

Detecting Tropical Forests' Responses to Global Climatic and Atmospheric Change: Current Challenges and a Way Forward

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ABSTRACT

Because of tropical forests' disproportionate importance for world biodiversity and for the global carbon cycle, we urgently need to understand any effects on these ecosystems from the ongoing changes in climate and atmosphere. This review, intended to complement existing data reviews on this topic, focuses on three major classes of challenges that we currently face when trying to detect and interpret directional changes in tropical forests. One is the very limited existing information on the historical context of study sites. Lasting effects from past climate, natural disturbances, and/or human activities could be significantly affecting current-day processes in tropical forests and need to be investigated for all active field sites. Second, while progress has been made in recent years on standardizing and refining research approaches, a number of methods- and data-limitations continue to affect efforts both to detect within-forest changes and to relate them to ongoing environmental change. Important outstanding needs are improved sampling designs, longer time-series of observations, filling key data gaps, and data access. Finally, forest responses to ongoing environmental change are complex. The effects of many simultaneously changing environmental factors are integrated by the plants, and their responses can involve significant lags, carryovers, and non-linearities. Specifying effects of individual environmental changes, however, is required for accurate ecosystem-process models and thus for projecting future impacts on these forests. After discussing these several types of challenges and ways to address them, I conclude with a priority agenda for this critical area of research.

RESUMEN

Debido a la importancia desproporcionada de los bosques tropicales para la biodiversidad mundial y para el ciclo global del carbono, es urgente identificar los impactos sobre estos ecosistemas provocados por los cambios actuales en el clima y en la atmósfera. Este artículo de revisión, escrito con el propósito de complementar otras revisiones recientes, se enfoca en tres principales clases de retos que enfrentamos actualmente en la detección e interpretación de cambios direccionales en los bosques tropicales. Primero es la gran escasez de información histórica acerca de los sitios de estudio. Los procesos actuales en los bosques tropicales pueden reflejar los efectos prolongados del pasado climático, las perturbaciones naturales y/o las actividades humanas, por lo que deben de ser investigados en todos los sitios actuales de estudio. Segundo, a pesar de avances recientes en la estandarización y el refinamiento de los métodos de investigación, nuestra habilidad para detectar cambios en los bosques y ligarlos a los grandes cambios ambientales sigue siendo limitada. Para garantizar avances en el área se requiere mejorar los diseños de muestreo, extender las series de observación en el tiempo a plazos mayores, llenar ciertos vacíos claves en el conocimiento, y facilitar el acceso a los datos existentes. Por último, se requiere de enfoques que tomen en cuenta la complejidad de las respuestas de los bosques a los cambios ambientales. Las plantas integran los efectos de cambios simultáneos en múltiples factores ambientales, y sus respuestas pueden ser no lineales e incluir efectos de retraso y acarreo. No obstante, es importante también especificar los efectos individuales de los diferentes cambios ambientales para afinar los modelos de procesos a nivel del ecosistema, y así poder proyectar los impactos futuros sobre estos bosques. Después de discutir dichos retos y estrategias para enfrentarlos, concluyo con una agenda de prioridades para esta área crítica de investigación.

Key words: carbon dioxide; climate change; data access; ecophysiology; forest ecology; global change; landscape sampling; monitoring; process modeling; tropical rain forest.

IN THIS TIME OF ACCELERATING CHANGES ON EARTH, what is happening to the world's tropical forests? One side of this question, the pan-tropical loss and degradation of forests due to land-use change, logging, and fire, has been summarized in several recent papers (Curran *et al.* 2004, Nepstad *et al.* 2004, Houghton 2005, Ometto *et al.* 2005, Wright 2005). A separate issue is how the remaining old growth tropical forests are being affected by changing climate and atmospheric composition, a question with its own global-scale implications. Negative effects on these ecosystems would translate into strong biotic impoverishment of the planet. Secondly, these forests are major players in the world's carbon cycle. They harbor globally significant amounts of carbon both in the vegetation and in the soil (Dixon *et al.* 1994), and they annually process vast amounts of carbon in photosynthesis and respiration (Melillo *et al.* 1993, Field *et al.* 1998). Changes in tropical forest carbon cycling can

therefore affect the pace of climate change (Clark 2004a). We thus urgently need to understand how this biome is responding to the rapid ongoing changes in environmental conditions. The existing field observations and laboratory studies related to this question have been the subject of multiple reviews (Clark 2004b, Lewis *et al.* 2004a, Wright 2005). In this paper, intended to complement the data reviews, I focus on the challenges that we currently face when trying to detect and interpret directional changes in old growth tropical forests, and I propose ways to address these challenges.

BACKGROUND: TRENDS ALREADY UNDERWAY?

The tropics have experienced large directional climatic and atmospheric changes just over the last 30 yr, a period of particular interest because it encompasses most existing tropical forest ecological data. Between 1975 and 2005 the atmospheric concentration of CO₂

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(atmospheric $[\text{CO}_2]$) increased 14 percent, from 330 to 377 ppm. During this entire period it far exceeded the 300 ppm maximum level for the 420,000 yr before industrialization (Petit *et al.* 1999). Since 1975 all tropical regions have experienced strong warming, with temperature increases of $0.26 \pm 0.05^\circ\text{C}$ per decade (Malhi & Wright 2004). Although solar radiation data for the tropics are sparse and conflicting (see Lewis *et al.* 2004a), directional changes in total radiation have occurred at the global scale: gradual “global dimming” from the 1960s to the late 1980s, “global brightening” (radiation increases of 0.2–0.3%/yr) from the late 1980s until 2000 (Wild *et al.* 2005), and another reversal during 2000–2005 due to increasing cloud cover (Pallé *et al.* 2006); these changes are also likely to have affected the photosynthetically important balance between direct and diffuse light. Stratospheric ozone has significantly declined over recent decades in the tropics, where UV-B levels are already the highest globally (Searles *et al.* 1995). Rainfall has significantly changed in some tropical regions, declining 3–4 percent per decade in northern tropical Africa and decreasing marginally in tropical Asia (Malhi & Wright 2004). Dry season intensity has increased in African and Indian rain forest areas (Malhi & Wright 2004).

Notable climatic excursions have also affected the tropics. Large jumps in temperature (Fig. 1) and (in many tropical areas) record droughts occurred in the strong El Niño events of 1982–1983, 1987–1988, and 1997–1998 (Malhi & Wright 2004). Up to 65 percent reductions in photosynthetically active radiation were caused by aerosols from exceptional fires in the 1997–1998 and 2002–2003 El Niño’s in parts of Southeast Asia (Kobayashi *et al.* 2005). Similar regional-scale decreases in total radiation must have been caused by the very widespread fires that have occurred elsewhere in some years of recent decades (*e.g.*, large areas of Amazonia in 1997–1998; Nepstad *et al.* 2004).

Tropical forests could reasonably be expected to have responded to these directional changes and short-term extremes. Temperature, rainfall, atmospheric CO_2 , and radiation (direct and diffuse) all affect photosynthesis and/or respiration and thus could alter plants’ net carbon balance, carbon allocation, or productivity. Such im-

pacts could lead to changes in many aspects of plant performance (mortality, recruitment, growth, reproduction, phenology). Related effects at the stand level could include shifts in floristics, in above-ground or belowground biomass, or in the big forest carbon fluxes (gross primary productivity, ecosystem respiration) that largely determine net carbon exchange with the atmosphere (Chapin III *et al.* in press). Global ecosystem-process models based on current understanding (*e.g.*, White *et al.* 2000, Cramer *et al.* 2001, Fung *et al.* 2005) have projected declining productivity for the world’s tropical forests as warming proceeds, in spite of physiological benefits from increasing atmospheric CO_2 . Some projections (*e.g.*, Jones *et al.* 2003, Cowling *et al.* 2004) have indicated massive tropical forest die-offs starting around mid-century. Significant uncertainties exist, however, with respect to key processes. One is the level at which physiological benefits to plants from increasing atmospheric CO_2 reach a plateau; this point may already have been reached (Körner 2003). Other key parameters that are poorly understood for tropical forests are the photosynthetic optimum temperature (*cf.* Tribuzy 2005) and the acclimation capacity of photosynthesis and respiration. Also little studied are nutrient constraints. While the critically important phosphorus inputs to the Amazon via Saharan dust have been increasing on a millennial scale (Okin *et al.* 2004), they are climatically sensitive (Swap *et al.* 1992). Anthropogenic increases in atmospheric nitrogen inputs could produce important cation losses from tropical forest soils (Asner *et al.* 2001). Current tropical UV-B levels could be reducing tropical forest productivity (*cf.* Searles *et al.* 1995). Finally, atmospheric constituents such as tropospheric ozone (*cf.* Lelieveld *et al.* 2004) and other types of anthropogenic pollutants such as pesticides could be affecting forest biogeochemistry but are largely unquantified for tropical forests.

