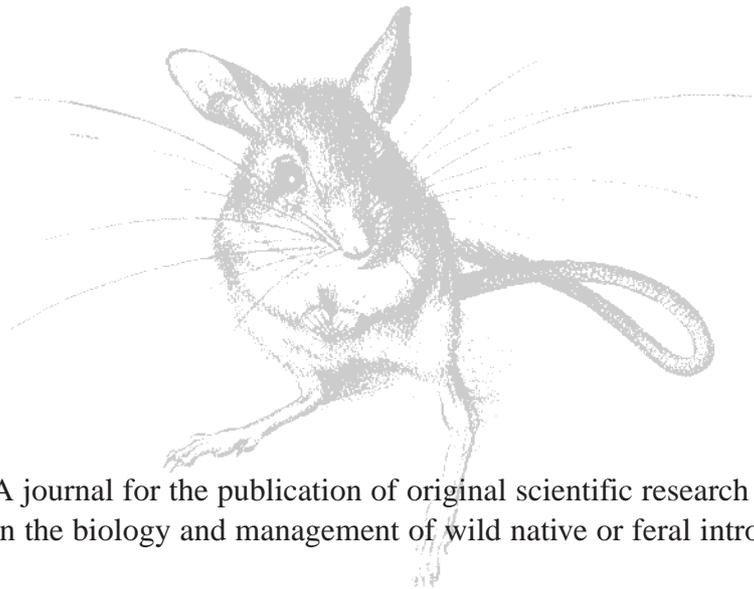

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Responses of Non-volant Mammals to Late Quaternary Climatic Changes in the Wet Tropics Region of North-eastern Australia

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Abstract

It is generally recognised that the distribution of vertebrates in rainforest and wet sclerophyll forest of the Wet Tropics region of north-eastern Australia is profoundly influenced by the formation of two rainforest refugia at the height of Pleistocene glacial periods. Anomalies in the distribution of non-volant mammals indicate that other events may be equally important. In this paper, past geographical occurrence of non-volant mammals is examined by equating the mammals' known temperature tolerance with palaeoclimatic temperature zones. It is hypothesised that dispersal and vicariant phases taking place since the most recent glacial period have had a profound influence on current patterns of distribution. A major dispersal phase of cool-adapted species occurred after the glacial period, and continuous populations were subsequently fragmented into upland isolates by expansion of warm rainforest during the late post-glacial period. These upland isolates remain substantially unchanged to the present day. Species shared either with New Guinea or south-eastern Australia arrived in the region during the most recent post-glacial period. Clarification of periods of vicariance and dispersal provides a conceptual framework for testing relative divergences of populations within and between regions.

Introduction

Rainforest and Faunal History of the Wet Tropics

The present rainforest fauna of the Wet Tropics region of north-eastern Australia has three components: endemics, those shared with New Guinea and those shared with south-eastern Australia (Winter 1988). The endemic rainforest specialists comprise eight marsupials and a rodent. The marsupials are Gondwanan in origin and a relict fauna as a consequence of major contraction of their rainforest habitat, from extensive coverage of the continent in the Miocene 15–20 million years ago, to the remnant patches of today (Webb and Tracey 1981; Archer 1984; Archer *et al.* 1991). The one rodent endemic to the Wet Tropics region belongs to a genus originating in New Guinea; it probably spread to Australia across a Pleistocene landbridge (Flannery 1990).

Marsupials and rodents shared with New Guinea have undergone little evolutionary differentiation, to subspecific level only, indicating recent separation of populations (Schodde and Calaby 1972). They probably used rainforest connections across landbridges between the two land masses during the Pleistocene (Flannery 1990), but later than did the endemic rodent, as evidenced by its greater differentiation.

The third group of Wet Tropics rainforest species is that shared with south-eastern Australia that are capable of inhabiting both rainforest and wet sclerophyll forests (Winter 1988). Included in this group are species restricted to the wet sclerophyll band of the Wet Tropics. As for the species shared with New Guinea, this group has also undergone little evolutionary differentiation between the Wet Tropics and southern populations, indicating recent separation, probably during the Pleistocene.

Climatic History of the Wet Tropics

A detailed and well-documented palynological history of the last 190000 years of the Wet Tropics region reveals cycles of rainforest expansion and contraction caused by climatic

fluctuations (Kershaw 1985; Walker 1990). During the most arid times, the rainforest contracted into moist refugia, smaller than the present-day area of rainforest. Webb and Tracey (1981) postulated that these refugia provided an uninterrupted presence of rainforest in the region, although the discovery of *Eucalyptus* charcoal in some of the refugia raises doubts about their actual spatial continuity (Hopkins *et al.* 1993).

For the first 150000 years of this period, the forest was dominated by gymnosperms, particularly *Auricularia*, during cooler drier times (Kershaw 1985; Walker 1990) and although the forest was drier with a more open canopy, it was still essentially a rainforest type. However, over the past approximately 38000 years, a radical change took place in this forest. It changed to a type dominated by sclerophyll vegetation containing *Casuarina* and *Eucalyptus* and with a much higher frequency of fire (Kershaw 1985; Hopkins *et al.* 1993), attributed to the influence of humans (Kershaw 1986). This reduced the moist rainforest refugia to fragments, surrounded by a habitat hostile to rainforest fauna. This fragmentation exacerbated the effects of habitat reduction on the ability of rainforest fauna to survive these drier times.

Using the palynological evidence, Nix and Switzer (1991) reconstructed palaeoclimates from the height of the most recent glacial period, about 18000 years before present (YBP) to the present day. Although they did not model earlier climatic periods, they estimated the present day climate to be similar to that of the previous interglacial period from 126000 to 115000 YBP. In this latest complete cycle, rainforest contracted to be replaced by sclerophyll forest at the height of the glacial period (Kershaw 1986). Earlier cycles would have followed the same pattern except that moist rainforest was replaced by dry gymnosperm forest rather than by sclerophyll forest. Nix and Switzer's (1991) modelling is fairly coarse and does not show short-term, high-amplitude climatic fluctuations, or 'flickers', characteristic of the Pleistocene (Roy *et al.* 1996), which may have blurred the glacial cycles.

Current Distribution Patterns of Fauna

At the height of the most recent glacial period, rainforest in the Wet Tropics region reduced to two discrete refugia centred on the Thornton and Atherton units (Nix and Switzer 1991). They were separated by a strip of woodland 80 km wide on a low section of coastal ranges, between the higher massifs of the Carbine Tableland to the north and the Lamb Range to the south, referred to as the Black Mountain Corridor or Gap (Bell *et al.* 1987; Joseph and Moritz 1994).

There is clear evidence of a major separation of the rainforest fauna of the region into northern and southern communities, which reflects the existence of these two refugia. On the basis of distributions of non-volant rainforest mammals, Winter *et al.* (1984) proposed two subregions also centred on the Atherton and Thornton uplands, which are the equivalent to Nix and Switzer's (1991) refugia. The influence of this separation is clearly shown in the distribution of the ringtail possum genus *Pseudochirulus*, which has sister-species, *P. cinereus* and *P. herbertensis*, each side of the Gap. They are distinguished from each other by morphological differences (Tate 1945), diploid chromosome numbers of 16 and 12 respectively (Murray *et al.* 1989) and a 2% sequence divergence for mitochondrial DNA, the latter suggesting a Pleistocene separation of the genus (Moritz *et al.* 1997).

Frogs also display northern and southern communities within the region (McDonald 1992), and genetic variation within species of reptiles and birds indicate a major division in populations across the Gap (Moritz *et al.* 1993; Joseph and Moritz 1994; Joseph *et al.* 1995). The degree of nucleotide divergence each side of the Gap suggests that vicariance has affected the species at different times with some at least antedating the Pleistocene (Joseph *et al.* 1995).

