History of vegetation and habitat change in the Austral-Asian region

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Abstract

Over 1000 marine and terrestrial pollen diagrams and some hundreds of vertebrate faunal sequences have been studied in the Austral-Asian region bisected by the PEP-II transect, from the Russian arctic extending south through east Asia, Indochina, southern Asia, insular Southeast Asia (Sunda), Melanesia, Australasia (Sahul) and the western south Pacific. The majority of these records are Holocene but sufficient data exist to allow the reconstruction of the changing biomes over at least the past 200,000 years. The PEP-II transect is free of the effects of large northern ice caps yet exhibits vegetational change in glacial cycles of a similar scale to North America. Major processes that can be discerned are the response of tropical forests in both lowlands and uplands to glacial cycles, the expansion of humid vegetation at the Pleistocene–Holocene transition and the change in faunal and vegetational controls as humans occupy the region. There is evidence for major changes in the intensity of monsoon and El Niño–Southern oscillation variability both on glacial–interglacial and longer time scales with much of the region experiencing a long-term trend towards more variable and/or drier climatic conditions. Temperature variation is most marked in high latitudes and high altitudes with precipitation providing the major climate control in lower latitude, lowland areas. At least some boundary shifts may be the response of vegetation to changing CO₂ levels in the atmosphere. Numerous questions of detail remain, however, and current resolution is too coarse to examine the degree of synchronicity of millennial scale change along the transect.

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1. Introduction

A review of the data available for vegetation reconstruction and of other biological proxies of environmental change across the Austral-Asian Pole–Equator–Pole (PEP-II) transect is timely because records are becoming increasingly scattered throughout a diversity of published and unpublished sources. To manage this voluminous data over the range of time scales in PEP-II, our approach is necessarily selective. We provide some overview for longer timescales where the number of records is limited but for the Late

Pleistocene and Holocene we focus on important aspects of particular periods.

The paper has uneven coverage with greater detail given to the Southern Hemisphere. While this is partly accidental, the south has many examples of climate–environment interactions with intact ecosystems, whereas the north is radically changed by widespread intensive human settlement which has tended to obscure the non-anthropogenic processes. Thus the south is in one sense a laboratory for changes in northern PEP-II and indeed the other PEP transects. Anthropogenic impact along PEP-II is treated in this volume by Bird *et al.*, so is not analysed here.

Ages used in this paper are generally tuned to marine stage chronologies for older periods. However, data

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from LGM to Holocene times are generally given in terms of the radiocarbon time scale.

2. Palaeo-vegetation data

PEPII includes all the major biomes of the planet and has the largest imbalance in area between the Northern and Southern hemispheres, although land extends further south than on the Europe–Africa (PEP III) transect. Major cratonic elements include the Indo-Australian plate, the Asian plate and the western Pacific plate, which are all in an active state of collision due to the northwards movement of the Indo-Australian plate since the Cretaceous. During the Cenozoic period, very significant changes to landmasses have occurred, with high tropical mountains appearing in New Guinea, Indonesia and Taiwan, while the Himalaya and Tibetan Plateau have been upthrust. The seaway that separates Australia from Asia has become restricted in the last 5 million years, leading to rearrangements in oceanic and atmospheric circulation. At the same time the Tibetan Plateau has become higher and colder (forming in effect a third pole), controlling the Asian summer and winter monsoons and preventing their entry into the northern steppes (Ruddiman et al., 1997; Dodson et al., *this volume*).

Dodson et al. (*this volume*) summarise the distribution of biomes on the PEPII. The major source of evidence for variations in the composition and distribution of vegetation on the transect is pollen and charcoal records from lake, swamp, cave and marine sediments and soils. About 1300 such records are available, although the vast majority are mid-Holocene to present in age range (Table 1). This can be contrasted to ca 5000 records from the PEP I and PEPIII transects. However they are fairly evenly spread along the PEP II transect whereas the bulk of sites of PEP I and PEPIII are in North America or northern Europe respectively. The coverage is nonetheless variable, since suitable sites are rare in arid areas and effort has been uneven. Thus the

publication since the onset of PEPII discussions in the early 1990s of results from studies in China (e.g., Winkler and Wang, 1993; van Campo et al., 1996; Yu et al., 1998, 2000; Jiang and Piperno, 1999; Tang et al., 1999, 2000; Yan et al., 1999; Zheng and Li, 2000; Shi et al., 2001; Liu et al., 2002; Ren and Beug, 2002; Li et al., 2003; Yi et al., 2003), Korea (e.g., Kong, 2000; Choi, 2001), Japan (Takahara et al., 2000), Australia, New Zealand (e.g., McGlone et al., 1993; Harle et al., 1998; Pickett et al., *in press*) and the subantarctic islands (McGlone, 2002a,b) have added greatly to what was already known about the vegetation history of parts of PEPII. Cambodia (e.g., Maxwell, 2001), Siberia and Mongolia (e.g., Tarasov et al., 1998, 2000; Edwards et al., 2000), India (e.g., Kajale and Deotare, 1997; Sutra et al., 1997; submitted), Thailand (e.g., Maxwell and Liu, 2002), Malaysia, Micronesia, Indonesia, Papua New Guinea, some Pacific islands (e.g., Farrera et al., 1999; Hope et al., 1999) have coverage for some habitats. By comparison, Nepal, Myanmar, Sri Lanka, Laos, Vietnam, Philippines and the Solomon Islands remain relatively poorly studied.

Longer records provide a basis, through examination of previous glacial and interglacial conditions, for examination of the degree to which the last glacial and Holocene are characteristic of conditions during the later part of the Quaternary. They are particularly important in the assessment of vegetation and habitat responses to Milankovitch-scale climatic variation and identification of the role that people may have played in the development of recent landscapes.

The data base upon which changes in the nature and distribution of vegetation types can be detected and explained at the PEPII scale is, unfortunately, small. However, the tectonically active Pacific margins of the transect have resulted in relatively youthful landscapes, many of which are volcanic, and have provided suitable sites for sediment accumulation and palynological study through one or more glacial cycles on land and in offshore basins. Terrestrial and marine records are essentially complementary. Terrestrial records provide detailed information on limited vegetation catchments. Their value for elucidation of past environments has been limited by the difficulty of accurate dating beyond the range of radiocarbon, although uranium/thorium disequilibrium dating has been used successfully in some instances (e.g., Colhoun et al., 1999; Harle et al., 1999, 2002) and perhaps less usefully in others (e.g., Longmore and Heijnis, 1999). Within this region the potential of regional correlation through the identification of dated tephra is substantial and has been applied in Japan (e.g., Miyoshi et al., 1999; Takahara and Kitagawa, 2000) and New Zealand (e.g., Okuda et al., 2001). Heavy falls of tephra may also preserve the buried vegetation cover more-or-less intact, thus providing an opportunity to examine the composition and

Table 1
Approximate number of pollen records for biomes in the PEPII region

Region	Total	Holocene	Late Pleistocene	> 100,000
Boreal 48–65°N	25	25	3	0
North temperature 22–48°N	240	200	55	8
Tropical 30°N–32°S	190	170	45	6
South temperature 20–54°S	550	520	92	14

structure of past communities of plants in some detail (e.g., late glacial *Larix–Picea* forests in northern Japan (Noshiro et al., 1997).

Marine records, by contrast, provide broad regional pictures of vegetation on adjacent land masses, often incorporating a number of biomes, are well dated through possession of oxygen isotope records, and can be directly correlated with conditions in oceans through combined pollen and marine micropalaeontological study. A potential major limitation of marine palynology, especially along this Pacific Rim with its extensive continental shelves, is that the vegetation signal can become distorted by changes in pollen catchment area through alternating exposure and drowning of coastal regions. Paired marine and terrestrial sites such as those of ODP 820 and Lynch's Crater in northeast

Queensland (Moss and Kershaw, 2000) and the Banda Sea and Bandung Basin records of Indonesia (van der Kaars, 1998) provide perhaps optimal data for assessment of patterns of vegetation change. The marine record also provides valuable chronological control for the terrestrial record. For example marine core analysis helped place sections of a volcanic maar record at Lake Wangoom, Victoria, Australia (Harle et al., 1999) in chronological context. In fact, the chronology of most long terrestrial records is inferred by correlation with marine records, through pattern matching.

Fig. 1 shows the location of all known pollen records in the Austral-Asian region that cover, or are considered to cover, at least the last 100 ka. They provide a reasonable latitudinal coverage from the northern taiga of Siberia to the southern temperate forests of the

Fig. 1. Location of long pollen records covering the last ca. 40 ka plus, in relation to major biomes along the eastern part of the PEPII transect reconstructed for the last glacial maximum.