Do tropical forests already show evidence of sensitivity to changing environmental factors? Is their carbon balance shifting? Have there been directional changes in other forest processes or in forest structure or composition? The limited relevant data are from three quite different research approaches.

1. *Atmospheric studies.* Global-scale indications come from global ecosystem-process models adjusted to match atmospheric gas measurements for the period 1980–2000 (“inverse models”). A robust finding (*cf.* review in Clark 2004a) has been globally significant interyear variation in the exchange of carbon between the terrestrial tropics and the atmosphere. The large inferred variation in tropical carbon fluxes is strongly correlated with the interannual variation in tropical temperatures (higher net emissions from the tropics in hotter years; *e.g.*, Clark *et al.* 2003). This signal is consistent with reductions across the world tropics in forest net primary productivity during the recent peak-temperature events. Atmospheric inversion studies differ notably, however, in their estimates of the carbon balance of global tropical vegetation; the decadal estimates for the 90s range from a sink to a source (Clark 2004a).
2. *Eddy covariance studies.* At a few Neotropical sites, this tower-based technique has been used to estimate local forest carbon

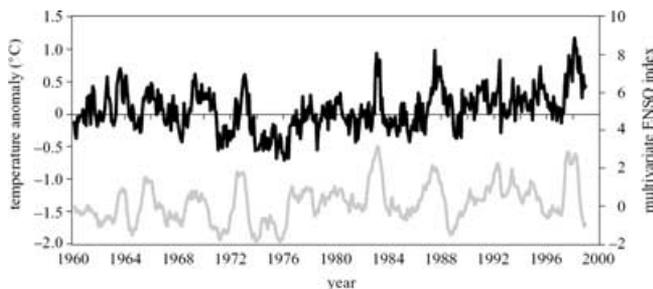


FIGURE 1. Temporal variation in the pan-tropical temperature anomaly (black line) and the multivariate ENSO index (gray line) over the period 1960–2000. Reproduced with permission from Malhi and Wright (2004, Fig. 4) and the Royal Society of London.

exchange with the atmosphere over several weeks to 1–3 yr. Data from the first such studies were initially interpreted (*e.g.*, Grace & Malhi 2002) as evidence that Amazonian forests were acting as strong net carbon sinks, perhaps in response to CO₂ fertilization. A study in a Costa Rican forest (Loescher *et al.* 2003) appeared to indicate similarly large net uptake in one of the 3 yr but approximate carbon balance in the hottest year. A very different perspective resulted, however, when researchers using eddy covariance at two towers in an eastern Amazonian site (Saleska *et al.* 2003, Miller *et al.* 2004) corrected for the still-air nighttime conditions typically found in tropical forests (Loescher *et al.* 2003, Miller *et al.* 2004, Ometto *et al.* 2005). The filtered eddy covariance data from these two nearby stands indicated they were either in carbon balance or acting as modest sources of CO₂ to the atmosphere. A separate finding from tropical forest eddy covariance studies (Loescher *et al.* 2003, Goulden *et al.* 2004) has been reduced net carbon uptake by the forests during half-hour periods with the highest current daytime temperatures, times when there is also maximal vapor pressure deficit.

3. *Ground-based studies.* By far most of the relevant observations have been from remeasurements of trees and lianas over varying lengths of time. One class of findings from such data has been large responses by tropical forests to interyear variation in drought and temperature. A 16-yr study in a Costa Rican lowland wet forest (Clark *et al.* 2003) revealed big changes among years in forest-level tree growth; the tree growth rates were strongly negatively related to annual temperatures (Fig. 2). In Neotropical and tropical Asian forests (studies reviewed in Clark 2004b; also Rolim *et al.* 2004, van Nieuwstadt & Sheil 2005), notable spikes in tree mortality were detected in recent strong El Niño events, periods of exceptional temperatures and drought. Long-term weekly monitoring of tree flowering patterns in a Panama forest (Wright & Calderon 2006) showed increased numbers of species flowering in recent El Niño events, periods of both elevated temperatures and greater accumulated solar radiation. Striking decadal-scale directional changes have also been inferred for tropical forests during the last 30 yr. These include: (a) increasing rates of tree turnover (Amazonia—Phillips *et al.* 2004); (b) increasing aboveground biomass (Amazonia—Baker *et al.* 2004a); (c) increasing liana abundance (Fig. 3, pantropical—Phillips *et al.* 2002a; Panama—Wright *et al.* 2004); (d) within-forest floristic changes (Central Amazon—Laurance *et al.* 2004; Panama—Hubbell 2004); and (e) long-term changes in patterns of tree and liana flowering or fruiting (Uganda—Chapman *et al.* 2005; Panama—Wright & Calderon 2006).

IDENTIFYING THE EFFECTS OF GLOBAL CHANGE

If these findings are accurate indicators of ongoing global-change effects on forests around the world tropics, much bigger forest responses could be expected as climatic/atmospheric changes inten-

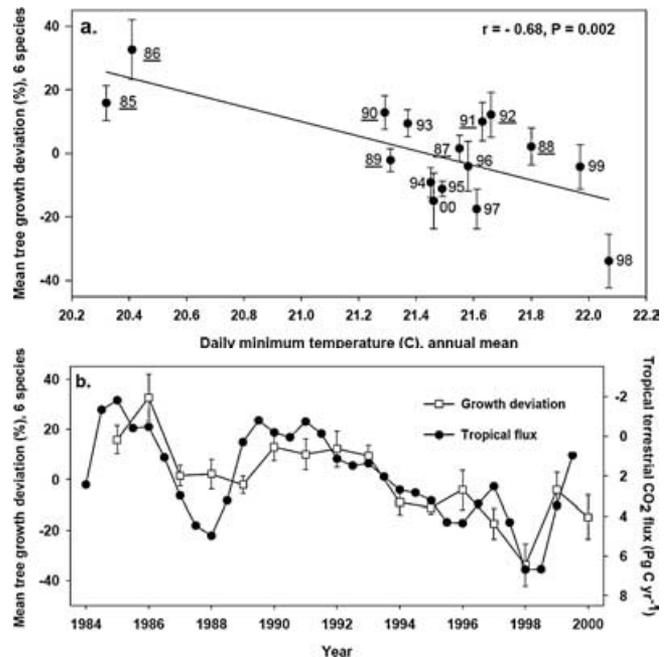


FIGURE 2. (a) Relative diameter growth of adult trees (detrended for size-dependence) and annual temperatures at La Selva, Costa Rica (Clark *et al.* 2003). (b) The correlation ($r = -0.77, N = 15$ yr, $P < 0.001$) between this interannual variation in tree growth and the interyear variation in the net CO₂ flux from the global terrestrial tropics (note inverted y-axis), as inferred from an atmospheric inverse model (see text).

sify. The resulting impacts on global biodiversity and the world's carbon cycle could have large political and economic ramifications, both within tropical countries and for international policy. It is thus critical for the research community to closely track the responses of these ecosystems to the environmental changes that are underway.