Anomalies in Mammalian Distributions

Certain anomalies exist in the concept of a simple dichotomy of faunal communities determined by the two glacial refugia. Current distribution of some species fails to fit with the notion that fauna separated into two communities equivalent to the two refugia at that time and remained constant to the present day. These incongruities indicate that more-recent rainforest cycles could have exercised an equally important influence on the biogeography of the region.

The anomalies are clearly demonstrated by the present distribution of two ringtail possums, *Hemibelideus lemuroides* and *Pseudochirops archeri*. They occur each side of the Black Mountain Gap but the level of divergence appears less than in *Pseudochirulus*. *H. lemuroides* exhibits significantly different levels of the white colour morph in the separate populations (Winter 1984; Trenerry and Werren 1993), thus indicating genetic divergence. However, the lack of other overt morphological differences is taken as evidence that it has not attained the specific level shown by *Pseudochirulus*. *P. archeri* is presently continuous across the Gap and reveals no signs of divergence to indicate population fragmentation at the time of the *Pseudochirulus* separation, nor signs of hybridisation to indicate subsequent amalgamation following such a separation.

In addition, the absence of *H. lemuroides* and *P. archeri* from the Thornton massif supports the hypothesis that they were later arrivals on the northern side of the Gap. This is emphasised by the prediction that the Thornton unit contained the largest area of rainforest at the time of greatest contraction of the habitat, 18000 YBP (Nix and Switzer 1991). *H. lemuroides* could have become locally extinct in the Thornton unit, because it is more prone to extinction than is *P. archeri* or *P. cinereus*, but this is unlikely to apply to *P. archeri*, which is the least prone to extinction (Laurance 1990a).

Previously, Winter *et al.* (1984) attempted to incorporate these anomalies into the subregional concept by proposing the Carbine unit as an overlap zone, but this was insufficient to adequately address the issue of multiple divergence times.

Consequently, this paper re-examines the aberrations by matching hypothetical distributions of non-volant mammals to Late Quaternary climatic changes. It presents evidence that post-glacial dispersal and vicariant phases played as important a part in determining the present-day distribution of species as the dramatic vicariant event at the height of the glacial period.

Methods

Mapping

Climatic modelling maps produced by Nix and Switzer (1991) were used to examine the distributions of non-volant mammals in the Wet Tropics during the late Quaternary in the following ways:

- (i) five temperature zones—Very Cool, Cool, Moderately Cool, Warm and Very Warm (Table 1)—were derived from the temperature classes of Nix and Switzer (1991, fig. 16);
- (ii) current known distributions of species were equated with present-day temperature zones (for example, the known distribution of *H. lemuroides* is closely mirrored by the extent of the two coolest zones, which have an annual mean temperatures lower than 21°C, and the distribution of *P. archeri* matches the zones with annual mean temperatures lower than 23°C);
- (iii) species were grouped into four categories according to geographical distributions and habitat (Winter 1988) (Table 1); and
- (iv) efficacy of geographical and woodland habitat barriers during changing climatic periods was assessed from present-day discontinuities in mammal populations (Fig. 1; Table 2).

Assumptions

This examination of palaeodistribution patterns assessment is based on three assumptions:

- (i) that mammalian species have been consistent in their temperature tolerance for at least the past 18000 years and thus have moved in unison with shifting temperature zones;
- (ii) that no significant change has occurred to the geomorphological barriers during the period under consideration; and
- (iii) that the rate of morphological divergence within vicariant populations is relative to the time of separation.

Palaeodistributions of Non-volant Rainforest Mammals

In this section, movements of temperature zones and their implications for rainforest distribution are examined, using Nix and Switzer's (1991) maps of four climatic periods. Consideration is then given to ways in which the four categories of non-volant mammals responded.

Table 1. Classification of non-volant mammals in relation to ecological-cum-geographical categories and the temperature zones of Nix and Switzer (1991)

Name abbreviations are those used in the figures. Altitude ranges in New Guinea from Flannery (1990).
Mod. Cool, Moderately Cool

Category, species (with abbreviation)	Altitude range (m)	Temperature zones (°C)					Altitude range in New Guinea (m)
		Very Cool (<19)	Cool (19–21)	Mod. Cool (21–23)	Warm (23–25)	Very Warm (>25)	
Wet Tropics rainforest-endemic species							
Ag <i>Antechinus godmani</i>	>600	■	■	■	■	■	
HI <i>Hemibelideus lemuroides</i>	>500	■	■	■	■	■	
Uh <i>Uromys hadrourus</i>	>500	■	■	■	■	■	
Ph <i>Pseudochirulus herbertensis</i> ^A	>350	■	■	■	■	■	
Pc <i>Pseudochirulus cinereus</i> ^A	>450	■	■	■	■	■	
Par <i>Pseudochirops archeri</i>	>300	■	■	■	■	■	
DI <i>Dendrolagus lumholtzi</i>	>0	■	■	■	■	■	
Db <i>Dendrolagus bennettianus</i>	>0	■	■	■	■	■	
Hm <i>Hypsiprymnodon moschatus</i>	>0	■	■	■	■	■	
South-eastern rainforest and wet sclerophyll species							
As <i>Antechinus stuartii</i>	>700	■	■	■	■	■	
SI <i>Sminthopsis leucopus</i>	>700	■	■	■	■	■	
Pp <i>Pseudocheirus peregrinus</i>	>700	■	■	■	■	■	
Tvj <i>Trichosurus vulpecula johnstoni</i>	>600	■	■	■	■	■	
Rf <i>Rattus fuscipes</i>	>0	■	■	■	■	■	
Af <i>Antechinus flavipes</i>	>0	■	■	■	■	■	
Dm <i>Dasyurus maculatus</i>	>0	■	■	■	■	■	
Pn <i>Perameles nasuta</i>	>0	■	■	■	■	■	
Mc <i>Melomys cervinipes</i>	>0	■	■	■	■	■	
Ts <i>Thylogale stigmatica</i> ^B	>0	■	■	■	■	■	
Pb <i>Petaurus breviceps</i> ^B	>0	■	■	■	■	■	
Hc <i>Hydromys chrysogaster</i> ^B	>0	■	■	■	■	■	
South-eastern wet sclerophyll species							
Pau <i>Petaurus australis</i>	>690	■	■	■	■	■	
Rlu <i>Rattus lutreolus</i>	>600	■	■	■	■	■	
Bt <i>Bettongia tropica</i> ^C	>430	■	■	■	■	■	
New Guinean rainforest species							
Cc <i>Cercartetus caudatus</i>	>0	■	■	■	■	■	1500–3450
Dt <i>Dactylopsila trivirgata</i>	>0	■	■	■	■	■	0–2300
Uc <i>Uromys caudimaculatus</i>	>0	■	■	■	■	■	0–1925
Pm <i>Pogonomys mollipilosus</i>	>0	■	■	■	■	■	800–3000
Rle <i>Rattus leucopus</i>	>0	■	■	■	■	■	0–1200

^ALower altitude limits are between zone boundaries.

^BAlso found in New Guinea but classified as south-eastern Australian.

^CTreated as a close sister-species to *B. penicillata*.

Full Glacial Period: 18000 YBP

The cooling and drying of the climate reached its zenith at the height of the glacial period. Rainforest greatly contracted, leaving two rainforest refugia of significant size: one centred on the Atherton unit and the other on the Thornton–Carbine units (Nix and Switzer 1991). They were separated by about 80 km of drier habitat in the Macalister unit. At the same time, a drop in sea level of 120 m (Nix and Switzer 1991) formed a new coastal plain, and it is assumed that the dry corridor of the Macalister unit extended to the new coastline (Fig. 2a). The Warm and Very Warm temperature zones disappeared, the Moderately Cool zone extended down to sea level in the Thornton unit and the Cool zone to sea level in the more southerly Atherton unit.

