined in area since the LGM.

3.3. Long-term stability of forest environments

By overlaying the maps for all four climates, three past and present, it is possible to determine the areas that remain suitable for any forest type in only one, two, three or all climates. From this, we infer the subregions that are most stable for each forest environment with respect to large climate changes (i.e., always suitable to the same forest type) and are possibly long-term refugia. Of the 15 forest types, four have areas that remain stable across all climates (Table 5). Not surprisingly, Medium and Low Woodlands have the largest area in all four climates. Simple Notophyll and Simple Microphyll Forests have approximately twice the stable area as Mesophyll Vine Forests.

Mapping these stability classes identifies locations that act as long-term refugia for any of the forest types (Fig. 3). The most stable regions for rainforest in aggregate roughly correspond to their presence at the LGM (Fig. 2) although the total area of stable environments is somewhat less than rainforest area at the LGM. The most important subregions, in terms of total stable area (present in all four climates), is the Cairns–Cardwell Lowlands (Table 6). The stable areas within this subregion are mostly in a large area south of the Bellenden-Ker/Bartle-Frere Uplands and part of the upper Tully drainage. In terms of percentage of sub-regions that remains stable in all climates, the most stable areas are the Bellenden-Ker/Bartle-Frere Up-lands, Malbon Thompson Uplands, Mossman Low-lands, Thornton Lowlands and Spec Uplands.

The most important stable regions for Mesophyll Vine Forest are parts of the Mossman and Thornton Lowlands with very small areas in the Central Wet

Table 5
Area (km^2) of each forest environment where it is predicted in one, two, three or all four climates (LGM, PHT, HCO and today)

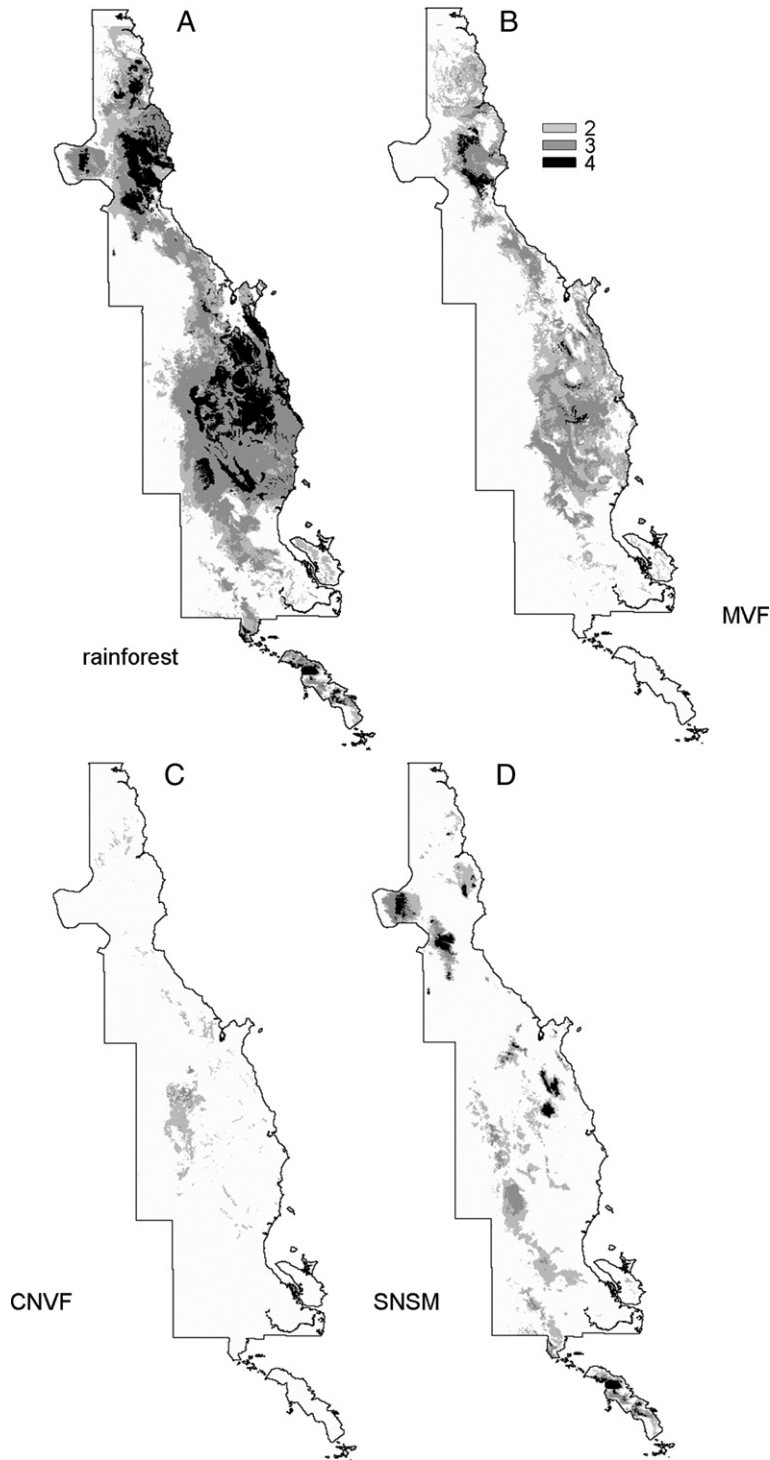| Forest class	1	2	3	4
MVF	5597	3472	2009	156
MVFP	61	0	0	0
SDMVF	1340	122	0	0
CNVF	3583	449	39	0
NVF	146	0	0	0
SNSM	5931	1821	700	316
DMVT	70	1	0	0
VFAE	3836	278	7	0
TOFTW	3944	1090	344	100
MOFW	1227	63	2	0
MLW	6843	2746	1544	1519
CC	1043	1070	606	0
MRP	687	199	63	0
AVF	103	23	8	0
NSEVF	200	65	6	0

