Impact of a drier Early–Mid-Holocene climate upon Amazonian forests

Francis E. Mayle* and Mitchell J. Power

School of GeoSciences, University of Edinburgh, Drummond Street, Edinburgh EH8 9XP, UK

This paper uses a palaeoecological approach to examine the impact of drier climatic conditions of the Early–Mid-Holocene (ca 8000–4000 years ago) upon Amazonia's forests and their fire regimes. Palaeovegetation (pollen data) and palaeofire (charcoal) records are synthesized from 20 sites within the present tropical forest biome, and the underlying causes of any emergent patterns or changes are explored by reference to independent palaeoclimate data and present-day patterns of precipitation, forest cover and fire activity across Amazonia. During the Early–Mid-Holocene, Andean cloud forest taxa were replaced by lowland tree taxa as the cloud base rose while lowland ecotonal areas, which are presently covered by evergreen rainforest, were instead dominated by savannahs and/or semi-deciduous dry forests. Elsewhere in the Amazon Basin there is considerable spatial and temporal variation in patterns of vegetation disturbance and fire, which probably reflects the complex heterogeneous patterns in precipitation and seasonality across the basin, and the interactions between climate change, drought- and fire susceptibility of the forests, and Palaeo-Indian land use. Our analysis shows that the forest biome in most parts of Amazonia appears to have been remarkably resilient to climatic conditions significantly drier than those of today, despite widespread evidence of forest burning. Only in ecotonal areas is there evidence of biome replacement in the Holocene. From this palaeoecological perspective, we argue against the Amazon forest ‘dieback’ scenario simulated for the future.

Keywords: Amazon tropical forest; pollen; charcoal; fire; Holocene; climate

1. INTRODUCTION

Understanding the direction and magnitude of climate change in Amazonia over the twenty-first century, and its impact upon Amazonian forests, constitutes a major international research effort that reflects the global importance of the Amazon forest biome and its associated climatic and hydrological systems (e.g. Malhi & Phillips 2004). The trend of rising temperatures in Amazonia (0.25°C per decade) measured over recent decades (Malhi & Wright 2004) is likely to continue, with a projected increase of 3.3°C this century under mid-range greenhouse gas emission scenarios, although this could be much higher (up to 8°C) under scenarios of widespread forest dieback (Betts et al. 2004; Christensen et al. 2007). However, trends of future precipitation change across Amazonia are much less clear, with the magnitude and direction of change depending on the climate model employed (e.g. whether or not ecosystem–climate feedbacks are included), the region of Amazonia considered and the timing of precipitation reduction (e.g. dry versus wet season; Bush & Silman 2004; Christensen et al. 2007; Malhi et al. 2008). The most alarming and controversial model result is the ‘Amazon dieback’ scenario by Cox et al. (2000) whereby positive feedbacks between increased forest dieback and increased aridity lead to a parched Amazon Basin completely denuded of forest by the end of the twenty-first century. This extreme scenario lies at one end of the range of hypothetical outcomes, the other being accelerated tree growth under conditions of enhanced fertilization due to higher CO2 levels (Lewis et al. 2004). Given the global implications of a deforested versus forested Amazon Basin, it is an urgent priority to better understand how its forests are likely to respond to drier climatic conditions.

Here, we address this issue by using a palaeoecological approach to examine how Amazonia’s forests were affected by climatic conditions of the Early–Mid-Holocene (approx. 8000–4000 years BP (calendar years before present)) when major lake-level low-stands point to a significantly drier climate than today. We also consider how fire regimes (defined here as changes in charcoal abundance) may have changed throughout the Holocene, given that drier climates would be expected to promote increased fire, either directly due to drier soils and reduced humidity or indirectly by favouring more flammable ecosystems (e.g. savannahs). If past fire activity is found to be unrelated to climatic conditions or vegetation flammability, then this would be indicative of anthropogenic, rather than natural, burning.