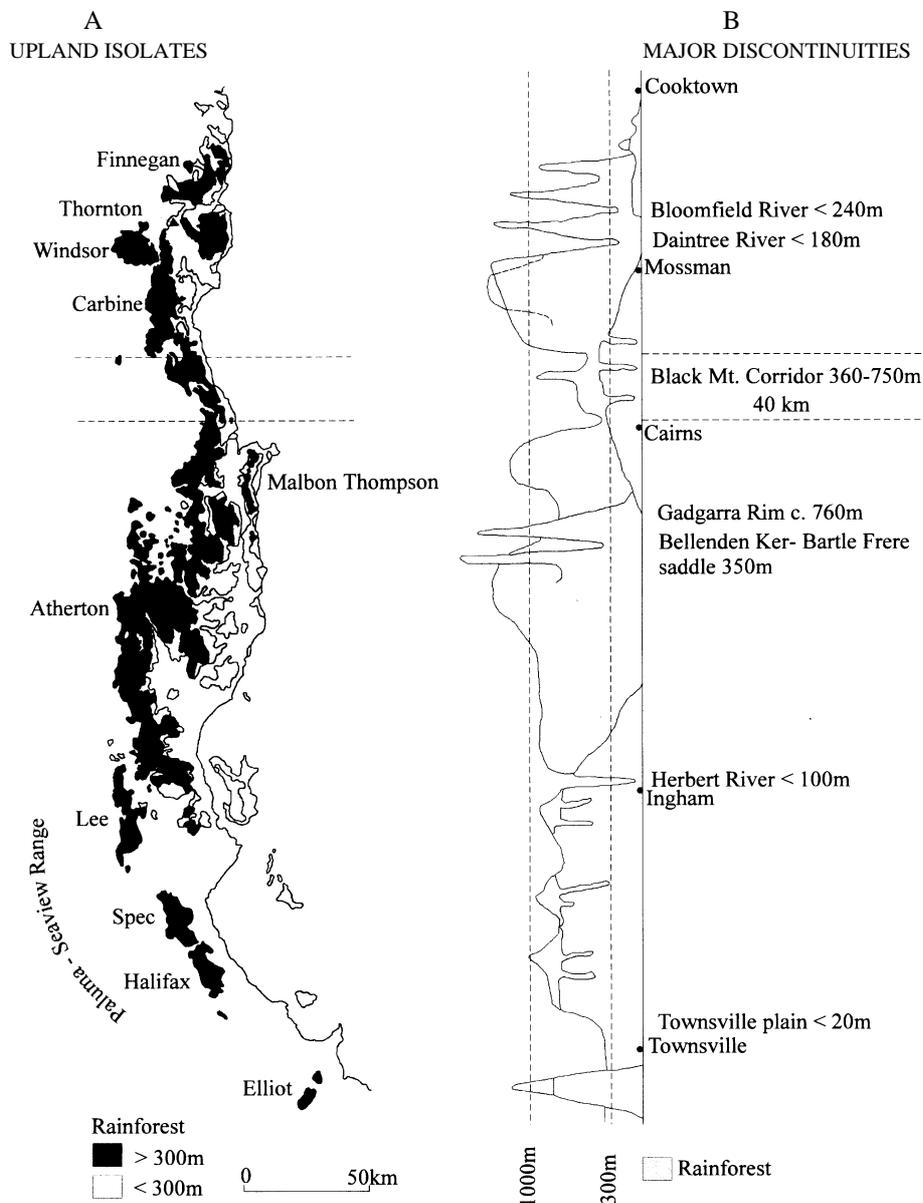


Fig. 1. Upland rainforest isolates in the Wet Tropics (after Bell *et al.* 1987) in relation to altitudinal and ecological discontinuities. (A) Plan view; (B) sectional view.

Although Nix and Switzer (1991) refer to the northern refuge as the Thornton–Carbine units, the core of the refuge is actually Thornton only. It is clearly visible on their map that Carbine sustains only minute fragmented areas of rainforest.

This contraction of rainforest had two major influences on its fauna. First, it reduced the total area of rainforest to less than half the present area, thus imposing a bottleneck on the number of species in relation to absolute area of habitat. Second, it instigated a major vicariant event by separating the fauna of the region into two isolated populations north and south of the Black Mountain Gap. Thus, the existing faunal diversity of the Wet Tropics region reflects the

Table 2. Within-region third-order and selected fourth-order discontinuities to faunal distributions in the Wet Tropics biogeographical region

First- and second-order discontinuities are between-region breaks (see Winter 1984)

Name	Maximum elevation (m)	Minimum width (km)	Vegetation type across discontinuity
Third-order discontinuities			
Bloomfield River	250	5	Woodland and riparian strips
Daintree River	160	2	Rainforest
Black Mountain Corridor	360–750	40	Rainforest
Cairns Coastal Plain	20	3	Rainforest–woodland mosaic
Herbert River	100	2	Woodland
Townsville Coastal Plain	60	25	Woodland
Fourth-order discontinuities			
Windsor–Carbine Saddle	720	5	Woodland
Bartle Frere–Bellenden Ker Saddle	350	0.5	Rainforest
Gadgarra Rim (Lamb Range–Lamins Hill)	c. 760	c. 10	Rainforest
Stone River Gap (Mt Lee–Mt Spec)	700	10	Woodland
Ollera Creek Gap (Mt Spec–Mt Halifax)	570	0.5	Woodland

species–area relationships of a reduced and fragmented habitat that existed during the glacial period (Crome 1990; Nix and Switzer 1991).

Rainforest-endemic species

The two species of *Dendrolagus* have a current distribution that equates with one existing in each of the glacial refugia: *D. bennettianus* in the northern Thornton refugium and *D. lumholtzi* in the southern Atherton refugium (Winter *et al.* 1991; Nix and Switzer 1991). However, speciation of the two almost certainly predates this vicariant event. An Australian origin for the genus (Flannery and Szalay 1982) and their positioning on opposite sides of a major dichotomy of the genus (Groves 1982) support the hypothesis of a much earlier divergence of the two species. The presence of *D. lumholtzi* on the northern side of the Black Mountain Gap is attributed to a subsequent dispersal event discussed later. In contrast to the *Dendrolagus* species, divergence of *Pseudochirulus* species, *P. cinereus* and *P. herbertensis*, whose present distribution is each side of the Black Mountain Gap, can be attributed to this vicariant event, because they are closely related species of a more recent origin.

Most other endemics are considered to have survived in only one or other of the refugia, even if the species was divided at the time into a northern and southern population.

Existing distributions of *H. lemuroides* and *P. archeri* indicate that they survived this time in the Atherton refugia and dispersed north later. Their absence from the Thornton unit, which is the core of the northern refugium, substantiates this statement.

The absence of any overt morphological variation in *Hypsiprymnodon moschatus* throughout its range supports the concept that it survived in one of the refugia during the glacial period and subsequently dispersed throughout the region. On the basis of species–area relationships, it is more likely that the potoroid survived in the larger Atherton unit.

Antechinus godmani is known only from the Atherton Uplands, but its perceived absence from the Carbine Tableland north of the Black Mountain Gap may be an artefact of inadequate sampling, particularly as Nix and Switzer (1991) give the Carbine Tableland as core habitat. Its discovery north of the Black Mountain Corridor would be indicative of dispersal similar to that of *H. lemuroides*. Alternatively, the discovery of a sister-species in the north would indicate a population divided by the glacial vicariant event.

The known presence of *Uromys hadrourus* in the Atherton Uplands, the Carbine Tableland and particularly the Thornton Uplands (Winter and Moore 1995) strongly indicates that a

previously continuous population was fragmented into subpopulations at the height of the last glacial period. Subsequent genetic divergence between the subpopulations is indicated by weight differences between individuals in the Thornton and Atherton unitspopulations (Winter and Moore 1995).

South-eastern rainforest and wet sclerophyll species

Species currently represented in both the Wet Tropics and south-eastern Australia are conjectured to be post-glacial arrivals in the Wet Tropics. This statement is based on the argument that genetic divergence would have proceeded beyond the current subspecific status in each region if separation of the populations had occurred during the glacial period as a result of the expanded dry Bowen Corridor.

