Prehistoric human impact on rainforest biodiversity in highland New Guinea

Simon G. Haberle*

Department of Archaeology & Natural History, Research School of Pacific and Asian Studies, Australian National University, Canberra, Australian Capital Territory 0200, Australia

In the highlands of New Guinea, the development of agriculture as an indigenous innovation during the Early Holocene is considered to have resulted in rapid loss of forest cover, a decrease in forest biodiversity and increased land degradation over thousands of years. But how important is human activity in shaping the diversity of vegetation communities over millennial time-scales? An evaluation of the change in biodiversity of forest habitats through the Late Glacial transition to the present in five palaeoecological sites from highland valleys, where intensive agriculture is practised today, is presented. A detailed analysis of the longest and most continuous record from Papua New Guinea is also presented using available biodiversity indices (palynological richness and biodiversity indicator taxa) as a means of identifying changes in diversity. The analysis shows that the collapse of key forest habitats in the highland valleys is evident during the Mid–Late Holocene. These changes are best explained by the adoption of new land management practices and altered disturbance regimes associated with agricultural activity, though climate change may also play a role. The implications of these findings for ecosystem conservation and sustainability of agriculture in New Guinea are discussed.

Keywords: pollen; palynological richness; biodiversity indicator taxa; swamp forest; Papua New Guinea

1. INTRODUCTION

New Guinea is one of the most biodiverse regions on the globe as it is believed to harbour over 5% of the world's biodiversity in less than 1% of the land area (Johns 1993; Miller et al. 1994; Heads 2001). In the current century, the greatest threat to regional New Guinea-Australian tropical biodiversity is an everincreasing human population and pressures from global economic activity that have led to accelerated forest clearing, ecological degradation and climate change (Sekhran & Miller 1994; Haberle 2003a; Hilbert et al. 2004). In contrast to conditions in Southeast Asia to the west, at least 70% of the natural environment of the island remains intact and represents the third most significant expanse of tropical rainforest wilderness on Earth after the Amazonian and Congoli forest blocks (Mittermeier et al. 2005). While largescale short-term assessments of the region's vulnerability to biodiversity loss have generally excluded New Guinea from the category of 'biodiversity hotspot' (Mittermeier et al. 2005), this approach ignores the potential that small-scale processes and long-term influence of human activity may also have a significant impact on biodiversity change.

The broad changes in vegetation since the arrival of humans in the highlands¹ of New Guinea around

30 000 calendar years before the present (yr BP; Kosipe record, White et al. 1970) have been established from 19 swamp and lake sites (Haberle 2003b). These records show that at the time of early deglaciation, beginning around 14 500 yr BP, the forest limit rises and montane forests invade valley floor grasslands in response to warmer temperatures and rising atmospheric CO₂, though conditions were not uniformly suitable for forest development until after 9000 yr BP. The palaeoecological records from highland valleys point to a sustained and gradual intensification of forest clearance and burning from at least 7000 yr BP (Haberle 2003b), though evidence from the archaeological site of Kuk Swamp in the Wahgi Valley (figure 1) suggests that at least here the valley floor was never completely forested during the Early Holocene. During this time, people were using fire to increasingly disturb and modify the montane forest and soils on the valley floor for the purpose of managing and harvesting significant food plants (Denham et al. 2004).

The development of agriculture as an indigenous innovation during the Early Holocene is considered to have resulted in increased population pressures, rapid loss of forest cover and increased land degradation over thousands of years (Haberle & David 2004). A review of the evidence for early agriculture in New Guinea supported by new data from Kuk Swamp demonstrates that cultivation had begun there by at least 7000 yr BP and probably much earlier (Denham *et al.* 2004). The focus of early agricultural activity was in the intermontane valleys between 1000 and 1900 m above sea level, where the Early Holocene organic-rich soils and swamp forest cover provided a suitable environment for

^{*}simon.haberle@anu.edu.au

¹ In this case, the term 'highlands' refers to the inland regions of the island of New Guinea above an altitude of about 1000 m and not exclusively to the present day Highlands provinces of Papua New Guinea.