Australasia, with concentrations of records in the northern and southern temperate latitudes, the Southern Hemisphere tropics and Northern Hemisphere marginal tropics. The critical equatorial region is poorly covered. Records are almost entirely restricted to more humid coastal and sub-coastal environments. Exceptions include Lake Baikal, that has, as yet, only been published in abstract form (Kataoka et al., 2000), and the records from offshore semi-arid to arid northwestern Australia. The recognised importance of fire as an environmental variable, particularly within the Australian region and more recently within the ENSO-influenced tropics, has resulted in the construction of fire histories, based upon down-core variations in the amounts of charcoal, within these regions (e.g., van der Kaars et al., 2000).

Other terrestrial palaeoecological sources include phytoliths, plant macrofossils and invertebrate and vertebrate faunas. Many analyses of deposits of vertebrates have been associated with archaeological investigations (Bellwood, 1997). However extinction of faunas is known from pre-archaeological contexts perhaps reflecting the increased stress of environmental change during the upper Pleistocene. In Australia some mid-Pleistocene faunas are lost or become restricted in the upper Pleistocene; for example, vombatids, giant lizards (*Megalania*) and pythons (*Wonambi naracoortensis*) are very rare after the last interglacial (Merrick et al. (2003) provide a full review of palaeofaunas in Australia and New Guinea). Stegodons and other endemic taxa such as giant tortoises have disappeared from the larger oceanic islands of Indonesia in the mid-Pleistocene (Morwood, 2001). Similar losses have occurred in mainland Asia (*Gigantopithecus*, large horned cattle, hippopotamus) but here the causes are even less clear, given the presence of hominids over several glacial cycles. The causes of extinction of faunas such as flightless birds and mammals provides lively debates across the transect with both climate change and human predation being proposed as a primary cause (e.g., Flannery, 1994). New Zealand (and many Pacific islands) provide a clear, well-dated example of human arrival coinciding with a major and rapid loss of vertebrates and giant invertebrates, that can only be attributed to human predation and introduction of the Pacific rat (*Rattus exulans*) (Worthy and Holdaway, 2002).

3. Long records of vegetation history

3.1. Cyclical variations

3.1.1. Temperate Northern Hemisphere

Within the north temperate region, the progressive reconstruction and analysis of marine pollen records in association with those for microfauna (Heusser and

Morley, 1985, 1997; Morley and Heusser, 1989, 1997; Heusser, 1990) combined with the recent terrestrial records of Miyoshi et al. (1999), Takahara and Kitagawa (2000) and Nakegawa et al. (2002) have revealed a remarkably consistent picture of vegetation change in relation to climate over the last three to four glacial cycles in the Japanese region. Global ice volume forcing, operating through changing intensities of the summer and winter monsoons and the location of the subarctic front, was the predominant influence with interglacials characterised by high representation of temperate and subtropical forest elements and glacial periods showing substantially higher values of boreal conifers with some increase in herbaceous vegetation, especially *Artemisia* steppe. A summary pollen record from marine core RC14-99 provides an illustration of these changes (Fig. 2). Due to the region experiencing high rainfall generally, temperature has exercised relatively greater control over vegetation variation, with a shift south of some 7 degrees latitude for boreal conifers during glacial periods. However, from high values of pollen from the moisture-loving endemic conifer *Cryptomeria*, the heights of interglacials are suggested to have received peak precipitation largely due to maximum intensity of the summer monsoon. Miyoshi et al. (1999) identify a characteristic succession for interglacials that begins with *Fagus*, followed by the deciduous oak *Lepidobalanus* under cool conditions and ends with significant representation of the temperate elements *Cryptomeria* and *Sciadopitys*. These phases are separated by significant values for the warm temperate taxa *Cyclobalanopsis* (evergreen oak) and *Castanopsis* in the interglacials of Marine Isotope Stage (MIS) 9 and 1, suggesting the achievement of higher temperatures within these periods. This succession is also evident in available data from the marine records, although the proposal of achievement of relatively warm conditions in the Holocene conflicts with evidence for lower sea surface temperatures in this interglacial (Heusser and Morley, 1997). In contrast to interglacials, glacial periods appear much less variable although Miyoshi et al. (1999) identify *Cryptomeria* peaks as characterizing interstadials. On the basis of the overall representation of *Cryptomeria*, Morley and Heusser (1997) calculate precessional (20 ka) frequency for the summer monsoon.

3.1.2. Temperate Southern Hemisphere

Records from the southeastern part of Australia and New Zealand form a distinct group that is divorced from direct monsoon influence, although, like those in the region of Japan, the sites lie within the westerly air stream, at least during part of the year. The longest and most continuous record from the southern westerlies is that of DSDP Site 594 off the southeast coast of New Zealand (Fig. 3). Cyclicity in vegetation is clearly related

Fig. 2. Core RC14-99 (northwest Pacific Ocean): ratio pollen diagram of major dry land taxon groups, and selected taxa expressed as percentages of the dry land pollen sum (from Heusser and Morley, 1997; and unpublished data).

Fig. 3. DSDP Site 594 (southwest Pacific Ocean): ratio pollen diagram of major dry land taxon groups, and selected taxa expressed as percentages of the dry land pollen sum (from Heusser and van de Geer, 1994; and unpublished data).

to global climate forcing, with interglacials exhibiting expansion of Podocarpaceae-hardwood and *Nothofagus* temperate rainforest and glacials dominated by open grasslands and Asteraceae herbfields in association with scrub. Temperature is considered to have been the

critical variable with glacials being several degrees cooler. Precipitation was probably also lower but high representation of sedges suggested to Heusser and van de Geer (1994) that moisture availability, due to reduced temperature, may have been similar to that of today. As

in the records from the Japanese region (Takahara et al., 2000), glacial vegetation was much more homogeneous than that of interglacials with each interglacial being more distinctive than its Japanese counterpart. MIS 9 is distinguished by a marked peak in *Nothofagus*, the double interglacial of MIS 7 is marked by the only high values of the conifer *Libocedrus* in the record, while only the latter two interglacials are dominated by podocarps (including *Dacrydium cupressinum*) that are characteristic of the Holocene climatic optimum over much of New Zealand. An early Holocene peak in the tree fern *Cyathea*, which also occurs in MIS 7, provides the clearest distinction between MIS 5a and 1. There is no underlying interglacial pattern as identified within Japan and this may be due to different regional responses of essentially migrational taxa that define latitudinal vegetation ranges and relict or orthoselected taxa (to use the terms of Grichuk, 1984) in addition to differences in orbital configurations.

Migrational taxa essentially expand from refugia occupied during glacial periods as in most New Zealand taxa and *Cryptomeria* and *Sciadopitys* in Japan and these are ones that vary dramatically between interglacials.

Heusser and van de Geer (1994) view the DSDP Site 594 record as representative of the vegetation of southern New Zealand: this has been generally borne out by the terrestrial sequences of Moar and Suggate (1996) and Okuda et al. (2001) for MIS 5 to MIS 1. However, Soons et al. (2002) suggest that there has been substantial regional vegetation variation and stress the necessity of testing marine records against compatible terrestrial ones. In particular, they suggest, primarily on the basis of glimpses of MIS 7 from a discontinuous record from the Banks Peninsula (which lies adjacent to DSDP Site 594) that changes in coastal configuration may have altered the composition of pollen reaching the marine site after MIS 7 and, consequently, that this is responsible for apparent cooler indicators within MIS 7 and 9 compared with the later interglacials.

Within the southeastern Australian region, long records from Tasmania (e.g., van de Geer et al., 1993) have similarities to those from New Zealand with expansion of rainforest, composed predominantly of *Nothofagus* and Podocarpaceae, defining interglacials and high levels of grassland/herbfield and subalpine scrub within glacial periods. Superimposed on this basic vegetation pattern is a major sclerophyll element, characterized by *Eucalyptus* and Casuarinaceae, which dominates a range of open vegetation types from wet to dry environments. From an examination of the most continuous and detailed terrestrial pollen record available, Lake Selina, Colhoun et al. (1999) conclude that, as with New Zealand records, temperature exercised the major control over cyclical vegetation changes, with the last interglacial being warmer and wetter than the

Holocene and MIS 2 being the coolest and driest phase of the last glacial cycle. The incompletely interpreted pollen record from Darwin Crater, covering several glacial cycles, demonstrates similar cyclicity back in time (Colhoun and van de Geer, 1988) although it possesses little chronological control.