There are three major classes of challenges for doing this, however. First, too little attention has been given to the historical context of tropical study sites. Lasting effects from past climate, natural disturbances, and/or human activities could be significantly contributing to current-day changes within tropical forests. Such possibilities need to be actively investigated for all active field sites. Second, while progress has been made in recent years on standardization and refinement of research approaches, a number of methods- and data-limitations continue to affect our efforts both to detect within-forest changes and to relate them to ongoing environmental change. Important outstanding needs are improved sampling designs, longer time-series of observations, filling key data gaps, and data access. Finally, forest responses to ongoing environmental change are necessarily complex. The effects of many simultaneously changing environmental factors are integrated by the plants, and their responses could also involve diverse kinds of temporal complications, such as lags and nonlinearities. Specifying effects of individual environmental changes, however, is a *sine qua non* for accurate ecosystem-process models and thus for projecting future impacts on these forests. In

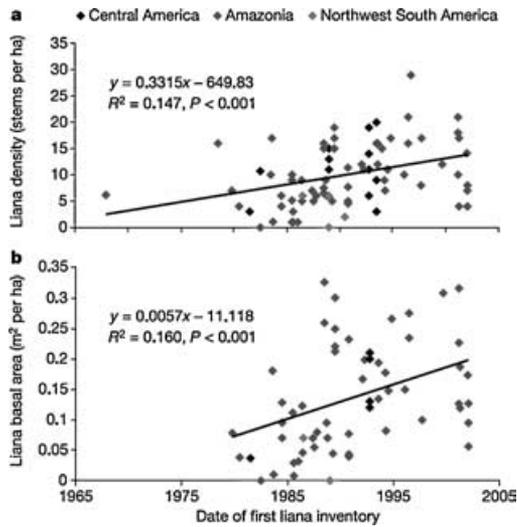


FIGURE 3. Importance of lianas (≥ 10 cm diameter) in each Neotropical site as a function of date of first inventory. (a) Liana stem density in stems per ha; (b) liana basal area in $\text{m}^2 \text{ha}^{-1}$. “Central America”: Panama and tropical countries to the north; “Northwest South America”: the Chocó bioregion, west of the Andes; “Amazonia”: the Amazon river basin and contiguous forested zones of Guyana and eastern Brazil. Linear regressions are fitted to the Amazonian data. Reprinted by permission from O. Phillips and from Macmillan Publishers Ltd: NATURE (Phillips *et al.* 2002a, Fig. 1), copyright 2002.

the following sections I discuss these challenges and propose ways to address them.

CHALLENGE 1: UNSEEN LEGACIES.—

... most landscapes and natural ecosystems bear strong legacies of past events. In fact, as we anticipate future changes in our forests, we fully expect that these will be driven as much by recovery from historical processes as by responses to novel conditions. (pp. 363–364)

To understand processes that have shaped current plant and animal assemblages through time and to document the slow progress of important ecological processes, we need to extend the time frame for our studies and our thinking by conducting truly long-term research and by using a creative array of historical approaches. ... we cannot make sound interpretations of the modern landscape solely by examining current conditions. We must always invoke a detailed knowledge of the history of the land and its people. (pp. xi–xii)

(Foster & Aber 2004)

The above quotes reflect recognition by temperate zone forest scientists of the importance of history for today’s forests. Tropical forest science has yet to fully incorporate such a perspective. While the issue of historical influences on tropical forests has recently received more attention in the literature (*e.g.*, Newbery *et al.* 1998, Whitmore & Burslem 1998, Chazdon 2003, Baker *et al.* 2005, Nelson 2005, Pitman *et al.* 2005, Wright 2005), tropical researchers still frequently neglect this dimension of their study sites.

In his 1996 survey of tropical forest research papers from the 2 yr prior, Clark (1996) found that in 53 of 57 cases the study

site was characterized with a term such as “primary,” “undisturbed,” “virgin,” “mature,” or “pristine.” Although progress has been made since then (notably, the recently described Center for Tropical Forest Science [CTFS] plot histories; Losos & Leigh 2004), published study-site descriptions often still include either an unsupported assertion of the forest’s undisturbed status, or indications that the researcher is making such an assumption. Stands that are speciose, have tall, large-diameter trees, and lack the even size-structure of obviously successional forest are still frequently assumed to have been essentially free of disturbances and stable in structure and function over many centuries, particularly if they are remote from current-day roads.

Diverse research findings, however, indicate that change and disturbance have permeated the histories of today’s old growth tropical forests. Some of this evidence has come from fields such as anthropology and archaeology. Some has been pieced together by tropical ecologists for their field sites (*e.g.*, Newbery *et al.* 1998, Baker *et al.* 2005, Pitman *et al.* 2005). The accumulating data are still fragmentary compared to the rich historical understanding of temperate and boreal forests. They nevertheless are leading to a similar vision for all tropical forests: one of large millennial- and regional-scale changes through the last 20,000 yr, combined with individualistic site histories due to local climatic events, natural disturbances and human activities.

It is now widely agreed (Piperno *et al.* 1990; Flenley 1998; Mayle *et al.* 2000, 2004; Cowling *et al.* 2004; Bush *et al.* 2004) that all three tropical regions (Neotropics, Africa, Southeast Asia) experienced dramatic climatic and vegetation shifts through the Holocene, roughly the last 10,000 yr. At the Last Glacial Maximum (LGM, *ca* 34–22,000 yr before present [ybp]; Smith *et al.* 2005) tropical land temperatures may have been as much as 5–10°C lower than today’s, with tropical montane plants showing large downslope elevational shifts. In succeeding millennia, the climatic changes included periods of relatively abrupt cooling or warming, as well as long phases of much drier climates in many areas. Atmospheric CO_2 increased from *ca* 200 ppm at the LGM to the pre-Industrial level of 280 ppm (Cowling *et al.* 2004), a 40 percent gain. These big environmental changes must have produced complex changes in forest extent and in forest structure, floristic composition, and productivity across the tropics. Thus, the current-day global change affecting this biome, while without question taking the planet into unprecedented conditions at accelerating rates, follows on a long history of environmental change.

Secondly, today’s tropical forests have been subject to diverse types of natural disturbances throughout their history (Clark 1990, Whitmore & Burslem 1998, Chazdon 2003, Cochrane 2003). The nonanthropogenic agents of abrupt change include: naturally ignited fires, ranging from forest-removing cataclysms to relatively low-impact ground-fires; landslides; anomalous floods; earthquakes; wind-damage events ranging from typhoons to local blowdowns to individual tree deaths; lightning; extreme climatic events such as severe drought or periods of cold, exceptional rains or high temperatures; outbreaks of pathogens or plant consumers (herbivores, seed predators); and population crashes of keystone species or guilds (*e.g.*, figs, pollinators, top predators, seed dispersers).

Then there are the many forms of local anthropogenic disturbances to tropical forests. Humans have inhabited all tropical regions for at least the last several thousand years (see Piperno *et al.* 1990, Roosevelt 1999). In some areas their forest clearing and agriculture, associated fires of different intensities, and/or selective logging drastically affected forest structure. In areas of intact forest cover, indigenous humans may have harvested forest products, in-planted useful species (*cf.* modern examples from the Guaymí in Panama, Gordon 1982), or hunted (thus affecting densities of important seed dispersers and seed predators). The possibly lasting effects of such human activities in “remote” tropical forest areas are only starting to be recognized by tropical ecologists.

Some impressive historical legacies over large geographic areas are now documented for tropical forests. A remote-sensing analysis of the meander dynamics of major rivers in the upper Amazon (Salo *et al.* 1986) highlighted the primary successional processes continually being initiated by the large lateral movements of the big rivers (horizontal displacements reaching 250 m per yr; Salo & Rasanen 1989); 12 percent of the lowland forest in a large sector of the Peruvian Amazon was determined to be in different stages of primary succession within the current floodplains, and 27 percent of the total forest area showed evidence of river-depositional processes. Based on historical accounts, dated charcoal, and archaeological indications of widespread simultaneous cultural discontinuities, Meggers (1994) concluded that mega-Niño events produced extreme droughts and widespread fires across the Amazon Basin at roughly 300–400 yr intervals over the last 2000 yr (*ca* 400, 700, 1000, and 1500 ybp); the most recent of these occurred within the lifetime of some extant trees (*cf.* Worbes & Junk 1999, Fichtler *et al.* 2003). A combination of archaeological and tree-ring evidence from Central Africa suggests that this region’s magnificent mahogany forests were initiated *ca* 800–900 ybp, when intensively cultivated landscapes were abandoned by rapidly declining iron age human populations; 60 percent of Gabon’s current forests are dominated by a light-demanding successional tree species (Justice *et al.* 2001). Analyses of pollen and charcoal in sediment cores from a remote Darien Peninsula site in Panama indicated that the well-developed rain forests there today were initiated *ca* 350 ybp, when multiple millennia of agricultural activities over that landscape ended abruptly with the Europeans’ arrival (Bush & Colinvaux 1994). Based on mapping the distribution patterns of useful plant species in the middle Rio Negro area of Brazil, Guix concluded that human activities over wide areas could have had lasting effects on the floristics of many extant Amazonian forests (Guix 2005, p.17):

Ecological and archaeological evidence suggests that pre- and post-Columbian settlers in the Caurés and Negro rivers confluence managed at least some of the forests and influenced their floristic composition . . . Indian mediated plant dispersal could be potentiated by an extensive network of Indian exchange in the region located in the confluences of the Negro, Caurés, Branco, Juaperi and Unini rivers.

