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Tropical forests and global atmospheric change: a synthesis

Yadvinder Malhi¹ and Oliver L. Phillips^{2*}

¹*School of GeoSciences, Darwin Building, University of Edinburgh, Edinburgh EH9 3JU, UK*

²*Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds LS2 9JT, UK*

We present a personal perspective on the highlights of the Theme Issue ‘Tropical forests and global atmospheric change’. We highlight the key findings on the contemporary rate of climatic change in the tropics, the evidence—gained from field studies—of large-scale and rapid change in the dynamics and biomass of old-growth forests, and evidence of how climate change and fragmentation can interact to increase the vulnerability of plants and animals to fires. A range of opinions exists concerning the possible cause of these observed changes, but examination of the spatial ‘fingerprint’ of observed change may help to identify the driving mechanism(s). Studies of changes in tropical forest regions since the last glacial maximum show the sensitivity of species composition and ecology to atmospheric changes. Model studies of change in forest vegetation highlight the potential importance of temperature or drought thresholds that could lead to substantial forest decline in the near future. During the coming century, the Earth’s remaining tropical forests face the combined pressures of direct human impacts and a climatic and atmospheric situation not experienced for at least 20 million years. Understanding and monitoring of their response to this atmospheric change are essential if we are to maximize their conservation options.

Keywords: Amazonia; carbon dioxide; carbon balance; forest dynamics; global change; vegetation modelling

1. THE CONTRIBUTION OF THIS ISSUE TO THE DEBATE

In the introduction to this Theme Issue, we outlined the various strands of research that have contributed to the papers presented. Here we try to synthesize contributions and insights from these diverse fields, with the aim of tackling a specific question that could be encapsulated as: what will mature old-growth tropical forests look like at the end of this century? Addressing this question has implications for conservation, global biodiversity and global biogeochemical cycling, as well as being a test of our understanding of natural ecosystems. At the end of this process, we cannot claim to be able to answer this question, but by examining it from a variety of perspectives we may have made significant progress. Some of the achievements in this issue that have caught our eyes as editors include:

- (i) Coherent global documentation of temperature and precipitation trends in tropical forest regions in recent decades.
- (ii) Quantitative comparison among climate model predictions of climate change in tropical land regions in the twenty-first century.
- (iii) Significant updating of observations of changing tropical forest biomass and dynamics, and for the

first time the links between them, with expanded datasets and improved exploration of methodologies.

- (iv) Evaluation of research priorities for reducing error in estimates of forest biomass.
- (v) Coverage of various sides of the active debate into the nature and causes of contemporary change in tropical forests.
- (vi) Presentation of a systematic framework within which to discuss and analyse causal agents of change in tropical forests.
- (vii) Evaluation of the effects of non-atmospheric influences, such as feedbacks between fragmentation, fire and climate, and the influences of changes in large fauna.
- (viii) Quantification of the impact of fire disturbance on mammal and bird populations.
- (ix) A comprehensive review of palaeo-evidence of change at the LGM, and of substantial climate change in tropical regions during the Holocene.
- (x) A new attention to the potential significance of seasonally dry tropical forests as an expanding biome at times of past and future climate change.
- (xi) A physiological exploration of possible high temperature thresholds to the viability of moist tropical forest biomes.

The main conclusions are reviewed below.

(a) *The nature and magnitude of atmospheric change in the tropics*

Malhi & Wright (2004) demonstrate that since the mid-1970s there has been a globally synchronous warming in

* Author for correspondence (o.phillips@geography.leeds.ac.uk).

One contribution of 17 to a Theme Issue ‘Tropical forests and global atmospheric change’.

tropical forest regions of 0.26 ± 0.05 °C per decade. As discussed by Cramer *et al.* (2004), global climate models suggest a further warming in all tropical forest regions of between 3 and 8 °C (typically 4 °C) by the end of the century. This suggests that by 2100 tropical temperatures will have moved outside the envelope of natural variability of at least the past 2 million years.

Changes in precipitation are particularly sensitive to changes in tropical oceanic and atmospheric circulation, and recent precipitation changes show strong spatial variability, with evidence of a strong drying trend in Africa but few significant trends elsewhere. Future scenarios of precipitation change are also highly variable between region and between climate model, with changes of up to $\pm 20\%$ predicted by the end of the century. The only consistent tropical rainfall scenario in the four climate models discussed by Cramer *et al.* (2004) is a rise in precipitation in Asian tropical forest regions.