Fig. 3. Maps of stability class (present in 2, 3, or 4 climates) for all rainforests combined (A), Mesophyll Vine Forest (B), Complex Notophyll Vine Forest (C) and Simple Notophyll and Simple Microphyll Forests (D).

Tropics. Complex Notophyll Vine Forests do not have locations that are consistently stable but the western Atherton Uplands are stable in two climates. Simple Notophyll and Simple Microphyll Forests are stable (present in all climates) in the Windsor, Carbine, Bellenden-Ker/Bartle-Frere, and Halifax Uplands with

Table 6

Stability analysis for subregions with greater than 10 km^2 area in stability class 4 when aggregating all closed rainforest types

Subregion	Modelled area (km^2)	km^2 of rainforest in each stability class				% of modelled area in stability class 4
		1.00	2.00	3.00	4.00	
Cairns–Cardwell Lowlands	4131	311	373	1804	1029	24.9
Atherton Uplands	3812	466	615	1869	571	15.0
Mossman Lowlands	648	72	141	96	296	45.7
Bellenden-Ker/ Bartle-Frere	309	0	4	72	233	75.3
Thornton Lowlands	529	17	118	191	203	38.4
Carbine Uplands	755	58	203	338	117	15.5
Finnegan Uplands	506	81	96	203	113	22.4
Thornton Uplands	302	0	28	172	103	34.0
Spec Uplands	203	17	54	70	62	30.3
Windsor Uplands	705	107	137	256	50	7.1
Malbon Thompson Uplands	84	0	22	17	45	54.2
Halifax Uplands	309	66	93	75	25	8.0
Lamb Uplands	351	13	155	160	24	6.8
Bloomfield Lowlands	546	150	191	98	20	3.7
Lee Uplands	737	239	146	132	20	2.7

Subregions are listed in descending order based on their area in stability class 4.

a small stable area in the Thornton Uplands. While not apparent at the scale of Fig. 3, several additional uplands retain at least small amounts of Simple Notophyll and Simple Microphyll environments in all climates (Table 7).

3.4. Correspondence with pollen and charcoal evidence

While it is difficult to test our predictions with a high degree of spatial and temporal resolution, they are qualitatively consistent with the past distributions of sclerophyll forests identified through carbon dating and electron microscopy of charcoal fragments taken from soil pits throughout the study area (Hopkins et al., 1990, 1993, 1996) and temporal changes observed in pollen sequences.