2. MATERIAL AND METHODS

We discuss a selection of previously published sites from tropical South America, which show strong evidence for precipitation change throughout the Holocene, all of which come from the tropical Andes (figures 1 and 2). We then synthesize previously published palaeovegetation (pollen...
Figure 1. Maps showing site locations, distribution of forest types, tree cover, precipitation patterns and fire regime across the Amazon Basin. Amazonian forests are delimited by a solid black boundary line, which encompasses not only humid evergreen rainforests in the lowland basin and Guyana Shield but also semi-deciduous Chiquitano dry forests in the south and all forest types on the eastern flank of the Andes. WORLDCLIM bioclimatic variables (Hijmans et al. 2005) of (a) annual precipitation and (b) precipitation of the driest quarter (driest three months) characterize present-day climatic variability across the Amazon. (c) Ecoregions (Olson et al. 2001) are shown for all forested areas. (d) The per cent tree cover map (Defries et al. 2000) illustrates the relative forest cover (available biomass) across the Amazon. (e) Simulated variations in historical (twentieth century) fire return intervals across the Amazon using LPJ-DGVM (Thonicke et al. 2001). Palaeovegetation and charcoal sites are shown by white circles; palaeoclimate sites are shown by white crosses.

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data) and palaeofire (charcoal) records from sites across the Amazon Basin (including the eastern flank of the Andes) that occur within the present tropical forest biome (including ecotonal savannah gallery forests) and show their locations with respect to present-day forest types (ecoregions; Olson et al. 2001), tree cover (Defries et al. 2000), precipitation regimes (Hijmans et al. 2005) and fire return interval (Thonicke et al. 2001; figure 1). Only those sites with reliable chronologies and continuous records spanning most of the Holocene (figure 3) are considered. We use the authors’ age–depth model from their published paper and, for sites without such a model, we produce our own based on linear interpolation between dates. Radiocarbon ages were calibrated into calendar years before present (BP) using the calibration curve by Fairbanks et al. (2005). The pollen records are summarized as simple schematic cartoons depicting significant biome shifts or compositional changes (figure 4). Raw charcoal data are presented alongside these vegetation records and are derived from the recently compiled, and publicly available, Global Charcoal Database (Power et al. in press; http://www.bridge.bris.ac.uk/projects/QUEST_IGBP_Glob_Palaeofire_WG). Site metadata are shown in table 1.

3. RESULTS AND DISCUSSION

(a) Holocene precipitation changes

There is widespread evidence that during the Early–Mid-Holocene (approx. 8000–4000 years BP) climatic conditions in the tropical Andes were significantly drier than present. Evidence comes from a variety of proxies (figure 2), e.g. peak dust concentrations and snow accumulation minima in Andean ice cores (Thompson et al. 1998), oxygen isotope ratios in lacustrine calcite (Seltzer et al. 2000) and, most convincingly, diatom, geochemical and seismic evidence for lake-level low-stands, particularly in Lake Titicaca (e.g. Baker et al. 2001) where lake-level dropped to 100 m below present between 6000 and 5000 years BP.

Given the complex spatial heterogeneity of precipitation patterns across Amazonia today (figure 1a,b), and the vast size of this region, it is unsurprising that the timing of these Holocene precipitation maxima and minima differs significantly among these records. Tropical Southern Hemisphere lake-level low-stands occur progressively later in the Holocene with increasing latitude (Abbott et al. 2003; Bush et al. 2005). For example, driest climatic conditions at Lake Junin (11°S), Lake Titicaca (14–17°S) and Sajama Mountain (18°S) were centred ca 10 000, 5500 and 4000 years BP, respectively (figure 2). This latitudinal, time-transgressive pattern points to the 20 000-year precession orbital cycle (Berger 1992) as the dominant driver of Holocene climate change (considered at multi-millennial scale), causing progressively greater austral summer insolation (and hence more southerly penetration of a stronger summer monsoon) throughout the Holocene.

Although the sites yielding these climate records occur in the tropical high Andes, they are relevant for this study because they receive most of their precipitation from the Amazon lowlands and, ultimately, the Atlantic Ocean (Nobre & Shukla 1996).
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(i) Lowland sites

The impact of the drier conditions of the Early–Mid-Holocene upon tropical forests varied across the Amazon Basin (figure 4), and, as expected, the magnitude of impact is inversely correlated with mean annual precipitation (figure 1a) and positively correlated with the length and severity of the dry season (figure 1b), and proximity to ecotones (figure 1c,d,e).