(b) *Insights from the past*

Mayle *et al.* (2004) present a comprehensive review and model study of changes in Amazonia since the LGM. Fossil pollen data and dynamic vegetation models now suggest that much of Amazonia remained forested through the cool arid conditions of the LGM, but the forest was of substantially different composition from modern-day forests, with drought-adapted forests covering much of southern Amazonia and cold-adapted Andean taxa migrating into the lowlands. Hence, it now seems unlikely that Amazonian forests retreated into refugia surrounded by savannah at the LGM, although 'within-forest' refugia of moist forest surrounded by seasonally dry forest remain a distinct possibility. This contrasts with Africa, for example, where the mean state of the forests is drier and there is clear evidence of large-scale retreat of the forest during arid periods (e.g. Morley 2000). During the Early–Mid-Holocene (*ca.* 8500–3600 calibrated yr BP), much of Amazonia experienced drying and perhaps warming, and Mayle *et al.* (2004) suggest that this period may give insights into ecological shifts to be expected in warming, drying tropical forest (although the direction of projected precipitation trends this century is far from certain). The Early–Mid-Holocene saw frequent widespread fires throughout southern and eastern Amazonia, which led to replacement of lowland evergreen rainforest taxa by drought- and fire-tolerant semi-deciduous dry forest and savannah taxa. The palaeo-analogue is not exact, however, as atmospheric CO₂ concentrations this century will be at least double those in the Early–Mid-Holocene, which would favour species with C3 photosynthetic pathways (such as lianas and dry forest trees) over those with C4 pathways (such as savannah grasses).

The potential importance of the SDTF is also emphasized by Pennington *et al.* (2004). Until recently, this ecosystem has been neglected in a debate largely focused on moist forests and savannahs. SDTF taxa have frequently shifted or expanded to replace moist forest taxa at times of aridity, and some phylogenetic analyses have suggested that current pockets of SDTF are refugia from a broad arc of SDTF that existed at the LGM. However, SDTF regions have been more affected by agriculture than moist forests, and it is likely that a possible future drying would see an expansion of agriculture rather than dry forests.

What stands out from the palaeo-analyses is the sensitivity of tropical forest structure and composition to climate variations in the Pleistocene (10 000 to 2 Myr BP), and even in the relatively stable Holocene (the past 10 000 years). Tropical forests are clearly dynamic ecosystems of constantly shifting composition and structure. Viewed from this perspective, the reports of ecological change in mature forests during the final quarter of the twentieth century are perhaps not surprising, and it is inevitable that the ecology and structure of intact tropical forests will respond to the atmospheric changes projected for the current century.

Cowling *et al.* (2004) also present a climate–vegetation model analysis of the recent past (the LGM and the Younger Dryas) and the near future. They suggest that the predominant mechanisms for maintenance of forest in cool periods are the reduced evapotranspiration and lowered respiration costs, and that tropical forests may now be near an upper temperature threshold where these physiological mechanisms become positive feedbacks that induce forest dieback. Will most plants have sufficient genetic and phenotypic flexibility to respond to rising temperatures by increasing these temperature thresholds? Recent evolutionary history suggests not, because the Pleistocene climates that tropical taxa have experienced for several million years have been predominantly much cooler than today's. Those (few?) taxa that are tolerant of higher temperatures may be expected to dominate ecosystem composition in a warming world. Identifying these taxa should be a research priority.

Some insight into the responses of tropical taxa to rising temperatures may come from examination of the Early Eocene (*ca.* 55 Myr ago), when there was a rapid rise of tropical temperatures (by 4–5 °C; Zachos *et al.* 2003), possibly at a rate similar to projected climate change over the twenty-first century. This was probably induced by volcanism or submarine seismicity and perhaps accelerated by a release of methane clathrates from ocean sediments. Many contemporary tropical families had evolved by then, and examination of which of these prospered and declined may give insights into their relative tolerance to high temperatures. Morley (2000) reports a worldwide decline in palms at equatorial latitudes at this thermal maximum and the appearance (and subsequent disappearance with cooling) of numerous new vegetation types without analogues in modern floras. By contrast, Wing *et al.* (2003) report little evidence of species turnover at a site in the warm 'paratropical' latitudes of North America. This is clearly a rich field for research. Incidentally, carbon isotope analyses and model simulations suggest that the terrestrial biosphere was a major carbon sink (1000–3000 Pg C) over this Early Eocene warming, because of a combination of CO₂ enrichment and global warming (Beerling 2000).

