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THE HISTORY, PALAEOCLIMATIC SIGNIFICANCE AND PRESENT DAY STATUS OF THE SOUTHERN CONIFER FAMILIES ARAUCARIACEAE AND PODOCARPACEAE

A HISTÓRIA, O SIGNIFICADO PALEOCLIMÁTICO E O ESTADO ATUAL DE CONHECIMENTO DAS CONIFERAS DO HEMISFÉRIO SUL PERTENCENTES AS FAMÍLIAS PODOCARPACEAE E ARAUCARIACEAE, COM ÊNFASE À AUSTRÁLIA

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Resumo: O atual estado de conhecimento das coníferas do Hemisfério Sul, pertencentes as famílias Araucariaceae e Podocarpaceae, e seu valor para a reconstrução paleoclimática levam em conta os aspectos de sua ecologia, distribuição atual e os registros fósseis. A ênfase desse trabalho está voltada para a região do Pacífico asiático, mais especificamente a Austrália, onde o registro fóssil é mais substancial. A atual distribuição, restrita e disjunta, dessas coníferas no hemisfério sul, é um resultado mais relacionado com a deterioração climática no Cenozóico Inferior do que a competição com as angiospermas ou pela deriva continental. A alta diversidade e abundância foram obtidas em vários momentos no passado, sob diferentes condições ambientais. A habilidade de dispersão dessas coníferas é bem ilustrada pela recente expansão geológica nas ilhas do Pacífico asiático, onde o equilíbrio climático é maior que o do continente e por severos distúrbios ocasionais. Isto é conclusivo para essas coníferas, com excessão de alguns casos de sobrevivência extrema, são bons indicadores climáticos, tendo um alto valor na reconstrução da variabilidade climática. A atuação dos seres humanos teve pouca influência no modelo de distribuição no passado, mas as coníferas do hemisfério sul são vulneráveis aos níveis de perturbações atuais assim como a sua intensificação futura.

Palavras-Chave: Coníferas do Hemisfério Sul; Podocarpaceae; Araucariaceae; Biogeografia; História da Vegetação; Alterações Climáticas.

Abstract: The present day status of the southern conifer families Araucariaceae and Podocarpaceae and their value for palaeoclimatic reconstruction are examined from a consideration of aspects of their ecology, present day distributions and fossil history. The present restricted and disjunct distribution of these conifers on southern hemisphere land masses is largely a product of late Cenozoic climatic deterioration rather than competition with angiosperms or continental movements. High diversity and high abundance have been achieved at various times in the past but under different environmental conditions. The dispersal ability of conifers is well illustrated by geologically recent expansion into the Asia-Pacific islands where survival has been facilitated by the maintenance of more equable climatic conditions than on continents and by occasional severe disturbances. It is concluded that the conifers, except in extreme relictual cases, are good indicators of climatic conditions, if their history is taken into account, and may be of special value in reconstruction of climatic variability. People appear to have had little influence on distributional patterns in the past but the southern conifers are likely to be vulnerable to current

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and predicted future intensive levels of disturbance.

Keywords: Southern Conifers; Podocarpaceae; Araucariaceae; Biogeography; Vegetation History; Climate Change.

INTRODUCTION

The southern conifers include the families Araucariaceae and Podocarpaceae together with those genera of the Cupressaceae that have essentially a southern hemisphere distribution. The general interest in the southern conifers lies in their ancient origins, being the oldest and often the most conspicuous components of extant southern hemisphere forest vegetation, their geographically broad but disjunct distribution on southern hemisphere continents and islands, their often unusual appearance and their timber values. Their significance to palaeobotanists lies primarily in the relatively good representation of macrofossil remains that allows examination of evolutionary and biogeographic patterns over a long period of geological time. Their primary interest to palynologists lies in their generally high representation of distinctive pollen that can be used, in conjunction with macrofossils, to examine the nature and causes of changing vegetation patterns. In more recent times, there has been an interest in using the pollen signatures from southern conifers to construct or refine palaeoclimatic estimates as the plants are frequently emergent above forest canopies and, being exposed to the atmosphere, reflect well mesoclimatic conditions. In tropical forests their representation is often critical to palaeoclimatic interpretation, as there are few other plants with wind dispersed pollen to provide a consistent record of environmental conditions.

For all these reasons, there is a strong interest in southern conifer conservation. In any formulation of conservation strategies, a consideration of the present day status of the southern conifers is required. Here, opinions vary as to whether many species are in balance with prevailing environmental conditions or they are essentially remnants of more extensive past distributions that do not reflect potential environmental ranges. Any lack of equilibrium would also have a major influence on the value of the conifers for palaeoclimatic reconstruction.

Arguments for relictual status come from both the fossil record and from present day ecological studies. The major fossil record argument is based on the belief that the conifers are declining due to competition from more recently evolved angiosperms. Here, the general patchy distribution of the southern conifers gives credence to the hypothesis of Regal (1997) that the greater flexibility of angiosperms with respect to reproduction, mobility and chemical defense is leading to their gradual take over of the landscape and isolation of southern conifer populations. Present day evidence for conifer decline comes from the apparent lack of regeneration in many conifer stands (*e.g.,* Holloway 1954, Womersley 1958, Wardle 1963). However, recent compilations of fossil records have suggested that conifer diversity, if not abundance, may have been maintained with angiosperm evolution (*e.g.,* Lidgard & Crane 1990), while evidence for lack of regeneration noted in many conifer stands may relate to their mode of regeneration. Many conifers are long lived and require only occasional recruitment that can be triggered by infrequent landscape disturbances such as volcanic activity, fire, landslides etc. (Enright & Ogden 1995).

This paper focuses on an examination of the present status and palaeoclimatic significance of the southern conifers through an examination of present distributions and past records at a variety of scales. It builds on the recent compilations of southern conifer ecology and history by Enright & Hill (1995) and Hill & Brodribb (1999). The Cupressaceae will be excluded from consideration because of limitations in identification of pollen to different genera, that might include northern as well as southern conifers in the past, and concerns over differential pollen preservation. In addition, the Cupressaceae, unlike the Araucariaceae and Podocarpaceae that are almost entirely restricted to rainforest, extend into more arid environments that have not preserved fossil evidence.

PRESENT DAY DISTRIBUTIONS – CONTINENTAL LANDMASSES

The Araucariaceae and Podocarpaceae are now restricted to the southern hemisphere, in relation to continental land masses, except for some representation in eastern Asia, despite their broad distribution in both hemispheres during the Mesozoic (Stockey 1990). A general contraction in range is also suggested from the relatively low species diversity and discontinuous distributions within the southern hemisphere (Figure 1). The Araucariaceae are represented by only two species of *Araucaria* in South America, one in the Andes of central Chile and the other on the plateau of southeastern Brazil and by two species of *Araucaria,* five species of *Agathis* and the recently discovered, monotypic genus *Wollemia* (Jones *et al*. 1995) in Australia. All Australian representatives occur in the topographically diverse east coastal and sub-coastal region. There is no representation of the family in Africa.

The Araucariaceae are generally contained within the broader, but still patchy, distribution of the more diverse Podocarpaceae. *Podocarpus* and the closely related and palynologically indistinguishable genus *Prumnopitys* are the only members of the family that extend to tropical to subtropical continental areas. Only in the cool, wet, high latitude areas of Tasmania and South America is there any generic diversity.

Despite these apparently remnant distributions, there are marked general similarities in conifer locations between continents suggesting a conservative ecology retained from more continuous distributions in Gondwana. Apart from the unusual occurrence of *Araucaria araucana* in Chile that extends to the treeline (Veblen *et al*. 1995) and the very restricted distribution of *Wollemia* in southeastern Australia, all Araucariaceae have a predominantly subtropical distribution. The Podocarps are concentrated in the cooler temperate as well as subtropical latitudes. Both families are best represented in areas of high relief. The degree of similarity in ecology between genera on different continents is well illustrated by the major concentrations of *Araucaria* in Australia and Brazil, a similarity noted by Webb (1966). Both have discontinuous distributions at similar latitudes in eastern sub-coastal areas (Figure 2). The species are emergent above angiosperm and podocarp rainforest taxa and show an interesting relationship with open grassy areas or ‘balds’ whose origin has not clearly been established.