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Figure 1. The island of New Guinea and location of sites mentioned in the text.

agricultural development. Today, these intermontane valleys have been substantially transformed through human activities associated with agriculture, leading to the original organic-rich soils and swamp forest cover being replaced by organic-depleted soils supporting grasslands (figure 4).

While swamp forests persist in the intermontane valleys, today the community is restricted to small patches that fringe the grass or sedge peat swamps of the valley floors (Paijmans 1976). Most swamp forest trees grow on hummocks separated by pools of water, creating a sparse or open canopy with dense layer of small trees and shrubs (figure 5). The common trees include Syzygium and other Myrtaceae, conifers (especially Dacrydium and Podocarpus), Pandanus and Nothofagus. Pandanus are often dominant as their stilt roots are ideally suited to an ever-wet soil environment. The conifers (e.g. Dacrydium nidulum) are also an important component in disturbed swamp forests where they form dominant stands in early stages of swamp forest recovery towards a diverse mixed swamp forest assemblage (Johns 1980). These swamp forests are assumed to represent the remnants of a once much more extensive forest community that covered the wet peaty soils of the intermontane valley floors. Here, I review the palaeoecological evidence from five major intermontane valleys in New Guinea (figure 1) and use two measures of past biodiversity to address the following questions:

- (i) Are the present day swamp forests remnants of a once much more extensive forest community?
- (ii) How rapidly did the transformation from swamp forest to grassland occur and was the change ubiquitous in time and space?

- (iii) What influence did anthropogenic fires and forest clearance activities have upon shaping the present day landscape?
- (iv) What has been the overall impact on biodiversity and are there key taxa now missing as a result of past human activities?
- (v) What were the consequences of biodiversity loss for human populations in the highlands during the Mid–Late Holocene?

2. METHODOLOGY AND STUDY SITES

(a) Measures of biodiversity through time using palaeoecological techniques

Estimating the diversity of past vegetation communities from pollen data is potentially a powerful tool to measure plant biodiversity through time. One approach is to use simple counts of pollen types in a sample as an estimate of diversity, though this requires a standardized or constant count size as the number of pollen types increases as the pollen count increases (Bennett & Willis 2001). The calculation of palynological richness was developed by Birks & Line (1992) as a way of standardizing the pollen count between samples and thus allowing comparisons within a pollen sequence. However, the taxonomic uncertainties associated with pollen morphological types means that species diversity may change but not be registered in pollen morphological type change (e.g. changes in Poaceae species are generally not visible in the pollen record), resulting in a potential underestimate of biodiversity change.

A second approach is to target key biodiversity indicator taxa in the pollen record, where these taxa (or taxon) are representative of a distinct diverse vegetation community of interest through time. The montane swamp forests of New Guinea are readily identified in the pollen records by high percentage representation in the pollen assemblage of Myrtaceae (mainly *Syzygium*), *Dacrydium* and *Pandanus* (Haberle 1998*b*). The assumption here is that a loss or reduction of all or part of these key indicators from the pollen record is indicative of a loss or reduction in the extent of the associated vegetation community and therefore a loss in local biodiversity. A major uncertainty in this approach is the temporal constancy of the association between the key indicator types and their vegetation community which could lead to a potential overestimate of biodiversity change.

(b) Study sites

The island of New Guinea lies within the humid tropics and is strongly influenced by seasonal fluctuations of the major equatorial circulation patterns. During the austral winter, New Guinea is under the influence of deep tropical easterly air flow (southeast trade winds), while during the austral summer monsoon, equatorial north-westerlies dominate. Throughout the year, the region is a locus of airstream convergence known as the intertropical convergence zone (ITCZ) and, as a result, is one of the most persistently cloudy regions around the equator (McAlpine et al. 1983). Circulation patterns over the region are strongly affected by the Southern Oscillation, though the influence is strongest during the pre-monsoon from September to November (McBride 1999). The severity of the 1997–1998 El Niño event was brought about by an anomalous eastwards displacement of the ITCZ from over the maritime continent towards the central Pacific and a subsequent failure of the austral summer monsoon (Webster et al. 1998).