An exception is *Trichosurus vulpecula johnstoni*, for two reasons. First, of the species with south-eastern affinities it appears to have proceeded furthest down the path of speciation. Flannery (1994) elevated *johnstoni* to full specific status and presumably did so on the evidence of Kerle *et al.* (1991). However, this elevation is premature, because although Kerle *et al.* (1991) found that the Atherton population stood apart from all other populations of *Trichosurus* on skull morphology and differed in some fixed allozymes, they considered their sample too small to resolve the possum's taxonomic status.

The second and more compelling piece of evidence is in the the present distribution of *T. v. johnstoni*: it is confined to the western part of the Atherton Tableland (Winter *et al.* 1991). Such a confined distribution is consistent with the hypothesis that a *Trichosurus* population became geographically isolated in the Atherton refugium at the time of the rainforest's greatest contraction. However, this highlights the anomaly that other taxa with south-eastern affinities were not similarly isolated during this period.

There are three possible explanations for the unique circumstances of *T. v. johnstoni*:

(i) *T. vulpecula* has a much wider habitat tolerance than do other south-eastern species, as exemplified by its wide distribution across central Australia in semi-arid habitats (Kerle *et al.* 1992), which may have placed the species in juxtaposition to the Atherton refugia during the glacial period;

(ii) geographical isolation of *T. vulpecula* may have occurred at the same time as for other south-eastern species, but taxonomic divergence has occurred more rapidly; or

(iii) *T. v. johnstoni* is merely a polymorphic population of *T. vulpecula* in which individuals in wetter areas are darker-coated than those in drier habitats, similar to the condition found in Tasmania (Guiler and Banks 1958).

Postulation that the time of isolation occurred during the height of the glacial period favours the first of these possibilities.

South-eastern wet sclerophyll species

Akin to the south-eastern rainforest species, the three non-volant mammals primarily restricted to wet sclerophyll are considered to be post-glacial arrivals in the Wet Tropics because they also have not diverged beyond subspecific status.

The most probable scenario is that during the height of the glacial period, wet sclerophyll forest in the Wet Tropics region underwent a more pronounced constriction than did the rainforest. It was thus reduced in area below that capable of supporting specialist species (Winter 1988) and continuity with southern habitat of the same type was broken.

New Guinean rainforest species

Elimination of Warm and Very Warm temperature zones resulted in regional extinction of strictly warm-adapted species.

As with the south-eastern species, if the warm-adapted New Guinean species had survived in the Wet Tropics region during the glacial period, speciation would have proceeded further

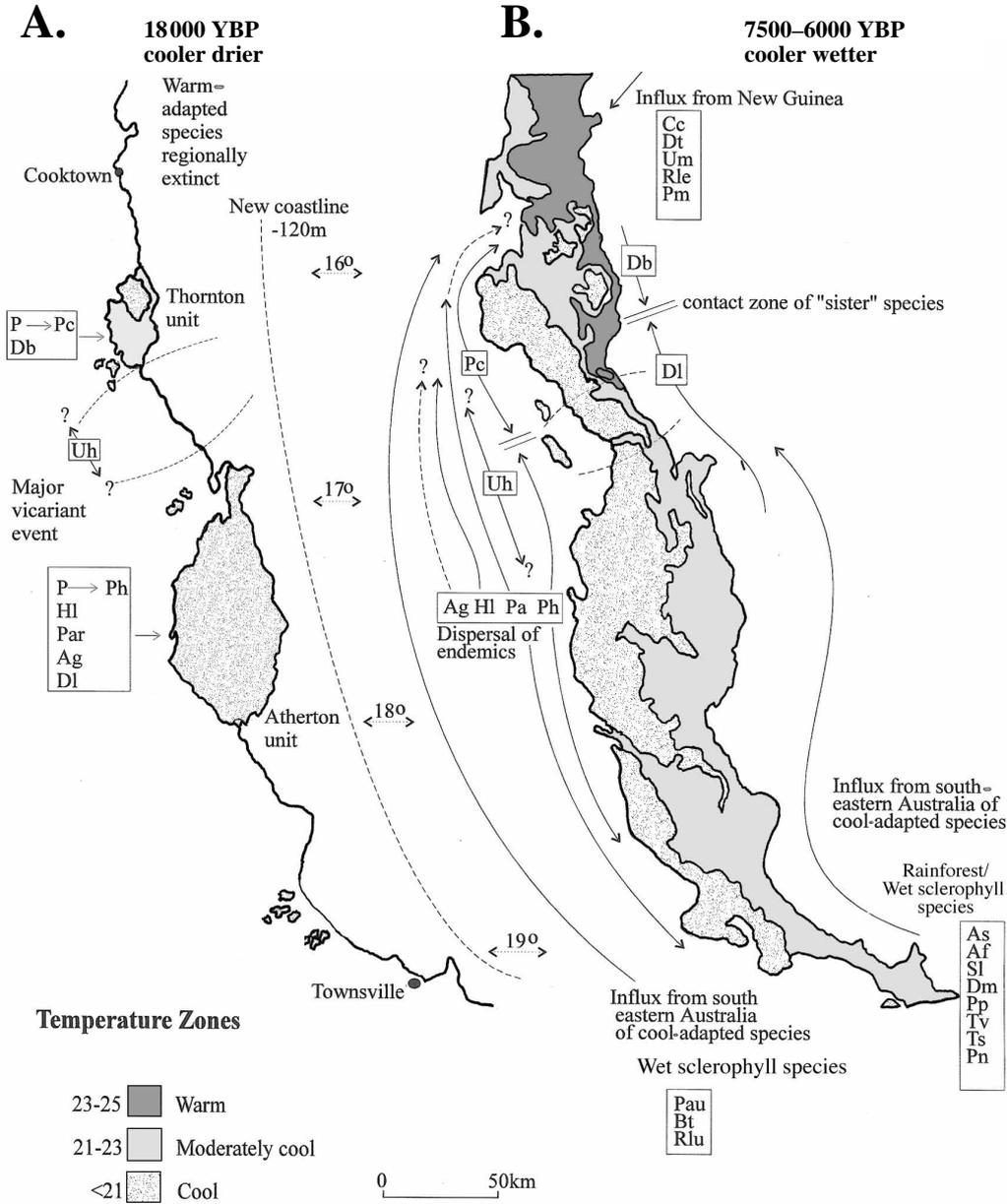


Fig. 2. Rainforest environment by temperature classes since the height of the last glacial period (after Nix and Switzer 1991) and postulated movements by non-volant rainforest mammals (see Table 1 for name abbreviations). (A) Glacial period, 18000 years before present (YBP); (B) early post-glacial period, 7500-6000 YBP.

according to the proposed scenario. Therefore, this group of animals are postulated to be later arrivals to the Wet Tropics.