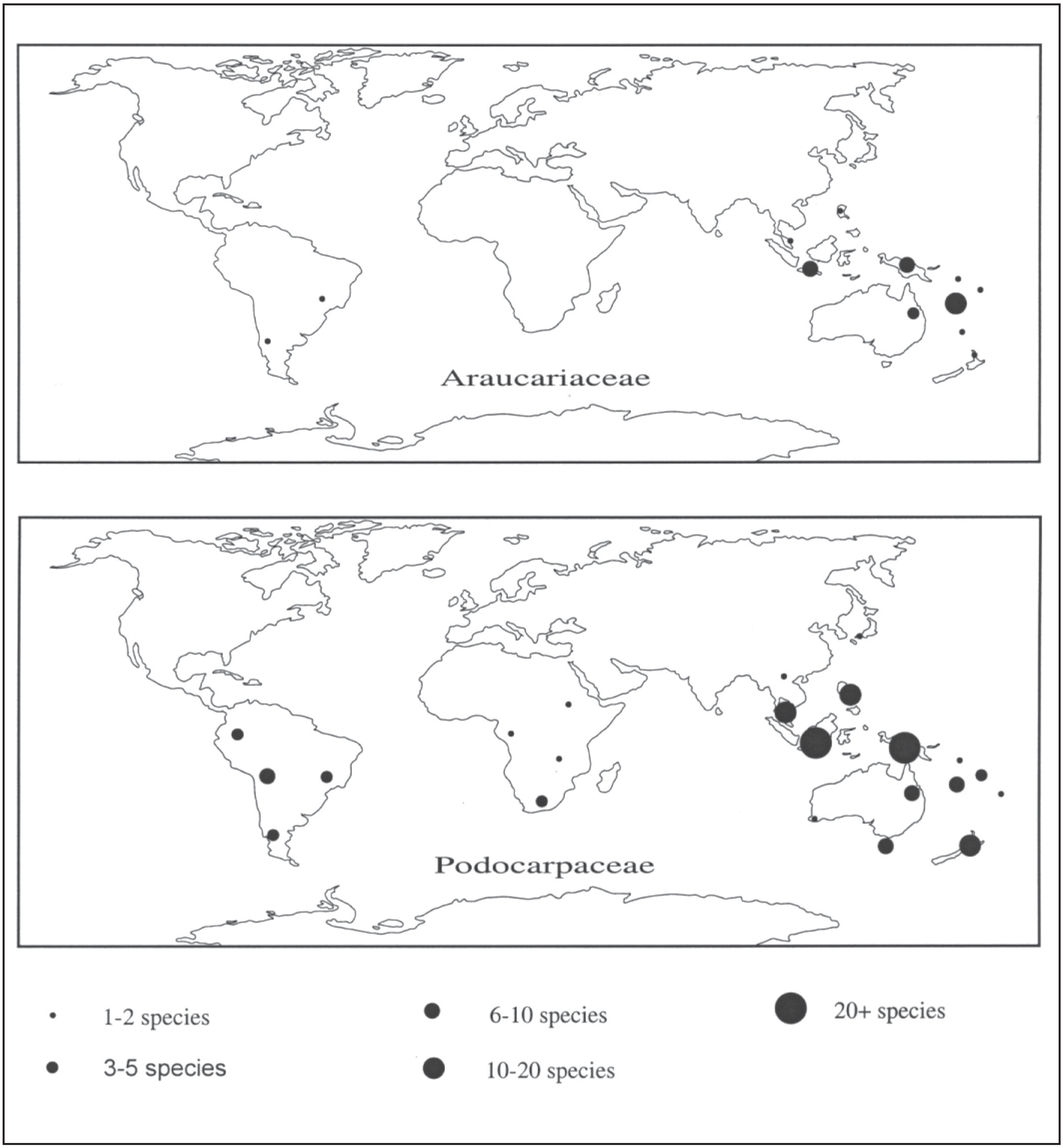

FIGURE 1: The global representation of species of Araucariaceae and Podocarpaceae (data from Enright & Hill 1995).
FIGURE 1: Representação global das espécies de Araucariaceae e Podocarpaceae (dados de Enright & Hill 1995).

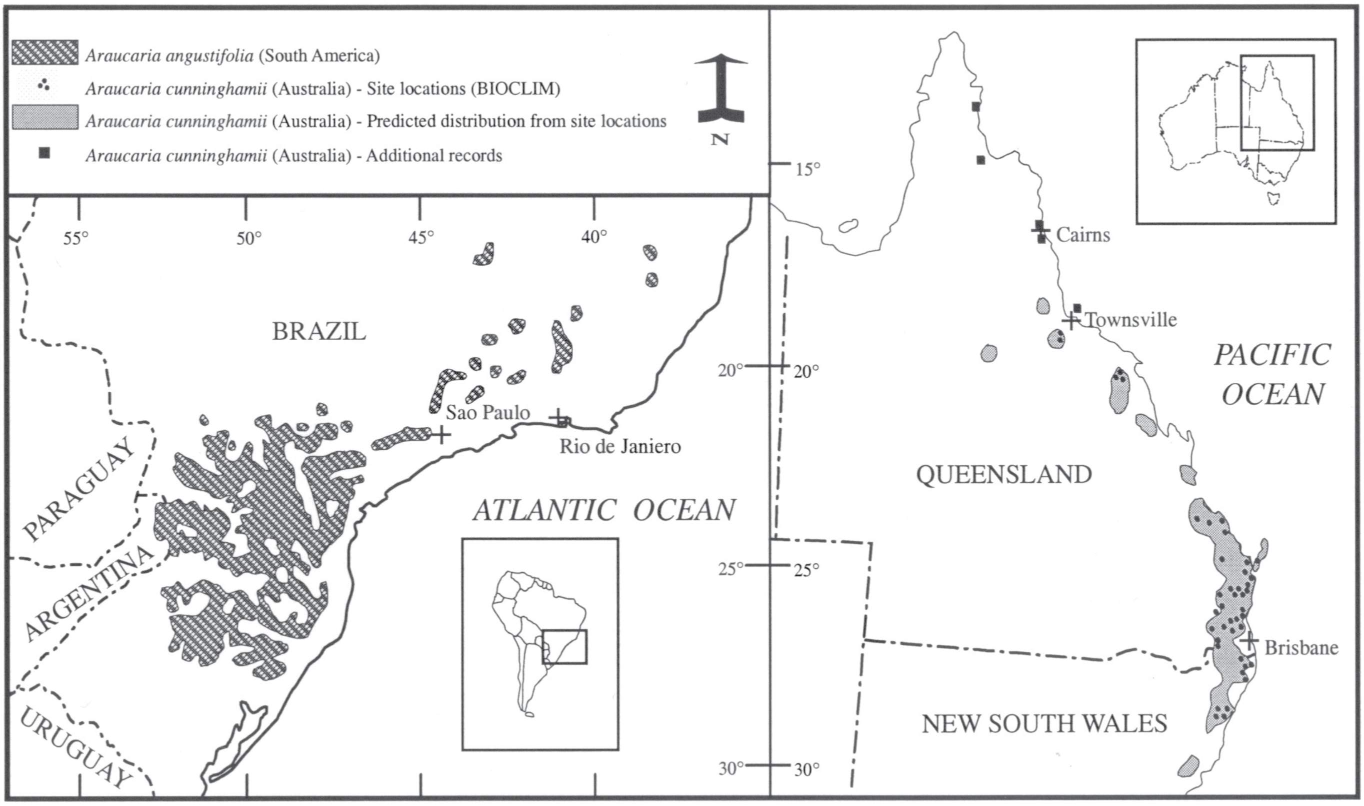

*FIGURE 2: Distribution of **Araucaria angustifolia** in southeastern South America (after Veblen **et al.** 1995), and site records and predicted bioclimatic distribution of **Araucaria cunninghamii** in Australia (after Nix 1991).*
*FIGURA 2: Distribuição de **Araucaria angustifolia** no Sudeste da América do Sul (após Veblen **et al.** 1995), e locais de registro e distribuição bioclimática prognosticada de **Araucaria cunninghamii** na Austrália (após Nix 1991).*

CONTINENTAL FOSSIL RECORDS

The places and times of origin of the Araucariaceae and Podocarpaceae are unknown but there is growing consensus that fossil taxa attributable to these families were present around the beginning of the Mesozoic. Macrofossils are recorded from at least the beginning of the Jurassic for the Araucariaceae (Stockey 1982) and the Triassic for the Podocarpaceae (Axsmith *et al.* 1998), while pollen likely to have derived from both families is recorded from the Early Triassic (de Jersey 1968). Data on the history of these groups is most complete for the Australian region, and these provide the basis for historical reconstructions.

Generalised stratigraphic ranges for selected taxa, together with independent evidence for major environmental variables and geological events, are shown on figure 3. Some information on diversity through time, largely for the Cretaceous and Cenozoic, is provided on figure 4 from macrofossil data collated by Hill & Brodribb (1999). This diagram, showing the number of identified species for each period, includes available, acceptable data from all southern hemisphere sites, but is heavily biased towards Australia. An indication of abundance, for Australian Araucariaceae only, is mapped as average site percentage values for individual time periods (Figure 5a and b).