Montane regions have an obvious conservation importance at times of warming, as the flight of many cold-adapted taxa to the Andes at the last glacial transition demonstrates (Mayle *et al.* 2004). Their protection should therefore be a conservation priority, not only to protect their current endemic-rich biota, but also as a refuge for mesic lowland taxa. The projected 4 °C warming over the twenty-first century can be expected to lead to an 800 m upward migration of ecotone, over half the current

altitudinal extent of cloud forest. Cloud forests may be the tropical ecosystems most sensitive to climate change, and monitoring of changes in composition and structure should give early clues to trends in ecosystem composition.

(c) *The expected response of tropical forests to contemporary change in the tropical atmosphere*

Several papers in this issue focus on contemporary drivers of change in tropical forests, and discuss a suite of possible responses: in forest ecophysiology, ecology, fire dynamics and human interactions.

Several papers (Chambers & Silver 2004; Clark 2004; Körner 2004; Lewis *et al.* 2004a) discuss the ecophysiological arguments for various responses to contemporary tropical atmospheric change, often taking opposing viewpoints. Some of the major arguments surrounding two potential drivers, increasing atmospheric CO₂ concentrations and increasing temperatures, are summarized in table 1.

Increased fire incidence is likely to be another important factor in driving changes in tropical forests (Barlow & Peres 2004). To some extent this may be driven by drying trends in some tropical forest regions, but human factors such as desiccation associated with fragmentation (Laurance 2004) and logging, and the spread of the human colonization frontier are likely to be important factors independent of any local background climate change. Whereas much of this Theme Issue concentrates on the response of tropical vegetation to climate change, Barlow & Peres (2004) provide a timely example of the potential of severe faunal shifts accompanying such vegetation change. Laurance (2004) demonstrates how forest deforestation and fragmentation can accelerate climate change, both locally by modifying microclimate and regionally by enhancing surface warming and perhaps suppressing precipitation.

(d) *Observations of contemporary change in tropical forests*

What is actually being observed in tropical forests today? Can we see any direct evidence of responses to contemporary atmospheric change? Three papers present such evidence from monitoring plots in old-growth tropical forests, much of which is emerging from the RAINFOR project (Malhi *et al.* 2002), which is supporting the development of a pan-Amazonian monitoring network. These results update and expand upon papers by Phillips & Gentry (1994) and Phillips *et al.* (1998), which first presented evidence of accelerating forest dynamics and increasing forest biomass in old-growth tropical forests.

Baker *et al.* (2004) present an updated analysis of changes of biomass in old-growth Amazonian forests, and conclude that there has been a net increase in biomass in recent decades at a rate of $1.22 \pm 0.42 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, slightly greater than that originally estimated by Phillips *et al.* (1998). They address several methodological issues, including uncertainties in measurement of large trees and choice of allometric equation to estimate biomass (cf. Chave *et al.* 2004), and find the results robust to these uncertainties. Applying adjustments for the biomass of

roots, small trees and lianas (following Phillips *et al.* 1998), this is equivalent to a net carbon sink in intact old-growth forests of $0.9 \pm 0.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, or, multiplying by the area of moist forest in Amazonia, ca. 0.6 Pg C yr^{-1} .

Phillips *et al.* (2004) present an updated analysis of changes in forest turnover in Amazonia (tree recruitment and mortality), using a spatially and temporally extended dataset to explore regional patterns and to separate turnover into tree recruitment and mortality. They confirm that turnover rates appear to have accelerated across Amazonia, with the greatest absolute increases on more fertile soils in western Amazonia. Moreover, the increase in recruitment has been greater than, and in advance of, the increase in mortality, implying that the increases are driven by an acceleration of growth, which eventually feeds back on mortality, rather than a direct acceleration of mortality through disturbance.