In contrast to Tasmania and New Zealand, records from the mainland of southeastern Australia are interpreted mainly in terms of changing precipitation and there is little indication of temperature variation. This situation is likely to be a result of a combination of factors including the limited representation and restricted distribution of temperature controlled rainforest taxa, the dominance of sclerophyll and herb taxa containing a number of species with different and often wide bioclimatic ranges, little topographic variation and environments more exposed to incursions of subtropical high pressure systems and therefore very sensitive to moisture variation. The basaltic western plains of Victoria have provided a focus for palynological research and vegetation variation is best illustrated by the Lake Wangoom record that covers the last two glacial cycles (Harle et al., 2002). Interglacials MIS 7, 5e and 1 show high values for forest or woodland taxa, especially *Eucalyptus*, while glacials are dominated by grasses and by herbaceous and shrubby members of the Asteraceae. Of the interglacials, MIS 5 is distinguished by its relative stability and high rainfall through the most notable representation of the rainforest taxon, *Nothofagus*, and tree ferns. There is no response of Casuarinaceae within this interglacial but the achievement of high peaks within MIS 7, between those of *Eucalyptus*, indicate relatively high climatic variability at this time. In common with the many short pollen records from the area, the Holocene shows an initial peak of Casuarinaceae and later emergence of *Eucalyptus*. A different interglacial relationship between these two taxa is shown in the long but discontinuous and contentiously dated record from Lake George in the eastern highlands of New South Wales (NSW) (Singh and Geissler, 1985). Here, interglacials tentatively attributed to MIS 11, 9 and 7, are characterized by high values for Casuarinaceae, with *Eucalyptus* only becoming prominent and essentially replacing Casuarinaceae within the last two interglacials. In contrast to almost all previous records examined, none from the mainland of southeastern Australia show clear responses to the interstadials contained within MIS 5 suggesting that perhaps moisture sources were not greatly influenced by the relatively minor changes in temperature.

3.1.3. Inter-tropical region

In comparison with generally good correspondence between terrestrial and marine pollen records in temperate areas, the records from lowland, marginal

northern hemisphere tropics, marine ODP Site 1144 (Sun and Luo (2001) and recently extended from ca 280 ka to a million years by Sun et al. (2003)) and Lake Tianyang (Zheng and Lei, 1999) within the north China Sea region, show marked differences. They also do not show substantial variation in arboreal vegetation types in relation to global forcing, despite being sensitively situated between tropical and temperate forests with montane forests existing at high altitudes. The terrestrial record, estimated to cover the last 400 ka from radiocarbon and thermoluminescence dating, is dominated by pollen from subtropical/submontane forests, particularly the evergreen oaks, *Quercus* and *Castanopsis*, derived from adjacent uplands. There is also good representation from montane forest taxa such as *Pinus*, *Altingia* and *Podocarpus*, but only sporadic values for a number of local tropical semi-evergreen forest taxa. Correspondence analysis reveals some consistent differences in representation between oak forest and montane forest taxa that are used, along with the radiometric dates, to tentatively assign MIS boundaries to the diagram and infer that glacials were cooler than interglacials. However, it is stated that the changes appear to be more moderate and irregular than those from higher latitude regions. The inferred isotope stratigraphy does not easily accommodate variation in non-arboreal taxa, whose peaks most likely indicate drier conditions. The only marked peak is assigned to the last glacial period where it is considered that high values of both grasses and *Artemisia* indicate drier as well as cooler conditions.

The South China Sea marine record is distorted by high values for *Pinus*, a taxon noted for its high pollen production and dispersal, which could have been derived from montane vegetation near the coast, as well as from more northerly areas of China and carried in by the winter monsoon. Rivers also transport terrestrial pollen from a range of altitudes and habitats to coastal and marine sedimentary environments. Values for the subtropical oaks are consistently low, as are all tropical/subtropical taxa. Temperate broadleaved taxa have higher values, presumably due to the influence of the winter monsoon, but existing variation cannot be related to glacial cyclicity. Glacial periods, especially MIS 6 and 4-2, are distinguished by higher values of both Poaceae and *Artemisia* with the latter dominant during the last glacial period. Conditions during the last two glacial periods at least were clearly cooler and drier than interglacials, and this could provide a basis for revision of the Lake Tianyang stratigraphy. The proposal by Sun et al. (1999, 2000) and Sun and Luo (2001) that *Artemisia*-dominated grassland may have colonized the exposed northern continental shelf, rather than demonstrating substantial terrestrial expansion of steppe from inland northern China, places some constraint on quantification of existing climatic conditions. Overall,

it would appear that, apart from grassland colonization of the exposed northern continental shelf, vegetation variation was largely restricted to changes in altitudinal range of montane communities and some replacement of lowland forest by grassland during glacial periods.

Lynch's Crater (Kershaw, 1986) and ODP Site 820 (Moss, 1999) within the northeast Australian region allow a similar comparison of marine-terrestrial records at an equivalent latitude in the Southern Hemisphere to those from the South China Sea. The northeast Australian region contains a core of tropical rainforest surrounded by eucalypt-dominated sclerophyll woodland and has a climate dominated by easterly (Trade) winds and a secondary monsoonal influence. An oxygen isotope curve provides a chronology for the ODP record and, from a comparison of pollen representation, this chronology has been applied to the Lynch's Crater record. Both records cover approximately the last two glacial cycles with detailed correlation provided for the last glacial cycle (Moss and Kershaw, 2000). Features of the pollen record from ODP Site 820 are shown in Fig. 4.

The response of vegetation in northeast Australia to global forcing is clearly evident although, unlike the China Sea situation, the signal is clearer in the terrestrial than the marine record. Interglacials were dominated by tropical to-submontane rainforest characterised by high values for taxa such as Cunoniaceae and Elaeocarpaceae indicating high rainfall. However, substantial variation in rainforest community composition is recorded within and between interglacials. Glacial periods are generally identified by high values for Poaceae, Casuarinaceae and *Eucalyptus*, and the conifers *Araucaria* and *Podocarpus*. This indicates expansions of sclerophyll woodland and moist rainforest respectively over much of the area currently occupied by humid rainforest under regionally drier conditions. There is no clear indication of any reduction in temperature during glacial periods, although this could be a result of the insensitivity of pollen of sclerophyll vegetation to this variable and the present restricted distribution of araucarian forest, as bioclimatic analysis of rainforest taxa reveals up to 3°C annual variation within interglacials (Kershaw and Nix, 1989).

A short record from marine core Fr10/95-GC17, located off the Cape Range Peninsula and covering no more than the last 120 ka, provides evidence for vegetation in the arid northwest of the Australian continent (van der Kaars and De Deckker, 2002). The site is in a zone intermediate between northern monsoon and southern westerly influences and, consequently, its low (200–300 mm) and variable rainfall falls in both summer and winter. The record is dominated by herbaceous and low shrub vegetation composed largely of Asteraceae, Poaceae and Chenopodiaceae that had a sparse and probably regionally variable cover of *Eucalyptus*, *Acacia* and, sometimes, the dryland conifer

Fig. 4. ODP Site 820 (Coral Sea): ratio pollen diagram of major dry land taxon groups, selected taxa expressed as percentages of the arboreal pollen sum, and charcoal particles expressed as numbers per cubic centimetre (from Moss, 1999).

Callitris. Alternation of dominance by Asteraceae and Poaceae suggests, from surface sample studies (van der Kaars and De Deckker, 2002), the relative importance of winter and summer rainfall respectively. The pattern is most marked during early phases, with the approximate 20 ka frequency suggesting precessional control that may or may not be in phase with substages of MIS 5. Highest rainfall is considered to have been achieved during MIS 5, with highest *Eucalyptus* and aquatic pollen values, and, to a lesser degree, in the Holocene, with high aquatic values and some *Eucalyptus* response. However, the major change occurs around 40 ka, when Chenopodiaceae increases relative to *Eucalyptus*.

The extent of reduction in rainforest and its distribution during the last glacial period has been the source of some conjecture (Ash, 1988). The Lynch's Crater record suggests that rainforest would have been restricted to areas receiving greater than 2500 mm of rainfall per year, but Hopkins et al. (1993), in their search for rainforest in presumed refugia from identification of dated soil charcoal, found only evidence of eucalypts at this time. The ODP record indicates the regional survival of a significant amount of rainforest during glacial periods. The most economical explanation is that, as the major source of pollen to this site is likely to have derived from rivers (Moss, 1999), rainforest existed essentially as gallery forests therefore over-representing rainforest taxa in the marine record, with survival aided by the complex physiography of the coastal ranges.