The southern conifers are one group of plants that appear to have evolved after the major extinction phase at the end of the Permian, prompted by arid conditions throughout much of Gondwana (Hill *et al.* 2000). The earliest pollen records of Araucariaceae, in the Triassic, are found in coastal Queensland perhaps only coincidentally within the present limited geographical range of the family. These early araucarians occurred with extinct genera displaying podocarpaceous affinities. Both families increased in abundance and diversity during the Jurassic, the time of major expansion into the northern hemisphere. The increase in Araucariaceae is indicated by high pollen values in both eastern and particularly western Australia. Both major extant araucarian genera, Araucaria and Agathis are recorded by the Middle Jurassic although the evidence for Agathis is equivocal and the genus may not have evolved until the Early Cretaceous (Hill & Brodribb 1999).

It is likely that rising sea levels through the Jurassic resulted in both increased precipitation and temperature that facilitated the development of forest vegetation. However, it should be noted that throughout the period of evolution of the bulk of Gondwanan vegetation, ie the Jurassic and particularly the Cretaceous and early Cenozoic, Australia was at much higher latitudes than it is today. Consequently, light would have been a major limiting factor, placing constraints on forest development. The emergent form of conifers could have imparted a great advantage on conifers with respect to light intervention. Another pertinent feature of Australia during the Jurassic and Early Cretaceous was that the continent was rotated with the west at lowest latitudes. The high araucarian values through this period within the western part of the continent may indicate an early preference of the family for lower latitudes where evidence suggests climates were relatively warm and dry (McLoughlin & Hill 1996).

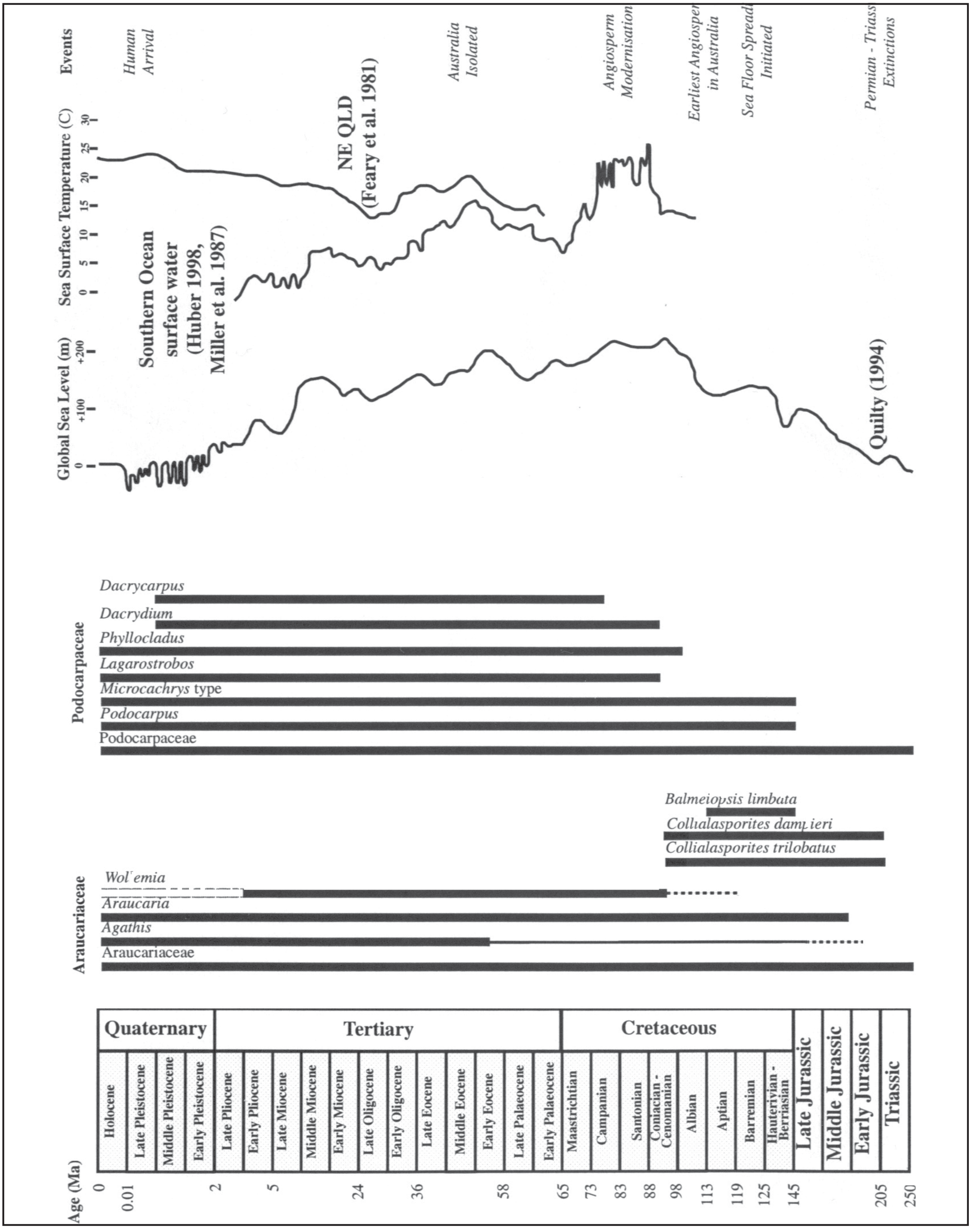

FIGURE 3: Stratigraphic ranges of Araucariaceae and Podocarpaceae taxa in relation to major environmental changes and events.
FIGURA 3: Distribuição estratigráfica de espécimes de Araucariaceae e Podocarpaceae em relação a eventos e às maiores variações ambientais.

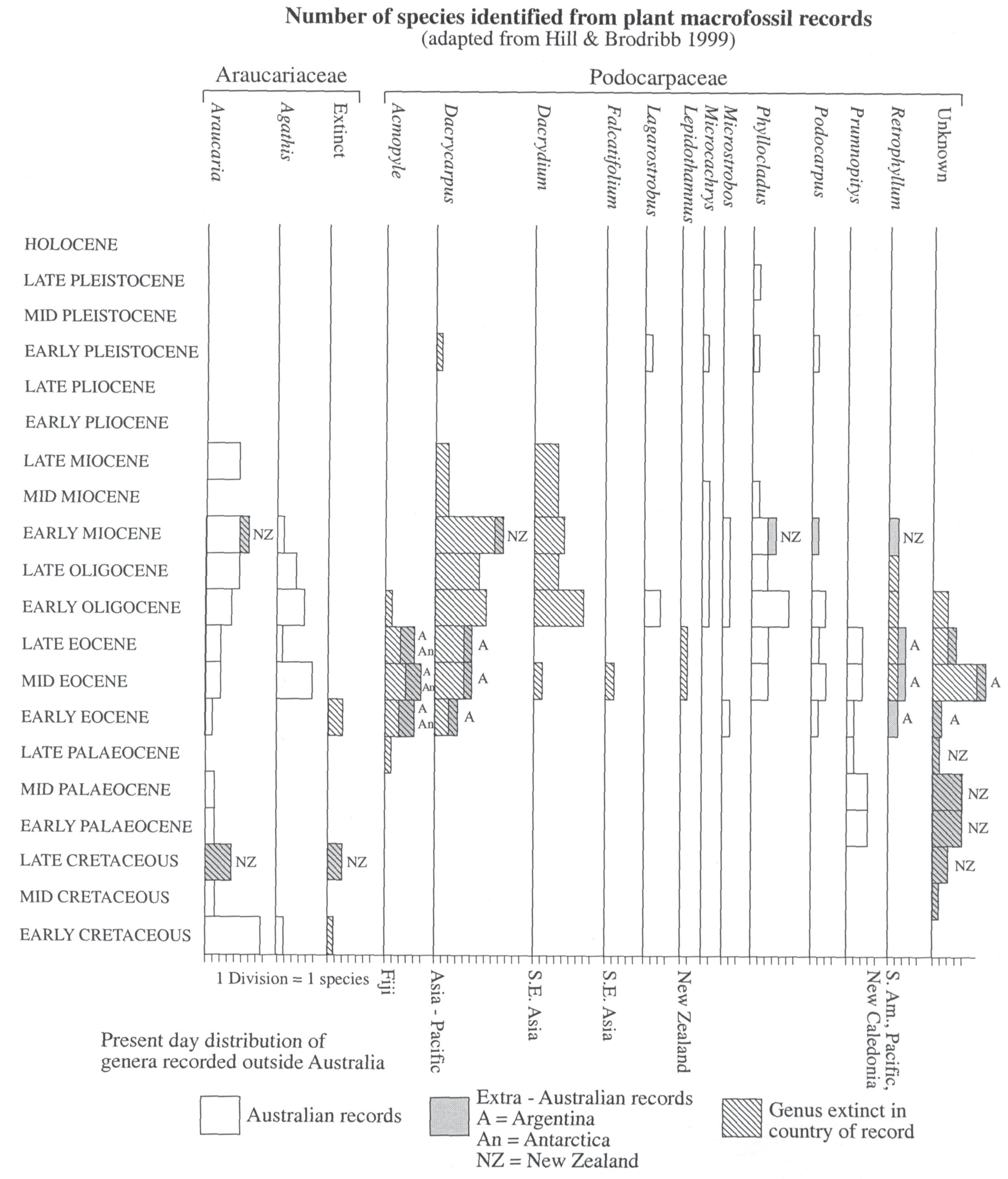

FIGURE 4: Numbers of species identified for Araucariaceae and Podocarpaceae taxa from plant macrofossil records presented in relation to geological age and geographic region (data from Hill & Brodribb 1999).