The greatest impact is evident at sites at the ecotonal margins of the basin where the dry season is longest and most severe (figure 1b). At Carajas (eastern Amazon ecotone), this reduction in precipitation caused replacement of forest by open savannah between ca 8900 and 4460 years BP, which in turn gave way to forest again when precipitation increased once more in the Late Holocene (figure 4; Absy et al. 1991; Sifeddine et al. 2001). Laguna Bella Vista and Laguna Chaplin lie at the southern Amazon ecotone within highly seasonal evergreen rainforest and are only 130 and 30 km, respectively, from semi-deciduous dry forests and savannahs to the south and east (figure 1c). Throughout most of the Holocene, these sites were dominated by a dry forest/savannah mosaic (figure 4; Mayle et al. 2000; Burbridge et al. 2004) when the climate was drier than today. Humid evergreen rainforests expanded to dominate the lake catchments only in the last two millennia, once precipitation had approached modern levels (reflected by rising water levels in Lake Titicaca following the Mid-Holocene low-stand). Similar biome shifts occurred at the northern Amazon ecotone, whereby gallery forests expanded within the Colombian llanos savannas (Lagunas Loma Linda and Chenevo) (figure 4; Behling & Hooghiemstra 2000; Berrio et al. 2002a,b). However, the onset of forest expansion in response to increased precipitation at these northern sites (6910 and 7750 years BP, respectively) occurred significantly earlier than in southern Amazonia, consistent with the latitudinal time-transgressive precipitation changes identified in Andean lake-level records discussed earlier.

Interestingly, the Parker and Gentry sites of southern Amazonia (Bush et al. 2007a,b) are within 200 km of the Beni savannahs of northern Bolivia (figure 1c) and yet the surrounding tropical forests have experienced little change over the past 6000–7000 years (figure 4). However, this is perhaps unsurprising when one considers that these Peruvian forests receive more precipitation than those further south near the southern margin of Amazonia (figure 1a,b), and, crucially, the Beni savannahs are not climatically controlled but are instead a function of edaphic and hydrological conditions that are unfavourable to woody plants (Mayle et al. 2007).

The cluster of five sites in eastern Amazonia (Sarucuri, Santa Maria, Comprida, Geral and Tapajos; figure 1) all show signs of forest disturbance, revealed by substantial peaks in pollen (30–40%) of the weed tree Cecropia (figure 4; Bush et al. 2000, 2007b; Irion et al. 2006). This region presently experiences a
significant dry season (figure 1b), which conceivably was longer and more severe earlier in the Holocene (if the Andean climate records are representative of the eastern Amazon). It is possible that increased severity and/or frequency of droughts led to greater tree mortality and hence more forest gaps, leading to a greater proportion of the forest in an early successional (i.e. Cecropia-dominated) state (Weng et al. 2002). However, as Weng et al. acknowledge, it is hard to envisage such a mechanism producing a Cecropia-dominated forest lasting several centuries or millennia, as one would expect that the short-lived, early pioneer, Cecropia trees would be rapidly out-competed by more drought-adapted (e.g. semi-deciduous) and longer-lived tree taxa. Furthermore, the marked variability in timing of this Cecropia phase among this tight cluster of sites does not fit with a regional climatic forcing and instead points to a non-climatic cause for this forest disturbance (e.g. humans) for at least some of the sites (see below).

Two riverine sites (Curuá and Calado), tributaries close to the main Amazon River channel (figure 1c), show a change from terra firme forests to predominantly varzea–igapó (seasonally flooded) forests in the Late Holocene (figure 4), consistent with higher flood levels of the Amazon River, although the extent to which this was caused by increasing precipitation and/or rising sea levels is unclear (Behling & da Costa 2000; Behling et al. 2001).

Lake Pata and Maxus-4 occur in the wettest part of the Amazon Basin (figure 1a,b), and each exhibits floristic changes during the Mid-Holocene, coincident with peak aridity in the high Andes. The Lake Pata pollen record has previously been interpreted by the site investigators (Colinvaux et al. 1996; Bush et al. 2002, 2004a) as indicative of a closed-canopy forest, throughout not only the Holocene, but also the last glacial–interglacial cycle. However, a close inspection of the Holocene sequence reveals a distinct pollen assemblage zone, centred ca 6000–7000 years BP, characterized by peaks in the herbs Borreria and Poaceae and the Mauritia palm, as well as the almost complete disappearance of Moraceae/Urticaceae pollen (figure 4; Bush et al. 2004a). Considered as a whole, this pollen assemblage is suggestive of a change from a closed-canopy forest to a forest/woodland sufficiently open to support a herbaceous understorey, consistent with a response to reduced precipitation. The latter is corroborated by geochemical evidence.