The large highland valleys with complex agriculture based on root cropping centred on the altitudes of 1400–1850 m were a major discovery of the twentieth century (Brookfield 1964). The outer flanks of the mountains are perhumid, with precipitation more than double evaporation in almost all months. In the highland or intermontane valleys, the mountains cut off the orographic rain and local circulations dominate in most seasons. Here, air rises each day up the warmed slopes and descends over the valley, giving sunny conditions with adequate rainfall from afternoon thunderstorms. Away from the large highland basins, even small valleys may have this effect and may thus support small hamlets. In these marginal settlements, techniques of ditching and mounding are used to shed water from the fields. There is a northwest-southeast gradient from aseasonal precipitation to the appearance of a weakly defined dry season, and from relatively infertile limestones and mudstones in West Papua to richer soils fertilized by volcanic ash falls in Papua New Guinea east of the Strickland River (Hope & Haberle 2005).

Despite the present day restriction of forested areas to the surrounding mountainous slopes and degraded patches on highland valley floors, the structure and composition of lower montane forest found between 800 and 2200 m altitude is highly variable with the common canopy trees including *Castanopsis*,

Nothofagus, Elaeocarpus, Beilschmiedia, Melastomataceae, *Phyllocladus* and the emergent gymnosperms Araucaria hunsteinii and Araucaria cunninghamii. Nothofagus is found as a scattered element of mixed lower montane forest, though it commonly forms a continuous forest between 2200 and 2700 m, possibly in response to persistent cloud cover and infrequent but large-scale disturbance (Read & Hope 1996). Grasslands resulting from anthropogenic activity have replaced much of the lower montane forests throughout the major highland valleys, with Leersia and Phragmites common in wetter areas and the tall Miscanthus floridulus common in areas experiencing more aseasonal precipitation. Where precipitation has a more pronounced seasonality and fires are more frequent, particularly in the east, the short Imperata grassland communities are dominant. Using the two biodiversity indices discussed above (palynological richness and key biodiversity indicator taxa) as a means of tracking changes in biodiversity through time, selected pollen records from five highland valley floors where intensive agriculture is practised today are examined (figure 1).

3. SWAMP FOREST LOSS DURING THE HOLOCENE IN NEW GUINEA

Pollen records from New Guinea spanning the Late Glacial to Holocene period show that vegetation, at least within montane and alpine regions, has a remarkable ability to track climate change (Hope 1976; Haberle 2003b). In highland valleys where human settlement and deforestation are prominent features of the contemporary landscape, palaeoecological records are generally not continuous, perhaps due to anthropogenic-related disturbance and lack of detailed chronological control. One exception to this is the Tari Basin record which is the longest and most continuous record from the island of New Guinea (Haberle 1998b). Despite these problems, five sites have been selected from highland valleys extending from the central ranges of Irian Jaya to the eastern highlands of Papua New Guinea, representing the general nature of vegetation change through the Holocene. A summary diagram (figure 2) is presented for each site that includes the relative proportions of forest trees, swamp forest (Myrtaceae), a disturbance and arboriculture indicator (Casuarina), and charcoal particle concentration as an indicator of fire. The *Casuarina* pollen type is most probably associated with *Casuarina oligodon* which is a nitrogen fixing tree that is commonly planted by people throughout the highlands and used for multiple purposes (house/fencing material, crop shade, fallow tree, etc.). Loss of local forest cover is believed to have led to the adoption of agroforestry techniques to compensate for loss of forest resources (Haberle 1998a).

(a) Baliem Valley

The western-most site in the transect is Kelela Swamp at 1400 m altitude in the Baliem Valley (Haberle *et al.* 1991), which has a long, possibly discontinuous, pollen record dating back to some time before 7000 yr BP. In the earliest phase, regional forest cover was dominated



Figure 2. Summary of major changes in pollen records from five highland valleys during the Late Glacial transition and through the Holocene. The four graphs show arboreal taxa, swamp Myrtaceae (dominantly *Syzygium*), *Casuarina* pollen percentages (of total pollen sum excluding aquatics) and charcoal density (500 years interpolated sample interval, note different *y*-axis scales).

by mixed *Castanopsis/Lithocarpus* forest in the valley. Accession of clays and silts to the site was followed by evidence for widespread forest disturbance, burning and Myrtaceae–*Pandanus* swamp forest clearance by around 7000 yr BP. After this, forest clearance and burning continued with only minor reversals through to 3000 yr BP, when extensive grassland areas were established. There is a marked rise in *Casuarina* pollen around 1100 yr BP, suggesting that deliberate planting of this tree may have become important at this time.