FIGURA 4: Número de espécies identificadas de Araucariaceae e Podocarpaceae provenientes de registros de macrofósseis de plantas presentes em relação à idade geológica e região geográfica (dados de Hill & Brodribb 1999).

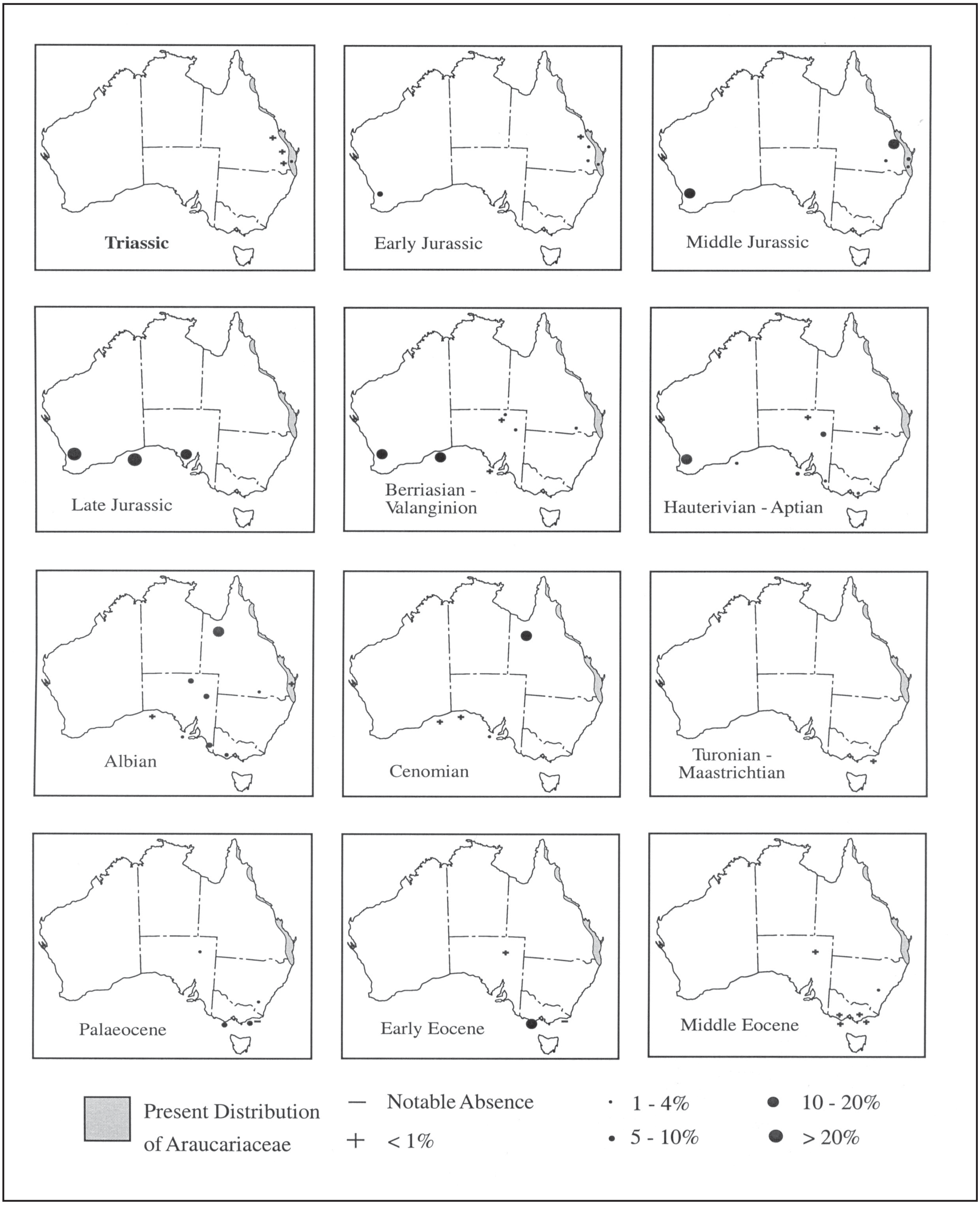

FIGURE 5a: Average percentages of Araucariaceae pollen for geological time periods from Australian fossil sites; a) Triassic –Middle Eocene;
FIGURA 5a: Média das porcentagens de polen de Araucariaceae para os períodos do tempo geológico dos sitios paleontológicos da Austrália; a) Triássico – Eoceno Médio;

FIGURE 5b: Average percentages of Araucariaceae pollen for geological time periods from Australian fossil sites; b) Late Eocene-Holocene.
FIGURA 5b: Média das porcentagens de polen de Araucariaceae para os períodos do tempo geológico dos sitios paleontológicos da Austrália; b) Eoceno Superior - Holoceno.

The initiation of continental rifting towards the end of the Jurassic resulted in the gradual separation of India and southern Africa from subsequent changes in Gondwanan vegetation that included a major phase of modernisation. The beginning of the Cretaceous saw the first appearance of modern podocarp genera, *Podocarpus* and *Microcachrys*, while the Araucariaceae has both high abundance and high diversity, especially of *Araucaria*. At this time there were at least four times the number of *Araucaria* species as what there are on the continent today. By contrast, in the Middle to Late Cretaceous, there are few araucarian macrofossils recorded and there is a corresponding fall in araucarian pollen, although Dettmann (1994) suggests that both Araucariaceae and Podocarpaceae were major canopy or canopy emergent dominants through most of the Cretaceous with a reduction in Araucariaceae towards the very end of this period. Due to the emergence of most of the continent above sea level (Dettmann 1994), fossil evidence is largely restricted to southeastern Australia. It is possible that araucarians flourished through the Middle-Late Cretaceous in the northern part of Australia, as there are high values in the Albian and Cenomanian when fossiliferous material is present.

Relatively low values for Araucariaceae in the southern part of Australia may have been a result of competition with evolving angiosperms, but were more likely excluded due to high precipitation until the end of the Cretaceous when high pollen producing *Nothofagus* would have had an additional affect on reducing araucarian percentages. It is unfortunate that there is little quantitative information from sites in southeastern Australia within the unstable area of continental rifting, that is considered to have been a major centre of the evolution of the extant Australian flora (Dettmann 1989). This evolution appears to have included conifers, questioning the idea that they were outcompeted by angiosperms. Certainly there were extinctions within the Araucariaceae that contributed to reduced abundance values, and probably also in the Podocarpaceae, but the period saw the first appearance of the majority of extant Podocarpaceae and probably the araucarian genus *Wollemia*. The Turonian marks the first pollen record of *Wollemia* (Macphail *et al*. 1995) although there is some suggestion from macrofossil evidence that the genus may date to the beginning of the Cretaceous (Chambers *et al*. 1998).

There is some increase in the representation of Araucariaceae in the Palaeocene and Early Eocene with the relatively high value in the latter period derived from *Wollemia* (Macphail *et al*. 1994). However, macrofossil evidence for both families, apart from *Prumnopitys*, is slight. There is then a substantial increase in macrofossil records, demonstrating high conifer diversity from the Middle Eocene to the Early Oligocene, especially in the podocarps and *Agathis*. In addition to extant podocarps, Australia supported a number of extinct genera that are now found in other parts of the world such as Fiji, Southeast Asia, New Zealand and South America. Similarly, there is evidence for a broader distribution of extra-Australian genera on other land masses. This peak in southern conifer diversity is perhaps surprising, as diversity of angiosperms was also high with complex rainforest covering much of the continent. Hill & Brodribb (1999) consider that the reason why the conifers were able to compete under the inferred warm, wet and equable climates of this period was their ability to expand their leaf surfaces and effectively capture light. However, pollen records for the Araucariaceae show consistent but low values suggesting that the conifers may have been largely restricted to unstable river valley environments on rainforest margins where they would have been recorded as macrofossils. Certainly, they appear not to have formed a consistent or substantial emergent layer above the forest canopy.