Our results are largely consistent with pollen data from Lynch's Crater (17°220′S, 145°420′E; Kershaw et al., 2007-this volume) within the south-eastern Atherton Uplands (Kershaw, 1985; Moss and Kershaw, 2000). At the LGM we predict this location to be on a boarder between Tall Open Forest and Woodland and Complex Notophyll Vine Forest environments with extensive Simple Notophyll and Simple Microphyll environments nearby. In the PHT climate we predict

similar conditions, Complex Notophyll Vine Forest with Simple Notophyll and Simple Microphyll and Mesophyll Vine Forest nearby but also very small patches of Tall Open Forests and Woodland environments nearby. With the HCO climate, Lynch's Crater has a Mesophyll Vine Forest environment, which it retains today (Moss and Kershaw, 2000), with Simple Notophyll and Simple Microphyll to the East on Mt Bartle-Frere and mostly Complex Notophyll Vine Forest to the west.

Similarly our results are consistent with the detailed pollen record from Lake Euramoo (Haberle, 2005; Tibby and Haberle, 2007-this volume) in the Atherton Uplands in a drier location north of Lynch's Crater. In the LGM climate we predict this area to be Tall Open Forests and Woodland environments with Medium and Low Woodland in close proximity and small areas of rainforest environments nearby on Mt. Edith (Simple Notophyll and Simple Microphyll) and the upper Mulgrave River (Mesophyll Vine Forest). At the PHT this locale has a Complex Notophyll Vine Forest environment with Simple Notophyll and Simple Microphyll Vine Forests, Tall Open Forests and Woodland and Medium and Low Woodland environments nearby. At HCO it still retains a Complex Notophyll Vine Forest environment with considerable Mesophyll Vine Forest in the area and, as today, Medium and Low Woodland to the West.

Charcoal collected from the Windsor Uplands, demonstrates the existence of sclerophyll forests from 26 860 to 12 750 BP (Hopkins et al., 1990). We predict Tall Open Forests and Woodland environments on the

Table 7

Stability analysis for subregions with greater than 0.0 km^2 area in stability class 4 for Simple Notophyll and Simple Microphyll Forest environments

Subregion	km^2 of SNSM in each stability class				% of modelled area in stability class 4
	1.00	2.00	3.00	4.00	
Bellenden-Ker/Bartle-Frere	79	70	51	81	26.4
Carbine Uplands	253	130	103	70	9.2
Spec Uplands	44	50	45	53	26.1
Windsor Uplands	99	152	156	50	7.0
Thornton Uplands	96	139	20	16	5.2
Halifax Uplands	86	78	44	14	4.5
Lamb Uplands	187	39	24	4	1.1
Lee Uplands	278	150	38	1	0.2
Malbon Thompson Uplands	45	17	7	1	0.7
Finnegan Uplands	163	26	5	1	0.1

Subregions are listed in descending order based on their area in stability class 4.

eastern and western margins with Simple Notophyll and Simple Microphyll environments in the centre of the Windsor Uplands at LGM. All but one of the charcoal sites in this area are consistent with our predictions of sclerophyll forests or woodlands in past climates. The one exception is within a few kilometers of predicted Tall Open Forests and Woodland environments. Charcoal collected throughout the rest of our study region occurs, with rare exceptions, in locations that we predict to have had sclerophyll forest environments in at least one of the three past climate scenarios. The two major exceptions are charcoal in the Thornton Lowlands in the Cape Tribulation region and several charcoal records from the Halifax Uplands in the southern Paluma Range. These discrepancies are probably due to especially intense burning activities by Aboriginal people (Hopkins et al., 1996). Charcoal sites in the Halifax Uplands are associated with Aboriginal trails that linked the lowlands and uplands and would have been kept open through repeated burning. These comparisons with pollen and charcoal data show that our model predictions of forest environments are qualitatively consistent with the observations of actual forest classes in the palaeo-record.