Two long records from the southern margin of the equatorial rainforest within Indonesia—the Bandung Basin of western Java (van der Kaars and Dam, 1995) and Core SHI-9014 from the Banda Sea (van der Kaars et al., 2000), supported by somewhat discontinuous

records extending into at least MIS 2 such as from the Wanda site, Sulawesi (Hope, 2001), Lake Hordorli, Irian Jaya (Hope and Tulip, 1994), Lake Sentarum, West Kalimantan (Anshari et al., 2001) and Nee Soon, Singapore (Taylor et al., 2001), demonstrate the survival of substantial areas of rainforest during the last glacial period at least. However, distribution and composition of rainforest communities exhibited notable changes. The dominance of pollen from freshwater swamp forest with some lowland forest elements at the marginal lowland site of Bandung (630 m altitude), suggests copious rainfall and temperatures slightly higher than today during the basal last interglacial phase of the record. Reduced temperatures are indicated by the expansion of lower montane oak (*Lithocarpus–Castanopsis*) forests during the latter part of MIS stage 5. High representation of upper montane taxa such as *Dacrycarpus* and *Engelhardia* during the last glacial period (MIS stages 4–2) indicates further altitudinal lowering of the vegetation belts and temperatures at least 4°C lower than today. A replacement of swamp forest by herbaceous swamp at the beginning of MIS 4 suggests that the fall in temperature was accompanied by drier conditions, most likely because of reduced monsoon rain with the drying of the Sunda continental shelf to the north. More detailed interpretation is hindered by the lack of a record for the last 20 ka.

The longer (180 ka) and more continuous Banda Sea record provides valuable regional support for the terrestrial Bandung record. It suggests substantial survival of lowland forest, dominated by Dipterocarpaceae, during glacial period although both lowland and upper montane forest were reduced relative to an expanded lower montane oak forest. High values for

Poaceae suggest the extension of grassland rather than rainforest over exposed continental shelf during glacial periods, although, as the major Sahul Shelf extends from the drier Australian region, there is no proof that rainforest would not have occupied shelf areas within the equatorial region. More certain evidence for reduced precipitation during glacial periods is provided by lower fern spore values: in fact fern spore abundance mirrors the oxygen isotope curve. The abundance of Poaceae pollen increases in the Banda Sea record during MIS2, possibly due to drier or more seasonal conditions. However Lake Hordorli remains fully forested at all times, supporting the notion that at least the core of the Western Pacific Warm Pool remained stable.

Pollen records from eastern Indian Ocean tropics, like that from the Banda Sea, provide evidence from both Indonesia and northern Australia, but within a region experiencing much less rainfall and where continental shelf expansion, although marked, may not be as critical to the pollen signal, directly through alteration of land–sea relationships or indirectly through the influence of continental exposure on regional climate. All records are strongly influenced by the northwest (Australian) summer monsoon. Core G6-4 from the Lombok Ridge, despite its close proximity to the Indonesian Lesser Sunda Islands, is dominated by pollen from Australia in the form of *Eucalyptus* and Poaceae (van der Kaars, 1991; Wang et al., 1999) (Fig. 5). There is a slight indication that Poaceae increased relative to *Eucalyptus* during the last three glacial periods, which may suggest

opening up of the dominant woodland canopy under lower rainfall or expansion of grassland with exposure of the continental shelf, but this is not the major pattern of variability exhibited. By contrast, rainforest and fern spores, derived predominantly from Indonesia, exhibit similar patterns to those from the Banda Sea, with increased abundance of lowland rainforest and fern spores during the two interglacials recorded and fern spores tracking closely the isotope curve. Well-dispersed fern spores show a similar clear signal in the 500 ka record from Core MD-982167 that is much closer to the Australian continent, but there is little pollen representation from Indonesian vegetation. The dominant Australian woodland taxa, Poaceae and *Eucalyptus*, show a great deal of variability, with the latter displaying approximately a 20 ka frequency through much of the record. On average, Poaceae values are higher during glacials and, together with highest representation of Cyperaceae, support evidence from the Gulf of Carpentaria that the exposed northern Australian continental shelves were colonized by a mosaic of grasslands and sedgelands (Chivas et al., 2001).

The presence of mangrove pollen in all records from the northern Australian-Indonesian region demonstrates the regional importance of this vegetation type. Strong fluctuations in representation are consistent between records with peak values coinciding with rising sea levels and consequently marine transgressions across continental shelves, especially around glacial–interglacial transitions (Grindrod et al., 2002). Mangrove

Fig. 5. Core G6-4 (Lombok Ridge, Indian Ocean): ratio pollen diagram of major dry land taxon groups, selected taxa expressed as percentages of the dry land pollen sum, and the charcoal/pollen ratio (from Wang et al., 1999).

representation is reduced at times of high sea level and also falling sea levels and regressive shorelines. There is little mangrove representation during low sea levels. Grindrod et al. (2002) conclude that mangrove histories, although tied to glacial–interglacial cyclicality, are not directly linked to climate change but to physiographic changes to coasts as they respond to Quaternary sea level adjustments.

The complexity of pollen records generally inhibits, from visual inspection, the elucidation of patterns other than those clearly linked to glacial–interglacial cyclicality. However, these records have the potential to reveal the relative influence of the individual components of insolation forcing as well as other forcing mechanisms that influence regional vegetation and climate variation. Time series or spectral analysis is required in order to detect frequencies evident within marine records with good chronological control.

A preliminary analysis of frequencies within selected pollen components and charcoal from marine records ODP Site 820, SHI-9014, G6-4 and Fr10/95-GC17 across northern Australia and southern Indonesia (Kershaw et al., in press b) revealed a variety of frequency responses to orbital forcing as well as others that could not easily be related to orbital forcing. Mangroves showed greatest correspondence with patterns from oxygen isotope records indicating northern hemisphere orbital control with dominant 100 ka eccentricity frequency, followed by 40 ka obliquity frequency and then 20 ka precession frequency. This correspondence is no doubt a result of mangrove response to ice-controlled sea level variation, as previously established. Tropical forest trees and ferns in the Banda Sea and Lombok Ridge records also show marked similarities to isotope frequencies, presumably a result of the influence of sea level on moisture availability although some tropical forcing is suggested by a diminution in the obliquity frequency relative to that of precession. Asteraceae, only analysed for the arid northwest Australian record, is also notable for its significant Milankovitch frequencies, possibly a result of higher latitude climate control over its distribution. Other components, such as Poaceae, *Eucalyptus*, rainforest gymnosperms (indicative of montane or drier rainforest) and charcoal, although displaying some relationship to global orbital forcing, show great variability in amplitude and significance between orbital frequencies, possibly a function of their non-stationary nature (see next section).

A major additional frequency on PEPH, significant in the majority of terrestrial components, but particularly so in the Pacific and Indian Ocean regions (Pisias and Rea, 1988; Beaufort et al., 2001), is 30 ka. Its greatest expression is in the charcoal and araucarian rainforest components of ODP Site 820, where peaks in charcoal, indicating intense burning, can be related to sustained

declines in fire sensitive araucarian rainforest. The close relationship between charcoal peaks and periods of high ENSO activity (a combination of high frequency El Niño and La Niña events), as proposed over the last 150 ka in the model of Clement et al. (1999), could provide an explanation for the 30 ka frequency. ENSO may also be influential in the explanation of the relatively strong 20 ka signal in the tropical records generally as, within the model, precession dominates the El Niño component of ENSO variation. It is interesting to note that a distinct tropical component has been suggested in the core RC14-99 record from off the coast of Japan through spectral analysis (Morley and Heusser, 1997). Although the record is dominated by orbital control over monsoon activity in general, and is clearly demonstrated at eccentricity and obliquity scales, the proxy for summer monsoon rainfall (the terrestrial conifer *Cryptomeria*) shows a precessional response that lags both the Northern Hemisphere solar radiation and ice volume minima by several thousand years, and is likely to have resulted from latent heat transported from the Indian or tropical Pacific oceans. No phase relationships were calculated for the tropical records examined by Kershaw et al. (2003), but preliminary analysis of the core off the Kimberley coastline suggests, from the pattern of representation of *Eucalyptus* through the last 300 ka, that precessional forcing of the summer monsoon through orbital variations in Southern Hemisphere insolation may provide the dominant control over terrestrial vegetation in northwestern Australia. There is a clear need for more rigorous examination of available detailed marine records to fully explore the nature and extent of tropical forcing on global climate variability at the Milankovitch scale.

3.2. Long-term trends

Many of the time series from the long records of palaeo-vegetation are not stationary, as they demonstrate that there have been sustained alternations in PEPH vegetation through the late Quaternary period.