Diversity decreases from the Late Oligocene due, according to Hill & Brodribb (1999), to the onset of continental drying although, from studies of pollen and lithotype variation in coal deposits of southeastern Australia, increased climatic variability rather than drying may have been the critical factor (Kershaw *et al.* 1991). The increase in representation of Araucariaceae pollen is consistent with drier or more variable climates as regeneration in some species of *Araucaria* is generally facilitated by a more open rainforest canopy that is promoted by such conditions. It is feasible to propose that a widespread emergent *Araucaria* layer, analogous to that in the Jurassic and Early Cretaceous, reformed, perhaps suggesting a return to similar climatic conditions.

The macrofossil record virtually ends in the Late Miocene with only single species of extant genera present in the Pleistocene, apart from one occurrence of the extinct genus *Dacrycarpus.* It is likely that expansion of the Antarctic ice sheet to close to present dimensions around the end of the Miocene and the establishment of current oceanic and atmospheric circulation patterns (Bowler 1982) did produce cooler and drier conditions over southeastern Australia that caused a decline in conifer diversity. However, the lack of macrofossil records is as much related to unfavourable conditions for preservation as it is to conifer representation, as a substantial pollen record is maintained after this time. In fact, a recently analysed site in the western highlands of Victoria on mainland Australia dated to 1.7 million years ago (the Early Pleistocene) has revealed 11 southern conifer genera, 5 of which are no longer present in Australia and all of which are absent from the region today (Kale Sniderman, *personnal communication*). This level of genetic diversity is as high as any site record in the Australian Cenozoic (Hill & Brodribb 1999). Furthermore, rather than having reduced representation after the Miocene, the Araucariaceae achieve highest Cenozoic values in the Early Pliocene although high values are virtually restricted to coastal and sub coastal locations along the eastern seaboard. In southeastern Australia, the transfer of high pollen values from more inland to more coastal locations from the Miocene to the Early Pliocene plots the drier margin of rainforest as it contracts to present high rainfall areas along the highland coastal fringe (Kershaw *et al.* 1994).

The subsequent contraction of the Araucariaceae to the northeastern part of the continent in the Late Pliocene to Pleistocene could relate to the intensification of the westerly wind system that extended over southeastern Australia (Bowler 1982) and subjected these conifers, for the first time, to a winter rainfall regime, or to the onset of Quaternary glacial/interglacial scale climatic oscillations. Increased global climatic variability in itself was probably not the major factor as high araucarian values are maintained in the northeastern part of the continent.

The ability of species of Araucariaceae to survive for long periods under adverse climatic conditions is provided by the continued minor presence of *Araucaria* pollen in a record from the western plains of Victoria through the whole of the Early Pleistocene (Wagstaff *et al.* in press) and by the survival of very small stands of *Wollemia* within protected gorges in New South Wales, 2 million years after the detection of pollen in fossil records (Macphail *et al.* 1995). However, it is likely that the increased amplitude of climatic oscillations that began in the Middle Pleistocene resulted in the final demise of *Araucaria*, if not *Wollemia*, within southeastern Australia.

Looking at times of major decline or extinction in the southern conifers as a whole (Figure 6), a number of interesting features emerge. One is that most regional extinctions appear to have taken place within Australia. This could suggest conditions unique to the continent, the marginal nature of the climate with respect to the climatic ranges of component taxa, or a lack of data from other parts of the world. The latter explanation has some validity but there have still been extinctions in China and West Africa that could be marginal for southern conifer survival. A second feature is that, as evidence accumulates, taxa are generally demonstrated to have survived for a longer period of time. Several taxa provide evidence of survival until the Late Pleistocene (the last 125,000 years) and judging by the length of time that *Wollemia* remained undiscovered and remained unsupported by a pollen record, it is likely that other taxa will be found to have survived into this period. A third feature is that there is no clear latitudinal pattern to extinction, suggesting that it is unlikely that temperatures, particularly global extreme temperatures at the heights of glacial periods, were not a primary cause of extinction. Although general drying and increasing amplitudes of glacial/ interglacial cyclicity (Shackleton *et al.* 1995) have clearly had an influence on general range reduction, this does not explain the survival of so many conifers into the most recent of these cycles.

A unique characteristic of the last glacial cycle in Australia is the arrival of people in the middle of this period, and the sustained decline in drier araucarian forest, including the southern conifers *Podocarpus* and *Dacrydium* around this time, in the pollen record from Lynch's Crater on the Atherton Tableland (Figure 7). The cause of these changes has long been attributed to an increase in burning associated with human activities (Kershaw 1986). This hypothesis is supported by sharp and sustained increases in charcoal and fire-promoting sclerophyll taxa, particularly *Eucalyptus* and the absence of any major global climate change at this time. The date of around 38,000 BP for these events also corresponded with the earliest known archaeological evidence for the presence of people on the Australian continent.

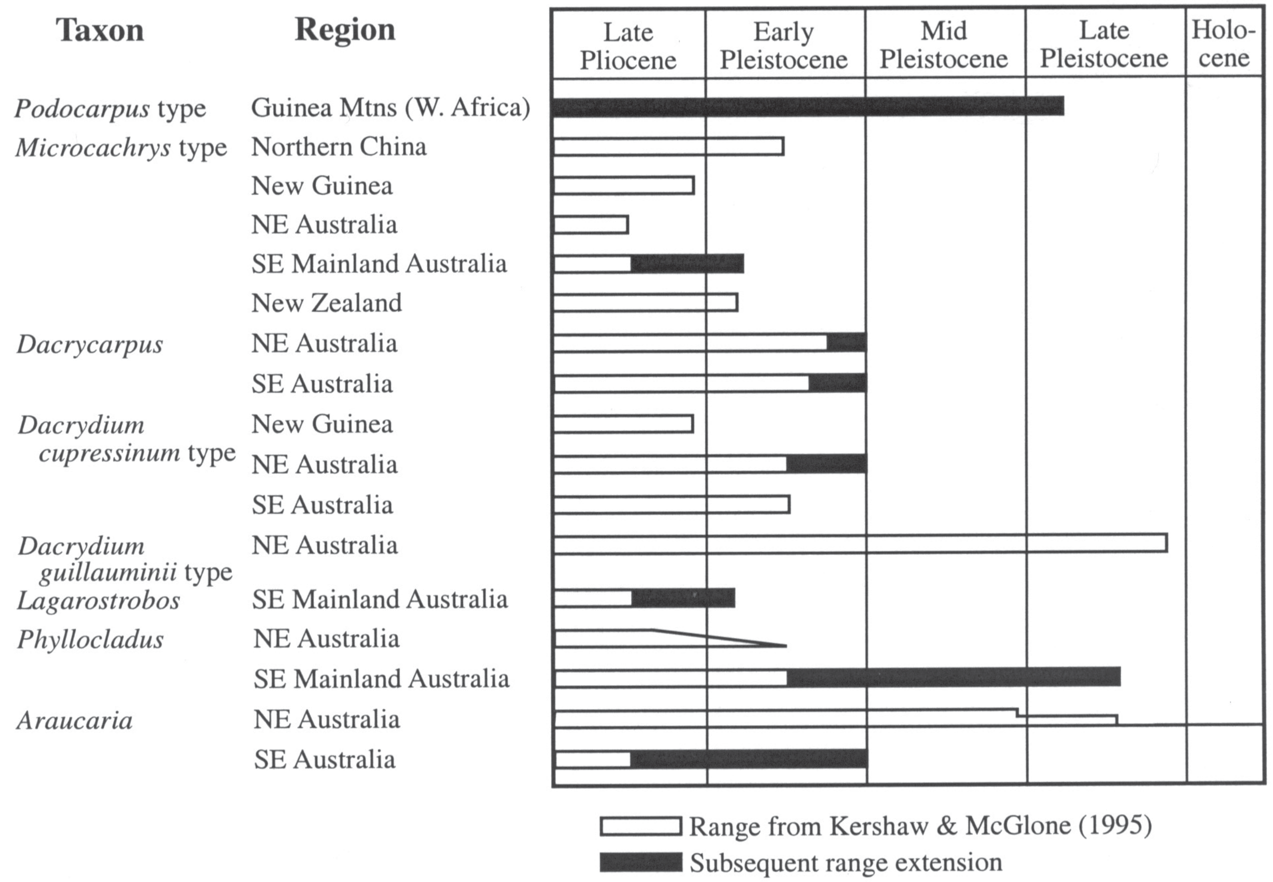

FIGURE 6: Pollen evidence for timing of major regional extinctions or range contractions of some southern conifers.
FIGURA 6: Evidências polínicas para a maior extinsão geológica regional ou distribuição das retrações de algumas coníferas do sul.