4. Discussion

4.1. Landscape dynamics

Our results confirm the highly dynamic nature of the Wet Tropics landscape and present a much more detailed picture of landscape change since the late Pleistocene than previously has been available. Our modelled rainforest refugia at the LGM, Fig. 2A, are largely consistent with previous estimates (Webb and Tracey, 1981; Nix and Switzer, 1991) although our analysis is more detailed and we predict small rainforest areas in the south (Paluma Range). The greater extent and connectivity of rainforest during the cool–wet PHT is supported by Kershaw and Nix (1988) and Hopkins et al. (1993). The presence of rainforest environments throughout the entire northern part of the study region under the PHT climate suggests that rainforest may have extended far north of the Wet Tropics and is consistent with an hypothesized rainforest connection with New Guinea in the late Pleistocene/early Holocene (Nix and Kalma, 1972).

Estimated distributions and stable locations for the various rainforest environment classes are our main, novel contribution. We show that Mesophyll Vine Forest, Complex Notophyll Vine Forest, and Simple Notophyll and Simple Microphyll Forest environments

respond individualistically to climate change. Mesophyll Vine Forests contract to very small refugia in the north and central parts of the Wet Tropics (corresponding too their most stable locations) and then expand from these areas to their greatest extent in the HCO climate. Complex Notophyll Vine Forest environments, on the other hand, shift across the landscape with minimal extent in the HCO climate and have no areas where they are consistently present. Simple Notophyll and Simple Microphyll Forest environments expand from many scattered glacial refugia during the cool, wet PHT and then contract again to their smallest extent during the warm HCO. Their numerous interglacial refugia correspond to their location in the HCO climate and are also the most stable locations.

The different behaviours of these three environments may help to explain broad biodiversity patterns today. For example, there are few endemic species limited to the lowland Mesophyll Vine Forest environments and the majority of endemics (plant and animal) occur in the cooler, upland forest environments. Mesophyll Vine Forest environments had a total extent of only 608 km^2 at LGM while the major upland and highland rainforest environments (Complex Notophyll and Simple Notophyll and Simple Microphyll) covered 2923 km^2 in that climate (see Table 4). Thus, lowland rainforest may have been extremely limited throughout the long glacial periods while the cooler rainforest classes moved down in elevation and represented the most significant part of the glacial rainforest refugia. A logical conclusion is that glacial cooling and aridity lead to the extinction of lowland specialists while cool-adapted species where less affected due to the larger area of upland rainforest that remained. In contrast, the upland rainforest environments (Complex Notophyll and Simple Notophyll and Simple Microphyll) contract to their minimum area in what we term interglacial refugia during the warmest interglacial climates (1234 km^2 at HCO). In this climate, Mesophyll Vine Forest environments have their greatest extent (9682 km^2). Thus, both glacial and interglacial contractions of rainforest types are probably important in determining present biogeographic patterns. For example, Winter (1997) presents evidence that postglacial dispersal and the contraction and fragmentation of upland forests are as important in determining the present-day distribution of mammals as the contraction of rainforests at LGM. Independent modelling of an upland endemic, the golden bowerbird (*Priona newtoniana*), in our four climate scenarios shows similar declines in habitat in the HCO climate (Hilbert et al., 2004). The much greater detail of our modelling than previous estimates of refugia should provide the basis for

a more complete understanding of today's distributions of various taxa.

4.2. Usefulness of the modelling approach

Estimating the geographic distribution and function of vegetation in the past or future is important in many contexts. For example, land-managers and conservation ecologists often need to know the spatial pattern of vegetation that existed before extensive clearing of the landscape. Understanding the geographic distributions of past environments and the vegetation communities associated with them is often necessary to explain current patterns of species diversity and the distributions of rare, endemic species.

Many researchers assume that the ideal model for predicting the impacts of past or future climate change on vegetation should: be mechanistic (explanatory) and rely on well established principles; be based on plant species or at least plant functional types; include physiology explicitly; predict community composition and/or vegetation structure, including novel associations; represent transient dynamics at the population and landscape level; and include disturbance explicitly.

Based on these subjective criteria, empirical or "correlational" models may appear to be much less than ideal. However, it is important to recall that "ideal" models do not exist, models can only be more or less effective for a specific set of objectives. Neither empirical nor mechanistic models are intrinsically better. While explanation, in the sense of "bottom–up" simulation, is an intellectually satisfying goal we must also be pragmatic when faced with immediate needs and recognise that explanations in a reductionist, mechanistic form are not always available or even necessary.