Figure 4. Palaeovegetation records, based upon previously published pollen data (see table 1 for site metadata), are presented in schematic cartoon form to illustrate the dominant changes (or lack thereof) in biome, forest type and/or species composition, in such a way as to illustrate the key vegetation responses and optimize inter-site comparisons. Site groupings are as follows: (a) lowland ecotonal sites, (b) southern sites, (c) eastern sites, (d) western and central sites and (e) Andean sites. Raw charcoal data are presented, which were obtained from the Global Charcoal Database (Power et al. in press; http://www.bridge.bris.ac.uk/projects/QUEST_IGBP_Globeal_Paleofire_WG). Asterisks denote horizons where charcoal was recorded, but not quantified. Where no charcoal is shown for a site, this is because either charcoal was searched for but none was found (Consuelo and Pata) or charcoal was not searched for (Loma Linda, Chenevo, Maxus-4 and Calado).
### Table 1. Site metadata.

| Site name         | Latitude  | Longitude | Elevation (m) | Country | Local vegetation          | Ecoregion                      | Investigator                      |
|-------------------|-----------|-----------|---------------|---------|---------------------------|-------------------------------|-----------------------------------|
| **Palaeoclimate records** |           |           |               |         |                           |                               |                                   |
| Junin             | 11.0000   | -75.0000  | 5700          | Peru    |                           | Peruvian Yungas                | Seltzer et al. (2000)            |
| Titicaca          | -16.1344  | -69.1553  | 3810          | Bolivia/Peru |                           | Central Andean wet puna         | Baker et al. (2001)              |
| Sajama ice cap    | -18.1000  | -68.8833  | 6542          | Bolivia |                           | Central Andean dry puna         | Thompson et al. (1998)           |
| **Palaeovegetation records** |           |           |               |         |                           |                               |                                   |
| Chaplin           | -14.4667  | -61.0667  | 200           | Bolivia | humid rainforest           | Madeira–Tapajós moist forests | Mayle et al. (2000) and Burbridge et al. (2004) |
| Bella Vista       | -13.6167  | -61.5500  | 190           | Bolivia | humid rainforest           | Madeira–Tapajós moist forests | Mayle et al. (2000) and Burbridge et al. (2004) |
| Carajas           | -6.5833   | -49.5000  | 750           | Brazil  | humid rainforest/savannah  | Xingu–Tocantins–Araguaia moist forests | Absy et al. (1991) and Sifeddine et al. (2001) |
| Loma Linda        | 3.3000    | -73.3833  | 310           | Colombia| gallery forest/savannah   | Apure–Villavicencio dry forests | Behling & Hooghiemstra (2000)    |
| **Lowland ecotonal sites** |           |           |               |         |                           |                               |                                   |
| Chenevo           | 4.0833    | -70.3500  | 150           | Colombia| gallery forest/savannah   | Negro–Branco moist forests     | Berrio et al. (2002)             |
| **Northern sites** |           |           |               |         |                           |                               |                                   |
| Parker            | -12.1406  | -69.0215  | 276           | Peru    | humid rainforest           | Southwest Amazon moist forests | Bush et al. (2007a)              |
| Gentry            | -12.1773  | -69.0977  | 258           | Peru    | humid rainforest           | Southwest Amazon moist forests | Bush et al. (2007a)              |
| **Eastern sites**  |           |           |               |         |                           |                               |                                   |
| Saracuri          | -1.6788   | -53.5703  | 18            | Brazil  | humid rainforest           | Uatuma–Trombetas moist forests | Bush et al. (2007b)              |
| Santa Maria       | -1.5783   | -53.6054  | 17            | Brazil  | humid rainforest           | Uatuma–Trombetas moist forests | Bush et al. (2007b)              |
| Tapajos           | -2.7758   | -55.0828  | 15            | Brazil  | humid rainforest           | Madeira–Tapajós moist forests | Bush et al. (2006)               |
| Comprida          | -1.6249   | -53.9966  | 130           | Brazil  | humid rainforest           | Uatuma–Trombetas moist forests | Bush et al. (2000)               |
| Geral             | -1.6469   | -53.5955  | 130           | Brazil  | humid rainforest           | Uatuma–Trombetas moist forests | Bush et al. (2000, 2007b)        |
| **Western and Central sites** |           |           |               |         |                           |                               |                                   |
| Rio Curua         | -1.7347   | -51.4549  | 3             | Brazil  | *varzea–igapó* forest     | Xingu–Tocantins–Araguaia moist forests | Behling & da Costa (2000)        |
| **Andean sites**  |           |           |               |         |                           |                               |                                   |
| Chochos           | -7.6363   | -77.4746  | 3285          | Peru    | sub-paramo/sub-Andean forest |                              | Peruvian Yungas                  | Bush et al. (2005)               |
| La Teta-2         | 3.0833    | -76.5333  | 1020          | Colombia| disturbed forest           |                              | Cauca Valley dry forests         | Berrio et al. (2002)             |
| Surucucho         | -3.0625   | -78.0000  | 3180          | Ecuador | sub-paramo/sub-Andean forest |                              | Napo moist forests               | Colinvaux et al. (1997)          |
| Consuelo          | -13.9500  | -68.9833  | 1360          | Peru    | cloud forest               |                              | Bolivian Yungas                  | Bush et al. (2004b) and Urrego (2006) |