The rapid growth and the exuberance of the tropical rainforests in the Amazon basin could mask old anthropic interferences in these ecosystems . . . Thus, ecological research in Amazonia must include the

possibility of long-term interferences and transformations promoted by Indians and Caboclos, in different degrees and scales, in forest ecosystems.

Further examples of regional-scale human influences are given by Willis *et al.* (2004).

Recent studies have also pointed to smaller-scale historical legacies. Based on long-term ecological observations in the Korup forest in Cameroon, Newbery *et al.* (1998) hypothesize that the monodominant stands within this forest originated opportunistically during a past period of exceptionally dry years. Both tree-ring analysis and ^{14}C dating were used to examine the tree age structure in another Cameroon forest (Worbes *et al.* 2003); the stand was found to be late-successional, dominated by a high-light demanding species, and with the oldest tree only 220 yr old. In the Ecuadorian Amazon, Pitman *et al.* (2005) observed greatly reduced plant species richness in a well-developed forest that they judged to be structurally indistinguishable from the speciose forests typical of the region. Their detective work based on archeological findings, remote-sensed data, and soils led them to conclude that this forest originated after a catastrophic flood breakthrough event *ca* 500 yr ago, and that colonization limitations have so far impeded many regional plant species from joining this community.

Profound effects from more recent disturbance events have also been documented by ecological studies in particular tropical forests. In the 1982–1983 mega-Niño event, which brought record temperatures and severe drought to East Kalimantan, Indonesia, Leighton and Wirawan (1986) found 71 and 37 percent, respectively, of the very large trees (> 60 cm diameter) had died in (unburned) forest plots on dry ridges and slopes. Such drastic mortality of the biggest trees would greatly alter forest structure and create a demographic and biomass void that would take many decades to refill. Equally striking is the structural and floristic change wrought in recent years in the 50 ha CTFS forest-dynamics plot at Pasoh, Malaysia, by the exploding population of native pigs; Ickes *et al.* (2005) found that extraordinary numbers of tree saplings in the plot were being destroyed annually by female pigs for their nests. These disturbances were recognized because of real-time ecological observations. Imagine, however, what might be guessed about the history of these two forests by ecologists seeing them for the first time 20–30 yr in the future.

It is also thought provoking in this regard to consider the historical information now accumulated for three of the most active sites of Neotropical forest research (Table 1). For all three, diverse legacy-generating events or changes have been documented or inferred. Such influences clearly need to be factored into analyses of these forests’ ongoing processes. While some of these historical influences apply to the entire study site (*e.g.*, widespread fires, droughts, hunting), others are spatially restricted or involve only certain taxa. Examples from all three sites (forest clearings associated with indigenous settlements in the Barro Colorado Island (BCI) plot, corn agriculture documented at La Selva, the flood in the Lecythidaceae plot; Table 1) illustrate the importance of developing spatially explicit and taxon-specific knowledge of such past or ongoing influences within study areas. While it is vital to recognize

TABLE 1. Evidence of natural and human disturbances and climatic shifts in old growth stands at three Neotropical sites: La Selva Biological Station, Costa Rica; Barro Colorado Island, Panama; and the Biological Dynamics of Forest Fragments Project, Brazil.

a. La Selva (“Old La Selva,” a 600-ha section of contiguous old growth)

- A widespread fire that occurred *ca* 500 B.C. is indicated by ^{14}C -dated charcoal in the soil both outside and within the old growth forest; the spatial extent of the fire suggests extreme drought conditions (Horn & Sanford 1992). The degree of forest damage from the fire (ground fire? forest destruction?) is unknown.
- Three pre-Colombian settlement sites existed during the period 1000 BC–1000 AD adjacent to the current old growth (Sol Castillo 2000). Pollen evidence from two small peripheral swamps (Kennedy & Horn 1997, Horn & Kennedy 2001) indicates corn agriculture in the adjacent fertile soils near rivers (770 BC to possibly 1500–1600 AD). Although the settlements and cultivation were both peripheral to the old growth, the indigenous people’s impacts within it likely included intensive hunting, extraction of plant products, and possibly in-planting of useful plant species (*cf.* Gordon 1982) that are currently present in the old growth, such as *Zamia neurophyllidia* D. W. Stev. (Zamiaceae), *Dipteryx panamensis* (Pittier) Record & Mell (Papilionaceae), *Aechmea magdalenae* (André) André ex Baker (Bromeliaceae) and palms.
- The valuable timber trees *Cedrela odorata* L. (Meliaceae) and *Minquartia guianensis* Aubl. (Olacaceae) may have been selectively extracted from those old growth areas with easy river access, before the La Selva reserve was created in 1968.
- The palm *Iriartea deltoidea* Ruiz & Pav. (Arecaceae), a multiuse plant (heart of palm, thatching, wood for furniture and construction), was apparently completely extracted from 20–25 ha of the old growth near the R. Puerto Viejo, probably sometime during 1930–1980 (Clark *et al.* 1995).
- All palms were experimentally removed from one hectare of old growth (W of the CEN trail), sometime between 1950 and 1968 (L. Holdridge, pers. comm.).
- Land-use change starting in the 1950s converted forest areas adjacent to Old La Selva to pasture and secondary forest (Butterfield 1994), creating the potential for significant edge effects and increased influence of biota from disturbed areas.
- Modern (post-1900) defaunation has included: local extinction of the Giant Anteater and White-Lipped Peccary in the 1960s–1970s; sporadic hunting (paca/peccary/currasow) to the present; a strong regional decline of the Great Green Macaw; and local declines of other forest bird species (Levey & Stiles 1994, Sigel *et al.* 2006).

b. BCI (the 50-ha Forest Dynamics Plot)

- A drying trend from 180 B.C. to 1310 A.D. has been inferred from a Panama stalagmite (^{18}O) record, which further suggested that modern climate in Panama is wetter than it was *ca* 1300 AD (Lachniet *et al.* 2004).
- As recently as 1139–1527 A.D. (and before), one or two pre-Columbian settlements occupied and probably patchily cleared *ca* 6–8 ha in the center of the plot; the remaining 42–44 ha of the plot retained forest cover during this period (Piperno 1990). These people certainly hunted and extracted plant products in the old growth forest and possibly in-planted (*cf.* Gordon 1982) useful plants that are currently found (Condit *et al.* 1996) in the plot (*e.g.*, *Brosimum alicastrum* Sw. [Moraceae], *Elaeis oleifera* (H.B.K.) Cort. [Arecaceae], *Dipteryx panamensis* (Pittier) Record & Mell (Papilionaceae), *Aechmea magdalenae* (André) André ex Baker (Bromeliaceae), *Licania platypus* (Hemsl.) Fritsch [Chrysobalanaceae], *Gustavia superba* (H.B.K.) Berg [Lecythidaceae], *Theobroma cacao* L. [Sterculiaceae], *Spondias mombin* L. [Anacardiaceae]).
- Two peripheral hectares within the 50-ha plot (and about half of the total island) were cleared in the 1800s for farming; these were abandoned *ca* 1900 (Leigh, Jr. *et al.* 2004).
- With the construction of the Panama Canal in 1910, BCI was converted from a hilltop within a larger landscape to an island; this brought intensified wind damage to forests of the western slope of the island (Foster & Brokaw 1990), adjacent to the plot.
- All trees of *Swietenia macrophylla* King (Meliaceae) and most *Cedrela odorata* L. (Meliaceae), valuable timber species, are likely to have been removed from BCI’s forests by modern colonists (Foster & Brokaw 1990); logging and other forest-product extraction ended in 1923, when BCI was declared a reserve (Leigh, Jr. *et al.* 2004).
- BCI historical and recent ecological records document exceptional events of famine and elevated mortality of diverse frugivorous mammals, in 1931–1932, 1958–1959, 1970–1971, and 1993–1994, suggesting island-wide fruiting failures (Wright *et al.* 1999); these events would have directly and indirectly affected diverse plant populations (missed recruitment, depressed populations of seed dispersers and seed predators).
- Defaunation on BCI since the building of the Panama Canal has included strong reductions or extirpation of the largest predators, white-lipped peccaries, and large poisonous snakes, and declines or losses of many bird species; effective protection from hunting has existed since *ca* 1980 (Leigh, Jr. *et al.* 2004).