3.2.1. Southern Hemisphere

The trend in the pollen record from ODP Site 820 over the last 250 ka is more apparent than the cyclicality (Fig. 4). During this period araucarian rainforest, which had been a major component of the northern Australian landscape for at least the last 10 million years (Kershaw et al., in press), was replaced by eucalypt woodland. It is proposed that increased disturbance linked to greater or more effective burning was the critical factor. This would have impacted most severely the fire sensitive araucarian rainforest and advantaged the fire tolerant or fire promoting eucalypts and grasses. Major stepwise decreases in araucarian rainforest taxa are recorded around 135 ka and around 45 ka, and are accompanied

by the most prominent charcoal peaks within the record (Moss and Kershaw, 2000). The dates of these impacts are intriguing in that the former is very close to the change from Casuarinaceae to *Eucalyptus* dominance of interglacials at Lake George, tentatively dated to 130 ka and considered to have resulted from a sustained increase in fire (Singh and Geissler, 1985), and the latter corresponds with the first major evidence for burning at Lynch's Crater that is considered to have initiated the replacement of araucarian forest by eucalypt woodland on the Atherton Tableland, a process completed in about 12,000 years (Kershaw, 1986). Also along the eastern fringe of the continent, a subtropical coastal interdune site on Fraser island, araucarian rainforest is replaced by eucalypt vegetation in association with increased burning during the late Quaternary (Longmore, 1997). However, some concern over dating inhibits a more detailed comparison with other sites. Apparently divorced from burning activity, at least visibly, is an early change in the ODP Site 820 record, dated to about 170 ka. Here there is a rise in Poaceae representation, corresponding with a decline in palm pollen and fern spores. This could indicate the replacement of lowland swamp forest, distinguished by high palm representation, by grasslands and could have resulted from some local alteration of river systems or coastal configurations, or have a more regional cause.

Sustained changes in vegetation and charcoal are notable in records from the north and northwest of Australia, although relationships between the two are not generally as clear as in sites along the eastern Australian fringe. In the Lombok Ridge record, charcoal particle values are relatively low until the MIS 8-7 boundary, which shows the first of many sharp peaks that include major ones at 130 ka and around 40 ka, and a general increase to present (Wang et al., 1999). Slightly higher charcoal values during interglacials may relate to greater fuel availability under higher precipitation levels. However, the regional vegetation pattern is dominated by a sharp increase in grasses relative to eucalypts around 180 ka, suggesting the development of a much more open woodland vegetation in northern Australia. To the north, in a more humid tropical source region, the Band Sea record shows a general pattern of high burning levels during glacial periods. However there is a sharp increase associated with a sustained decline in the Indonesian dominant lowland rainforest family, Dipterocarpaceae, around 35 ka (van der Kaars et al., 2000). The record from the semi-arid Kimberley coast shows generally stable charcoal values until a peak around 115 ka and a subsequent general increase to present, dating from about 40 to 45 ka. The initiation of this latter rise is accompanied by the abrupt disappearance of a taxon considered most likely to have been present in dry vine thicket, the inland extreme of rainforest-related

vegetation. The record off the arid northwest coast of Australia is unusual in showing a clear reduction in charcoal towards present, both in percentage and influx terms (van der Kaars and De Deckker, 2002). The fall from relatively high and variable values to consistently low values corresponds with that in *Eucalyptus*, between 46 and 40 ka, and, as in the Lombok Ridge record, lower charcoal values probably result from a reduction in fuel availability.

Within the southeast Australian region there are indications of vegetation alteration such as a relative increase in *Eucalyptus* relative to Casuarinaceae and rainforest over the last glacial cycle at Lake Selina and increased grass representation within the Lake Wangoom record, but the lack of longer records prohibits the separation of trends from variability. However, the apparent final disappearance of *Phyllocladus* from the Australian mainland (McKenzie and Kershaw, 2000) and extinction of *Nothofagus* on King Island to the north of Tasmania (D'Costa, 1997) demonstrate a contraction of temperate rainforest within the region at some time during the last glacial period. In contrast to Australia, there is no clear evidence of trends within New Zealand records during the latter part of the Quaternary although some range alterations have no doubt occurred.

3.2.2. Northern Hemisphere

The two records from the northern part of the South China Sea both show trends towards more open vegetation within glacial periods. In ODP Site 1144, increased herbaceous values are largely a result of *Artemisia* that first shows marked expansion in MIS 6 and this expansion is repeated in MIS 4-3 with maximum *Artemisia* representation in MIS 2 (Sun and Luo, 2001). In Lake Tianyang, the major increase in herbaceous vegetation, involving *Artemisia* but more particularly Poaceae, did not occur until the LGM but the whole of the major part of the last glacial period (MIS 4-2) was marked by increased representation of temperate forest elements, in comparison with previous glacial periods. Similar, although less dramatic, trends are evident further north in the Lake Biwa record with sustained increases in Poaceae, Cyperaceae and fern spores during the last two glacial periods. There are also significantly lower *Fagus* values from the earlier part of MIS 7.

3.3. Possible forcing factors

It is clear that the later part of the Quaternary has witnessed long term changes in vegetation that have influenced the nature and present day distribution of vegetation. They also indicate that patterns of change indicated in the numerous records from the latest Pleistocene and Holocene cannot be considered as

representative of previous glacial cyclicality. From the very limited number of longer records, it may appear that an underlying trend was initiated within the last 300 ka and may correspond with the so-called mid-Brunhes event detected in many marine proxies particularly from the Pacific Ocean but whose cause is uncertain (Pisias and Rea, 1988). The vegetation changes within this period are variable in nature and also in timing, but many broadly relate to periods around 200–170 ka, 135–125 ka and 35–45 ka. It is probable that the pattern is complicated by varying sensitivities of vegetation to forcing factors in space and time.

Geographically, the most marked changes are in northeastern Australia with extension along the northern part of this continent and diminution of the trend latitudinally along the Pacific Rim to the north and south. If there is any overall forcing, it most likely originated within the West Pacific Warm Pool region with oceanic conveyance to higher latitudes northwards through the Kuroshio Current and southwards through the East Australian current, and atmospheric conveyance through monsoon and ENSO activity. Some development, intensification or expansion of the West Pacific Warm Pool in the mid-Brunhes has been suggested by marine isotope evidence for a systematic shift to lower $\delta^{18}\text{O}$ in records from the Coral Sea including the ODP Site 820 record (Peerdeman et al., 1993; Isern et al., 1996) that indicates a rise of some 3–5°C in sea surface temperatures. Such an increase in build up of warm water in the western Pacific would have a great influence on ENSO activity that, as already mentioned, could help explain equally dramatic changes in the pollen record from ODP Site 820, especially when high ENSO activity coincided with times when other environmental conditions were conducive to vegetation change. The somewhat different responses to increased variability in records from off northern Australia could perhaps be explained by the distinct influence of the monsoon (e.g., Webster et al., 1998), strong linkages to ENSO, and probably such links in the past (Beaufort et al., 2001).

A possible mechanism for altered climate forcing is a constriction of the Indonesian gateway between the Pacific and Indian Oceans as a result of tectonic and volcanic activity related to the continuing movement of the Australian continent towards Asia. However, it is suggested by Sun and Luo (2001) that the increased representation of grassland in the northern South China Sea was a function of progressive glacial exposure of the continental shelf associated with uplift of the Tibetan Plateau around 150 ka as well as to climatically drier and cooler conditions. Sun et al. (2003) found evidence for a long-term trend to more extreme steppe-like conditions during glaciations in a marine core from shallow water on the continental shelf south of China.

This can be compared with reconstructions of the vegetation that formed interglacial soils found between loess layers (Chen et al., 1997) that establish that temperate and subtropical forest has extended further north in earlier interglacial stages than the early Holocene when it reached 38°N. This indicates that at times the summer monsoon may have penetrated more deeply into China.

The impact of people, through biomass burning, has long been proposed as a major cause of alteration to Australian vegetation and the suggestion of impact from the Lake George (Singh and Geissler, 1985) and ODP Site 820 records (Kershaw et al., 1993), well before evidence for Aboriginal occupation of the continent, provided the source of a great deal of debate (see Bird et al., this volume). The current consensus of an arrival date (e.g., Bowler et al., 2003) around 45–50 ka restricts discussion of potential, initial human impact to the period of altered vegetation and burning around 35–45 ka. There has been general acceptance that this event is primarily anthropogenic because there had been no evidence for a major climate change within this part of MIS 3 in addition to the archaeological record. However, the suggestion from the ODP 820 record that this was a time of high ENSO variability, and the evidence for a strong precessional monsoon signal in core MD982167 does introduce the possibility of a climatic contribution. Perhaps the most parsimonious explanation is that people were present on the continent before 45 ka but that their effect on the vegetation was limited until the onset of a period of high climatic variability.

4. Pleniglacial environments

The best studied time phase is from the last glaciation, when the most dramatically different environments are found right across the transect. The BIOME program (Prentice et al., 1993) has mapped available pollen records throughout the transect. In the north the mean position of the polar front and the relative strengths of summer and winter monsoons controlled the position of the treeline (Tarasov et al., 2000). Forested areas were converted to grasslands and steppe, as far south as south China. In the mountains of Taiwan the shift in the lower boundary of conifer forest was about 1500 m (from 2400 m today to 800 m during MIS 4) but steppe or forest steppe existed for a short time during the LGM (Tsukada, 1967; Kuo and Liew, 2000). The northern part of the exposed South China Sea coastal plain appears to have been an open *Artemisia*-dominated grassland. Woodland-forest dominated by pine extended into central Thailand and subtropical forest was restricted (Maxwell and Liu, 2002). However pollen from marine cores west of India (van Campo, 1986)

suggests that humid tropical vegetation was maintained through the stadial in southwestern India. Similarly subtropical vegetation was maintained in Yunnan, southern China (Walker and Sun, 1988), while lowland rainforest colonised the emerged southern continental shelf of the South China Sea (Sun et al., 1999, 2002).