One basic premise of empirical approaches is that the best information available on the relationships between environments and vegetation (whether individual species, plant functional types or vegetation classes) is the current geographic distribution of vegetation and environmental variables describing climate and soils. While mechanistic explanations for these patterns are very useful, these hypotheses are still ultimately dependent on the objective distributions themselves. That is, the explanatory models are *hypotheses* used to explain the *observed* distributions. For example, the validity of mechanistic, ecophysiological explanations for maximum leaf area index across the globe (Woodward et al., 1995) must be evaluated by comparing predicted values with the empirical geographic data. Similarly, simulation models often use known geo-graphic distributions of species to set parameter values (e.g., temperature minima and maxima for species' growth functions in gap models). As another example, macrofossils and pollen in sediments are used to infer past climates from the present distribution of taxa with respect to climate. In each case, the basic observable information is the current spatial distribution of more or less subjective biological categories (species, plant functional types, communities, biomes, structural vegetation classes) and measured abiotic variables.

Our empirical approach appears to be quite useful for climate change studies (Hilbert et al., 2001), especially in poorly understood and floristically complex regions. We argue that empirical modelling approaches have an important role in palaeoecology and global change research that is complementary to the developing mechanistic methods and that the full potential of empirical models has not yet been realized. Perhaps there is value in returning to empirical approaches and attempting to improve them, in parallel with developments in the mechanistic approaches.

5. Conclusions

This research demonstrates the great utility of empirical classification of environments using the present distributions of structural/physiognomic forest classes and their environments. It provides a very rich picture of environmental change in the recent geological past and, considering its apparent correspondence with pollen and charcoal evidence, may represent actual forest distributions fairly well. Disaggregating rainforest into its various structural/environmental classes is very important for a full picture of Quaternary dynamics of rainforests, especially in mountainous regions like the Wet Tropics. It is especially important to consider refugia of upland and highland rainforests during the warmest parts of the interglacials. Future research will investigate whether our detailed projections of past climates can improve our understanding of today's distributions of the flora and fauna of the region.

References

Adam, P., 1992. Australian Rainforests. Clarendon Press, Oxford.

Aide, T.M., Rivera, E., 1998. Geographic patterns of genetic diversity in *Poulsenia Armata* (Moraceae): implications for the theory of Pleistocene refugia and the importance of riparian forest. Journal of Biogeography 25, 695–705.

AUSLIG, 1994. TOPO-250K Data User Guide. Australian Surveying and Land Information Group, Canberra.

Burnham, R.J., Graham, A., 1999. The history of neotropical vegetation: new developments and status. Annals of the Missouri Botanical Garden 86, 546–589.

Colinvaux, P.A., De Oliveira, P.E., 2001. Amazon plant diversity and climate through the Cenozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 166, 51–63.

Colinvaux, P.A., Liu, K.B., De Oliveira, P.E., Bush, M.B., Miller, M.C., Kannan, M.S., 1996. Temperature depression in the lowland tropics in glacial times. Climatic Change 32, 19–33.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. Quaternary Science Reviews 19, 141–169.

Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., De Beaulieu, J.L., Hamilton, A.C., Maley, J., Marchant, R., Perez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H., 2000. Pollen-based biome reconstruction for Southern Europe and Africa 18,000 Yr Bp. Journal of Biogeography 27, 621–634.

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., Yu, G., 1999. Tropical climates at the last glacial maximum: a new synthesis of terrestrial palaeoclimate data: I. Vegetation, lake levels and geochemistry. Climate Dynamics 15, 823–856.

Flenley, J.R., 1998. Tropical forests under the climates of the last 30,000 years. Climatic Change 39, 177–197.

Graham, A.W., Aide, T.M., Kanowski, J., 2006. Floristic relationships between the plots. In: Graham, A.W. (Ed.), The CSIRO Rainforest Permanent Plots of North Queensland – Site, Structural, Floristic and Edaphic Descriptions. CSIRO and the Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns, p. 17.

Haberle, S.G., 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. Quaternary Research 51, 27–38.

Haberle, S.G., 2005. A 23,000-yr pollen record from Lake Euramoo, Wet Tropics of NE Queensland, Australia. Quaternary Research 64, 343–356.