Lewis *et al.* (2004b) explore the changes in structure and dynamics in greater detail by examining simultaneous changes in forest biomass, growth, mortality and stem number in 50 Amazonian forest plots. They demonstrate that there appears to have been an acceleration of growth in most of these plots, accompanied by a lagged acceleration of mortality and a general increase in biomass and stem number. This suggests that the observed increase in biomass is unlikely to be explained by recovery from past disturbance, but instead suggests a direct forcing from CO₂, solar radiation and/or possibly temperature. One unexpected feature is that the observed acceleration of growth, at $2.55 \pm 1.45\% \text{ yr}^{-1}$, is an order of magnitude higher than that expected from CO₂ fertilization alone. If CO₂ fertilization is indeed the primary driver of this acceleration, this discrepancy could be explained if trees are disproportionately allocating carbon to stem growth, or there are positive feedbacks through changes in forest structure and composition, or the shift in the compensation point between photosynthesis and respiration is more important than the overall boost in photosynthesis. Alternatively, some other driver such as a possible increase in sunshine may be involved (Nemani *et al.* 2003).

In sum, there is now unequivocal evidence that the biomass of monitored intact forest plots in the Neotropics has increased in recent time. There is perhaps still room for debate in the interpretation of this increase within the natural disturbance–discovery dynamic of a tropical forest landscape, although the evidence presented by Lewis *et al.* (2004b) of a simultaneous increase in both biomass and turnover does suggest the presence of an external driver (such as CO₂ or light) accelerating growth.

Can such changes in dynamics be verified by satellite observation? The dramatic increases in turnover reported by Phillips *et al.* (2004) might have a visible effect on canopy gap fractions or canopy texture. There is some evidence from Landsat imagery of concerted changes in mature forest canopy texture across the biome, consistent with a large-scale shift in forest behaviour (Weishampel *et al.* 2001). Other evidence may lie hidden in radar or lidar estimates of forest height, or the spectral signature of forests canopies, and as the satellite record improves in temporal duration, it may be rewarding to look for trends in these signals.

Table 1. Arguments to expect, or not to expect, substantial effects of increasing CO₂ concentrations on tropical forest growth and carbon balance. Direct and indirect effects are considered, including climate change.

zero or negative effect on growth and carbon storage	positive effect on growth and carbon storage
leaf level	
increased respiration and photorespiration caused by rising temperatures	direct fertilization of photosynthesis by high CO ₂
warming temperatures lead to increased evaporative demand, inducing stomatal closure and reducing photosynthesis	reduced photorespiration caused by high CO ₂
increased emissions of volatile hydrocarbons at higher temperatures consume assimilated carbon	improved water-use efficiency caused by high CO ₂
	photosynthetic rates increase with moderate warming optimum temperature for photosynthesis rises with rising CO ₂
plant level	
plants are often saturated with respect to non-structural carbohydrates?	excess carbon may be used preferentially above ground to acquire rate-limiting resource (light) by investing in wood
plant growth limited by nutrients other than carbon (N, P, K, Ca)	excess carbon may be used preferentially below ground to acquire rate-limiting resource (nutrients) through fine root development or supporting P-scavenging mycosymbionts
rising soil temperatures increase soil acidification and mobilize aluminium, reducing soil nutrient supply	rising temperatures increase soil mineralization rates and improve nutrient supply
plant carbon balance is limited by respiration costs rather than by photosynthesis gains?	
acclimation (downregulation of photosynthesis) limits any response to increasing CO ₂	
stand level	
biomass ultimately limited by disturbance (e.g. windthrow risk) rather than by resources	faster growth leads to some biomass gains, with mortality gains lagging
forest canopies are close to physical limits of forest structure which cannot be increased (e.g. maximum tree height is limited by hydraulics or mechanics)	rising CO ₂ improves water-use efficiency and reduces tension in the water column, allowing an increase in maximum tree height for a given cross-sectional area
faster growth and turnover may favour disturbance-adapted taxa, with less dense wood	faster growth and turnover may prevent stand dominance by senescent 'over-mature' trees with high respiration costs, creating positive feedback on stand-level growth rates
lianas may benefit from increased CO ₂ and disturbance, limiting biomass gains by trees	improved forest water balance leads to reduced drought mortality and fire incidence
mortality rates increase because of climatic warming and/or drying, or increased climatic variability	
climatic drying combined with forest fragmentation and degradation lead to increased fire frequency	