The core tropical forests of mainland southeast Asia, Borneo, Sumatra, Java, Sulawesi and New Guinea remained in the lowlands (e.g. Kershaw et al., 2001; van der Kaars et al., 2001; Weiss et al., 2002) despite encroachment in some areas by grasslands in Thailand, Sulawesi (Dam et al., 2001; Hope, 2001) and probably southern New Guinea. There appears to be greater evidence of aridity in the western part of the region than to the east in New Guinea. In fact, Kershaw et al. (2001) consider that the total area under forest may have increased, as extensive continental shelves were occupied. However higher altitude montane forests advanced to lower altitudes, reaching 800 m in some areas such as Kerinci, Sumatra (Newsome and Flenley, 1988), Central Java and Bandung (Stuijts, 1993; van der Kaars and Dam, 1995; Polhaupessy 2002), Sulawesi (Hope, 2001), Maluku (Barmawijaya et al., 1993) and the Cyclops Mountains (Hope, 1996).

At very high altitudes the treeline was depressed to around 2200 m (Hope, 1996; Peterson et al., 2002). Above this were shrubby grasslands with treeferns until glacial ice was reached at around 3500 m. The treeline depression of approximately 1800 m compared to the modern is much greater than that of the snowline, of about 1100 m. Since the snowline depression equals or exceeds that noted in the tropical mountains in the other transects, an explanation beyond aridity must be sought. Palynology shows that the shrub-rich grasslands have been replaced in the Holocene by low closed forest, so that the glacial maximum was a time of reduced tree success (Hope, 1989, 1996). At some time after 40 ka the specialised marsupial fauna that grazed these grasslands disappears (Heinsohn and Hope, 2003).

In Australia wet forests retreated to the mountainous scarps and were replaced by sclerophyll woodlands or grassland. Across northern Australia and the plain connecting it to southern New Guinea, semi-arid sclerophyll woodlands and steppe grasslands expanded north. The shift in the boundary between rainforest and *Eucalyptus*–*Casuarina* woodland is most clearly demonstrated at Lynches Crater in northeast Queensland (Moss and Kershaw, 2000; Kershaw et al., 2001) but cores northwest of Australia (Wang et al., 1999; van der Kaars et al., 2000; Kershaw et al., 2002) also clearly delineate an expansion of Poaceae and Chenopodiaceae. A phytolith and macro-botanical record from Carpenters Gap rock shelter in northwestern Australia (O'Connor, 1999; Wallis, 2001) shows an expansion of desert grasses by 34 ka but some occasional moist elements are still present around 19 ka. Faunal records

of woodland species such as wallabies, from Lemdubu Rock shelter, Aru Islands, show that this site at 6°S on the Arafura plain, now surrounded by rainforest, was within the sclerophyll zone on the exposed shelf from 30 to 14 ka (O'Connor et al., 2002). In southwestern Australia there was a distinct expansion of arid environments (Pickett, 1997).

In the tropical Pacific Islands there are only relatively minor indications that conditions were cooler and drier. In Fiji, montane forest was well developed and some lower altitude taxa excluded, suggesting temperatures may have been lower (Hope, 1996). In New Caledonia more open forest is present and there is evidence for natural fire (Stevenson et al., 2001). This seems to have been associated with major erosion and the spread of *Gymnostoma* maquis after 23 ka (Hope and Pask, 1998). The Easter Island evidence suggests lower rainfall was experienced in the eastern temperate Pacific (Flenley et al., 1991).

In southeastern Australia treelessness was widespread down to sea level (Hope, 1989; Dodson, 1998) although woodland was preserved in patches, and closed forest persisted in mountain valleys or small refugia (e.g., Harle et al., 1993; McKenzie, 1997; McKenzie and Kershaw, 2000). Large trees seem to have been lost from riparian sites in the south, resulting in changes to fluvial regimes and widespread building of source bordering dunes and sand sheets (Hesse et al., this volume). This seems to have been a response to drier and possibly windier conditions since forest was maintained along the eastern scarp and was not excluded by temperature. A peculiar mixture of taxa now widely separated occurs in several sites, for example Kangaroo Island, South Australia, where a desert fauna including, hopping mice, is mixed with a wet scrub fauna now restricted to Tasmania (Hope et al., 1977). This suggests that a mosaic of desert steppe and swamp shrub vegetation may have been present under conditions of low rainfall and low evaporation that led to raised groundwater levels. Steep rainfall gradients are indicated by the persistence of rainforest near areas that developed dune fields and other aeolian landforms in the glacial stage (McKenzie and Kershaw, 2000). Cold temperatures up to 10°C colder than present are indicated in central Australia from amino acid racemisation data from eggshells (Miller et al., 1997; Hesse et al., this volume).

Change in southwestern Australia seems more muted but analysis of charcoal demonstrates that the dominant eucalypt species were different (Dortch, 2000) and cave deposits record some desert faunas from 30 to 15 ka (Baynes et al., 1975). This vegetation change is not extreme, however, being explicable by increased continentality caused by migration of the coastline onto the continental shelf, as first pointed out for the Nullarbor Plain by Martin (1973). Marine changes suggest that the

shallow southward flowing warm Leeuwin current was reduced or diverted offshore (De Deckker et al., 2002).

New Zealand was extensively glaciated and forest is absent in numerous sites in the area now forming the South Island (McGlone et al., 1993). Warm temperate forests with *Agathis* were restricted to an area north of Auckland, while beech forest was nearly wiped out in the South Island (Newnham, 1992). In the place of forests were widespread subalpine scrubs and herbfields. During the pleniglacial in the New Zealand region, cool southern ocean water masses pushed up against the Chatham Rise to the east, depressing sea surface temperature by 4–6°C and steepening the north–south temperature gradient by 8°C (Weaver et al., 1998; Nelson et al., 2000). The far southern island groups Campbell and Auckland, and the axial mountain ranges of the South Island were heavily glaciated, with limited areas of glaciation on higher peaks in the southern and central North Island. Equilibrium glacier line depressions of around 800–850 m suggest a lowering of mean annual temperature by 4–5°C on the mainland (Porter, 1975), and depressions of between 850 and 1000 m in the far southern islands by 5–6°C (McGlone, 2002a, b). Erosion of tephra mantles and loess sheets suggest that vegetation cover was unstable or incomplete above around 500 m in the central North Island (Pillans et al., 1993), and above 300 m in the southern South Island (McIntosh et al., 1990). A cool-climate forest dominated by *Nothofagus* occupied the Northland Peninsula north of 36°S, and extended south along the coastline to 38°S (Lees et al., 1998). However, inland districts from Auckland south had highly variable mosaics of *Nothofagus* forest (with very minor Podocarpaceae contributions), scrub and grassland, and the further south, the less the forest contribution became (McGlone et al., 1993; Sandiford et al., 2002). The drier, eastern coast of the South Island was largely in open herb fields, grassland, and small-leaved scrub; in the west, grassland and shrubland with scrub conifers prevailed (Moar, 1971; Vandergoes, 2000).

The very far south of the South Island, being adjacent to the extremely cold glacial waters pushed up against the Chatham Rise, may have approximated a cold, dry desert (Nelson et al., 1993). Many lake basins dried out and peat-filled basins show hiatuses during the pleniglacial, suggesting much drier climates at this time (Pillans et al., 1993; McGlone et al., 1993). Despite this cooler, drier climate, forest patches containing much of the present regional floras appear to have survived throughout the pleniglacial along coastlines and in inland microclimatic sites provided by the mountainous terrain (McGlone et al., 2001). Glacial ice restricted the area available for tussock grassland and herbfield on the sub-Antarctic islands (McGlone, 2002a, b). On Heard Island, the vascular flora was probably almost exterminated. Survival of forest trees and scrub on other far

southern islands is not certain, but the balance of the evidence indicates that most current species did persist through the pleniglacial.