(b) Ifitaman Valley

The township of Telefomin lies in the Ifitaman Valley at an altitude of around 1500 m. In contrast to the Baliem Valley, Nothofagus-rich forest remains a relatively important forest element throughout the 20 000-year pollen record, despite the relatively low elevation (Hope 1983). Around 12 000 yr BP, regional warming produced a shift in forest composition to a more mixed Nothofagus forest, with only a slight rise in Castanopsis/ Lithocarpus. The Telefomin pollen record shows a major disturbance event between 11 500 and 8500 yr BP, which is possibly discontinuous (inferred from Hope 1983; figure 3), and is interpreted as anthropogenic burning and local forest clearance followed by abandonment and reestablishment of primary forest. Another period of disturbance occurs only after 4500 yr BP, when grassland expands rapidly to its present extent, and forest and Myrtaceae swamp forest are cleared from the site. Casuarina appears to be grown in the valley only after 1000 yr BP, in line with the evidence from the Tari Basin and the Baliem Valley. However, unlike these two regions, the extensive grasslands around Telefomin today are rarely used for agricultural purposes and are infrequently burnt.

(c) The Tari Basin

Haeapugua lies at an altitude of 1650 m in the Tari Basin and is the only published continuous pollen record from the highlands of New Guinea that spans at least 30 000 yr BP to the present (Haberle 1998b). The record shows that the montane tree *Nothofagus* is important throughout the record, though other trees, including *Castanopsis/ Lithocarpus*, Myrtaceae, *Dacrydium* and *Pandanus*, attain dominance at different times. The Early Holocene is marked by the development of swamp forest vegetation and a peak in the pollen diversity. This is maintained until around 3000 yr BP when there are indications of swamp forest disturbance, a decline in the pollen diversity and the key indicator taxa, followed by swamp forest clearance commencing around 1700 yr BP.

(d) Jimi Valley

Nurenk Swamp (Gillieson *et al.* 1989) lies at an altitude of 1900 m in the Jimi Valley and shows that a Myrtaceae swamp forest existed around the site prior to 3500 yr BP. Possible watertable changes, tephra-fall events and human activity may have disturbed the site and resulted in the loss of swamp forest cover. Forest disturbance continues until 300–400 yr BP when increased burning and a rise in *Casuarina* pollen indicated a strong human influence on the site.

(e) Kainantu Valley

Norikori Swamp (Haberle 1996) lies at an altitude of 1750 m in the Kainantu Valley and shows that a Myrtaceae–*Pandanus* swamp forest existed on the site for an undetermined time before 5000 yr BP. Disturbance of forest and clearance is already evident by the time Holocene sedimentation begins around 5000 yr BP. Features purported to be fossil agricultural structures in the nearby Arona Valley are dated to around 4500 yr BP and are associated with pollen assemblages representing deforested conditions (Golson & Gardner 1990; Haberle 1996). Forest clearance and burning continue gradually until 1500 yr BP when rapid vegetation change towards an extensive grassland landscape, similar to the present, occurs. *Casuarina* begins to increase around 600 yr BP.

4. PALYNOLOGICAL RICHNESS AS AN INDICATOR OF BIODIVERSITY LOSS IN SWAMP FORESTS DURING THE HOLOCENE

Palynological richness and the presence of key indicator taxa are used to develop an understanding of biodiversity change through time in the Tari Basin, the one site in the highland valleys that has a continuous record over at least 30 000 years (Haberle 1998*b*). The pollen diagram (figure 3) and a summary



Table 1. Description of pollen zones from the Haeapugua record (figure 3), Tari Basin, Papua New Guinea. (Palynological richness provides a comparative estimate of the expected number of taxa in each sample and is determined by rarefaction analysis (Birks & Line 1992). *Key indicators of swamp forest biodiversity are Myrtaceae, *Dacrydium* and *Pandanus*.)