In contrast to the araucarian forest, wetter and more complex rainforest dominated by angiosperms did survive through the whole of the last glacial period, presumably because its denser canopy maintained a more humid microclimate, reducing its vulnerability to fire penetration. This complex rainforest then expanded over the Tableland during the Holocene (the last 10,000 years) as it had in previous interglacials (isotope stages 7 and 5) as a result of increased precipitation. Araucarian forest appears to have remained in small isolated patches within the general region, while *Dacrydium* is no longer found on the Australian mainland.

The interpretation of araucarian forest decline has been questioned recently by evidence provided from a similar long pollen record constructed from marine core ODP 820 taken off the coast of northeastern Australia adjacent to the Atherton Tableleland (Moss 1999, Moss & Kershaw 2000). Salient features of this record are shown on figure 7. The record demonstrates that, regionally, the decline in *Araucaria* commenced much earlier than around Lynch's Crater and well before any archaeological evidence for people, whose arrival is now considered to have been between around 50,000 to 60,000 years ago (Roberts *et al.* 1993). It is also apparent, from the charcoal curve, that fire has been a continuous feature of the region through at least the last 250,000 years. The first substantial decline in araucarian forest occurred around 130,000 years ago, at the height of the penultimate glacial period and was associated with a peak in fire activity and an initial increase in eucalypt vegetation. A further sustained decline occurs about 35,000 years ago that is again associated with a major peak in burning and a further increase in abundance of *Eucalyptus*. These latter changes can be correlated with those at Lynch's Crater.

It could be argued that the earlier change was climatically induced with fire promoted by dry glacial conditions while the second *Araucaria* decline was the result of increased burning due to human activity. However, this proposal does not explain why araucarian forest remained intact through earlier glacial periods. The key to understanding this geologically late vegetation transformation may lie in evidence provided by the extended oxygen isotope record from the ODP 820 core (Peerdeman *et al.* 1993). The record shows a systematic shift in isotope values, superimposed on those attributed to glacial-interglacial cyclicity, between about 300,000 and 250,000 years BP (Figure 7) that has been interpreted as an increase in sea surface temperatures of some 4^{0}C. Such an increase, not recorded beyond this region, could relate to the development of the West Pacific Warm Pool (WPWP), centred off eastern New Guinea, to the north of this area (Isern *et al.* 1996).

Although a temperature increase may be expected to lead to an increase in precipitation within the region, and consequently to an expansion of rainforest vegetation, the presence of the WPWP is a prerequisite for oscillations in the temperature gradient across the Pacific Ocean that gives rise to wet and dry events within the region and climatic variability over a large part of the earth's surface. The decline in araucarian forest might then have been a result of increased burning during dry El Niño events, regardless of mean precipitation values. The potential for increased burning and forest destruction during El Niño phases has been well documented in Indonesia within recent years (Goldammer 1999**).** El Niño – Southern Oscillation variability is noted for its activity on scales of a few years but it is predicted that activity may have varied on scales of thousands of years (Clement *et al.* 1999) with a most recent increase in activity about 5,000 to 6,000 years ago (eg McGlone *et al.* 1992). It is interesting to note that variability in both the charcoal and southern conifer curves from the ODP record has a preferred periodicity of 30,000 years, from spectral analysis (Moss & Kershaw 1999), that is not a Milankovitch frequency which controls glacial-interglacial cyclicity. It is therefore argued that this is an ENSO frequency that, over the last 250,000 years, has been the major influence on the dynamics of the araucarian forests with major impacts occurring around 130,000 years ago when high ENSO activity corresponded with a dry glacial period, and between 40,000 and 35,000 years ago when high ENSO activity coincided with the presence of people on the continent.

In a consideration of the reason why sea surface temperatures increased within the Middle Pleistocene, the continued movement of Australia into the Southeast Asian region and alteration of land-sea configurations could have had a major influence. Any blockage of the major ocean current that transports warm water from the Pacific to the Indian Ocean through this seaway, that is part of the global oceanic circulation system, would have caused the build up of warm water in the equatorial west Pacific and had a climatic influence in this region and perhaps also over other parts of the globe.

The continued movement of Australia northwards might also have had a direct influence on the decline in *Araucaria*, through the attainment of critical temperature levels, as this movement has brought northern Australia, for the first time in the history of *Araucaria* on the continent, into tropical latitudes. However, there is also evidence for a recent decline in the subtropics (Longmore 1997), although araucarian forests have remained much more abundant in these latitudes.

Although climatic variability may have had a significant influence on the decline of araucarian forest, it may have also have had a positive influence on conifers within wetter forest systems. It has been suggested that increased representation of *Agathis* in the more complex rainforests of the Atherton Tableland within the last 5,000 years was due to increased levels of instability with the onset of the latest phase of high ENSO activity (McGlone *et al.* 1992). This activity may also have led to a similar expansion of *Agathis* in the warm-temperate to subtropical forests of New Zealand (Ogden *et al.* 1992) and of *Araucaria* in southeastern Brazil (Behling 1998).

PRESENT DAY DISTRIBUTION – ASIA PACIFIC ISLANDS

In contrast to the relatively low diversity of conifers today on major southern hemisphere landmasses, diversity is substantially higher on islands in Pacific-Asia. In the cases of New Zealand and New Caledonia that are considered to have been components of Gondwana within the period of existence of the Araucariaceae, high diversity has traditionally been attributed to survival and evolution in isolation of original Gondwanic stock due to the moderating influence on climate change of island systems and reduced competition from evolving angiosperms. In addition, the greater impact of occasional disturbances resulting from volcanic and tectonic

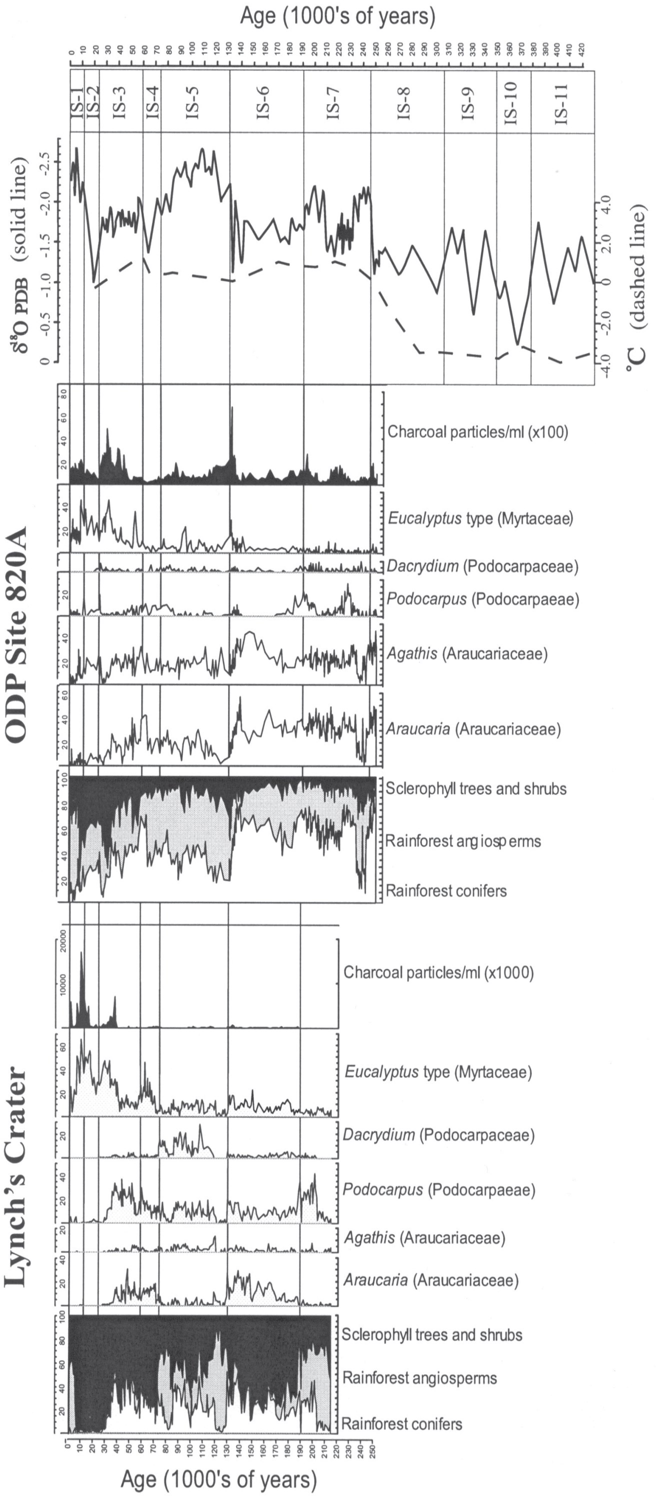

FIGURE 7: Selected attributes of the pollen records of Lynch's Crater (Kershaw 1986) and ODP 820 (Moss 1999) in relation to the oxygen isotope and inferred sea surface temperature change records from ODP 820 (Peerdeman ***et al****. 1993). All pollen values are expressed as percentages of the sum of total dryland forest taxa for each sample.*

FIGURA 7: Atributos selecionados do registro polínico de Lynch's Crater (Kershaw 1986) e ODP 820 (Moss 1999) em relação aos isótopos de oxigênio e às variações nos registros inferidos do mar, de ODP 820 (Peerdeman ***et al.*** *1993). Os valores de polen total são expressos como porcentagens da soma polínica total do total de taxa de florestas secas para cada amostra.*

activity as well as climatic events, and outpourings of ultramafic rocks on New Caledonia, that disrupted any angiosperm-dominated forest canopy, would have favoured longer lived conifers. In fact it has been proposed by Jaffré (1994) that the emplacement of the ultramafics in New Caledonia during the Eocene is likely to have caused an expansion of conifers.