5. The Pleistocene–Holocene transition

The advent of Holocene climates with increased moisture is marked by the commencement of sedimentation in numerous sites across the transect from the late Pleistocene (younger than 15 ka) to the early Holocene. These records provide evidence for a widespread environmental change towards conditions supporting swamp and lake development. In some cases, such as glacial retreat from glacial basins, the cause of initiation of sediment is quite clear. In others it is less so, although a general shift to increased organic sediments points to increasing ground cover and slope stability in catchments. Chronological problems loom large in many records from the tropical regions for the period after the LGM, although the reasons are not well understood. There are gaps in the record that may extend across LGM times (e.g. from ca 24 to <12 ka) or occur after the LGM until well into the Holocene (e.g., at Lake Sentarum, Kalimantan (Anshari et al., 2001)). Extreme examples are a gap from 31 to 2 ka within a 350 cm peat section in West Papua (Hope, 1998) and suspected substantial gaps in the record from Lake George, New South Wales (Singh and Geissler, 1985). Where many dates of initiation of sedimentation are available there is usually a wide range of ages, suggesting that individual site characteristics can delay transitions for thousands of years. Thus peatland initiation dates are very variable in southeastern Australia (Kershaw and Strickland, 1989), and to some extent in western China (Winkler and Wang, 1993). In New Zealand, the problems with hiatuses in sedimentation across the transition are largely confined to peatland sites north of 36°S in the Northland peninsula (e.g. Newnham, 1992).

The ecological response to the warming climates of the late Pleistocene are dependent on the various controlling factors in place in different localities. Responses to warming on the northern parts of the PEPH transect include the invasion of tundra and steppe by woodlands and taiga. At Lake Baikal, tree pollen is almost absent until about 9.7 ka. In Japan, the response of trees to warmer climates is apparent by 11.5 ka but conditions stayed colder than present until about 9 ka, possibly due to the landlocked Sea of Japan (Takahara et al., 2000).

In southern China, India and southeast Asia the transition has been reviewed by Maxwell and Liu (2002) who argue for a stepped increase in monsoon strength (with warming and increasing summer moisture) commencing about 13.1 ka. The vegetational effects of this

may lag in Tibet by up to 1500 years, but in other areas the response is immediate. The sparsely dated site at Nilgiris, in the Western Ghat Range, southern India (J.P. Sutra, pers comm.) appears to have had only a short dry period at the height of the LGM. In Sichuan, China, Roergai Marsh is surrounded by alpine meadow and desert steppe until 18 ka (Shen et al., 1996). Gradual increases then occurred in sub-alpine shrubs, which in turn finally give way to forest at 11 ka. In Taiwan, Liew and Tseng (1999) find increasing moisture at 15 ka and forest expansion after 13.9 ka, with humid episodes at 12.5 ka. Final warming at the start of the Holocene is indicated by decrease in cool temperate elements and an increase in subtropical elements at 10.1 ka.

In tropical southeast Asia, Penny (2001) infers slightly drier conditions and raised fire regimes in the late Pleistocene with an expansion of oak and pine forest. Tropical broadleaf forest abruptly replaces the more open forest between 12 and 10 ka. This record contrasts with those from Yunnan, where the late Glacial was a time of fluctuation as lower altitude elements invaded at the same time as montane elements expanded, suggesting simultaneously wetter and warmer climates that may have experienced a series of short reversals from 14 to 10 ka (Sun et al., 1986). If seasonality was less pronounced, as Maxwell and Liu (2002) postulate, then this condition continues into the early Holocene until around 7.5 ka. Newsome and Flenley (1988), Stuijts (1993) and van der Kaars et al. (2001) record the transitions from 14 ka until 11 ka in Sumatra and Java as lower altitude taxa invade.

In New Guinea, glacial retreat had started by 15 ka and revegetation of the alpine follows a three stage process. Shrublands replace tundra by 13 ka and there is a second increase in diversity and rise in the treeline about 10.2 ka. The highest sites do not reach an equilibrium subalpine forest until around 9 ka (Peterson et al., 2002). The subalpine forest appears to form from elements that were part of a mixed montane forest in the Pleistocene so that effectively a forest biome replaces an open shrubland–treefern–grassland biome (Hope, 1989). This may be a response to increasing CO₂ (Street-Perrott et al., 1997). Sukumar et al. (1995) also propose rising CO₂ levels as an important driver of forest expansion on the Western Ghat Range during the deglaciation phase of the last glacial. Forests in New Guinea vary widely floristically even between adjacent mountains, indicating an individualistic formation from variable elements. At montane altitudes *Nothofagus* forest loses ground after 14 ka to mixed montane forests that include *Castanopsis*, a change that may reflect increased seasonality of moisture since it is more pronounced in the south and east of the island (Haberle, 1998). At low altitude the lowland forest expands after 10.5 ka, both at the expense of montane forest (Hope, 1996; van der Kaars et al., 2000) and by invading

woodland habitats as shown by a shift in fauna to rainforest taxa on the Aru islands (O'Connor et al., 2002) at about 11.5 ka. At Lake Hordorli on the northern coast of New Guinea there is an apparent reversion to higher altitude forest around 9.5 ka, which is in agreement with an early Holocene record of marine cooling in the Banda Sea (van der Kaars et al., 2000).

The sites at Atherton, northeast Queensland, also show development of closed forest, but this is delayed until 8–9 ka possibly due to extensive dry coastal plains to the east and northwest which are only substantially flooded at this time (Moss and Kershaw, 2000). At Carpenters Gap, northwest Australia, an increase in monsoon forest fruits occurs at 7 ka, or possibly earlier (O'Connor, 1999). It thus seems likely that warming was accompanied by increased evaporation in the terminal Pleistocene, which kept water balances negative until the early Holocene. In the Pacific Islands the transition to increased moisture commences about 13.5 ka (Stevenson et al., 2001) but is not complete until 11 ka. The transition to forest similar to the present day is achieved at perhumid Lake Tagamaucia in Fiji around 10.5 ka (Hope, 1996), suggesting that temperatures had reached present day levels by then.

In southeastern Australia, cooler alpine conditions are still marked at 12.5 ka but trees are already invading the uplands. Peat initiation dates range from around 13 ka in moist sites at 1000 m to 8.5 ka at sites above 1500 m (Kershaw and Strickland, 1989; Martin, 1999). These dates generally accord with those in Tasmania (Macphail, 1986; Colhoun, 1996). Moist alpine conditions are lost from the eastern ranges by around 11.6 ka but eucalypts seem slower to invade drier montane sites, being apparently delayed until ca 8 ka at Lake George, New South Wales (Singh and Geissler, 1985).

In New Zealand, a range of sites display deglaciation dates and the spread of forest across South Island that had appeared to be largely vegetated by alpine scrub or grassland until 12 ka. The rapid spread of regional moist forests demonstrates that they had survived in refugia amongst the lower ranges. Their individualistic return parallels the New Guinea case (McGlone et al., 1993). The subsequent Holocene history is also instructive, as some areas remain occupied by their founder forests for thousands of years longer than others. This may be an example of the resilience of communities in the absence of anthropogenic or disturbance-forced readjustment to changed climates. Humans only disturb the record within the last 700 years (McGlone and Wilmshurst, 1999b) unlike the remainder of the PEP II transect where human interference has probably hastened the adjustment of vegetation boundaries to new equilibria with local climates and disturbance regimes. Resurgence of

peat growth and reforestation by tall Podocarpaceae forest (south of 36°S) began around 15 ka in the northern and central North Island and was accompanied by major increases in rainfall, temperature (a rise of around 3°C) and stabilisation of the landscape (McGlone et al., 1993; Newnham et al., 2003; Turney et al., 2003).

Retreat of glaciers on New Zealand's South Island was underway by around 14 ka (Suggate, 1990) and replacement of pleniglacial grasslands by shrubland had occurred in the west by 15.3 ka (Vandergoes and Fitzsimons, 2003), and in the east by 14 ka (Turney et al., 2003). Tall Podocarpaceae forest occupied most lowland and montane South Island sites by 10–9.5 ka (McGlone et al., 1993), an interval which marks a sharp transition to a warm-temperate, drought-intolerant forest over much of the North Island (Newnham et al., 1989; McGlone, 2001; Turney et al., 2003) and warm but drier facies forest in eastern districts (Hall and McGlone, 2001; McGlone, 2002a, b). Full forest cover was delayed in the semi-arid central districts of the southern South Island until 8 ka (McGlone and Wilmshurst, 1999a), and in the far southern islands was not dominant until 6 ka (McGlone, 2002a, b). The rapid spread of regional moist forests demonstrates that they had survived in refugia either along the coast or inland in mountainous terrain.