Early Post-glacial Period: 7500-6000 YBP

During this time the climate became wetter than at the height of the glacial period, although it remained cool. Rainforest expanded to become continuous throughout the length of the region

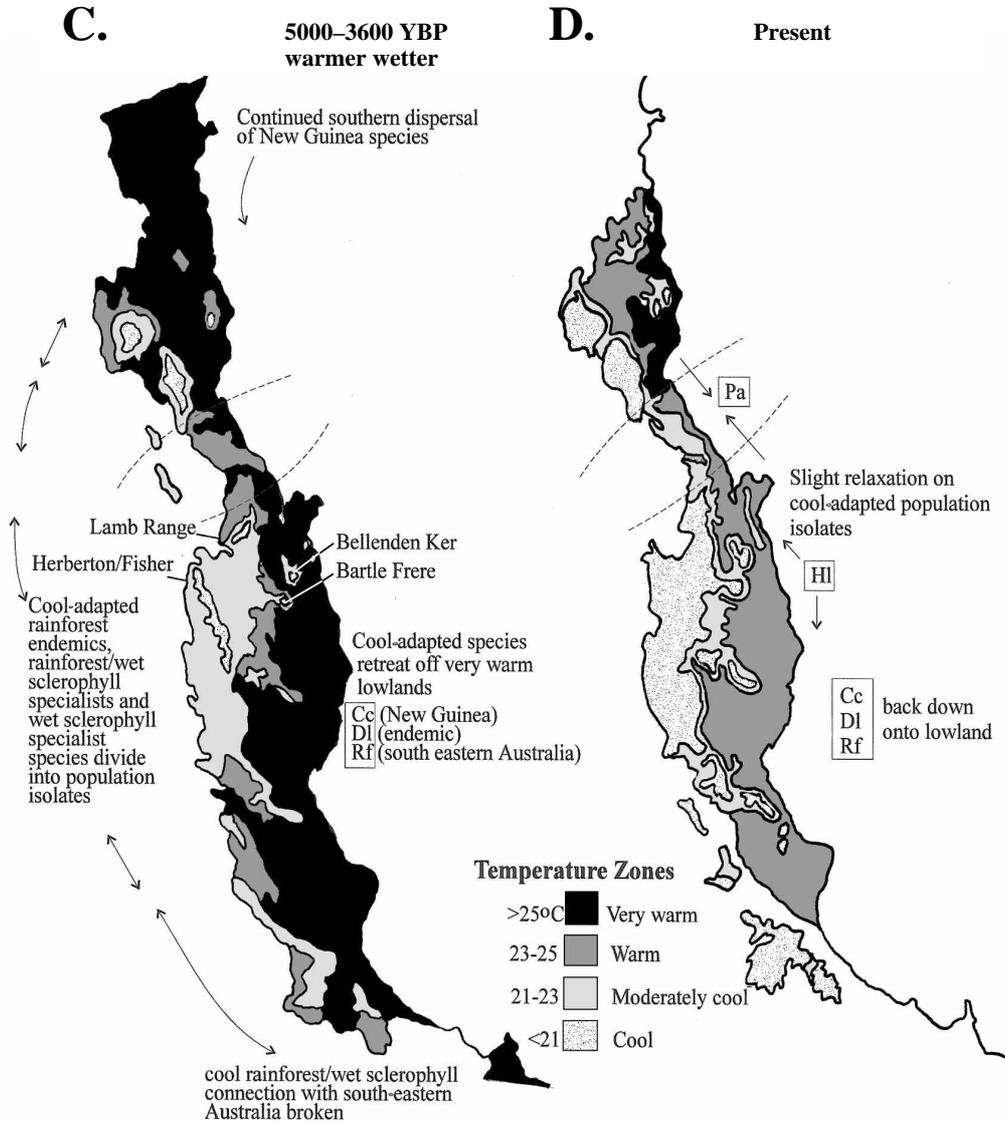


Fig. 2. (C) Late post-glacial period, 5000–3600 YBP; (D) present day.

(Fig. 2b) and even along the eastern seaboard of Australia, north and south of the region. For a period during this time, rainforest was also continuous between Cape York Peninsula and New Guinea across a landbridge, before it was obliterated by rising sea levels (Nix and Kalma 1972). South of the Wet Tropics region, wet sclerophyll forest was an integral component of the moist-forest connection.

The climate was still cool enough for the Moderately Cool zone to extended down to the coast south of Mossman and across the inland end of the Daintree and Bloomfield valleys north of Mossman. The Cool zone became virtually continuous from the Mt Windsor Tableland in the north to the Herbert Gorge in the south with only minor discontinuities in the Black Mountain Corridor. North of Windsor, Cool zone continuity was broken by the Daintree and Bloomfield valleys, resulting in Cool zone isolates in the Thornton and Finnigan units. To the south of the Herbert Gorge, an extensive Cool zone was present along the crest of the Seaview and Paluma

Ranges. These Cool zone isolates were separated from the main area by Moderately Cool zone climates as was the small Cool zone isolate on Malbon Thompson.

Wet Tropics rainforest-endemic species

This was a major dispersal phase for non-volant mammals in the region. During this period, cool-adapted rainforest-endemic mammals were able to traverse most of the barriers that form discontinuities in current species' distributions and the following scenarios for species are consistent with this ability.

(i) *H. moschatus*, with its ability to use all temperature zones, expanded its range to cover the entire region.

(ii) *P. cinereus* spread across the Carbine, Windsor, Thornton and possibly Finnigan units. In the Black Mountain Corridor, it may have come in contact with *P. herbertensis*, but by this time reproductive isolation kept them as distinct species.

(iii) Both *H. lemuroides* and *P. archeri* dispersed north across the Black Mountain Corridor. The former colonised the Carbine unit but apparently failed to reach the Windsor unit. The latter possum, with superior powers of dispersal (Laurance 1990a), attained the Windsor unit and may even have extended into the Thornton and Finnigan units through the connecting Moderately Cool zone. However, the window of opportunity allowing *P. archeri* to cross the Daintree and Bloomfield valleys may have closed, because of climatic warming, before it could take advantage of this connection. *A. godmani* may have acted in a similar fashion, but survey information is inadequate to speculate on its possible dispersal onto the Carbine Tableland.

(iv) The two *Dendrolagus* species expanded out from the two glacial refugia to come into contact with each other. Although this contact zone may have altered over subsequent time, it appears to persist today in the Carbine Unit (Nix and Switzer 1991; Winter *et al.* 1991).

(v) South of the former glacial refuge in the Atherton unit, both *P. herbertensis* and *P. archeri* traversed the Herbert River discontinuity to colonise the expanded rainforest on the Seaview and Paluma Ranges. Again, with its greater ability to disperse, *P. archeri* moved further south. However, the Moderately Cool climate of the Herbert River valley proved an impediment to the southern movement of both *H. lemuroides* and *A. godmani*.

To the west, Bakers Blue Mountain and Hann Tableland remained isolated, thus preventing colonisation by rainforest species from the main area.

South-eastern rainforest and wet sclerophyll species

The connection to rainforest and wet sclerophyll forest to the south-east of the region allowed a dispersal phase of southern species to the north. This resulted in a selection of species reaching the Wet Tropics and some, for example *Perameles nasuta* and *Thylogale stigmatica*, even reaching as far as Cape York Peninsula and New Guinea respectively. During this period *Antechinus flavipes* may have dispersed into the rainforests of Cape York Peninsula as a precursor to *Antechinus leo* (Van Dyck 1980).

Why was there not an equivalent dispersal of Wet Tropics endemics to the south? The most probable reason is that the link between the Wet Tropics and south-eastern Australia included wet sclerophyll forest, which acted as a barrier to the specialist rainforest endemics but not to the more generalist south-eastern species (Winter 1988).

South-eastern wet sclerophyll species

During this period, wet sclerophyll forest probably extended as a continuous belt along the western edge of the rainforest, from the Mt Windsor Tablelands in the north to the southern end of the Paluma Range. North of Windsor this forest may have occurred as isolated patches on the western slopes in the Thornton and Finnigan units, and probably also played an important part in the connection to rainforest and wet sclerophyll forest in south-eastern Australia.

All three wet sclerophyll species dispersed northwards and existed as continuous populations throughout their range from south-eastern Australia to the Wet Tropics. *Petaurus australis* and

Bettongia tropica reached the Windsor unit. The northern limit of *Rattus lutreolus* was at least the Atherton unit and the apparent absence of this species further north is possibly sampling oversight.

New Guinean rainforest species

For a relatively brief period, the Torresian landbridge bridge offered New Guinean rainforest mammals the opportunity to cross into north-eastern Australia before it was flooded by rising sea levels (Nix and Kalma 1972). Species that made this crossing extended their distribution southwards. Some, such as *Phalanger intercastellanus*, *Spilocuscus maculatus* and *Echymipera rufescens*, extended no further than the McIlwraith Range on Cape York Peninsula. The five species that are now resident in the Wet Tropics (Table 1) began their journey south in this period. *Cercartetus caudatus* is the most cool-adapted of this group, as indicated by its present distribution in New Guinea between elevations of 1500 and 3450 m, and must have arrived in the Wet Tropics region by this time. The remaining four species are warmer-adapted and need not have reached their destination until the next climatic period.