Hamilton, A.C., 1976. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. Palaeoecology of Africa and the Surrounding Islands 9, 63–97.

Heine, K., 2000. Tropical South America during the last glacial maximum: evidence from glacial, periglacial and fluvial records. Quaternary International 72, 7–21.

Hilbert, D.W., in press. The dynamic forest landscape of the Australian Wet Tropics: present, past and future. In: Stork, N., Turton, S., (Eds.), Living in a Dynamic Tropical Forest Landscape, Blackwell, Oxford.

Hilbert, D.W., Ostendorf, B., 2001. The utility of empirical, artificial neural network approaches for modelling the distribution of regional to global vegetation in past, present and future climates. Ecological Modelling 146, 311–327.

Hilbert, D.W., van den Muyzenberg, J., 1999. Using an artificial neural network to characterise the relative suitability of environments for forest types in a complex tropical vegetation mosaic. Diversity and Distributions 5, 263–274.

Hilbert, D.W., Graham, A.W., Parker, T.A., 2000. Tall open forest and woodland habitats in the Wet Tropics: responses to climate and implications for the Northern Bettong (*Bettongia tropica*). Tropical Forest Research Series, vol. 1. CSIRO and the Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns. 45 pp.

Hilbert, D.W., Ostendorf, B., Hopkins, M., 2001. Sensitivity of tropical forests to climate change in the humid tropics of North Queensland. Austral Ecology 26, 590–603.

Hilbert, D.W., Bradford, M., Parker, T., Westcott, D.A., 2004. Golden bowerbird (*Prionodura newtonia* (sic)) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. Biological Conservation 116, 367–377.

Hopkins, M.S., Graham, A.W., Hewett, R., Ash, J., Head, J., 1990. Evidence of late Pleistocene fires and eucalypt forest from a North Queensland humid tropical rainforest site. Australian Journal of Ecology 15, 345–347.

Hopkins, M.S., Ash, J., Graham, A.W., Head, J., Hewett, R.K., 1993. Charcoal evidence of the spatial extent of the Eucalyptus woodland expansion and rain-forest contractions in North Queensland during the late Pleistocene. Journal of Biogeography 20, 357–372.

Hopkins, M.S., Head, J., Ash, J., Hewett, R.K., Graham, A.W., 1996. Evidence of Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. Journal of Biogeography 23, 737–745.

Kershaw, A.P., 1985. An extended late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. Proceedings of the Ecological Society of Australia 13, 179–189.

Kershaw, A.P., 1986. Climate change and Aboriginal burning in north-eastern Australia during the last two glacial/interglacial cycles. Nature 322, 47–49.

Kershaw, A.P., 1989. Was there a "Great Australian Arid Period?". Search 20, 89–92.

Kershaw, A.P., 1994. Pleistocene vegetation of the humid tropics of Northeastern Queensland, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 399–412.

Kershaw, A.P., Nanson, G.C., 1993. The last full glacial cycle in the Australian region. Global and Planetary Change 7, 1–9.

Kershaw, A.P., Nix, H.A., 1988. Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. Journal of Biogeography 15, 589–602.

Kershaw, A.P., Bretherton, S.C., 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 (this volume). doi:10.1016/j.palaeo.2007.02.015.

McMahon, J.P., Hutchinson, M.F., Nix, H.A., Ord, K.D., 1995. ANUCLIM User's Guide, Version 1. Centre for Resource and

Environmental Studies, Australian National University, Canberra. 90 pp.

Metcalfe, D.J., Ford, A.J., in press. Floristic biodiversity in the Wet Tropics. In: Stork, N., Turton, S., (Eds.), Living in a Dynamic Tropical Forest Landscape, Blackwell, Oxford.

Moss, P.T., Kershaw, A.P., 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 155–176.

Nix, H.A., 1991. Biogeography: pattern and process. In: Nix, H.A., Switzer, M.A. (Eds.), Rainforest Animals: Atlas of Vertebrates Endemic to Australia's Wet Tropics. Australian National Parks and Wildlife Service, Canberra, pp. 11–40.

Nix, H.A., Kalma, J.D., 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. In: Walker, D. (Ed.), Bridge and Barrier: The Natural and Cultural History of Torres Strait. Department of Biogeography and Geomorphology Publication BG=3, Research School of Pacific Studies, Australian National University, Canberra, pp. 61–91.