Evidence for a reversion to more glacial conditions at the time of the Younger Dryas is not well accepted from all parts of the PEPII transect, although coarse resolution and limited dating control does not allow the question to be settled. Despite some evidence for short episodes of glacial advance, palaeoecologists in the region have resisted the impulse to label any and all late transitional excursions in their diagrams as the Younger Dryas event. It may be that rising CO₂ values and increasing moisture availability with the advancing sea levels mask any temporary temperature reversions that may be occurring, evidence for which exists in the form of variations in the extent of glaciers in New Zealand (e.g., Denton et al., 1999). The late glacial, and the Younger Dryas chron in particular, is now represented by several well-dated sequences in New Zealand. The vegetation evidence shows increasing scrub forest cover, and the inclusion of more warmth and moisture requiring taxa from 12 to 9.5 ka (Turney et al., 2003; Vandergoes and Fitzsimons, 2003). This suggests that the climate was, overall, in a warming phase and that the well established evidence for glacial advances at around this time (Denton et al., 1999) can be explained either by brief cool intervals or the positive effect on glacier balances of increasing precipitation and more persistent westerly wind flow in summer (McGlone, 1995). However there is some pollen evidence for a weak cooling earlier in the late glacial (Newnham and Lowe, 2000; Turney et al., 2003).

6. The impact of Holocene variability

While Holocene climate change appears less dramatic than the stadial-interstadial transition, it has not been a time of environmental stability. In fact understanding the Holocene of the PEPII transect is complicated by the spread of agriculture in Asia and New Guinea, particularly after 6 ka (Ren and Zhang, 1998; Haberle et al., 2001; Bird et al., this volume) and out into the Pacific over the last 4000 years. Everywhere, increasing human populations have had widespread and progressively greater influence on vegetation and faunas. There are undoubtedly feedback effects from these changes on the sedimentary and climate systems. Australia, which did not experience agriculture, and New Zealand, settled only in the past 700 years, provide test beds for assessing the response of ecosystems to Holocene variability.

Precessional insolation data indicates reduced seasonality at low latitudes in the early Holocene with warmer Southern Hemisphere winters and cooler Southern Hemisphere summers, compared to the present. That an increase in El Nino strength and frequency occurs after 5 ka has been debated (e.g., Haberle and Ledru, 2001) as a potential cause of vegetational shifts towards more secondary forest and increased burning from this time.

Treelines reach higher limits in the mid-Holocene (8–5 ka) and some tropical rainforests incorporate more warm elements at the same time. In China, warm temperate forest is more extensive at 6 ka than subsequently (Ren and Zhang, 1998; Yu et al., 1998, 2000; Ren, 2000; Liu et al., 2002) but in Japan little difference was found (Takahara et al., 2000). In India, freshwater conditions in the Rajasthan desert are replaced by fluctuating saline conditions in the last 3–4 ka (Kajale and Deotare, 1997; Maxwell and Liu, 2002), while in the central Himalaya an increased extent of evergreen oak between 3.5 and 4 ka suggests cooler conditions and reduced activity of the southwest monsoon (Phadtare, 2000). Maxwell (2001) inferred that the summer monsoon was strengthened in Cambodia from 8.4 to 5.3 ka followed by drier climates marked by more frequent fires. Some recovery towards moist forest takes place in the last 2.4 ka, but disturbance may be preventing a full recovery. The early Holocene marks very extensive peat expansion from core areas in Kalimantan (e.g., Page et al., 1999), triggered in part by sea level rise but also reflecting increased moisture and perhaps CO₂ concentrations. While fire occurs in the peatlands throughout the Holocene, it appears to increase in frequency after 3–2 ka (Fig. 6), and historical fires are linked to anthropogenic burning during strong El Nino events.

In New Zealand, the early Holocene (10–7.5 ka) is marked by dry warm climates to the east of the axial mountain ranges, and moist, mild climates in the west

Fig. 6. Enggelam 2 P23, Kutai Peatlands, East Kalimantan Indonesia: pollen sum = total pollen. The site has supported swamp forest but shows that fire events have become common in the last 2.5 ka (Hope, unpublished data).

and north, and is followed by a progressive deterioration in which climates became increasingly variable and cool (McGlone et al., 1993; Wilmshurst et al., 2002). Over the mid to late Holocene, *Nothofagus*-dominant forest spread in central and southern districts, creating complex phytogeographic patterns that appear to reflect both the historical effect of glacial refugia and resistance of established Podocarpaceae forest and the timing and degree of climate change (McGlone et al., 1996).

In southeastern Australia, the mid-Holocene is marked by increased wet elements in forests that would seem to indicate moister conditions. Bega Swamp is a high resolution record from an orographically complacent swamp site (Fig. 7) that is surrounded by eucalypt forest (Green et al., 1988; Hope, unpublished). The eucalypt forest dominant switches abruptly to another type on several occasions, but this may represent quite minor transitions across environmental limits or even autogenic processes that are not driven by external changes. A similar scenario applies to Barrington Tops in New South Wales (Dodson et al., 1986). The virtually constant fire regime typical of the Australian Holocene may have acted as an adjustment force that kept the forests in equilibrium with small climatic shifts. A few sites on islands that appear to have experienced a more episodic fire regime show large fluctuations in fire activity and vegetational response (Bowman, 1998). This contrast suggests that episodic disturbance such as anthropogenic fire or swidden clearing, or storm events

such as tropical typhoons, can allow climatic change to be expressed in new vegetational equilibria.

It is clear that a simple model of late Holocene cooling and drying relative to the early Holocene does not adequately explain the observed relatively small but complex vegetational responses. In fact minor shifts in mean conditions may conceal variations in the frequency of extreme events that may be the significant controlling factor. A possible example may be the comparison of pollen based reconstructions with other proxies. Monthly isotopic records from the growth bands of fossil corals in north Queensland, Australia (Gagan and Chappell, 2000) demonstrate temperature and rainfall means at 5.8–5.7 ka that are slightly below the present values. This is a time in which Kershaw et al. (1991) suggest that warmer wetter lowland elements were better represented in the montane forests on land nearby than later in the Holocene. The striking difference between the fossil and recent coral proxies, however, is the absence of major droughts and floods, which are represented in every decade of the modern coral record and which are associated with some ENSO events. This demonstrates that the frequency of extreme events may control vegetation floristics and structure in the tropical and warm temperate regions at least.

This potential equilibrium of vegetation with events on 50–100 year timescales rather than annual means presents a problem for attempts to model regional climates using a BIOME approach (Prentice et al., 1993)

Fig. 7. Bega Swamp, southeastern Australia: pollen sum = dryland taxa. Bega Swamp is a high resolution Holocene site from an orographically stable location, showing a lengthy mid-Holocene development of wet forest elements (Hope, unpublished data).

in which plant functional types are related to pollen spectra and used to infer the dominant biome. These may not match biomes reconstructed from climate models based on modern vegetational distributions in all regions. BIOME also has difficulty reconstructing moisture boundaries, particularly as many pollen deposition sites may have atypically humid settings.

7. Conclusions

The evidence for environmental change is only indirectly a proxy for climate change, being mediated through vegetational cover that may have lags or respond to other factors as well as being buffered by site characteristics. This may help explain why parallel ecological changes along the PEPH transect may be diachronous, although resolution is so far quite poor. They might also be attributed to variable sensitivity to climate change or differential controlling factors for biomes. Finally, the regions themselves may reflect local controls. The role of the marginal seas is a good example, apparently delaying the onset of moister conditions until the shelf areas have been inundated, so that the increase in moist forests is delayed by some lengthy period. Similar effects have been noted on the PEPH transect (Markgraf, 2000).

At the orbital scale of climatic variation, vegetation response along most of the PEPH transect has been dominated by ice-volume forced, global glacial–interglacial cyclicity resulting in general synchronicity in vegetation responses between hemispheres. Glacial periods have been characterized by more open vegetation than interglacials, a result of both cooler and drier conditions. Temperature is the major variable influencing vegetation at high latitudes and in the humid tropics at high altitude. Moisture availability has had the major effect on low latitude, lowland vegetation and has been greatly influenced by alternate drowning and exposure of extensive continental shelves as a result of sea level fluctuations. Greatest variation in vegetation is shown both within and between interglacial periods, while glacial periods, apart from interstadials, have been characterized by greater vegetation homogeneity. This pattern may largely be explained by the prominence, in glacials, of herbaceous vegetation, including Poaceae, Asteraceae and Chenopodiaceae, whose contributing taxa cannot easily be differentiated palynologically. In the northern temperate high latitudes, there is clear latitudinal migration of forest taxa, but in other parts of the transect there is only evidence for expansion and contraction within essentially the same geographical range.

Records showing least global forcing are those of the northwestern part of northern Australia, where some

direct Indian Ocean forcing of monsoon rainfall is apparent. Tropical monsoon and ENSO influences also become apparent in frequency analysis of drier rainforest, sclerophyll and charcoal components of marine records with good chronological control. Even clearer tropical forcing is evident from examination of long-term trends in vegetation. Progressive or step-wise changes towards more open vegetation as a result of drier or more variable climatic conditions are most evident in the northern Australian region, but the influence extends to higher latitudes along the Pacific rim probably through major oceanic currents as well as monsoon and ENSO atmospheric circulation. Alteration of the West Pacific Warm Pool as a result of tectonic activity may provide the underlying cause of these trends.

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