However, the actual age of the conifers on both these islands has recently been questioned. There is some geological evidence to suggest that both New Caledonia (Robert Hall *personal communication*) and New Zealand (Pole 1994) that continuity of conifer occupation was disrupted by the submergence of the islands in the early or mid Cenozoic. Consequently, if this evidence is correst, then colonisation had to be by long distance dispersal, across ocean barriers, from more recent taxa from the Australian region, followed by relatively rapid speciation. The high diversity of conifers noted for the mid Cenozoic in Australia would have provided a diverse source of conifers available for colonisation.

By contrast to New Caledonia and New Zealand, New Guinea has always been a part of the Australian landmass. Any conifers existing on the limited and lowly lying extent of the island in the early Cenozoic would have been augmented by higher latitude and altitude Australian sources with the formation of mountains in the late Cenozoic. Opportunities for colonisation may have been short lived, however, as continental drying resulted in the formation of a dry corridor between New Guinea and Australia.

In relation to Southeast Asia, the paucity of southern conifers on the Asian mainland combined with the dynamic state of these islands, suggests a major colonisation from essentially Australian sources as this continent came into contact with Southeast Asia during the Miocene (Whitmore & Page 1980). The mountains of New Guinea would have formed a major transit. It is perhaps surprising that diversity on many islands is so high considering the dominance of the region by angiosperm-dominated diverse rainforest. The situation appears almost the reverse of angiosperm replacement of conifers. However, conifers are largely restricted to mountain areas and peatland forests where angiosperm competition is reduced. The sparse but emerging fossil record also provides a more complex picture of possible origins of conifers within this region and their environmental controls.

FOSSIL RECORDS FROM ASIA-PACIFIC ISLANDS

The most substantial fossil record derives from New Zealand although the data are insufficient to test the hypothesis of Pole (1994) that there was a total conifer turnover in the Cenozoic period. In general terms, the evidence, largely derived from pollen, indicates a similar high diversity to Australia in the mid Cenozoic with a loss of taxa in the latter part of this period, attributed to increased global climatic variability (Kershaw 1988, Kershaw & McGlone 1995). In contrast to the larger southern hemisphere masses, New Zealand though has retained a substantial cover of conifers, with a variety of niches, that have been very important in Quaternary climate reconstruction.

In the Southeast Asian region, the fossil record compiled by Morley (1998) clearly demonstrates that the majority of extant conifers have had a relatively recent geological history in the region. As shown on figure 8, *Dacrydium* and *Podocarpus* are first recorded in the Middle Eocene before Australia had finally separated from Antarctica and begun its rapid northwards movement towards Southeast Asia. It is possible that these taxa arrived by long distance transport, perhaps assisted by slithers of Gondwana that had broken away prior to the separation of the Australian continent. However, a very feasible alternative is that the taxa were transported from Gondwana on the Indian continent that came into contact with Asia around this time (Morley 1998). At the time of contact with India, the complex rainforest of Southeast Asia had not yet developed, facilitating entry of these conifers. Subsequent cooler conditions, as suggested by the immigration also of northern conifers into the region, may have promoted evolution of the southern taxa. These southern taxa managed to survive the ensuing wet and warm conditions in the later part of the Miocene that resulted in the regional extinction of most northern conifers. They probably survived in drier and more unstable areas as well as in peat swamps, where competition from angiosperms would be reduced. Only the genera *Dacrycarpus* and *Phyllocladus* are first recorded after contact with Australia and, as these taxa occur predominantly in montane environments, they most likely did disperse from the highlands of New Guinea.

The different times of arrival and different ecologies of these conifers have bearing on the interpretation of Quaternary records from equatorial Indonesia that have been used in attempted resolution of the debate over whether temperatures in the tropics were significantly lower than today during the Last Glacial Maximum (LGM), centred on 17,000 years ago (Rind & Peteet 1985). This is an important consideration for understanding and modelling changing atmospheric circulation patterns (Kutzbach & Guttner 1986).

Selected information from three pollen records that have addressed this issue are presented in figure 9. The Rawa Danau record is derived from a lowland swamp in a volcanic crater on West Java, marginal to the humid core of the tropical rainforest while the other two records are from lowland peatland forests well within the humid core - Nee Soon in Singapore and Lake Pemerak swamp in West Kalimantan. There are clearly higher values for podocarps, including *Dacrycarpus*, in the Rawa Danau record during the LGM than subsequently, but there are also very high levels of Poaceae (indicating rainforest replacement by savanna vegetation) and charcoal, suggesting much drier conditions than today. Consequently, van der Kaars *et al.* (in press) suggest that the higher podocarp values were most likely to have been the result of higher relative representation of pollen from highland areas due to reduced pollen production in plants from the lowlands, rather than any major expansion of montane podocarps into lowland areas. Some podocarps may also have been growing closer to the site due to reduced competition from angiosperm forest taxa. They conclude that the record can not be used to support significant temperature lowering during the LGM.