Nevertheless, the four warm-adapted New Guinean species were sufficiently tolerant of cool temperatures, as expressed by their present upper altitudinal limits in New Guinea (Table 1), to place them at the northern end of the landbridge bridge, even when temperatures were cooler during this post-glacial period.

Late Post-glacial Period: 5000–3600 YBP

This period was the second vicariant phase in the past 18000 years. Climate during this time continued to be wet but temperatures became warmer than the period prior to this and warmer than the present-day.

With this warming, the cooler climatic zones migrated up the mountain slopes and became a series of cool upland rainforest isolates, smaller than currently exist (Fig. 2c). All three of the cooler zones were totally eliminated from the Finnigan and Malbon Thompson Units and, in contrast to the earlier glacial period, separators of the remaining upland isolates were Warm zone rainforests rather than dry woodlands. Rainforest persisted to the north and south of the region in the Very Warm zone.

Wet sclerophyll forest within the region contracted during this warmer period into a series of habitat isolates on the western and cooler edges of the Windsor, Carbine, Atherton, Seaview and Paluma units. It was obliterated in the Finnigan unit by the elimination of the Cool zone and in the Thornton unit it was reduced to minute remnants, at best. To the south of the region, the disappearance of cool-adapted wet sclerophyll forest broke the continuity of habitat for cool-adapted species between the southern end of the Wet Tropics and the Clarke Ranges about 350 km further south.

Wet Tropics rainforest-endemic species

Any cool-adapted species that had reached the Finnigan or Malbon Thompson units across bridges in Moderately Cool zones in the preceding dispersal phase would have vanished as a result of the warmer climate. Possible candidates include *P. cinereus*, *P. archeri* and *U. hadrourus* from Finnigan and *P. herbertensis* and *P. archeri* from Malbon Thompson. Species confined to the Cool zone, such as *H. lemuroides* and *A. godmani*, would not have made the earlier crossing to these outliers.

The fact that *P. archeri* is not known in the Thornton unit today suggests that it never reached this sector during the previous dispersal phase. If any of the rainforest ringtail possums was to have survived in the greatly reduced cooler zones in the Thornton unit, one would expect it to be *P. archeri*, rather than a *Pseudochirulus* species, because of its superior survival powers in a fragmented landscape (Laurance 1990a).

The Black Mountain Corridor once again became a barrier to cool-adapted species but not to species capable of existing in warmer rainforest. Thus, the Carbine populations of *P. archeri* and

H. lemuroides became isolated from populations in the Atherton unit. During this warmer time, the Very Cool and Cool zones in the Carbine unit were approximately half today's size, subjecting *H. lemuroides* to a severe population bottleneck. At this time genetic drift may have occurred, resulting in the significantly higher proportion of white colour morphs. While *P. archeri* experienced a similar bottleneck, it was not as severe because of the possum's wider temperature tolerance and therefore had less influence on the genetics of the population. Furthermore, the *P. archeri* populations north and south of the Corridor were subsequently reunited during relaxation of isolating factors when it became cooler, whereas *H. lemuroides* populations remained discrete.

In the Atherton unit, the Cool zone was reduced to four main isolates: Lamb Range, Bellenden Ker, Bartle Frere, and Herberton Range and Mt Fisher. This change resulted in four isolated populations of *H. lemuroides*. The Lamb Range, Bellenden Ker and Bartle Frere populations were small compared with the population from the Herberton Range and Mt Fisher. It is postulated that the perceived current absence of this possum on Bellenden Ker resulted from local extinction at this time and its subsequent inability to recolonise across the saddle between Bellenden Ker and Bartle Frere, which is below the possum's lower altitudinal limit. The small Lamb Range population survived and remains isolated to this day by the Gadgarra Rim discontinuity. The Bartle Frere population subsequently became continuous with the Herberton Range and Mt Fisher population.

Antechinus godmani was reduced to population isolates in the fragmented cool zones of the Atherton units. Its current presence on Bellenden Ker indicates that, unlike *H. lemuroides*, it did not become extinct in this isolate, presumably because of smaller area requirements. *U. hadrourus* once again became restricted to population isolates within the Thornton, Carbine and Atherton units.

South of the Herbert River, the Cool zone fragmented into two or more isolates separated by continuous warmer rainforest along the Seaview and Paluma Ranges. Both cool-adapted *P. archeri* and *P. herbertensis* were then restricted to these isolates. The present-day absence of the latter in the Paluma unit, the larger more southerly isolate, supports the contention that this possum failed to reach the southern end of these ranges during the previous dispersal phase.

Dendrolagus lumholtzi, intolerant of the Very Warm zone temperatures, was forced off the coastal lowlands throughout its distribution but retained continuity of population in the uplands with perhaps a break across the Herbert gorge. In contrast, *H. moschatus*, which is tolerant of warmer temperatures in the Very Warm zone, maintained its extensive coverage of the region.

South-eastern rainforest and wet sclerophyll species

With disruption of the southern link through disappearance of cool rainforest and cool wet sclerophyll forest, populations of the south-eastern Australian mammals became isolated in the Wet Tropics and the process of genetic divergence began. If the geographical isolation of *T. vulpecula* had not been initiated at the height of the glacial period, as argued in this paper, it would have commenced during this second vicariant phase.

The present distribution pattern of *Pseudocheirus peregrinus* may have become established during this period. It currently occurs in woodland to the west of the Wet Tropics region, throughout its length, and is found in rainforest, but only at the extreme southern end of the region in the cooler zones of the Paluma unit. Its absence from other rainforest areas within the Wet Tropics may partly be competitive exclusion by *Pseudochirulus*, as the two taxa are allopatric. However, it does not re-enter the rainforest north of the range of *Pseudochirulus*, even though suitable temperature zones exist in the Finnigan unit. This suggests that it is unable to survive in Warm zone rainforest around the base of the Finlayson Range and that this has prevented the possum's colonisation of the cooler zones in the Finnigan unit.

Rattus fuscipes was probably forced off the coastal lowlands by the spread of the Very Warm zone, as suggested by its present absence from this zone north of Mossman (Taylor and Horner 1973). Likewise, the *A. flavipes* population may have been displaced from the coastal plain by the expansion of the Very Warm zone. This would have resulted in the isolation of the Finnigan,

Thornton, Malbon Thomson and Seaview–Paluma populations from the continuous Windsor to Atherton population.

South-eastern wet sclerophyll species

All three species persisted in wet sclerophyll refugia on the western edge of the cooler zone isolates and, as for the south-eastern rainforest species, became isolated from populations further south.

Wet sclerophyll forests in the Windsor, Carbine and Atherton units were sufficiently extensive to support populations of *Petaurus australis* and *B. tropica*, which persist to this day. However, *P. australis* probably became locally extinct at this time on the Lamb Range, a separate isolate within the Atherton unit, and in the Seaview and Paluma units south of the Herbert River. This change came about because *P. australis* is the species most restricted to wet sclerophyll through its dependence on *Eucalyptus grandis* and *E. resinifera* (Russell 1984) and because the area of forest available to it was smaller than that available to the other two species. Although the presence of *B. tropica* is confirmed only within the Windsor, Carbine and Atherton units (Winter and Johnson 1995), apparently suitable habitat exists in the Seaview unit, but its presence has yet to be confirmed. The third wet sclerophyll species, *R. lutreolus*, survived in these isolates and is known today from the Atherton unit and those to the south.