pollen zone description	palynological richness	key indicators*
zone H3 (>30 000–18 000 yr BP)	low to high	present
Nothofagus-rich montane forest on valley floor	-	-
zone H4 (18 000–8500 yr BP)	low	present
Grassland dominates with high fire incidence followed by an expansion of mixed montane forest taxa after 14 500 yr BP		-
zone H5 (8500–1700 yr BP)	high	dominant
Mixed montane swamp forest dominated by Myrtaceae until around 3000 yr BP when increased disturbance of swamp forest leads to increased dominance of <i>Dacrydium</i> and <i>Pandanus</i>		
zone H6 (1700 yr BP to the present)	low	declining
Grass and sedge dominated swampland with loss of swamp forest taxa resulting from burning and the initiation of artificial drainage of section of the swamp near the site for agricultural purposes. The increased abundance of <i>Casuarina</i> after 900 yr BP may reflect deliberate planting in nearby gardens		

of the pollen zone interpretations are given in table 1. Palynological richness analysis shows that there has been considerable change in pollen-type diversity over at least the past 30 000 years coinciding with major changes in vegetation in this region. Prior to the Last Glacial Maximum, the basin floor is forested with a diverse mosaic of Nothofagus-rich montane forest and mixed swamp forest in the wetter areas and palynological richness is high. At around the time of the Last Glacial Maximum, grassland is established under the influence of increased burning which is considered to be the consequence of climate change as well as the arrival of humans in the region. Between 18 000 and 9000 yr BP, burning is sufficient to maintain grasslands in the valley floors and while forest is present in the valley the overall diversity is low as are the key indicators of biodiversity. The Early Holocene is marked by the development of swamp forest vegetation and a peak in both the key indicator types and the pollen diversity. This is maintained until around 3000 yr BP when there are indications of swamp forest disturbance, a decline in the pollen diversity and the key indicator taxa, followed by swamp forest clearance commencing around 1700 yr BP (figures 4 and 5).

In the Haeapugua record, lower palynological richness generally coincides with the establishment of open vegetation on the site, which may be explained by a true loss of overall plant diversity from the site or it may reflect the lower pollen taxonomic resolution available from grasslands relative to forests. While there is no evidence to support or deny the latter assertion, this may serve as a cautionary note for interpretation of palynological richness as an indicator of biodiversity. What is certain is that forest biodiversity is reduced through the retreat or total loss of forests from the site. Currently, Haeapugua Swamp does not support any swamp forest, though remnant swamp forest patches survive in other parts of the Tari Basin. The extirpation of swamp forest from the Haeapugua catchment is indicative of a much wider phenomenon evident through an examination of the key pollen indicators of swamp forest from the five major valleys where local swamp forest loss outstrips the overall

forest loss under pressure from increased burning and forest clearance activity for agriculture (figure 2). In the Haeapugua record, the combination of both indicators of biodiversity provides a useful insight into the relationship between vegetation community change and biodiversity change. The coincidence in loss of swamp Myrtaceae with lower palynological richness between approximately 18 000 and 14 500 yr BP and after 3000 yr BP to the present provides a strong argument for true biodiversity loss at the site as the former tends to overestimate biodiversity change and the latter underestimates biodiversity change. In contrast, the phases of vegetation change prior to 18 000 yr BP show a lack of consistency between the two indicators in table 1. The low palynological richness values associated with forest cover that included swamp forest indicators during the earliest phase (prior to around 27 500 yr BP; figure 3) in the record may point to a shift in relative dominance of tree species cover (particularly Nothofagus). In this case, swamp forest dynamics driven by disturbance factors or climate change may have led to greater dominance of a single taxonomic group and a perceived loss of diversity at the site.

5. DISCUSSION

(a) Are the present day swamp forests remnants of a once much more extensive forest community?