A key feature of all these spatially extensive analyses, whether based on direct or remotely sensed measurements, is that analysis of the spatial patterns should be able to reveal further clues about the causal mechanisms behind these observed changes. For example, if the primary driver were increased CO₂ levels stimulating growth by improved water-use efficiency, we would expect to see the greatest growth and biomass gains in seasonally dry forests. Alternatively, if the primary driver is a possible increase in solar radiation, this increase would have a distinct geographical pattern, which could be compared with forest plot observations.

To the extent that intact forests are increasing in biomass, they act as a carbon sink and a moderate buffer

on the rate of rise of atmospheric CO₂. Although the contemporary debate about the magnitude of the carbon sink is clearly of current global scientific and societal interest, in the longer term it may become rather less significant. All contributors to this Theme Issue seem to agree that any contemporary carbon sink is likely to be a transient benefit, which will either flatten out as CO₂ fertilization saturates or tropical forests reach a structural limit, or perhaps reverse through ecological or physiological responses to increased temperatures, regional drought and ecological shifts such as increased liana abundance. Moreover, as pointed out by Cramer *et al.* (2004), deforestation and forest degradation are likely to be more important factors in determining tropical carbon stores than the carbon

dynamics of the remaining intact forests. Finally, any change in the terrestrial biosphere is likely to be swamped by expected fossil fuel emissions of CO₂ in the coming decades. For example, the entire live biomass carbon pool of the Amazonian forest is *ca.* 120 Pg C (Houghton *et al.* 2002; extrapolated to all of Amazonia). If we include soil carbon reserves, this store increases to *ca.* 200 Pg C. This is equivalent to *ca.* 20 years of anthropogenic CO₂ emissions under the most likely future emissions scenarios (IPCC 2001), and *ca.* 29 years of atmospheric CO₂ increase assuming a constant combined oceanic and non-tropical biomass sink of 3 Pg C yr⁻¹. Hence, even a 25% increase in the vegetation biomass of Amazonia (i.e. 30 Pg C) would delay future anthropogenic global warming by only 4 or 5 years.

Perhaps a more important issue is the extent to which we can expect shifts in forest ecology and biodiversity in response to atmospheric change, such that even protected areas will undergo rapid change. Here, the observations of changing biomass and dynamics have value as early indicators of the direction of change. The sensitivity of tropical forest composition to climatic change in the Pleistocene and Holocene suggest that it is inevitable that tropical forest composition will change in response to atmospheric change, as particular species are favoured by higher CO₂ and changing climate. This is regardless of whether tropical forests are sources or sinks of carbon. Much greater scientific effort is warranted in understanding this complex and emerging threat, both in terms of the focus of theoretical and modelling effort, and in the monitoring of tropical biodiversity changes on the ground.

2. RECOMMENDATIONS FOR THE FUTURE

In the Anthropocene (Crutzen 2002) we have embarked on an unplanned experiment with global ecosystems, mainly through direct action (e.g. deforestation), but also through the indirect effects of climate change. Given the inertia of the ocean–atmosphere system, we have already committed the planet to some further warming even if the world emissions were to shrink by half or more. Given the more realistic time-scales for stabilizing global climate, substantial climate change by the end of the century is very likely. Understanding how ecosystems such as tropical forests will respond as they are pushed into environmental regimes unexplored for at least 20 Myr (Prentice *et al.* 2001) is still riddled with uncertainty, but this issue has tried to cast some light on possible future trends.

(a) *Expect change*

Analysis of both contemporary climate records and environmental change since the LGM shows that tropical climates can vary substantially over time. Examination of both the palaeo-record and contemporary observations, suggests that the species composition of tropical forests may be sensitive to even small shifts in climate and atmospheric composition. Therefore, it seems almost inevitable that intact tropical forests are undergoing substantial ecological shifts in response to contemporary global atmospheric change, but our ability to predict what exactly these changes should be remains poor. Moreover, the relationships between changes in species composition and resulting shifts in ecosystem function appear complex and currently difficult to trace.