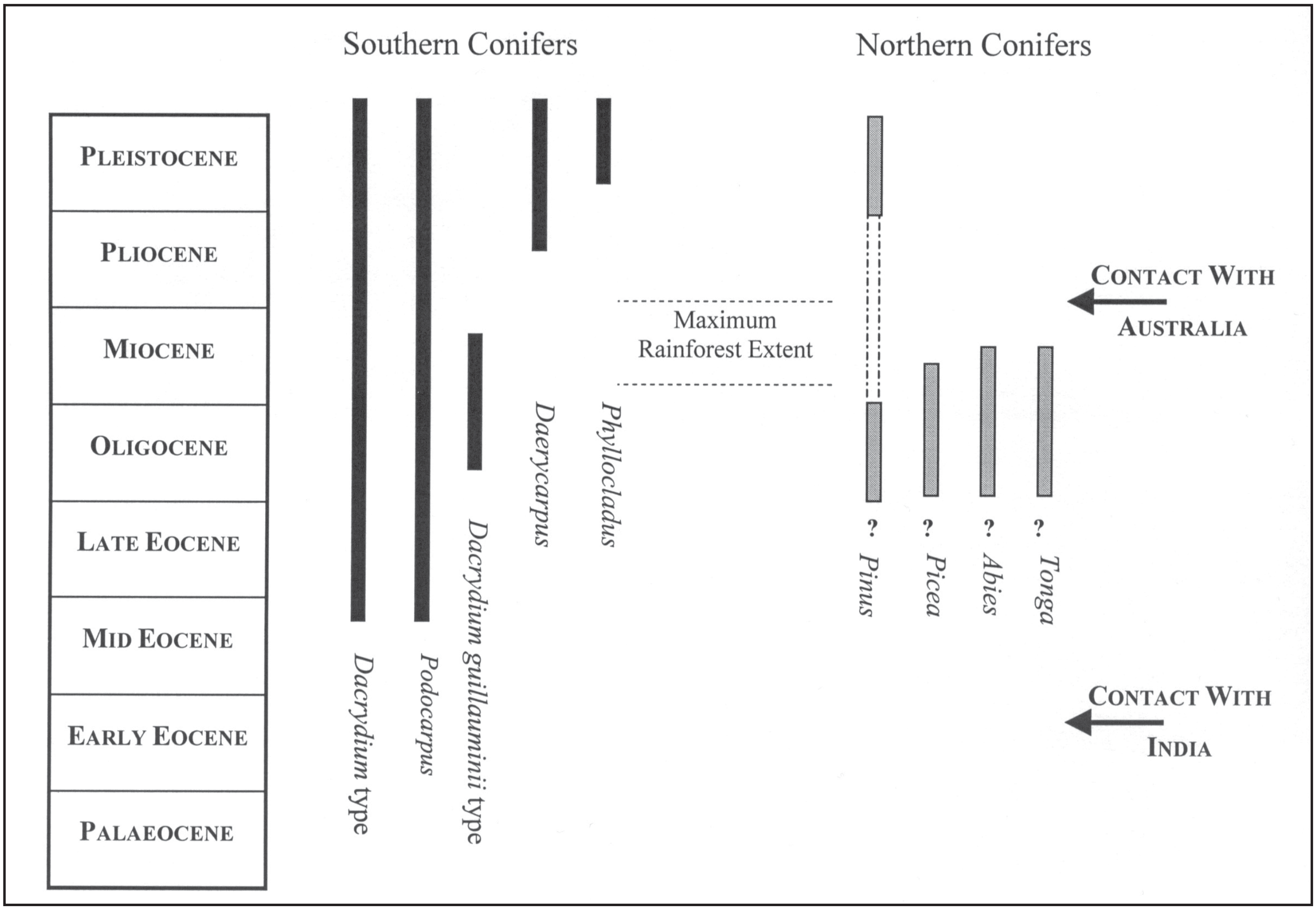

FIGURE 8: Stratigraphic ranges of selected conifers in the Cenozoic of Southeast Asia (adapted from Morley 1998).
FIGURA 8: Distribuição estratigráfica de coníferas selecionadas no Cenozóico do Sudeste da Ásia (adaptado de Morley 1998).

The higher representation of podocarps in the pre-Holocene part of the record from Nee Soon is interpreted by Taylor *et al*. (in press) as most likely indicating substantially lower temperatures than today. However, the lack of differentiation of the podocarps, that may not include the purely montane elements, combined with higher Poaceae values, makes it possible that, like Rawa Danau, substantially lower temperatures than today need not be invoked.

The record from Lake Pemerak swamp shows a clear concentration of podocarps around the LGM. Although *Podocarpus* is the major taxon, the representation of the more certain high altitude taxa *Dacrycarpus* and *Phyllocladus* does suggest that temperatures were reduced, especially as Poaceae and charcoal values, indicative of drier conditions, have relatively low values. Anshari *et al*. (in press) suggest that the conifers were a component of the lowland forest although values for the more certain montane taxa may not be sufficiently high to demonstrate such a local presence. The degree of temperature depression during the last glacial maximum is therefore difficult to quantify.

An extension of this debate is evident in the equatorial Amazon Basin. Colinvaux (1989) inferred a temperature depression during the LGM of about 6^0C based largely on increased pollen percentages of montane *Podocarpus* in lowland pollen records. However, Hooghiemstra & van der Hammen (1998) question this estimate on the basis that *Podocarpus* had a lowland distribution before the uplift of the Andes and that precipitation, in addition to temperature, has a marked influence on its distribution.

Additional research is needed to provide realistic quantitative temperature estimates from southern conifer data.

CONCLUSIONS

Despite the diversity and variable ecology of the southern conifers, there are some generalisations that can be made concerning their past and present distribution patterns. The group evolved in response to ameliorating climatic conditions after a major extinction event associated with dry conditions at the end of the Permian period. They increased in abundance and diversity through the Jurassic and Early Cretaceous periods and maintained an important presence in the vegetation of the southern hemisphere major land masses through the Late Cretaceous and early Tertiary, only to become areally restricted and genetically depauperate with continental drying and increased climatic variability during the later part of the Cenozoic period. There were extinctions related to angiosperm evolution and establishment in the Middle Cretaceous, or to conditions favouring this evolution. However, the conifers showed adaptability in light of competition from angiosperms and many

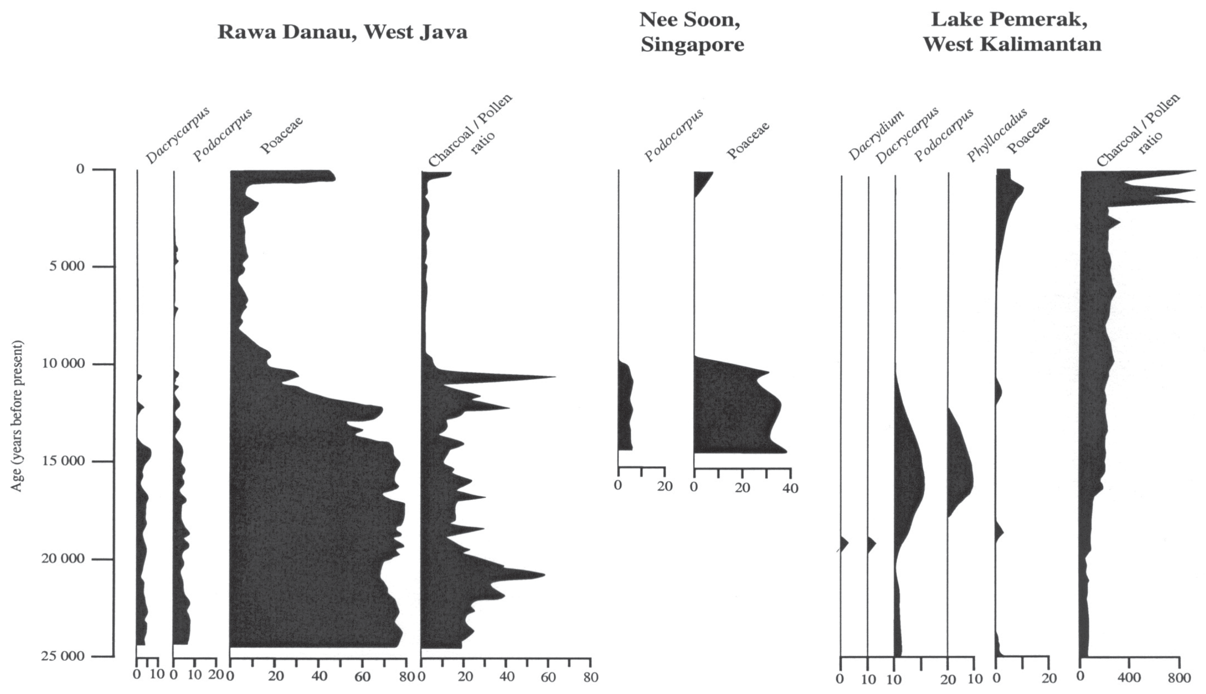

FIGURE 9: Selected features of late Quaternary pollen records from the equatorial rainforests of Southeast Asia. Pollen taxon values are expressed as percentages of total pollen for each sample.
FIGURA 9: Aspectos selecionados do registro polínico do Quaternário Superior de florestas equatoriais do Sudeste da Ásia. Valores de Táxon polínicos são expressos como porcentagens do polen total para cada amostra.

extant taxa date from this time. Many of these taxa that evolved during the global peak in temperatures during the Middle Cretaceous have succumbed to late Cenozoic climatic deterioration, while older taxa, extending back to the Jurassic period have survived. *Araucaria,* in fact, regained high levels of abundance in some communities within the late Cenozoic that it enjoyed during the Jurassic and Early Cretaceous, suggesting a return to similar climatic conditions. The disparity evident between abundance and diversity is best illustrated in the Eocene period where high temperatures and rainfall, conducive to angiosperm rainforest development also showed high macrofossil conifer diversity but consistently low pollen abundance.

In contrast to declining conifer diversity on the southern hemisphere continents within the late Cenozoic, high diversity was largely maintained or enhanced on Asia-Pacific islands where a combination of more equable climatic conditions and infrequent disturbances appear to have been critical influences. This island pattern demonstrates a dispersal ability not evident in the southern conifers on continental masses.

A number of conifer taxa now have very restricted and presumably relict distributions, some to the extent that they are unlikely to provide any indication of their potential climate range. Other taxa, however, perhaps due to their sensitivity and vulnerability to climatic conditions at present and in the recent past, can be considered to be very useful indicators of climate change. Even in Australia, where it was considered that climatic influences were subordinate to those of human activity and the expansion of fire-promoting sclerophyll vegetation in recent times, leading to a contraction of conifer populations, climate is now seen as a major driving force.

The conifers can be used as indicators of mean temperature or rainfall levels depending on their location, but perhaps their special value may be in determination of degrees and patterns of variability, of which ENSO variability is a major climatic component.

The longer term historical record of conifer activity can be useful in assessment of the climatic significance of particular conifers in recent times. Conversely, more recent conifer history allows more confidence to be placed on the use of conifers for climatic reconstruction in geologically distant past.

Although past human influence on conifer distributions has not been substantial, present and predicted future human activity does provide a real threat to the long term survival of many component species. Despite their ability to survive occasional disturbances, their longevity, regeneration patterns and desirability for timber products, do not equip them well for survival under persistent logging and burning activities that now characterise the landscape of many parts of the world. They are a precious resource that deserve maximum protection.

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