c. BDFP Project (the 100-ha Lecythidaceae Plot in Area 41):

- Based on ubiquitous ^{14}C -dated charcoal in the top *ca* 60 cm of soil, fires occurred in the plot at various times between *ca* 4050 B.C. and 1820 (\pm 140 yr) A.D. (Bassini & Becker 1990, Piperno & Becker 1996, Santos *et al.* 2000). The extent of forest damage (ground fire? forest destruction?) from each of these fires is unknown. Overlapping ^{14}C dates of abundant charcoal indicate that between *ca* 650 and 850 A.D., either frequent smaller fires or a few large ones burned throughout the site (Piperno & Becker 1996).
- Mega-Niño events causing extreme drought and fires across the Amazon Basin have been inferred from archeological evidence and charcoal to have occurred around 450 A.D., 950 A.D., 1250 A.D., and 1550 A.D. (Meggers 1994).
- Phytoliths indicate strong floristic change in the plot sometime during the Holocene (the shift cannot be dated with certainty); in the earlier period, the forest contained taxa typical of much wetter habitats (*e.g.*, Marantaceae); diverse tree and shrub groups (*e.g.*, Burseraceae, Chrysobalanaceae) increased in abundance more recently (Piperno & Becker 1996).

TABLE 1. *Continued.*

-
- Although archeological evidence indicates extensive use of Amazonian terra firme forests (plant products and animals) by paleo and prehistoric Indians (Roosevelt 1999), no human artifacts have been reported from the plot (Piperno & Becker 1996). It is thus not known whether indigenous peoples affected the forest or fauna of the area. Phytolith analysis of the plot soil, however, revealed no evidence of cultivation of maize or other crops (Piperno & Becker 1996).
 - Over the last century, exceptional strong droughts occurred in the El Niño events of 1906, 1925–1927, 1948, 1982–1983, and 1997–1998 (Sombroek 2001). The months-long smoke and haze associated with related widespread fires could also have significantly lowered light levels in these years (*cf.* Davison *et al.* 2004).
 - An extreme, prolonged rain event in 1989 led to localized flooding and elevated tree mortality in a small portion of the plot (Mori & Becker 1991).
 - Hunting continues to occur within the plot and surrounding forest; the effects on the fauna have not been documented.
-

such influences, overgeneralizing their extent could produce highly inaccurate ecological conclusions.

In summary, there is now abundant reason to think that all extant tropical forests are likely to have been affected by significant past disturbances and environmental changes other than those normally thought of as part of current global change. Without first identifying such legacies, we cannot judge their potential contribution to current forest processes. All active tropical forest study sites need to be evaluated both for possible lasting effects from past events and for contemporary local influences (*e.g.*, hunting, pesticide spraying). When no such effort has been made, the lack of evidence of historical and modern influences clearly does not demonstrate their absence. Focused cross-disciplinary detective work regarding each site's historical and modern context may turn out to be key for understanding current forest structure or trends. Further, because this contextual knowledge is likely to be incomplete, a cautious, open-minded attitude will be important when interpreting processes at each site and how they might relate to current-day environmental changes.

CHALLENGE 2: DATA AND METHODS LIMITATIONS.—Substantial efforts have recently been focused on improving and standardizing the methods used in tropical forest monitoring (*e.g.*, Sheil 1995, Clark 2002, Phillips *et al.* 2002b). Considerable progress has been made during just the last several years. Best-practice tree-measurement methods (*e.g.*, ladders and diameter tapes replacing around-buttress and optical methods) are now standard in most tropical forest plots (*cf.* Condit 1998, Baker *et al.* 2004a). New analyses (Lewis *et al.* 2004b) have quantified the biases in tree demographic rates caused by multiyear census intervals (Sheil & May 1996), enabling corrections when the biases are large. A comparative evaluation of tropical tree biomass allometries has identified the best available equations for different tropical forest types (Chave *et al.* 2005), and wood density is now being explicitly considered in studies of trends in biomass and biomass increment (*e.g.*, Malhi *et al.* 2004, Baker *et al.* 2004b). A set of census protocols for the notoriously difficult lianas (*cf.* Gerwing 2004) have just been published (Gerwing *et al.* 2006) as a result of a Working-Group effort at the National Center for Ecological Analysis and Synthesis.

While all these steps are bringing major research improvements, there are still unresolved issues that constrain our ability to assess the responses of tropical forests to global changes:

1. *Cross-site versus within-forest trends.* Long time-series of measurements for multiple forests are not yet available for even a single tropical region such as Amazonia. The regional-scale reported trends (increases in aboveground biomass: Phillips *et al.* 1998; in tree dynamics: Phillips & Gentry 1994, Phillips *et al.* 1994; and in the abundance of lianas: Phillips *et al.* 2002a) were inferred from composite analyses of data from many plots that were set up and measured by different researchers over different periods. The analyses were based either on each plot's first year of data (Fig. 3, two liana analyses) or on cross-plot means for those plots that were active each year (turnover, biomass, some liana analyses). Strengths of this approach were that it integrated information from multiple decades and large geographic areas. On further consideration, however, the authors and others identified two issues meriting attention.

The first was the possibility of biases due to method differences across studies and through time. Phillips and his collaborators revisited and refined their meta-analyses from this perspective, for two of the three trends: aboveground biomass (Baker *et al.* 2004a) and turnover rates (Phillips *et al.* 2004). After excluding some problematic plots, they ran replicate analyses to assess the potential effects of other concerns such as measurement ambiguities and plots possibly sited to be in “majestic forest.” Going forward, such problems will be obviated by increasingly general use of community-consensus best-practice field measurement protocols and by better data documentation. A remaining need, however, is for the methods histories of the plots included in these analyses to be published (see below; *Data transparency/access*). Secondly, now that a study of liana-censusing protocols has led to consensus recommendations (Gerwing *et al.* 2006), it would be valuable for the liana trend analysis to be revisited, taking into account the methods used in the different plots.

A second question is whether the statistically significant *across-plot* trends found in the composite analyses (*e.g.*, Fig. 3) accurately indicate trends occurring through time *within forests*. This issue was explored analytically for forest turnover by Hall *et al.* (1998). They first determined characteristic levels of within-landscape variation in tree mortality and recruitment rates, based on subplots within two of the CTFs 50 ha plots (Pasoh and BCI; see Losos & Leigh 2004), and then used these data to investigate the conditions for detecting

turnover trends. Their first conclusion was that, based on the variation in those particular datasets, at least 1000 trees would need to be monitored per site to detect, *within sites*, the level of temporal trend indicated by the *cross-plot* analysis. They next asked if within-site trends existed in the data from the 17 plots in the original study (Phillips & Gentry 1994) that had been censused more than twice (Fig. 4). For only three plots did they find statistical support for an increase in forest turnover. Third, they used the turnover statistics from these 17 plots to simulate forest turnover through time either with (1) no temporal trend or (2) a fixed progressive increase in turnover. In the simulations of unchanging forest dynamics, 20 percent of the cases with fewer than ten plot censuses tested falsely positive for increasing turnover; the false positives disappeared with additional censuses. In the simulations of increasing plot turnover, 15–20 censuses were required to detect the trend with 95% confidence. For monitoring turnover rates of a given tropical forest, therefore, the results of these analyses suggested that: (1) at least 1000 trees should be followed; and (2) reliable detection of a trend in turnover is likely to require at least ten censuses.

This guidance is just based on one set of plot dynamics data and therefore cannot be taken as a hard and fast rule for all tropical forests. It is nevertheless thought provoking to assess the tropical forest plots being monitored around the world in terms of the two recommendations. Although there are many currently active plot studies (*e.g.*, 62 in the RAINFOR network across Amazonia, Phillips *et al.* 2004; 15 in the pan-tropical CTFS network, Losos & Leigh 2004; the CARBONO plot system at La Selva, Costa Rica, Clark & Clark 2000a; the Canguk Research Station plot system in Sumatra, M. Kinnaid & T. O'Brien, pers. comm.), most include fewer than 1000 stems (46 of 79, 58%), and the mean number of recensuses is 2.6. Only three plots have been censused 10 times, and none fulfills both of the suggested conditions for reliable detection of a within-site trend in turnover rates.