Palaeoecological records from the five major highland valleys examined in New Guinea point to a sustained and gradual intensification of forest clearance and burning from at least 7000 yr BP that led to the loss of swamp forest cover at different times. This process is widespread across the highlands and within the valleys as well. The loss of swamp forest cover reflected in the Haeapugua record is not simply restricted to the local swamp environment. Buried wood in peat sections recorded throughout the basin attest to a much more widespread phenomenon in the Tari Basin (Haberle 1998*b*), though the variability in the timing of these changes in one single valley has yet to be determined.



Figure 4. Remnant swamp forest on the valley floor surrounded by anthropogenic grasslands south of the Kainantu Valley, Papua New Guinea.

The composition of swamp forests that covered these valley floors is similar across the highlands, with all pollen records that contain pollen assemblages from the Early Holocene depicting a mixed montane swamp forest with Myrtaceae (mostly Syzygium), Pandanus and to a lesser extent Dacrydium, dominating the forest taxa assemblage. The dominance of the latter two taxa appears to be determined by increased frequencies of disturbance that may have impacted upon the ecosystem through natural processes (climate, competition) or human impact (selective exploitation of useful plant species, fire). What is clear from this analysis is that the present day swamp forests are remnants of a once much more extensive forest community.

(b) How rapidly did the transformation from swamp forest to grassland occur and was the change ubiquitous in time and space?

The pace at which this change took place appears to vary from as much as around 1500 years in the Baliem Valley to less than 500 years in the Kainantu Valley (figure 2). A comparison of the timing of swamp forest loss between the five valley records in figure 2 shows that at this scale the loss is neither strictly time transgressive nor is it synchronous along the transect. This is not consistent with what might be expected under a 'Neolithic Transition' model where diffusion of agricultural techniques and crops may have been rapid and the impacts widespread. Nor is it consistent with a climate change model in which a shift to more frequent and intense El Niño-related drought events around 4500 yr BP (Gagan et al. 2004) may have contributed to increased disturbance, burning and water loss which could have led to widespread loss of swamp forest cover after this time. A more complex model of landscape history is suggested by the palaeoecological results for swamp forest loss in which an increased focus on wetland agriculture during the Mid-Late Holocene (Denham et al. 2004), perhaps in combination with ongoing climate changes, led to rapid clearance of the swamp forest type at different times across the highlands.



Figure 5. *Pandanus* and conifer (*Dacrydium* and *Araucaria*) dominated swamp forest in the Erave District of the Southern Highlands, Papua New Guinea.

(c) What influence did anthropogenic fires and forest clearance activities have upon shaping the present day landscape?

While the timing and nature of these changes can be identified, the reason for these changes at different times is not clear. Part of the reason may lie in the relative intensity of exploitation of each site and its vulnerability to the external forces of change. These forces may have included direct forest clearance or alteration of the forest disturbance regime, perhaps through selective forest clearance practices, burning activity or climate change. For example, a shift in fire regimes may be human or climate driven. Climate changes are generally considered to be relatively minor during the past 10 000 years, though it has been suggested that the impact of short-term climate variability, such as increased drought stress and fire associated with El Niño-Southern Oscillation (ENSO) events, has had a significant influence on vegetation dynamics in the New Guinea region over the past five millennia (Haberle & Chepstow-Lusty 2000; Haberle et al. 2001). This has been supported further by records showing landscape destabilization from the South American coast (Sandweiss et al. 1996) and increased disturbance of vegetation in Australia (Shulmeister & Lees 1995) between 5000 and 4000 years ago. Neoglacial advances of highland glaciers during the past 3500 years have been reported by Hope & Peterson (1976), suggesting that minor temperature fluctuations were probably experienced in the occupied valleys.

Recent studies have shown that, under increasing pressures from external forces of change, ecosystems are vulnerable to loss of resilience which may lead to switches to alternative states with consequential species losses (Molinari et al. 2005). In the Tari Basin example (figure 3), the swamp forest appears to have responded to an increase in fire-related disturbance after 3000 yr BP with a shift from Myrtaceae to Dacrydium-Pandanus dominated swamp forest. The reason for the final loss of forest cover and its replacement by grass-sedge swampland by 1700 yr BP may have been direct clearance or a switch to an alternate state under continued high fire-related disturbance frequencies. Either way, human activity appears to be the primary driver of ecosystem change, though it remains difficult to exclude the possibility that El Niño-related climate change may have played a partial role in enhancing the rate of swamp forest loss during the Mid-Late Holocene.