New Guinean rainforest species

The warm-adapted species were not affected by changes in temperatures in the Wet Tropics during this period and were able to use the full range of temperature zones within the region. The cooler-adapted *C. caudatus* was displaced from the Very Warm zone of the coastal lowlands at this time. Its present-day absence from the rainforests of the McIlwraith Range on Cape York Peninsula, between the Wet Tropics and New Guinea, can be attributed to local extinction caused by the presence of the Very Warm zone only on this range during this period.

Present Day

This period has culminated in a slight expansion of cooler forests but an overall reduction in rainforest area. Slightly cooler and drier conditions than those in the previous period have led to a moderate expansion of cool upland isolates to their present size and location (Fig. 2d). This has resulted in amalgamation of most of the Very Cool zones in the Atherton unit, except for Bellenden Ker, which remains separate. It re-established a Moderately Cool zone link across the Black Mountain Corridor, and this zone also reappears in the Finnigan and Malbon Thomson units, but they remain isolated by surrounding Warm zone. Similarly, although the cooler zones in the Thornton unit have expanded, they remain separated from cool isolates to the south by the Warm and Very Warm zones in the Daintree valley. At the southern end of the region, drier conditions have led to loss of rainforest south of the Herbert River. As a result, the Very Cool and Cool zone isolates on the Seaview and Paluma Ranges are now surrounded by dry forest.

Wet Tropics rainforest endemic species

Populations of *Pseudochirops archeri* in the Carbine and Atherton units once again become continuous with the linking of the Moderately Cool zone across the Black Mountain Corridor. However, with the lack of continuity of the Cool zone in this corridor, both the *H. lemuroides* and *Pseudochirulus* populations remain separate. Amalgamation of Very Cool zones in the Atherton unit allowed population isolates of *H. lemuroides* and *A. godmani* to coalesce, although populations of *H. lemuroides* remain as discrete entities each side of the Gadgarra Rim and the species has been unable to recolonise Bellenden Ker because of the low saddle between Bellenden Ker and Bartle Frere.

Reappearance of Cool and Moderately Cool zones on Finnigan and Malbon Thomson has not been followed by recolonisation by cool-adapted species because both remain separated from source areas of upland species by warm rainforest zones across the warm Bloomfield Valley and on the Cairns Coastal Plain respectively. Likewise, the Thornton unit remains

isolated by the warm Daintree valley, preventing additions of cool-adapted endemics from the Carbine and Windsor units.

The loss of warmer rainforest south of the Herbert River has deprived *D. lumholtzi* and *H. moschatus* of much of their habitat. The remaining fragments of cooler forest appear to be too small to support *D. lumholtzi*, which has disappeared from rainforest south of the river, whereas *H. moschatus* has managed to survive in the Seaview unit.

Uromys hadrourus could be expected to have expanded its range in the Atherton unit with the amalgamation of the Very Cool zones, but currently it is known only from a very restricted area in the Lamins Hill locality west of Bartle Frere (Winter and Moore 1995), despite extensive mammal collection over the past 70 years. This distribution suggests that the rat has very specialised habitat requirements that restrict it to small, localised populations even in apparently continuous habitat, plus it may avoid capture by conventional methods.

South-eastern rainforest and wet sclerophyll species

The only significant change in distribution of this group through relaxation in the size of cool isolates was for *R. fuscipes*. This species was able to recolonise the coastal plain south of the Daintree River owing to the retreat of the Very Warm zone to the north of the river.

However, the loss of rainforest continuity south of the region has emphasised the isolation of these species within the Wet Tropics region. The most extreme example is *Sminthopsis leucopus* inhabiting rainforest and wet sclerophyll forest in the Wet Tropics region (Van Dyck 1985; Laurance 1990b). Its closest neighbouring population is in southern New South Wales (Van Dyck 1985), a distance of some 1600 km. For others such as *Perameles nasuta*, *Thylogale stigmatica* and *Melomys cervinipes* and for the rainforest populations of *Pseudocheirus peregrinus* and *Trichosurus vulpecula*, the gap is a relatively narrow 350 km to the Clarke Range. Another group, which includes *Antechinus stuartii*, *A. flavipes* and *R. fuscipes*, did not persist in the small area of suitable habitat on the Clarke Range (Winter and McDonald 1986; Van Dyck and Longmore 1991) and the gap is in the order of 800 km to south-eastern Queensland.

South-eastern wet sclerophyll species

Relaxation to the limits of this cool-adapted forest, with the advent of cooler temperatures, has achieved little more than a slight expansion of the existing refugia rather than an amalgamation. It has been insufficient to enable *Petaurus australis* to recolonise wet sclerophyll forest on the western slopes of the Lamb Range, nor has it enabled the glider to cross the Herbert River into the Seaview and Paluma units.

Wet sclerophyll specialists in the Wet Tropics, as for the rainforest species, have become isolated from populations further south. The closest neighbouring populations of *P. australis* (P. Walsh, personal communication) and *R. lutreolus* (Van Dyck and Longmore 1991) are on the Clarke Ranges in the Mackay district.

Bettongia tropica appears to have had a major contraction of range within the past 100 years to its present limit within the Wet Tropics region (Winter and Johnson 1995). This may have resulted from human interference, although it is tempting to speculate that changing climate has also contributed to this contraction.

New Guinea rainforest species

All species occur throughout the full range of elevations within the region and are therefore not affected by any altitudinal barriers. The only species known to have a restricted distribution within the region is *Rattus leucopus* which, south of Tully, is confined to the lowlands below about 400 m (Winter, unpublished data). *Pogonomys mollipilosus* may show a similar pattern of restriction to lowlands at the southern end of the region. It is known from the lowlands at Cairns and to the north, but further south the only records are from the uplands, the most southerly being at Millaa Millaa in the Atherton unit (Winter and Whitford 1995).

Summary of Vicariant and Dispersal Phases

It is postulated that the following stages of fragmentation and dispersal took place.

(i) During the glacial period, cool-adapted rainforest species survived in one or other of the main refugia, mainly the larger Atherton refugium. An exception was *Pseudochirulus*, which diverged into two species at this time. Warm-adapted species became extinct with the elimination of warmer temperature zones.

(ii) In the dispersal phase of the early post-glacial period, endemic species dispersed across previous environmental barriers, particularly the wide Black Mountain Gap. Species currently shared with New Guinea now began the exchange through rainforest corridors open for a short time across the connecting landbridge, before it was obliterated by rising sea levels. Concurrently, rainforest-cum-wet sclerophyll species from south-eastern Australia were able to colonise the Wet Tropics along the cool-forest link between the two regions.

(iii) In the late post-glacial period, cool-adapted rainforest and wet sclerophyll species, both endemics and those shared with south-eastern Australia, underwent population fragmentation into a number of upland isolates. These isolates were smaller than those existing at the present day. The isolates were separated by warm rainforest rather than sclerophyll woodland present at the time of the glacial period. The warm-adapted species shared with New Guinea completed dispersion through the Wet Tropics at this time and some may not have arrived until as late as this period through a rainforest connection to Cape York that persisted.

(iv) Finally, a slight cooling of temperatures to the present day re-established the connection between some population isolates of cool-adapted species, particularly across the Black Mountain Corridor and between populations within the Atherton unit.

Discussion

The present-day pattern of distribution of non-volant mammals in the Wet Tropics is consistent with the proposition that it was established since the most recent glacial period, 18000 YBP. It is consistent with the notions that (1) endemic species were confined to one or other of the glacial refugia and subsequently dispersed; (2) another vicariant phase took place for cool-adapted species, during the warm and wet time of the late post-glacial, which has determined the present-day upland population isolates; and (3) shared species, shared with either New Guinea or south-eastern Australia, arrived during a post-glacial period. In the case of south-eastern cool-adapted species, it was the early post-glacial period, whereas the warm-adapted species arrived from New Guinea at the same time, or even later during the late post-glacial period.