2. How to assess tropical forest landscapes.

A single plot corresponds to one sample of the forest, and it is unlikely to represent the whole landscape-scale environmental variability. Among the possible biases, there is a tendency for researchers to select attractive forests (the 'majestic effect' of Sheil 1995) or to avoid disturbed forests. The landscape-level AGB [aboveground biomass] estimate should be assessed by establishing a network of plots randomly distributed over the landscape, to assess the variability of forest types.

(Chave *et al.* 2004, p. 412)

For accurate detection of change, a further need is to observe a representative sample of each forest through time. Obtaining such a sample is not easy, however. As highlighted in the above quote, marked within-landscape variation in old growth tropical forests is caused by the combined effects of edaphic variation, the gap cycle, and the occurrences of very large trees. When this within-forest structural variation was quantified in different Neotropical forests by measuring all trees in replicate plots of different sizes (Brown *et al.* 1995, Clark & Clark

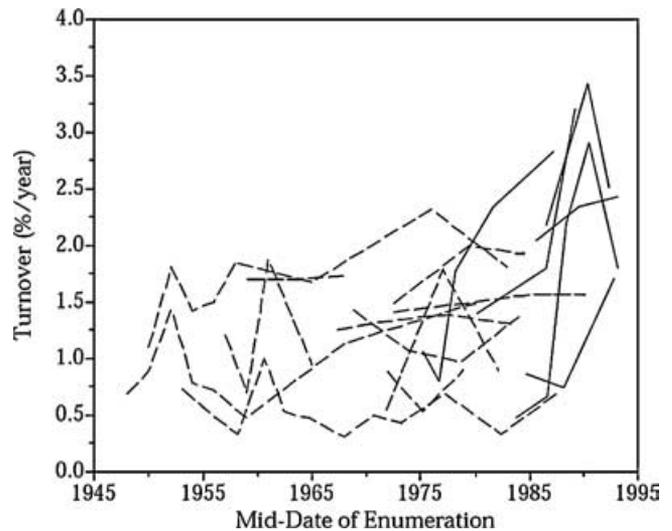


FIGURE 4. Temporal pattern of stand turnover (mean of annual mortality and recruitment) for 17 tropical forests. Each curve represents an individual site at which permanent plots were enumerated many times. The mid-date of enumeration is the mid point of each interval for which mortality, recruitment and hence turnover could be computed. Neotropical sites are indicated by solid lines. Figure 4 of Hall *et al.* 1998, reproduced with permission from P. Hall and UNESCO Publishing.

2000a, Keller *et al.* 2001, Chave *et al.* 2003), high among-plot variance was consistently found. These studies found that a total sample area of 3–10 ha was needed to estimate aboveground biomass to ± 10 –20 percent. A second important finding was that sampling efficiency increases when a larger number of smaller plots are spread over the landscape. For example, in an eastern Amazonian site, 21 0.25-ha plots (5.25 ha total), 15 0.5-ha plots (7.35 ha total), and 10 1-ha plots (10 ha total) all enabled estimating forest aboveground biomass within 20 percent with 95% confidence (Keller *et al.* 2001). At the same time, however, multiple researchers (Laurance *et al.* 1999, Clark & Clark 2000a, Keller *et al.* 2001, Chave *et al.* 2004) have recommended a minimum plot size of 0.25 ha for such landscape sampling, because biomass estimates based on smaller plots are strongly affected by the spotty distributions of large trees and heterogeneity in recent disturbance history.

As with forest structure, forest processes are expected to vary spatially within old growth tropical forests. Even if an old growth forest were at steady-state at the landscape scale, the large *biomass losses* caused by natural disturbances would tend to be localized and sporadic, while, in contrast, most areas of the forest should show (smaller) *biomass increases* (Fearnside 2000, 2003; Körner 2004). Such within-landscape patterns could plausibly resolve the opposite biomass trends that have been inferred from studies using contrasting sampling methods. A long-term increase in aboveground biomass was inferred (Baker *et al.* 2004a) from a set of Amazonian forests where the assessments were largely based on one or a few small plots (≤ 1 ha total plot area per site at 51 of the 59 sites;

Baker *et al.* 2004a, Table 1). In contrast, in the two Neotropical sites with long-term monitoring of many hectares (50 ha, Chave *et al.* 2003; 18 ha, Laurance *et al.* 2004), the forests showed no change in aboveground biomass/basal area over 15 yr.

3. *Multiyear versus annual intervals.* The active tropical forest monitoring studies around the world are nearly all based on intercensus intervals of 2–5 yr. I know of only two ongoing studies that have maintained long-term monitoring at annual intervals (La Selva, Costa Rica [18 0.5-ha plots, since 1997; Clark & Clark 2000a], and Canguk, Sumatra, Indonesia [100 0.05-ha plots, since 1997, M. Kinnaird & T. O'Brien, pers. comm.]). The Conservation International TEAM Initiative now underway is aiming to establish sets of replicated annually censused plots within each of up to 50 old growth tropical forests worldwide (S. Andelman, pers. comm.). To date, however, the multiyear time intervals that have dominated tropical forest monitoring constrain assessments of how tropical forests are responding to changing environmental factors.

One limitation they bring is decreased temporal sampling. Most tropical forest plots have only been remeasured a few times, far fewer than the ten enumerations suggested to be necessary for detecting a directional change in turnover rates (Hall *et al.* 1998). Eleven of the 15 large CTFS forest-dynamics plots have so far been measured ≤ 3 times (Losos & Leigh 2004). With the currently used intercensus interval of 5 yr, it will take another 35 yr or more to achieve ten censuses of these important plots. Only 7 yr would be required, however, if within-plot sub-samples were henceforth measured annually.

The power of annual censuses goes beyond speeding the accumulation of data points, however. Yearly censuses enable two important kinds of process-level analyses. First, because climatic factors vary strongly among years (see Fig. 1), the range of interannual climatic variation over periods such as 10–20 yr enables a first assessment of the climatic sensitivity of tropical forest processes, without having to await the slower pace of long-term directional climate change. Such understanding is needed for improving the process models currently being used to project biotic responses to global change. Secondly, data on annual-scale performance of forests across the tropics would greatly inform interpretation of the large differences among years in the rate of atmospheric CO₂ accumulation (see below). In contrast, data based on multiyear census intervals merge years of contrasting climate and of varying forest performance, thus blurring such relationships.

A remarkable example (Fig. 2) of the power of an annual time-series is the strong correlation that was found (Clark *et al.* 2003) between forest-level tree growth at La Selva, Costa Rica and the annual contribution of the global terrestrial tropics to atmospheric CO₂ dynamics, as inferred from an atmospheric inverse model. The combined datasets suggest that a negative response of tropical forest productivity to higher annual temperatures is already affecting the pace of atmospheric CO₂ accumulation (greater tropical CO₂ emissions in hotter years).

These links would not have been detected had the La Selva record been based on multiyear census intervals.

An additional benefit of annual censusing is increased quality of field data. Diverse practical problems progressively increase data uncertainties as time elapses between measurements. When errors are made in a given census, such as omitting a tree, mistakenly classifying it as dead, or transposing digits in a tree measurement, they are more likely to be detected and corrected effectively when the next census is only a year later. Further, yearly checks and adjustments ensure that the active point of diameter measurement is unaffected by the upward growth of buttresses and other bole irregularities, a source of data bias or loss that occurs with longer census intervals (*cf.* Condit 1998, Appendix 3.3, *POM Problems at BCI*). Annual censuses also minimize the underestimates in turnover rates (*cf.* Lewis *et al.* 2004b) and in forest growth and recruitment (Clark *et al.* 2001) that are a function of intercensus interval length.

4. *Big data gaps: environment & ecophysiology.* We know far too little about how climate has varied at tropical study sites over the last decades. There is a general scarcity of long-term meteorological records in tropical regions. Further, data quality issues affect the extant records (see Aguilar *et al.* 2005). Until the 1990s, even the more well-developed tropical forest research sites had only minimal meteorological measurements, usually restricted to daily maximum/minimum temperature and daily rainfall. In recent years the availability of automated meteorological stations has greatly increased the scope of such monitoring at the better-equipped field sites, but even in these cases there can be recurring sensor failure due to biota/lightning/humidity, and sensor maintenance and calibration require dedicated personnel. Most tropical forest study sites that are currently included in trend analyses have no local records of climatic variation through recent decades. There may or may not be extrapolatable records for air temperature and rainfall from elsewhere in the country or local region. For nearly all tropical forest sites, multidecade records are lacking for many other potentially important factors: solar radiation; cloud cover; soil moisture; atmospheric deposition of nitrogen, pesticides, or other pollutants; soil nutrients; tropospheric ozone; and UV-B.