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for lower lake levels at Lake Pata during the Early–Mid-Holocene (Bush et al. 2002). The most compelling evidence for such a vegetation change at this site comes from the negligible percentages of Moraceae/Urticaceae pollen, which are in marked contrast to the consistently high values of this pollen type (20–30%) not only throughout the rest of the Quaternary record of this site, but also in modern rainforest pollen samples elsewhere across the Amazon rainforest biome (e.g. Gosling et al. 2005). However, the very low sedimentation rate at Lake Pata means that the duration and timing of this Mid-Holocene vegetation zone is uncertain.

In contrast to Lake Pata, where Cecropia is absent ca 6600 years BP and never exceeds 10% anywhere in the record, the Ecuadorian site, Maxus-4, was dominated by Cecropia (approx. 60%) between 8700 and 5800 years BP (figure 4). The timing of this Cecropia peak, and the proximity of this site to the neighbouring Andes, raises the possibility that it might be due to episodic droughts under a drier climate causing increased gap formation, and thus favouring this pioneer species (Weng et al. 2002), although, as argued above, there are problems with this hypothesis, strengthening the case for other types of disturbance (e.g. burning by Palaeo-Indians) considered below.

(ii) Andean sites
Pollen records from the Andean flank of the Amazon Basin show how past drier conditions affected different kinds of forest in different ways. At Lago Consuelo, located in the lower montane cloud forest of Peru (1360 m elevation; figure 1c), reduced precipitation (9000–5000 years BP) caused local replacement of cloud forest taxa by lowland rainforest taxa (figure 4; Bush et al. 2004b). Further north in Peru, at the higher elevation site Laguna de Chochos (3285 m), cloud forest was replaced by Polylepis forest ca 10 000 years BP, which persisted until 7300 years BP, consistent with drier conditions (figure 4; Bush et al. 2005). In the Colombian Andes (Teta-2, 1020 m), the replacement of cloud forest by semi-deciduous dry forest ca 8000 years BP is also indicative of a change to a drier climate (figure 4; Berrio et al. 2002). In contrast, however, pollen from Lake Surucucho, located at the sub-paramo/sub-Andean forest ecotone in Ecuador (3180 m; figure 1c), shows surprisingly little change in forest composition throughout the Holocene (Colinvaux et al. 1997).

(c) Holocene fire activity
Figure 4 demonstrates that there is considerable heterogeneity in fire regimes, both spatially and temporally. To what extent are these palaeofire records a function of climate, vegetation type and/or human activity? At Chaplin and Carajas, fire activity closely follows changing extent of flammable savannahs, demonstrating that past fires have long been a natural feature of savannahs in these ecotonal areas. Given that even drought-tolerant semi-deciduous dry forests are rarely subject to natural fire (as indicated by the presence of fire-intolerant acti; Pennington et al. 2006), and some Holocene records are largely, or completely, devoid of charcoal (e.g. Pata and Consuelo), our working hypothesis is that the charcoal records from the remaining sites that have been forested throughout the Holocene reflect anthropogenic fires set, either intentionally or accidentally, by Palaeo-Indians. However, heterogeneity in the charcoal signals, even among densely clustered sites, suggests that such fires were localized and much smaller in scale than those of today (Bush et al. 2007a).