Nix, H.A., Switzer, M.A., 1991. Rainforest animals: atlas of vertebrates endemic to Australia's wet tropics. Kowari, vol. 1. Australian National Parks and Wildlife Service, Canberra.

Specht, R.L., 1970. Vegetation. In: Leeper, G. W. (Ed.) The Australian Environment. CSIRO & Melbourne University Press, Melbourne. pp. 44–67.

Stanisic, J., Eddie, C., Hill, A., Potter, D., 1994. A Preliminary Report on the Distribution of Land Snails Occurring in the Wet Tropics Area. Report to the Wet Tropics Management Authority, Cairns.

Stevenson, J., Hope, G., 2005. A comparison of late Quaternary forest changes in New Caledonia and northeastern Australia. Quaternary Research 64, 372–383.

Taylor, D., Saksena, P., Sanderson, P.G., Kucera, K., 1999. Environmental change and rain forests on the Sunda Shelf of southeast Asia: drought, fire and the biological cooling of biodiversity hotspots. Biodiversity and Conservation 8, 1159–1177.

Tibby, J., Haberle, S.G., 2007. A late glacial to present diatom record from Lake Euramoo, Wet Tropics of Queensland, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 251, 46–56 (this volume). doi:10.1016/j.palaeo.2007.02.017.

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

Tracey, J.G., Webb, L.J., 1975. Vegetation of the humid tropical region of North Queensland. (15 maps at 1 : 100,000 scale + key.) CSIRO Aust. Long Pocket Labs: Indooroopilly, Qld.

Truswell, E., 1993. Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors. Australian Systematic Botany 6, 533–557.

Turney, C.S.M., Kershaw, A.P., Moss, P., Bird, M.I., Fifield, L.K., Cresswell, R.G., Santos, G.M., Di Tada, M.I., Hausladen, P.A., Youping, Z., 2001. Redating the onset of burning at Lynch's Crater (North Queensland): implications for human settlement in Australia. Journal of Quaternary Science 16, 767–771.

van der Kaars, S., Dam, R., 1997. Vegetation and climate change in West-Java, Indonesia during the last 135,000 years. Quaternary International 37, 67–71.

Walker, D., Chen, Y., 1987. Palynological light on tropical rainforest dynamics. Quaternary Science Reviews 6, 77–92.

Walker, D., Flenley, J.R., 1979. Late Quaternary vegetational history of the Enga Province of upland Papua New Guinea. Philosophical Transactions of the Royal Society of London, B 286, 265–344.

Walker, D., Hope, G.S., 1982. Late Quaternary vegetation history. In: Gressitt, J.L. (Ed.), Biogeography and Ecology of New Guinea. W. Junk, The Hague, pp. 263–285.

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 forests. Australian Plants 9, 349–363.

Webb, L.J., 1984. Conservation status of the rainforests of north Queensland. In: Werren, G.L., Kershaw, A.P. (Eds.), Australian Rainforest Study. Proceedings of a Workshop on the Past, Present and Future of Australian Rainforests, vol. 3. Griffith University, Brisbane.

Webb, L.J., Tracey, J.G., 1981. Australian rainforest: patterns and change. In: Keast, A. (Ed.), Ecological Biogeography of Australia. Junk, The Hague, pp. 607–694.

Whitehead, P.W., Stephenson, P.J., Mcdougall, I., Hopkins, M.S., Graham, A.W., Collerson, K.D., Johnson, D.P., in press. Temporal development of the Atherton Basalt Province, North Queensland Australian Journal of Earth Sciences.

Williams, S.E., Pearson, R.G., Walsh, P.J., 1996. Distributions and biodiversity of the terrestrial vertebrates of Australia's wet tropics: a review of current knowledge. Pacific Conservation Biology 2, 327–362.

Winter, J.W., 1997. Responses of non-volant mammals to Late Quaternary climatic changes in the Wet Tropics region of northeastern Australia. Wildlife Research 1997, 493–511.

Woodward, F., Smith, T.M., Emanuel, W.R., 1995. A global land primary productivity and phytogeography model. Global Biogeochemical Cycles 9 (471), 490.