There is also still quite limited understanding of the physiological responses of tropical forest plants to these environmental factors (see Körner 1995, Clark 2004b, Lewis *et al.* 2004a, Wright 2005). Many fundamental questions are currently unanswerable. For example, what is the stand-level photosynthetic temperature optimum? How/(do) respiration responses of roots, stems, and leaves vary with soil fertility (particularly nitrogen and phosphorus)? How do tropospheric ozone levels affect photosynthetic rates? How much of the photosynthetically fixed carbon is currently being lost due to temperature-sensitive emissions of isoprene (Keller & Lerdau 1999, Geron *et al.* 2002) and other volatile organic compounds? Such responses could vary significantly among plant functional groups, among species, and between life stages of

the same species (e.g., understory seedlings/saplings vs. adult trees in the canopy). Tropical plants' capacities to acclimate photosynthesis and respiration to increasing temperatures are poorly studied; their ability to acclimate could decline abruptly at certain threshold conditions and may already be quite limited (see Read 1990). Changes in plant performance over the same range of climatic variation may differ greatly between abrupt extreme events and long-term progressive environmental change. A quantitative and broadly generalizable grasp of all these aspects of the physiological responses of tropical forest plants, particularly canopy trees, is needed for improving the realism of global ecosystem-process models.

5. *Data transparency/access.* Given the globally significant implications of any directional changes in tropical forests, a particular concern is that the relevant data have largely remained inaccessible to the scientific community. It is time for tropical forest researchers to overcome the cultural barriers (inertia, data "territoriality") and emulate the Human Genome Project. For strong science, full documentation and transparency are needed to enable informed peer evaluation of research findings. Accessibility of the data to the broader community is also likely to produce new ways of learning from the field observations.

Fortunately, new tools make this constraint easy to address, and they are starting to be used. All research teams can now make their field data and associated metadata freely available as downloadable files on public websites. The CI-TEAM Initiative for tropical biodiversity monitoring will put all data and metadata on the web, without restrictions, within 2 yr of the field measurements. The CTFs plot network is currently implementing web-based open access to all plot data taken ≥ 5 yr prior; the data from all six censuses of the BCI forest-dynamics plot are now available online. Individual researchers can publish their datasets in the Ecological Society of America's peer-reviewed data journal, *Ecological Archives* (e.g., Clark & Clark 2000b, 2006), contribute them to public web-based data archives (NCEAS, Google), or post them on personal web sites. Published papers that present original findings should now as a matter of course include electronic appendices including all the data necessary for readers to replicate the analyses in the paper (see, for example, Wright & Calderon 2006). All these steps will strengthen efforts to detect trends in tropical forests.

CHALLENGE 3: TANGLED THREADS OF CAUSATION.—If a tropical forest is found to be changing, a particularly tough nut to crack will be correctly identifying the "why" of the changes. In addition to the possibility that study sites are continuing to respond to historical influences, as discussed above, other factors will complicate attempts to link forest responses to particular environmental factors. This section focuses on these additional layers of complexity and then illustrates a number of them with two case studies.

A fundamental difficulty is caused by the simultaneous changes in climatic and atmospheric factors. For example, recent strong El Niño events brought both intensified drought stress and peak temperatures to SE Asia and parts of the Neotropics (Malhi & Wright

2004). Similarly, canopy-leaf photosynthetic rates in an Amazonian forest (Tribuzy 2005) and eddy-covariance estimates of forest carbon uptake in a Costa Rican forest (Loescher *et al.* 2003) declined in periods with both higher temperatures and greater leaf water stress. In these examples, the co-occurring factors were both stressors, but were they coequal in effect, or was one dominating? Or, were they synergistic? When there is also change in a factor, such as increasing atmospheric CO₂, with potentially opposite effect(s), distinguishing the influence of each factor becomes even more problematic. Locally parameterized ecosystem-process models may be the most effective way to estimate the relative contributions of such simultaneous changes.

Secondly, context can greatly influence outcomes. For example, the effect of a given set of environmental conditions on a tropical forest could be expected to vary depending on preceding climatic history. Although similar sharp peaks in pan-tropical temperatures occurred in the strong El Niño events of 1982–1983 and 1997–1998 (Fig. 1), the 1982–1983 temperatures may have had stronger negative impacts because of their greater contrast with those of the preceding decade. A second example is given by tropical elevational gradients. Global warming is an intensifying stress on the already-warm forests in the lowlands, but it may enhance productivity of tropical forests at (cooler) higher elevations, at least for a while (but see Chapman *et al.* 2005).

There is also an important question of how to assess climatic factors (*cf.* Aguilar *et al.* 2005). In the case of water stress, for example, forest responses may be more strongly linked to soil-moisture minima or the number of consecutive days without rain, than to annual or monthly rainfall totals. Mean monthly air temperature, commonly used to indicate site conditions, may correlate less with observed plant responses than other temperature metrics; when a plant response is photosynthesis-driven, for example, a more relevant index might be the proportion of the daytime with temperatures above some threshold. For solar radiation, valuable metrics might be the direct and diffuse radiation accumulated when vapor pressure deficit is below some critical value. Discerning the most appropriate climatic indicators may require creative exploratory analyses or iterative process-level modeling.

Biotic responses to environmental factors can involve hysteresis, lags, and carryover. Climatic variability and extreme events ("tipping points") can lead to ecosystem state-change, such as the conversion of forest to grassland or savanna in the drier parts of the Amazon when sufficiently intense drought and/or high temperatures occur (*cf.* Hutyra *et al.* 2005). The occurrence of a given forest response at one time can preclude a similar response later. An example is the die-off of most very large trees in a Borneo forest in the 1982–1983 El Niño (Leighton & Wirawan 1986); the extreme temperatures and drought in 1997–1998 could not have provoked a similar die-off, because the very large trees had been lost and insufficient time had passed for them to be replaced. Similarly, a strong mass-flowering event of Asian dipterocarp trees in 1 yr can preclude a big masting in the following year(s), regardless of whether the appropriate environmental conditions or trigger reoccur. In the case of floristic responses to intensifying stressors, if there is a progressive shift toward more resistant species due to mortality of the

more sensitive taxa, the forest-level responses to the stressor may diminish or disappear. A distinct effect is interannual carryover; for example, elevated tree mortality in one climatically extreme year might continue into the next year, even though those conditions have abated. Such temporal complexities can obviate simple correlations between time series of forest function and time series of environmental factors, even when there is a strong causal link.

All these issues need to be recognized and factored into assessments of ongoing change in tropical forests. Other key ingredients include: consistent long-term monitoring; ongoing development of new kinds of information as understanding deepens; the use of process-level modeling constrained by local field data to assess the likelihood of competing possibilities; and thoroughly testing the evidence in hand for alternative explanations. Two ongoing studies illustrate some of these issues and approaches:

1. *La Selva tree growth versus temperature, 1984–2000.* As discussed earlier, the large temporal variation shown by adult tree growth at La Selva was strongly negatively related to annual temperatures (Fig. 2a). Still, multiple issues need to be considered.

Three possibly confounding factors that can be satisfactorily ruled out are related to tree mortality and ontogeny. The growth record did not include numerous dying trees with progressively slowing growth rates (Lewis *et al.* 2004a); 96 percent of the measured trees survived at least a further 4 yr (D. A. Clark & D. B. Clark, pers. comm.). Any size-dependent (ontogenetic) changes in growth rates were identified from a large accumulated growth dataset for the six species (Clark & Clark 1999, 2000b, 2006) and were removed from the focal trees' increments before analysis. This detrending also ruled out a third possibility (Lewis *et al.* 2006), that the very large interannual changes in relative diameter growth among years (Fig. 2) could be due to "switches in allocation from wood to reproduction as trees mature."