(d) What has been the overall impact on biodiversity and are there key taxa now missing as a result of past human activities?

None of the pollen records from New Guinea indicates an extinction event in the swamp forest plant community as a result of past human activities. What is evident is that widespread extirpation of diverse swamp forest communities has occurred at different times over the past 7000 yr BP. The implications for vulnerability to extinction of the plant and animal species within swamp forest communities are the same as for any species whose spatial distribution is reduced through human activity: the vulnerability to extinction may increase with fragmentation and aerial reduction of the community. The current lack of knowledge about the nature of species diversity within swamp forests of the highlands also hinders any definitive measure of potential extinction. However, given the extremely high diversity and local endemism in families such as the Orchidaceae, it may be reasonable to assume that loss of swamp forest habitat in a single

valley may have led to extinctions in a number of plant species that are not registered in the pollen records.

Extinctions in the animal kingdom have been recorded in the highlands of New Guinea during the past 50 000 years. Fossil fauna have been recovered from swamp forest sites in the Tari Basin and elsewhere in New Guinea. The now extinct large forest-browsing mammal group known as *Hulitherium tomasettii* is believed to have browsed within swamp forest environments and may have been a target for early human hunting, which is considered the primary cause of their extinction during the Last Glacial Period (Menzies & Ballard 1994).

(e) What were the consequences of biodiversity loss for human populations in the highlands during the Mid-Late Holocene?

The story of agricultural development in the highlands of New Guinea is one of the continued indigenous innovation in agricultural techniques in the face of increased land degradation and climate change (Haberle & David 2004). The adoption of Casuarina agroforestry techniques around 1200 years ago as a strategy to alleviate the local loss of forest resources previously available in swamp forests is an example (figure 2). Furthermore, Bayliss-Smith & Golson (1992) believe that the widespread planting of Casuarina facilitated the rehabilitation of soils after gardening through nitrogen fixation, its use for firewood and building material and the elimination of taro beetle infestation in gardens where it was planted, and that this practice was successful enough in the dryland for labour-intensive wetland cultivation and swamp forest clearance to be reduced or given up. Bourke (1997) cautions placing too much emphasis on the importance of Casuarina tree-fallowing alone throughout the highlands and suggests that the initial rise in Casuarina pollen may have been related to people planting Casuarina trees in and near villages to provide timber as supplies became scarce with the continued clearance of forests. Either way, the innovation of planting of utilitarian forest products close to settlements would have reduced the need for further primary forest clearance and perhaps reduced further biodiversity loss.

The remaining highland swamp forests should be considered as a conservation priority as their current relict distribution within densely populated valley floors makes them an extremely vulnerable plant community. Part of this conservation effort has been underway in the indigenous community as some swamp forest patches are conserved as significant sacred sites by land owners. Although agrarian populations in the highlands of Papua New Guinea have almost doubled over the past 25 years, the area of agricultural land has expanded by only 11% (MacAlpine & Freyne 2001). This implies ongoing intensification of existing agricultural areas through the incorporation of new crop species and agricultural techniques. While this is a positive indication of potential buffers for forest resource management, ongoing population increases will lead to further pressures to clear forested land and particularly valley floor swamp forests. The impacts of continued intensification on land degradation and the long-term sustainability of relict forest communities have yet to be realized.

6. CONCLUSIONS

An evaluation of the change in biodiversity of forest habitats through the Late Glacial transition to the present in five palaeoecological sites from highland valleys in New Guinea, where intensive agriculture is practised today, has shown that people have had a significant impact on forest community composition, function and diversity over many thousands of years. The palaeoecological record of vegetation change can provide a deeper time perspective on the relative vulnerability of any given vegetation community to external forces that may result in biodiversity change. Consideration of long-term (1000-100 000 years) as well as short-term (10-100 years) time-scales should be incorporated into biodiversity planning. The conservation of relict forest communities most at risk from recent agricultural intensification will require an integrated approach between current land owners, government, conservation biologists and ecologists with an understanding of long-term biodiversity change.

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