It could be argued that the present composition and pattern of distribution of the Wet Tropic's non-volant mammals was established during an earlier glacial cycle and merely preserved during more recent cycles. The main claim against this argument is that radical change took place in the type of vegetation that replaced moist rainforest during dry stages of a cycle. In the earlier cycles, it was gymnosperm forest that, although substantially drier than moist rainforest, still retained many characteristics of rainforest suitable for the continued survival of rainforest mammals. In stark contrast, sclerophyll forest replaced rainforest during dry phases of the most recent cycle and sclerophyll forest is a hostile environment to rainforest mammals. Consequently, patterns of mammalian distribution established during earlier cycles would not have fitted the environmental changes taking place during the most recent cycle. Thus, this best-fit model applies only to the most recent cycle.

In addition, evidence from differential evolutionary divergence occurring during the Pleistocene supports the hypothesis of a recent establishment. The presence of two species of *Uromys*, one endemic and the other shared with New Guinea, indicates two invasions. The genus is thought to have originated in New Guinea and reached Australia across landbridges formed during the Pleistocene (Flannery 1990). The two species are at the opposite ends of the spectrum of divergence within the genus: *U. hadrourus* has had time to evolve into an endemic species that has no obvious vicar in New Guinea. Thus, it is an earlier arrival than

U. caudimaculatus, which has diverged to subspecific status only. Such a large difference suggests that their respective invasions took place at the opposite limits of the Pleistocene.

Furthermore, the absence of *H. lemuroides* north of the Carbine unit and *Pseudochirops archeri* north of the Windsor unit supports the notion of their dispersal from the Atherton unit, through the Black Mountain Corridor, during post-glacial times, and that they failed to progress further north in the time available. If this dispersal had occurred in an earlier cycle, both species would have gained a more northerly springboard from which to commence a northern advance during the last cycle, implying that they would then have reached the Thornton unit. The divergence of *H. lemuroides* populations being less than that of the two *Pseudochirulus* vicars, each side of the Black Mountain Gap, also supports the proposed absence of the former species north of the Black Mountain Gap, until after the glacial period.

Finally, although equating patterns of distribution to palaeoclimates is conjectural, relative times of isolation and convergence can be tested by mitochondrial DNA analysis (Moritz *et al.* 1993; Joseph and Moritz 1994; Joseph *et al.* 1995). Some immediate questions that can be verified by this method are grouped below in regional categories.

Intra-regional Questions

(i) Did the vicariant event that separated the sister-species *Pseudochirulus herbertensis* and *P. cinereus* take place prior to that which isolated the Carbine and Atherton populations of *H. lemuroides*, as postulated in this paper, or at the same time?

(ii) Did fragmentation of the *Petaurus australis* population in the Wet Tropics occur within the past 5000 years, as postulated in this paper, or at an earlier time?

(iii) Did fragmentation and recombination of the Atherton unit populations of *H. lemuroides* occur? If so, when, in relation to the isolation of the Carbine Tableland population?

(iv) Did the *H. moschatus* population fragment into two population isolates at the height of the last glacial period and subsequently recombine to form the single continuous population of today?

(v) Is *T. v. johnstoni* a subspecies, as presently accepted, or a full species? If the latter, how does this relate to the time of isolation of other species with south-eastern affinities within the Wet Tropics?

Other divergences and recombinations of species populations, as depicted in Fig. 3, can also be tested.

Inter-regional Questions

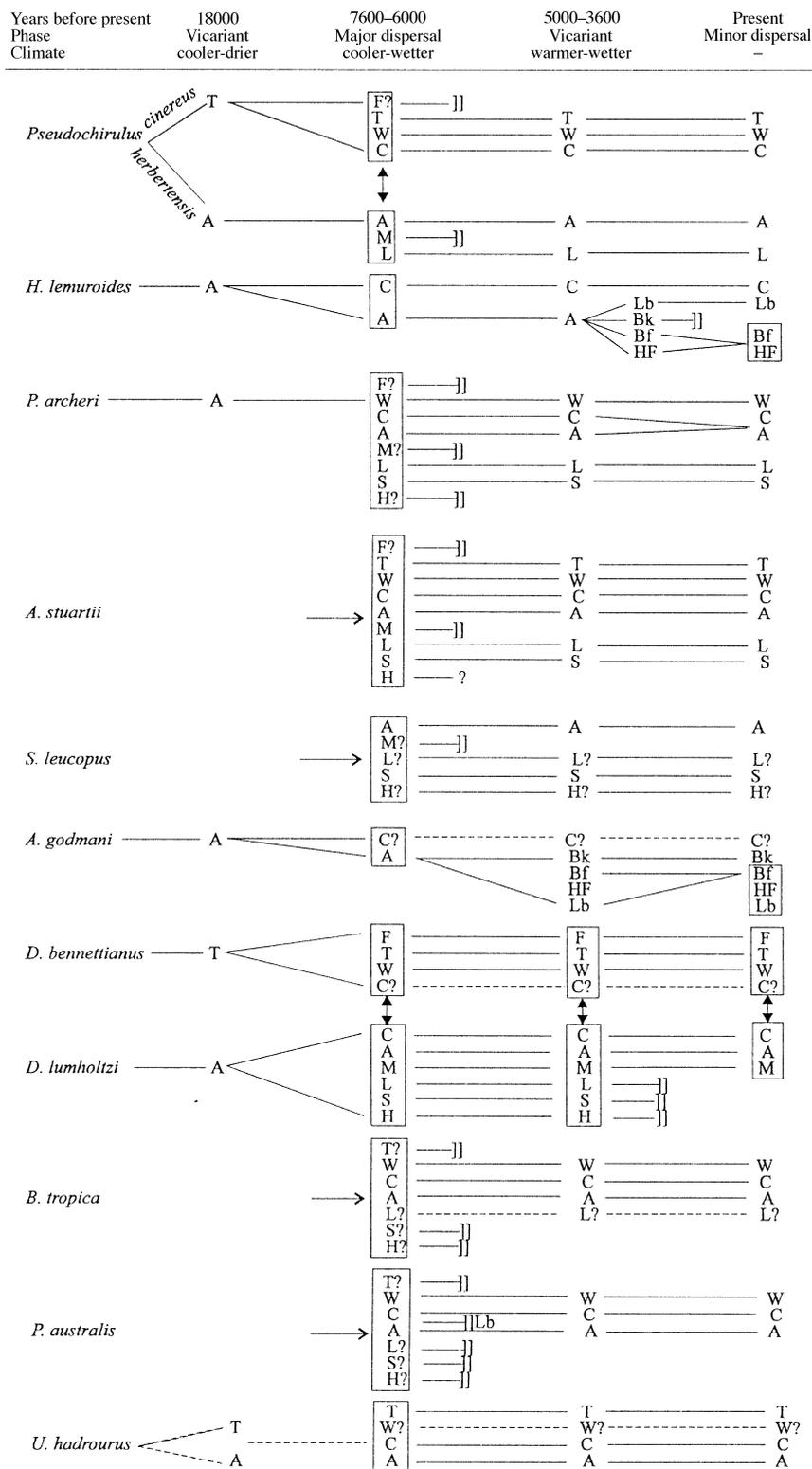
(i) Did the vicariant event that isolated the populations of New Guinean and Wet Tropics species occur after the height of the last glacial period, as postulated here, or earlier?

(ii) Did the vicariant event that isolated the Wet Tropics and South-eastern Australian populations of both rainforest and wet sclerophyll species occur after the height of the last glacial, as postulated here, or earlier?

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Fig. 3. Hypothetical flow-chart of selected non-volant mammal distributions in the Wet Tropics region depicting vicariant and dispersal phases since the height of the last glacial period. Continuous populations are boxed;]] = local extinction; vertical arrows between species represent contact zones. Upland units: A = Atherton, Bf = Bartle Frere, Bk = Bellenden Ker, C = Carbine, F = Finnigan, H = Halifax, HF = Herberton Range/Mt Fisher, L = Lee, Lb = Lamb Range, M = Malbon Thompson, S = Spec, T = Thornton, W = Windsor.



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