Despite this heterogeneity, there is a hint of a broader scale regional pattern, suggesting that climate forcing may also have played a role in Holocene fire regimes. Several sites (e.g. Santa Maria, Geral, Surucucho, Chochos) show clear Mid-Holocene (6000–4000 years BP) charcoal peaks, perhaps due to the drier climate at this time making forests more combustible. The absence of charcoal at Consuelo, and near-absence at Pata, is unsurprising, given that these sites occur in the wettest parts of the basin (figure 1a,b), although the presence of charcoal in a single sample at Pata ca 5000 years BP (M. Bush 2007, personal communication) raises the possibility that it might be causally related to reduced Mid-Holocene precipitation.

Although the impact of past fires on the structure and species composition of Holocene Amazonian forests is difficult to discern from pollen records, correlative peaks in charcoal and Cecropia and/or grass, spanning several millennia, in particular at Santa Maria, Geral and La Teta-2, point to burning of sufficient frequency to maintain forests in a continually disturbed, early successional state.

4. Conclusions and implications for the future
In the most seasonal, ecotonal regions of the Amazon lowlands, the drier climate of the Early–Mid-Holocene caused either the replacement of forest by savannah (Carajas) or supported the continued presence of savannahs in regions which were previously unforested (e.g. Chaplin, Loma Linda). On the eastern slopes of the Andes, reduced cloud cover caused replacement of cloud forest taxa by lowland tree taxa. Even in the wettest central part of the Amazon (Pata), closed-canopy forest may have given way to more open vegetation, consistent with Mid-Holocene drying.

Many sites show Early–Mid-Holocene peaks in Cecropia pollen, constituting clear evidence of disturbance. This disturbance may have been caused by drought, fire or humans, or a combination of all three, the probable cause at a given site depending on how well the palaeoclimate, pollen and charcoal patterns match one another, as well as the precipitation regime and fire return interval of the locality today. Even where it is clear that the disturbance was driven by fire (e.g. Santa Maria), the cause of fire may itself be an issue. Palaeo-Indians are the most probable source of ignition, even at seasonal sites such as Santa Maria, where the charcoal peak supports the hypothesis that a Cecropia phase spanning several millennia is best explained by Palaeo-Indians maintaining the forest in an early successional state using fire. In fact, the widespread evidence for these long-lasting Cecropia phases suggests that humans, rather than climate, may
have been the key agents of disturbance of Holocene forests in many parts of the basin, especially if ‘pre-
Conquest’ Amazonia was much more densely populated than previously thought (Erickson 2000;
Heckenberger et al. 2003, 2007). However, a drier climate would have had an important influence by
making forests more combustible. Anthropogenic burning would therefore have been a more effective
tool for forest clearance and, through more frequent fire leakage, would have led to an increase in large
wildfires as occurs today during particularly severe droughts (Aragão et al. 2007).

Our analysis shows that, notwithstanding floristic changes, the forest biome in most parts of Amazonia
appears to have been remarkably resilient to climatic conditions significantly drier than those of today,
despite widespread evidence of forest burning. Only in ecotonal areas did forests give way to savannahs (e.g.
Carajas). Although the effects of continually rising CO₂ and different climate change scenarios, upon
Amazonia’s forests over the twenty-first century remain uncertain (Cramer et al. 2004), our insights from the
distant past suggest that the Amazon forest ‘dieback’ scenario simulated by Cox et al. (2000) and Betts et al.
(2004) is unlikely. However, the absence of Holocene palaeotemperature records from lowland Amazonia
means that the degree to which Early–Mid-Holocene Amazonian ecosystems can be considered an appro-
priate analogue for the future is uncertain. A projected temperature increase of 3°C over the twenty-first
century (Malhi & Wright 2004), in combination with drying and forest fragmentation, would be expected to
increase water stress and vulnerability to dieback, although this may be offset by higher CO₂ concen-
trations. Of much greater cause for concern should be the unprecedented rates of deforestation (Laurance
et al. 2001), forest fragmentation (Laurance et al. 1997, 2000) and uncontrolled burning (Cochrane et al. 1999;
Nepstad et al. 1999), which are much more serious and immediate threats than climate change.

We thank Yadvinder Malhi, for the invitation to write this paper and present these ideas at the ‘Climate Change and the
fate of the Amazon’ meeting at Oriel College, University of Oxford, 20–22 March 2007; Mark Bush and Dunia Urrego,
for discussions on the manuscript and contributing charcoal data; and the two referees, Herman Behling and Miles
Silman, for their detailed comments and suggestions which substantially improved the paper. We acknowledge the Global
Palaeofire Working Group (GPWG) of the International Geosphere–Biosphere Programme (IGBP) cross-project Data
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