Other questions to consider, however, concern the complexity of real-life environmental conditions and of the trees' integrated responses to them. The only other environmental data available for this time period at La Selva were rainfall (all 16 yr) and solar radiation (8 yr). Although their annual means were not related to annual tree growth (Clark *et al.* 2003), such annual metrics may mask important aspects of climatic variation, as noted earlier. Forest process models being parameterized for La Selva and driven by local climatic data will enable improved assessment of the complex relations between these factors and both photosynthesis and respiration, at physiologically relevant time-steps (half-hours). The longer time-series of growth data that are accumulating from this study, along with the data from annual stand-level monitoring at La Selva since 1997 (the CARBONO Project), will help to address new questions that will likely emerge from this modeling and will show whether the link between tree growth and temperature over the first 16 yr is maintained through time and at the stand level. Whether or not unmonitored factors such as tro-

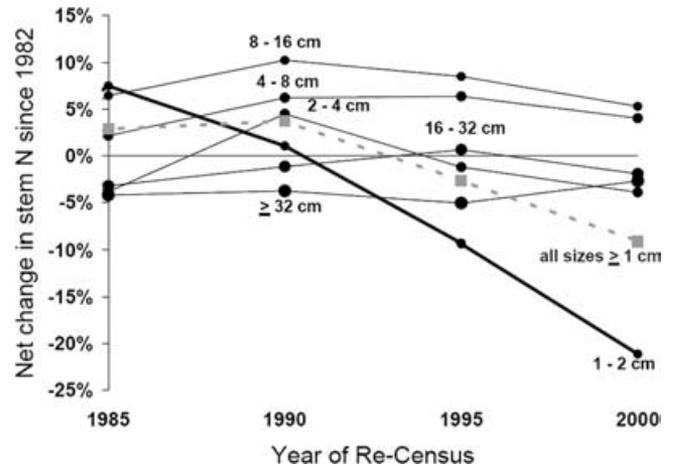


FIGURE 5. Net change (%) over time in the number of live stems, by size class, in the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama (data from Table 2.1 of Hubbell 2004). Numbers in subsequent censuses are compared to those from the initial census ("1982"), which took place over the period 1981–1983 (Leigh, Jr. *et al.* 2004).

pospheric ozone or UV-B are affecting the forest will remain an important open question, however.

2. *Dramatic changes on BCI.* The 50-ha forest dynamics plot on BCI, Panama, the longest studied of the CTFs plots, provides a fascinating case study of recent within-forest change. In a review of the findings from the first 18 yr (1982–2000) of research in the plot, Hubbell (2004) discussed the striking floristic changes that took place over this period. A third of the plant species changed >50 percent in abundance, and many rare species declined in all four census intervals. A parallel large change in the plot was a remarkable net decline (21%) in the number of live 1–2 cm diameter saplings between 1982 and 2000 (Fig. 5). What caused such major changes?

There are several plausible possibilities, not necessarily mutually exclusive. As suggested by several researchers (Hubbell & Foster 1990, Bush & Colinvaux 1994, Sheil & Burslem 2003), this forest may still be in the late stages of a successional process entrained by the pre-Columbian human activities within the plot and/or by more recent influences from adjacent agricultural activities (see Table 1). A second possibility noted by Hubbell (2004) is a progressive stand-level recovery from the elevated tree mortality that was found to have occurred in the plot by 1985–1986 (Condit *et al.* 1995), the first census after the strong 1982–1983 El Niño. Annual canopy mapping in the plot indicated temporarily higher frequencies of low gaps in 1986 (Hubbell 2004), perhaps stimulating the short-term increase (Fig. 5) in the smallest sapling class seen in the 1985–1986 census (and in the next-larger saplings in the 1990 census). Third, BCI may be continuing the long-term drying trend that was documented for the period 1925–1986 (Windsor 1990), and the flora may be directionally changing in response to this (Hubbell 2004). The large long-term loss

in the smallest saplings has two other possible explanations: recruitment to this size class may have declined due to the effects of human traffic in the plot on seedlings or saplings, or this smallest measured size class may be more affected than larger stems by directional changes to date in drought and/or temperature.

Several kinds of evidence can help in the process of weighing these possibilities. If successional processes are dominant, there should be predictable guild-dependence in the floristic changes (e.g., excess mortality of adults of high-light demanders). If they reflect influences from the 6–8 ha pre-Columbian settlement on the central plateau (Piperno 1990) or from adjacent agricultural activities in more recent times (Hubbell 2004), such patterns should have a predictable spatial signal within the plot. Spatially explicit analysis can also be used to test the proposed link between sapling recruitment and the availability of gaps. If a drying trend is playing a large role, ecophysiological data indicating species' relative drought tolerance (cf. Engelbrecht *et al.* 2005) should help to identify the relevant floristic signal. Developing a spatial analysis of the compositional changes and of soil moisture patterns across the plot could also be valuable; however, in this case, such a link might be confounded by the pre-Columbian occupancy of the central plateau. The "human-traffic" hypothesis with respect to the loss of 1–2 cm saplings is testable by comparison of seedling/sapling densities in the plot with those in similar areas outside the plot. Targeted ecophysiological studies of seedlings and small saplings would be needed to evaluate the possibility that temperatures and/or soil moisture have already reached lethal stress levels for these small plants.

A great strength of this large plot for answering many of these questions is the huge number of identified and spatially located individuals that have been monitored. A limitation with the current protocols, however, is the 5 yr time step for censuses. There is currently discussion of annually measuring subsamples of the BCI plot. Such enhanced temporal sampling intensity would likely increase understanding of the large ongoing changes in the plot, while at the same time providing valuable internal checks on the all-plot 5 yr data.

MOVING FORWARD

There are clearly many challenges for understanding how tropical forests may already have been affected by the changing climate and atmosphere and how they are likely to respond to the intensifying environmental changes in the future. Tropical forest ecology has greatly matured as a science over the last 20 yr, however, and we now have a much stronger basis for addressing these complex issues. I conclude with an agenda of priority needs for this effort:

1. *Recognizing historical legacies.* For all monitored tropical forest plots, a spatially explicit understanding needs to be developed of site history during the last 500–1000 yr, including any recent or current impacts of natural or anthropogenic disturbance. This will take interdisciplinary teamwork. A minimal research agenda for each site would be thorough sampling for phytoliths and charcoal, as well as an analysis of the flora for patterns indicating previous human activities or natural disturbance.
2. *A "fingerprint" of succession.* Research needs to be focused on developing quantitative, objective ways of distinguishing forests that are at different stages of succession, and that result from different types of human-generated and natural disturbances (see Chazdon 2003). Relevant data need to be actively collected in the field from sites with very well-documented histories, rather than basing conclusions on *a priori* assumptions. Spatially explicit analysis of remote-sensed forest structural data (e.g., LIDAR-derived forest height distributions at varied distances from rivers across tropical floodplains, followed through time) will help this effort.
3. *A frontal attack on tropical plant physiology.* Focused studies of the sensitivities of canopy-level plant processes to climatic/atmospheric factors (e.g., temperature, radiation, water stress, ozone) are a high priority. We need to develop clever ways in such studies to separate the effects of correlated factors. At the same time, the iterative development and use of locally parameterized process models will greatly aid attempts to understand forest responses to the simultaneous changes in many environmental factors.
4. *Maintaining the long-term forest data.* The relatively few active tropical forest plots that now have decadal or longer records are irreplaceable. Efforts and resources need to be focused on maintaining these plots into the future, alongside the growing number of more recently initiated plots. For all of these, maintaining the continuity of the core measurements (tree growth, tree mortality, floristics) through the coming decades will be key for efforts to understand the effects of changing environmental conditions on these ecosystems.
5. *Environmental monitoring.* Improved climatic data are greatly needed for interpreting forest processes. They need to cover a more comprehensive set of environmental factors than just daily rainfall and maximum/minimum temperatures, and there needs to be a greater focus on consistent quality control of the data. Satellite-borne sensors may lead to global tropical coverage of some climatic factors, but such data must first be ground-truthed at tropical field sites.
6. *Elevational transects and biome ecotones as early warning tools.* As recently illustrated by an analysis of frog extinctions in Costa Rica (Pounds *et al.* 2006), elevational transects of continuous tropical forest offer an important opportunity for detecting the effects of climate change on tropical forest plants. Similar opportunities exist at between-biome ecotones, such as boundaries between closed-canopy tropical forest and savannas. Efforts should be focused on establishing monitoring programs at such sites in all major tropical regions.
7. *Integration and collaboration.* With the advent of the Internet, tropical scientists can much more effectively work as a community on these urgent research issues. With an increasing pool of researchers, the growing networks of plot studies, and

the current tools for communication and data sharing, tropical forest science is now capable of greatly advancing understanding of the current status and future of the world's remaining tropical forests.

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