(b) *Observe and monitor*

The changes in tropical forests reported in several papers in this issue would not have been observed if some forest monitoring studies had not been established in the 1980s, and in no case were these early plots established with the aim of detecting the impact of global change drivers. These serendipitous findings pose a powerful challenge to the dominant hypothetico-deductive approach to science, which tends to devalue observation for observation's sake and favours short-term (3 year cycle) research into simpler, more easily delineated problems.

For complex ecosystems with the potential of unforeseen emergent changes, long-term 'field-truthing' of ecosystem shifts is an irreplaceable complement to laboratory studies or modelling projects. This is a much greater challenge in hyperdiverse low-income tropical countries than in bio-impooverished but materially wealthy temperate ones. A systematic long-term programme for monitoring tropical forests (and other ecosystems) to standard protocols must become a global science priority. Important steps have been made in this direction by networks such as the CTFS (Center for Tropical Forest Science) 50 ha plots network, the RAINFOR network of widespread smaller plots (Malhi *et al.* 2002), and Conservation International's Tropical Ecosystems and Monitoring (TEAM) programme, but there is a need for global standardization and integration, and, critically, real commitment to long-term funding. A useful analogy is perhaps the global network of meteorological observations that have proved invaluable in confirming and detailing climate change initially predicted by model simulations. A similar monitoring of 'ecosystem weather' would be relatively inexpensive and prove invaluable, both as a test of our understanding and as a 'miner's canary' to provide early warning of unforeseen ecological changes.

(c) *Bring more ecology into the models*

The current generation of vegetation–climate models represent significant advances in our understanding of the relationship between climate and biome distribution. They are, however, based largely on an understanding of bulk physiology and biogeochemical cycling, and divide potential vegetation into a few 'functional types' such as evergreen broadleaf and evergreen deciduous. This is a substantial degree of complexity and can hardly be considered a failing, but it is likely that critical interactions will occur at a finer degree of resolution of functional types. For example, an increase in abundance of lianas (Phillips *et al.* 2002) or shade-tolerant species may have a greater influence on forest biomass and dynamics than a direct ecophysiological response to temperature, but no current model is able to address such possible changes. This largely reflects a current lack of data and understanding, but an important target for a future generation of ecosystem models would be to incorporate a finer degree of resolution of plant functional types.

(d) *Do not take a tropical carbon sink for granted*

There is some evidence that intact tropical forests may be increasing in biomass and acting as a moderate carbon sink (of the order of 1 Pg C annually), and therefore buffering to some extent the rate of anthropogenic global warming. Although significant compared with contemporary

annual fossil fuel CO₂ emissions of 7 Pg C, it is likely to be reduced in importance when compared with the projected emissions of 15–20 Pg C by the mid-twenty-first century. Moreover, almost all researchers agree that this sink cannot be relied on, and may even reverse in the coming century, acting as a moderate accelerator rather than a moderate sink.

(e) Do not forget land use change

The debate in this issue has focused on relatively intact tropical forests. It is, of course, vital to remember that in most tropical forest regions deforestation and degradation will still dominate over climate change effects for at least the medium term (decades), as demonstrated by Cramer *et al.* (2004). In many regions, the debate about the effects of climate change may be rendered irrelevant by the almost complete disappearance of tropical forests. However, even if only a small fraction survive in reserves or inaccessible regions, their ecological stability may depend on the degree to which they will be affected by atmospheric change, and the ease with which vulnerable species can migrate to nearby refuges. Moreover, as highlighted by Barlow & Peres (2004) and Laurance (2004), the feedbacks between the land use change and local microclimate and fire regimes may play a critical part in determining the viability and sustainability of forest reserves and corridors.

(f) Plan conservation with atmospheric change in mind

Tropical forests face dual pressures this century: direct deforestation and degradation, and atmospheric change. In the face of rapid tropical deforestation, it is essential that what conserved areas remain are designed to be as robust as possible in the face of atmospheric change. Several conservation organizations already take climate change into account, focusing more on 'conservation corridors' rather than isolated reserves, and incorporating elevational gradients that allow easier migration to cooler climates. Our understanding of ecosystem responses to atmospheric change is still in its infancy, however, and these strategies will need to incorporate new insights as they emerge.

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GLOSSARY

- LGM: last glacial maximum
SDTF: seasonally dry tropical forest